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Distribution of viable resting stage cells of diatoms in sediments and water columns of the Chukchi Sea, Arctic Ocean

Chiko Tsukazaki[1]*, Ken-Ichiro Ishii[2], Kohei Matsuno[1], Atsushi Yamaguchi[1] and Ichiro Imai[1]

[1]*Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan*
[2]*Graduate School of Global Environmental Studies, Kyoto University, Yoshida-nihonmatsu-cho, Sakyo-ku, Kyoto 606-8501, Japan*

Abstract: The distribution of resting stage cells of diatoms in the surface sediments and water samples collected in the Chukchi Sea was investigated using the most probable number (MPN) analysis to understand the mechanism underlying diatom blooms in the Arctic region. High densities (3.5×10^5 to 6.8×10^6 MPN cells cm^{-3} wet sediment) of viable resting stage cells of typical Arctic diatom species were found in the surface sediments of the Chukchi Sea. Resting stage cells of the sea-ice–related diatom genus *Fragilariopsis* were more abundant (2.6×10^6 MPN cells cm^{-3} wet sediment) than *Chaetoceros* (2.18×10^6 MPN cells cm^{-3} wet sediment) or *Thalassiosira* (1.76×10^6 MPN cells cm^{-3} wet sediment) in the southern Chukchi Sea. This reflected a previous bloom of *Fragilariopsis* ahead of typical planktonic blooms of *Chaetoceros* and *Thalassiosira* and suggests that sea-ice–related blooms are a substantial factor for primary production in this area. During the sampling period, diatom assemblages in the *in situ* water columns were dominated by *Pseudo-nitzschia delicatissima*, *Cylindrotheca closterium*, *Proboscia alata*, and *Thalassionema* spp. After storage of water samples for 6 months in the dark, viable diatom resting stage cells of typical Arctic species such as *Attheya longicornis* and *Chaetoceros socialis* were detected. These autochthonous species formed resting stage cells that remained viable in the dark for more than 6 months, while diatom species of Pacific origins could not survive under conditions of extremely limited light. The resting stage cells provide an advantage for autochthonous diatoms to endure the unfavourable light conditions of the Arctic winter. In the Chukchi Sea, resting stage cells of diatoms were supplied by current inflows from shallow sea areas. Densely distributed viable resting stages at the bottom are also a possible source for seeding the diatom cells into phytoplankton communities and ice assemblages in shallow marginal ice zones.

Key Words: Chukchi Sea, Diatom, Ice algae, Phytoplankton bloom, Resting stage cells

INTRODUCTION

The Chukchi Sea is a shallow Arctic marginal ice zone (average depth, about 50 m) covered with ice for about 6 months in a year, with freeze-up starting in November and melt-back in June (Woodgate *et al*. 2005). Between 1998 and 2009, an open water season (mean, 105 ± 25 days) occurred (Arrigo & Van Dijken 2011). A nutrient-rich flow from the Bering Sea sustains high phytoplankton productivity and biomass dominated by diatoms (Springer & McRoy 1993) and enriches the ecosystem of the Chukchi Sea (Walsh *et al*. 1989).

During winter, photosynthetic algae receive insufficient light because of the polar night and ice cover (Perovich 1998; Sakshaug 2004; Perovich & Polashenski 2012). In early July, dense blooms break out along the marginal ice zone and develop under the ice immediately after an increase in light transmission through the ice (Sukhanova *et al*. 2009; Perrette *et al*. 2011; Arrigo *et al*. 2012, 2014). Diatoms are the most important primary producers in the Arctic area. The sea-ice–related blooms occur with the growth of ice algae and are dominated by pennate diatoms (Horner & Alexander 1972; Hsiao 1980; Horner & Schrader 1982; Gosselin *et al*. 1997; Von Quillfeldt 1997; Ratkova & Wassmann 2005; Poulin *et al*. 2011). Certain pennate diatoms such as *Fragilariopsis* initiate plankton blooms through a process of releasing cells from the ice, and the diatom populations are gradually replaced by centric diatoms such as *Thalassiosira* and *Chaetoceros* (Grøntved & Seidenfaden 1938; Bursa 1961; McRoy & Goering 1976; Saito & Taniguchi 1978; Horner & Schrader 1982; Gosselin *et al*. 1997; Von Quillfeldt 1997).

Many planktonic diatoms form resting stage cells (i.e. resting spores or resting cells), which ensure high viability in variable coastal environments (Hargraves & French 1983; Imai *et al*. 1990; McQuoid & Hobson 1996; Itakura *et al*. 1997). Resting spores and resting cells are thought to have almost the same physiological characteristics, which allow them to endure environmental stresses such as darkness and nutrient depletion. They differ in that resting spores are morphologically distinct from vegetative cells, while resting cells are externally similar to vegetative cells (Hargraves & French 1983; Garrison 1984; Kuwata & Takahashi 1990; Itakura *et al*. 1997). Several studies have suggested that resting stage cells sink rapidly after a bloom because of an increase in weight from thickening of the frustule or entanglement and aggregate formation (Hargraves & French 1983; Smetacek 1985; Odate & Maita 1990; Sugie & Kuma 2008). As a result, resting stage cells of diatoms are frequently abundant in the sediments of productive shallow sea areas (Imai *et al*. 1990; Itakura *et al*. 1999; McQuoid 2002). Germination of resting stage cells is triggered by appropriate light intensity (Hollibaugh *et al*. 1981; Hargraves & French 1983; Imai *et al*. 1996b). Therefore, resuspension of resting stage cells in the euphotic layer from the bottom is essential to initiate vegetative growth (Pitcher *et al*. 1991; Ishikawa *et al*. 2001). The composition of resting

* Corresponding author (tskzkuaai@gmail.com).
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Table 1. Positions of the stations, bottom depths, sampling dates, and depths of the water and core samples.

Station no.	Position			Water samples sampling depth (m)	Core samples remark	Sampling date
	Lat. (°N)	Lon. (°W)	Bottom depth (m)			
1	71-00	162-00	45	0, 5, 10, 20, 35.6, Bottom[1]	○	11 Oct
2	70-30	164-45	45	0, 5, 10, 20, 35.1, Bottom	○	11 Oct
3	70-00	168-00	45		○	5 Sept
4	68-30	168-50	52		○	12 Oct
5	67-00	168-50	47	0, 5, 10, 20, 36.2, Bottom	○	12 Oct
6	65-46	168-30	56	0, 5, 10, 20, 46.4, Bottom	no sample	13 Oct

[1] Seawater samples from bottom depths (45 m) at Station 1 were available only for cell counts.

stage cells in sediments, which serve as seed populations, is one of the most important factors affecting the appearance of phytoplankton blooms in upwelling or shallow seas where water columns are frequently mixed from the bottom to the surface (Garrison 1984; Pitcher 1990). Resting stage cells are thought to play an important role in Arctic regions that are similar to temperate coastal areas. Therefore, it is important to focus on the distribution of diatom resting stage cells in surface sediments to understand the mechanism underlying spring blooms in the Arctic region. In this study, we investigated the possibility that distributions of viable resting stage cells of diatoms in surface sediments and water samples collected in the Chukchi Sea and Bering Strait serve as seed populations that precede the blooms.

MATERIAL AND METHODS

The survey was conducted at six stations in the Chukchi Sea and Bering Strait during the cruise MR10-05 of the R/V *Mirai* in September and October 2010, when the stations were completely ice free (Table 1; Fig. 1). A conductivity–temperature–depth (CTD; SBE911plus CTD system, Sea-Bird Electronics Inc., Bellevue, Washington USA) cast was made at each station to measure water temperature and salinity. Concentrations of nutrients [dissolved inorganic nitrogen (DIN), silicate, and phosphate] were determined using a nutrient analyser (QuAAtro 2-HR, BL TEC K.K., Osaka, Japan). Chlorophyll *a* concentration was determined using a Turner Design Fluorometer (10-AU-005, Turner Designs, San Jose, California USA). Sediment cores were obtained using a multiple corer (internal diameter, 74 mm) at five stations (1, 2, 3, 4, and 5), and the top 3 cm of each core was placed in an airtight container and stored at 1°C in the dark. Seawater samples were collected using Niskin bottles from several depths and a multiple corer from bottom depths at four stations (1, 2, 5, and 6) (Table 1). No water sample was collected from stations 3 and 4 because of adverse weather. Seawater samples for phytoplankton cell counts were preserved with glutaraldehyde (1% final concentration) immediately after sampling. Seawater samples for most probable number (MPN) analyses of diatom resting stage cells were stored at 1°C in the dark. Seawater samples from bottom depths (45 m) at station 1 were not available for MPN analysis.

The sediment samples were stored in the dark for more than 6 months to determine the viability of the resting stage cells under assumed Arctic winter conditions. After storage, the sediment samples were incubated according to the MPN method (Imai *et al*. 1984, 1990), and the abundance of viable resting stage cells of diatoms in the sediments was estimated. Homogenized wet sediment samples were suspended in sterile filtered seawater at a concentration of 0.1 g wet weight ml^{-1} and then diluted with modified SWM-3 culture medium (Chen *et al*. 1969; Imai *et al*. 1996a) to obtain several dilution series. Aliquots of five dilution series (10^{-2} to 10^{-6}) were inoculated in five parallels in tissue culture microplate wells (1 ml per well) at 5°C, 50 μmol photons m^{-2} s^{-1}, and a 14:10 h light:dark cycle. Each microplate well was monitored for detection of vegetative cells by using an inverted epifluorescence microscope (Eclipse TE200, Nikon, Tokyo, Japan). Identification of the species or taxonomic groups was determined every 3 days until the end of incubation at 14 days. The MPN of viable resting stage cells (MPN cells cm^{-3} wet sediment) was estimated based on the number of positive wells (appearance of vegetative cells) in the five wells of each dilution series, according to a statistical table (Throndsen 1978; Itoh & Imai 1987). The specific gravity of the wet sediment was determined as described by Kamiyama (1996), and it was then used to calculate the densities of viable diatom resting stage cells per 1 cm^3 of the sediment.

Water samples (500 ml) for MPN analyses of diatom resting stage cells were stored at 1°C in the dark for more than 6 months and concentrated tenfold after the sedimentation procedure. The water samples were diluted with modified SWM-3 culture medium to obtain the inoculation concentrations (10^{-1} to 10^{-3} dilution series). The MPN of viable resting stage cells in the water column was estimated after incubation by using the MPN method mentioned above. Phytoplankton distribution and species composition in the *in situ* water columns were determined using the preserved water samples. Appropriate aliquots (0.1–1.0 ml) of the concentrated samples were observed using an inverted microscope (Eclipse TE200, Nikon, Tokyo, Japan) at ×300–600 magnification. To observe diatoms, 150–600 cells were counted per sample. Analysis of similarities (ANOSIM) was performed using the Bray–Curtis similarity method with PRIMER v6 to evaluate similarity of the diatom species composition detected in the sediment, water, and fixed water samples from each station. The separate datasets were standardized and fourth-root transformed prior to analysis.

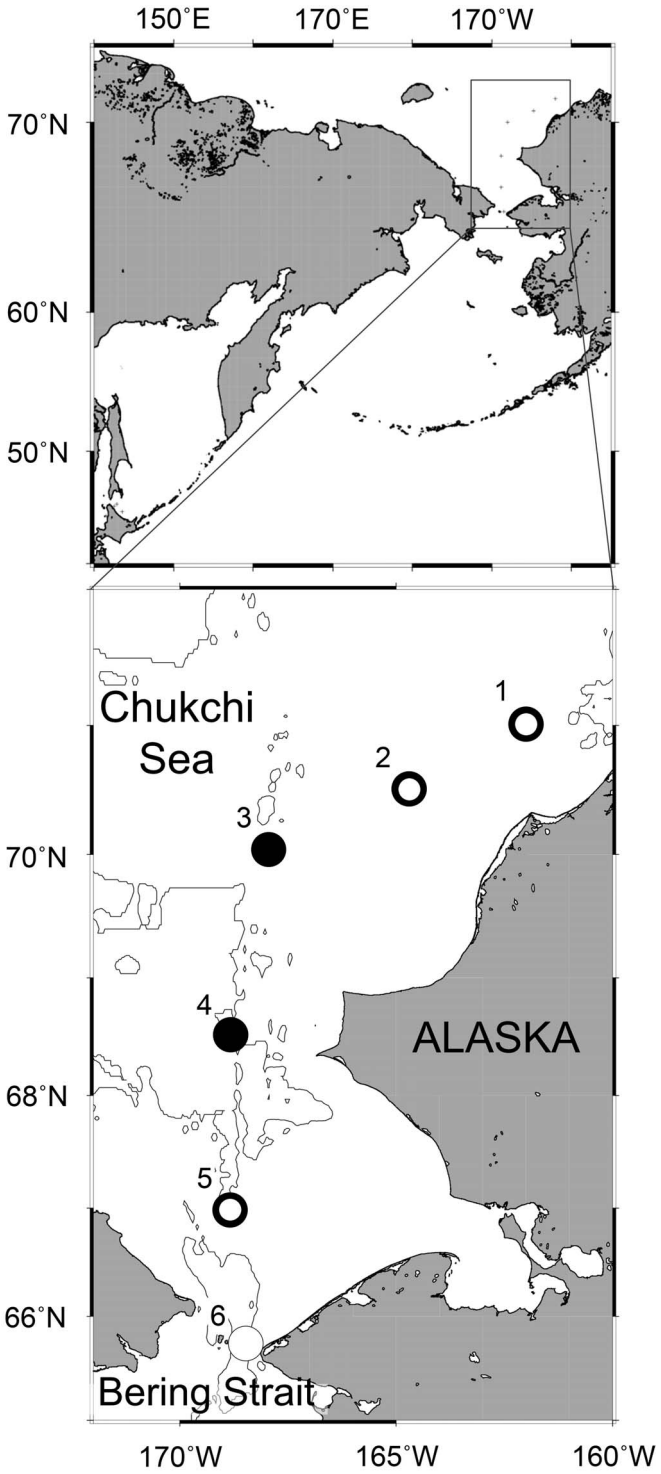


Fig. 1. Locations of the sampling stations in the Chukchi Sea and Bering Strait. Filled circles, core sampling stations; open circles, water sampling stations; open circles with black borders, core and water sampling stations.

RESULTS

Hydrographic conditions

The northward flow through the Bering Strait is generally defined as three water masses. The nutrient-poor Alaska Coastal Water (ACW, salinity $\leq$ 31.8, temperature $>$ 4°C) is distinct from the nutrient-rich Anadyr Water (AW, salinity = 32.5 to 33.0). Furthermore, temperature/salinity profiles distinguish the salty AW from Bering Shelf Water (BSW, salinity = 31.8 to 32.5) (Coachman *et al.* 1975; Grebmeier *et al.* 1988; Walsh *et al.* 1989). Consequently, the water masses have variable characteristics in the Chukchi Sea, such as surface mixed layer water (SMLW, salinity $<$ 30); Eastern Chukchi summer water (salinity = 31 to 32), which corresponds to the nutrient-poor ACW; and Western Chukchi summer water (salinity $>$ 32), which corresponds to the nutrient-rich AW (Shimada *et al.* 2001).

South of the Chukchi Sea (station 5) and Bering Strait (station 6), the temperatures of the water columns were uniformly 3–4°C, with a halocline at 10–20 m (Fig. 2). In the western Chukchi Sea (stations 1 and 2), the temperatures of the deeper layers were low, forming a thermocline under 30 m depth, particularly at station 1 where the cold water ($<$ 0°C) was possibly related to sea-ice formation. The low salinity water in the upper layer at station 1 was related to SMLW. The surface water was depleted of dissolved inorganic nitrogen (DIN) and silicate, which was in contrast to the large amount of nutrients (5.5–12.6 μM DIN and 19–28.5 μM silicate) present in the upper 10 m layer of station 5 (south of the Chukchi Sea) and station 6 (Bering Strait). The nutrient-poor water in the upper layer at station 2 is presumably affected by ACW. The water mass south of the Chukchi Sea (station 5) and Bering Strait (station 6) corresponded to BSW and AW, and the surface layer appeared to be affected by ACW.

Dissimilarity of the diatom species compositions in different datasets

In this study, a total of 25 genera, including 41 species, of diatoms were identified in the water and sediment samples. After incubation of sediment samples, 17 genera, including 27 species, of diatoms were observed; after incubation of water samples, 21 genera, including 35 species, of diatoms were identified. A total of 19 genera, including 21 species, of diatoms were identified in the fixed water samples (Table 2).

Analysis of the similarities showed no significant differences ($0.511 <$ Global R < 0.822, $P > 0.05$) between the diatom species compositions detected during the resting stage with the MPN method in the sediment and water samples (Table 3). Significant differences ($0.994 <$ Global R, $P < 0.01$) were observed between diatom species compositions in the fixed water samples and postincubation by using the MPN method in the water samples from stations 1, 2, 5, and 6.

Phytoplankton in the *in situ* water columns

The diatom assemblages in the *in situ* water columns were dominated by *Pseudo-nitzschia delicatissima* (Cleve) Heiden, *Cylindrotheca closterium* (Ehrenberg) Reimann & J.C.Lewin, *Proboscia alata* (Brightwell) Sundström, and *Thalassionema* spp. (Fig. 3). The resting spores of *Chaetoceros* spp. (including *C. furcellatus* Yendo, *C. diadema* (Ehrenberg) Gran, *C. debilis* Cleve, and *Chaetoceros* cf. *socialis* H.S.Lauder) occurred at all sampling depths of the *in situ* water columns, ranging from 200 to 1000 cells litre^{-1} in the upper 20 m, 200 to 7000 cells

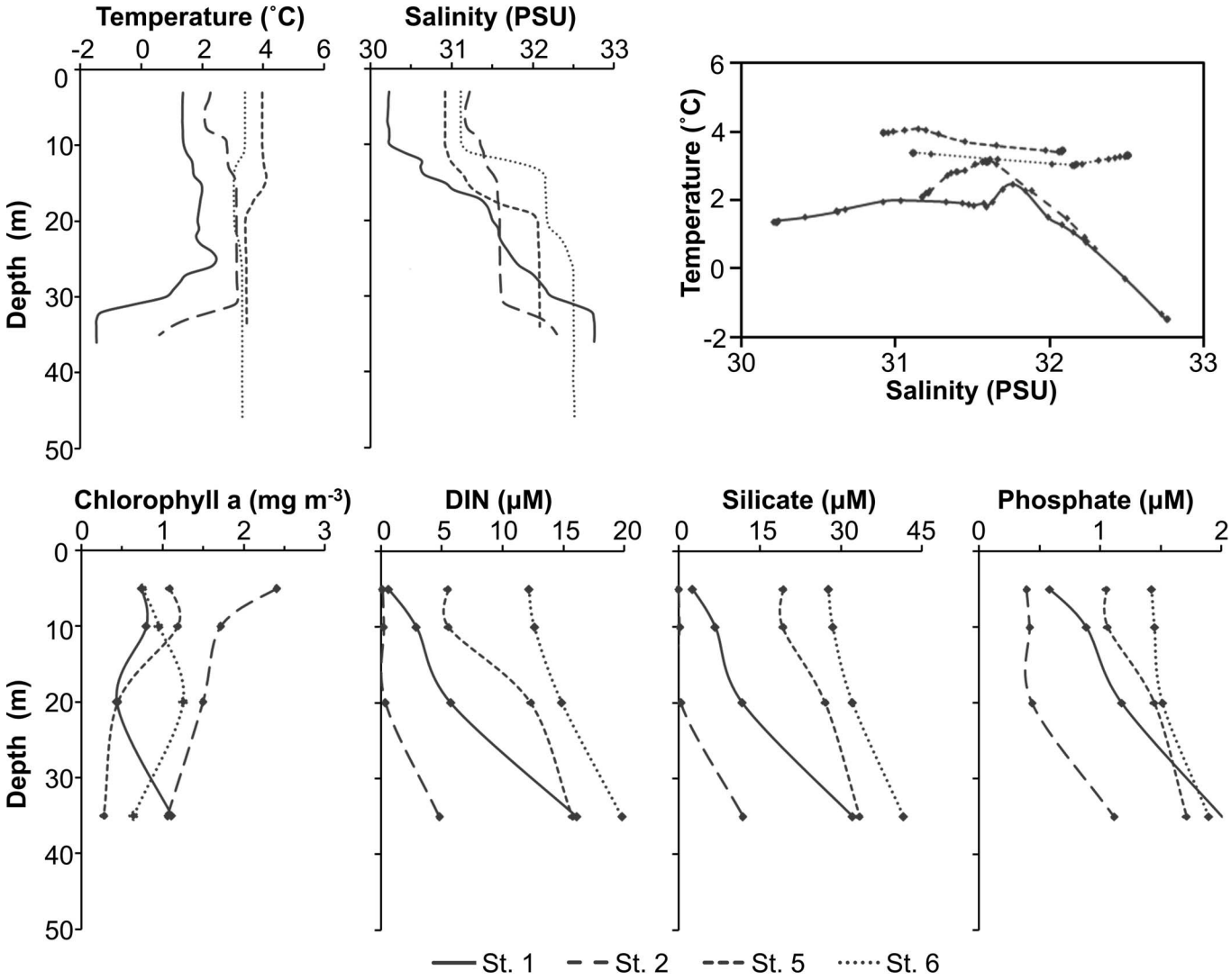


Fig. 2. Vertical profiles of temperature (°C), salinity, T–S diagrams, chlorophyll *a* (mg m^{-3}), dissolved inorganic nitrogen (DIN, μM), silicate (μM), and phosphate (μM) at stations 1, 2, 5, and 6.

$litre^{-1}$ above the sea bottom (55 m depth) in the Bering Strait, 100 to 2400 cells $litre^{-1}$ below 20 m, and 10 to 130 cells $litre^{-1}$ in the upper layer of the Chukchi Sea.

Diatom resting stages in the sediments

The distribution of the resting stage cells in the sediments varied spatially with respect to abundance and species composition. The estimated numbers of resting stage cells in the surface sediments according to the MPN analysis ranged from 3.5×10^5 to 6.8×10^6 (MPN cells cm^{-3} wet sediment) throughout the core sampling stations (Fig. 4). The maximum concentrations were found south of the Chukchi Sea (station 5), where pennate diatoms *Fragilariopsis* spp., including *F. cylindrus* (Grunow ex Cleve) Helcke & Krieger and *F. oceanica* (Cleve) Hasle, were abundant and accounted for about 39% of all the diatom resting stages. *Chaetoceros socialis* (30%) and *Thalassiosira nordenskioeldii* Cleve (21%) were the second and third most dominant species. *Chaetoceros socialis* markedly dominated and accounted for 70% of all the resting stage cells at station 3 and 71% at station 4. *Chaetoceros* spp. including *C. tenuissimus* Meunier, *C. diadema*, *C. debilis*, *C. furcellatus*, *C. wighamii* Brightwell and *C. subtilis* Cleve, were also observed. In the Chukchi Sea, a relatively large population of resting stage cells of the common Arctic species *Attheya longicornis* R.M.Crawford & C.Gardner (21% at station 1 and 37% at station 2) was found. With respect to other taxa, the centric diatoms *Bacterosira bathyomphala* (Cleve) Syvertsen & Hasle, *Detonula confervacea* (Cleve) Gran, and *Porosira glacialis* (Grunow) Jørgensen were relatively abundant (10^3 to 10^4 MPN cells cm^{-3} wet sediment). *Leptocylindrus danicus* Cleve, *Leptocylindrus minimus* Gran, and *Odontella aurita* (Lyngbye) C.Agardh were also identified in all the samples. Cells of *Rhizosolenia* spp. were detected at low abundances at stations 2, 4, and 5. Among pennate taxa, the genus *Fragilariopsis* was dominant in the sediments, while *Navicula* spp. (average 2.6×10^3 MPN cells cm^{-3} wet sediment), *Nitzschia* spp. (9.3×10^1 to 1.6×10^4 MPN cells cm^{-3} wet

Table 2. Occurrence (+) of diatoms in the sediments and water columns according to different datasets (cell count or MPN method).

	Cell count	MPN method	
	water	Water	Sediment
Actinoptychus senarius		+	
Asteroplanus karianus		+	+
Attheya longicornis		+	+
Attheya spp.	+		
Bacterosira bathyomphala		+	+
Chaetoceros debilis		+	+
Chaetoceros diadema		+	+
Chaetoceros didymus		+	
Chaetoceros furcellatus		+	+
Chaetoceros mitra		+	
Chaetoceros similis		+	
Chaetoceros simplex		+	
Chaetoceros socialis		+	+
Chaetoceros subtilis		+	+
Chaetoceros tenuissimus		+	+
Chaetoceros wighamii		+	+
Chaetoceros spp.	+	+	+
Cylindrotheca closterium	+	+	+
Detonula confervacea		+	+
Entomoneis spp.		+	
Eucampia spp.	+		
Fragilariopsis cylindrus			+
Fragilariopsis oceanica			+
Fragilariopsis spp.	+	+	+
Leptocylindrus danicus	+	+	+
Leptocylindrus minimus	+	+	+
Navicula spp.	+	+	+
Nitzschia spp.	+	+	+
Odontella spp.	+	+	+
Paralia sulcata	+	+	
Pauliella taeniata	+	+	+
Pleurosigma spp.	+	+	+
Porosira glacialis	+	+	+
Proboscia alata	+		
Pseudo-nitzschia delicatissima	+		
Pseudo-nitzschia spp.	+		
Rhizosolenia spp.	+		+
Skeletonema spp.	+	+	+
Synedropsis spp.		+	
Thalassionema spp.	+	+	
Thalassiosira angustelineata		+	
Thalassiosira gravida		+	+
Thalassiosira nordenskioeldii		+	+
Thalassiosira spp.	+	+	+

sediment), and *Cylindrotheca closterium* (2.0×10^1 to 3.5×10^3 MPN cells cm^{-3} wet sediment) were abundant in all the samples, as was *Pauliella taeniata* (Grunow) F.E.Round & Basson (4.0×10^1 to 2.0×10^3 MPN cells cm^{-3} wet sediment) at station 2 and station 3. *Pleurosigma* spp. were detected at low abundances (3.1×10^2 to 6.2×10^2 MPN cells cm^{-3} wet sediment) at stations 2, 3, and 4.

MPN analysis underestimates the abundance of viable resting stage cells of diatoms and is insensitive to detecting species with cell densities less than 50 cells ml^{-1} (Harris *et al.* 1998) or cell densities around or less than 100 cells g^{-1} wet sediment (Montresor *et al.* 2013). In this study, species with cell densities around or less than 30 cells cm^{-3} wet sediment were unlikely to be detected with MPN analysis.

Table 3. Results of the analysis of similarities (ANOSIM), in which the similarity of diatom species compositions in different datasets (diatom species detected in the sediments and water after incubation by using the MPN method and diatom species detected in the fixed water samples) at each station was evaluated.

	Stations			
ANOSIM	1	2	5	6
Sediment (MPN) vs water (MPN)				
Global R*[1]	0.72	0.822	0.511	—
Significance level (%)	16.7	14.3	14.3	—
Sediment (MPN) vs water (cell count)				
Global R	1	1	1	—
Significance level (%)	14.3	14.3	14.3	—
Water (MPN) vs water (cell count)				
Global R**[1]	1	0.989	0.994	1
Significance level (%)	0.2	0.2	0.2	0.2

[1] $*P > 0.05$, $**P < 0.01$.

Diatom resting stages in the stored water samples

In the water columns, viable diatom resting stage cells were detected at all sampling depths with the MPN method after storage for 6 months under both cold and dark conditions. Maximum density (average, 1.6×10^4 MPN cells $litre^{-1}$) was observed at a depth of 5 m above the seabed (35 to 45 m) at all water sampling stations. Dominant taxa were *Chaetoceros socialis* [68% at peak cell density layer (20 m depth) at station 5 and 74% at peak cell density layer (45 m depth) at station 6], *Attheya* spp. [53% at peak cell density layer (35 m depth) at station 1 and 98% at peak cell density layer (35 m depth) at station 2], and *Chaetoceros* spp. [36% at peak cell density layer (35 m depth) at station 1], including *C. furcellatus* and *C. diadema* (Fig. 5). *Thalassiosira nordenskioeldii* was detected at all sampling depths south of the Chukchi Sea (station 5), where its resting stages were abundant in the sediments (21% of total resting stage cell concentration). *Thalassiosira nordenskioeldii* abruptly appeared at 20 m depth and in the sediment of station 1, and at 35 m depth in station 2. Planktonic diatoms *Cylindrotheca closterium* and *Thalassionema* spp. were also detected within the water column. South of the Chukchi Sea (station 5), heavy silicified *Paralia sulcata* (Ehrenberg) Cleve, a predominantly tychopelagic species, was distributed throughout the water column; however, its density was the highest in deeper layers (37 to 47 m). Species detected in the deeper layers (20 to 55 m) totalled 12 ± 4 genera, including 14 ± 4 species, and they were more varied than the 9 ± 7 genera, including 8 ± 4 species, detected in shallower layers (0 to 10 m) at each water sampling station (1, 2, 5, and 6). In only the deeper layers, did we observe *Actinoptychus senarius* (Ehrenberg) Ehrenberg, *Bacterosira bathyomphala*, *Chaetoceros debilis*, *Chaetoceros didymus* Ehrenberg, *Chaetoceros mitra* (Bailey) Cleve, *Chaetoceros similis* Cleve, *Chaetoceros simplex* Ostenfeld, *Chaetoceros wighamii*, *Leptocylindrus minimus*, *Pauliella taeniata*, *Porosira glacialis*, and *Thalassiosira angustelineata* (A.W.F.Schmidt) G.Fryxell & Hasle; whereas, we observed *Thalassionema* spp. and *Synedropsis* spp. only at the upper 20 m depths.

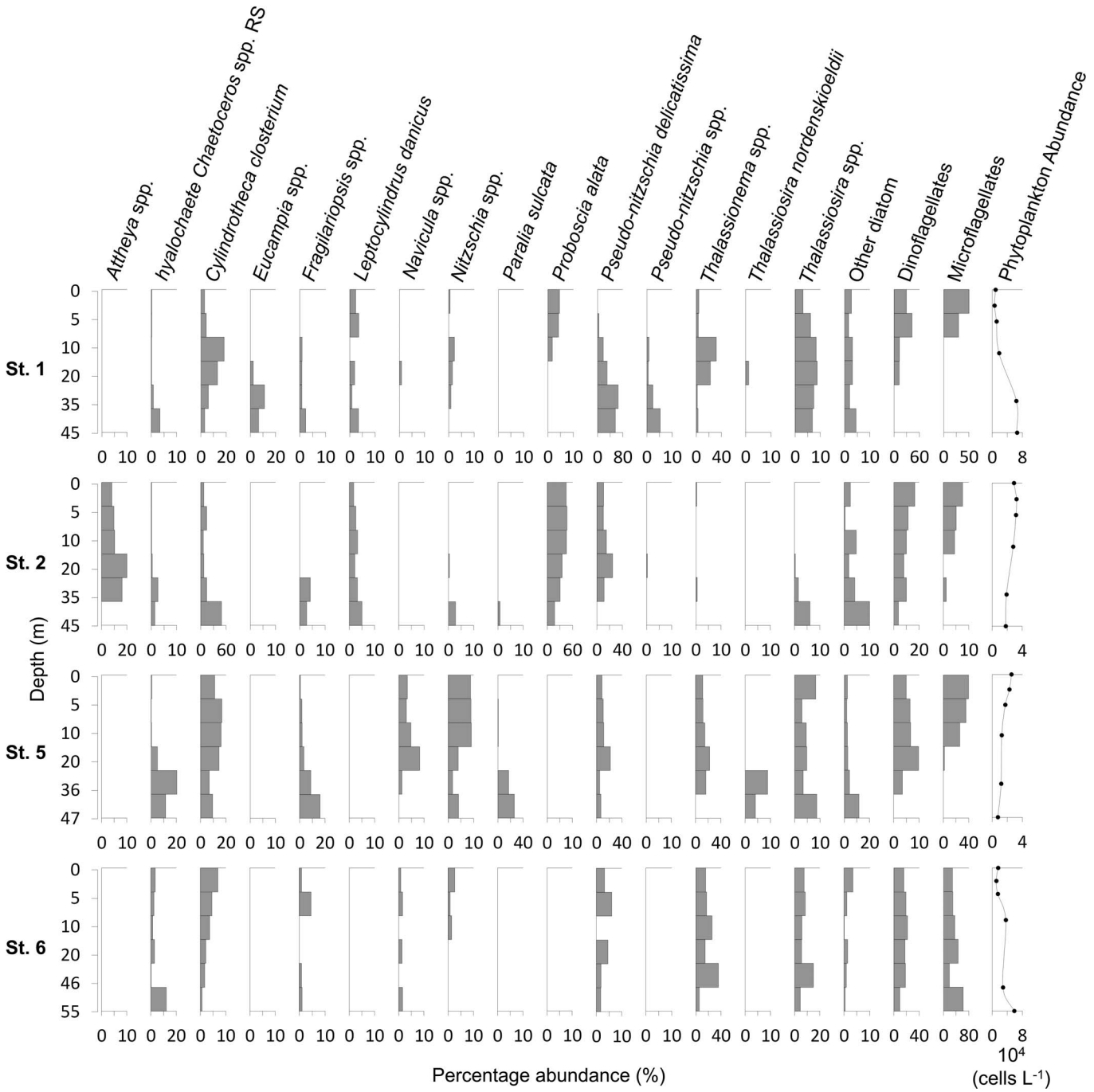


Fig. 3. Vertical distribution of cell abundance ($\times 10^4$ cells litre^{-1}) and taxonomic group composition of diatoms detected in the fixed water samples from Stations 1, 2, 5, and 6.

DISCUSSION

Advantages of autochthonous diatoms

During the sampling period, phytoplankton populations in the water columns were composed mainly of oceanic species that occur seasonally in the Bering shelf water from summer to fall (Taniguchi *et al.* 1976; Sukhanova *et al.* 2006); they clearly differed from species in the water columns as resting stage cells by using the MPN method after 6 months of storage in the dark. Diatom species detected after incubation with the MPN method were mainly planktonic diatoms that form resting stage cells, and few differences were observed between the species detected in the water columns and sediment samples (Tables 1, 2). According to Zhang *et al.* (1995), the mechanisms underlying energy storage and metabolic activity reduction are important for the survival of diatom cells during dark polar winters. Kuwata *et al.* (1993) reported that the resting stage cells (both resting spores and cells) of *Chaetoceros pseudocurvisetus* Mangin exhibited low respiratory and

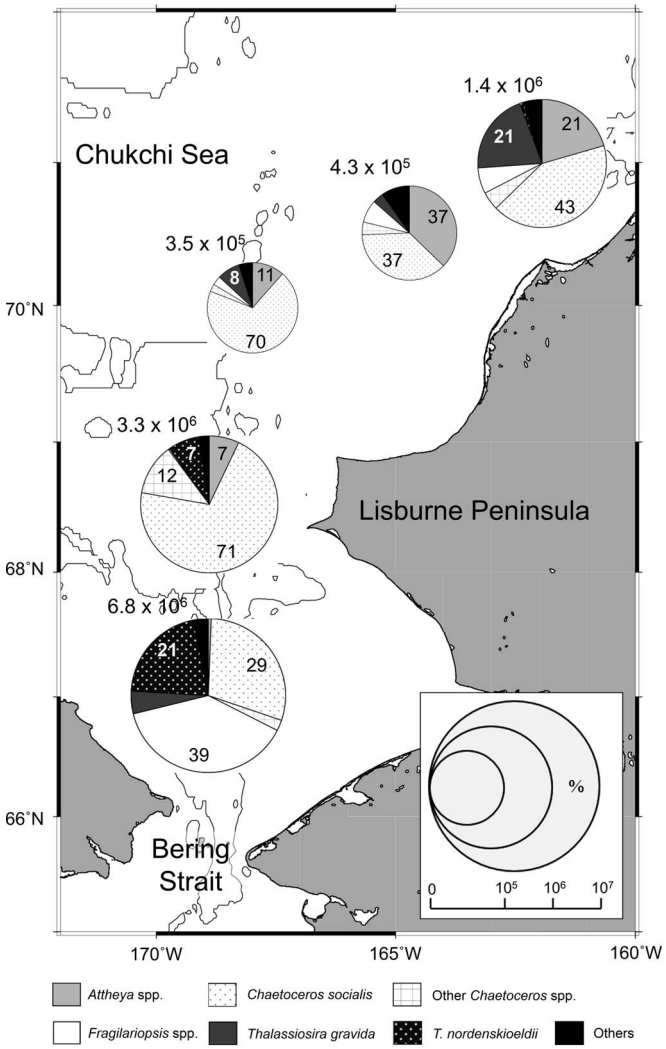


Fig. 4. Spatial distribution of total diatom resting stage cells (MPN cells cm^{-3} wet sediment) and composition of diatoms detected as dominant resting stage cells in the sediments of the Chukchi Sea. The numerals above the circles indicate the values of MPN. The numerals inside the circles indicate the percentages of diatom species compositions.

photosynthetic activities and accumulated more neutral lipids as an energy source with increased unsaturated fatty acids than the vegetative cells. In this study, diatoms that form resting stage cells, such as the hyalochaete *Chaetoceros* (e.g. *C. socialis*), remained viable under dark and cold conditions for more than 6 months and were capable of repropagation. With respect to the other planktonic pennate diatoms, such as *Cylindrotheca closterium* and *Thalassionema* spp., 10% of the total cells were capable of repropagation; whereas, dominant planktonic species in the *in situ* water columns during the sampling periods (e.g. *Pseudo-nitzschia delicatissima* and *Proboscia alata*) disappeared after 6 months of dark storage. The resting stage of *P. alata* has not been observed since the study by Cupp (1943). Hoogstraten *et al.* (2012) reported that *P. alata* is well adapted to natural variability in light availability in the modern Southern Ocean; however, this species appeared unable to overcome long dark periods like Arctic winters, along with *P. delicatissima*, which is not known to form resting stage cells. It is thought that these planktonic species were originally distributed in Pacific waters and do not develop indigenously in spring blooms along the ice edge soon after melting. Consequently, the life cycle–forming resting stage cells are essential for autochthonous species to endure severe Arctic environments and grow and bloom as dominant species.

Seed population of diatoms in the Chukchi Sea

In the Chukchi Sea, the abundance of viable resting stage cells in the sediments exceeded the general range (10^3 to 10^6 MPN cells cm^{-3} or g^{-1} wet sediment) of the temperate coastal areas, e.g. Seto Inland Sea of Japan (Imai *et al.* 1990; Itakura *et al.* 1997), Swedish Coast (McQuoid 2002), Indian Ocean (Mitbavkar & Anil 2002), East China Sea (Ishikawa & Furuya 2004). In particular, resting stage cells accumulated in the southern Chukchi Sea, where primary production is enhanced by the inflow of nutrient-rich water from the Bering Sea (Springer & McRoy 1993).

Besides physical and chemical factors, planktonic biomass and species composition in water columns influence the distribution of resting stage cells in sediments. Therefore, the distribution of diatom resting stage cells includes information about past diatom blooms (Pitcher 1990; Itakura *et al.* 1997; McQuoid 2002; McQuoid & Nordberg 2006). In general, planktonic centric diatoms such as *Chaetoceros* and *Thalassiosira* (or *Skeletonema*, especially in eutrophic regions) are the dominant taxa that contribute to spring phytoplankton blooms in coastal areas, and they are also dominant in sediments in the form of resting stage cells (Imai *et al.* 1990; Itakura *et al.* 1997). In this study, resting stage cells in the sediment samples determined using the MPN method were dominated mostly by typical Arctic planktonic species such as *Attheya* spp., *Chaetoceros socialis*, *Thalassiosira nordenskioeldii* and *Thalassiosira gravida* Cleve (Horner 1984; Booth & Horner 1997; Melnikov *et al.* 2002; Sergeeva *et al.* 2010; Zheng *et al.* 2011; Poulin *et al.* 2011). Unprecedentedly, in the southern Chukchi Sea, resting stage cells of *Fragilariopsis*, an important sea-ice–related pennate diatom, dominated the benthos. Previous studies have reported a massive phytoplankton bloom that develops beneath first-year sea ice on the Chukchi Sea continental shelf, which was dominated by *Chaetoceros*, followed by *Fragilariopsis* and *Thalassiosira* (Arrigo *et al.* 2012; Laney & Sosik 2014). The dominance of resting stage cells in the sediment appeared to correspond to their dominance as vegetative cells in phytoplankton blooms. Significantly, the large population of resting stage cells of *Fragilariopsis* estimated in this study indicates that sea-ice–related blooms dominated by *Fragilariopsis* possibly outweigh planktonic blooms of more typical species of *Chaetoceros* and *Thalassiosira* in the southern Chukchi Sea.

While 114 species of marine centric diatoms form resting spores, only a few rare marine pennate diatoms, such as *Fragilariopsis cylindrus*, *Fragilariopsis oceanica*, and *Pauliella taeniata*, form resting spores (Doucette & Fryxell 1983; McQuoid & Hobson 1996; Tomas 1997) and are important components of ice algal populations. In particular, *F. cylindrus* and/or *F. oceanica* were dominant species in both sea ice and water columns (Horner & Alexander 1972; Hsiao 1980, 1992; Horner & Schrader 1982; Hasle 1990; Syvertsen 1991; Von

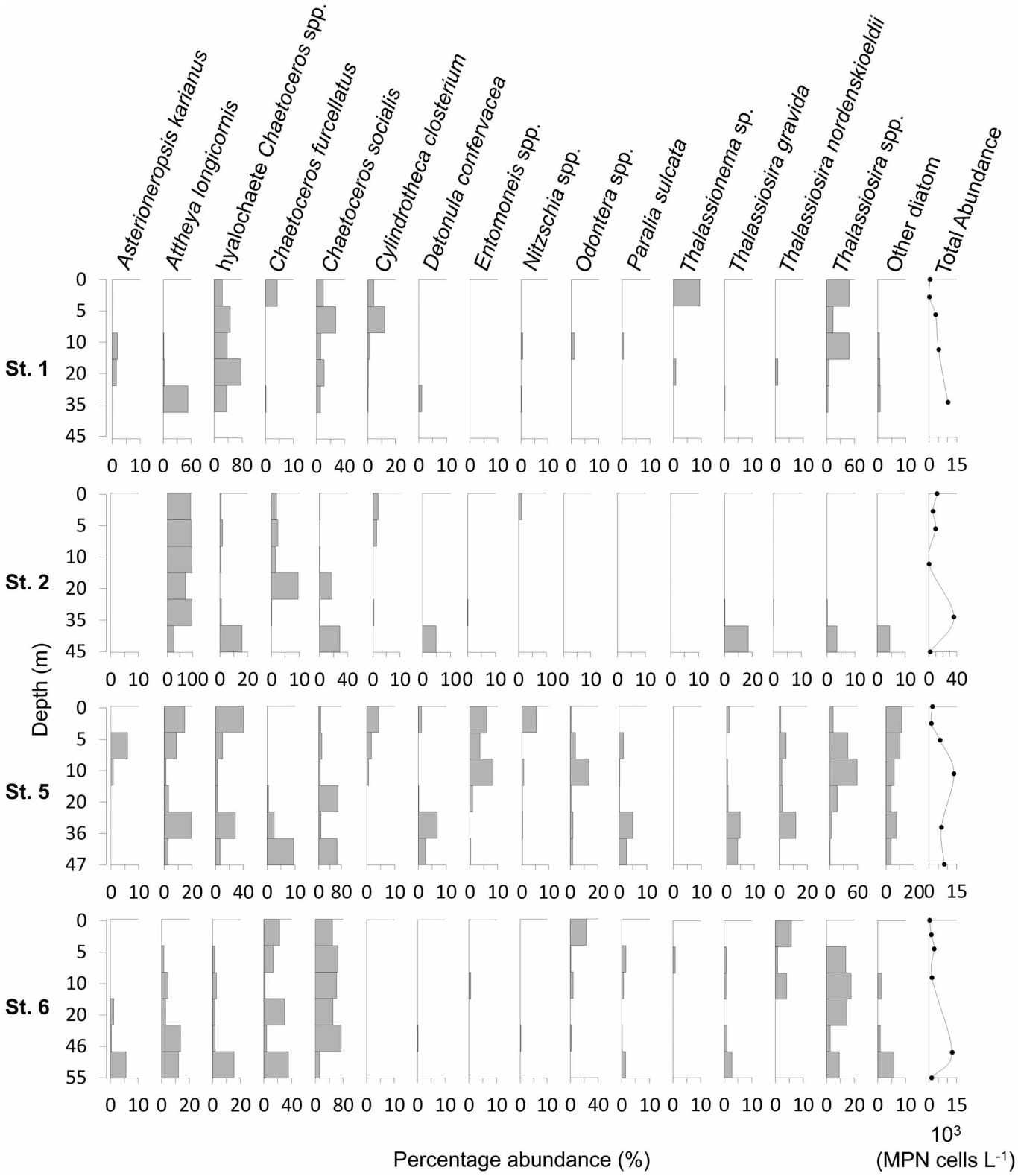


Fig. 5. Vertical distribution of resting stage cells ($\times 10^3$ MPN cells litre^{-1}) and taxonomic group composition of diatoms detected after incubation by using the MPN method at stations 1, 2, 5, and 6.

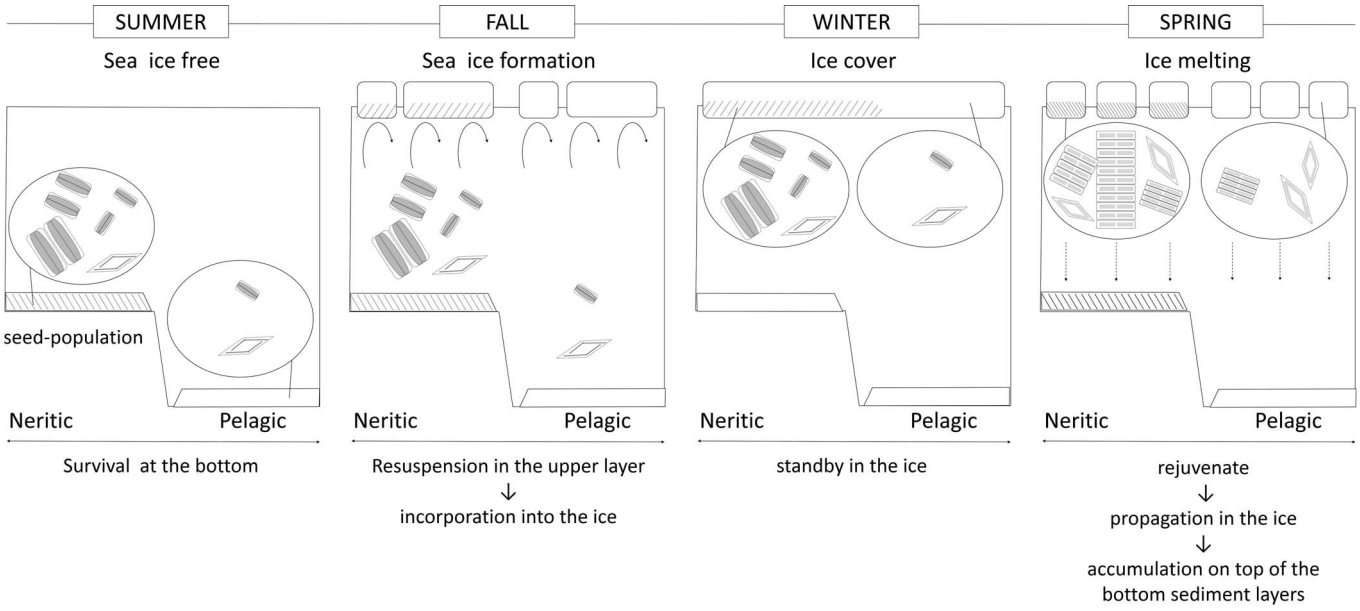
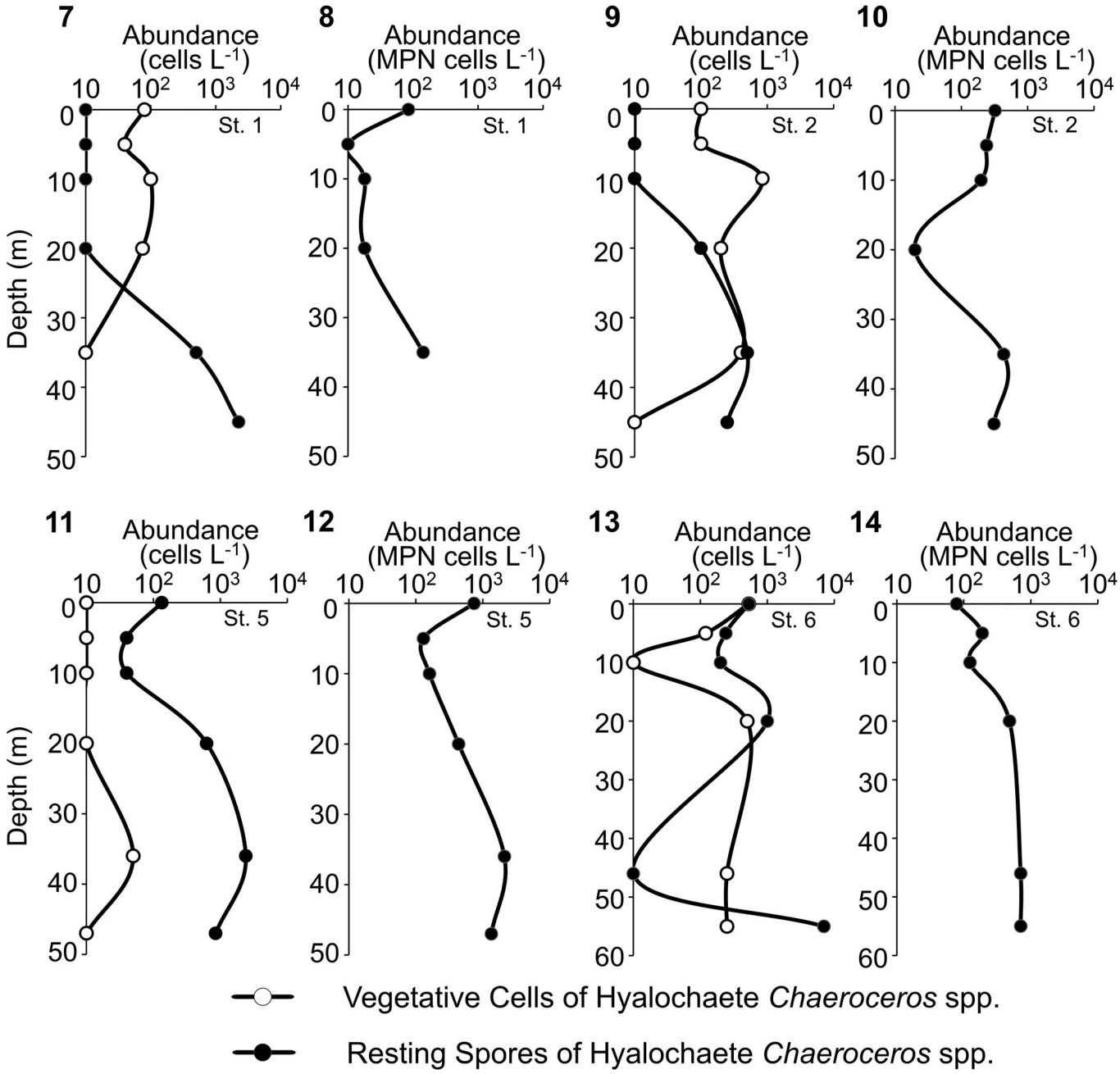


Fig. 6. Schematic representation of the cycles of the seed population of ice algal diatoms in the marginal ice zone.

Quillfeldt 1997, 2004; Von Quillfeldt *et al*. 2003; Sukhanova *et al*. 2009; Zheng *et al*. 2011). In addition to *Fragilariopsis*, other pennate diatoms in ice algal assemblages, such as *P. taeniata*, *Cylindrotheca closterium*, *Navicula* spp., *Nitzschia* spp., and *Pleurosigma* spp., remained viable as seed populations in the surface sediments during the warm season free of sea ice. These sea-ice–related diatoms surviving at the bottom have the potential to initiate future blooms. The resting stage cells at the sea bottom need to be embedded into the sea ice during ice formation to develop as sea-ice–related blooms. In the southern Chukchi Sea, upwelling and turbulent mixing are derived from northward flow through the Bering Strait (Walsh *et al*. 1989), and vertical mixing is driven by wind, cooling, and brine from sea ice between autumn and winter (Aagaard & Roach 1990; Weingartner *et al*. 1998, 2005). Subsequently, large seed populations can be resuspended from the surface sediments in the water columns. In addition, inorganic sediment particles and microorganisms are incorporated and accumulated within sea ice (Garrison *et al*. 1983; Syvertsen 1991; Reimnitz *et al*. 1993; Weissenberger & Grossmann 1998). Even benthos on shallow shelves adhere to frazil ice possibly formed at a depth of 25 to 30 m (Reimnitz *et al*. 1992). Thus, resting stage cells can be incorporated into the newly forming sea ice (Von Quillfeldt 1997; Von Quillfeldt *et al*. 2003; Werner *et al*. 2007). Consequently, the formation of an ice algal assemblage begins with sea ice formation (Hsiao 1980; Horner & Schrader 1982; Niemi *et al*. 2011). Certain diatoms, including sea-ice–related species and planktonic species, can survive in the ice by using stored energy and reduced metabolic activity, supposedly via formation of resting stage cells. Eventually, resting stage cells that survive in the ice will develop into ice algal blooms and/or plankton blooms associated with the return of daylight and melting of the sea ice. Several factors are essential for the occurrence of an ice algal bloom: benthic resting stage cells, physical processes that allow resuspension of resting stage cells in the water column, and ice formation. Von Quillfeldt (1997) indicated different sources of ice algae that originate seasonally from the water column, benthos, and freshwater, after observing great variation in species composition in the assemblages of ice algae. Algal cells in multiyear ice may also be a source of ice algal blooms, especially ice that forms over deep Arctic basins (Olsen *et al*. 2017). However, in the shallow marginal ice zone, the seeding of ice algae from the seafloor can be most successful for ice formation where viable diatom resting stage cells are densely distributed (Fig. 6).

Distribution of resting stage cells in the water columns

The MPN method revealed that vegetative cells in the upper layers of station 1 and station 2 changed to resting stage cells during storage in the dark (Figs 7–10). The formation of resting spores and cells depends upon differences in nutrient deficiency induced by nitrogenous nutrients and silicic acid in the case of *C. pseudocurvisetus* (Kuwata *et al*. 1993). Because there was not enough nitrate and silicic acid available in the water samples from the upper layers of the western Chukchi Sea, dark storage under may have initiated the formation of resting cells rather than resting spores, which need large amounts of silica to produce new thickened cell walls. The principal triggers for resting spore formation are depletion of nutrients (especially nitrate) and insufficient light (Garrison 1981; Hollibaugh *et al*. 1981; Hargraves & French 1983; Kuwata & Takahashi 1990; Itakura *et al*. 1993), and the likelihood of resting stage formation increases when DIN concentration is less than 1 μM (Garrison 1981; Itakura & Imai 1994). Kuwata & Takahashi (1990) reported that *Chaetoceros pseudocurvisetus* formed resting spores under a nitrate to silicate ratio of 3.1:1 to 9.3:1, and the resting spore formation terminated when the silicate concentration decreased to around 4 μM. During the sampling periods, resting spores of hyalochaete *Chaetoceros* spp., including *C. furcella-*



Figs 7–14. Comparison of the vertical distribution of hyalochaete *Chaetoceros* spp. including *Chaetoceros furcellatus*, *Chaetoceros diadema*, and *Chaetoceros debilis* in different datasets.

Figs 7, 9, 11, 13. Resting spores and vegetative cells distributed in the *in situ* water column of stations 1, 2, 5, and 6 verified using cell counts.

Figs 8, 10, 12, 14. Viable resting spores detected in the water column of stations 1, 2, 5, and 6 after incubation by using the MPN method.

tus, *C. diadema*, and *C. debilis*, were found below 20 m depth in the *in situ* water columns at stations 1 and 2 (Fig. 7, 9). Because the sinking rate of resting spores is five times faster than that of vegetative cells (Bienfang 1981), resting spores were supposedly formed in the upper layers and promptly sank to the deeper layers of the water columns in the Chukchi Sea. South of the Chukchi Sea (station 5) and in the upper 20 m and bottom layers of Bering Strait (station 6), resting spores were present throughout the water column during the sampling period (Figs 11–14); however, it cannot be assumed that they formed at these layers because of favourable nitrate and silicate conditions. Because the water masses at stations 5 and 6 have sources in BSW and AW and the surface layer is affected by ACW, the resting stage cells in the southern Chukchi Sea were probably carried by these currents. In shallow areas, especially, physical events (e.g. vertical mixing by wind, cooling, tidal currents, upwelling, or convection) and human activities (e.g. bottom trawlings or dredging) resus-

pend the resting stages cells of surface sediments in the euphotic layer (Pitcher 1990; Ishikawa *et al*. 2001; McQuoid & Godhe 2004). Once the resting stage cells are incorporated into the water column, the current transports cells to another area, where favourable environmental conditions allow vegetative cells to sometimes develop into blooms. Short innate dormancy, usually from several days to several weeks, has been shown in diatom resting stage cells [e.g. *Chaetoceros diadema, Chaetoceros didymus, Leptocylindrus danicus, Skeletonema costatum* (Greville) Cleve] before germination and/or repropagation (Hargraves & French 1983; Itakura *et al*. 1992; Itakura *et al*. 1993). However, resting cells that maintain their vegetative cell form can respond more quickly to favourable environments than resting spores, allowing them to recover the population (Kuwata & Takahashi 1990). In the southern Chukchi Sea where nutrients are supplied by currents, allochthonous resting stage cells, especially resting cells, would be responsible for seeding the populations of occasional blooms.

In summary, several typical Arctic diatom species form resting stage cells, an adaptation for the dark Arctic winters and dominate as autochthonous species among ice algae or phytoplankton immediately after the recovery of daylight in marginal ice zones. Several sources seed diatom populations into phytoplankton communities and sea-ice assemblages associated with currents or resuspended from sediments. In the shallow marginal ice zone of the Chukchi Sea, where resting stage cells of sea-ice–related diatoms and planktonic diatoms are dense at the bottom, resuspension of seed populations from the sediments during ice formation may be an effective source for initiating ice algae and subsequent plankton blooms.

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