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Distribution of viable diatom resting stage cells in bottom sediments of the eastern Bering Sea shelf

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ABSTRACT

Information on diatom resting stages is fundamentally important to understanding the population dynamics of diatoms including bloom formation. The distribution of viable diatom resting stage cells in bottom sediments of the eastern Bering Sea in July 2009 was investigated by the most probable number (MPN) method. The abundances of diatom resting stage cells ranged from 1.7×10^3 to 1.2×10^6 MPN cells cm^{-3} wet sediment, comparable to those in shallow eutrophic areas where diatom blooms frequently occur. Common species during the spring phytoplankton bloom in the eastern Bering Sea were also dominant in sediments as resting stage cells. It should be noted that relatively high numbers of ice algae species, especially ribbon-shaped chain forming pennate diatoms, were found in the sediments. The life cycle strategy using resting stage cells allows planktonic and ice algal species to survive unfavorable environmental conditions such as the dark winter season, and potentially contribute to form blooms of several types (subsurface of ice, ice edge, plankton) through vertical mixing.

1. Introduction

Diatoms are important primary producers within marine ecosystems, and contribute to efficient primary production. Many diatom species are large and often form colonies in chains. Diatom blooms occur extensively in the spring and fall along the coastal areas of middle to high latitudes. It is well known that many diatoms, especially coastal planktonic species, form resting stage cells associated with unfavorable conditions such as low nitrogen concentration and low light intensity (Durbin, 1978; Garrison, 1984; Hargraves and French, 1975; Hollibaugh et al., 1981; McQuoid and Hobson, 1996). Vegetative cells of these diatom species temporarily disappear from the water column, and then reappear and bloom again after some period. The life cycle including resting stages ensures they survive variable coastal environments, leading to domination among phytoplankton populations.

High abundances of diatom resting stage cells ($\sim10^6$ MPN cells cm^{-3} wet sediment) have been reported from bottom sediments of temperate coastal areas such as the Seto Inland Sea, Japan (Imai et al., 1990; Itakura et al., 1997). The distribution of resting stage cells in sediments is likely related to the distribution of phytoplankton populations in the water column (Pitcher, 1990). Viable resting stage cells potentially affect the occurrence of autochthonous plankton species in the water column (Itakura et al., 1997). Therefore information, for example distribution and abundance, on resting stage cells is fundamentally important in determining the spatial distribution of diatoms population dynamics and species succession (McQuoid, 2002).

The eastern Bering Sea shelf is the widest continental sea shelf outside the Arctic. The wide shallow shelf, more than 500 km wide, is seasonally covered by sea ice in all years. This is a region well known for high productivity of upper trophic level organisms including crabs, fish, birds, and mammals (McRoy et al., 1986). The annual increase in primary production usually begins with the growth of ice algae on the underside of sea ice (e.g. *Acnanthes taeniata*, *Fragilaria striatula*, *Fragilariopsis cylindrus*, *Fragilariopsis oceanica*; Saito and Taniguchi, 1978), followed by a phytoplankton bloom in the water column in the ice front zone (e.g. *Thalassiosira gravida*, *Thalassiosira hyalina*, *Thalassiosira nordenskioeldii*; Saito and Taniguchi, 1978), and the conventional spring bloom in the water column upon thermal stratification (e.g. *Chaetoceros convolutus*, *Chaetoceros debilis*, *Chaetoceros furcellatus*, *Chaetoceros diadema* , dinoflagellates; McRoy and Goering, 1976; Saito and Taniguchi, 1978). When the ice retreats early in late winter, the open water bloom begins in late spring in the stratified water columns due to solar heating without ice associated spring bloom (Eslinger and Iverson, 2001; Hunt et al., 2002; Stabeno et al., 1998, 2001).

The southeastern Bering Sea shelf is separated into distinguishable hydrographic domains by three fronts, and these domains have different circulation features with distinct temperature,

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salinity and stratification properties (Coachman et al., 1980; Coachman, 1986). In the coastal shelf domain (CSD: < 50 m isobath), the water column tends to be vertically homogeneous due to the overlapping of wind and tidal mixing energies. The middle shelf domain (MSD: $50 < H < 100$ m isobaths) water column is generally homogeneous during fall and winter. Throughout late spring and summer, the surface wind mixed layer is separated from the tidally mixed bottom layer by a pronounced thermocline. The outer shelf domain (OSD: $100 < H < 170$ m isobaths) is a zone of little or no mixing energy characterized by persistent fine structuring of properties between the surface wind mixed layer and tidally mixed bottom layer. The shelf break front separating shelf water from basin water along the shelf edge zone, the Bering Slope Current (Kinder et al., 1975; Schumacher and Reed 1992), is an important physical feature (Springer et al., 1996).

The life cycle of diatoms, including resting stages, is considered essential to their survival and dominance over the Bering Sea shelf, similar to the situation of temperate coastal areas where there is a mutually intimate interaction between water column and sea bottom. In this manuscript, we report on the distribution of viable resting stage cells of diatoms in the eastern Bering Sea shelf bottom sediments, and discuss the dynamics of diatom populations.

2. Materials and methods

Sampling was conducted at 22 stations in the eastern Bering Sea shelf from 8 to 15 July 2009 during a cruise OS202 of the T/S Oshoro-Maru of Hokkaido University (Fig. 1). A CTD cast was made at each station to measure water column temperature, salinity, density and collect discrete samples for nutrient analysis. Major nutrient concentrations were measured with a Technicon auto-analyzer basically employing the methods reported by Parsons et al. (1984) and Matsunaga et al. (1990). Sediment sampling was carried out at 17 stations using a Smith-McIntyre grab sampler or a gravity core sampler. The top 3 cm of sediment core was extruded and stored in darkness at 2 °C for more than 3 months for the purpose of eliminating vegetative cells . Sediment samples were analyzed following the procedure of the most probable number (MPN) method (Imai et al., 1984, 1990) to estimate the abundance of viable resting stage cells in sediments. Homogenized sediment samples were suspended in sterile filtered seawater at a concentration of 0.1 g wet weight mL^{-1} (10^0 dilution). This 10^0 dilution of suspension was used to prepare a 10^{-1}–10^{-6} dilution series with modified SWM-3 culture medium (Chen et al., 1969; Imai et al., 1996a). Five aliquots (1 mL) of each dilution series were incubated using tissue culture microplates under an illumination of 30 μmol-photons m^{-2} s^{-1} and a 14:10 h light:dark cycle at a temperature of 5 °C on the assumption of representing the sea surface environmental conditions. Appearance of vegetative cells was measured for each well of the microplates, and species or taxonomic groups identified using inverted microscopy every 3 days until the end of incubation at 7–14 days. Wells in which vegetative cells were identified were scored as positive. MPN of viable diatom resting stage cells (MPN cells g^{-1} wet sediment) was estimated according to statistical tables (Itoh and Imai, 1987; Throndsen, 1978), based upon the number of positive scores in the five wells of each dilution. MPN per cubic centimeter of wet sediment was calculated with the apparent specific gravity of wet sediment determined according to Kamiyama (1996).

Water samples were collected from the sea surface at each station and from several depths at St. 11 and St. 18 for phytoplankton and chlorophyll *a* analyses. Water samples were sequentially filtered through 20 μm mesh, a membrane filter (2 μm) and a GF/F filter, then analyzed for chlorophyll *a* using a Turner Designs fluorometer (Suzuki and Ishimaru, 1990). Phytoplankton samples were preserved with glutaraldehyde at a final concentration of 1% and then settled and concentrated to ten to twenty fold. Appropriate aliquots (0.2–1 mL) of concentrated samples were transferred to a slide glass and phytoplankton cells counted using an inverted microscope. Species were further identified using a light microscope at 1000 × magnification and a scanning electron microscope.

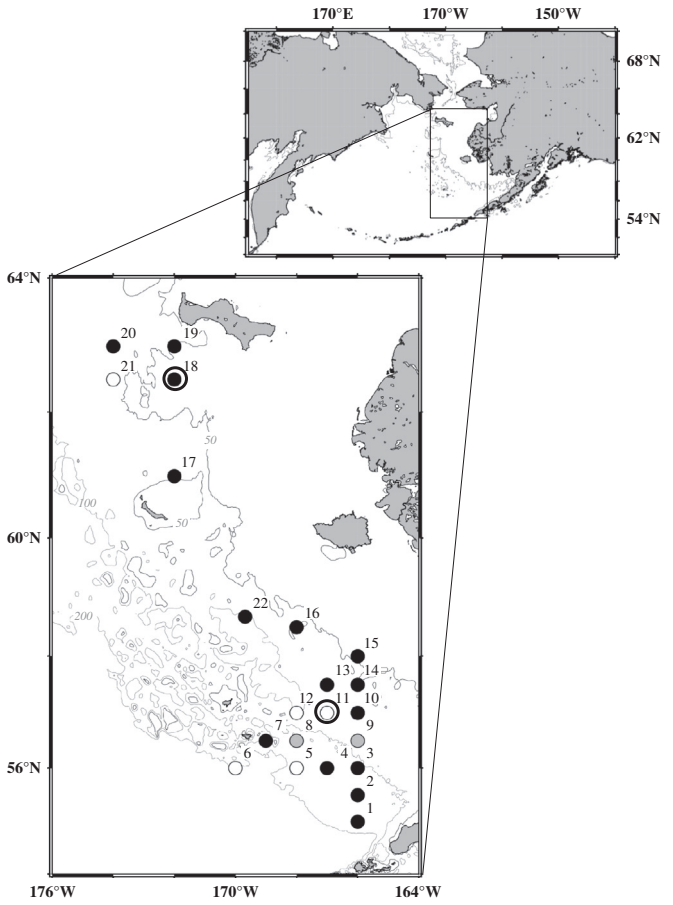

Fig. 1. Sampling stations in the eastern Bering Sea. •: stations for collection of sediment core and surface water, ◯: sediment core, ○: surface water, ◯: water samples from several depths.

3. Results

3.1. Hydrography

According to the theory of Coachman et al. (1980), stations were divided into three distinct depth domains. Thermoclines were generally found at 20–30 m in the MSD during the cruise (Fig. 2A). The pycnocline was exceptionally clear at stations with about 20 m depth in the Saint Laurence Island Polynya region (Smith et al., 1990) (Fig. 2B). These stations were separated from other MSD stations by characteristics of bottom temperature. Surface nutrients were depleted over the eastern Bering Sea shelf during the cruise (Table 1).

3.2. Distribution of phytoplankton

High surface chlorophyll *a* concentrations (St. 5; 6.1 μg L^{-1}, St. 7; 4.7 μg L^{-1}) and phytoplankton cell abundances (6.1×10^5–1.8×10^6 cells L^{-1}) were patchy at stations along the shelf edge. The dominant species was *Pseudo-nitzschia* cf. *delicatissima* (St. 5; 85%, St. 7; 45%).

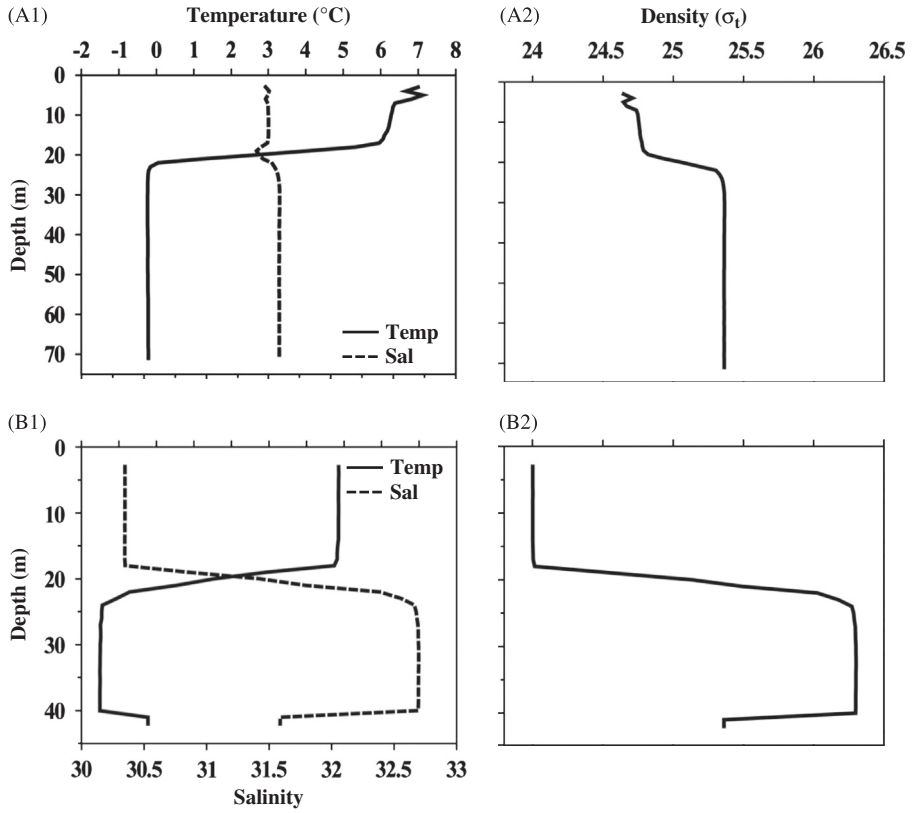

Fig. 2. Vertical profiles of temperature and salinity at station 11 (A-1) and station 18 (B-1), and density profiles at station 11 (A-2) and station 18 (B-2) in water columns of the eastern Bering Sea during the cruise in July 2009.

Table 1
Surface nutrient (NO_3+NO_2,SiO_2, PO_4) concentration (μM) in the Bering Sea in July 2009. Stations were divided into four domains, OSD (outer shelf domain: $100 < H < 170$ m isobaths), MSD (middle shelf domain: $50 < H < 100$ m isobaths), CSD (coastal shelf domain: < 50 m isobaths) and SLIP (St. Lawrence Island Polynya region).

St.	Domain	Depth (m)	Day (July 2009)	NO_3+NO_2 (μM)	SiO_2 (μM)	PO_4 (μM)
1	OSD	135	8	14.25	28.34	1.25
2	OSD	121	8	1.74	13.20	0.55
3	OSD	113	9	0.58	10.35	0.50
4	OSD	133	9	0.40	7.58	0.29
5	OSD	136	9	1.62	20.85	0.59
6	OSD	220	9	6.28	24.77	0.88
7	OSD	102	10	0.37	16.92	0.29
8	OSD	115	10	0.09	2.03	0.22
9	MSD	84	10	0.10	1.83	0.16
10	MSD	70	10	0.08	2.42	0.41
11	MSD	75	10	0.05	1.30	0.15
12	MSD	77	11	0.05	1.30	0.15
13	MSD	70	11	0.09	1.71	0.57
14	MSD	64	11	0.08	2.36	0.41
22	MSD	70	15	0.03	1.06	0.18
15	CSD	54	11	0.06	1.59	0.48
16	CSD	45	11	0.08	2.42	0.48
17	SLIP	55	12	0.09	4.36	0.57
18	SLIP	45	13	0.11	2.12	0.32
19	SLIP	53	13	0.03	3.18	0.43
20	SLIP	74	13	0.06	5.71	0.37
21	SLIP	68	14	0.31	4.06	0.42

In the southern region (St. 11; MSD), there was a maximum in chlorophyll *a* concentration (1.62 μg L^{-1}) and cell abundance (1.1×10^5 cells L^{-1}) above the pycnocline (Fig. 3). The small phytoplankton size fractions (< 20 μm) contributed to high chlorophyll *a* concentrations, and were dominated by small dinoflagellates and microflagellates (78–92%). Diatoms dominated below the pycnocline, but chlorophyll *a* concentrations and cell abundances were relatively low. In the northern region (St. 18; Polynya region), there was a maximum of chlorophyll *a* concentration (1.3 μg L^{-1}) and cell abundance (3.8×10^5 cells L^{-1}) below the pycnocline dominated by large (> 20 μm) diatoms (71–95%). At this station, dinoflagellates and microflagellates dominated in the abundance in the upper layer but chlorophyll *a* concentrations and cell abundances were relatively low.

Fig. 4 illustrates the vertical distributions of diatoms at St. 11 and St. 18. Vegetative cells of *Chaetoceros* spp. were observed in the upper layer, and resting spores of *Chaetoceros* spp., especially *C. furcellatus*, were abundant in the lower layer of both stations. The diatom species characteristically found in the water column were *Paralia sulcata* at St. 11, and *T. nordenskioeldii* and *Porosira glacialis* at St. 18.

3.3. Abundances of resting stage cells in sediments estimated by the MPN method

The numbers of resting stage cells in bottom sediments estimated by the MPN method were in the range of 1.7×10^3 (St. 1) to 1.2×10^6 (St. 20) MPN cells cm^{-3} wet sediment (Fig. 5). Eighteen centric diatom taxa and 4 pennate diatom taxa were observed as vegetative cells after the incubation for the MPN method (Table 2). Almost all species were already reported as species found in the Bering Sea (Goering and Iverson, 1981; Motoda and Minoda, 1974; Saito and Taniguchi, 1978; Schandelmeier and Alexander, 1981). Dinoflagellate cysts were also estimated ($\sim 1.2 \times 10^3$ MPN cells cm^{-3} wet sediment). The highest concentrations were found south of St. Lawrence Island (St. 20). The number of viable cells ranged from 6.1×10^4 to 9.2×10^5 MPN cells cm^{-3} wet sediment (average 2.4×10^5) in the MSD and CSD. There were small numbers of resting stage cells in the OSD and shelf edges where the bottom depths were greater

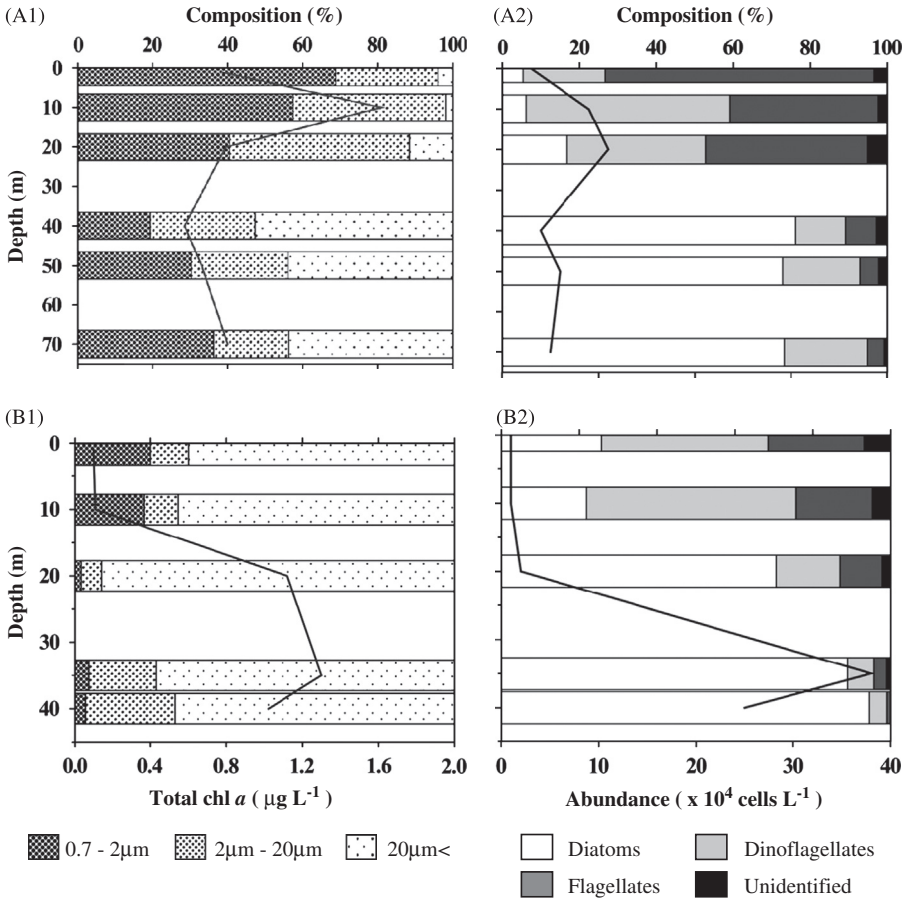

Fig. 3. Vertical profiles of chlorophyll *a* concentrations (μg L^{-1}) of three size fractions at station 11 (A-1) and station 18 (B-1), and cell abundances (× 10^4 cells L^{-1}) and taxonomic group composition of phytoplankton at station 11 (A-2) and station 18 (B-2) in water columns of the eastern Bering Sea in July 2009.

than 100 m, and the numbers ranged from 1.7×10^3 to 6.8×10^4 MPN cells cm^{-3} wet sediment (average 2.1×10^4).

Fig. 6 shows the dominant diatom species of viable resting stage cells in sediments. The numbers of resting stage cells in the southern region and south of St. Lawrence Island are summarized in Table 2. *Chaetoceros* spp. (~1.3×10^5 MPN cells cm^{-3} wet sediment), *Thalassiosira* spp. (~1.8×10^5 MPN cells cm^{-3} wet sediment) and *Attheya longicornis* (~8.7×10^5 MPN cells cm^{-3} wet sediment) were the dominant taxa. *C. diadema* (~6.8×10^4 MPN cells cm^{-3} wet sediment), *Chaetoceros socialis* (~6.3×10^4 MPN cells cm^{-3} wet sediment) and *C. furcellatus* (~2.4×10^4 MPN cells cm^{-3} wet sediment) were abundant species of the genus *Chaetoceros*. *T. nordenskioeldii* (~1.8×10^5 MPN cells cm^{-3} wet sediment) and *T. gravida* (~5.5×10^4 MPN cells cm^{-3} wet sediment) were abundant species of the genus *Thalassiosira*. *P. sulcata* was detected at high abundances in the southern region (~6.3×10^4 MPN cells cm^{-3} wet sediment). *Skeletonema* spp. and *Odontella* spp. were also identified but the abundances were relatively low. Other species with high abundances were the pennate diatoms of ribbon-shaped colony forming species, *F. cylindrus*, *F. oceanica*, *Fragilaria* cf. *capucina*, *Fragilaria oblonga*, *Pauliera taeniata* (~1.1×10^5 MPN cells cm^{-3} wet sediment) and solitary *Navicula* spp. (~3.6×10^4 MPN cells cm^{-3} wet sediment).

4. Discussion

4.1. Phase of phytoplankton populations during the study cruise

Phytoplankton populations were changing from a phase dominated by diatoms to one dominated by flagellates during this sampling period. The phase transition was observed above the pycnocline and low latitudes (St. 11). Surface nutrient concentrations were depleted when surface stratification developed, and chlorophyll concentrations declined to low levels over the eastern Bering Sea shelf (Whitledge et al., 1986). Observed phytoplankton assemblages suggest that the study period was near the end of a diatom bloom. High abundances of *Chaetoceros* spp. resting spores were observed in the lower layer whereas the vegetative cell abundances were low in the upper layer (Fig. 4). This result strongly suggests that diatom resting stage cells would have formed before the cruise and had been sinking near the end of the bloom.

It is well known that there is a current of water originating at the Bering Sea shelf edge that is rich in nutrients and plankton (Springer et al., 1996). During this cruise, relatively high chlorophyll *a* concentrations and phytoplankton (diatoms) cell abundances were observed only at the shelf edge, suggesting the contribution to primary productivity in summer season.

4.2. Distribution of resting stage cells in the bottom sediments

The viable resting stage cells in sediments are potentially important seed banks for planktonic blooms. The population size of resting stage cells distributed in the eastern Bering Sea shelf was comparable to that distributed in the Seto Inland Sea of Japan (~10^6 MPN cells cm^{-3} wet sediment: Imai et al., 1990; Itakura et al., 1997, 1999), and that in the coastal Swedish fjord (~5.7×10^4 MPN cells g^{-1} wet sediment: McQuoid et al. 2002). The study area of the Seto Inland Sea and coastal Swedish fjord are mostly inshore areas (shallower than depth of 30 m) where

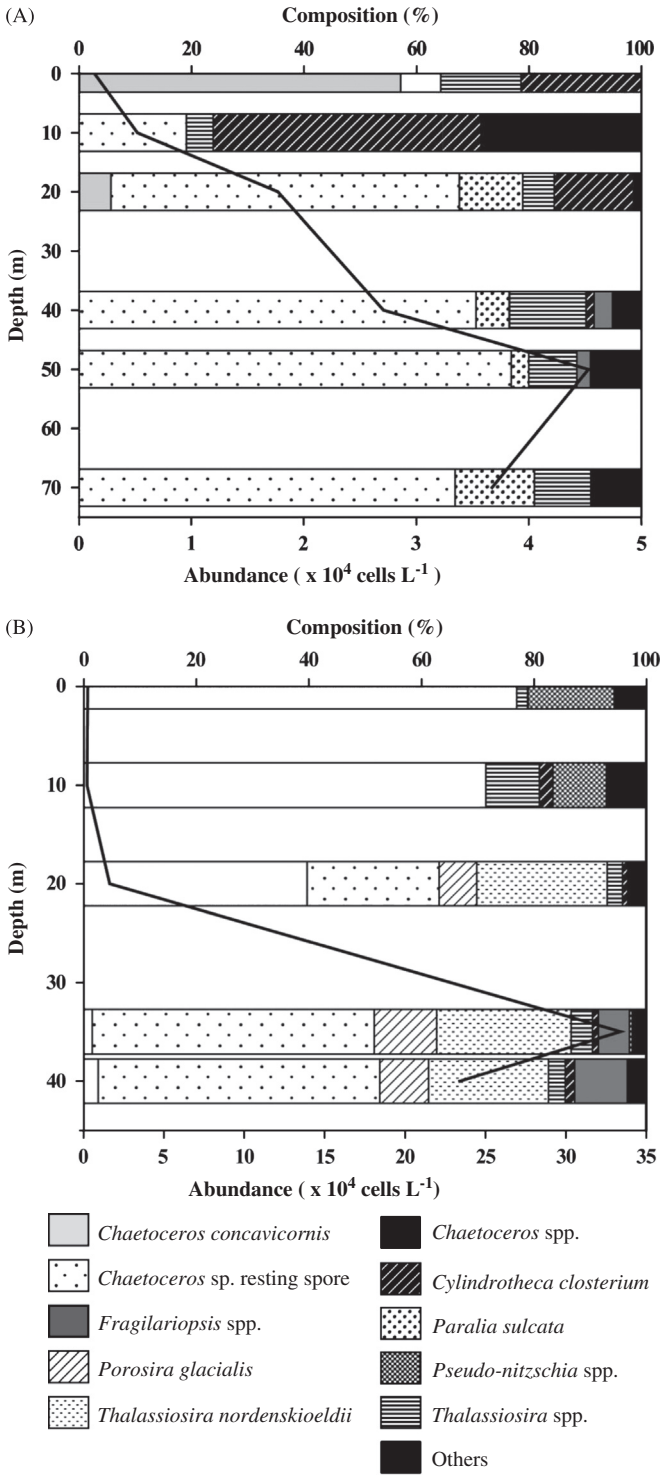

Fig. 4. Vertical distributions of cell abundance ($\times 10^4$ cells L^{-1}) and species composition of the dominant diatoms in water columns at station 11 (A) and station 18 (B).

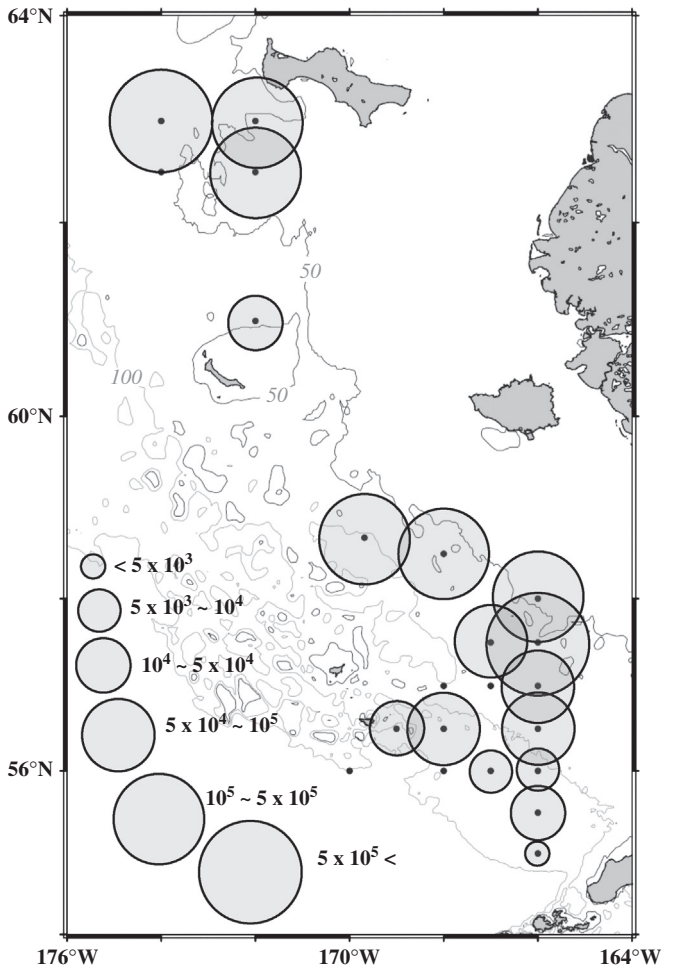

Fig. 5. Spatial distribution of total diatom resting stage cells (MPN cells cm^{-3} wet sediment) in surface sediments (top 3 cm depth) of the study area. Stations without circle indicate no data.

intercommunication of diatoms between water column and sea bottom is capable and frequent. Although the study area of the Bering Sea shelf was offshore and a deeper depth (average 83 m), the diatom resting stage cells also appeared abundantly in sediments.

Plankton biomass largely influences the population size of the diatom resting stage cells (Itakura et al., 1999; McQuoid, 2002). High abundances of resting stage cells in sediments are believed to reflect dense bloom of diatoms predominant among the plankton community on the Bering Sea shelf. There is a relationship between the dominant phytoplankton species in the water columns and resting stage cells in sediments. Similarities in species composition of the resting stages and typical plankton populations reveal that resting stage cells were formed locally after the blooms in the water columns.

Viable resting stage cells of *Skeletonema* spp. were most abundant in the bottom sediments of the Seto Inland Sea and coastal Swedish Fjord, but less so over the Bering Sea shelf. *Skeletonema* spp. usually occurs in high abundance in eutrophic to extremely eutrophic regions (Yamada et al., 1980); therefore, the supply of resting stage cells from the water column is presumably low in the Bering Sea where the degree of anthropogenic eutrophication is limited.

P. sulcata grows primarily at the sea bottom of shallow areas, but this species is sometimes found with high cell abundances in the water column (Abrantes, 1988; Hobson and McQuoid, 1997) presumably due to physical forces such as strong winds or tidal mixings (Blasco et al., 1980; Oh and Koh, 1995). In this study, *P. sulcata* cells were abundant in bottom sediments at MSD and CSD, and the lower water column at St. 11 (MSD). Cells of *P. sulcata* were also distributed at the surface of CSD in the study period. This fact suggests that cells were transported from bottom to surface layer by physical forces such as storms and strong tidal action at the bottom.

Chaetoceros concavicornis and *Ch. convolutus*, both dominant species in summer in the Bering Sea, were found in the water

Table 2
Abundance ranges and means (MPN cells cm^{-3} wet sediment) of diatom resting stage cells and dinoflagellate cysts in bottom sediments of the study area.

Species	Southeastern Bering Sea		St. Lawrence Island Polynya region	
	min–max	mean	min–max	mean
Class Bacillariophyceae				
Order Centrales				
Actinoptychus senarius	N. D.~2.6×10^3	2.9×10^2	N. D.	
Attheya longicornis	N. D.~5.6×10^5	5.0×10^4	7.2×10^2–8.7×10^5	2.3×10^5
Total *Chaetoceros* spp.	N. D.~6.9×10^4	1.6×10^4	3.1×10^3–1.3×10^5	7.5×10^4
Chaetoceros curvisetus	N. D.		N. D.~2.5×10^3	6.3×10^2
Chaetoceros diadema	N. D.~3.3×10^4	5.0×10^3	N. D.~6.8×10^4	2.6×10^4
Chaetoceros didymus	N. D.~2.8×10^3	2.7×10^2	N. D.~2.7×10^3	6.9×10^2
Chaetoceros mitra	N. D.~1.0×10^4	8.0×10^2	N. D.	
Chaetoceros socialis	N. D.~2.6×10^4	5.7×10^3	3.1×10^3–6.3×10^4	3.4×10^4
Chaetoceros furcellatus	N. D.~2.4×10^4	3.9×10^3	N. D.~1.7×10^3	4.4×10^2
Chaetoceros laciniosus	N. D.~1.6×10^3	1.2×10^2	N. D.	
Chaetoceros debilis	N. D.~3.2×10^3	2.5×10^2	N. D.	
Other *Chaetoceros* spp.	N. D.~7.1×10^2	5.4×10^1	N. D.~5.1×10^4	1.3×10^4
Detonula spp.	N. D.~1.0×10^4	1.6×10^3	N. D.~1.9×10^4	4.9×10^3
Skeletonema spp.	N. D.~6.9×10^3	1.4×10^3	N. D.~3.2×10^2	8.1×10^1
Total *Thalassiosira* spp.	N. D.~1.1×10^5	1.7×10^4	N. D.~1.8×10^5	9.0×10^4
Thalassiosira nordenskioeldii	N. D.~7.4×10^4	7.4×10^3	N. D.~1.8×10^5	7.7×10^4
Thalassiosira gravida	N. D.~5.5×10^4	9.1×10^3	N. D.~3.7×10^4	1.3×10^4
Other *Thalassiosira* spp.	N. D.~7.7×10^3	7.2×10^2	N. D.	
Paralia sulcata	N. D.~6.3×10^4	1.1×10^4	N. D.~3.6×10^2	1.7×10^2
Porosira glacialis	N. D.~3.3×10^3	5.4×10^2	N. D.	
Odontella spp.	N. D.~1.6×10^3	4.1×10^2	N. D.~2.7×10^3	9.6×10^2
Delphineis spp.	N. D.~6.0×10^3	8.2×10^2	N. D.	
Navicula spp.	N. D.~1.8×10^4	2.1×10^4	N. D.~3.6×10^4	1.2×10^4
Pennate species (ribbon forming)	N. D.~9.6×10^4	1.9×10^4	3.6×10^2–1.1×10^5	2.8×10^4
Fragilaria spp.	N. D.~2.3×10^4	1.1×10^4	N. D.	
Fragilariopsis spp.	N. D.~9.4×10^4	1.7×10^4	N. D.~1.1×10^5	2.8×10^4
Pauliera taeniata	N. D.		N. D.~3.6×10^2	9.1×10^1
Class Dinophyceae	N. D.~2.8×10^2	1.5×10^2	N. D.	
Total	1.74×10^3–9.2×10^5	1.4×10^5	1.0×10^4–1.2×10^6	4.9×10^5

N. D. : not detected.

samples during this study. However, we could not detect the appearance of them after incubation of the sediments with the MPN treatment. These *Chaetoceros* species appear to have a life strategy different from those forming resting stage cells.

There is no report of resting stage cells for *Pseudo-nitzschia* spp. Although *Pseudo-nitzschia* spp. were dominant at the shelf edge during the study period, they are presumably unable to overwinter in the Bering Sea without resting stages due to poor light conditions. It is considered that they are allochthonous populations transported by the current from the southern areas to the Bering Sea.

There are several pennate diatom species forming resting stage cells (McQuoid and Hobson, 1996). The pennate species found in sediments in high abundance were ribbon-shaped colony forming species (*F. cylindrus*, *F. oceanica*, *Fragilaria* cf. *capunica*, *P. taeniata*) and solitary *Navicula* spp. They frequently comprise the ice algae populations. These species are known to grow at the subsurface of sea ice in late winter to early spring in the Bering Sea (Saito and Taniguchi, 1978; Schandelmeier and Alexander, 1981; Goering and Iverson, 1981). Benthic *Delphyneis* species were also observed in the sediments, but already attaching to the substrata such as sand grains with several cells before incubation. Resembling the centric diatom species, ice algae species form resting stage cells, and they survive in bottom sediments after sinking from sea ice melted during the warm season and then serve as a source of seed stock for ice algae was suggested to be sediments (Horner and Schrader, 1982). The present study confirmed the existence of resting stage cells of ice algae species in the bottom sediments during summer season. The resting stage cells presumably play an important role as a seed population in developing large biomass of ice algae when they were resuspended and incorporated into the ice during freeze-up.

Attheya sp. were usually found in the plankton associated with *Chaetoceros* species (Crawford et al., 1994) and from undersurface of sea ice (Melnikov et al., 2002; Schandelmeier and Alexander, 1981; von Quillfeldt, 2000; Werner et al., 2007). They possibly contribute to primary productivity as plankton and also as ice algae. High abundances of resting stage cells in sediments indicate the importance of the genus *Attheya* as primary producers in the Bering Sea.

4.3. Contribution of resting stage cells to bloom formation

Germination and rejuvenation of diatom resting stage cells are generally affected by light (Hargraves and French 1983; Hollibaugh et al., 1981; Imai et al., 1996b), and hence the resting stage cells in the sea bottom need to be resuspended to the euphotic zone where they can germinate or rejuvenate and resultant vegetative cells commence to grow (Itakura et al., 1997). In regions of upwelling, the prevalence of resting spores of the genus *Chaetoceros* in newly upwelled waters (Abrantes, 1988; Pitcher, 1990) indicate that upwelling events have enough energy to resuspend the resting stage cells from the benthos into the water column (Pitcher et al., 1991). In the Funka Bay of Japan, the resting spores of *Chaetoceros* spp. in the bottom layer were brought back into the euphotic zone during the vertical mixing of the water column (Odate and Maita, 1990), implying that vertical mixing also has sufficient energy to resuspend the resting stage cells into the water column. It was reported that artificial stirring of stable water columns led to larger cell size diatom blooms in marine environment (Eppley et al., 1978).

In a study of the Bering Sea (Sambrotto et al., 1986; Eslinger and Iverson, 2001), the spring phytoplankton bloom onset occurred when the water column was vertically mixed to the sea bottom,

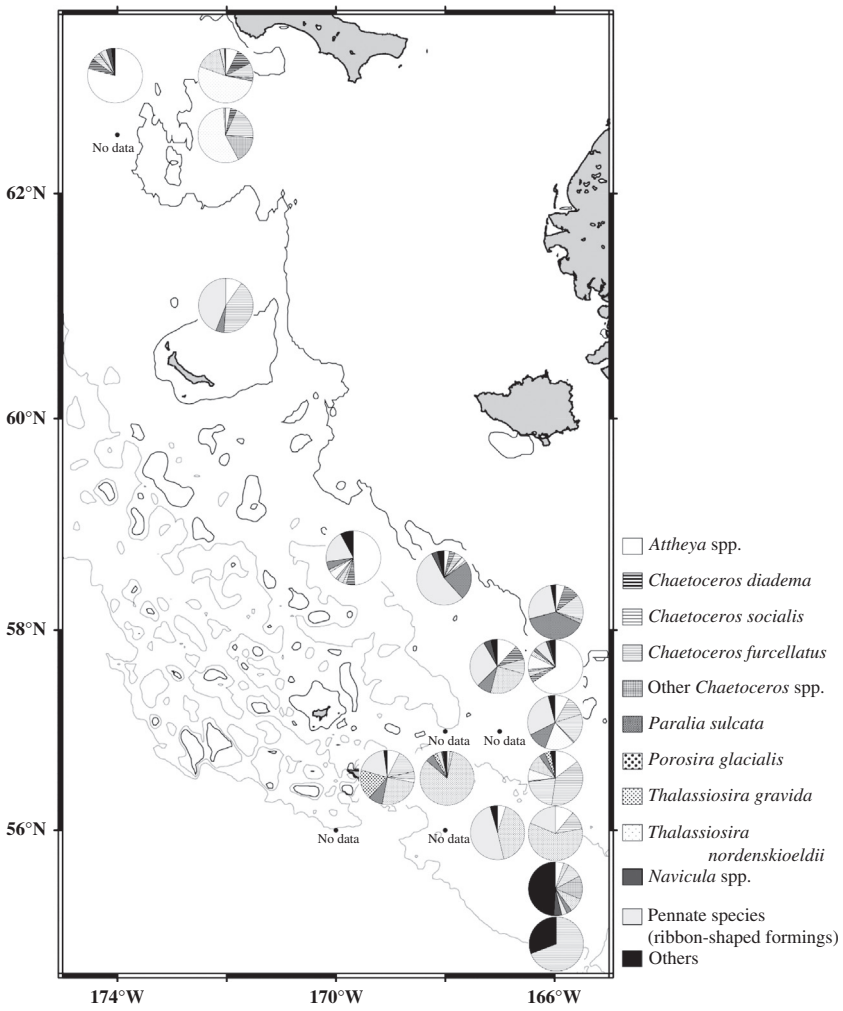

Fig. 6. Species composition of the diatom resting stage cells observed in surface sediments (top 3 cm depth) of the study area detected with the most probable number (MPN) method. The stations without circle indicate no data.

and chlorophyll maxima were associated with the shoaling of the mixed layer. Blooms often tend to appear suddenly because vegetative cells originated from resting stage cells are supposed to divide rapidly with the organic matter already stored in the cells (Shakshaug, 1989). Hence, the trigger of the spring bloom was not only supply of inorganic nutrients, but also probably the resuspension of resting stage cells into the euphotic layer.

As is the case in temperate seas, the seasonal decrease in atmospheric temperature and increase turbulence enhance the vertical mixing in fall and winter in the Bering Sea shelf. When the sea surface was covered with ice, wind driven mixing ceases but the convective mixing layer deepens to a depth about 50 100 m in response to brine drainage of freezing ice (Ikeya and Kawanobe, 2002; Ohtani, 1969, 1973; Sullivan et al., 1988). Upwelling plumes of circulation cell have also been observed at the ice edges in the Bering Sea (Alexander and Niebauer, 1981; Okkonen and Niebauer, 1995). These physical processes have the potential to mix resting stage cells from the benthos to the water column. A cold water mass (−1.7 to 0° C) remained under the pycnocline in the southern part of the St. Lawrence Island Polynya and MSD during the study period suggesting that the sea ice possibly formed in that region and the vertical convection reached the benthos.

Fig. 7 gives a schematic representation of the life cycles of ice algae and phytoplankton in the eastern Bering Sea shelf. Horner and Schrader (1982) reported that microalgae were present in the sea ice as soon as it formed in the fall and generally were scattered throughout the ice thickness. In the winter period, resting stage cells of ribbon-shaped pennate species and solitary *Navicula* spp. would be mixed to the water column from the bottom by convection. If those species are incorporated or attached to the sea ice, they would develop in ice algae. Similarities in composition of benthic and ice algae species (Matheke and Horner, 1974) support this hypothesis. As an alternate explanation, plankton species could survive the winter period as resting stage cells and be resuspended in the water column the following spring and bloom, when they are successfully trapped to the euphotic layer. Resting stage cells probably are resuspended non-selectively, but the germination/ rejuvenation in response to favorable light and temperature conditions (French and Hargraves, 1985; Hollibaugh et al., 1981;Imai et al., 1996b) will affect vegetative growth, and so initiation and composition of bloom.

In a past study, benthic *P. sulcata* cells existed in the sea ice (Schandelmeier and Alexander, 1981), suggesting that cells suspended from the sea bottom were incorporated into ice. Resting spores of *C. socialis* and *F. oceanica* were also found in the ice (von Quillfeldt, 1997). There is a strong possibility that the resting stage cells of plankton species are incorporated into the sea ice together with ice algae species. Those resting stage cells of plankton species could germinate in the upper layer when the sea ice is melting, and probably contribute to the ice edge bloom accompanied with ice algae species. When the water column is vertically mixed to the sea bottom by the process of wind and tidal mixing, the resting stages of planktonic species probably contribute to the open water bloom after the water has stabilized.

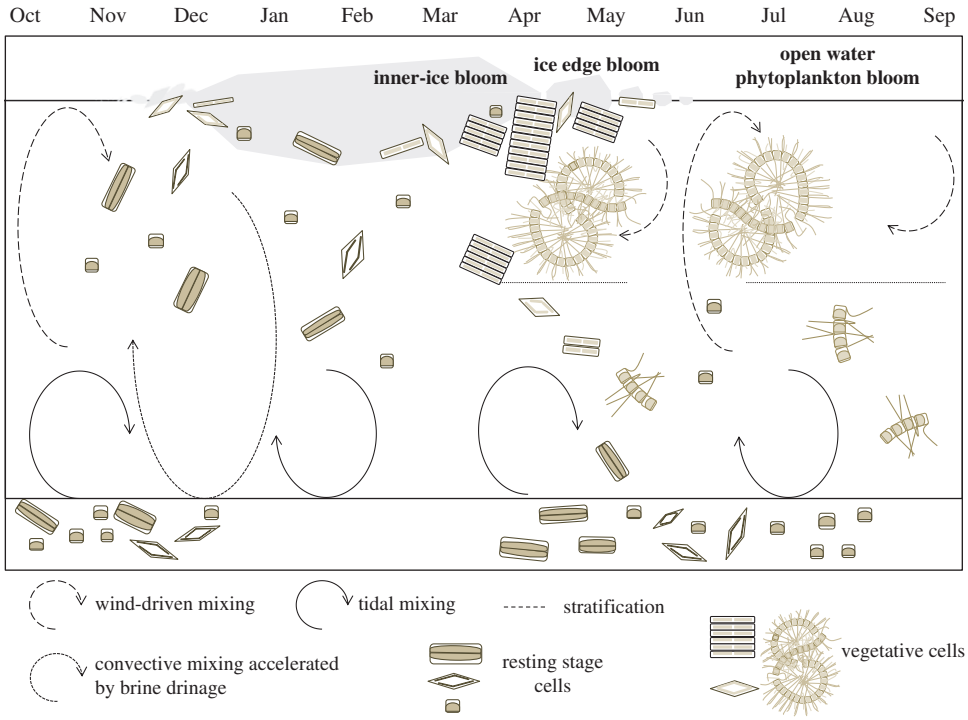

Fig. 7. Schematic representation of the life cycles of ice algae and planktonic diatoms in the eastern Bering Sea shelf based on the present study and partially following Coachman et al. (1980), Sullivan et al. (1988) and Ikeya and Kawanobe (2002).

Under conditions that favor extensive spatial and temporal extent of sea ice, more resting stage cells could be incorporated into the ice as seed populations and contribute to a rich bloom. In contrast, when sea ice has limited spatial and temporal extent, there is insufficient light to support a bloom (Hunt et al., 2002) and a smaller seed population to contribute to a bloom. Thus there is a possibility that year to year variations in ice extent and duration have large effects in the scale and period of the spring blooms in the Bering Sea.

5. Conclusion

Diatom species of plankton and ice algae employ resting stages as survival strategies in the Bering Sea as is the case of the resting stages of many diatoms in temperate waters. It is strongly suggested that resting stage cells play a crucially important role in overwintering of diatoms in the Bering Sea, where vegetative cells are exposed to extremely severe conditions (low temperature, sea ice formation, extreme light limitation) in winter, and in supplying a seed populations for spring blooms through germination and/or rejuvenation in water columns and sea ice.

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