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Influences of sea ice on eastern Bering Sea phytoplankton*

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Abstract The influence of sea ice on the species composition and cell density of phytoplankton was investigated in the eastern Bering Sea in spring 2008. Diatoms, particularly pennate diatoms, dominated the phytoplankton community. The dominant species were *Grammonema islandica* (Grunow in Van Heurck) Hasle, *Fragilariopsis cylindrus* (Grunow) Krieger, *F. oceanica* (Cleve) Hasle, *Navicula vanhoeffenii* Gran, *Thalassiosira antarctica* Comber, *T. gravida* Cleve, *T. nordenskiöeldii* Cleve, and *T. rotula* Meunier. Phytoplankton cell densities varied from 0.08×10^4 to 428.8×10^4 cells/L, with an average of 30.3×10^4 cells/L. Using cluster analysis, phytoplankton were grouped into three assemblages defined by ice-forming conditions: open water, ice edge, and sea ice assemblages. In spring, when the sea ice melts, the phytoplankton dispersed from the sea ice to the ice edge and even into open waters. Thus, these phytoplankton in the sea ice may serve as a "seed bank" for phytoplankton population succession in the subarctic ecosystem. Moreover, historical studies combined with these results suggest that the sizes of diatom species have become smaller, shifting from microplankton to nannoplankton-dominated communities.

Keyword: phytoplankton; sea ice; Bering Sea; community structure

1 INTRODUCTION

The Bering Sea is a complex, semi-enclosed basin that lies north of the North Pacific Ocean, one of the most productive areas in the world's oceans (Iverson et al., 1979a). In recent years, increases in air temperature and dramatic decreases in the extent and thickness of sea ice have occurred throughout the Bering Sea (Schumacher et al., 2003). Anomalies in regional weather in the southeastern Bering Sea have resulted in significant changes in climate (calm wind, warm air temperature, reduction of cloud et al.), sea surface temperature, and plankton communities (species composition, coccolithophorid bloom et al.), (Napp and Hunt, 2001; Whitledge et al., 2001). Because the effects of climate change may be first seen in polar regions, the Bering Sea may serve as an example for similar systems of how changes in sea ice alter the entire ecosystem by affecting the populations and communities that sea ice supports (Alexander and Niebauer, 1981; Hunt et al., 2002).

As primary producers and the main food source for zooplankton, phytoplankton play an important role in energy flow and nutrient cycling in marine ecosystems. Previous studies in the Bering Sea have examined phytoplankton community structure under variable environmental conditions; however, most have focused only on net phytoplankton collected with a regular phytoplankton net of which the net pore size is 67 μm (Aikawa, 1932; Motoda and Kawarada, 1955; Karohji, 1958). Compared with studies of phytoplankton in the western Bering Sea (McQuoid and Hobson, 1998; Hobson and McQuoid, 2001;

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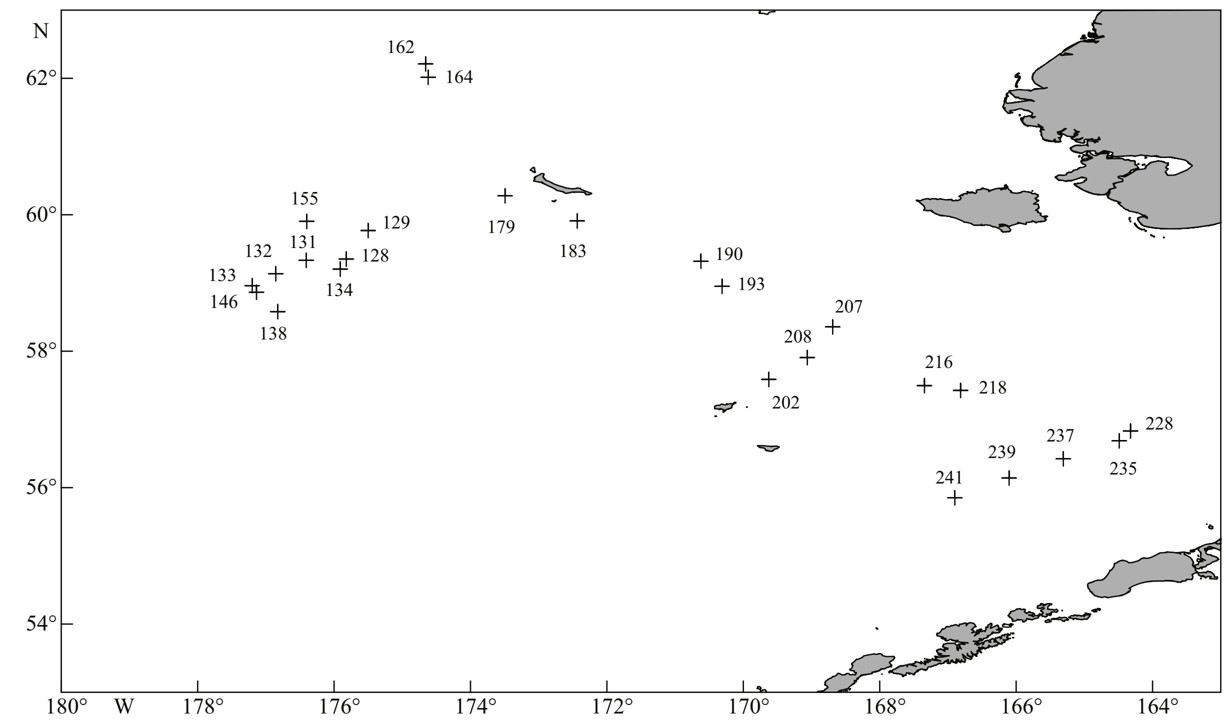

Fig.1 Location of sampling stations in the eastern Bering Sea

Yang et al., 2002; Hay et al., 2003; Aizawa et al., 2005), there are few in the eastern Bering Sea (Taniguchi et al., 1976; Iverson et al., 1979a, b; Schandelmeier and Alexander, 1981). Ice algae alter the phytoplankton community of the Bering Sea when they are released into open water (He et al., 2005), as shown by Taniguchi et al. (1976) and Schandelmeier and Alexander (1981), who found that the sea ice species *Thalassiosira* spp., *Fragilariopsis* spp., and *Navicula* spp. dominated springtime phytoplankton communities in the eastern Bering Sea. Centric diatoms and chain-forming pennate diatoms have also been found in some ice samples (Schandelmeier and Alexander, 1981). Certain diatom taxa (e.g. *Thalassiosira rotula* and *Chaetoceros* spp.) are only found after the intrusion of water with elevated levels of dissolved inorganic nitrogen (Hobson and McQuoid, 2001), suggesting that some diatom species (e.g. *Paralia sulcata*) can be used as indicators of environmental change (McQuoid and Hobson, 1998).

The Bering Sea is a high-nutrient, low-chlorophyll (HNLC) regime with high concentrations of nitrate in particular (Banse and English, 1999). In the Bering Sea, upwelling caused by tidal fronts may extend springtime phytoplankton bloom duration along the ice edge by supplying nutrients (Niebauer and Alexander, 1985). Sambrotto et al. (1986) documented the temporal development of a spring diatom bloom in the southeast Bering Sea middle shelf during three consecutive years without sea ice. They found signals generated by periodic factors such as the neap-spring tide and aperiodic storm events that were resolved during the spring bloom. They also showed that ~37% of new nitrogen productivity was caused by wind mixing events that occurred after initial water column stabilization and prolonged high rates of nitrate uptake (Sambrotto et al., 1986). These processes critically altered the physical environment, influencing phytoplankton community structure and ecosystem properties.

We examined the phytoplankton community composition, cell density, and the depth of water samples in the eastern Bering Sea between April and May 2008. The objective was to determine 1) the effects of varying sea ice conditions on phytoplankton community structure, and 2) if sea ice diatoms can provide a seed bank for open sea phytoplankton assemblages.

2 MATERIAL AND METHOD

To examine phytoplankton community structure under varying sea ice conditions (open water, ice-edge and sea ice), water samples were collected with Niskin bottles (0.25 L) from 25 locations (hereafter called stations) in the eastern Bering Sea (53°–63°N, 163°–180°W) between April 24, 2008 and May 6, 2008 (Fig.1). Each water sample was collected from chlorophyll maximum layer and transferred to a

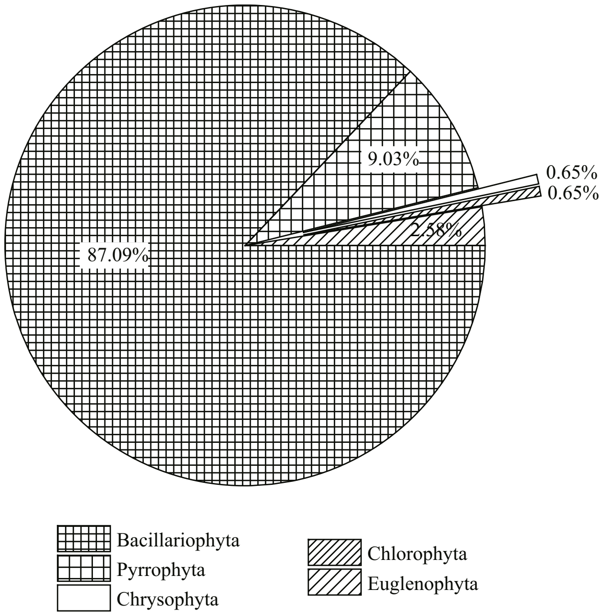

Fig.2 Composition of phytoplankton community in the eastern Bering Sea

250 mL polyethylene bottle for phytoplankton analysis. Samples were fixed in 1% Lugol's solution, concentrated to a final volume of 10 mL after sedimentation, and stored in darkness until counted. Formaldehyde (1–2 drops) was added to each sample for permanent storage.

Every phytoplankton species were identified and counted using an inverted microscope (Olympus BH-2, Japan) at (100–600)× magnification. Initially unknown species were later identified using a JEM-100 CXII (Japan) transmission electron microscope. To prepare for imaging, diatom cells were cleaned with H_2SO_4 and rinsed with distilled water to neutrality. A drop of each sample was then placed on Formvar-coated copper grids, dried, and imaged.

Survey data were visualized using Surfer 10.0 (2011) to map the distribution of phytoplankton. To determine the phytoplankton community structure, cluster analysis was used with Primer 5.29 software (Shannon and Wiener, 1949; Margalef, 1958; Pielou, 1966).

3 RESULT

3.1 Phytoplankton species composition

In total, 155 phytoplankton species were identified, including 135 species of 35 genera of Bacillariophyta, 14 species of seven genera of Pyrrophyta, four species of two genera of Euglenophyta, and one species each of Chrysophyta and Chlorophyta. The overall plankton assemblage was dominated by Bacillariophyta at 87.09%, with the remaining composed of 9.03% Pyrrophyta, 2.58% Euglenophyta, and 0.5% each Chrysophyta and Chlorophyta. (Fig.2). The dominant species were *Grammonema islandica* (Grunow in Van Heurck) Hasle, *Fragilariopsis cylindrus* (Grunow) Krieger, *F. oceanica* (Cleve) Hasle, *Navicula vanhoeffenii* Gran, *Thalassiosira antarctica* Comber, *T. gravida* Cleve, *T. nordenskiöeldii* Cleve, and *T. rotula* Meunier.

The phytoplankton community in the eastern Bering Sea was mainly composed of eurythermal groups and cold-water groups (Table 1). In open waters, phytoplankton density was high, and both eurythermal species (e.g. *Chaetoceros socialis* and *T. rotula*) and cold-water species (e.g. *T. antarctica* and *T. hyalina*) were common. Within sea ice, phytoplankton density was low and dominated by cold-water species (e.g. *C. concavicornis*, *N. vanhoeffenii*, *Amphidinium extensum*, and *Pyramimonas grossii*), whereas at the ice edge, phytoplankton communities contained both eurythermal species and cold-water species.

3.2 Phytoplankton community structure

The number of phytoplankton species (*S*) found in each sample ranged from 8–38, with the maximum number found at station 207, and the minimum at station 131. Cell density ranged from 0.08×10^4 to 428.8×10^4 cells/L (Table 2).

High-density phytoplankton assemblages were mainly found in the western part of the study area, as seen by the horizontal distribution map (Fig.3), although the maximal cell density was found in the east at Site 239, where blooms of *T. nordenskiöeldii* occurred, reaching up to 10^6 cells/L.

Cluster analysis showed that the phytoplankton assemblage could be divided into three groups defined by sea ice-forming conditions: open waters, ice edge, and sea ice. The highest cell densities were found in open waters and at the ice edge; densities were low in sea ice (Fig.4). Despite compositional differences among groups, two dominant species *F. oceanica* and *T. nordenskiöeldii* were found in all conditions (Table 3). The open water assemblage was characterized by *Thalassiosira* spp. (e.g. *T. antarctica*, *T. nordenskiöeldii*, *T. gravida*, *T. hyalina* (Grunow) Gran, and *T. rotula*) and *Fragilariopsis* spp. (e.g. *F. oceanica*). The ice edge assemblage was similar to that of open waters. The sea ice assemblage differed in the identity of the dominant species, which included *Navicula* spp. (e.g.

Table 1 Ecological groups and distribution areas of the dominant species in the eastern Bering Sea

Dominant species	Ecological groups	Distribution areas	Phylum
Chaetoceros socialis	●	Open water	Bacillariophyta
Chaetoceros concavicornis	○	Ice	Bacillariophyta
Thalassiosira antarctica	○	Open water	Bacillariophyta
Thalassiosira nordenskioeldii	○	Open water, ice edge, ice	Bacillariophyta
Thalassiosira gravida	○	Open water, ice	Bacillariophyta
Thalassiosira hyalina	○	Open water	Bacillariophyta
Thalassiosira rotula	●	Open water, ice	Bacillariophyta
Grammonema islandica	●	Ice edge	Bacillariophyta
Fragilariopsis cylindrus	○	Ice edge	Bacillariophyta
Fragilariopsis rhombica	○	Ice edge	Bacillariophyta
Fragilariopsis oceanica	○	Open water, ice edge, ice	Bacillariophyta
Navicula vanhoeffenii	○	Ice	Bacillariophyta
Nitzschia closterium	●	Ice	Bacillariophyta
Nitzschia longissima	●	Ice	Bacillariophyta
Pleurosigma angulatum	●	Ice	Bacillariophyta
Amphidinium extensum	○	Ice	Pyrrophyta
Pyramimonas grossii	○	Ice	Chlorophyta

● and ○ stand for eurythermal species and cold-water species, respectively.

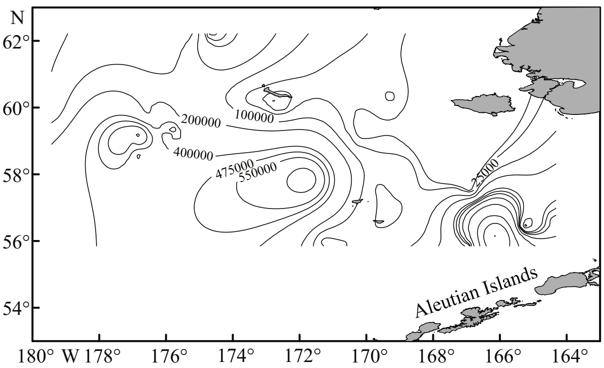

Fig.3 Horizontal distribution of phytoplankton cell density (cells/L)

Table 2 Phytoplankton diversity indices among sites in the eastern Bering Sea

Sample ID	*S*	*N*	*D*	*J'*	*H'* ($\log_2$)
128	14	56.44	0.68	0.53	2.02
129	15	11.76	0.88	0.89	3.49
131	**8**	41.60	**0.37**	0.51	1.53
132	20	76.40	1.03	0.75	3.26
133	22	73.20	1.08	0.50	2.24
134	18	35.80	0.91	0.54	2.26
138	12	39.04	0.59	0.36	**1.31**
146	18	45.24	0.90	**0.33**	1.36
155	25	29.28	1.37	0.91	4.23
162	21	60.36	1.12	0.68	2.97
164	17	46.00	0.85	0.48	1.95
179	15	**0.18**	0.88	0.92	3.61
183	12	**0.18**	0.71	0.92	3.30
190	25	2.24	1.43	0.94	4.36
193	9	0.90	1.57	0.95	4.53
202	27	2.82	**2.17**	**0.96**	**5.02**
207	**38**	8.34	1.33	0.80	3.66
208	24	5.89	1.67	0.81	3.96
216	30	1.22	1.21	0.94	4.13
218	21	53.20	0.68	0.71	2.71
228	14	56.32	0.83	0.77	3.15
235	17	3.12	1.24	0.93	4.10
237	21	1.13	0.53	0.93	2.96
239	17	**428.80**	0.73	0.48	1.96
241	35	45.24	1.81	0.69	3.55

S: species number; *N*: cell density ($\times 10^4$ cells/L); *D*: Margalef species abundance index; *J'*: Pielou's species uniform; *H'*: Shannon-Wiener diversity index; Boldface numbers indicated the minimum and maximum values of every index.

N. vanhoeffenii) and *Nitzschia* spp. (e.g. *N. closterium* (Ehr.) W. Smith, *N. longissima* (Breb.) Ralfs), in addition to *Fragilariopsis* spp. and *Thalassiosira* spp.

3.3 Phytoplankton abundance

Total phytoplankton abundance in the eastern Bering Sea peaked most noticeably in open waters (station 229, Fig.5a), with lesser peaks located at the ice edge. Chlorophyta occurred only at two stations, both of which were located in the sea ice (208 and 216, Fig.5b). Chrysophyta and Euglenophyta were distributed variably, but rarely exceeded 8×10^3cells/L (Fig.5c, d), whereas Pyrrophyta were widely distributed throughout the eastern Bering Sea (Fig.5e). Bacillariophyta were responsible for the peaks in

Table 3 Dominant species of phytoplankton in the three groups in the eastern Bering Sea

Different areas	Sample ID	Dominant species
Open water	228 235 239 241	*Chaetoceros socialis*; ***Fragilariopsis oceanica***; *Fragilariopsis* sp.; *Thalassiosira antarctica*; ***Thalassiosira nordenskioeldii***; *Thalassiosira gravida*; *Thalassiosira hyalina*; *Thalassiosira rotula*
Ice edge	128 129 131 132 133 134 138 146 155 162 164	***Fragilariopsis oceanica***; *Grammonema islandica*; *Fragilariopsis cylindrus*; *Fragilariopsis rhombica*; ***Thalassiosira nordenskioeldii***
Sea ice	179 183 190 193 202 207 208 216 218 237	*Chaetoceros concavicornis*; ***Fragilariopsis oceanica***; *Navicula vanhoeffenii*; *Nitzschia closterium*; *Nitzschia longissima*; *Pleurosigma angulatum*; *Thalassiosira gravida*; ***Thalassiosira nordenskioeldii***; *Thalassiosira rotula*; *Amphidinium extensum*; *Pyramimonas grossii*

Species that occurred in all areas are in bold face.

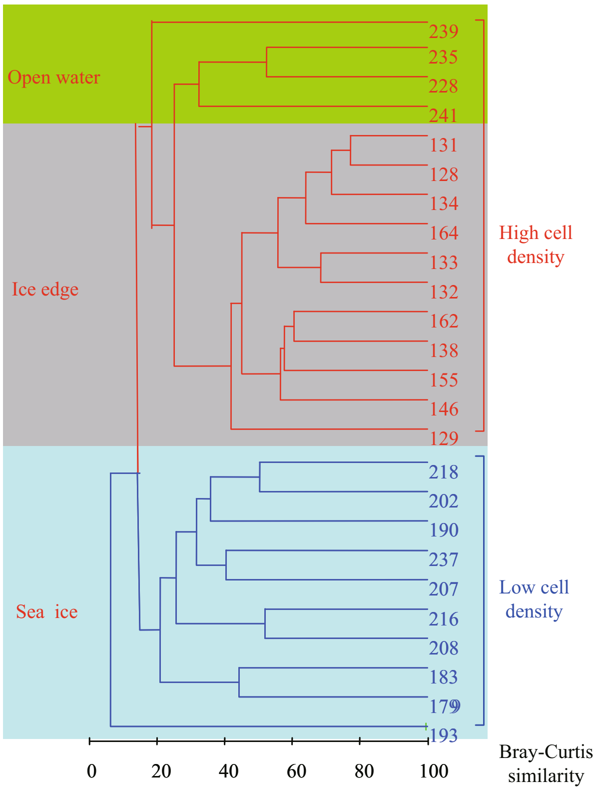

Fig.4 Dendrogram of cluster analysis of phytoplankton assemblage collected in the eastern Bering Sea

abundance in open waters (Fig.5f).

Total diatom density in the eastern Bering Sea also peaked in open waters (Fig.6a) and was caused largely by the occurrence of centric diatoms (Fig.6b). Density peaks at the ice edge were produced primarily by pennate diatoms (Fig.6c). Overall, 49 centric species and 86 pennate species of diatoms were identified.

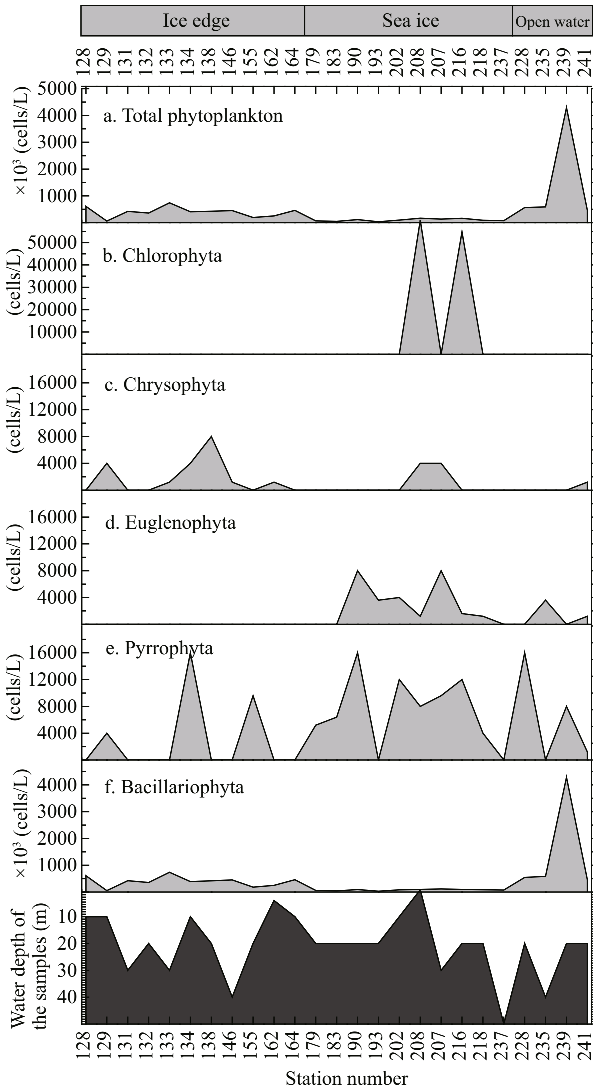

Fig.5 Absolute abundance profiles of (a) total phytoplankton, (b) Chlorophyta, (c) Chrysophyta, (d) Euglenophyta, (e) Pyrrophyta, (f) Bacillariophyta, and the depth of samples

4 DISCUSSION

4.1 Phytoplankton species and distribution

Our study found higher similarity between the phytoplankton communities of open waters and the ice edge compared with that of sea ice. However, with the rise in sea surface temperature and gradual sea ice melt in the spring, phytoplankton species characteristic of sea ice began to appear at the ice edge and even in open waters. For example, the cell density of *T. nordenskiöeldii* gradually increased from the ice to the ice edge and significantly increased from the ice

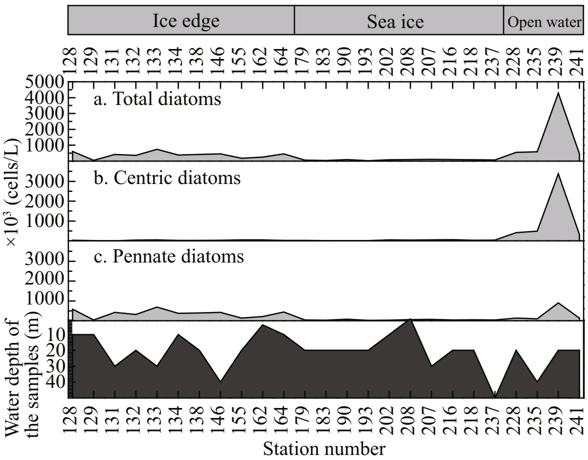

Fig.6 Absolute abundance profiles of (a) total diatoms, (b) centric diatoms, (c) pennate diatoms, and the depth of samples

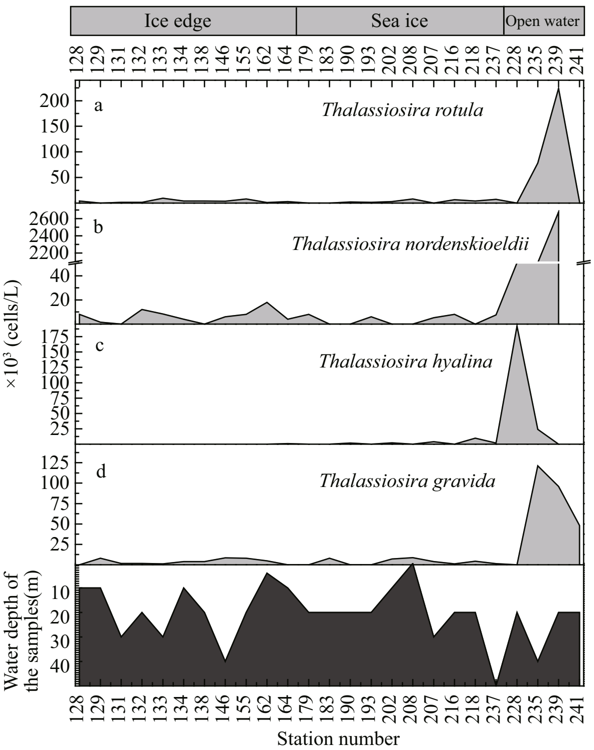

Fig.7 Absolute abundance profiles of four dominant centric diatoms

a. *Thalassiosira rotula*; b. *T. nordenskioeldii*; c. *T. hyalina*; d. *T. gravida* and the depth of samples.

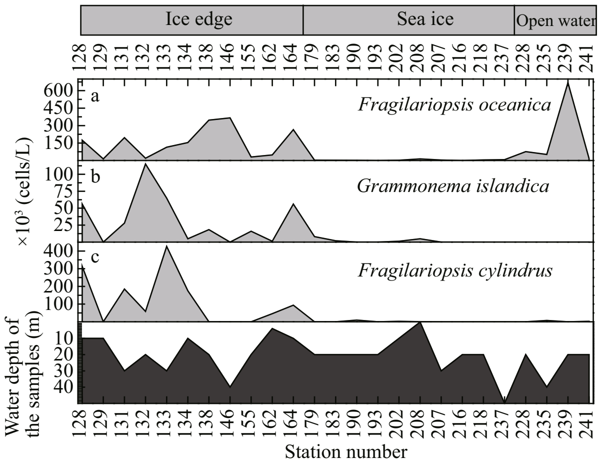

Fig.8 Absolute abundance profiles of three dominant pennate diatoms

a. *Fragilariopsis oceanica*; b. *Grammonema islandica*; c. *Fragilariopsis cylindrus*, and the depth of samples.

edge to the open waters (Figs.5, 7). As melting of sea ice continued, blooms of *T. nordenskiöeldii* spread throughout the eastern Bering Sea. This suggests that phytoplankton in the sea ice may serve as a "seed bank" for phytoplankton population succession in the subarctic ecosystem. The abundance of pennate diatoms such as *Grammonema islandica* and *Fragilariopsis cylindrus* characterized close to the ice edge region (Fig.8), but in the open water, the centric diatom genus *Thalassiosira* (Fig.7) dominated. Taniguchi et al. (1976) previously showed that when the shelf water of the Bering Sea was influenced by sea ice melt in May, particularly dense populations of *T. nordenskiöeldii* and *T. hyalina* as well as large populations of *Fragilariopsis* occurred. In a 3-year study of phytoplankton across 109 stations in the southeast Bering Sea, Schandelmeier and Alexander (1981) also determined that the ice edge spring bloom was a distinct community, and suggested that early in the spring, the ice flora might seed the bloom as the ice melts. Hunt et al. (2002) also concluded duration of ice cover, timing of melt, and water temperature determine the onset of spring net primary production in the subarctic.

In the Bering Sea, interactions between the Siberian High and the Aleutian Low determine regional changes in circulation and the thermal state (Luchin et al., 2002). While changes in salinity and temperature at the ice edge contribute to ice melting, they may also, at times, cause wind-driven upwelling (Alexander and Niebauer, 1981). Upwelling brings nutrients to surface waters, potentially enhancing production depending on light availability. In our study, phytoplankton cell density in the eastern Bering Sea increased from east to west, mostly toward open waters (Fig.3) where blooms of *T. nordenskiöeldii* occurred. Potential causes of high phytoplankton densities near the Aleutian Islands could be the input of terrigenous material or nutrients supplied by upwelling in the Bering Slope Current. High rates of nitrate uptake that can occur after upwelling may strongly influence phytoplankton community structure and ecosystem properties (Niebauer and Alexander, 1985). Additionally, effects of sea ice on water temperature, salinity and ocean currents may have caused the low cell densities observed in sea ice compared with the high densities in open waters.

4.2 Ecological considerations and groupings

After melting, dispersal of diatoms growing in brash ice is dependent on the ice habitat and surrounding environment. We found that diatoms were dominant in the eastern Bering Sea and primarily responsible for peaks in cell density (Fig.5f). High densities of primarily eurythermal phytoplankton species in open waters were likely caused by lower latitudes, relatively higher water temperature, good light conditions, and effective exchange with surrounding nutrient and species-rich waters. However, in the sea ice with low temperature, poor light conditions, and inadequate nutrients, phytoplankton abundance was low and dominated by cold-water species. In the ice edge, which serves as the transition between these areas, environmental conditions are more variable and both eurythermal and cold-water species were common. Thus, there were distinct phytoplankton assemblages associated with ice, with the water column at the ice edge, and with the ice-free water of the outer and inner continental shelf in the eastern Bering Sea. Moreover, some species distributions were limited to certain regions, presumably constrained by ecological preferences (see Table 1 for a summary).

The class Bacillariophyta can be subdivided into centric diatoms and pennate diatoms. In the study region, centric diatoms were more abundant in open waters than in sea ice or at the ice edge, whereas pennate diatoms dominated at the ice edge (Fig.6). Nutrients strongly influence diatom distributions, with pennate diatoms preferring oligotrophic pelagic conditions, and centric diatoms preferring eutrophic conditions, such as areas of upwelling. The genus *Thalassiosira* in the family Thalassiosiraceae are always the dominant centric diatom taxa. Both *T. nordenskiöeldii* (Fig.7b) and *T. gravida* (Fig.7d) were common to abundant throughout most of the study region, while *T. hyalina* was only found in open waters. The pennate diatoms *Fragilariopsis* and *Grammonema* also had distinct distribution patterns. *F. oceanica* (Fig.8a) was present in open waters and at the ice edge, whilst *G. islandica* (Fig.8b) and *F. cylindrus* (Fig.8c) were more abundant at the ice edge, but absent or rare in open waters. Finally, some cold-water species were only found in the sea ice, including *C. concavicornis*, *N. vanhoeffenii*, *Amphidinium extensum*, and *Pyramimonas grossii*.

4.3 Diatom community succession

Physical and biological anomalies have been documented in the Bering Sea shelf ecosystem since 1997 (Napp and Hunt, 2001; Merico et al., 2004). These included unusual climatic conditions that have resulted most notably in high sea surface temperatures and a shallow mixed-layer depth (Merico et al., 2004). During 1997, weaker-than-average winds resulted in a decrease in nutrient flux from the continental slope to the shelf (Napp and Hunt, 2001). Since then, a study on the effects of future CO_2 and temperature increases on marine phytoplankton communities concluded that the Bering Sea ecosystem is particularly vulnerable to these effects of climate change (Hare et al., 2007). The authors concluded that increasing temperatures in the Bering Sea could drive shifts in algal dominance from diatoms towards smaller nannoplankton groups. Dramatic shifts in phytoplankton species composition from microplankton- to nannoplankton-dominated assemblages have been found in the Black Sea (Humborg et al., 1997) and in Jiaozhou Bay (Shen, 2002).

Phytoplankton communities in the Bering Sea have been studied for many decades. The dominant species of phytoplankton found in each of these studies are given in Table 4. In most regions and most seasons, diatoms dominated the communities. Pyrrophyta and *Phaeocystis pouchetii* (Haptophyta), however, were at certain times in some regions important components of the phytoplankton community. In general, Pyrrophyta make up a major portion of the phytoplankton population in the eastern Bering Sea. Historical data (Table 4) show that the genera *Corethron* and *Rhizosolenia* occurred commonly before 1978, but after 1997 the dominant genera shifted to *Thalassiosira*, *Emiliania*, and *Fragilariopsis*, although different investigators have reported different species assemblages. Differences may have resulted if collections were made during different stages of species succession, as phytoplankton species dominance can change in a few days or weeks. It is also likely that differences in collection, preparation and observation methods could have resulted in different findings. Additionally, a shift in the cell size of the dominant diatom species has been observed. For example, a small coccolithophore bloom was present

Table 4 Cell density and dominant taxa of phytoplankton in the Bering Sea

Area	Year	Density	Dominant species	Reference
Bering Sea	1928	-	*Chaetoceros atlanticus*, *Corethron criophilum*, *Rhizosolenia alata*, *R.hebetata* f. *semispina*, *R. hebetata* f. *hebetata*, *Thalassiothrix longissima*	Aikawa, 1932
Aleutian waters	1953	10^5–10^7 cells/m^3	*Chaetoceros* spp., *Corethron criophilum*, *Denticula* sp., *Pseudo-nitzschia seriata*, *Rhizosolenia hebetata* f. *semispina*	Motoda and Kawarada, 1955
Bering Sea	1955	10^5–10^9 cells/m^3	*Chaetoceros convolutus*, *C.compressus*, *C.debilis*, *C.radicans*, *C.constrictus*, *Pseudo-nitzschia delicatissima*, *P. seriata*, *Nitzschia closterium*, *N.longissima*, *Rhizosolenia hebetata* f. *semispina*, *Thalassiothrix longissima*, *Denticula* sp.	Kawarada, 1957
Northern Bering Eastern Bering	1955	10^4–10^7 cells/m^3	*Thalassiothrix longissima*, *Rhizosolenia hebetata* f. *hebetata*, *R. hebetata* f. *semispina*, *Pseudo-nitzschia seriata*, *Denticula* sp., *Fragilariopsis* spp., *Chaetoceros atlanticus*, *C. debilis*, *C. concavicornis*, *C. didymus*, *C. constrictus*, *C. radicans*, *Coscinodiscus* sp., *Paralia sulcata*	Karohji, 1958, 1959
Bering Sea	1960	10^4–10^7 cells/m^3	*Chaetoceros atlanticus*, *C. concavicornis*, *C. convolutus*, *C. compressus*, *C. constrictus*, *C. debilis*, *C. decipiens*, *Corethron criophilum*, *Denticula* sp., *Grammonema islandica*, *Rhizosolenia alata*, *R. hebetata* f. *hebetata*, *R. hebetata* f. *semispina*, *Pseudo-nitzschia seriata*, *Nitzschia closterium*	Ohwada and Kon, 1963
Eastern Bering Sea	1972	-	*Thalassiosira hyalina*, *T. nordenskioldii*, *Fragilariopsis*, *Navicula*	Taniguchi et al., 1976
Southeast Bering Sea	1975, 1976, 1977	10^4–10^7 cells/L	Ice edge: *Chaetoceros* spp., *Thalassiosira* spp., *Fragilariopsis* spp., *Navicula vanhoffeni*, *N. pelagica*, *Achnanthes* spp. Shelf-break: *Chaetoceros socialis*, *C. compressus*, *C. radicans*, *Thalassiosira nordenskioldii*, *Phaeocystis*	Schandelmeier and Alexander, 1981
Southeastern Bering Sea shelf	1978	Middle shelf (2–5)× 10^4 cells/m^3 Outer shelf (7–12)× 10^5 cells/m^3	Middle shelf domain: *Rhizosolenia alata*, *Chaetoceros debilis*, *Thalassiosira aestivalis*, *Thalassiosira nordenskiöldii* Outer shelf region: *Phaeocystis pouchetii*	Iverson et al., 1979a, b
Bering Sea	1997	(2.1–2.8)×10^6 cells/L	*Emiliania huxleyi*	Merico et al., 2003
Bering Sea	1999	-	*Emiliania huxleyi*, *Nitzschia* spp.	Olson and Strom, 2002
Bering Sea	1999	10^5 cells/L	*Thalassiosira trifulta*, *T. conferta*, *T. gravida*, *Fragilariopsis pseudonana*, *Neodenticula seminae*, *Pseudo-nitzschia* spp.	Aizawa et al., 2005
Bering Sea	2003	-	*Cylindrotheca* sp.	Hare et al., 2007
Bering Sea	2003, 2008	-	*Fragilariopsis cylindrus*, *F. oceanica*, *Bacterosira bathyomphala*, *Thalassiosira antarctica*, *T. nordenskiöeldii*, *Neodenticula seminae*	Ran et al., 2013
Eastern Bering Sea	2008	(0.08–428.8)×10^4 cells/L	*Grammonema islandica*, *Fragilariopsis cylindrus*, *F. oceanica*, *Navicula vanhoeffenii*, *Thalassiosira antarctica*, *T. gravida*, *T. nordenskiöeldii*, *T. rotula*	This study
Eastern Bering Sea	2009	(6.10×10^5)–(1.80×10^6) cells/L	*Pseudo-nitzschia* cf. *delicatissima*, *Chaetoceros* spp., *Thalassiosira nordenskiöeldii*, *T. gravida*, *Fragilariopsis* spp.	Tsukazaki et al., 2013
Bering Sea	2010	(10^2–10^5) cells/L	*Neodenticula seminae*, *Chaetoceros atlanticus*, *C. compressus*, *C. furcellatus*, *C. curvisetus*, *Thalassionema nitzschioides*, *Thalassiosira nordenskiöeldii*, *Leptocylindrus danicus*	Lin et al., 2013

in 1996, while in 1997 blooms that were unprecedented in extension and intensity were caused by a species of nannoplankton, *Emiliania huxleyi* (Table 4). Diatom community succession has also changed over time from *Chaetoceros*-*Rhizosolenia*-*Nitzschia* to *Chaetoceros*-*Fragilaria*-*Nitzschia* to *Chaetoceros*-*Thalassiosira*-*Fragilaria* (Table 4). Increases in recent years in the nannoplankton diatom genera *Chaetoceros* and *Thalassiosira* over other microplankton genera *Navicula* and *Nitzschia* provide evidence that, in general, diatom cell size has decreased, and the diatom community has tended to shift from microplankton to nannoplankton in the Bering Sea.

5 CONCLUSION

Sea ice phytoplankton may serve as a “seed bank” for phytoplankton population succession in open waters in the subarctic ecosystem. In open waters, phytoplankton abundance was mainly dominated by eurythermal species. In contrast, cold-water species were dominant in sea ice. At the ice edge, both eurythermal species and cold-water species were abundant. Spatial differences in the distribution of phytoplankton cell density as well as the different ecological groups in the eastern Bering Sea suggest causative factors of latitude, temperature, light, nutrients, and ocean stratification.

Historical data and the present study demonstrate that in the Bering Sea, diatom community succession has changed from dominance by microplankton species to nannoplankton groups, and it is suggested that these have been caused by physical and biological anomalies in the Bering Sea shelf ecosystem since 1997.

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