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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.

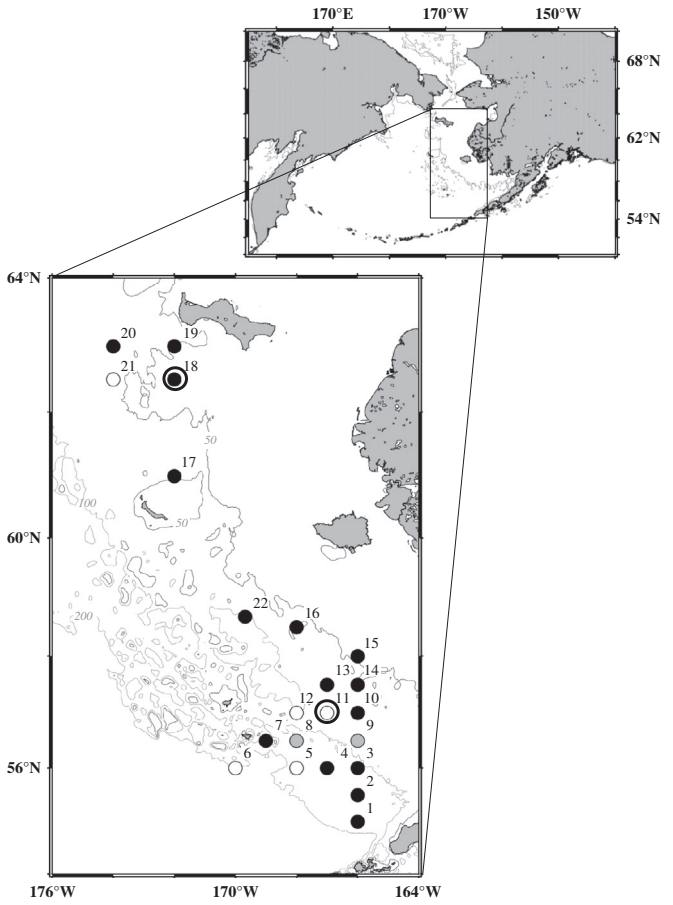

Fig. 1. Sampling stations in the eastern Bering Sea. •: stations for collection of sediment core and surface water, ◯: sediment core, ○: surface water, ◯: water samples from several depths.

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%).