Origin of *Thalassiosira* diatoms that cause the spring phytoplankton bloom in Funka Bay, southwestern Hokkaido, Japan

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Abstract: Seed populations of *Thalassiosira* diatoms were examined from sediments in Funka Bay, southwestern Hokkaido, Japan, and the spatial distribution of vegetative cells in the bay and adjacent areas was studied to investigate the origin of the diatoms that form the largest component of the spring diatom bloom in the bay. After the spring bloom, the standing stock of the *Thalassiosira* seed population in bay sediments was much lower than that of *Chaetoceros*. Bottom temperature is likely to be one of the major factors influencing the survival of the *Thalassiosira* seed population. A survey on the spatial distribution of diatom vegetative cells revealed that *Chaetoceros* were concentrated in the nearshore regions of the bay, while *Thalassiosira* were abundant in offshore regions (>500-m bottom depth) outside the bay. These results suggest that *Thalassiosira* from the Coastal Oyashio Water mass is the main source of diatom contributing to the spring diatom bloom in the bay.

Key words: spring diatom bloom, Coastal Oyashio Water, Thalassiosira

Introduction

In boreal seas, spring diatom blooms are an integral component of annual primary production, but bloom mechanisms vary greatly among regions (e.g., Graf et al. 1982; Lignell et al. 1993; Fernandez et al. 1991; Nejstgaard et al. 1997). In Funka Bay, a semi-closed shallow bay that is located in southwestern Hokkaido, Japan, the annual spring diatom bloom usually occurs in February or March (Nakata 1982; Tanaka 1984; Odate 1987), and its magnitude and species composition are influenced by the intrusion of the Coastal Oyashio Water mass, which facilitates rapid stratification of the water column (Shinada et al. 1999). Thalassiosira diatoms predominate during the early phase of the bloom, with Chaetoceros diatoms thereafter becoming the dominant phytoplankton species, with a concurrent increase in grazers such as dinoflagellates and copepods (Nakata 1982; Odate & Maita 1990).

Resting spores in sediments have been reported to be the source of some spring diatom blooms (Garrison 1979, 1981; Smetacek 1985). In neritic waters, these spores remain on the sea floor in summer, and then are reintroduced into the euphotic zone by vertical mixing of water during winter (Davis et al. 1980; Kido & Ohtani 1981; Odate 1987). Many resting spores of *Chaetoceros* diatoms have been found in bottom sediments in Funka Bay (Asami 1987), however there are no reports of the occurrence of resting spores of *Thalassiosira* diatoms in the bay's sediments. This may in part be due to the difficulty in distinguishing *Thalassiosira* resting spores from vegetative cells (cf. Hargraves & French 1983).

The present study aimed at discerning the source of seed populations of the *Thalassiosira* diatoms that cause the spring bloom in Funka Bay by examining diatom seed populations on the sea bottom during summer-winter and surveying the spatial distribution of diatoms in the bay and adjacent seas during the spring bloom.

Funka Bay is located in the southwestern portion of the island of Hokkaido Japan, and is a semi-closed shallow bay (area, 2270 km^2 ; mean depth, 59 m; maximum depth, 107 m; Ohtani 1971) open to the Pacific Ocean (Fig. 1). The water column structure is characterized by two major water masses: the Coastal Oyashio Water mass (temperature <3°C, salinity <33.3‰), and the Tsugaru Warm

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Fig. 1. Sampling stations for the survey on the spatial distribution of diatoms in Funka Bay and neighboring waters, southwestern Hokkaido, during 5–11 March 1996. Station 30 (*open circle*), where bottom sediments were collected from June 1995 to January 1996, is also shown. The typical intrusion pattern of the Coastal Oyashio Water in superimposed as a *shaded arrow*.

Water mass (>6°C, >33.6‰), the latter originating from the Tsushima Warm Current (Ohtani 1971; Ohtani et al. 1971b). The Coastal Oyashio Water mass occupies the bay from spring to summer and is replaced by the Tsugaru Warm Water mass from fall to winter. The Tsugaru Warm Water that overwinters in the bay (termed Funka Bay Water) is denser than the Coastal Oyashio Water. Consequently, the intrusion of the Coastal Oyashio Water mass into the bay during February-March induces an immediate stratification of the water column. The Coastal Oyashio Water mass and the Funka Bay Water mass have similar concentrations of nutrient (nitrate, 5.0–9.3 μ M; phosphate, 0.8–1.0 μ M; silicate, 18–20.6 μ MM; cf. Maita 1982).

Materials and Methods

Collection and counting of diatom seed populations in bottom sediments

Diatom seed populations were counted using the MPN method (Throndsen 1978; Imai et al. 1984). Bottom sediments were collected with a gravity core sampler at Stn 30 (central portion of the bay; 42°15.9'N, 141°36.3'E, 92-m depth) from June 1995 to January 1996 (Fig. 1). Bottom (ca. 90-m) temperatures were determined using a CTD unit

(Seabird 19). Surface sediments (ca. top 1 cm of the core sample) were stored in a cool box (ca. 5°C) immediately after collection and then transferred to the laboratory. A 1-g (wet weight) subsample was suspended in 10 ml of modified "Erd-Schreiber" medium (Throndsen 1978), and serial 8-fold dilutions were made. Diluted 1-ml subsamples were placed in triplicate in the wells of a 24-well polystyrene tissue culture plate. The plates were incubated at 12.5°C (the optimum temperature for germination of diatoms, cf. McQuoid & Hobson 1995) under a light intensity of 2200 lux (12 L : 12 D). The presence or absence of vegetative cells of *Chaetoceros* and *Thalassiosira* was observed under an inverted microscope after 6 to 8 d from inoculation. The most probable number (MPN) was calculated using the MPN statistical table (Throndsen 1978).

Spatial distribution of diatom vegetative cells

A field survey was carried out at 11 stations inside and 20 stations outside of Funka Bay during 5–11 March 1996 (Fig. 1). Water samples (500 ml) were collected at 10-m depth with a Niskin bottle and preserved with 1% buffered formalin (final concentration) to examine the diatom species and to calculate the biomass. At each sampling station, water temperature, salinity and density were determined concurrently using a CTD unit (Neil Brown Mark IIIB).

In the laboratory, the samples were settled and concentrated to 20 ml. Enumeration and dimensional measurements of diatom cells were done under the inverted microscope using 0.2 to 4 ml of the concentrated samples (Utermöl 1958). Diatoms that could not be identified to species level were assigned to higher taxonomic groups. Cell volumes of the diatoms were calculated assuming the appropriate geometry of the cell and then converted to cell carbon by using the formula of Strathmann (1967).

Results

Diatom seed populations in bottom sediments

Bottom temperatures were low (ca. 5°C) from June 1995 to January 1996 (Table 1). Vegetative cells of Thalassiosira nordenskioeldii, Thalassiosira spp., Chaetoceros sociale, Ch. compressum and Chaetoceros spp., which are the dominant species during the spring diatom bloom in Funka Bay (Shinada et al. 1999), occurred in the sediments collected at Stn 30 during the present study. The MPN of Th. nordenskioeldii was 460 cells (g wet wt mud)⁻¹ in June, decreasing to 4-110 cells (g wet wt mud)⁻¹ in the other months. The MPNs of Chaetoceros sociale, Ch. compressum and Chaetoceros spp. were higher than those of Thalassiosira during the present investigation (43 to 1.1×10^6 cells [g wet wt mud]⁻¹), although data on Thalassiosira spp. was lacking from July to October. The MPN of Chaetoceros was lowest (43–240 cells [g wet wt mud]⁻¹) during August, and then increased $(460-4.6 \times 10^4 \text{ cells [g wet wt mud]}^{-1})$ from

	June-95	July	Aug.	Sep.	Oct.	Jan96
Thalassiosira nordenskioeldii	460	4	93	15	110	93
Thalassiosira spp.	1100	no data	no data	no data	no data	43
Chaetoceros sociale	1100000	11000	240	930	1100	46000
Chaetoceros compressum	1100	2400	43	430	1100	1500
Chaetoceros spp.	30000	4600	240	430	460	11000
Bottom temperature (°C)	4.8	4.9	4.8	no data	5.6	5.3

Table 1. Seasonal change in the most probable number (MPN) of spring bloom forming diatoms (6-8 d incubation of sedimented samples). and bottom temperature as Stn 30, central portion of Funka Bay. Figures are expessed as cells (g wet wt mud)⁻¹.

October to January. The potential seed population of *Chaetoceros* was 2 or 3 orders higher than that of *Thalassiosira* in January 1996.

Spatial distribution of vegetative cells

The Coastal Oyashio Water mass occupied the entire survey area during 5–11 March 1996 (Fig. 2). The lowest values for both temperature and salinity were also recorded outside the bay (<1°C and 32.6‰, respectively). Slightly warmer and more saline waters were recorded at almost all the stations inside the bay (2.2°C and >32.8‰, respectively) except at Stn 19 (Fig. 2).

A high biomass of total diatoms (ca. 100 mgC m^{-3}) was observed during 5–11 March 1996 both at outside and inside the bay (Fig. 3a). *Thalassiosira* and *Chaetoceros* showed different spatial distribution patterns; *Thalassiosira* was most abundant outside the bay, whereas *Chaetoceros* occurred in larger numbers inside the bay (Fig. 3b,c). High concentrations of *Chaetoceros* inside the bay is indicative of the late-phase of the diatom bloom, as *Thalassiosira* pre-



Fig. 2. Spatial distribution of temperature (a) and salinity (b) at 10-m depth in Funka Bay and neighboring waters during 5-11 March 1996.

dominates during the early-phase of the bloom (Shinada et al. 1999).

We compared the species composition of *Thalassiosira* and *Chaetoceros* between the inside (Stns 17-19, 24-26,



Fig. 3. Spatial distribution of biomass (mg C m^{-3}) of total diatoms (**a**), *Thalassiosira* (**b**) and *Chaetoceros* (**c**) at 10-m depth in Funka Bay and neighboring waters.



Fig. 4. Species composition of *Thalassiosira* and *Chaetoceros* inside (upper panel) and outside (lower panel) the bay at 10-m depth during 5–11 March 1996.

27, 29–31 and 33) and the outside (Stns 101 and 103–108) of the bay (Fig. 4). Inside the bay, *Chaetoceros debile* (maximum 18% of the total biomass), *Ch. sociale* (17%) and *Ch. compressum* (14%) were dominant. *Thalassiosira nordenskioeldii* (31%) was dominant only at a north eastern station (Stn 19). Outside the bay, *Chaetoceros sociale* (12%) and *Ch. radicans* (11%) were common only at coastal stations (Stns 106–108). *Thalassiosira norden-skioeldii* (16–55%) was a major component at all the stations outside the bay.

Discussion

This is the first report on seed populations of Thalas-

siosira diatoms in the bottom sediments of Funka Bay and it showed that the abundances of the Thalassiosira seed population were 2-3 orders of magnitude lower than those of Chaetoceros in January (before spring bloom). Bottom temperature in the central part of the bay ranges between 2-8°C throughout the year (Kido & Ohtani 1981). Resting spores of Chaetoceros are viable in sediments at about 5°C for more than one year (Hollibaugh et al. 1981). However, the resting spores of Thalassiosira nordenskioeldii, which was the most dominant species of Thalassiosira found in this study, are not viable after 200 d under the same temperature regime (Durbin 1978). Bottom temperatures were around 5°C throughout the study period (Table 1), so that the survival rate of the Thalassiosira nordenskioeldii seed population would be low by the beginning of the spring bloom. Therefore, temperature is likely to be one of the major factors influencing the survival of the Thalassiosira (mostly Th. nordenskioeldii) seed populations. The seed populations of Chaetoceros decreased rapidly from June to August, and again increased from September to January. Maita & Odate (1988) reported that the fall phytoplankton bloom occurred in November in Funka Bay. The increase in seed populations during this period may be attributable to the sedimentation of diatom from this phytoplankton bloom. Our results suggest that seed populations in the bay's sediments might be important for the Chaetoceros spring bloom, but not for Thalassiosira.

Chaetoceros was concentrated only inside the bay, whereas Thalassiosira was distributed at the offshore stations outside the bay during 5-11 March. Seed populations of Thalassiosira in offshore sediments cannot be a source of blooming since the mixed layer was <200 m throughout the year in this offshore region where bottom depths are >500 m (Yamaguchi & Shiga 1997). Lateral advection by the Coastal Oyashio Water mass is considered to be the most plausible explanation for the abundance of Thalassiosira in the offshore surface layer (Fig. 3b). The seed populations for Thalassiosira blooms that occurred outside Funka Bay probably originate from the southern part of the Kuril Islands (Karohji 1986) and the Okhotsk Sea (Iizuka & Tamura 1958; Ohwada 1957), and are transported with the Coastal Oyashio Water into the bay. The Coastal Oyashio Water mass intrudes into the bay from the northeast (Ohtani et al. 1971a). In this study, Thalassiosira nordenskioeldii was dominant in the northeastern part of the bay (Stn 19) (Fig. 4). The present results suggest that the Coastal Oyashio Water mass transports Thalassiosira from the offshore region into Funka Bay.

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