Bull. Fac. Fish. Hokkaido Univ.
41(1), 1-7. 1990.

Seasonal Distribution and Vertical Flux of Resting Spores of *Chaetoceros* (Bacillariophyceae) Species in the Neritic Water of Funka Bay, Japan*

Tsuneo ODATE** and Yoshiaki MAITA**

Abstract

Seasonal distribution and vertical flux of *Chaetoceros* spp. resting spores were determined using seawater samples and sediment trap samples in Funka Bay (Hokkaido, Japan). The spores of *Chaetoceros sociale* were predominant in both samples. The spore density was high in the 50-80 m depth layer in late April ($>10^5$ spores$\cdot L^{-1}$), just after the spring bloom. The maximum flux of spores occurred at 74 m depth in late April (2.0×10^8 spores$\cdot m^{-2}\cdot d^{-1}$). Apparent sinking velocity was estimated to be 0.04-10.05 m$\cdot d^{-1}$. The high velocity was obtained during and after the blooms, suggesting that spore formation occurred during this period. Fewer spores were collected with traps deployed at 30 m during the same period, implying that spore formation probably occurred between the 30 to 74 m depth. The spore density in the bottom layer (90 m) was high ($>10^4$ spores$\cdot L^{-1}$) from July to August, whereas their vegetative cells could not be found in the surface water (0 m). The results showed that a large number of spores sink rapidly after the bloom, stay in the bottom layer throughout summer, and then were brought back into the euphotic zone during the vertical mixing of the water column. The spores then germinate and the vegetative cells probably over-winter in the water column, becoming the seed stock for the next bloom.

Introduction

In boreal waters, phytoplankton blooms usually occur in spring (Raymont, 1980). In Funka Bay, southern Hokkaido also, an annual spring bloom of phytoplankton dominated by diatoms is observed during a short period in February or March (Nishihama et al., 1976; Nakata, 1982; Odate, 1987). Studies conducted in 1984 (Shiomoto, 1987), 1985 (Maita and Odate, 1988), and 1986 (Odate and Maita, in preparation) also showed that the peaks of the spring bloom occurred in mid-March. At the end of a bloom, an increase in resting spore density is usually observed (Odate, 1987). Formation of resting spores is considered to be a survival strategy triggered by unfavorable growth conditions (e.g. nutrient depletion or temperature stress) (Durbin, 1978; Davis et al., 1980; Garrison, 1981; Hollibaugh et al., 1981; Smetacek, 1985; Ishizaka et al., 1987). The spores sink to the cold bottom water in summer and during the vertical mixing of water in winter, they are brought back to the euphotic layer (Davis et al., 1980; Kido and Ohtani, 1981; Odate, 1987). These may then serve as seed stocks for the coming spring bloom.

* *Contribution No. 219 from the Research Institute of North Pacific Fisheries, Faculty of Fisheries, Hokkaido University*
(北海道大学水産学部北洋水産研究施設業績第219号)
** *Division of Marine Biochemical Science, Research Institute of North Pacific Fisheries, Faculty of Fisheries, Hokkaido University*
(北海道大学水産学部北洋水産研究施設海洋生産学部門)

Although the spore standing crop in Funka Bay has been partly reported (Odate, 1987), little is known about the *in situ* flux or sinking rates. Using sediment trap samples, Pitcher (1986) observed that a rapid formation and settling of *Chaetoceros* spp. resting spores occur in the southern Benguela system. Moreover, he pointed out that using typical field sampling procedures may not show the transient spore formation. In this study, the flux of *Chaetoceros* resting spores in Funka Bay was determined using sediment trap samples.

Materials and Methods

Vertical distribution of resting spores was determined using seawater samples collected from different depths using a Van Dorn smapler in the central part of the bay (Fig. 1), from March 1984 to May 1985, and from February to April, 1986. One liter of the seawater sample was fixed with Lugol's solution (3%, v/v) and the excess solution decanted after several days.

The sediment trap system described by Maita et al. (1986) was moored at 74 m depth in the same station (Fig. 1) from August 21 to October 1, 1984 (three times), from November 15 to December 3, 1984 (once), from February 1 to March 15, 1985 (three times) and from May 10 to 23, 1985 (once). The following year, the traps were deployed again at the same station at two depths, 30 and 74 m, from February 27 to April 30 (four times). The sediment from a cylinder treated with 1% formalin containing 1.5 M NaCl was mixed thoroughly and 1/2,000-1/4,000 subsamples were

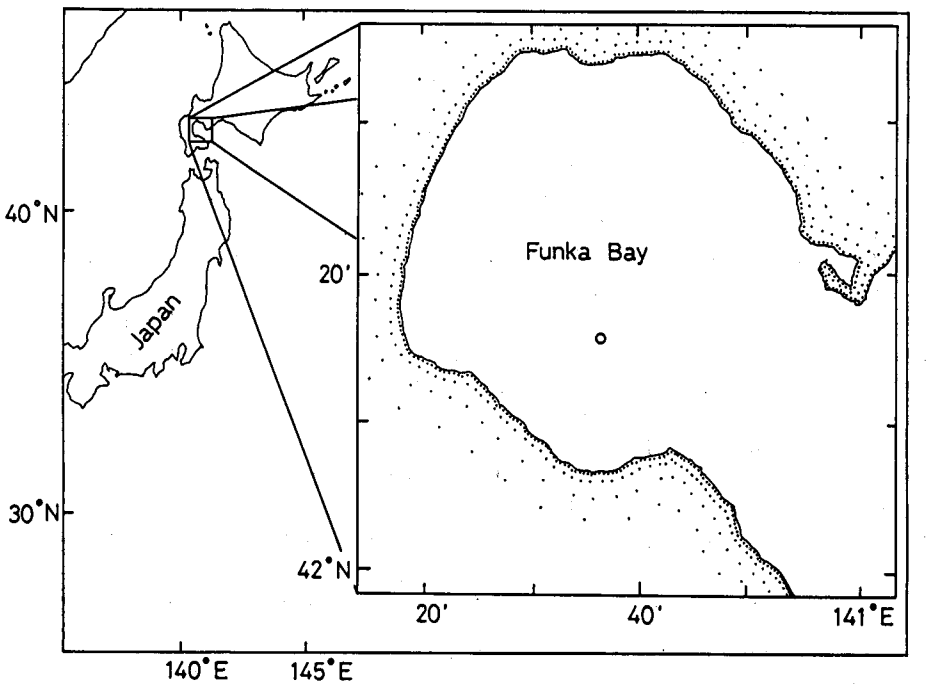

Fig. 1. Location of sampling station (open circle) in Funka Bay. Depth at the sampling station is 92 m.

set aside.

Aliquots (1/20–1/200) from the water samples and sediment trap samples were examined using an ordinary light microscope at a magnification of 200×. Vegetative cells and resting spores of *Chaetoceros* were counted.

Results and Discussion

In this study five species belonging to the genus *Chaetoceros* (*C. sociale*, *C. debile*, *C. compressum*, *C. furcellatum*, and *C. subsecondum*) were identified. Vegetative cells of these species were commonly observed in Funka Bay during spring phytoplankton blooms (Nakata, 1982; Odate, 1987). The most dominant spore in both the water and trap samples was that of *C. sociale*.

Vertical distribution of *Chaetoceros* resting spores is shown in Fig. 2. A high spore density ($>10^5$ spores$\cdot L^{-1}$) was observed between the 50 m to 80 m depth in April of 1984, after the spring phytoplankton bloom had occurred. From May, however, the density gradually decreased reaching a minimum in July. Resting spores were not observed in the upper 40 m from May to July, 1984. In the bottom layer (90 m depth), however, a high spore density ($>10^4$ spores$\cdot L^{-1}$) was observed during this period, and their vegetative cells could not be found in the surface water (0 m) from July to August, 1984 (Fig. 3). The contour line corresponding to 10^3 spores$\cdot L^{-1}$ reached 50 m depth in August and 10 m depth in November (Fig. 2), after which time the presence of the vegetative cells in the surface water in September (10^3–10^4 cells$\cdot L^{-1}$) and December ($>10^5$ cells$\cdot L^{-1}$) was noted (Fig. 3). The increase in spore density in August coincided with the inflow of the Tsugaru warm water, a branch of the Kuroshio, into this bay (Maita and Odate, 1988). It is known that the intrusion occurs in the mid-layer of the water column (Ohtani and Kido, 1980). In fact, the warm water mass was noted at the 30–60 m depth layer between August 21 and September 3, 1984 (Maita and Odate, 1988). It may be considered that the inflow of the warm water disturbed the bottom layer, such that the spores were

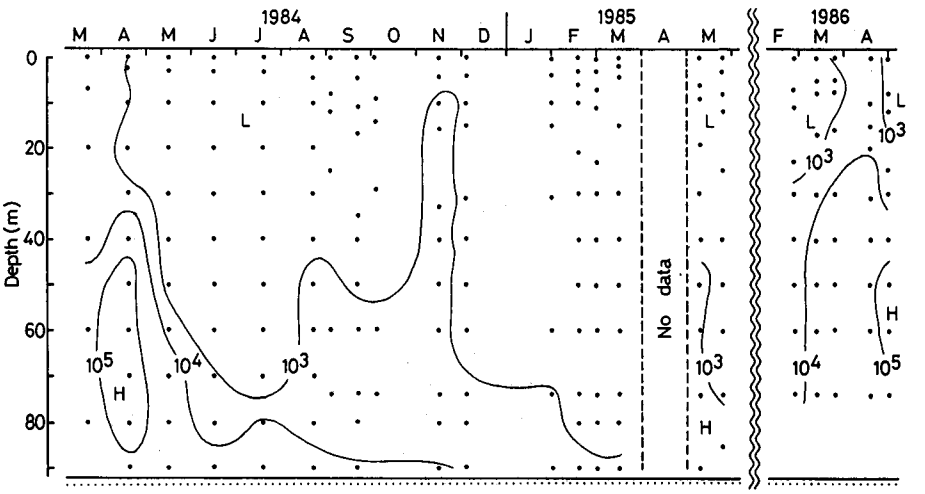

Fig. 2. Seasonal distribution of resting spores of *Chaetoceros* spp. (spores$\cdot L^{-1}$).

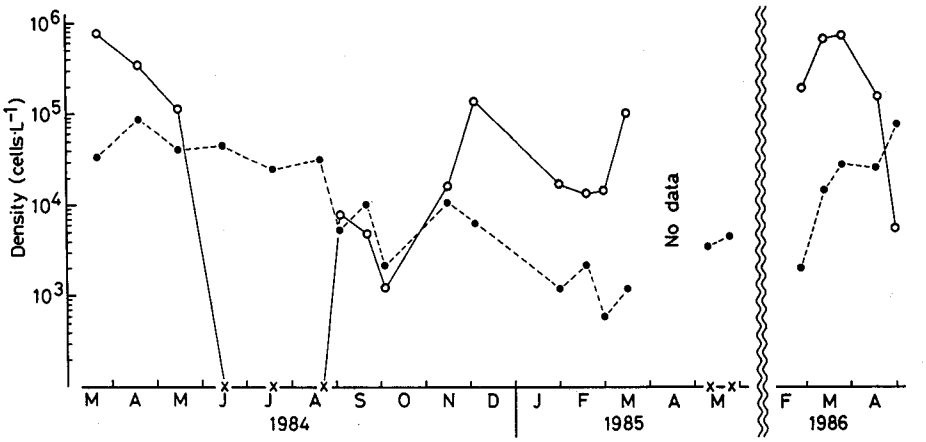

Fig. 3. Seasonal changes in *Chaetoceros* spp. Open circles, vegetative cells in the surface layer (0 m); closed circles, resting spore in the bottom layer (74 or 90 m). Cross signs denote no occurrence.

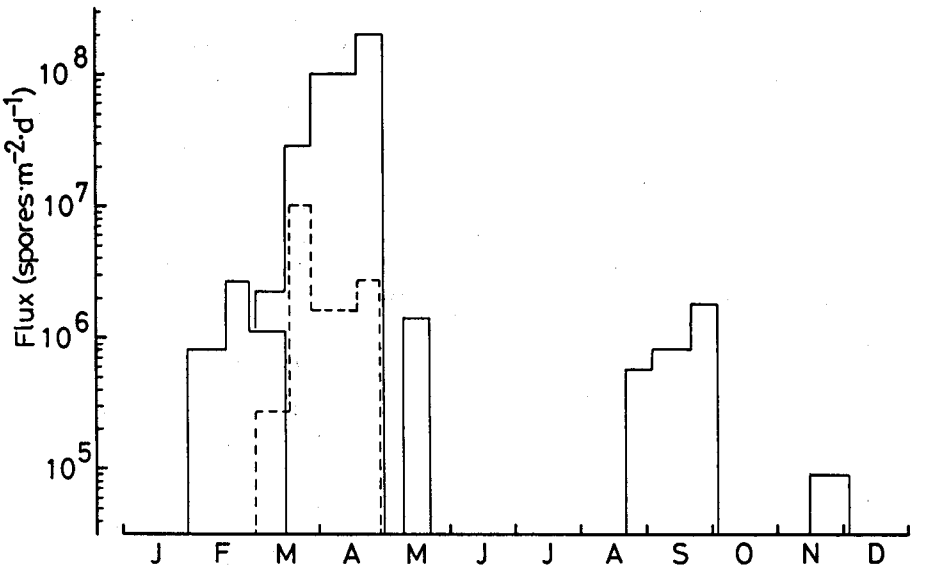

Fig. 4. Seasonal variations in vertical flux of resting spore of *Chaetoceros* spp. at 30 m depth (broken line) and 74 m depth (solid line).

brought back into the upper layer. The larger increment noted in November may be due to the vertical mixing of water, since a thermally homogenous water column had been reported at this time (Maita and Odate, 1988). From December to March, the spore density was low. A high density was observed again in late April 1986, whereas the vegetative cell density dropped.

Figure 4 shows the vertical flux of *Chaetoceros* spp. resting spores during

Table 1. Percent composition of *Chaetoceros* resting sopores collected with a sediment trap during autumn (from September 21 to October 1, 1984) and spring (from April 17 to April 30, 1986) at 74 m depth in Funka Bay. Data in parentheses denotes percentage of spores observed in chains.

		Autumn	Spring
Chaetoceros	*sociale*	60.4 (0)	88.3 (82)
C.	*debile*	28.3 (0)	3.8 (63)
C.	*compressum*	11.3 (0)	3.6 (83)
C.	*furcellatum*	0.0 (0)	4.0 (98)
C.	*subsecondum*	0.0 (0)	0.2 (100)
C.	sp.	0.0 (0)	0.1 (100)

different seasons of the year. The flux increased from mid-March, the peak of the spring phytoplankton bloom, reaching a maximum of 2.0×10^8 spores$\cdot m^{-2}\cdot d^{-1}$ in late April, 1986, after the bloom. The increased flux resulted from the active formation of resting spores triggered probably by nutrient depletion, since the nutrient concentrations decreased rapidly during this period as observed by Maita and Odate (1988). After the spring phytoplankton bloom, spore flux at 30 m depth was several orders of magnitude lower than that at 74 m depth (Fig. 3). This strongly suggests that spore formation occurred between the 30 to 74 m depth. Hence, the spore density between the 50 m to 80 m depth was higher than that in the upper 30 m depth (Fig. 2). The flux observed between August and October was almost the same as that in February, early half of March, and May (ca. 10^6 spores$\cdot m^{-2}\cdot d^{-1}$). The lowest flux was obtained between November and December, when there was vertical mixing of the water column (Maita and Odate, 1988).

In autumn (September 21 to October 1, 1984), the spores of *C. sociale*, *C. debile*, and *C. compressum* collected in sediment traps were observed to be solitary (Table 1). In spring (April 17 to 30, 1986), spores belonging to three more species, *C. furcellatum*, *C. subsecondum*, and *C.* sp., were identified. During this period, most of the spores were observed either associated with vegetative cell colonies or as chains of two or more spores. It is quite natural to think that the solitary spores originated from the associated ones. Our observations suggest that the spores collected in spring were newly formed whereas those in autumn were old. The spores observed in autumn may be considered to have been re-suspended from the bottom layer as mentioned earlier.

An estimate of the sinking velocity ($m\cdot d^{-1}$) was obtained based on the flux ($m^{-2}\cdot d^{-1}$) and density (m^{-3}) of spores (Table 2). Here, the rate of spore formation during the descent was not considered. The values may only be a conservative estimate of the apparent sinking velocity. The apparent sinking velocity was estimated to be 0.04–10.05 $m\cdot d^{-1}$ (Table 2). Although this range was wider than that of an earlier study (2.75 ± 0.61 $m\cdot d^{-1}$; Bienfang, 1981), the mean sinking rates (2.36 $m\cdot d^{-1}$) were comparable. The faster velocity (>3 $m\cdot d^{-1}$) was obtained at 74 m depth between February 18 and March 15, 1985 (during the bloom), and between March 26 and April 30, 1986 (after the bloom). At 30 m depth, the high velocity was also calculated between March 14 and 26, 1986 (during the bloom).

Table 2. Resting spore standing stock, flux, and apparent sinking velocity within water column (0–74 m).

	Standing stock	Flux	Sinking velocity
	$\times 10^6$ spores$\cdot m^{-3}$	$\times 10^6$ spores$\cdot m^{-2}\cdot d^{-1}$	$m\cdot d^{-1}$
	(A)	(B)	(B/A)
1984			
Aug. 21–Sep. 3	2.35	0.56	0.24
Sep. 3–Sep. 21	1.45	0.80	0.55
Sep. 21–Oct. 1	1.28	1.73	1.35
Nov. 16–Dec. 3	2.12	0.09	0.04
1985			
Feb. 1–Feb. 18	0.43	0.81	1.89
Feb. 18–Feb. 28	0.26	2.61	10.05
Feb. 28–Mar. 15	0.15	1.09	7.52
May 10–May 23	1.03	1.45	1.40
1986			
Feb. 27–Mar. 14	0.96[1)]	0.26[1)]	0.27[1)]
	7.54	2.16	0.29
Mar. 14–Mar. 26	2.97[1)]	10.17[1)]	3.43[1)]
	16.57	28.69	1.73
Mar. 26–Apr. 17	6.89[1)]	1.61[1)]	0.23[1)]
	20.07	99.96	4.98
Apr. 17–Apr. 30	5.87[1)]	2.65[1)]	0.45[1)]
	58.99	199.49	3.38

[1)] 0–30 m water column.

These faster sinking velocities imply that rapid spore formation occurs during, as well as after the blooms when nutrients are depleted.

On the other hand, an extremely low velocity was noted between November and December, 1984. Since vertical mixing of water starts in November (Ohtani and Kido, 1980; Maita and Odate, 1988), the spores present near the bottom may have been brought back into the upper layer, which may sink again causing an increased flux. However, the actual spore flux was lowest in December (Fig. 4). The spores remained in the euphotic zone and eventually germinated. Hence, an increase in the cell density of *Chaetoceros* spp. was observed in November and December (Fig. 3). These vegetative cells may over-winter in the water column, and bloom when favorable conditions for growth occur (i.e. spring).

These results suggest that the dynamics of resting spores in the water column play an important role in the onset of the next bloom as noted also by Davis et al. (1980), Kido and Ohtani (1981), Odate (1987). Furthermore, our results suggest that the germination of spores occurred not just before the spring bloom but earlier, during the vertical mixing of the water.

Acknowledgements

We would like to express our sincere gratitude to the captain and crew of T/S *Ushio Maru*, Hokkaido University, for their excellent performance in mooring and recovering the sediment trap system and for their support during the field samplings. Thanks is extended to Ms. L.V. Castillo for reading of this manuscript.

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