Structure and magnitude of diatom spring bloom in Funka Bay, southwestern Hokkaido, Japan, as influenced by the intrusion of Coastal Oyashio Water

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Abstract: Effects of the intrusion of the Coastal Oyashio Water on the magnitude and species composition of the diatom spring bloom were investigated in the center of Funka Bay, southwestern Hokkaido, Japan from 1994 through 1996. Inflow of the Coastal Oyashio Water into Funka Bay occurred in 1995 and 1996, but not in 1994. Water-column stability among the three years was ranked (strong to weak) 1995>1996≫1994, and diatom abundance in the euphotic zone also coincided with this ranking. Diatoms of the genera *Thalassiosira* and *Chaetoceros* were most abundant throughout the three years, but the proportion of *Thalassiosira* was much lower in 1994 (24%) than in 1995 (72%) and 1996 (74%). *Thalassiosira* were abundant in the early phase of the diatom spring bloom and *Chaetoceros* were most abundant toward the end of the blooms in 1995 and 1996, but *Chaetoceros* were dominant throughout the entire bloom in 1994 (80–91%). These results indicate that the intrusion of the Coastal Oyashio Water into Funka Bay leads to a rapid increase in water column stability which facilitates the onset off *Thalassiosira* blooms.

Key words: diatom spring bloom, Coastal Oyashio Water, Funka Bay, *Thalassiosira*

Introduction

A large portion of the annual primary production in temperate and boreal waters is produced by diatom-dominated spring phytoplankton blooms (Riley 1957; Wassman & Aadnesen 1984; Lignell et al. 1993). Since understanding this process is important for evaluating carbon flow dynamics in high latitude marine ecosystems, intensive field studies have been conducted in Narragansett Bay (Smayda 1957; Pratt 1959,1965; Durbin et al. 1975), Monterey Bay (Garrison 1979), the Gulf of Maine (Townsend 1992) and the ice-melt zones of the Weddel Sea (Fryxell & Kendrick 1988) and Bering Sea (Niebauer et al. 1990, 1995) and the Oyashio region (Yoshimori et al. 1995; Kasai et al. 1997).

Funka Bay, located in southwestern Hokkaido, Japan, is a semi-closed shallow bay (area, $22.7 \times 10^2 \, km^2$; mean depth, 59 m; maximum depth, 107 m) open to the Pacific Ocean. The bay is of special importance to local fisheries, because it is a nursery ground for walleye pollock (*Theragra*

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chalcogramma). The bay's spring phytoplankton bloom is a short-term event, usually starting in early March and ending after a month (Nishihama et al. 1976; Nakata 1982; Odate 1987). The spring phytoplankton bloom accounts for an estimated 66% of the annual primary production in Funka Bay (Maita & Odate 1988), though the magnitude of the spring bloom varies considerably from year to year (Nishihama et al. 1976; Nakata 1982; Odate 1987). The hydrography of Funka Bay is characterized by two major water masses; the Coastal Oyashio Water (temperature <3°C, salinity <33.3‰), and the Tsugaru Warm Water (>6°C, <33.6‰) originating from the Kuroshio (Ohtani & Akiba 1970; Ohtani 1971; Ohtani et al. 1971a,b). The Coastal Oyashio Water occupies the bay from spring to summer, and the Tsugaru Warm Water occurs from fall to winter. The Tsugaru Warm Water that occurs in the bay during winter is named Funka Bay Water (3–6°C, >33.8‰). The density of Funka Bay Water is greater than that of Coastal Oyashio Water, so the inflow of the Coastal Oyashio Water into Funka Bay induces stratification of the water column. The Coastal Oyashio Water and the Funka Bay Water have similar high nutrient concentrations (nitrate, 5.0–9.3 μM; phos-
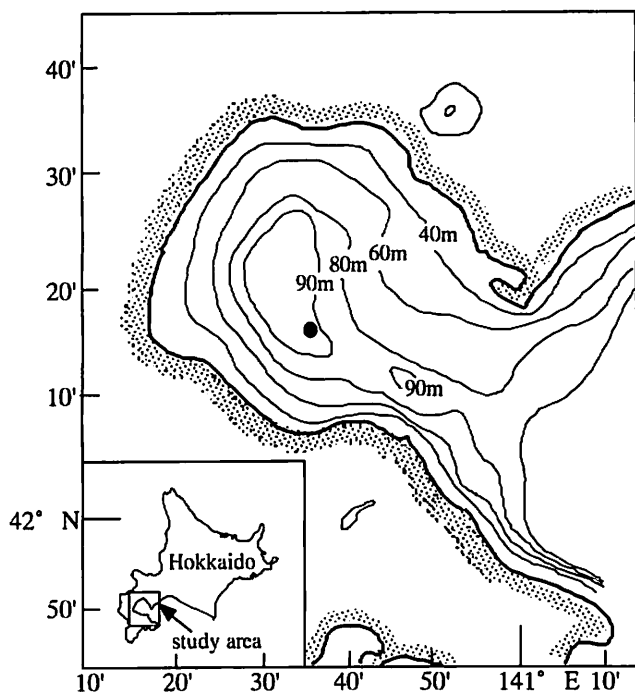
Fig. 1. Sampling station (solid circle) in Funka Bay, southwestern Hokkaido, Japan. Depth contours of 40, 60, 80 and 90 m are superimposed.

phate, 0.8–1.0 μM; silicate, 18.2–20.6 μM; cf. Maita 1982).

A previous study indicated that the timings of the intrusion of the Coastal Oyashio Water and the spring phytoplankton bloom are closely matched (Ohtani 1971), which led to the hypothesis that the Coastal Oyashio Water triggers the development of the spring bloom (Iwasaki 1978). In this study, we investigated the structure and magnitudes of phytoplankton blooms in relation to intrusions of the Coastal Oyashio Water in Funka Bay for three consecutive years to test this hypothesis.

Materials and Methods

The field survey was carried out from January to March/April in 1994, 1995 and 1996 at a station (42°15.9′N, 141°36.3′E; 92-m depth), located in the center of Funka Bay (Fig. 1). During each survey, water samples (0.5–1 liter) were collected at 10-m intervals between 10- and 90-m depth using 1.3-liter or 5-liter Niskin bottles. Surface water samples were collected with a plastic bucket. Subsamples (500–1000 ml) of these water samples were preserved with 1% buffered formalin (final concentration) for examination of diatom species and their biomasses. At each sampling, a Secchi disk reading was taken, and temperature and salinity profiles were determined using a CTD unit (SeaBird 19 or Neil Brown Mark IIIB).

At the land laboratory, the subsamples were settled and subsequently concentrated to 20 ml. Diatom cells in 0.2 to 4 ml of the concentrated subsamples were counted and measured using an inverted microscope (Utermöhl 1958).
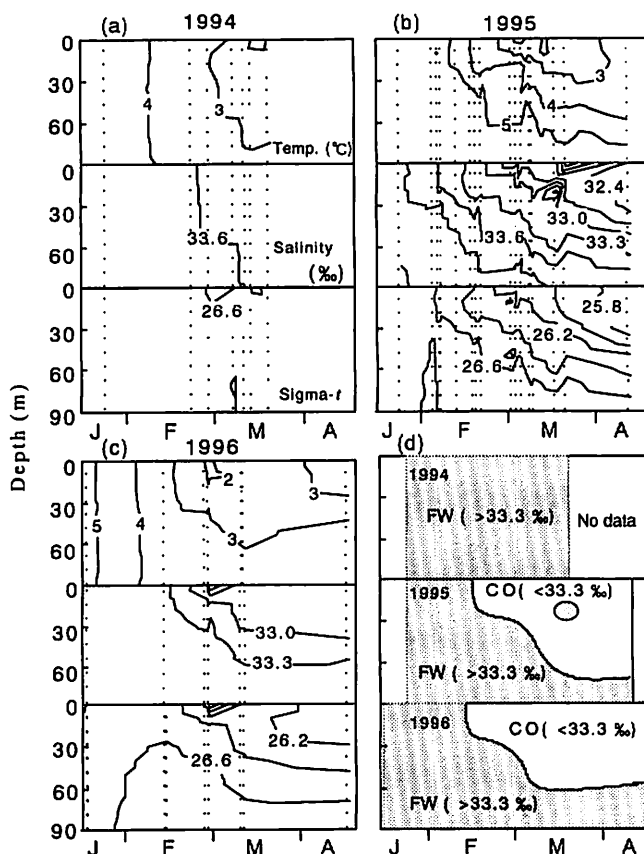

Fig. 2. Vertical profiles of temperature, salinity and sigma-t at the sampling station in Funka Bay from January to April in 1994 (a), 1995 (b) and 1996 (c). According to the results, temporal and spacial separation of the Coastal Oyashio Water (CO) from the Funka Bay Water (FW) is shown schematically (d).

Diatom species were identified using diagnostic features given by Tomas et al. (1996). Diatoms that could not be identified to species level were grouped into higher taxonomic groups. Cell volumes of diatoms were calculated assuming appropriate geometry of the cells, and then converted to cell carbon using the formula

$$\log_{10}C = 0.758 \log_{10}V - 0.422 \text{ (Strathmann 1967)},$$

where C is cell carbon (pg C μm^{-3}) and V is cell volume (μm^3).

Results

Hydrography

In 1994, temperature, salinity and density (sigma-t) were almost uniform throughout the water column from January through mid-March (Fig. 2a). As a result, the stability of the water column, as judged by sigma-t, was very weak over the entire 1994 survey period. In 1995, temperature and salinity were near uniform until early February, thereafter both decreased gradually at the surface toward mid-April. Reflecting these changes in temperature and salinity,
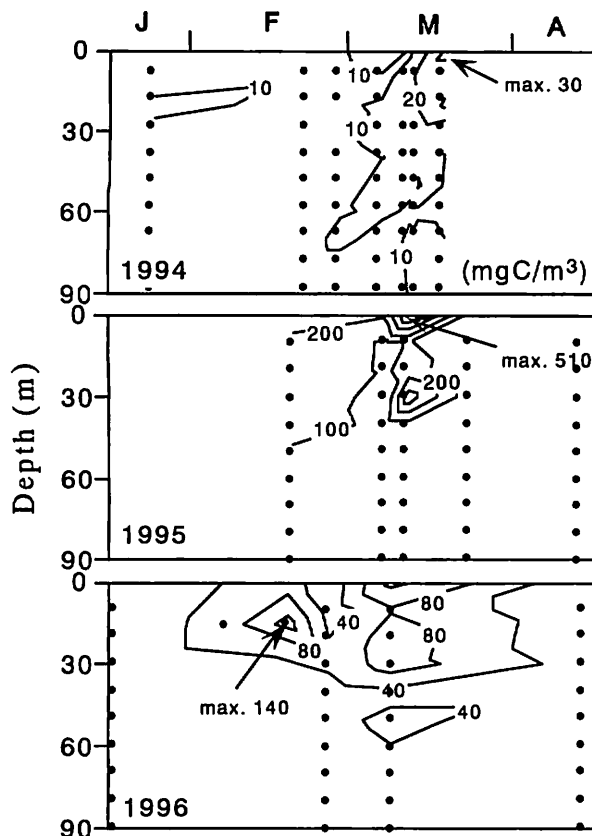
Fig. 3. Vertical profiles of diatom biomass at the sampling station in Funka Bay from January to April in 1994 (top), 1995 (middle) and 1996 (bottom). Note that biomass contour values are not the same between the years.

the water column became more stable from early February to mid-April in 1995 (Fig. 2b). Water column features in 1996 were similar to those in 1995; a gradual decrease occurred for both temperature and salinity in mid-February initially at the surface layer and extended to depth by mid-April. Sigma-t profiles indicated that the water column became stratified from mid-February in 1996 (Fig. 2c). From the results of sigma-t profiles over the three-year period, the stability of the water column was ranked (strong to weak) as 1995>1996≫1994.

Based on the definition of the Coastal Oyashio Water (<33.3‰, Ohtani 1971), the results in Fig. 2a–c indicate that the Coastal Oyashio Water had not flowed into Funka Bay by mid-March in 1994. On the other hand, in 1995 and 1996, the Coastal Oyashio Water intruded into the upper 20 m in mid-February and extended down to 60 m in March (Fig. 2d).

Diatom biomass

Sequential changes in the vertical distribution of diatom biomass in 1994, 1995 and 1996 are summarized in Fig. 3. In 1994, the diatom biomass increased slowly throughout the water column from January to mid-March. Reflecting

the weak stability of the water column in this year, diatoms were distributed near uniformly throughout the water column. The maximum biomass ($30\,\text{mg}\,C\,m^{-3}$) was recorded at 0 m in mid-March. Although there is no data for the period after mid-March, no increase in diatom biomass is expected to have occured because of low nitrate concentrations ($0.2\,\mu M$ at 0 m depth, data not shown).

In 1995, diatom biomass increased rapidly in mid-March in the presence of the Coastal Oyashio Water. The biomass ($>100\,\text{mg}\,C\,m^{-3}$) above 50 m in mid-February was much higher than in mid-February of the previous year. The diatom biomass peaked in mid-March at 0 m depth ($510\,\text{mg}\,C\,m^{-3}$), after which the biomass decreased rapidly to $<100\,\text{mg}\,C\,m^{-3}$ by late March in 1995. In 1996, the diatom biomass was much higher than in 1994, but slightly lower than in 1995. The maximum diatom biomass ($140\,\text{mg}\,C\,m^{-3}$) occurred in mid-February at 30 m depth.

Standing stock and species composition of the diatoms

The succession of the dominant diatom species (>10% of estimated total diatom carbon) in the top 30 m of the water column is shown in Fig. 4. The 0–30 m depth range was selected because most of the diatom biomass was concentrated in this range (see Fig. 3), and it encompassed the estimated euphotic zone of 26 m (the mean Secchi disk reading of 9.6 m×2.7, cf. Poole & Atkins 1929).

In the 1994 survey, *Corethron criopholum* (51% of total biomass) was dominant in January, followed by *Chaetoceros sociale* (15–45% of biomass), *Ch. decipiens* (13–15%), *Ch. radicans* (27%) and *Ch. compressum* (15–23%) as the season progressed. In the 1995 survey, *Thalassiosira nordenskioeldii* (22–69%) was most abundant from February to mid-March; later *Ch. compressum* (23%) and *Ch. concavicorne* (37%) became dominant. As in 1995, the initial predominant species from January to mid-February in 1996 was *T. nordenskioeldii* (40–60%). Later *Ch. radicans* (13–31%) and *Ch. sociale* (16%) both became dominant in succession.

The species succession observed suggests that the diatom community could be divided into three major groups (those belonging to the genus *Thalassiosira*, genus *Chaetoceros* and other diatoms), and that structural changes in the phytoplankton community occurred together with changes in total diatom carbon in the same strata (0–30 m) (Fig. 5).

In 1995 and 1996, when inflow of the Coastal Oyashio Water was confirmed, the early phytoplankton blooms observed around mid-February of each year were dominated by *Thalassiosira* (72% in 1995 and 74% in 1996). In both years, the proportion of *Thalassiosira* decreased rapidly with time and that of *Chaetoceros* increased. In 1994, when intrusion of the Coastal Oyashio Water was not evident, total diatom carbon was much lower than in 1995 and 1996. The proportion of the total diatom carbon comprised by *Thalassiosira* was lower than 25%, though a progressive increase in *Chaetoceros* abundance was observed, as also

1994	25 Jan.	24 Feb.	3 Mar.	10 Mar.	14 Mar.	16 Mar.	22 Mar.
Corethron criopholum	●						
Thalassiosira nordenskioeldii		○					
Other *Thalassiosira*	○	○					
Chaetoceros sociale		●	○		○	●	○
Chaetoceros decipiens		○	●	●			
Chaetoceros debile		○	○			○	
Chaetoceros diadema							○
Chaetoceros radicans				○	●	○	○
Chaetoceros compressum		○		○	○	○	●
Other *Cheatoceros*						○	○
Thalassionema nitschioides						○	○
Rhizosolenia spp.							

1995	21 Feb.	10 Mar.	15 Mar.	27 Mar.	19 Apr.
Thalassiosira nordenskioeldii	●	●	●		○
Chaetoceros decipiens		○	○		
Chaetoceros debile		○		○	
Chaetoceros radicans				○	
Chaetoceros compressum				○	
Chaetoceros concavicornis					●
Other *Cheatoceros*			○	●	○
Odontella aurita			○		

1996	17 Jan.	8 Feb.	22 Feb.	28 Feb.	11 Mar.	17 Apr.
Corethron criopholum	●					
Thalassiosira nordenskioeldii		●	●			
Other *Thalassiosira*	○	○	○			
Chaetoceros sociale					○	○
Chaetoceros decipiens					○	
Chaetoceros diadema					○	
Chaetoceros radicans				●		●
Chaetoceros compressum				○		○
Other *Cheatoceros*					●	
Thalassionema nitschioides				○		

Fig. 4. Species succession of diatoms at the sampling station in Funka Bay from January to April in 1994 (top), 1995 (middle) and 1996 (bottom). Open and closed circles denote dominant species (>10% of total diatom biomass) and the most dominant species, respectively.

seen in 1995 and 1996. *Chaetoceros* comprised 80–91% of the diatom carbon during the final phase of the survey each year.

Discussion

Development of water column stability is an important condition for the onset of the spring phytoplankton bloom in subarctic and temperate waters (Sverdrup 1953; Levasseur et al. 1984; Smetacek 1990), and this is usually achieved by warming of the surface layer due to increasing solar radiation in spring. In contrast, the present results clearly indicated that the intrusion of the Coastal Oyashio Water is the most important physical process responsible for establishing water column stability in Funka Bay, because its salinity is considerably lower than that of the Funka Bay Water and the Tsugaru Warm Water which over-

winters in the bay (Ohtani 1971). A similar physical process has been reported in ice-melt zones, where water column stratification is developed more rapidly by a salinity gradient than by a temperature gradient (Niebauer et al. 1990, 1995). Although the spring phytoplankton bloom in Funka Bay has been shown to occur even without inflow of the Coastal Oyashio Water (Nakata 1982; Tanaka 1984), the present study revealed that the bloom of 1994, which occurred without inflow of the Coastal Oyashio Water, was characterized by lower diatom biomasses (maximum 30 mg $C\,m^{-3}$) than the blooms of 1995 and 1996 which had concurrent inflows of the Coastal Oyashio Water (maximum 510 mg $C\,m^{-3}$ and 140 mg $C\,m^{-3}$, respectively). While no appreciable differences in nutrient concentrations were seen between the Coastal Oyashio Water and the Funka Bay Water (Maita 1982), nutrients transported with the Coastal Oyashio Water may be of significance in maintaining the spring diatom bloom in Funka Bay. To estimate the quantity
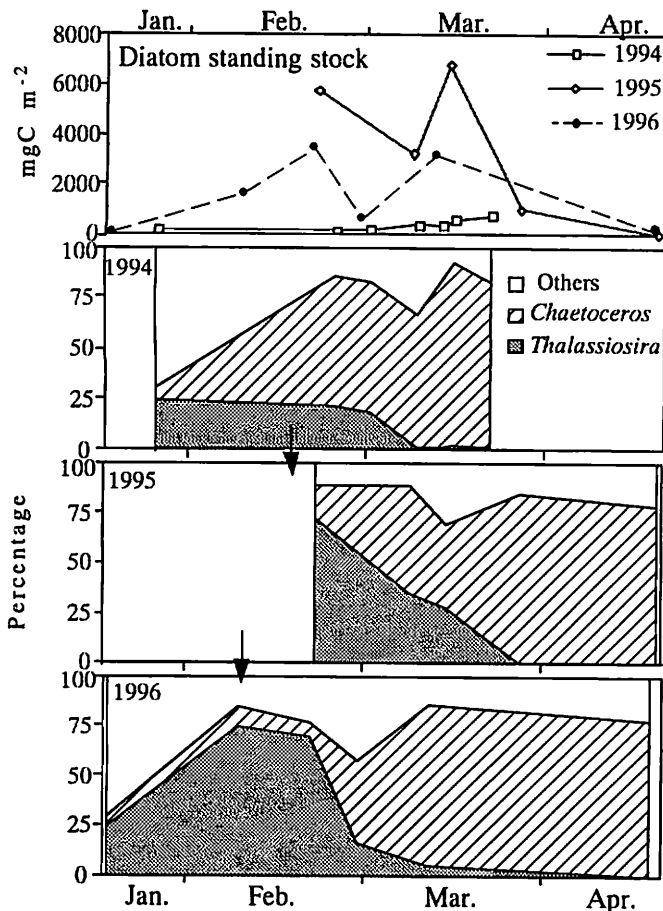
Fig. 5. Changes in total diatom standing stock (0–30 m) (top panel) and associated succession of three major diatom groups (*Thalassiosira*, *Chaetoceros*, others) at the sampling station in Funka Bay from January to April in 1994, 1995 and 1996 (bottom three panels). Arrows in bottom two panels denote the dates of intrusion of the Coastal Oyashio Water.

of nutrients brought with the Coastal Oyashio Water into the bay, monitoring of the intrusion mode of the Coastal Oyashio Water during the diatom blooming period should be carried out in future studies.

Thalassiosira nordenskioeldii was an integral component of the 1995 and 1996 spring diatom blooms in Funka Bay (Fig. 4). *T. nordenskioeldii* is adapted to low temperatures (<5°C) (Jitts et al. 1964; Durbin 1974), and is commonly found in the Coastal Oyashio Water (Shinada, unpublished data). At present, we are unable to discuss whether the *T. nordenskioeldii* blooms in both 1995 and 1996 were due to seed populations brought with the Coastal Oyashio Water, or due to resting spores that lay on the sea floor, as has been reported in various environments (Garrison 1979, 1981; Smetacek 1985). In Narragansett Bay, no seed population of *T. nordenskioeldii* occurs in the bay, being rather supplied from outside the bay, because temperatures in the bay during summer are too high for the resting spores to survive (Durbin 1978). In Funka Bay, regular inflow of the Tsugaru Warm Water occurs every fall (Ohtani & Akiba 1970;

Ohtani 1971; Ohtani et al. 1971a,b). Thus, the origin of the seed population of *Thalassiosira* that causes blooming in Funka Bay may be similar to that in Narragansett Bay.

In conclusion, the intrusion of the Coastal Oyashio Water significantly affects the magnitude and species composition of the spring bloom in Funka Bay. The magnitude of the spring phytoplankton bloom in turn affects the production of herbivorous zooplankton, such as copepods, flagellates and ciliates, and animals at higher trophic levels, such as walleye pollock. Recent studies suggest that the wind field in this area is a key mechanism causing the intrusion of the Coastal Oyashio Water into Funka Bay (Kasuga 1996; Shimizu & Isosa 1997). Therefore, the timing and the amount of the Coastal Oyashio Water transported into Funka Bay are governed ultimately by local weather conditions, and the monitoring of these may allow predictions of the magnitude of the spring diatom bloom.

Acknowledgments

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