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RESEARCH ARTICLE

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The role of diatom resting stages in the onset of the spring bloom in the East China Sea

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Abstract The abundance and species composition of diatoms were investigated along the PN line from the Okinawa Islands to the inner continental shelf in the East China Sea in the early spring of 1996. Viable diatom resting stages in sediments on the shelf were also enumerated by the extinction dilution method (most probable number method). Clear differentiation in the water masses was observed, with less saline, cold water (shelf water) on the shelf region, and warm, saline water (Kuroshio water) prevalent off the shelf and on the shelf edge. In the Kuroshio water, the abundance of diatoms was generally low but species diversity of diatoms was relatively high. In contrast, the spring bloom of diatoms was clearly observed in the shelf water where the water column was weakly stratified. The bloom was dominated by *Chaetoceros debilis*, contributing occasionally > 80% of the diatom community. Resting stages of this species were also the most abundant taxon in the sediments on the shelf. Resuspension of the sediment during winter mixing of the water column should have enabled the resting stages to germinate at the surface. Subsequent vegetative growth after germination led to the formation of an early spring bloom of *C. debilis* when the water column was stratified and light availability had increased. Intermittent resuspension of sediment on the shelf, driven by strong winds and tidal currents, probably provides opportunities for diatoms with a resting stage to exploit favorable conditions for their germination and subsequent vegetative growth. It is further suggested that complex hydrographic conditions in the East China Sea result in a dynamic bloom with contributions by both autochthonous and allochthonous species.

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Introduction

Continental shelves have generally been characterized as areas where biological productivity is much higher than that in the open ocean, due to the enormous input of terrigenous nutrients (see Walsh 1987). The East China Sea possesses a wide continental shelf shallower than 200 m, occupying approximately 70% of the total sea area. Two major rivers, viz. Changjiang and Huanghe, drain into the shelf region. This is, thus, one of the most productive areas in the world's oceans.

Studies conducted as a part of the MASFLEX program (Tsunogai et al. 2003), which particularly focused on biochemical cycles in the East China Sea, clearly revealed that biomass and productivity of phytoplankton are highest during the spring (e.g. Furuya et al. 1998). Satellite images obtained by the coastal zone color scanner (CZCS) and sea-viewing wide field of view sensor (SeaWiFS) have also shown a prolonged period of high concentration of phytoplankton pigments between March and June (Takagi et al. 1993; J. Ishizaka, personal communication).

By subjecting the pigment data obtained by high-performance liquid chromatography (HPLC) analyses to interpretation by CHEMTAX, Furuya et al. (2003) estimated the contribution of various phytoplankton classes to the total concentration of chlorophyll *a* from the Okinawa Islands to the inner continental shelf in the East China Sea during the spring of 1996. Eight major phytoplankton groups were classified, viz. prochlorophytes, cyanobacteria, chrysophytes, chlorophytes, prymnesiophytes, cryptophytes, dinoflagellates and diatoms. Among them, diatoms were observed to be the most abundant group on the shelf, contributing 40–66%

of the total chlorophyll *a*, followed by chlorophytes, cryptophytes, chrysophytes and primnesiophytes.

Many diatoms have been recorded as producing ''resting spores'' and ''resting cells'' (hereafter referred as ''resting stages'' for both types) during their life histories (Hargraves and French 1983; Garrison 1984). Numerous studies have reported that resting stages play crucial roles in survival under adverse conditions for vegetative cells and in seeding blooms (see McQuoid and Hobson 1996; Itakura et al. 1997). Since light is an essential factor in inducing germination of diatom resting stages (Hollibaugh et al. 1981; French and Hargraves 1985; Imai et al. 1996), resuspension of bottom sediments into the water column must be an important process for the cells to recruit as vegetative forms (see McQuoid and Hobson 1996; Itakura et al. 1997).

On the shelf of the East China Sea, winter monsoon, storm and tidal currents often resuspend bottom sediments throughout the water column (Milliman et al. 1985; Tanaka et al. 1987; Tanaka 1992; Iseki et al. 1995; Furuya et al. 1996). This resuspension in the East China Sea makes it a good location to study the role of the resting stages. On the basis of sediment incubations in laboratory, Ishikawa et al. (2001) postulated that the resting stages on the shelf are important for seeding the bloom. In this study we investigated the abundance and species composition of the diatoms in the spring bloom of 1996 in the East China Sea, along with enumeration of the viable resting stages in the sediments on the shelf. As a whole, this study was designed to evaluate the importance of diatom resting stages in the onset of the bloom and eventually to draw the relationship between diatom bloom formation and hydrographic conditions in the East China Sea.

Materials and methods

Field observations and sample collection

Physical oceanographic observations and water sampling were carried out at 10 stations along the PN line in the East China Sea during the SE96–01 cruise of T/S Seisui Maru (Mie University) from 15 April 1996 to 19 April 1996 (Fig. 1). Although the PN line originally comprised 12 stations (e.g. Furuya et al. 1996), stations PN-2 and PN-12 were not surveyed in this cruise. As described in Furuya et al. (2003), stations PN-1, PN-3 and PN-4 are located off the continental shelf, station PN-5 at the shelf edge, and stations PN-6 through PN-11 on the shelf. A Kuroshio water mass was observed around PN-4. Water temperature, salinity and density were obtained using a Niel Brown Instrument Systems CTD (mark III) at stations PN-1 and PN-4, and a Sea Bird electronic CTD at other stations (i.e. PN-3, and PN-5 through PN-11). Seawater samples were collected at all the stations, using rosette Niskin bottles fitted to the CTD.

Sediment samples were also obtained from seven stations (i.e. PN-5 through PN-11) on the shelf and at the shelf edge with a Smith-McIntyre grab sampler. Four sub-samples were taken from the bucket of the sampler, using polycarbonate coring tubes of 3.5 cm diameter. The top 1 cm of each core was then sliced off and pooled together into a sample bottle to avoid small-scale heterogeneity in the distribution of resting stages within a sampled area (26×23 cm). These samples were brought to the laboratory and stored at 4°C in the dark.

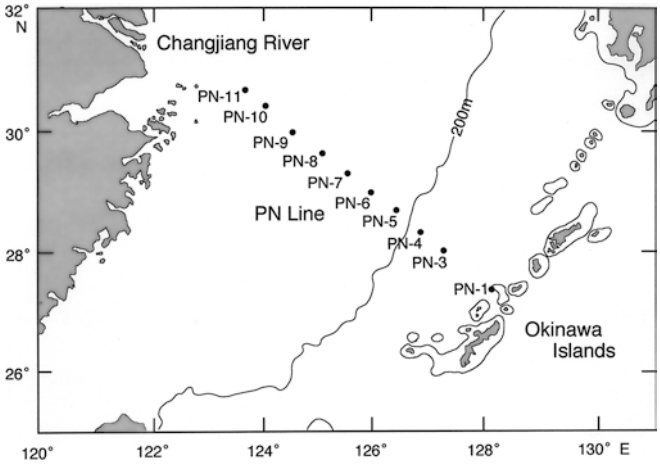

Fig. 1 Location of sampling stations on the PN line in the East China Sea

Phytoplankton biomass and composition

For estimation of chlorophyll *a*, a 200-ml aliquot of seawater was filtered through a Whatman GF/F glass fiber filter (25 mm) at < 100 mm Hg pressure. The filters were soaked in *N*, *N*-dimethylformamide, kept at −20°C (Suzuki and Ishimaru 1990) for pigment extraction and the chlorophyll *a* concentration was determined fluorometrically (Parsons et al. 1984) using a Turner Design fluorometer (Model 10-005).

For species identification and cell counts of diatoms, seawater samples were immediately fixed by adding borax-buffered formaldehyde at a final concentration of 2% (v/v). To investigate the horizontal distribution of diatoms, samples collected from three depths (0, 10 and 40 m) along the PN line were used for microscopic observation. In addition, at stations PN-8, PN-10 and PN-11, cell counts were particularly made on all samples collected vertically for analysis of the vertical distribution. An aliquot (50–100 ml) of the water sample was settled in an Utermöhl chamber for at least 24 h and the cells counted under an inverted microscope at 200× magnification.

During this cruise, analyses of phytoplankton pigments using HPLC, and nutrients (nitrate and phosphate) were carried out simultaneously (Furuya et al. 2003).

Enumeration of viable diatom resting stages in the sediments

Sediment samples stored at 4°C in the dark for more than 3 months in the laboratory were used for enumeration of viable resting stages of planktonic diatoms in the sediments. The samples were incubated following the extinction dilution method [most probable number method (MPN)] (Imai et al. 1984). This method allows us to enumerate the number of viable (i.e. able to germinate) resting stages in the sediment. Wet sediment (1 g) was suspended in 10 ml of f/2 medium (Guillard and Ryther 1962) to make a suspension at a concentration of 0.1 g wet sediment ml^{-1} (10^0 dilution). This suspension was subsequently diluted with f/2 medium and dilutions from 10^{-2} to 10^{-5} were obtained. Each 1-ml aliquot of the diluted samples (10^{-2}–10^{-5}) was incubated in five wells on a 24-well tissue culture plate (Corning) at 15°C under illumination at 170 μmol m^{-2} s^{-1} with a 12 h light/12 h dark photoperiod. The temperature maintained during the incubation simulated the average surface temperatures recorded in situ between stations PN-5 and PN-11, and light intensity during the incubation experiment was similar to levels within the euphotic zone at these stations (Ishikawa et al. 2001). The number of positive wells where vegetative cells germinated was counted on the seventh day using an inverted microscope. The most probable number of the resting

stages in the sediments (MPN g^{-1} wet sediment) was then calculated from a statistical table (Throndsen 1978) and the number was finally converted into density cm^{-3} of wet sediment by measuring the specific gravity of the original sediment.

Results

Hydrographic conditions

Detailed hydrographic conditions along the PN line during the cruise are described in Furuya et al. (2003). In brief, the water mass along the line was distinguished as being of two types, viz. a less saline (32.7–34.3) and cold water mass (<15°C), and a saline (34.0–34.5) and warmer (16–22°C) mass that was either the Kuroshio water or modified Kuroshio water. The former water mass was present on the shelf west of station PN-7, and the latter water mass occurred off the shelf, at the shelf edge, station PN-5, and station PN-6. Thus, the boundary between the two water masses was located between stations PN-6 and PN-7. These water masses are referred to here as "shelf water" and "Kuroshio water" respectively. The shelf water was weakly stratified at stations PN-8, PN-9 and PN-11(Fig. 2). A marked vertical gradient of σ_t was observed at depths of 10–16 m at station PN-9 and at depths of 30–38 m at station PN-11 with $\Delta\sigma_t$ /Δdepth values of 0.023 and 0.065, respectively. At station PN-8, σ_t increased steadily along with depth from the surface. These observations indicate vertical stability in the upper water column. The pycnocline was mainly associated with the halocline (Furuya et al. 2003). In contrast, no stratification in the water column was observed at station PN-10. Concentration of nitrate was high in the shelf water, varying from 1.9 to 8.0 μM, whereas it was mostly <1 μM in the Kuroshio water (Furuya et al. 2003).

Chlorophyll *a*

In the shelf water, chlorophyll *a* was generally >1.0 μg l^{-1} in surface waters at stations PN-8, PN-9 and PN-11 (Fig. 3). The highest concentration of chlorophyll *a* (2.75 μg l^{-1}) was observed at 20 m at station PN-8. However, at station PN-10, where the water column was not stratified, the concentration was consistently

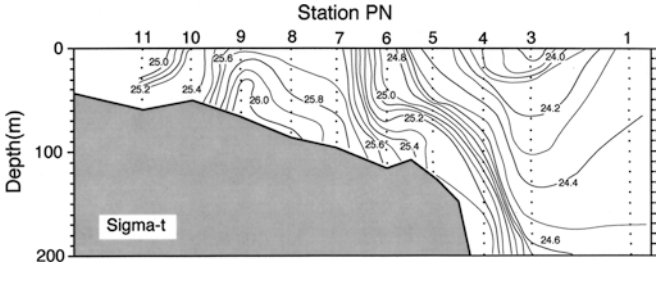

Fig. 2 Distribution of σ_t along the PN line during the period 15 April 1996 to 19 April 1996

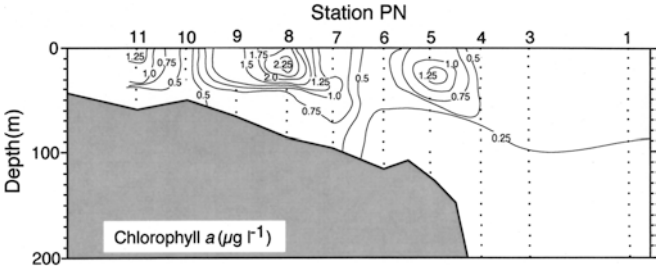

Fig. 3 Distribution of chlorophyll *a* along the PN line during the period 15 April 1996 to 19 April 1996

low (<0.5 μg l^{-1}) throughout the water column. In the Kuroshio water, chlorophyll *a* was always low (usually <0.5 μg l^{-1}), although a chlorophyll *a* patch (>1.0 μg l^{-1}) was found at around 30 m at the shelf edge (station PN-5) (Fig. 3). The results of chlorophyll *a* detected by the fluorometric method in this study corresponded to those detected by HPLC analysis (Furuya et al. 2003).

Phytoplankton community

The abundance of diatoms varied horizontally along the PN line (Fig. 4). In the shelf water, at 0 and 10 m at stations PN-7, PN-8, PN-9 and PN-11, where less saline and cold water dominated and the pycnocline was formed, diatoms were abundant ($>10^4$ cells l^{-1}). In contrast, at station PN-10, where the water column was mixed, the cell concentration was low and uniform throughout the water column ($3.0–3.3\times10^3$ cells l^{-1}). In the Kuroshio water, the cell concentration was generally low, except at station PN-5, where saline and warmer water predominated. A maximum concentration of 1.0×10^5 cells l^{-1} was observed at 10-m depth at station PN-8. In this study, 111 species belonging to 37 genera of diatoms were identified. In the shelf water, the diatom community was dominated by *Chaetoceros debilis* and three other *Chaetoceros* species, *Thalassiosira* sp. 1, *Pseudo-nitzschia pungens* and *Paralia sulcata* (Fig. 4). Each of these species contributed >10% to the total number of diatoms. In the waters where diatom concentration exceeded 10^4 cells l^{-1}, *C. debilis* was dominant (mean $= 54 \pm 25$%), followed by *Thalassiosira* sp. 1 (mean $= 12 \pm 17$%) and *Pseudo-nitzschia pungens* (mean $= 7 \pm 8$%). The contribution of *C. debilis* to the total diatoms was particularly high (72–83%) at 0- and 10-m depths at stations PN-8 and PN-11. *Paralia sulcata*, another characteristic species in the shelf water, comprised 34–60% of the diatom community throughout the water column at station PN-10, and 29% and 89% at 40-m depth at stations PN-9 and PN-11, respectively. In contrast, east of station PN-6, the dominant species varied among the stations with no consistent trend (Fig. 4). At station PN-5 where the diatoms were abundant ($>10^4$ cells l^{-1}), 78–100% of the diatoms had a relative abundance less than 10%, indicating a high species diversity.

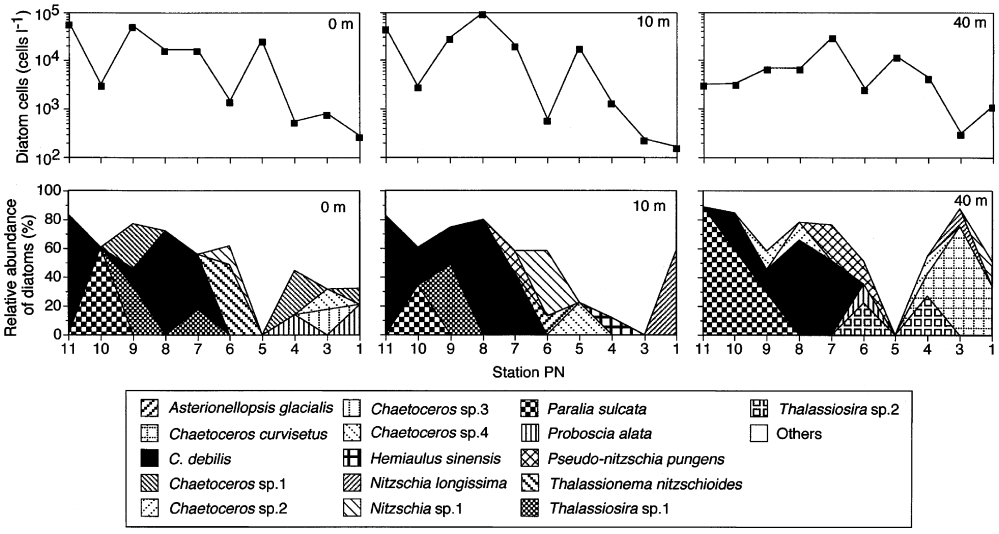

Fig. 4 Variations in diatom abundance (*upper panel*) and relative abundance of dominant species to the total diatom numbers (*lower panel*) at 0-, 10- and 40-m depths along the PN line during the study period. Species showing relative abundance >10% of total diatoms are considered dominant species

At stations PN-8 and PN-11 (Fig. 5), diatoms showed higher abundance (10^4–10^5 cells l^{-1}) above 30-m depth and decreased below this depth. *C. debilis* was the dominant species, contributing 57–80% of the diatom community above 50 m at station PN-8, and 76–86% above 30 m at station PN-11. Concentration of diatoms was relatively uniform ranging between 1.5–4.9×10^3 cells l^{-1} throughout the water column at station PN-10, where *P. sulcata* dominated (34–80%) the diatom community (Fig. 5). This species was also a dominant component below 60-m (18–44%) and 30-m (48–89%) depths at stations PN-8 and PN-11, respectively.

In general, along the PN line, diatom abundance was significantly correlated with chlorophyll *a* ($r^2=0.66$, $P<0.001$).

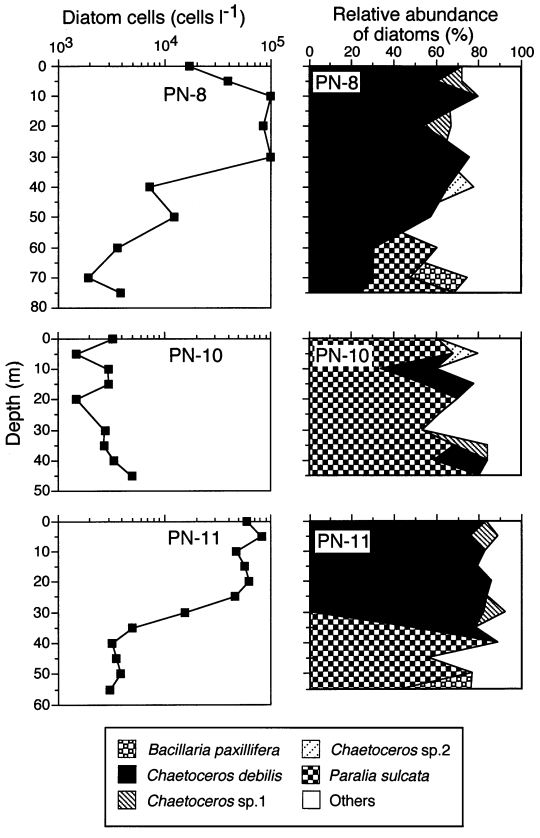

Fig. 5 Vertical distributions of diatom abundance (*left panel*) and relative abundance of dominant species within total diatom numbers (*right panel*) at stations PN-8, PN-10 and PN-11 during the study period. Species showing relative abundance >10% of total diatoms are considered dominant species

Diatom resting stages in the sediments

Seven diatom taxa, *C. debilis*, *C. curvisetus*, unidentified *Chaetoceros* spp., *Skeletonema costatum*, *Thalassiosira rotula*, *Thalassiosira* sp. 1 and *Thalassiosira* sp. 2, were detected in the sediment incubation based on the extinction dilution method. Since *C. debilis*, *T. rotula* and *Thalassiosira* sp. 1 were frequently observed in the experiment, the MPNs of these three species were selectively enumerated (Fig. 6). The resting stages of *C. debilis* were distributed in the sediments on the shelf west of station PN-6. *C. debilis* resting stages were relatively abundant (around 4×10^3 cells cm^{-3}) at stations PN-7, PN-10 and PN-11, with a maximum number of 4.4×10^3 cells cm^{-3} observed at station PN-11. Cells of this species were not detected at station PN-5. The resting stages of both the *Thalassiosira* species, with an exception at station PN-10 where the cells of *T. rotula* were not detected, were widely distributed in the sediments over the shelf and its edge, and the cell number ranged between 2.9×10^2 and 2.1×10^3, and between 3.0×10^2 and 1.9×10^3 cells cm^{-3} for *T. rotula* and *Thalassiosira* sp. 1, respectively.

Discussion

In the shelf water between stations PN-7 and PN-11, the chlorophyll *a* concentration observed in spring (Fig. 3)

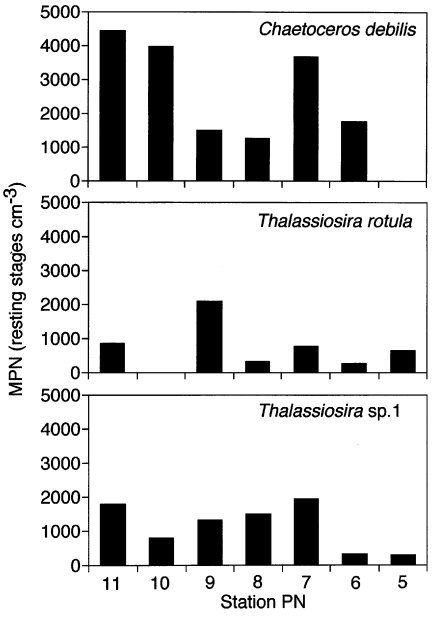

Fig. 6 *Chaetoceros debilis*, *Thalassiosira rotula*, *Thalassiosira* sp. 1. Horizontal distribution of the numbers of viable resting stages in the sediments on the continental shelf along the PN line during the study period

was much higher than is usually observed in other seasons (see Furuya et al. 1996; Hama et al. 1997), indicating that spring bloom occurred on the shelf during this study period. Based on the HPLC analyses and subsequent CHEMTAX interpretation of the pigment data, Furuya et al. (2003) reported that the spring bloom in 1996 in the shelf water of the East China Sea was mostly made up of diatoms.

The present study reveals that diatom resting stages were distributed in the sediment on the shelf (Fig. 6). Since light is essential for their germination (Hollibaugh et al. 1981) and the bottom depths from stations PN-5 to PN-11 are deep (53–128 m), germination of resting stages must follow resuspension. Furuya et al. (1996) reported that, during winter, the water column in the East China Sea was well mixed and the benthic diatom, *P. sulcata*, dominated throughout the water column, proposing that the occurrence of this species near the surface is a good indicator of enhanced vertical mixing. This species was reported to be widely distributed on the shelf sediments of the PN line (Asaoka 1975; Furuya et al. 1996). In the present study, direct microscopic observation of the sediments also revealed that the abundance of *P. sulcata* cells in the sediments ranged from 4.4×10^3 cells cm^{-3} to 3.8×10^4 cells cm^{-3} along the PN line on the shelf (data not shown). Furthermore, uniform distribution of *P. sulcata* was found from the bottom to the surface at station PN-10 (Fig. 5), suggesting that vertical mixing processes were sufficient to resuspend benthic diatoms and any resting stages of planktonic diatoms. In contrast, the water column at other stations on the shelf, west of stations PN-7, started to be weakly stratified (Fig. 2). These hydrographical conditions on the shelf coincide with those generally hypothesized for diatom resting stages to promote blooms, namely resting stages in the sediments are resuspended throughout the water column by vertical mixing and germination of theses cells occur when the mixed layer becomes shallower, potentially resulting in the formation of diatom blooms (see McQuoid and Hobson 1996).

The present study further revealed microscopically that the main component of the diatom community in the shelf water was *C. debilis* (Figs. 4, 5), whose resting stages were also the most abundant in the sediments on the shelf (Fig. 6). *C. debilis* is a species distributed mainly in cooler water (Hasle and Syvertsen 1997). Asaoka (1975) reported the occurrence of the vegetative cells of this species in winter of 1963. Although no data on the diatom community in winter of 1996 is available, this species might occur even at low concentration in the water column. If so, the vegetative cells possibly originated from the resting stages, which could have been resuspended to the surface light field from the bottom sediments after late autumn. However, the hydrographic conditions in winter did not allow the vegetative cells to build a large population because cells would have been mixed below the critical depth. In contrast, stratification in early spring reduced the depth of the mixed layer and kept the germinated cells above the euphotic layer, a more favorable condition for the growth of this species. This is most probably the reason that the diatom bloom led by *C. debilis* occurred in the upper layer of the stratified stations on the shelf during early spring. Thus, this study strongly supports the view proposed by Ishikawa et al. (2001) that diatom resting stages resuspended in winter seed the onset of the spring bloom on the shelf of the East China Sea.

During this study period, concentration of chlorophyll *a* at the surface shallower than 10 m at station PN-8 increased drastically from 2 $\mu g\ l^{-1}$ in the day time (0900 hours) to 9 $\mu g\ l^{-1}$ in the night time (2100 hours) (Furuya et al. 1998). The night community was dominated by *C. debilis*, contributing 95% of the total diatom cells (8.2×10^5 cells l^{-1}) (data not shown). The rapid increase of the biomass, being equivalent to a growth rate of 3.0 day^{-1}, cannot be explained only by the net growth rate (0.54 day^{-1}) which was estimated by the "dilution method" (Landry and Hassett 1982) for this spring phytoplankton community at 0 m at station PN-8 (Furuya et al. 1998). Therefore, increased diatom cell concentration within a short period was probably the result of combined biological growth and advection of cells. Concurrent with the rapid increase in biomass was a decrease of nitrate from 3 μM during the day to 0.1 μM during the night (Furuya et al. 2003), suggesting the possibility that the diatom bloom would decline immediately after this study period. However, the observations of phytoplankton pigments by CZCS and SeaWiFS have shown a prolonged period of high phytoplankton abundance from March through June (Takagi et al. 1993; J. Ishizaka, personal communica-

tion). This may suggest that phytoplankton blooms are repeated in the East China Sea from spring to the early summer.

On the shelf of the East China Sea, typhoon, storm and tidal currents cause intermittent mixing in the water column (Milliman et al. 1985; Tanaka et al. 1987; Tanaka 1992; Iseki et al. 1995). This mixing supplies the sea surface with nutrients from deep waters and resting stages from the sediments. The intermittent mixing enables the resting stages of various species, such as *C. curvisetus*, *C. debilis*, *S. costatum*, *T. rotula, Thalassiosira* sp. 1 and others, to exploit the favorable conditions at the sea surface, light, temperature and photoperiod, for their germination. Since vegetative growth after germination is largely controlled by complex factors, e.g. water temperature, light intensity, nutrient concentrations, competition with other phytoplankton and grazing by zooplankton, vegetative growth can then develop into a bloom not only in spring but also in other seasons if such environmental factors are favorable when the water column is stratified again. The shelf of the East China Sea may also receive allochthonous phytoplankton cells via water from the Kuroshio current (Kawarada et al. 1966, 1968; Guo 1991). Once they are brought in, the stratified waters of the shelf may promote the growth of these allochthonous cells. Phytoplankton growth on the shelf may also be enhanced by introduction of nutrients from Changiang River (Furuya et al. 1998). The effects of the riverine nutrient enrichment, however, are limited to local areas around the estuary. Over the growing season, meteorological and topographical characteristics in the East China Sea lead to complex hydrographic conditions that might prolong the bloom period from spring to early summer. Variations in hydrography may also lead to change in the dominance of autochthonous and allochthonous species in the phytoplankton.

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