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Responses of lower trophic-level organisms to typhoon passage on the outer shelf of the East China Sea: an incubation experiment

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Abstract

Typhoons can induce vertical mixing, upwelling, or both in the water column due to strong wind stress. These events can induce phytoplankton blooms in the oligotrophic ocean after typhoon passage. However, little is known about the responses of lower trophic-level organisms or changes in the community structure following the passage of typhoons, particularly in offshore regions. Therefore, we evaluated community succession on the outer shelf of the East China Sea through on-deck bottle incubation experiments simulating hydrographic conditions after the passage of a typhoon. Under all of the experimental conditions we tested, chlorophyll *a* concentrations increased more than 9-fold within 6 days, and these algal cells were mainly composed of large diatoms (> 10 µm). Ciliates also increased along with the diatom bloom. These results suggest that increases in diatom and ciliate populations may enhance biogenic carbon export in the water column. Typhoons can affect not only phytoplankton productivity, but also the composition of lower trophic-level organisms and biogeochemical processes in oligotrophic offshore regions.

1 Introduction

Tropical cyclones with strong winds represent extreme cases of disturbance impacting hydrographic conditions. Cyclone wind stress induces upwelling and deepening of the surface mixed layer while cooling the sea surface (Price, 1981). Such events caused by wind stress have been known to supply significant nutrients to the surface layer and lead to phytoplankton growth in coastal regions (Eppley and Renger, 1988; Marra et al., 1990). Because of difficulty observing such events, phytoplankton dynamics after tropical cyclone passage have not been evaluated quantitatively or qualitatively. However, recent studies using satellite images have revealed phytoplankton growth induced by tropical cyclones not only in coastal and shelf regions (Hung et al., 2010; Subrahmanyam et al., 2002), but also in offshore regions (Babin et al., 2004; Shibano et al., 2011; Walker et al., 2005). Advances in observation methods have enabled estimates of the contribution of tropical cyclones to regional productivity (e.g. Lin et al., 2012), with some studies showing significant effects (Lin et al., 2003; Siswanto et al., 2009). These satellite studies were based only on chlorophyll *a* concentrations in the surface layer, although ideally we would also evaluate the phytoplankton biomass in the subsurface layer and the community structures of phytoplankton and zooplankton to clarify changes in primary production.

Community structure after cyclone passage has been well studied in coastal regions, defined as regions affected by river discharge and terrestrial materials (Chang et al., 1996; Chen et al., 2009; Chung et al., 2012; McKinnon et al., 2003; Zhou et al., 2011). In coastal waters, the passage of cyclones generates nutrient-rich river runoff (Chang et al., 1996; Chen and Chen, 2006; Chen et al., 2009) and at times, eddies induced by cyclones entrain this river water (Yuan et al., 2004). These events induce floral shifts from small to large phytoplankton-dominated assemblages after cyclone passage (Chen, 2009; Chung et al., 2012; McKinnon et al., 2003). The subsequent decline of the phytoplankton bloom has been suggested to be triggered by depletion of nutrients (Lin et al., 2003) and high grazing pressure from mesozooplankton (Chung et al., 2012). However, there are few studies of the effects of passage of typhoons in offshore regions without riverine or bottom effects, because of the logistical difficulties of in situ observation.

Moreover, few studies have investigated the “seed” population that has the potential to initiate the bloom after cyclone passage. McKinnon et al. (2003) reported that post-cyclone diatom assemblages were dominated by pelagic genera on the continental shelf. This result indicates that resuspension was not a major source of the diatoms to the water column. In offshore regions, most of the seed population would be derived from the water column. Moreover, there may be differences in seed populations between upwelling and vertically mixed waters. The seed population likely originates at subsurface depths in the case of upwelling, while seed populations may be present in both the surface and subsurface layers in the case of vertical mixing. Identifying the origin of the seed population is important for clarifying the mechanisms of the bloom. However, there is no existing information on which populations contribute to blooms induced by typhoon passage in offshore regions.

The outer shelf of the East China Sea is located northwest of the subtropical North Pacific and is along the flow path of the Kuroshio. Because the Kuroshio originates from subtropical and tropical regions, the outer shelf of the East China Sea is an oligotrophic region characterized by year-round limitations in nutrients (nitrate below the detection limit of 0.05 µM in the upper 50 m; Kanda et al., 2003) and low chlorophyll *a* concentrations ($< 0.25\,\mu g\,L^{-1}$ in the upper 100 m in spring and summer; Furuya et al., 2003). Tropical cyclones, known as typhoons, frequently pass through this region (Digital Typhoon, http://agora.ex.nii.ac.jp/digital-typhoon/index.html.en). Siswanto et al. (2008) observed a phytoplankton bloom after typhoon passage in this area. In the present study, we carried out bottle incubation experiments simulating hydrographic conditions (upwelling and vertical mixing) after the passage of a tropical cyclone to evaluate: (1) community succession induced by typhoon passage unaffected by terrestrial materials or riverine discharge and (2) contributions of seed populations to the bloom.

2 Materials and methods

2.1 Sampling and incubation experiments

The incubation experiments were conducted in the East China Sea (29.5° N, 127° E) from 26 September to 2 October 2010 aboard the *R.V. Tansei-Maru*, Japan Agency for Marine-Earth Science and Technology (Fig. 1). Water samples were collected using Niskin bottles attached to a CTD multi-bottle sampler (Sea-Bird Electronics, Inc., USA). The experiment was conducted in 3 sets of duplicate 10 L polycarbonate bottles. To remove contamination by nutrients and trace metals, the bottles were prewashed with HCl. We defined two hydrographic scenarios to represent passage of a tropical cyclone. The first scenario (UP) was upwelling around the typhoon's center, which induces nutrient-rich water to rise, bringing a subsurface seed population to the euphotic zone. The second scenario (MIX) was vertical mixing, which increases the mixed layer depth, causing nutrients and a subsurface seed population to rise into the euphotic zone, mixing with a surface seed population. Bottles of UP were prepared with subsurface water (collected from the bottom of the subsurface chlorophyll maximum (SCM) layer at 110 m where the concentration of chlorophyll *a* was $< 0.02\,\mu\text{g}\,\text{L}^{-1}$). The bottles for MIX were prepared by mixing three layers (10 m + SCM + 200 m) in equal amounts. The third scenario (SN) was surface water (10 m) with added nutrients ($NaNO_3$ and NaH_2PO_3) to evaluate the contributions of seed populations in surface water. The concentrations of nutrients added to the SN bottles were much greater than those under in situ conditions in the study area. However the results of SN were similar to those of MIX; thus, we believe the data are sufficient to determine the origin of the seed population in the water column.

All bottles were covered with black mesh to simulate natural light equivalent to 30 % of surface radiation as would be found at 10–25 m (e.g. Kanda et al., 2003) during summer. The bottles were incubated for 6 days in a temperature-controlled tank at the surface temperature minus 3 °C to simulate the water column after typhoon passage, as described in previous reports (Hung and Gong, 2011; Siswanto et al., 2008). Subsampling for analysis was conducted each day.

2.2 Pigment analysis

Chlorophyll *a* subsampling from the bottles was carried out daily on days 0–6. To evaluate chlorophyll *a* concentrations, seawater (200 mL) was filtered onto a Whatman GF/F filter (~ 0.7 µm pore size) under gentle vacuum (< 100 mm Hg). Size fractionation of chlorophyll *a* samples was conducted on days 0, 3, and 6. Seawater (500 mL) was sequentially filtered with Nuclepore filters (10, 2, and 0.2 µm pore size) to estimate the contributions of picophytoplankton (0.2–2 µm), nanophytoplankton (2–10 µm), and microphytoplankton (> 10 µm) under the same vacuum as for chlorophyll *a* concentrations. The filtered samples were extracted with 6 mL of *N*,*N*-dimethylformamide (DMF) for 24 h at 4 °C (Suzuki and Ishimaru, 1990) and fluorescence was measured using a Turner Designs fluorometer (Welschmeyer, 1994).

Subsampling for HPLC pigment analysis was conducted on days 0, 3, and 6. Seawater samples (2 L) were collected from each bottle and filtered onto Whatman GF/F filters under a gentle vacuum (< 0.013 MPa). The filter samples were folded once, blotted with filter paper, stored under liquid nitrogen, and then deep-frozen (−80 °C) until analysis. In the laboratory, the frozen filter was blotted with filter paper again, broken into small pieces, and soaked in 3 mL DMF containing a known amount of canthaxanthin (Extrasynthase, France) as an internal standard. The samples were then sonicated using a Branson Sonifier Model 250 to break the cell walls. The samples were filtered through 0.45 µm PTFE filters to remove fine particles. All procedures described above were conducted under subdued light to prevent photodegradation of pigments. A mixture of 250 µL each of 28 mM ammonium acetate and the extract was injected into a Shimadzu Class-VP HPLC system incorporating a Zorbax Eclipse XDB-C8 column (4.6 × 150 mm) following the method of Van Heukelem and Thomas (2001), except for a flow rate of 1.1 $\mathrm{mL\,m^{-1}}$.

2.3 Phytoplankton community structure

To quantitatively estimate the community composition of the phytoplankton, the matrix factorization program CHEMTAX developed by Mackey et al. (1996) was used following the method of Latasa (2007) with minor modifications. In CHEMTAX, the initial pigment matrices (Table 1) were constructed as follows: full, double, one-half, and one-third of the matrix of Mackey et al. (1996) for equatorial Pacific populations, and full, double, one-half, and one-third of the matrix of Jeffrey and Wright (1997). Due to variations in pigment compositions, the initial pigment matrices were constructed separately for each treatment as described below. Prasinoxanthin and lutein were excluded from all matrices because lutein was not quantified and the concentration of prasinoxanthin was relatively low. Peridinin and 19′-butanoyloxyfucoxanthin were excluded from the

UP and SN matrices, respectively, because their concentrations were relatively low. In addition, since prasinoxanthin was barely detected but chlorophyll *b* was often found in this study, the term "green algae" (i.e. prasinophytes and chlorophytes) is used in this study. The initial ratios for green algae were the same as for chlorophytes. CHEMTAX was run separately for compositions before and after incubation, because light and nutrient conditions changed during the experiment.

Total chlorophyll *a* concentrations, including chlorophyll *a* and divinyl chlorophyll *a*, were compared to the compositions of flagellates, prymnesiophytes, dinoflagellates, green algae, chrysophytes, *Synechococcus*, *Prochlorococcus*, and diatoms.

2.4 Flow cytometry (FCM)

Seawater (1.5 mL) from each bottle was transferred into cryovials and fixed with paraformaldehyde (0.2 % final concentration) on days 0, 2, 3, 4, 5, and 6. The samples were stored in deep freezers (−80 °C) or under liquid nitrogen until analysis. Heterotrophic bacteria were counted using a PAS-III flow cytometer (Partec, Germany) equipped with a 10 mW 488 nm argon-ion laser with a sample flow rate of $\sim 10\,\mu\text{L}\,\text{s}^{-1}$. Before analysis, each sample was returned to room temperature. Samples were stained with the nucleic acid stain SYBR Green I and incubated at room temperature for 30 min before analysis. Forward light scatter (FSC), side light scatter (SSC), and red fluorescence (630 nm, FL3) were measured and analyzed using FloMax® software (Partec, Germany).

2.5 Microscopic observation

Seawater (500 mL) from each bottle on days 0, 3, and 6 was preserved with acid Lugol's solution (5 % final concentration) for enumeration of microphytoplankton and microzooplankton (> 10 µm). The samples were allowed to settle and concentrate in the dark. Ciliates, heterotrophic dinoflagellates, and crustacean nauplii were counted with an inverted microscope at a magnification of 200 ×. For ciliates, aloricate ciliates and tintinnids were counted separately.

2.6 Nutrient concentrations

Seawater (10 mL) was sampled daily from each bottle on days 0–6 and kept frozen (−20 °C) until analysis. NO_3, PO_4, NH_4, and SiO_2 concentrations were analyzed using an AACS nutrient analyzer (BRAN + LUEBBE, Germany).

3 Results

The sea surface (10 m) temperature and salinity were 28.3 °C and 33.8, respectively. The thermocline, SCM, and bottom of the SCM layer were located at 30, 47, and 110 m in depth, respectively. The temperature and salinity of the SCM and bottom of the SCM layer were 26.5 °C, 18.0 °C, 33.9 and 34.6, respectively. The weather was clear on days 0, 1, 2, 4, 5, and 6 and cloudy on day 3.

3.1 Chlorophyll *a* and nutrient concentrations

Chlorophyll *a* concentrations increased throughout the experiment in all treatments (Fig. 2). The final concentration was 16-fold higher for UP, 22-fold higher for MIX, and 9-fold higher for SN than the initial concentration. Picophytoplankton (∼ 0.2–2 µm) were dominant in all treatments on day 0 (Fig. 2). Picophytoplankton in UP remained at low concentrations of 0.01–0.04 $\mu g\,L^{-1}$ and their relative proportion decreased during incubation. Picophytoplankton had increased in concentration in MIX and SN by day 3, although their relative proportions had decreased. Their concentrations had stabilized by day 6 at 0.30 $\mu g\,L^{-1}$ in MIX and 0.18 $\mu g\,L^{-1}$ in SN.

In all treatments, microphytoplankton and nanophytoplankton became dominant by day 6, accounting for 81–95 % of the chlorophyll *a* concentration. Concentrations of microphytoplankton particularly increased and were dominant on day 6. The final concentrations of microphytoplankton were 83-fold higher in UP, 241-fold higher in MIX, and 52-fold higher in SN than the initial concentrations.

Apparent growth rates of phytoplankton were positive in MIX and SN from day 0 to day 1, suggesting an immediate increase (Fig. 3). The growth rate of phytoplankton was negative from day 0 to day 1 but positive from day 2 to day 3 in UP, suggesting a time lag in growth.

Concentrations of the nutrients NO_3, PO_4, and SiO_2 continuously decreased during incubation (Fig. 4), but were not entirely depleted.

3.2 Phytoplankton pigments determined by HPLC

Chlorophylls and carotenoids detected in this experiment were chlorophyll *a*, divinyl chlorophyll *a*, chlorophyll *b*, chlorophyll $c1+2$ (chlorophyll *c*1 and *c*2 coeluted in our HPLC), chlorophyll *c*3, fucoxanthin, 19′-hexanoyloxyfucoxanthin, 19′-butanoyloxyfucoxanthin, peridinin, diadinoxanthin, zeaxanthin, and β,β-carotene. Trace amounts of violaxanthin, alloxanthin, and neoxanthin were detected on day 3 and day 6 in MIX and SN.

Fucoxanthin, which is a biomarker for diatoms, prymnesiophytes, and chrysophytes in oceanic waters (Ondrusek et al., 1991), was the dominant accessory pigment on days 3 and 6 (Fig. 5). Its final concentration was 87-fold higher in UP, 167-fold higher in MIX, and 90-fold higher in SN than the initial concentration. The concentrations of peridinin, 19′-butanoyloxyfucoxanthin, and 19′-hexanoyloxyfucoxanthin, which are mainly derived from dinoflagellates (Johansen et al., 1974), chrysophytes (referred to as pelagophytes in Andersen et al., 1993), and prymnesiophytes (Jeffrey and Wright, 1994), respectively, slightly increased in all treatments during the experiment. On the other hand, zeaxanthin and divinyl chlorophyll *a* concentrations, which derive mainly from prokaryotic cyanobacteria (Jeffrey and Wright, 1997; Latasa and Bidigare, 1998), had increased by day 3 and decreased by day 6 in MIX and SN. The chlorophyll *b* concentration, which is a biomarker for green algae (prasinophytes and chlorophytes; Jeffrey, 1974), increased gradually and became the second-most abundant carotenoid by day 6 in all treatments. However, neither prasinoxanthin nor violaxanthin were detected in UP and were detected only at trace levels in SN and MIX on day 3 and day 6. This may be related to the presence of green algae, which does not contain prasinoxanthin (Ricketts, 1970) or violaxanthin (Mackey et al., 1996).

3.3 Phytoplankton community structure

Phytoplankton community structure markedly changed in all treatments. Chrysophytes were dominant in UP (83.5 %) and green algae in MIX (43.9 %) and SN (37.7 %) at day 0. In contrast, the ratio of diatoms to chlorophyll had increased to 91.2 %, 80.0 %, and 73.0 % in UP, MIX, and SN, respectively, by day 6 (Fig. 6). These results indicate that diatoms bloomed in all treatments. The proportions of *Prochlorococcus* and *Synechococcus* in MIX and SN were relatively high and stable by day 3, but had declined substantially by day 6. *Prochlorococcus*, which was initially subdominant in UP (11.0 %), was not detected on day 3, but was detected at trace levels on day 6. The proportions of dinoflagellates and prymnesiophytes were fairly stable through the experiment.

The concentrations of diatoms increased linearly with total chlorophyll *a* concentrations of microphytoplankton (i.e. chlorophyll *a* concentrations in the $> 10\,\mu$m fraction) measured by the fluorometric method (Fig. 7).

The microscope observations indicated that the pennate diatom *Pseudo-nitzchia* spp. was the dominant diatom in all treatments. In addition to *Pseudo-nitzchia* spp., *Cylindrotheca closterium* and *Nitzschia* sp., as well as the centric diatoms *Chaetoceros* spp. and *Skeletonema* spp., became more abundant during the high-chlorophyll period.

3.4 Microbial abundance and microzooplankton community structure

Ciliates (tintinnids and aloricate ciliates) substantially increased in MIX and SN (Fig. 8). Tintinnids and aloricate ciliates in MIX increased from 61.0 to 2450 cells L^{-1}, and from

133 to 3010 cells L^{-1}, respectively. Tintinnids and aloricate ciliates in SN also increased from 48.0 to 660 cells L^{-1} and from 204 to 794 cells L^{-1} during the experiment, respectively. In contrast, heterotrophic dinoflagellates and crustacean nauplii had low abundances throughout the experiment. Microzooplankton in UP had very low abundances throughout the incubation as follows: nauplii, 4 ± 5 ind L^{-1}; dinoflagellates, 1±1 cells L^{-1}; tintinnids, 6 ± 5 cells L^{-1}, and aloricate ciliates, 7 ± 1 cells L^{-1}.

Heterotrophic bacteria initially gradually increased, but ultimately became constant or decreased in all treatments, although there was no apparent increase in SN due to the changes in chlorophyll *a* (Figs. 2 and 9). The maximum densities of heterotrophic bacteria were 4.3, 2.4, and 1.7 times the initial densities in UP, MIX, and SN, respectively.

4 Discussion

4.1 Typhoon-induced floral shift

The goal of this study was to clarify community succession after typhoon passage on the outer shelf of the East China Sea. We experimentally tested two processes of bloom formation under provable hydrographic conditions after passage of a typhoon. One process was an upwelling event (UP), which increases light availability to phytoplankton in the subsurface layer. The other process was vertical mixing (MIX), which increases nutrient availability to surface phytoplankton and increases light availability to subsurface phytoplankton. The effect of typhoon passage to lower trophic level organisms is expected to depend on the strength of the typhoon, the size of the eye of the typhoon, local hydrographic conditions, and existing community structures. Therefore, our experiment could not replicate all typhoon conditions, but nevertheless approximated a relatively strong typhoon passage in the East China Sea.

The sea surface (10 m) temperature and salinity were 28.3 °C and 33.8, respectively. According to Siswanto et al. (2008), temperature and salinity derived from the Argo float in the East China Sea near our study site were 28.00 °C and 34.08 on 20 September and 28.08 °C and 34.00 on 24 September, respectively. According to Chen et al. (1993), who summarized the typical hydrography of the Kuroshio current in the southern East China Sea, typical temperatures and salinities in the surface water are 24.5–29.0 °C and 34.3–34.7, respectively. The concentration of NO_3 at the sea surface was 0.06 µM in this study. Kanda et al. (2003) reported an NO_3 concentration < 0.05 µM in the upper 50 m. The sea surface chlorophyll *a* concentration was 0.08 $\mu g\,L^{-1}$ in this study, and Furuya et al. (2003) reported a chlorophyll *a* concentration of $< 0.25\,\mu g\,L^{-1}$ in the upper 100 m in spring and summer. These results indicate that our study was conducted in a relatively low salinity and high nutrient, but not high productivity, period in the East China Sea.

Both UP and MIX resulted in significant increases in the chlorophyll *a* concentration. Before incubation, the mean chlorophyll *a* concentrations were 0.02 $\mu g\,L^{-1}$ in UP and 0.08 $\mu g\,L^{-1}$ in MIX. After incubation, the chlorophyll *a* concentrations increased to 0.40 $\mu g\,L^{-1}$ in UP and 1.74 $\mu g\,L^{-1}$ in MIX (Fig. 2). These results strongly suggest that changes in the irradiation and nutrient environment produced significant phytoplankton increases.

The phytoplankton community structure also changed during the bloom in each treatment. At day 0, chrysophytes in UP and cyanobacteria, *Synechococcus*, and *Prochlorococcus* in MIX were dominant among the chlorophyll biomass (Fig. 6). The most prominent change was the increase in large diatoms by day 6, although there were other minor changes early in the experiment (Figs. 6, 7). The dominant taxonomic group in the upper 100 m layer in summer on the outer shelf of the East China Sea is small phytoplankton (< 2 µm), such as *Synechococcus* (cyanobacteria) and *Prochlorococcus* (Furuya et al., 2003). These organisms have an advantage in low-nutrient areas because of their relatively large surface areas. However, addition of nutrients or subsurface seawater improved nutrient availability, providing a favorable environment for large phytoplankton to grow in MIX and SN. In particular, diatoms are known as opportunistic phytoplankton and can quickly dominate with an improvement in environmental conditions (Benitez-Nelson et al., 2007; Smetacek et al., 2012; Tsuda et al., 2003). Similar to previous studies, this study demonstrated the high growth rates of diatoms (Figs. 6, 7).

In addition to rapid growth by diatoms, grazing control on picophytoplankton (< 2 µm) may have been important in MIX and SN. Chlorophyll concentrations of picophytoplankton were dominant initially, but their relative percentages decreased in MIX and SN (Fig. 2). In addition, both *Synechococcus* and *Prochlorococcus* increased until day 3 in MIX and SN, then decreased to their initial abundances from day 3 to day 6 even though the nutrients were not depleted (Figs. 4, 5). These results suggest that increases in picophytoplankton abundance were initially induced by changes in nutrient conditions, but these small phytoplankton were then grazed down by feeding pressure from picoplankton feeders such as heterotrophic nanoflagellates and ciliates during incubation. In this experiment, neither the production nor grazing rates of phytoplankton were measured, but ciliates known to be pico- (Rassoulzadegan et al., 1988) and nanoplankton (Gifford, 1985; Verity, 1985) feeders significantly increased with decreases in pico- and nanoplankton during incubation.

4.2 Trophic upgrading with typhoon passage

The abundance of ciliates (aloricate ciliates and tintinnids) increased in MIX and SN, reaching a maximum of 2460 cells L^{-1} in MIX and 1450 cells L^{-1} in SN on day 6, by which time picophytoplankton and bacteria had decreased (Figs. 2, 8, 9). These results indicate that the growth of ciliates in the surface layer was induced by grazing of increased phytoplankton and bacteria. Protozoa such as ciliates can ingest small phytoplankton and bacteria that mesozooplankton cannot directly feed on due to their small size. Therefore, protozoa serve as a link between microbial food webs and mesozooplankton, producing an increase in the food quality known as “trophic upgrading” (Breteler et al., 1999).

In addition, the phytoplankton bloom induced by typhoon passage was mainly composed of large diatoms in both the surface and subsurface layers. These results suggest that typhoons induce an increase in food supply to higher trophic-level organisms (e.g. copepods). This change may enhance export flux by enhancing fecal pellet production and vertical migration (Wassmann et al., 1997). In addition, the typhoon-induced bloom was mainly composed of large diatoms in this study. Large diatom blooms play an important role in export production due to the high rate of sinking induced by their size and the ballast effect (Armstrong et al., 2001). Chung et al. (2012) reported that a diatom bloom induced by a typhoon was terminated within 24 h about a week after typhoon passage over a shelf break in the southern East China Sea near Taiwan, because of a concurrent increase in copepods. In addition, some studies of nearshore blooms have reported a sudden decrease in phytoplankton (e.g. Chang et al., 1996). In contrast, blooms induced by typhoons may remain for as long as a month offshore in the Northwest Pacific (Toratani, 2008) and in the middle of the South China Sea (Sun et al., 2010). Moreover, chlorophyll concentrations gradually decreased over a month in one report (Toratani, 2008). One possible explanation for these differences is the abundance of grazers that can ingest large plankton such as diatoms. Lee et al. (2009) reported that copepod abundances are higher in continental shelf waters and lower in outer shelf waters.

4.3 Origin of the seed population

Seed populations with the potential to seed the bloom after typhoon passage were present in both the subsurface and surface layers. However, the chlorophyll *a*-specific apparent growth rate was negative from day 0 to day 1 in UP, while its growth rate in MIX and SN was positive (Fig. 3). These results suggest that there are physiological differences between seed populations in the subsurface and surface layers. These differences may be related to the need for photoadaptation to higher light conditions in UP and/or physiological states such as resting cells and resting spores (Hargraves and French, 1983), which require a certain period before growth can begin. The surface seed population may have an advantage in immediately responding to enrichment in nutrients under high light conditions, leading to rapid growth. Satellite images have revealed that blooms induced by hurricanes or typhoons are observed 3–4 days after typhoon passage in offshore regions (Babin et al., 2004; Siswanto et al., 2008). Therefore, the surface seed population likely is the main contributor to bloom formation.

The dominant diatoms in the present study were very different from those reported at the outer shelf and the shelf break of the East China Sea in spring near the study area (Ishikawa and Furuya, 2004). Ishikawa and Furuya (2004) reported that the dominant species (relative abundance > 10 % of the total) were *Hemiaulus sinensis* and *Nitzschia longissima* at 10 m and *Thalassiosira* sp., *Chaetoceros curvisetus*, *Chaetoceros* sp., and *Nitzschia longissima* at 40 m on the outer shelf. In this study, the most abundant species was *Pseudo-nitzschia* sp. in all treatments. This result suggests that the seed population responding to a typhoon is different from the normally dominant species of diatoms. The seed population responding to a typhoon may be able to grow rapidly and adapt to unpredictable changes in hydrographic conditions, including higher nutrient and light availability and lower temperatures.

5 Conclusions

Under all experimental conditions simulating hydrographic conditions after typhoon passage, chlorophyll *a* concentrations increased several tens of times. The seed population of the bloom appeared to be mainly derived from the surface layer. Increased algal cells were mainly composed of large diatoms, not the small phytoplankton dominant under normal conditions. This shift may enhance export production due to a high sinking rate according to Stokes' law and mineral ballast effects (Armstrong et al., 2001). Moreover, this study demonstrated that ciliate microzooplankton also increased during incubation and may contribute to trophic upgrading of food quality. These results suggest that typhoons can affect not only phytoplankton productivity, but also higher trophic-level organisms and export production. Therefore, the passage of a typhoon could have a significant influence on the biogeochemical cycle, even in offshore regions. Some studies have suggested that the intensity and frequency of tropical cyclones will likely increase with global warming (Elsner et al., 2008; Emanuel, 2005). Thus, we should continue to evaluate the effects of tropical cyclones on the biogeochemical cycle.

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Table 1. Initial and final accessory pigment to chlorophyll *a* ratios for major phytoplankton groups in the CHEMTX analysis during the incubation experiments simulating hydrographic conditions after typhoon passage.

Seed Matrix/ group	Peri	19′-BF	Fucox	19′-HF	Diadino	Zeax	Chl *b*	DV Chl *a*	Chl *a*
UP									
Initial ratio									
Prymnesiophytes				2.051	0.061	–	–	–	1
Green algae						0.071	2.382	–	1
Chrysophytes		0.396	0.153	–	0.004	–	–	–	1
Synechococcus						0.380	–	–	1
Prochlorococcus						0.044	–	1	–
Diatoms			0.526	–	0.028	–	–	–	1
Final ratios for samples before incubation									
Prymnesiophytes				1.775	0.001	–	–	–	1
Green algae						0.065	2.128	–	1
Chrysophytes		0.370	0.163	–	0.00				1
Synechococcus						0.376	–	–	1
Prochlorococcus						0.00		1	–
Diatoms			0.537	–	0.005	–	–	–	1
Final ratios for samples after incubation									
Prymnesiophytes				1.389	0.066	–	–	–	1
Green algae						0.070	2.552	–	1
Chrysophytes		0.479	0.184	–	0.00				1
Synechococcus						0.088	–	–	1
Prochlorococcus						0.044	–	1	–
Diatoms			0.532	–	0.034	–	–	–	1
MIX									
Initial ratio									
Prymnesiophytes				2.547	0.016	–	–	–	1
Dinoflagellates	1.203	–	–	–	0.249	–	–	–	1
Green algae						0.026	0.696	–	1
Chrysophytes		0.596	0.478	–	0.004	–	–	–	1
Synechococcus						0.485	–	–	1
Prochlorococcus						0.292	–	1	–
Diatoms			0.599	–	0.050	–	–	–	1
Final ratios for samples before incubation									
Prymnesiophytes				2.606	0.00				1
Dinoflagellates	1.275	–	–	–	0.002	–	–	–	1
Green algae						0.023	0.486	–	1

Experimental groups: upwelling (UP), vertical mixing (MIX), surface water with additional nutrients (SN).
19′-BF, 19′-butanoyloxyfucoxanthin; 19′-HF, 19′-hexanoyloxyfucoxanthin; Chl *a*, chlorophyll *a*; Chl *b*, chlorophyll *b*; Diadino, diadinoxanthin; DVChl *a*, divinyl chlorophyll *a*; Fucox, fucoxanthin; Peri, peridinin; Zeax, zeaxanthin.

Table 1. Continued.

Seed Matrix/ group	Peri	19′-BF	Fucox	19′-HF	Diadino	Zeax	Chl *b*	DV Chl *a*	Chl *a*
Chrysophytes		0.561	0.460	–	0.00				1
Synechococcus						0.483	–	–	1
Prochlorococcus						0.292	–	1	–
Diatoms			0.566	–	0.008	–	–	–	1
Final ratios for samples after incubation									
Prymnesiophytes				2.547	0.016	–	–	–	1
Dinoflagellates	1.435	–	–	–	0.014	–	–	–	1
Green algae						0.024	0.348	–	1
Chrysophytes		0.292	0.535	–	0.004	–	–	–	1
Synechococcus						0.495	–	–	1
Prochlorococcus						0.292	–	1	–
Diatoms			0.623	–	0.051	–	–	–	1
SN									
Initial ratio									
Prymnesiophytes				1.353	0.022	–	–	–	1
Dinoflagellates	0.862	–	–	–	0.191	–	–	–	1
Green algae						0.017	0.503	–	1
Synechococcus						1.016	–	–	1
Prochlorococcus						0.268	–	1	–
Diatoms			0.666	–	0.043	–	–	–	1
Final ratios for samples before incubation									
Prymnesiophytes				1.355	–	–	–	–	1
Dinoflagellates	1.124	–	–	–	0.001	–	–	–	1
Green algae						0.015	0.296	–	1
Synechococcus						1.012	–	–	1
Prochlorococcus						0.245	–	1	–
Diatoms									1
Final ratios for samples after incubation									
Prymnesiophytes				0.665	0.172	–	–	–	1
Dinoflagellates	0.683	–	–	–	0.022	–	–	–	1
Green algae						0.030	0.904	–	1
Synechococcus					0.00	2.200	–	–	1
Prochlorococcus					0.00	0.255	–	1	–
Diatoms			0.546	–	0.017	–	–	–	1

Experimental groups: upwelling (UP), vertical mixing (MIX), surface water with additional nutrients (SN).
19′-BF, 19′-butanoyloxyfucoxanthin; 19′-HF, 19′-hexanoyloxyfucoxanthin; Chl *a*, chlorophyll *a*; Chl *b*, chlorophyll *b*; Diadino, diadinoxanthin; DVChl *a*, divinyl chlorophyll *a*; Fucox, fucoxanthin; Peri, peridinin; Zeax, zeaxanthin.

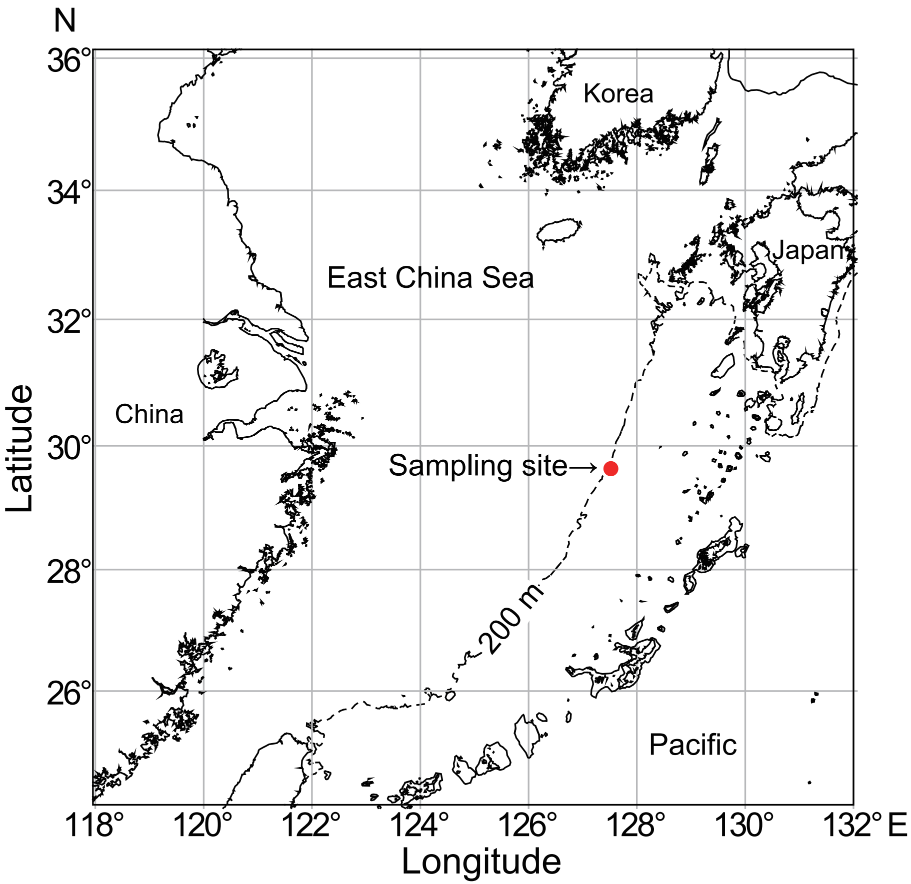

Fig. 1. Sampling location on the outer shelf of the East China Sea. The broken line shows the continental shelf (200 m depth) in the East China Sea.

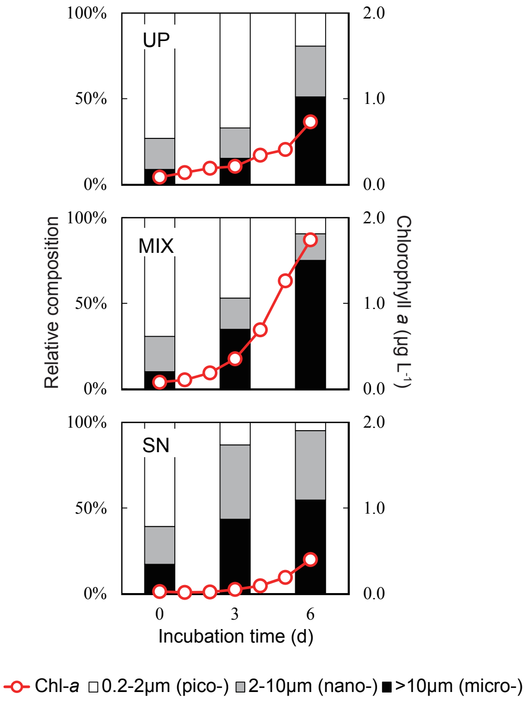

Fig. 2. Temporal variations in the concentrations of chlorophyll *a* and the relative compositions of size-fractionated chlorophyll *a* in the incubation experiments simulating hydrographic conditions after typhoon passage: upwelling (UP), vertical mixing (MIX), and surface water with additional nutrients (SN).

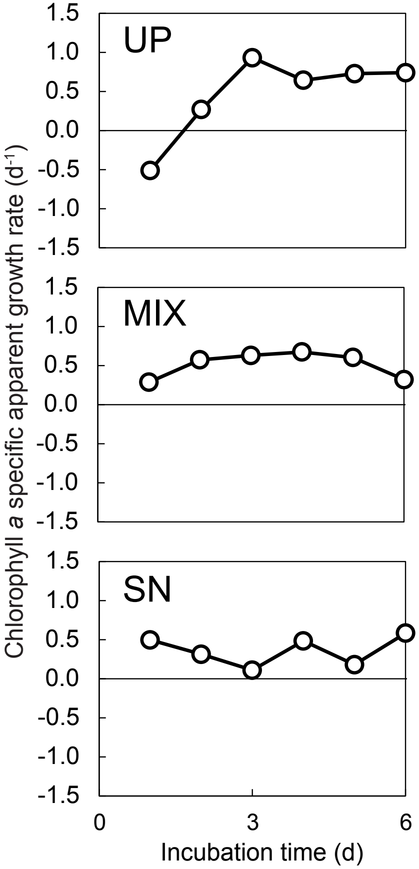

Fig. 3. Temporal variations in the chlorophyll *a*-specific apparent growth rate in the incubation experiments simulating hydrographic conditions after typhoon passage: upwelling (UP), vertical mixing (MIX), and surface water with additional nutrients (SN).

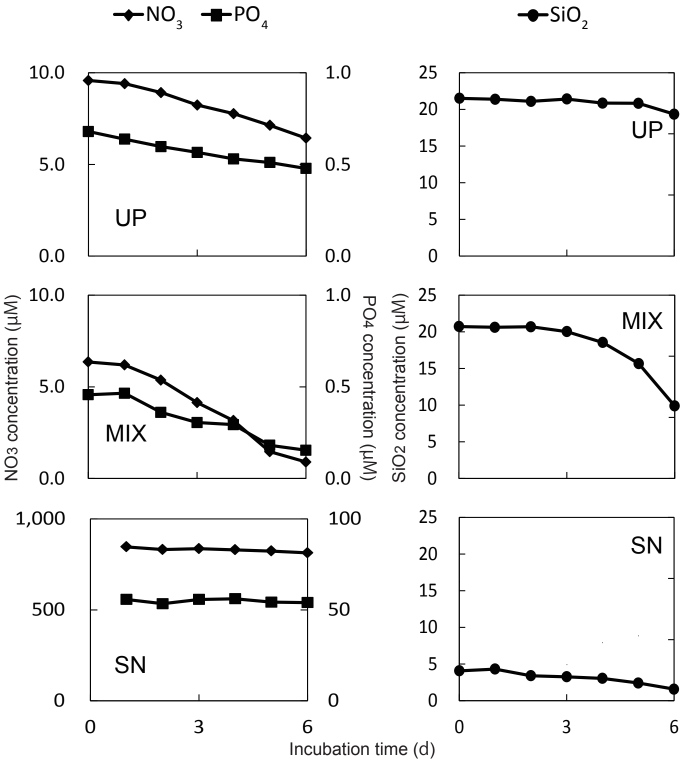

Fig. 4. Nutrient concentrations in the incubation experiments simulating hydrographic conditions after typhoon passage: upwelling (UP), vertical mixing (MIX), and surface water with additional nutrients (SN). All data are averages of duplicate bottles. Nitrate and phosphate were added to the SN bottles on day 0.

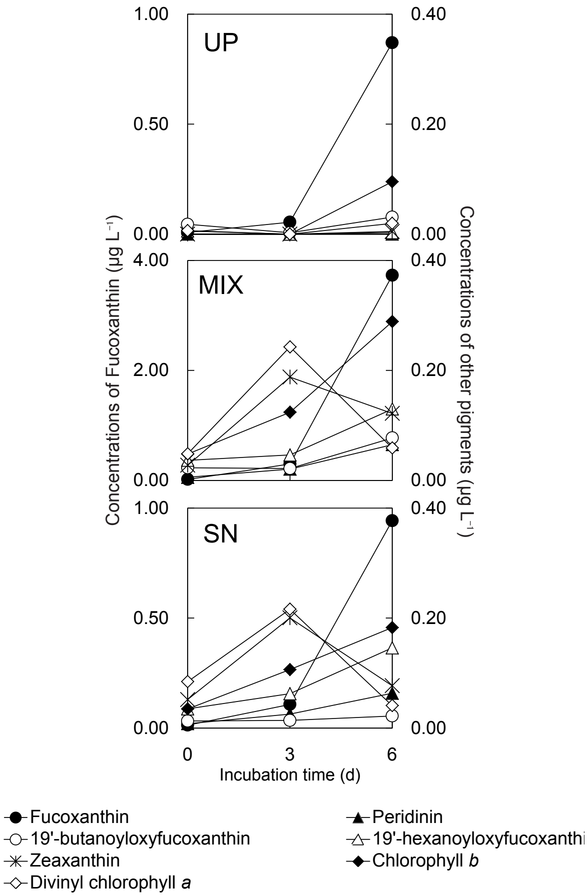

Fig. 5. Temporal variations in accessory pigment concentrations in the incubation experiments simulating hydrographic conditions after typhoon passage: upwelling (UP), vertical mixing (MIX), and surface water with additional nutrients (SN).

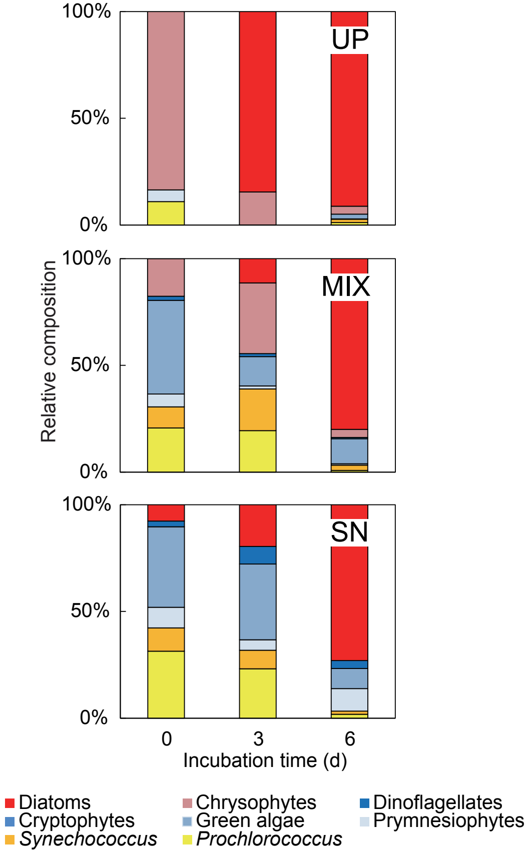

Fig. 6. Temporal variations in the relative contributions of phytoplankton groups to chlorophyll *a* concentrations in the incubation experiments simulating hydrographic conditions after typhoon passage: upwelling (UP), vertical mixing (MIX), and surface water with additional nutrients (SN).

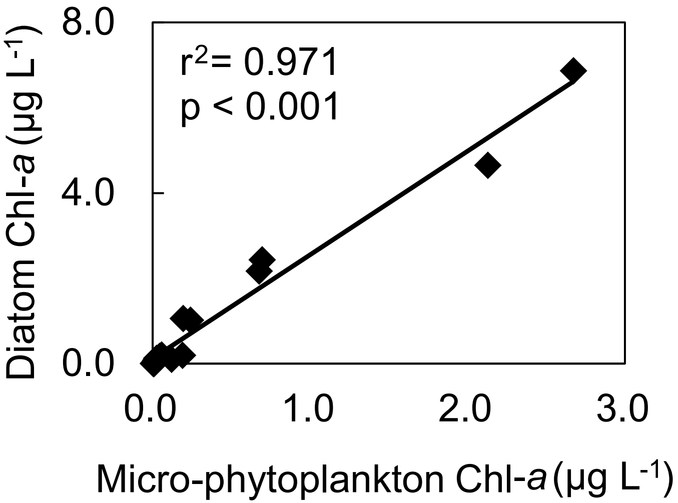

Fig. 7. Relationship between the chlorophyll *a* concentration in microphytoplankton estimated by size fraction and the chlorophyll *a* concentration in diatoms determined by HPLC in the incubation experiments simulating hydrographic conditions. All data were used in the correlation. r^2, coefficient of determination; p, p value.

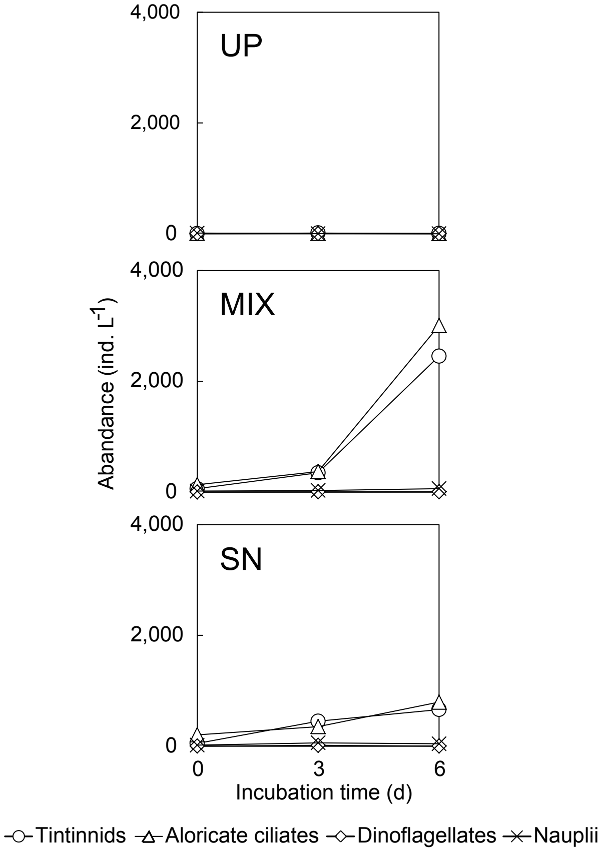

Fig. 8. Temporal variations in microzooplankton (tintinnids, aloricate ciliates, dinoflagellates, nauplii) abundance in the incubation experiments simulating hydrographic conditions after typhoon passage: upwelling (UP), vertical mixing (MIX), surface water with additional nutrients (SN).

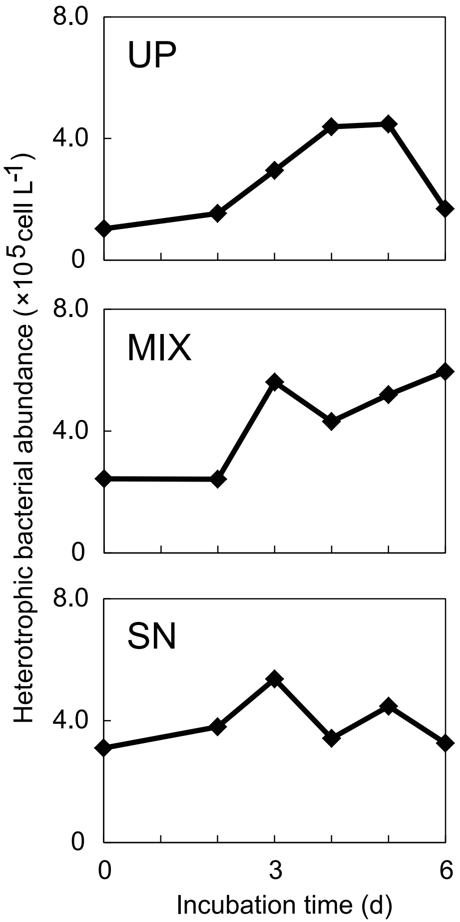

Fig. 9. Temporal variations in heterotrophic bacterial abundance in the incubation experiments simulating hydrographic condition after typhoon passage: upwelling (UP), vertical mixing (MIX), surface water with additional nutrients (SN).