



Effects of Typhoon Kaemi on coastal phytoplankton assemblages in the South China Sea, with special reference to the effects of solar UV radiation

Gang Li,^{1,2} Yaping Wu,¹ and Kunshan Gao¹

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[1] In order to see how physical and chemical changes in coastal environment caused by tropical cyclones would affect primary productivity of phytoplankton, we investigated the photosynthetic carbon fixation, the chlorophyll *a* concentration, and the species composition of phytoplankton assemblages in the surface coastal waters of the South China Sea, during 18 July to 7 August 2006, before and after Typhoon Kaemi's landing (on 25 July, 122 km away from the experimental site). Chlorophyll *a* concentration started to decrease from $12.3 \mu\text{g L}^{-1}$ 30 h before to $1.5 \mu\text{g L}^{-1}$ 40 h after its landing, reducing the capacity of photosynthetic carbon fixation in the seawater to one eighth. Prior to the typhoon's arrival, microplankton ($>20 \mu\text{m}$) accounted for 50% of the total chl *a*, being mainly dominated by the diatom *Thalassiosira* sp.; during the period 30 h before and 6 days after the typhoon, however, pico-nanoplankton ($<20 \mu\text{m}$) comprised 98% of the total chl *a*. By 2 weeks after the typhoon, microcells ($>20 \mu\text{m}$) dominated the species again, and occupied 60% of the total chl *a*, with the diatom *Nitzschia* sp. being the dominant group. Since the typhoon induced changes in taxonomic structure and environmental factors, the apparent photosynthetic efficiency (α) of phytoplankton assemblages was markedly enhanced after the typhoon, while both the light-saturating point (E_k) and noontime photosynthetic rates were significantly reduced. Solar ultraviolet radiation (UVR, $>55 \text{ W m}^{-2}$) significantly inhibited the photosynthetic carbon fixation by 17% and 28% before and after the typhoon, respectively, reflecting a higher UVR sensitivity of the posttyphoon phytoplankton assemblages.

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1. Introduction

[2] Typhoons or tropical cyclones often cause devastating influences on human properties and coastal facilities [Huigen and Jens, 2006]. They also trigger a lot of environmental changes in pelagic as well as coastal waters, such as surface seawater temperature (SST), salinity (SSS), pH, concentration of nutrients, mixing dynamics and light penetration in the water column [Frenette *et al.*, 1996; Shiah *et al.*, 2000; Babin *et al.*, 2004; Son *et al.*, 2006; Shi and Wang, 2007; Fujii and Yamanaka, 2008]. Such physical and chemical changes associated with the passage of a typhoon can exert temporal influences on biological production in aquatic ecosystems [Lin *et al.*, 2003; Babin *et al.*, 2004; Shi and Wang, 2007; Zheng and Tang, 2007; Fujii and Yamanaka, 2008]. Remote sensing studies revealed that Typhoon Kai-Tak in 2000 triggered a thirtyfold increase in

surface chlorophyll *a* concentration over the South China Sea [Lin *et al.*, 2003]. Phosphorus limitation could be compensated for and size fraction was altered for the phytoplankton species in Biwa Lake by typhoons 9313 and 9314 in 1993 [Frenette *et al.*, 1996; Robarts *et al.*, 1998]. *Synechococcus* abundance and total chlorophyll *a* concentration were raised after a typhoon in subtropical coastal waters [Chang *et al.*, 1996]. The runoffs associated with rainfall during typhoons and resuspension of particles or up-mixed benthic cells affect the attenuations of visible and ultraviolet radiation (UVR, 280–400 nm) through the water column and thus lead to changes of solar radiation in terms of both quality (wavelength ratio) and quantity to which phytoplankton cells are exposed [Frenette *et al.*, 1996]. Cells stirred up from deeper water layers during typhoons maybe physiologically sensitive to high photosynthetically active radiation (PAR, 400–700 nm) as well as UVR at surface. However, little has been documented on in situ photophysiological features of phytoplankton after a typhoon. Although nutrients redepletion after Typhoon Kai-Tak was considered to be responsible for the disappearance of the phytoplankton bloom [Lin *et al.*, 2003], UVR-related damages on phytoplankton cells after the typhoon might also be accountable. Therefore, it is of general interest

¹State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen, China.

²Key Laboratory of Marine Bio-resources Sustainable Utilization, South China Sea Institute of Oceanology, Guangzhou, China.

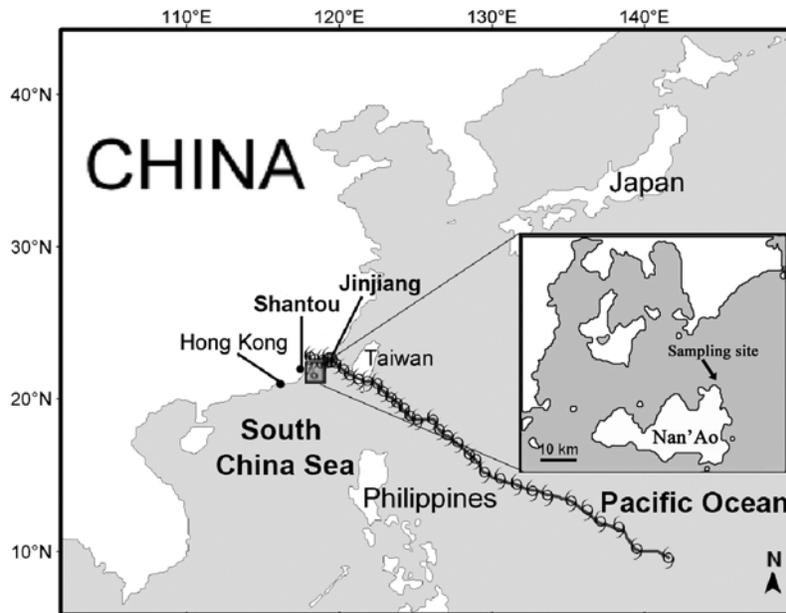


Figure 1. Map of the South China Sea, showing the path (19–26 July 2006; days 199–206) of the typhoon Kaemi and the location of Nan'ao Island where experiments were carried out from 18 July to 7 August (days 198–218).

to see how sensitive phytoplankton is to solar UVR before and after the tropical typhoons.

[3] Phytoplankton cells within the euphotic zone (down to 1% surface visible radiation) utilize PAR for carbon fixation; in this layer, they also tolerate harmful UVR that can penetrate to considerable depths [Hargreaves, 2003]. Solar UVR can reduce photosynthetic rates [Neale *et al.*, 1998; Litchman and Neale, 2005], and harm cellular components such as D1 proteins [Sass *et al.*, 1997] and DNA molecules [Helbling *et al.*, 2001; Buma *et al.*, 2003]. It can also decrease the growth [Litchman and Neale, 2005], alter cyanobacterial morphology [Wu *et al.*, 2005], and even lead to cell death [Llabrés and Agustí, 2006]. On the other hand, UVR has also been found to have positive effects on phytoplankton, so that ultraviolet A (UV-A, 315–400 nm) can be used to photorepair ultraviolet B (UVB, 280–315 nm) damaged DNA [Karentz *et al.*, 1991; Buma *et al.*, 2003] and to enhance the photosynthetic carbon fixation under conditions of fast mixing [Barbieri *et al.*, 2002; Helbling *et al.*, 2003] or low levels of solar radiation [Gao *et al.*, 2007a]. UVA is capable of driving photosynthesis either in phytoplankton or macroalgal species in the absence of PAR [Halldal, 1967; Gao *et al.*, 2007b]. Physical and chemical changes associated with typhoons, as mentioned above, may alter the responses of phytoplankton to solar PAR and UVR.

[4] In the South China Sea (SCS), typhoons occur annually at a mean frequency of 14 per year. Typhoon-induced changes in biomass density of primary producers as well as hydrographical features have been studied in its pelagic areas using remote sensing techniques in SCS [Lin *et al.*, 2003; Zheng and Tang, 2007]; however, little is known about the typhoon-induced changes in phytoplankton taxonomic structure and physiological responses to the environmental changes induced by typhoons. Although it is impossible to launch the investigations in pelagic areas

immediately before or after it due to the great dangers involved, it is possible and of significance to investigate how the physical and chemical changes caused by typhoons affect primary production in coastal waters, where sea farming of economic animals and seaweeds are actively performed. This study provides new information about the solar UVR effects on natural phytoplankton assemblages from SCS, where only a few field photobiological studies have been done [Helbling *et al.*, 2003; Gao *et al.*, 2007a, 2007b].

[5] Here we show that Typhoon Kaemi affected the species composition, total chl *a* concentration, photosynthetic carbon fixation and responses to solar UVR of phytoplankton assemblages from the coastal waters of the SCS.

2. Materials and Methods

2.1. Study Area and Sampling Protocol

[6] Surface seawater with phytoplankton assemblages was taken from a coastal area (10 m deep, 500 m off the coast) of Nan'ao Island (23°24'N, 117°07'E) in the SCS (Figure 1) prior to and following Typhoon Kaemi during the period of 18 July to 7 August 2006 (days 198–218). Water samples were collected at 10 cm depth every morning at 0900 (also on the day of Kaemi's landing on 25 July) with an acid-cleaned (1 N HCl) polycarbonate carboy immediately after the measurements of vertical profiles of temperature and salinity. The collected seawater samples were used within 15 min for determination of photosynthetic carbon fixation and related analyses as described below.

2.2. Measurement of Solar Radiation and Other Environmental Factors

[7] Incident solar radiation was continuously monitored with a broadband filter radiometer (ELDONET, Real Time

Computers Inc., Germany) installed on the roof of the Marine Biological Station (23°24'N, 117°07'E) of Shantou University. This instrument measures every second the solar irradiance in three wave bands: UVB (280–315 nm), UVA (315–400 nm), and PAR (400–700 nm), and records the mean for each minute [Häder *et al.*, 1999]. The reliability of this device has been certificated with the correspondence error less than 0.5% in comparison with the most accurate instrument (certificate No. 2006/BB14/1). The instrument has been calibrated regularly with assistance from the manufacture.

[8] Ahead the sampling proceeded, profiles of salinity and temperature in the water column of the study area were measured at 20 cm intervals with a SONDE (YSI 600XL, Yellow Springs Instruments, USA), and the pH values of the surface seawater were measured using an Oakton[®] pH meter.

2.3. Experimentation

[9] For determination of photosynthetic carbon fixation rates, water samples were prefiltered through 180 μm pore mesh and then dispensed into 30 ml quartz tubes and inoculated with $\text{NaH}^{14}\text{CO}_3$ solution (see below). To determine the effects of UVR, two radiation treatments (triplicates for each) were implemented: (1) samples receiving PAR + UVR (PAB, 280–700 nm, unwrapped quartz tubes); and (2) samples receiving only PAR (P, 400–700 nm), tubes wrapped with Ultraphan UV Opak DigeFra film (50% transmission at 395 nm), the transmission spectra of which was published elsewhere [Sobrino *et al.*, 2004]. Additionally, three tubes with seawater were wrapped in aluminum foil and incubated as the control. The tubes containing the samples were incubated for 3 h (1030–1330 local time) beneath the surface (2 cm) of running surface seawater within a water bath for the control of temperature (25–29°C) similar to the SST. A total of 13 experiments were conducted to determine the UVR impacts on phytoplankton photosynthetic rate during the study period.

[10] To determine the UVR-related effects on photosynthesis versus irradiance (P versus E) parameters, different levels (i.e., from 100 to <2%) of incident solar irradiance (with or without UVR) were obtained by covering the quartz tubes with none to 6 layers of neutral density screen. Three P versus E curves were obtained at days 204 (pretyphoon), 210 and 211 (posttyphoon), respectively.

2.4. Determination of Photosynthetic Carbon Fixation

[11] Prefiltered (pore size, 180 μm) water samples (30 ml each) were inoculated with 100 μl of 5 μCi (0.185 MBq) $\text{NaH}^{14}\text{CO}_3$ solution (ICN Radiochemicals, USA), and incubated under the conditions mentioned above. After incubation, the sample was filtered onto a Whatman GF/F glass fiber filter (25 mm), and the filter was placed in a 20 ml scintillation vial that was exposed to HCl fumes overnight and dried (55°C, 6 h) to expel the inorganic carbon as CO_2 . Then, 3 ml scintillation cocktail (Perkin Elmer[®]) was added to each vial and the incorporated ^{14}C was measured using a liquid scintillation counter (LS 6500 Beckman Coulter, USA). The rate of photosynthetic carbon fixation was determined according to Holm-Hansen and Helbling [1995].

2.5. Determination of Chlorophyll a and Species Analysis

[12] At the beginning of each experiment, chlorophyll a (chl a) concentration was measured by filtering 2–3 L of prefiltered surface seawater onto a Whatman GF/F glass fiber filter (47 mm), extracting with 10 ml absolute methanol for 3 h at room temperature (28–30°C) under dark condition, and determining the optical density with a scanning spectrophotometer (UV 2501-PC, Shimadzu, Japan). Chl a concentration was estimated according to Porra [2002]. To determine the pico-nanoplankton fraction, a subsample was prefiltered through a Nitex[®] mesh (20 μm), and the chl a concentration was determined as described above.

[13] For species analysis, phytoplankton samples were fixed with buffered formalin (final concentration of 0.4%). Following the description by Villafañe and Reid [1995], samples were settled in the 10 or 50 ml cylinder of an Utermöhl Chamber (Hydro-Bios Kiel, Germany) for 24 h, qualitative and quantitative analyses were then carried out with an inverted microscope (IX51, OLYMPUS, Japan).

2.6. Statistical and Other Analyses of the Data

[14] The parameters of P versus E curves were obtained using the model of Eilers and Peeters [1988] and fitting of the data by iteration:

$$P^B = E / (aE^2 + bE + c) \quad (1)$$

where P^B is the productivity ($\mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$), E the irradiance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), and a , b , and c the adjustment parameters. The initial slope (i.e., α), maximum production rate (P_{max}^B) and light saturation parameter (E_k) were expressed as a function of the adjustment parameters as follows:

$$E_k = (c/a)^{1/2}; \alpha = 1/c; P_{\text{max}}^B = 1 / [b + 2(ac)^{1/2}] \quad (2)$$

[15] Since the Ultraphan filter reflects 4% PAR under seawater [Gao *et al.*, 2007b], the levels of PAR for the treatments without UVR were calibrated by multiplying by 0.96 to establish the P versus E relationships.

[16] One way analysis of variance (ANOVA) was used to determine the significant differences among the estimated parameters (confidence level = 0.05); the correlation between variables was established using a Kendall's τ test.

3. Results

3.1. Physical Characteristics

[17] Kaemi originated from the western Pacific (11°42'N, 140°48'E) on 19 July (day 199) with a wind speed of 18 m s^{-1} , speeded up gradually thereafter to a maximal velocity of 40 m s^{-1} , and landed at a speed of 33 m s^{-1} on Jinjiang (24°30'N, 117°18'E), Fujian province, at 1550 on 25 July (day 205) (Figure 1). In the study area which is 122 km away, the maximum wind speed reached $\sim 20 \text{ m s}^{-1}$ (Shantou weather station) during the passage of the typhoon. Prior to the typhoon (30 h before landing), the water column of the study area as measured at day 204 was

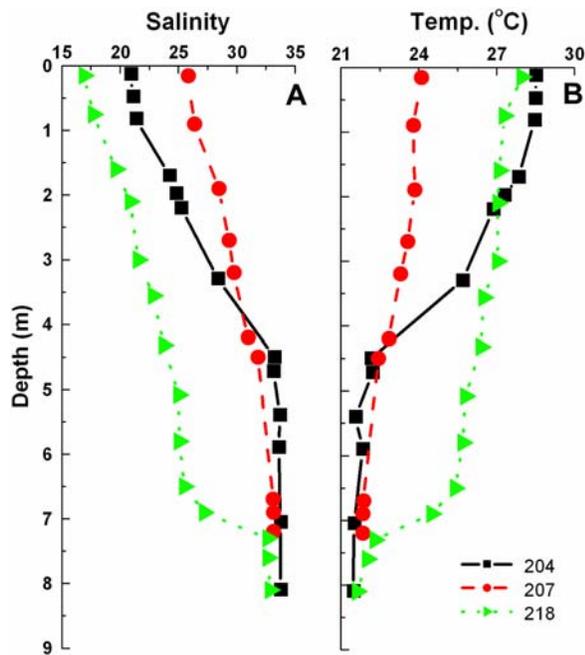


Figure 2. Representative profiles showing the underwater (a) salinity and (b) temperature (in °C) during the pretyphoon and posttyphoon periods in the study area. Profiles were obtained at day 204 (pretyphoon) and days 207 and 218 (posttyphoon).

intensively stratified with a temperature (salinity) gradient $\sim 6^{\circ}\text{C}$ (12) and an upper mixed layer (UML) of 3.5 m deep (Figure 2). The stratification was interrupted by the typhoon, and reestablished again in 2 weeks, with a temperature (salinity) gradient over 5°C (15) and the UML depth of 7 m (Figure 2).

[18] Daily doses of solar radiation, surface seawater temperature (SST) and salinity (SSS) as well as pH values during the study period, 18 July to 7 August 2006 (days 198–218), are shown in Figure 3. Due to the heavy overcast conditions associated with the typhoon, incident solar irradiance displayed a high variability (Figure 3a): of PAR daily doses varied from 0.51 to 12.3 MJ m^{-2} , whereas that of UVR varied from 0.08 to 1.64 MJ m^{-2} with variation of UVB to UVA ratio between 3.6% and 4.1%. Within one week before Kaemi's arrival, the sunny days prevailed; while the cloudy and rainy days played the major roles in 5 days following the typhoon (Figure 3a). About 6 h before Kaemi's landing, the SST decreased by 2°C and SSS increased by 4.2, compared with that of the previous day (day 204), because of the intensive mixing forced by strong winds. About 40 h after Kaemi's departure, the lowest SST of 24.3°C and highest SSS of 25.8 were detected at day 207. The SST then increased gradually, however, the SSS decreased drastically to 16.7 at day 210 due to the heavy rains at days 205, 206, and 208 and associated runoff, as well as the weakened mixing after the typhoon's departure (Figure 3b). The SSS increased to 24.7 at day 213, then decreased sharply to the lowest value of 14.9 at day 218 due to rain on the consecutive days 214, 215, and 216. The pH values in the surface seawater decreased from 8.13 (30 h before the landing) to 7.75 after the typhoon's passage

(40 h later), and then increased gradually to 8.14 (day 218) one week later (Figure 3c). Kaemi consequently caused higher salinity and lower pH and temperature in the surface seawater, which lasted for 6 days in the study area (Figures 3b and 3c).

3.2. Chlorophyll Concentration and Dominating Species

[19] Great variability of phytoplankton biomass (chl *a*) and species composition was found in periods before, during, and after the typhoon (Figure 4a). The highest value of $12.3 \mu\text{g chl } a \text{ L}^{-1}$ was observed at day 203 (pretyphoon), which decreased sharply to $1.5 \mu\text{g chl } a \text{ L}^{-1}$ at day 205: 6 h before Kaemi's landing (Figure 4a). Following the typhoon's departure, chl *a* concentration increased gradually to $7.87 \mu\text{g L}^{-1}$ (day 211) within one week, followed by a decrease to $3.19 \mu\text{g L}^{-1}$ (day 213), but increased thereafter to $8.68 \mu\text{g L}^{-1}$ at day 218 (Figure 4a). Prior to the typhoon (e.g., days 201–204), microplankton ($>20 \mu\text{m}$) accounted for $\sim 50\%$ of the total chl *a*; whereas 6 h before Kaemi's landing, the proportion of pico-nanoplankton ($<20 \mu\text{m}$) in chl *a* increased drastically up to $\sim 98\%$ and maintained for 6 days (Figure 4a), reflecting an effect of offshore water (with an abundance of small cells) currents forced by strong winds. The proportion of small cells ($<20 \mu\text{m}$) declined from day 211 on, but total phytoplankton biomass (chl *a*) increased gradually and peaked again at day 218 due to the blooming of microcells ($>20 \mu\text{m}$) that accounted up to 60% of the total chl *a* (Figure 4a), implying that a stabilized

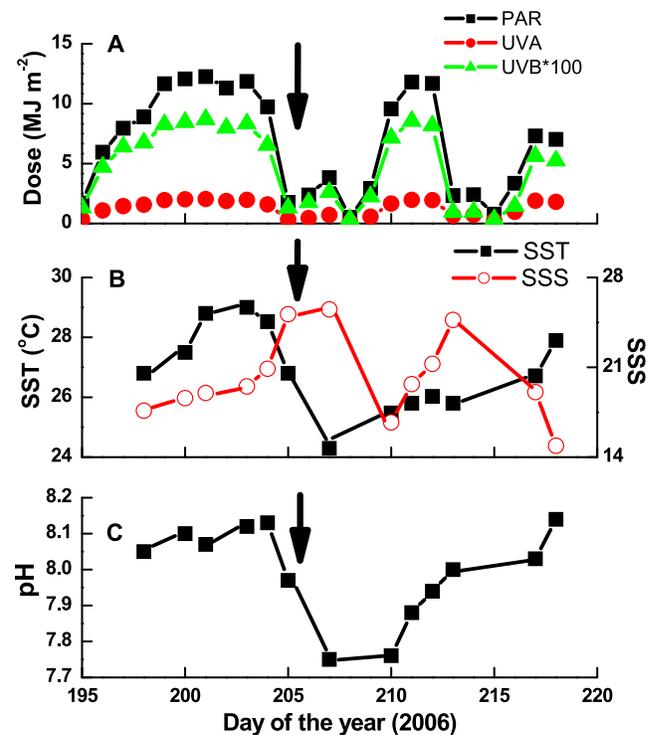


Figure 3. Solar radiation, surface seawater temperature (SST, in °C), salinity (SSS), and pH from 18 July to 7 August 2006 (days 198–218). (a) Daily doses of PAR (400–700 nm), UVA (315–400 nm), and UVB (280–315 nm) in MJ m^{-2} ; (b) SST and SSS, and (c) pH levels in the surface seawater.

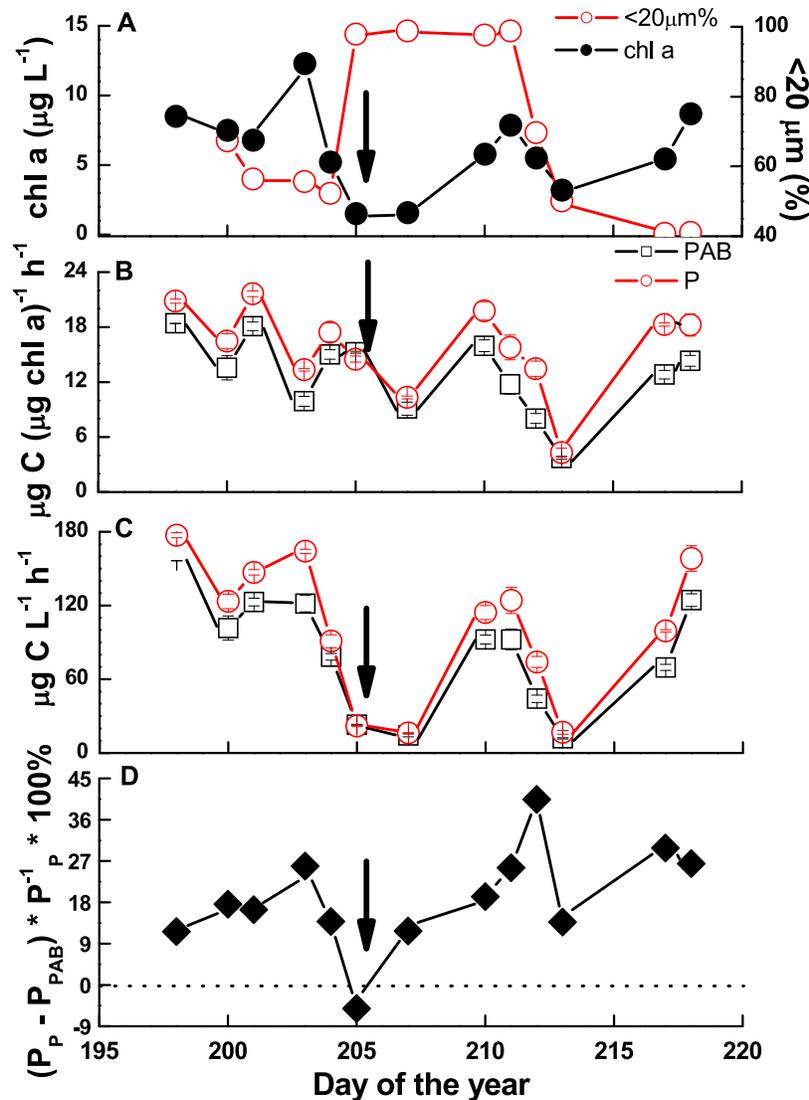


Figure 4. Biological characteristics in the surface seawater of the study area from 18 July to 7 August 2006 (days 198–218). (a) Total chlorophyll *a* concentration, chl *a* (in $\mu\text{g L}^{-1}$), and percentage of chl *a* in the pico-nanoplankton fraction (<20 μm); (b) photosynthetic rates [in $\mu\text{g C } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$], and (c) carbon fixation (in $\mu\text{g C L}^{-1} \text{ h}^{-1}$) of phytoplankton assemblages exposed to PAB (280–700 nm) and P (400–700 nm) treatments; and (d) UVR-induced inhibition (in %). Vertical bars represent standard deviations ($n = 3$ for each treatment).

water condition favored more the growth of larger cells. For the pretyphoon period (e.g., day 203), phytoplankton assemblages were dominated by the chain-formed diatoms (mainly *Thalassiosira* sp.), while pico-nanoplankton accounted for most of the cells within 7 days (i.e., days 205–211) following the typhoon's landing, diatoms (mainly *Nitzschia* sp.) dominated the species composition again later on (data not shown). Other diatoms (e.g., *Skeletonema costatum*, *Asterionella japonica*) and dinoflagellates (e.g., *Ceratium furca*) were also present during the study period, and benthos were found during the posttyphoon period, though they never became the dominant species (data not shown).

3.3. Photosynthetic Carbon Fixation and UVR Effects

[20] Photosynthetic carbon fixation rate, in P treatment at noon time, ranged from 13.4 to 21.6 $\mu\text{g C } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$

in the pretyphoon period (i.e., days 198–204) and 4.3 to 19.8 $\mu\text{g C } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$ in the posttyphoon period (i.e., days 207–218). Such a fluctuation coincided well with the solar radiation (Figures 3a and 4b). The carbon fixation capacity of seawater showed a similar pattern to the changes in chl *a* concentration (Figures 4a and 4c), and varied from 177 to 21.9 $\mu\text{g C L}^{-1} \text{ h}^{-1}$ (6 h prior to KEMI's landing) in the pretyphoon period and from 158 to 16.2 $\mu\text{g C L}^{-1} \text{ h}^{-1}$ in the posttyphoon period. The lowest photosynthetic capacity was observed at day 207: 40 h after Kaemi's landing. In contrast to the photosynthetic carbon fixation under PAR alone, the presence of solar UVR significantly reduced the rate either on the base of chl *a* or per volume of seawater for most of the days except day 205 (Kaemi's landing day) when the rate was lower under the PAR than PAR + UVR treatments (Figures 4b and 4c). The UVR-induced inhibition evaluated from the differences between

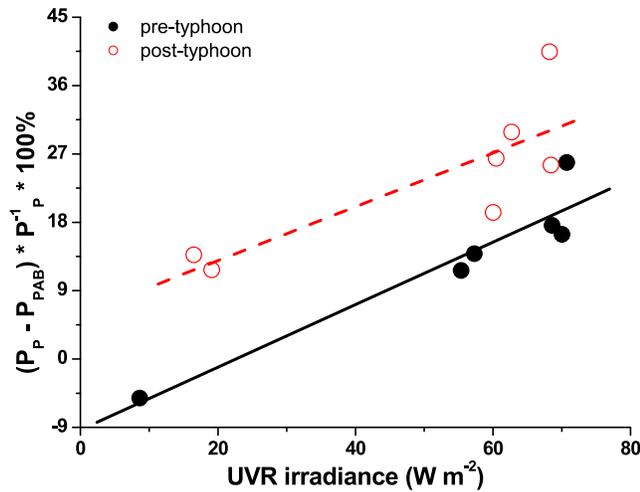


Figure 5. UVR-induced inhibition (in %) as function of UV irradiance (in W m^{-2}) within the incubation periods. The significant linear relationships of the inhibition and UV irradiance are shown with solid line for pretyphoon (days 198–205; $R^2 = 0.90$, $n = 6$, $p < 0.01$) and dashed line for posttyphoon (days 206–218; $R^2 = 0.66$, $n = 7$, $p < 0.05$) periods, respectively.

the solar radiation treatments with or without UVR ranged from 11.6% to 25.9% during the period of days 198–204 and decreased to -5.1% 6 h prior to the landing of Kaemi. This inhibition increased to 11.8% at day 207, and then to 13.7% at day 213 and to 30% at day 217, respectively (Figure 4d). The change pattern of the UVR-related inhibition mirrored that of the solar radiation (Figure 3a). We plotted the UVR-induced inhibition of the photosynthetic carbon fixation against the irradiance of UVR; it increased greatly with the increasing UVR, respectively, to $\sim 20\%$ and $\sim 33\%$ (at $\sim 70 \text{ W m}^{-2}$) in pretyphoon and posttyphoon seawater (Figure 5). The inhibition caused by UVR was $\sim 40\%$ higher ($p < 0.05$) in posttyphoon than that of pretyphoon phytoplankton assemblages, indicating that the pico- and nano-plankton ($< 20 \mu\text{m}$) and blooming diatom *Nitzschia* sp. in posttyphoon were more sensitive to UVR compared to the pretyphoon cells.

[21] The characteristics of the P versus E curves obtained before and after the typhoon are shown in Figure 6 and Table 1. Thirty hours before Kaemi's landing (i.e., day 204), responses of phytoplankton assemblages to solar radiation displayed less photoinhibition compared with that after its departure (e.g., days 210 and 211), especially under the PAB treatment (Figure 6). The maximal photosynthetic rate ($P_{\text{max}}^{\text{B}}$) under PAR alone ranged from 21.7 to $17.4 \mu\text{g C} (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$; whereas the photosynthesis-saturating irradiance (E_k) varied from 477 to $233 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Table 1). Both the $P_{\text{max}}^{\text{B}}$ and E_k were significantly inhibited by solar UVR ($p < 0.05$) (Table 1). The light saturation points (E_k) were higher at day 204 (pretyphoon) than that of days 210 and 211 (posttyphoon), while the photosynthetic apparent efficiency [α , 0.041 – $0.072 \mu\text{g C} (\mu\text{g chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$] was higher in the later than in the former (Table 1), indicating the responses of phytoplankton to solar radiation were conditioned by typhoon-induced changes in

the environment and taxonomic structure. Particularly, the presence of UVR significantly ($p < 0.05$) enhanced the light-limited slope (α) of photosynthesis by the phytoplankton assemblages (mostly large cells) at day 204 (pretyphoon), reflecting an UVA utilization; however, this phenomena was not observed at days 210 and 211 (posttyphoon) in seawater dominated by smaller cells (Table 1).

4. Discussion

[22] Kaemi's passage had provided us an opportunity to investigate the effects of the typhoon on the biological production associated with hydrological and chemical changes. Contrasts between the pretyphoon and posttyphoon were found in chlorophyll a concentration, phytoplankton composition, photosynthetic carbon fixation, and responses to solar PAR and UVR. The passage of Kaemi reduced chlorophyll concentration and photosynthetic carbon fixation and raised the photoinhibition caused by UVR.

[23] In the study area, heavy rains usually prevail in summer, lowering the seawater salinity (i.e., < 28). The stratification in the pretyphoon period disappeared due to the disturbance caused by Kaemi's passage (Figure 2). Vertical mixing caused by the typhoon in the open ocean

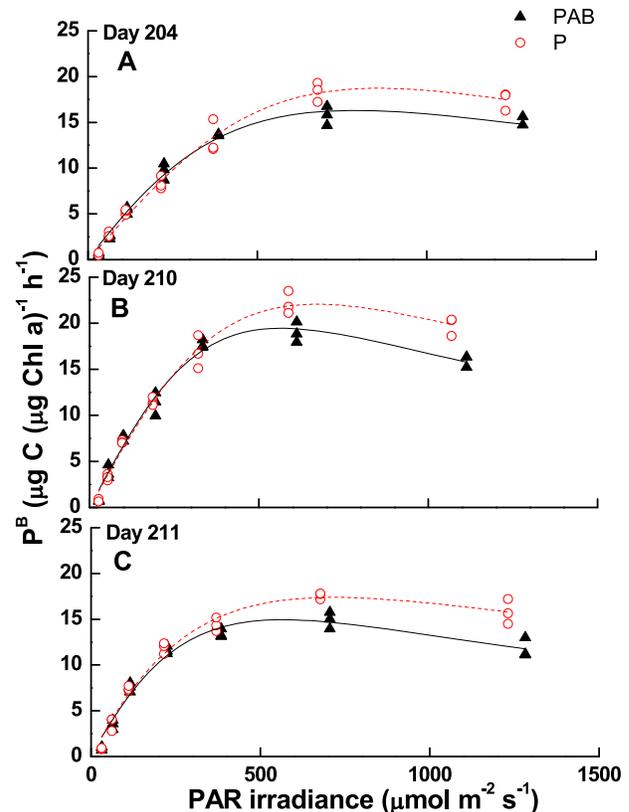


Figure 6. Phytoplankton assimilation number [P^{B} , in $\mu\text{g C} (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$] as a function of PAR irradiance (in $\mu\text{mol m}^{-2} \text{ s}^{-1}$) to which samples from Nan'ao were exposed. The experiments were carried out in (a) pretyphoon (day 204) and (b and c) posttyphoon (days 210 and 211) typhoon periods under PAB (280–700 nm) or P (400–700 nm) treatments. R^2 values of photosynthesis versus irradiance (P versus E) curves ranged from 0.96 to 0.98 ($n = 21$).

Table 1. Photosynthetic Parameters^a

	Radiation Treatment	Pretyphoon Day 204	Posttyphoon	
			Day 210	Day 211
P_{\max}^B	PAB	16.9 ± 0.40*	19.8 ± 1.08*	14.9 ± 0.25*
	P	19.4 ± 1.12	21.7 ± 0.67	17.4 ± 0.69
E_k	PAB	344 ± 12.8*	294 ± 4.71*	210 ± 5.73*
	P	477 ± 26.0	351 ± 25.8	233 ± 18.1
α	PAB	0.049 ± 0.001*	0.070 ± 0.008	0.069 ± 0.007
	P	0.041 ± 0.005	0.066 ± 0.001	0.072 ± 0.009

^aMean ± SD for the P versus E curves obtained on day 204 (pretyphoon) and days 210 and 211 (posttyphoon). P_{\max}^B [$\mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$], the maximal photosynthetic rate; E_k ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), the photosynthetic saturating PAR; α [$\mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$ ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)⁻¹], the apparent photosynthetic efficiency. These parameters were compared under full spectrum of solar radiation (PAB) with those under PAR alone (P). The asterisks represent significant ($p < 0.05$) differences between the radiation treatments with or without UVR. The values are the means ± SD ($n = 3$ for each treatment).

usually reduces SST by up to 1°C [Stramma and Cornillon, 1986; Babin et al., 2004]. In the present study, the change in SST before the arrival and after the departure of Kaemi was ~5°C (Figure 3b), which could be caused by the mixing of deep oceanic water with coastal water and the decrease of air temperature. Similar SST changes after the typhoon were also observed from offshore area of SCS [Lin et al., 2003; Zheng and Tang, 2007]. Currents forced by strong winds might bring open oceanic water with high salinity into coastal areas [Delesalle et al., 1993; McKinnon et al., 2003], then increased the coastal water salinity (Figure 3b); however, the rainfalls and associated runoff could balance the changes and lower the SSS, and also lead to the decrease in pH of seawater (Figure 3c). Moreover, typhoon-induced phytoplankton bloom and/or resuspension of particles or benthic cells are accountable for the great variability in field light conditions [Frenette et al., 1996; Fujii and Yamanaka, 2008]. Unfortunately, light profiles of our sampling site have not been developed due to the unavailability of a diving spectro-radiometer for the study period. Nevertheless, according to the attenuation coefficients obtained in the summer and winter of 2006, depths of the euphotic zone could be ~10 m prior to and <3 m following the typhoon, and 1% surface UVR level could be reduced from ~4 m to <1.5 m, respectively.

[24] The most immediate effect of the typhoon was the sudden decrease in the phytoplankton biomass and changes in species composition (Figure 4a). Sudden decreases in chl a density associated with typhoons' passage have been observed using satellite images [Lin et al., 2003; Zheng and Tang, 2007]; unfortunately, there has been no remote sensing data available in the study area for the period (Y. Bai, personal communication, 2009). According to Delesalle et al. [1993], a decreased chl a concentration occurred after a typhoon event in a lagoon area, while the total chl a concentration in the coastal waters of the present study was reduced to 1/5 after the typhoon's landing (Figure 4a). Apart from the dilution effects of oceanic water and runoffs due to the typhoon [Delesalle et al., 1993], grazing pressure and reduced temperature might have also contributed to the reduced phytoplankton biomass [Alpine and Cloern, 1992]. On the other hand, coastal waters usually have abundant microphytoplankton, and

offshore waters are usually rich in picophytoplankton [Chang et al., 1996; Froneman et al., 2001]. Mixing of the coastal and offshore water caused by the strong winds could lead to the increased proportion of pico-cells (Figure 4a); whereas the consecutive cloudy days after the typhoon (Figure 3a) could have sustained their dominant status for almost one week, as smaller cells with a large surface per unit volume could photosynthesize more efficiently in terms of light use under low-light conditions [Raven, 1998; Raven and Kübler, 2002]. After Kaemi's passage, peak of chl a concentration was observed at the sixth day (Figure 4a), which coincided well with the data derived from remote sensing [Zheng and Tang, 2007; Shi and Wang, 2007]. Phytoplankton biomass (chl a) was dominated by microcells (>20 μm) 1 day before and 6 days after Kaemi's landing (Figure 4a), indicating that the growth of larger cells was favored under the shallow and stable water conditions [Froneman et al., 2001; Villafañe et al., 2004a; Gao et al., 2007a]. Additionally, a dramatic pH decrease from pretyphoon to posttyphoon periods (Figure 3c) might be another reason for the species transition, as pH variation can lead to changes in inorganic carbon composition (CO_2 , HCO_3^- , and CO_3^{2-}) that may alter species composition because of their differential acquisition mechanisms [Raven and Beardall, 2003]. Since acidification of seawater results in higher partial pressure of CO_2 and can increase the photosynthesis of phytoplankton [Hein and Sand-Jensen, 1997], the decrease of pH by 0.4 after the typhoon's landing might enhance the photosynthesis to some extent due to raised pCO_2 and subsequent increased supply CO_2 to carboxylation, though the reduced SST could have eliminated such an effect.

[25] The phytoplankton assemblages were more sensitive to solar UVR in posttyphoon than pretyphoon periods (Figure 5). Such an enhanced sensitivity to UVR can be attributed to the environmental changes as well as species composition of the phytoplankton assemblages [Villafañe et al., 2004a, 2004b], since different species may possess different protective strategies against UVR [Roy, 2000]. During the period from pretyphoon to posttyphoon, dominant phytoplankton species (Figure 4a) changed from microcells (mainly *Thalassiosira* sp.) to piconano-cells, then to microcells (mainly *Nitzschia* sp.) again. Small cells (<2 μm) are more sensitive to solar UVR in view of their DNA damage [Helbling et al., 2001] and their inability to accumulate sufficient sunscreen substances [Raven 1991; Garcia-Pichel, 1994], compared with larger cells. Increased proportion (i.e., 98%) of piconano-cells due to the typhoon could have led to the higher sensitivity to solar UV radiation. In addition, the blooming diatom *Nitzschia* sp. after the typhoon might also be sensitive to UVR due to its acclimation to the reduced levels of solar radiation associated with the typhoon (Figure 3a). On the other hand, acute decrease of SST caused by the typhoon could also increase their sensitivity to UVR due to decreased ability at low levels of SST of protection and repairment against UVR [Buma et al., 2003; Gao et al., 2008]. Additionally, lowered pH due to the effects of the typhoon can affect the speciation of dissolved metals [Zirino and Yamamoto, 1972], which might be harmful to cells, and thus raised their sensitivity to UVR. Finally, phytoplankton cells that have acclimated to low-light conditions at deeper layers

could also become more sensitive to UVR after being mixed up because of the typhoon. These cells from deeper layers can result in lower light saturation point (E_k) and higher apparent photosynthetic efficiency (α) of the P versus E curves (Figures 6b and 6c and Table 1). The lower E_k and higher α values (Table 1) could also be contributed by the higher proportion of pico-nanoplankton cells (Figure 4a) that usually show higher efficiency of light harvesting and utilization [Raven, 1998; Raven and Kübler, 2002]. The cells with lower E_k and higher α (i.e., posttyphoon) values often needs to dissipate more excessive energy [Müller *et al.*, 2001], thus showing higher sensitivity to UVR under high-light conditions as shown in Figure 6. On the other hand, higher α value in the presence of UVR (Table 1) appeared to indicate a positive effect caused by UVA [Gao *et al.*, 2007b] during the pretyphoon period.

[26] Transitional changes in phytoplankton fraction, photosynthetic activity, and UVR sensitivity can happen in large areas after passage of the tropical typhoons, as demonstrated in this study at a site about 122 km away from the location of Kaemi's landing. However, such changes can differ according to geographical and topographical features. Changes in water cycle and frequency of typhoons can also lead to different patterns of the ecological and physiological behaviors of phytoplankton assemblages in the water column.

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K. Gao, G. Li, and Y. Wu, State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen, Fujian 361005, China. (ksgao@xmu.edu.cn)