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Seasonal Impacts of Solar UV Radiation on Photosynthesis of Phytoplankton Assemblages in the Coastal Waters of the South China Sea

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ABSTRACT

We carried out experiments to evaluate seasonal changes in the impacts of UV radiation (UVR, 280–400 nm) on photosynthetic carbon fixation of phytoplankton assemblages. Surface water samples were obtained in the coastal area of the South China Sea, where chlorophyll *a* ranged 0.72–3.82 μg L^{-1}. Assimilation numbers (photosynthetic carbon fixation rate per chl *a*) were significantly higher during summer 2005 than those in spring and winter 2004. The mean values obtained under photosynthetically active radiation (PAR) were 2.83 (spring 2004), 4.35 (winter 2004) and 7.29 μg C (μg chl *a*)$^{-1}$ h^{-1} (summer 2005), respectively. The assimilation numbers under PAR + UVR were 1.58, 2.71 and 5.28 μg C (μg chl *a*)$^{-1}$ h^{-1}, for spring, winter and summer, respectively. UVR induced less inhibition of photosynthesis during summer 2005 than during the other seasons, in spite of the higher UVR during summer. The seasonal differences in the productivity and photosynthetic response to UV were mainly due to changes in water temperature, while irradiance and vertical mixing explained >80% of the observed variability. Our data suggest that previous studies in the SCS using UV-opaque vessels might have overestimated the phytoplankton production by about 80% in spring, 61% in winter and 38% in summer.

INTRODUCTION

The ozone hole appearance since the 1980s (1) over the Antarctic area, and decreased ozone levels at other locations (2) have resulted in enhanced UV-B radiation reaching the Earth's surface. Such an anthropogenically induced phenomenon promoted great interest due to its potential deleterious effects on both humans and ecosystems. Although the chlorofluorocarbons in the stratosphere have been reduced since the implementation of the Montreal Protocol, the time for the recovery still largely depends on the climate change that affects thermal condition in the stratosphere (3).

UV radiation (UVR, 280–400 nm) is a permanent component of solar radiation that influences biological processes in aquatic and terrestrial ecosystems (4). Biologically effective levels of solar UVR can penetrate to significant depths in the open ocean, at least 30 m for UV-B (280–315 nm) and 60 m for UV-A (315–400 nm), while the penetration in coastal areas is less and largely depends on the properties of water (5). Due to this penetration of solar radiation, phytoplankton cells within the euphotic zone are normally exposed to these radiation wavelengths. UVR damages DNA (6), destructs PSII (7), bleaches pigments (8), increases membrane permeability (9) and depresses nitrate and phosphorus uptake (9), among other things. The ultimate impacts are reduction in primary production (10), changes in species composition (11) and subsequent influence on the food web (12). Despite the negative effects caused by UVR, the longer UV wavelength, mostly UV-A, sometimes has positive effects, such as enhanced photosynthetic carbon fixation by phytoplankton assemblages (13), photorepairing of DNA damage (14) and induction of antioxidant genes (15). In addition, UVR stimulates the accumulation of mycosporine-like amino acids (MAAs) (16) that protect cells from UVR-induced damage.

Phytoplankton sustains the largest ecosystem on the Earth, accounting for less than 1% of photosynthetic biomass, but contributing to about half of the primary production on our planet (17). Recently, UVR has been considered as a factor in model calculations for primary production (18). The physiological response of phytoplankton to UVR varies latitudinally (19,20). Impacts of UVR on subtropical phytoplankton differed completely from that of cells in the Antarctic area (21,22). These responses changed both spatially and temporally and might interact with other environmental factors, such as nutrients (23) and temperature (24). Moreover, primary production of coastal phytoplankton was higher when the cells were exposed to UVR than when it was screened off (25). Thus, the prediction of global primary production requires collection of data in different waters taking into account not only photosynthetically active radiation (PAR, 400–700 nm) but also the role of UVR.

The South China Sea (SCS), the second largest marginal sea, has a surface area of 3.5×10^6 km^2, supporting millions of people living along the coast based on its fisheries and other natural resources. Previous studies (26,27) on natural phytoplankton assemblages in the SCS have addressed phytoplankton

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distribution and production. However, few studies focused on the effects of solar radiation, especially UVR on phytoplankton productivity (28). In SCS, solar radiation reaches levels equivalent to those found in equatorial zones, but temporal solar UV effects on phytoplankton may be more complicated than other locations due to its contrasting seasonal variations in radiation. The aim of this study, therefore, was to investigate the photosynthetic carbon fixation of phytoplankton assemblages in different seasons and to establish the relationship of the primary production with solar UVR in the SCS's coastal waters adjacent to one of the most populated areas on our planet.

MATERIALS AND METHODS

Study area and sampling. Surface seawater samples were obtained at 500 m away from the shore of Nan'Ao island (in the SCS, Fig. 1) using 10-L acid-cleaned carboy during the period March 2004 to September 2005 (encompassing three seasons: spring 2004, winter 2004 and summer 2005). The samples were taken early in the morning (around 0930 h), and carried to the laboratory (15 min away) for experimentation and determination of chlorophyll concentration, spectral absorbance characteristics and species composition. Weather conditions precluded the routine collection of samples; nevertheless, we were able to obtain between 3 and 10 samples per season.

Solar radiation treatments. To determine UVR effects upon phytoplankton primary production, three solar radiation treatments were implemented using UV-cutoff foils:

1. PAB treatment: PAR + UV-A + UV-B (cells exposed to full spectrum of solar radiation), uncovered quartz tubes.
2. PA treatment: PAR + UV-A (cells exposed to irradiance above 320 nm), quartz tubes covered with Folex 320 filter (block UV-B, 50% transmittance at 320 nm).
3. P treatment: PAR (cells exposed to visible light), quartz tubes covered with Ultraphan 395 filter (block UVR, 50% transmittance at 395 nm).

The transmission spectra of the filters are presented elsewhere (29) and there was no significant differences (< 4% transmission) in the PAR levels between covered and uncovered tubes. For all the treatments mentioned above, we had duplicate (in summer 2005) or triplicate (in spring and winter 2004) tubes; in addition, two tubes covered with aluminum foil were incubated in the same water bath to determine the dark fixation. A total of 3, 10 and 9 experiments were performed during spring 2004, winter 2004 and summer 2005, respectively.

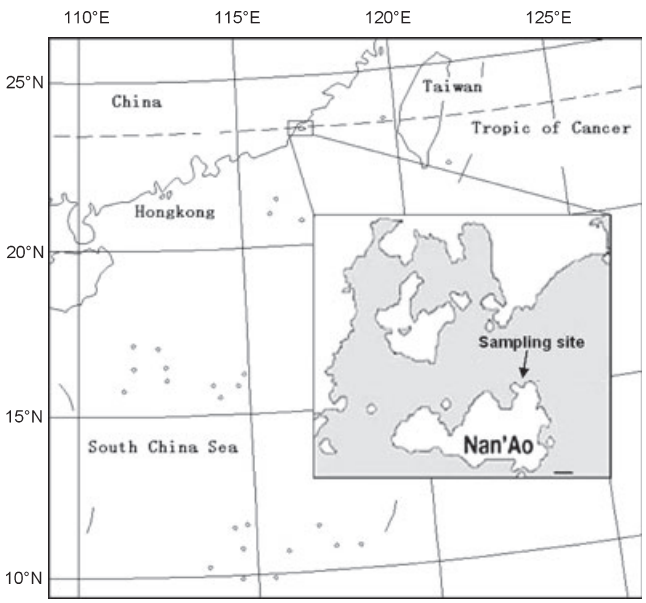

Figure 1. Location of Nan'Ao island and sampling site.

Solar radiation measurements and wind data. A solar radiometer (ELDONET; Real Time Computer, Inc., Germany) (30) was placed on the roof of a building within a 30 m distance from the incubation bath. This instrument monitors simultaneously three wavebands every second, 280–315 nm (UV-B), 315–400 nm (UV-A) and 400–700 nm (PAR), and records the means over 1 min. A diving version of this instrument with the same channels as above and a temperature sensor was used to determine the underwater radiation field and temperature profiles. The attenuation coefficients for solar radiation were calculated from the irradiance profiles obtained with this latter radiometer. Wind speed data for Nan'Ao area were obtained from T7online Corporation (http://www.t7online.com).

Measurements of chlorophyll a and species determination. Chlorophyll *a* concentration was determined by filtering 1 L of seawater onto 25 mm GF/F filter, extracting in absolute methanol for 3 h at room temperature, centrifuging at 5000 ***g*** for 10 min (5804R; Eppendorf, Hamburg, Germany), and scanning the supernatant with a spectrophotometer (DU530; Beckman Coulter, CA) between 280 and 750 nm. The chl *a* concentration (μg L^{-1}) of the seawater was calculated as (31):

$$[\text{Chl } a] = [16.29 \times (A_{665} - A_{750}) - 8.54 \times (A_{652} - A_{750})] \times V_e/V_f$$

where A_{652}, A_{665} and A_{750} represent absorbance at 665, 652 and 750 nm, respectively, V_e (mL) and V_f (L) is the volume of the extraction solution and filtered seawater.

The taxonomic analysis of phytoplankton assemblages was carried out using an inverted microscope (IX51; Olympus, Tokyo, Japan) after settling 10–50 mL of sample (fixed with buffered formalin of 0.4% final concentration of formaldehyde) for 24 h.

Determination of photosynthetic carbon fixation. Water samples, prefiltered through a 180 μm pore size mesh (to remove large zooplankton specimens), were dispensed into 20 mL quartz tubes, inoculated with 100 μL–5 μCi (0.185 MBq) of labeled sodium bicarbonate (Amersham, Buckinghamshire, UK), and then incubated for 3 h centered on local noon (1030–1330 h). The tubes were maintained in a water tank with running surface seawater as temperature control. After incubation, cells were filtered onto Whatman GF/F glass fiber filters (25 mm) that were placed into 20 mL scintillation vials, exposed to HCl fumes overnight and dried (45°C). To each vial, 3 mL of scintillating cocktail (Hisafe3, Perkin Elmer, MA) was added, and the photosynthetic carbon fixation was estimated from the CPM (counts per minute) using a liquid scintillation counter (LS 6500; Beckman Coulter) according to Holm-Hansen and Helbling (32).

Data analysis. The relative inhibition caused by UVR, UV-A or UV-B was estimated as follows:

$$\text{Inh}_{UVR} = (P_{PAR} - P_{UVR})/P_{PAR} \times 100\%$$
$$\text{Inh}_{UV-A} = (P_{PAR} - P_{UV-A})/P_{PAR} \times 100\%$$
$$\text{Inh}_{UV-B} = \text{Inh}_{UVR} - \text{Inh}_{UV-A}$$

where P_{PAR}, $P_{UV\text{-}A}$ and P_{UVR} represent assimilation numbers under P, PA and PAB treatments, respectively.

One-way ANOVA, nonparametric analysis and Kendall test were used to establish differences among treatments, with significance level set at 5% ($P = 0.05$). An ANCOVA, multiple regression analysis was used to estimate the main factors controlling seasonality of primary productivity and UV sensitivity.

RESULTS

The annual pattern of solar daily doses showed a high day-to-day variability due to changes in cloud cover (Fig. 2A,B), with PAR ranging from 0.46 to 14 MJ m^{-2} (Fig. 2A), UV-A from 0.074 to 2.37 MJ m^{-2} and UV-B from 1.73 to 73.2 kJ m^{-2} (Fig. 2B). There was a clear seasonal variation, with highest values in summer 2005 and lowest in winter 2004. The mean daily doses of PAR for the experimental periods were

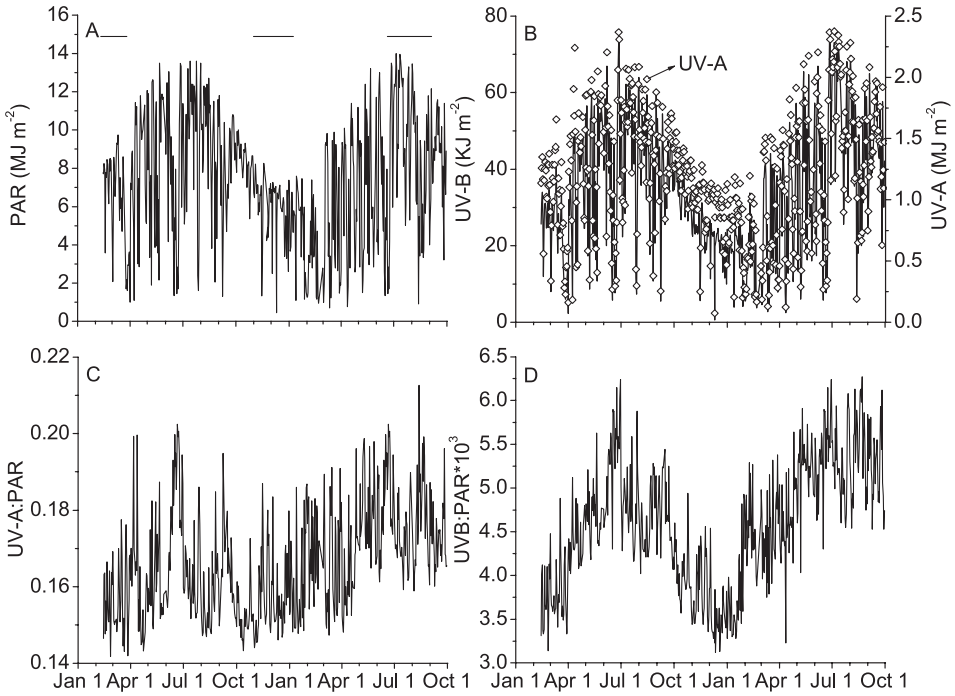

Figure 2. The annual patterns of daily solar doses from 14 February 2004 to 30 September 2005 in Shantou area (A, B), UV-A to PAR ratio (C) and UV-B to PAR ratio (D). Horizontal lines in (A) represent experimental periods.

6.98 (±1.80), 5.72 (±1.63) and 8.35 (±2.80) MJ m^{-2}, for spring 2004, winter 2004 and summer 2005, respectively. The highest incident irradiances recorded on 5 July 2005, time of the highest solar doses, were 539.64, 91.15 and 3.13 W m^{-2} for PAR, UV-A and UV-B, respectively. UV-A to PAR dose ratios ranged from 0.14 to 0.21 (Fig. 2C), while UV-B to PAR dose ratios showed highest values in summer 2005 (up to 0.0063) and the lowest in winter 2004 (down to 0.0031) (Fig. 2D).

The wind speeds during the experimental periods had a seasonality due to the monsoon (Fig. 3A), with mean speeds of 5.33 and 5.28, and 2.54 m s^{-1} in spring 2004, winter 2004 and summer 2005, respectively. The temperature profiles (Fig. 3B) indicated that the water column was stratified in summer 2005, with upper mixing layer (UML) being around 3.50 m, while in spring and winter 2004, the water column was mixed down to the bottom (*i.e.* 8.0 m) (Fig. 3B, Table 1). The attenuation coefficients of PAR, UV-A and UV-B were 0.72, 1.75 and 1.92 during spring 2004, and 0.79, 1.82 and 1.35 during winter 2004, and 0.54, 1.81 and 1.89 m^{-1} during the summer 2005 period, respectively (Fig. 3C,D, Table 1). The 1% depth (in meters) for penetration of PAR, UV-A and UV-B were 6.39, 2.63 and 2.40 during spring 2004, 5.82, 2.54 and 2.53 during winter 2004, and 8.52, 3.40 and 2.43 during summer 2005, respectively (Table 1). During spring 2004, the ELDONET sensor had a problem in the depth gauge, so in this case the attenuation coefficients were calculated based on 3 m depth measurements carried out with marks on the rope. The mean daily PAR irradiances on the surface and through the UML were 159.21, 124.93, 179.15, and 27.55, 19.73, 80.47 W m^{-2} during spring 2004, winter 2004 and summer 2005, respectively. The mean daily doses for PAR, UV-A and UV-B were 8.51 MJ m^{-2}, 1.34 MJ m^{-2}, 34.08 kJ m^{-2} during spring 2004, 6.82 MJ m^{-2},

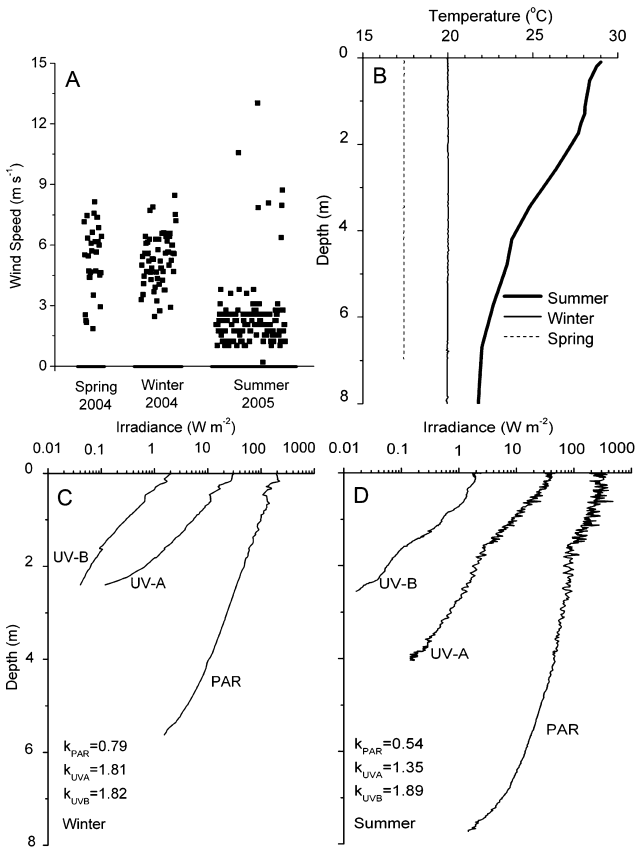

Figure 3. Mean daily wind speed (A), and representative underwater profiles of temperature (B) and PAR, UV-A, UV-B (C, D) in spring 2004, winter 2004 and summer 2005, respectively.

Table 1. The upper mixing layer depth (m), the attenuation coefficient (m^{-1}) and 1% depth (m) for PAR, UV-A and UV-B, and the daily solar radiation doses (MJ m^{-2} for PAR and UV-A, kJ m^{-2} for UV-B) and the mean daily PAR irradiance (W m^{-2}) at the sea surface and throughout the upper mixing layer during spring 2004, winter 2004 and summer 2005, respectively.

	Spring 2004	Winter 2004	Summer 2005
UML depth	8.00	8.00	3.50
K_{PAR}/1% depth	0.72/6.39	0.79/5.82	0.54/8.52
$K_{UV\text{-}A}$/1% depth	1.75/2.63	1.81/2.54	1.35/3.40
$K_{UV\text{-}B}$/1% depth	1.92/2.40	1.82/2.53	1.89/2.43
Sea surface PAR	159.21	124.93	179.15
PAR mean daily dose	8.51	6.82	10.90
UV-A mean daily dose	1.34	1.06	1.82
UV-B mean daily dose	34.08	24.80	53.69
UML PAR	27.55	19.73	80.47

UML = upper mixing layer; PAR = photosynthetically active radiation.

1.06 MJ m^{-2} and 24.80 kJ m^{-2} during winter 2004, and 10.90 MJ m^{-2}, 1.82 MJ m^{-2} and 53.69 kJ m^{-2} during summer 2005, respectively (Table 1).

The solar dose during the incubation period is presented in Fig. 4A; the PAR, UV-A and UV-B ranged between 2.30–4.28, 0.35–0.64 MJ m^{-2} and 12.41–21.62 kJ m^{-2} during spring 2004, between 2.79–3.78, 0.46–0.60 MJ m^{-2} and 12.94–18.21 kJ m^{-2} during winter 2004, and between 3.06–5.28, 0.54–0.91 MJ m^{-2} and 17.83–31.37 kJ m^{-2} during summer 2005, respectively. During November and December 2004, the sea surface temperature (SST) decreased gradually from 23.5 to 17.3°C (Fig. 4B), due to the frequent cold air in winter 2004; the SST reached the lowest value in March 2004 (16.5°C). High SST was found throughout summer 2005, with the highest value (28.3°C) recorded on 5 August 2005; the mean SST during the experimental period was 16.9 (±0.35), 19.6 (±2.13) and 27.6 (±0.76)°C in early spring 2004, winter 2004 and summer 2005, respectively. During the experimental periods, the chl-*a* concentration in surface seawater varied from 0.99 to 1.12, 0.90 to 1.90 and 1.12 to 3.82 $\mu g\ L^{-1}$ for spring 2004, winter 2004 and summer 2005, respectively (Fig. 4C). There was a significant positive correlation between chl-*a* and both SST ($R^2 = 0.58$, $P < 0.0001$) and the surface solar daily dose of PAR from the previous day ($R^2 = 0.36$, $P < 0.01$).

Photosynthetic carbon fixation rates (assimilation numbers) during spring 2004 (Fig. 5A) of samples exposed only to PAR varied from 2.33 to 3.74 μg C (μg chl *a*)$^{-1}$ h^{-1}, the highest value during spring 2004 was found on March 19, when SST was 16.9°C and the solar PAR dose was 6.43 MJ m^{-2}. During this season, photosynthetic inhibition due to UVR varied from

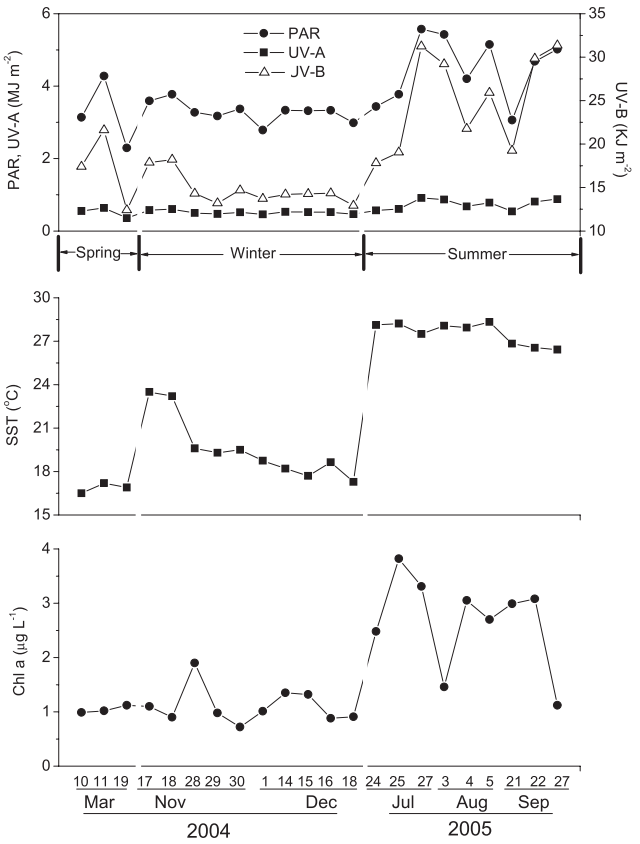

Figure 4. The solar dose (PAR, UV-A and UV-B) during incubation periods (1030–1330 h) (A), and surface seawater temperature (SST) (B) and Chl *a* concentrations (C) during the experimental period.

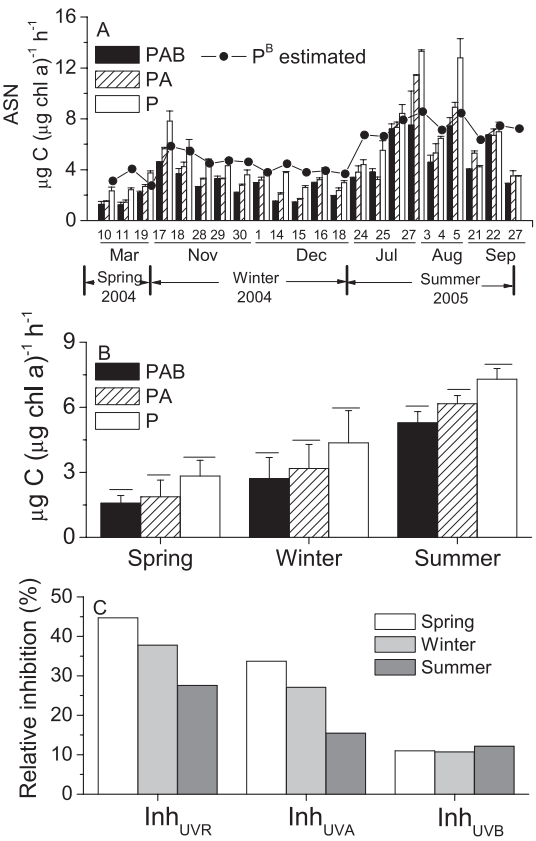

Figure 5. Photosynthetic carbon fixation rates under P, PA and PAB treatments and estimated values under P (P^B) during the experimental period (A), and the mean photosynthetic carbon fixation rates under P, PA, PAB treatments (B), the mean UVR, UV-A and UV-B caused inhibition (C) in spring 2004, winter 2004 and summer 2005, respectively. Vertical bars in (A) represent half of the range ($n = 2$) or SD ($n = 3$); vertical bars in (B) represent SD, $n = 3$–10; horizontal lines represent significant difference at the 0.05 level.

42% to 49%. Similarly, and during winter 2004, the assimilation numbers varied from 2.60 to 7.82 μg C (μg chl *a*)$^{-1}$ h^{-1}; the highest photosynthesis was found on 17 November when SST was also the highest (Fig. 5A) and solar PAR dose was 6.89 MJ m^{-2}; UVR caused an inhibition of photosynthesis in the range of 23–60%. During summer 2005, the assimilation numbers ranged from 3.49 to 13.31 μg C (μg chl *a*)$^{-1}$ h^{-1}) under solar PAR, with the highest rates observed on 3 August; UVR caused a photosynthetic inhibition that varied from 4% to 44%. Although UVR inhibited C-fixation during most of the days, there were exceptions on some dates (*i.e.* 21 and 27 September 2005 [cloudy days]) when the assimilation numbers of samples exposed in the PAB or PA treatments were equal or higher that those under the P treatment.

We used multiple linear regression to predict the assimilation numbers under PAR and the inhibition due to UVR. The best fits were obtained using temperature, wind speed and PAR dose as independent variables, with equation models of the form:

$$P_{\mathrm{PAR}} = 0.183 \times T - 0.225 \times W + 0.605 \times \mathrm{PAR} \quad (R^2 = 0.84)$$

$$\mathrm{Inh_{UVR}}(\%) = -0.751 \times T + 4.866 \times W + 7.837 \times \mathrm{PAR} \quad (R^2 = 0.89)$$

where T is the temperature, W is the wind speeds in m s^{-1} and PAR is the PAR dose during the incubation in MJ m^{-2}. So our model indicates that assimilation numbers under PAR increased with increasing temperature and PAR dose during the experiment; however, they decreased as wind speed increased. On the other hand, the percentage inhibition by UVR decreased with increasing temperature, but had a positive correlation with wind speed and PAR dose, indicating that the higher the dose and wind speed, the higher the inhibition.

In order to compare the three studied seasons we calculated the mean assimilation numbers (and SD) based on the data presented in Fig. 5A, for each studied season and for each radiation treatment. The mean assimilation numbers of samples exposed to PAR were significantly different ($P < 0.005$) among the different seasons, with the lowest values in spring 2004 (2.83 $\pm$ 0.73 μg C [μg chl *a*]$^{-1}$ h^{-1}), intermediate in winter 2004 (4.35 $\pm$ 1.49 μg C [μg chl *a*]$^{-1}$ h^{-1}) and highest in summer 2005 (7.29 $\pm$ 3.60 μg C [μg chl *a*]$^{-1}$ h^{-1}) (Fig. 5B). In addition, UVR caused significant inhibition ($P < 0.02$) during each season, reducing assimilation numbers even further. The mean UVR inhibition was 44.71%, 37.78% and 27.57% for spring 2004, winter 2004 and summer 2005, respectively (Fig. 5C). The inhibition caused by UV-A in spring 2004, winter 2004 and summer 2005 was 33.72%, 27.07% and 15.45%, respectively; while the UV-B inhibitory effects were not significantly different ($P > 0.05$) in the three seasons, with values of 10.99%, 10.71% and 12.12%, respectively.

The OD:Chl *a* (normalized to 0.1 at 665 nm) of the methanol-extracts from natural phytoplankton assemblages in spring 2004, winter 2004 and summer 2005 are shown in Fig. 6. The absorption characteristics indicate higher OD:Chl *a* in winter 2004 than in spring 2004 and summer 2005 between 300 and 640 nm, especially in the UVR range, with winter 2004 samples being 46% higher than the other two seasons on average.

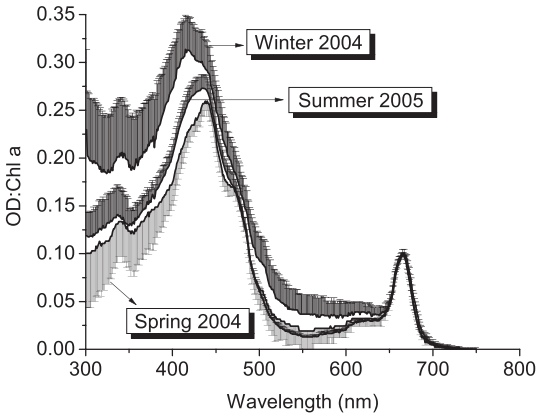

Figure 6. Optical density of methanol-extracts from the natural phytoplankton assemblages normalized to chl *a* during the study periods (spring 2004, winter 2004 and summer 2005). Vertical bars represent 1 SD (n = 3–10).

The taxonomic composition in spring 2004 and summer 2005 was dominated by diatoms: *Chaetoceros* sp., *Rhizosolenia* sp., *Pseudonitzschia* sp., *Skeletonema* sp. and *Asterionella* sp., while the dominant species in winter 2004 were *Pseudonitzschia* sp., *Ceratium* sp. and *Chaetoceros* sp. Additionally, benthic phytoplankton species (*e.g.* *Navicula* sp., *Rhizosolenia* sp., *Biddulphia* sp.) were observed in spring and winter 2004 samples.

DISCUSSION

The SCS is a high productive zone, with an annual primary production up to 0.88 Pg carbon (33). Investigations into the primary production in the coastal SCS have been carried out mainly during summer (28). The lack of time series data makes it difficult to assess the variations of primary production in this area. In addition, most of the studies have been conducted under complete or partially UV-free conditions (34). In this paper, however, we found that solar UVR significantly decreased photosynthetic carbon fixation of surface phytoplankton assemblages in the SCS. The productivity and photosynthetic responses of phytoplankton assemblages to solar UVR showed an inter-seasonal variation in the SCS coastal waters. Such a seasonal change was mainly attributed to the difference in the water temperature, while other factors, such as irradiance, mixing (evaluated through wind speed), also contributed to the observed variations.

Phytoplankton productivity often shows high variability in space and time scales (35). In the present study, it ranged from 2.31 to 34.54 mg C m^{-3} h^{-1} under PAR treatments, with the highest value observed in the summer of 2005, this being related to high values in SST, as high water temperature was shown to increase phytoplankton photosynthesis (36). Such a large variation of the primary production may affect the productivity of aquacultures (37). In the study area, the farmed oysters and scallops that filter-feed phytoplankton directly may be affected by the variation of phytoplankton cell concentration. The seasonal variation of phytoplankton productivity, as shown in this study, can be useful to optimize the aquaculture system by regulating the density of farmed animals to yield the best input–output ratio.

Besides the variation of primary production, we have determined a general trend of low photosynthetic carbon

fixation under treatments that included UVR as found in other studies (23). Samples collected during summer 2005 were less affected by UVR (Figs. 4 and 5), while the samples obtained during spring and winter 2004 were more sensitive to UVR. The high UVR resistance of cells during summer 2005 was mainly due to the relatively high temperature that might have induced a higher metabolism in the cells to cope with UVR. In addition, other factors might have also contributed, such as the high UV levels (*i.e.* pre-acclimation) and high proportion of UV-B to PAR ratios that could have induced more efficient defensive and repairing mechanisms in the phytoplankton (4). Also, the dominant species composition could have shifted to more UV-resistant ones (*e.g.* diatoms in summer) as seen in previous studies that showed a better fit of diatoms after long-term UV exposures (23). Light history can also be an important factor in regulating UVR effects (38). In our study area, the wind-driven mixing in spring and winter 2004 circulated phytoplankton cells through the water column, the cells therefore receive much less solar radiation (20–28 W m^{-2}) compared to the summer 2005 cells (80 W m^{-2}) that were less mixed (Fig. 3B). In fact, the negative relationship obtained between the assimilation numbers in PAR and wind speed suggest that cells were light limited during spring and winter. Cells in the UML, during spring and winter 2004, were exposed to about 25–34% of the solar PAR and 22–30% UVR of the summer 2005-exposed cells. Thus, the differences in the light intensity and history that the cells experienced among different seasons could account for part of the observed seasonal variation in their response to UVR. On the other hand, in addition to the negative effects caused by UVR throughout the year, insignificant or positive effects of UVR were observed on the cloudy days during summer 2005. On these days, solar radiation fluctuated rapidly from about 508 (maximum) to 86 W m^{-2} (minimum) during the incubation periods (*i.e.* 21 and 27 September 2005, data not shown), reflecting a rapid fluctuation in radiation as in a rapid vertical mixing condition (13); therefore, UV-induced damage and repair could be better balanced and UV-A-driven photosynthesis became important (25).

Temperature affects all biochemical reactions catalyzed by enzymes in cells (39), so it can affect the efficiency of repair and protection mechanisms in the cells exposed to UV. As shown above, the assimilation number under PAR increased, while the UVR inhibition decreased with increasing temperature. The higher SST in summer 2005 would increase the activity of enzymes involved in photorepair. Enhanced repair of UV-induced damages could have ameliorated the observed inhibition caused by UVR (24), thus leading to less UV-inhibited photosynthetic carbon fixation in summer 2005. During winter 2004, the phytoplankton assemblages showed higher UV-absorption than that during summer 2005 (Fig. 6), and this might play a protective role in screening off UVR, especially UV-B, leading to lower UV-B-induced inhibition in winter 2004, while the lowest UV-B dose during winter (Table 1) could also contribute to the low UV-B inhibition. The relatively high UV-absorption during winter 2004 could be due to higher proportion of dinoflagellates that synthesize more MAAs than diatoms (40).

The differences in sensitivity to UVR led to different degrees of photosynthetic inhibition among the seasons, ranging from 4% to 60%, of which UV-A accounted for up to 32–90% and UV-B up to 10–68%. Considering the effects of UVR, traditional measurements using UV-opaque vessels might have overestimated the photosynthetic carbon fixation of phytoplankton from the coastal SCS by about 80% in spring, 61% in winter and 38% in summer. As energy of UV-A can be utilized to drive photosynthetic carbon fixation of the coastal phytoplankton assemblages (25), the balance between the negative and positive effects of UVR could have influenced the overall UVR inhibitions in the different seasons. The balance between UVR-induced inhibition at surface and UV-A-triggered enhancement of photosynthetic carbon fixation at deeper depths (13,25) would give a measure of the error if the effects of UVR were neglected using the traditional UV-opaque vessels.

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