

Article

Experimental Assessment of Ultraviolet Radiation Impact on the Primary Production of Phytoplankton in the East/Japan Sea

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Abstract: Solar radiation, particularly ultraviolet radiation (UVR, 280–400 nm), is known to play a significant role in driving primary production in marine ecosystems. However, our understanding of the specific effects of UVR on the primary production of natural phytoplankton communities is still limited. We utilized the ¹³C stable isotope to quantify primary production and conducted experiments using different types of incubation bottles (polycarbonate and quartz bottles) to compare the primary production in the absence and presence of UVR. Although we observed a weak inhibitory effect at the surface of the water column, UVR exposure resulted in an approximately 1.5-fold increase in primary production over the euphotic zone. The enhanced primary production during the study period can be attributed to the combined effect of low UVB (280–320 nm) dose and abundant nutrient conditions. Notably, our size-fractionated measurements revealed that UVR exposure led to a two-fold increase in primary production in large cells (>2 µm) compared to the exposure of solely photosynthetically active radiation (PAR). In contrast, there was no significant difference in the primary production of small cells (<2 µm) between the absence and presence of UVR. These findings highlight the advantages of large cells when exposed to UVR, emphasizing the importance of phytoplankton cell size in determining their response to UVR. However, it is important to note that the effects of UVR on phytoplankton are influenced by various environmental factors, which interact with solar radiation, shaping the dynamics of phytoplankton responses to UVR.

Keywords: cell size; phytoplankton; polycarbonate bottle; primary production; quartz bottle; ultraviolet radiation



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1. Introduction

Primary production by phytoplankton is a fundamental biological process in the ocean, providing the primary source of organic matter for sustaining the growth or metabolic demands of marine organisms [1]. The magnitude of primary production (i.e., primary productivity) regulates the flow of biological energy in ecosystems [2]. The primary productivity is essentially a function of the incident irradiance because it determines the magnitude of primary production in the ocean [3]. As a result, solar radiation could affect community structure and ecosystem function in marine planktonic organisms [4,5]. Generally, photosynthetically active radiation (PAR; 400–700 nm) is the most important waveband for the photosynthetic process [6–10]. On the other hand, ultraviolet radiation (UVR; 280–400 nm) is regarded as having harmful effects on the photosynthesis and respiration of plankton communities [6,7,11]. Particularly, the UVB spectrum (280–320 nm) is recognized for its potential to damage cellular components such as DNA, protein molecules, and pigments,

thereby affecting phytoplankton growth and photosynthesis [5,12,13]. Previous studies have indicated that UVB can lead to a substantial decrease in phytoplankton carbon fixation rates [6,14–19]. Heterotrophic bacteria production can also be inhibited under UVB [20], and intense UVB radiation partially inhibits planktonic net community production [10]. In comparison, UVA (320–400 nm) has been shown to stimulate the carbon fixation of phytoplankton under relatively low solar irradiance levels [21,22]. Moreover, UVA enables the photo-repair of UVR-induced DNA or protein damage in natural organisms [12,13,23,24].

However, some studies have reported no significant effects of UVR on primary production and heterotrophic bacteria production [24–26]. The influential effects of UVR can be attributed to its interaction with various environmental factors, such as nutrients, temperature, and vertical mixing [26–28], or the high acclimation capacities of organisms in high-UVR conditions [28,29]. For example, nutrient availability can mitigate the harmful effects of UVR on phytoplankton and/or bacterial production [30,31]. Elevated temperatures can reduce the UVR stress and lessen the inhibition of photosynthetic carbon fixation by UVB [32,33]. Helbling et al. (2003) [34] found that UVR enhances the carbon fixation of phytoplankton under fast mixing conditions compared to slower circulation periods. Beyond the interactive effects between environmental forcings and UVR on phytoplankton, the cell size of phytoplankton appears to be crucial in determining their responses to UVR. Some studies have reported that smaller cells have been shown to be more vulnerable to UVR than larger cells [35,36], resulting in a decrease in the proportion of picophytoplankton under increased UVB exposure [37]. However, the sensitivity of phytoplankton to UVR can vary among different species [38].

Previously, the effects of UVR on marine phytoplankton have been reported mainly in high-latitude polar environments where UVB can be affected by seasonally severe depletion of stratospheric ozone [16,17,39] or in coastal waters with high concentrations of colored dissolved organic matter (CDOM) [40]. For example, Erga et al. (2005) [41] observed a reduction in primary production due to enhanced UVB radiation in the waters surrounding Antarctica during the occurrence of an ozone hole. However, UVR can also exert significant effects on biological processes in low latitudes and open ocean waters, where high solar irradiance and low CDOM allow for increased UVR penetration [40]. Furthermore, recent notable environmental changes could lead to different phytoplankton responses to UVR in open oceans. The East/Japan Sea, located in the northwestern Pacific Ocean, is a marginal sea and a seasonally productive region [42,43]. This region has experienced rapid increases in sea surface temperature and ocean acidification, resulting in changes in the duration and intensity of phytoplankton blooms, annual primary production, and phytoplankton community structure [43–45]. Previously, some studies examined the response of natural phytoplankton assemblages to UVR in the coastal waters of the Japan Sea [46,47]. However, little information is available on the radiation dependence of phytoplankton in the East/Japan Sea during productive periods for phytoplankton.

Two approaches have been widely used to assess UVR effects on phytoplankton, either attenuating some of the solar UVR reaching with filters or supplementing solar UVR levels with UV fluorescent lamps [48] (reference therein). Here, we experimentally assessed the effect of UVR on phytoplankton primary production using the different types of incubation bottles (polycarbonate and quartz bottles). Polycarbonate bottles can prevent the penetration of UVR [49] and are commonly used for primary production measurements in various oceans [42,50–54]. In contrast, quartz bottles allow the entire light spectrum (PAR: 400–700 nm, UVA: 320–400 nm, and UVB: 280–320 nm) to pass through [10,55,56]. Thus, comparing primary production in polycarbonate and quartz bottles could allow the estimates of the primary production in the absence and presence of UVR, respectively.

This study aims to experimentally assess the effect of UVR on phytoplankton primary production in order to extend our understanding in the less studied East/Japan Sea regarding UVR roles in primary production. Additionally, we examine how the impact of UVR differs between two phytoplankton size groups (large cells; $>2\ \mu\text{m}$, and small

cells; $<2\ \mu\text{m}$), as the cell size of phytoplankton plays a crucial role in determining primary production [33,57,58].

2. Materials and Methods

2.1. Experimental Design

The experiments were performed aboard the R/V *Haeyang 2000* between 14 and 22 March 2012 in the East/Japan Sea (Figure 1). Five stations were selected for sampling. Water temperature and salinity measurements were obtained using a CTD SBE-911 plus (Sea-Bird model) mounted on a rosette. Seawater samples were collected from three different optical depths (100, 30, and 1% of surface irradiance) using a rosette sampler equipped with 20 L Niskin-type bottles to assess the vertical radiation effect on primary production with depth, i.e., the impact of the differential radiation reaching different water depths.

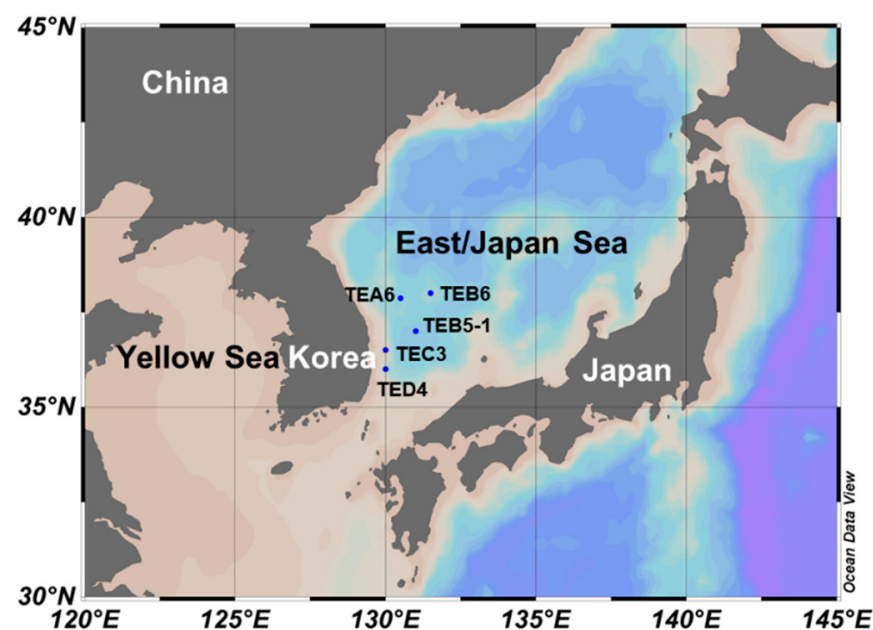


Figure 1. Location of the study area in the East/Japan Sea.

Two radiation treatments in the primary production measurements were implemented to distinguish between the absence and presence of UVR, i.e., (a) samples exposed to PAR+UVR in quartz bottles (1 L) and (b) samples exposed solely to PAR in polycarbonate bottles (1 L) (Nalgene, Thermo Fisher Scientific, Waltham, MA, USA) (Figure S1). To attenuate light intensity equivalent to the optical depths, the bottles were covered with layers of neutral density mesh. Duplicate light bottles were prepared in both polycarbonate and quartz bottles for each light depth. Additionally, a dark bottle representing the dark uptake rate was prepared without replicates. To eliminate the bacterial process, the dark bottle values were subtracted from the light bottle values.

2.2. Inorganic Nutrients, Chlorophyll *a* (*chl a*), and Primary Production Measurements

Water samples for major dissolved inorganic nutrients (nitrate, nitrite, ammonium, silicate, and phosphate) analysis were prefiltered through the glass-fiber filters (Whatman GF/F; diameter = 25 mm) on board and immediately frozen in a freezer ($-20\ ^\circ\text{C}$). After returning to the home laboratory, nutrient concentrations were analyzed using an automated nutrient analyzer (QuAatro, Seal Analytical, Norderstedt, Germany).

For chlorophyll *a* (*chl a*) analysis, 0.3 L samples were collected at the same depths (100, 30, and 1% of surface irradiance) and filtered through Whatman GF/F glass-fiber filters with a diameter of 24 mm. The samples were extracted for 24 h with 90% acetone at $4\ ^\circ\text{C}$ in

the dark, following the method described by Parsons et al. (1984) [59]. Chl *a* concentration was estimated using a Turner Design Trilogy Fluorometer that was previously calibrated with a pure chl *a* standard.

Primary production was measured using the ^{13}C isotope tracer [58], a method widely employed in various oceans [42,45,50–54,60–63]. Labeled carbon ($\text{NaH}^{13}\text{CO}_3$) substrates were added immediately to a final concentration of 0.16 mM in the primary production bottles. The bottles were incubated on deck in a large transparent water tank with continuously running surface seawater under natural light conditions. Incubated waters were divided into two filtration sets for total and small ($<2\ \mu\text{m}$) phytoplankton after approximately 4 to 5 h of incubation. The water samples (0.3 L) for total phytoplankton were filtered onto pre-combusted ($450\ ^\circ\text{C}$, 4 h) glass-fiber filters (Whatman GF/F; diameter = 25 mm). For small phytoplankton collection, the water samples (0.6 L) were first passed through $2\ \mu\text{m}$ polycarbonate nuclepore filters (47 mm diameter) to eliminate large phytoplankton, and then the filtrate was passed through GF/F filters (25 mm diameter). It should be noted that, in this study, polycarbonate nuclepore filters were not used due to incompatibility with the current combustion procedure of the mass spectrometry analysis. Therefore, the production of large phytoplankton ($>2\ \mu\text{m}$) was determined by calculating the difference between the small and total fractions. All samples were filtered under a gentle vacuum ($<100\ \text{mmHg}$). The filtered samples were treated with HCL fumes overnight to remove carbonate and were dried in a vacuum desiccator, following the procedure described by Hama et al. (1983) [64]. Particulate organic carbon (POC) and an isotopic ratio of $^{13}\text{C}/^{12}\text{C}$ were determined using a Thermo Finnigan Delta+XL mass spectrometer at the Alaska Stable Isotope Laboratory of the University of Alaska, Fairbanks, AK, USA. The measurement uncertainty for $\delta^{13}\text{C}$ was ± 0.17 .

2.3. Satellite-Derived Solar Radiation

PAR, UVA (ultraviolet-A, 320–400 nm), and UVB (ultraviolet-B, 280–320 nm) datasets were obtained from the NASA Langley Research Center's (LaRC) Atmospheric Science Data Center (ASDC) (<https://asdc.larc.nasa.gov/project/CERES>) (accessed on 2 May 2022). Incident intensities of ambient PAR, UVA, and UVB were collected at the nearest point to the sampling station and analyzed for each sampling date. The data were provided in Network Common Data Form (NetCDF) format, and at a spatial resolution of $1^\circ \times 1^\circ$. To accurately determine the surface flux at the sampling date, only All-sky surface UVA, UVB, and PAR fluxes were used for analysis. Even though the estimation of surface UVR using satellite data does not necessarily resemble the underwater light environment experienced by phytoplankton over the euphotic zone, the previous study revealed no significant systematic bias against ground-based measurements, except for snow-covered environments [65] (Arola et al. 2002).

2.4. Data Analysis

The depth-integrated primary production (IPP) rates were calculated by the trapezoidal rule. The trapezoidal integration involved dividing the water column into three light depths (100, 30, and 1% of surface irradiance) and calculating the area under the primary production rate within each depth range. By summing up the areas from three depths, IPP rates were obtained. The production/biomass ratio (h^{-1}) was calculated by dividing the integrated primary production rates ($\text{mg C m}^{-2} \text{h}^{-1}$) by the integrated POC concentration (mg C m^{-2}). An independent *t*-test was performed to determine significant differences between the variables. Pearson's correlation was used to examine the linear relationships between UVR and primary production (PP) from normal distribution. The interpretation of all the data focused on the comparison in the absence and presence of UVR, respectively. All statistical analyses were conducted using SPSS 12.0 software.

3. Results

3.1. Environmental Conditions

The surface seawater temperature ranged from 25.72 to 26.57 °C during the cruise period (Table 1). There were no significant differences in the ambient nutrient concentrations integrated over the euphotic zone among the stations ($p > 0.05$) (Table 1). The concentrations of DIN ($\text{NO}_3 + \text{NO}_2 + \text{NH}_4$) ranged from 205.0 to 268.0 mmol m^{-2} , with a mean of 244.4 mmol m^{-2} ($\text{SD} = \pm 25.1 \text{ mmol m}^{-2}$). The silicate concentrations ranged from 330.6 to 437.8 mmol m^{-2} , while the phosphate concentrations (PO_4^{3-}) ranged from 13.9 to 19.1 mmol m^{-2} .

Table 1. Water temperatures, integrated concentrations over the euphotic zone for dissolved inorganic nitrogen (DIN; $\text{NO}_2 + \text{NO}_3 + \text{NH}_4$), silicate (SiO_2), phosphate (PO_4), surface chlorophyll *a* (chl *a*), and integrated (I-chl *a*) concentrations over the euphotic zone of each sampling stations. Incident intensities of ambient PAR (photosynthetically active radiation, 400–700 nm), UVA (ultraviolet-A, 320–400 nm) and UVB (ultraviolet-B, 280–320 nm) during the incubation. Units are W m^{-2} .

Station	Date (dd/mm/yy)	Temperature (°C)	DIN (mmol m^{-2})	SiO_2 (mmol m^{-2})	PO_4 (mmol m^{-2})	Surface chl <i>a</i> (mg chl a m^{-3})	I-chl <i>a</i> (mg chl a m^{-2})	PAR (W m^{-2})	UVA (W m^{-2})	UVB (W m^{-2})
TED4	15 March 2012	26.14	205.0	330.6	13.9	0.48	20.1	86.88	20.66	0.46
TEC3	16 March 2012	25.72	262.5	391.2	18.3	0.42	20.0	184.46	25.21	0.57
TEB5-1	17 March 2012	26.10	268.0	437.8	19.1	0.82	26.0	70.61	13.30	0.32
TEA6	20 March 2012	26.32	249.4	382.1	18.8	0.95	55.6	218.42	39.86	0.78
TEB6	21 March 2012	26.57	237.1	388.8	16.3	0.92	63.2	244.17	38.13	0.66

The surface chl *a* concentration ranged from 0.42 to 0.95 mg chl a m^{-3} , and the water column-integrated chl *a* ranged from 20.0 to 63.2 mg chl a m^{-2} (Table 1). Incident solar radiation varied widely among stations due to weather conditions. The PAR was highest at station TEB6, reaching 244.17 W m^{-2} , while the lowest value was at station TEB5-1 (Table 1). The levels of UVA and UVB radiation varied from 13.30 to 39.86 W m^{-2} and from 0.32 to 0.78 W m^{-2} , respectively, across the stations. The average PAR intensity during the study period was $160.91 \pm 78.15 \text{ W m}^{-2}$. The average UVA and UVB intensities were $27.43 \pm 11.40 \text{ W m}^{-2}$ and $0.56 \pm 0.18 \text{ W m}^{-2}$, respectively. The ratio of UVA to PAR varied from 0.14 to 0.24, with an average of 0.18 ± 0.04 . The UVB intensity was considerably lower compared to UVA, accounting for approximately 0.4% of PAR.

3.2. Specific and Absolute Carbon Uptake Rates

The specific carbon uptake rates (h^{-1}) of phytoplankton (without considering carbon biomass) at different irradiance levels (100, 30, and 1% of surface irradiance) under PAR (UVR absence) and PAR+UVR conditions are presented in Table 2. Under PAR conditions, the specific carbon uptake rates of phytoplankton ranged from 0.008 to 0.018 h^{-1} at 100% irradiance level (Table 2). Under PAR+UVR conditions, the surface carbon uptake rates were slightly lower, ranging from 0.006 to 0.016 h^{-1} (Table 2). The specific carbon uptake rates at 30% and 1% irradiance levels were significantly higher under the presence of UVR than in the absence of UVR (t -test, $p < 0.05$) (Table 2). The specific uptake rates at 30% irradiance level under PAR ranged from 0.003 to 0.020 h^{-1} , whereas they varied from 0.007 to 0.024 h^{-1} under PAR+UVR. Similarly, the specific carbon uptake rates at 1% irradiance level were 0.000–0.002 h^{-1} for PAR and 0.000–0.012 h^{-1} for PAR+UVR, respectively.

The absolute carbon uptake rates ($\text{mg C m}^{-3} \text{ h}^{-1}$) under the absence and presence of UVR at the different irradiance levels are shown in Figure 2a. At the surface, the average absolute carbon uptake rate was $1.5 \pm 0.9 \text{ mg C m}^{-2} \text{ h}^{-1}$ under PAR alone, while it decreased to $1.2 \pm 0.5 \text{ mg C m}^{-2} \text{ h}^{-1}$ under PAR+UVR. Under UVR exposure, the average absolute carbon uptake rates were $1.8 \pm 1.2 \text{ mg C m}^{-2} \text{ h}^{-1}$ for 30% light depth and $0.6 \pm 0.5 \text{ mg C m}^{-2} \text{ h}^{-1}$ for 1% light depth (Figure 2a). In contrast, without UVR, the rates were $1.2 \pm 1.0 \text{ mg C m}^{-2} \text{ h}^{-1}$ and $0.1 \pm 0.1 \text{ mg C m}^{-2} \text{ h}^{-1}$ at 30% and 1% light

depths, respectively. With exposure to UVR, the highest absolute carbon uptake rates were observed at the depth receiving 30% of the surface irradiance (Figure 2a). The $IPP_{PAR+UVR}$ ranged from 22.1 to 78.5 $\text{mg C m}^{-2} \text{ h}^{-1}$ among the stations, while the rates without UVR (IPP_{PAR}) ranged from 12.7 to 63.1 $\text{mg C m}^{-2} \text{ h}^{-1}$ (Figure 2b). The station-averaged IPP_{PAR} was $31.4 \pm 21.7 \text{ mg C m}^{-2} \text{ h}^{-1}$, whereas $IPP_{PAR+UVR}$ was $49.5 \pm 26.7 \text{ mg C m}^{-2} \text{ h}^{-1}$.

Table 2. Specific carbon uptake rates (h^{-1}) of phytoplankton in three irradiance levels under PAR and PAR+UVR, respectively. All given values are mean values (standard deviation in parenthesis).

Station	PC Bottles (PAR)			Quartz Bottles (PAR+UVR)		
	Specific Carbon Uptake Rates (h^{-1})			Specific Carbon Uptake Rates (h^{-1})		
	100%	30%	1%	100%	30%	1%
TED4	0.009 (0.001)	0.006 (0.000)	0.006 (0.001)	0.007 (0.000)	0.008 (0.001)	0.002 (0.001)
TEC3	0.008 (0.002)	0.007 (0.000)	0.000 (0.000)	0.012 (0.005)	0.015 (0.003)	0.008 (0.004)
TEB5-1	0.013 (0.000)	0.003 (0.000)	0.000 (0.000)	0.016 (0.000)	0.007 (0.001)	0.000 (0.000)
TEA6	0.009 (0.002)	0.012 (0.004)	0.001 (0.001)	0.009 (0.001)	0.023 (0.008)	0.012 (0.004)
TEB6	0.018 (0.002)	0.020 (0.005)	0.002 (0.000)	0.006 (0.000)	0.024 (0.000)	0.006 (0.000)

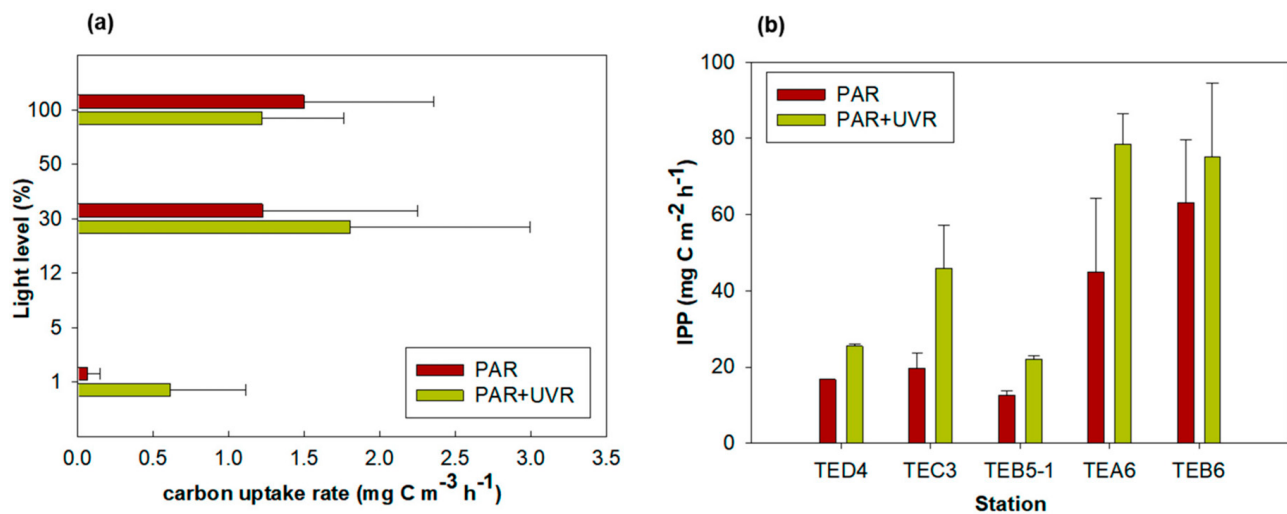


Figure 2. Comparison of (a) absolute uptake rates between PAR and PAR+UVR under the different light depths and (b) integrated primary production (IPP) rates at 5 stations under PAR and PAR+UVR.

3.3. Carbon Uptake Rates per Unit of Chlorophyll *a*

Figure 3 illustrates the comparison of the average carbon uptake rate per unit of chl *a* at three irradiance levels between PAR and PAR+UVR conditions. Under solely PAR exposure, carbon incorporation was highest at the surface and rapidly decreased with increasing depth. In contrast, UVR exposure led to higher carbon incorporation at the 30% irradiance level compared to the surface (Figure 3). Additionally, the presence of UVR distinctly increased carbon incorporation, even at the 1% irradiance level.

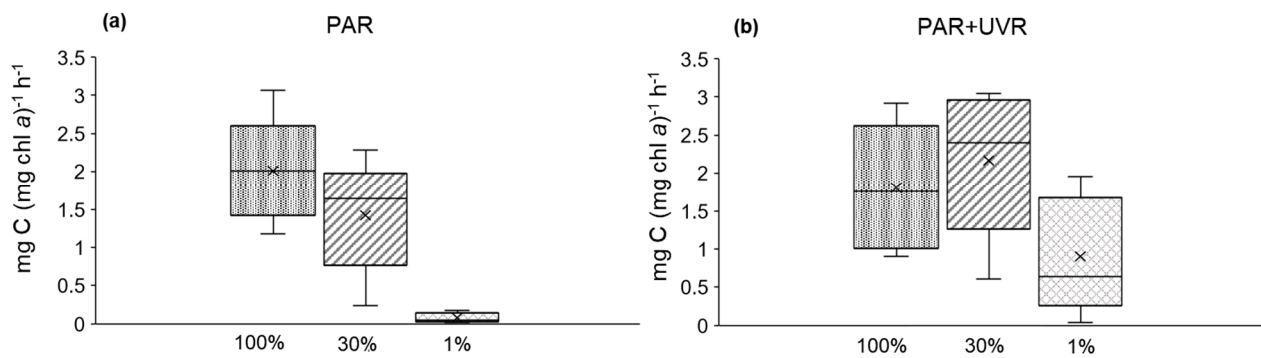


Figure 3. Comparison of carbon uptake rate per chl *a* by phytoplankton in three irradiance levels under exposure to PAR (a) and PAR+UVR (b). Cross marks represent average values.

3.4. Relationships between UVR and Primary Production

To demonstrate the effect of UVR on primary production, the surface primary production and integrated production values were compared with UVR (Figure 4). A highly significant positive correlation was observed between UVR and IPP ($r = 0.98$, $p < 0.01$), whereas a negative correlation was found with surface PP ($r = 0.67$, $p < 0.05$).

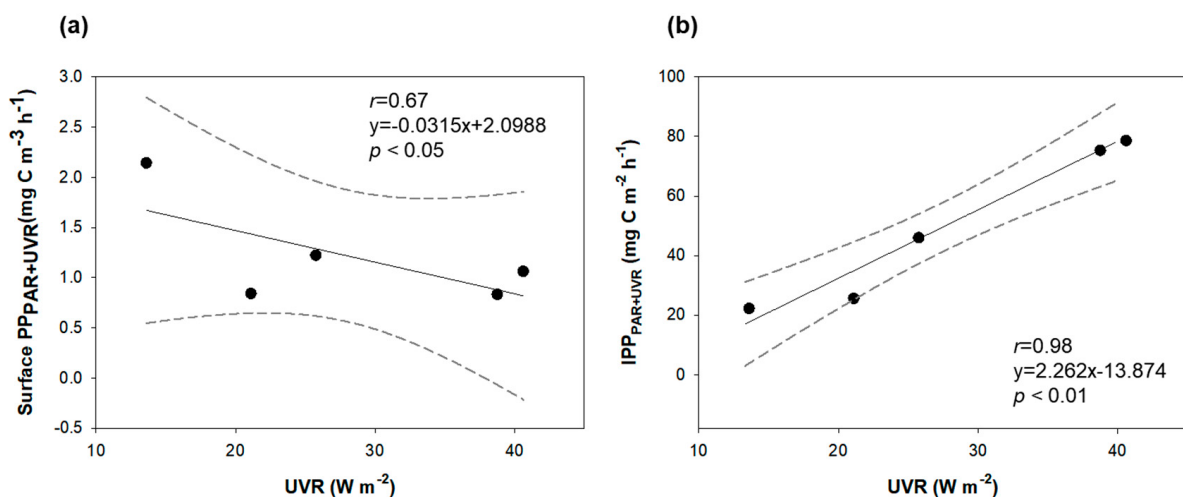


Figure 4. Relationships between (a) UVR (W m⁻²) and surface PP (primary production) (mg C m⁻³ h⁻¹) and (b) integrated primary production (IPP) (mg C m⁻² h⁻¹). The dot area is the 95% confidence band.

3.5. Effects of Solar UVR on Different Size Fractions of Phytoplankton

The effects of solar UVR on different size fractions (>2 μ m and <2 μ m) are shown in Figure 5. The IPP_{PAR} of large phytoplankton (>2 μ m) was 6.81 to 37.10 mg C m⁻² h⁻¹ among the stations, while the IPP_{PAR} of small phytoplankton (<2 μ m) was 5.29 to 26.03 mg C m⁻² h⁻¹ (Figure 5a). Large phytoplankton contributed 41.6 to 58.8% of the total primary production under PAR conditions, whereas the small phytoplankton accounted for $49.0 \pm 7.6\%$ (41.2–58.4%) (Figure 5a). In comparison, the IPP_{PAR+UVR} were 14.39–54.74 mg C m⁻² h⁻¹ for large cells and 7.70–35.35 mg C m⁻² h⁻¹ for small cells (Figure 5b). The contributions of large and small phytoplankton to total primary production were 53.1–69.7% and 30.3–46.9%, respectively, under exposure to UVR (Figure 5b).

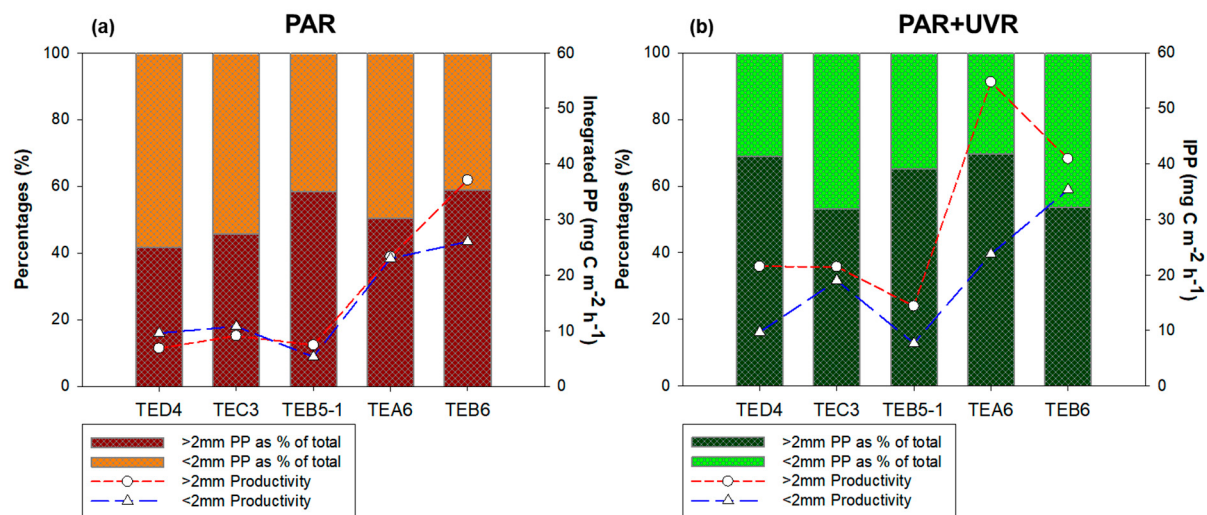


Figure 5. Contribution of different size fractions (>2 μm , <2 μm) to total primary production in % (columns) and the corresponding integrated primary production (IPP) of each group in $\text{mg C m}^{-2} \text{ h}^{-1}$ (symbol and line) for each of the 5 stations under (a) PAR and (b) PAR+UVR.

Table 3 illustrates the impact of UVR on two different size fractions (small and large cells) and their contribution to total primary production. Under PAR conditions, no significant difference in IPP was observed between the two size fractions (t -test, $p > 0.05$) (Table 3). Both small and large cells contributed similarly to the total primary production, accounting for 49.0% and 51.0%, respectively, under PAR (Table 3). However, UVR exposure resulted in a greater increase in primary production in large cells compared to small cells. Large phytoplankton exposed to UVR+PAR exhibited a two-fold increase in primary production compared to samples receiving only PAR. Additionally, the contribution of large cells to total primary production increased to 62.1% under UVR penetration, while the proportion of small cells decreased to 37.9% (Table 3). The comparison of production to biomass ratio further highlighted the highest photosynthetic efficiency in large cells when exposed to PAR+UVR (Table 3).

Table 3. Comparison of integrated primary production (IPP), contribution to total primary production, production to biomass (P/B) ratio of different size fractions (small and large cells) under PAR and PAR+UVR. All given values are mean values (standard deviation in parenthesis).

	PAR		PAR+UVR	
	Small (<2 μm)	Large (>2 μm)	Small (<2 μm)	Large (>2 μm)
IPP ($\text{mg C m}^{-2} \text{ h}^{-1}$)	14.9 (9.0)	16.7 (13.2)	19.1 (11.2)	30.6 (16.7)
Contribution (%)	49.0 (7.6)	51.0 (7.6)	37.9 (8.2)	62.1 (8.2)
P/B ratio	4.6 (2.7)	11.6 (11.0)	5.8 (3.6)	21.1 (17.6)

4. Discussion

4.1. The Effect of UVR Penetration on Primary Production

In this study, we investigated the impact of UVR exposure on primary production rates. The findings revealed a slight inhibitory effect of UVR exposure on surface primary production rates, resulting in a reduction in carbon incorporation compared to conditions without UVR (Figure 3). The inhibition of primary production due to UVR exposure at the surface was approximately 3.5%. This decrease can be attributed to the significant attenuation of UVR near the sea surface, as UVR is strongly absorbed by seawater. Previous studies have reported that UVR can diminish the synthesis of chl *a* and primary production at surface waters by up to 50% under the ambient levels of UVR, particularly when related to UVB radiation [6,38,66]. While this study did not differentiate between

the effects of UVA and UVB on primary production, the UVR data indicated considerably lower UVB to PAR ratios (mean $\pm$ S.D. = $0.38 \pm 0.11\%$) compared to UVA to PAR ratios (mean $\pm$ S.D. = $18.03 \pm 3.83\%$). This suggests that the impact of UVB radiation on phytoplankton may be less pronounced compared to UVA. Specifically, the UVB to PAR ratio in our study was approximately two times lower than those (UVB/PAR, 0.71–0.86%) reported in the South China Sea [9], although UVA to PAR ratios from this study are close to those (UVA/PAR, 15.5–17.8%) given by Gao et al. (2007a) [9]. The high UVB to PAR ratio reported by Gao et al. (2007a) [9] could result in a notable inhibition by UVB for phytoplankton carbon fixation in their study, whereas we observed the weaker inhibition of UVR on surface primary production. Additionally, the balance between UVR-induced damage (mainly UVB) and repair (mainly UVA) is known to play an important role in controlling primary production [41]. Thus, the relatively low UVB dose in our study may have resulted in a mild inhibition of surface primary production. However, this approach should be considered with some caution because UVB doses are often sublethal or do not cause damage when different filters are used to discriminate between UVA and UVB.

Unlike at the surface, UVR exposure has not affected negatively on primary production rates at deeper depths (Figure 2a). Phytoplankton exposed to UVR assimilated more carbon than those under only PAR conditions, suggesting that UVR can act as an additional energy source for photosynthesis at those depths. Overall, the results demonstrated an approximately 1.5-fold increase in the IPP over the euphotic zone under the UVR penetration. These findings align with previous laboratory studies [22] and field investigations [34,67], which have showcased the ability of solar UVR to stimulate phytoplankton photosynthesis and enhance primary production. Notably, Gao et al. (2021) [68] demonstrated that solar UVR (predominantly UVA radiation) facilitates CO₂ concentrating mechanisms (CCMs) and the carbon fixation of phytoplankton. Indeed, our study showed a highly significant positive correlation between UVR and IPP ($r = 0.98$, $p < 0.01$) (Figure 4). This could be associated with the relatively low PAR conditions ($160.9 \pm 78.2 \text{ W m}^{-2}$) during the incubation period, although some studies revealed that a PAR irradiance of $>160 \text{ W m}^{-2}$ is a value sufficient to saturate photosynthesis in natural phytoplankton communities [18,69].

Previous studies have reported that solar UVR, particularly UVA radiation, can drive photosynthesis in phytoplankton communities under relatively low irradiance conditions, such as during cloudy days [9,68]. According to Li and Gao (2013) [33], microplankton (not the case for nano- and pico-phytoplankton) exposed to both PAR and UVR exhibit higher carbon fixation rates compared to those exposed only to PAR exposure under low PAR intensity conditions (i.e., $<200 \text{ W m}^{-2}$). Therefore, under the combination of low PAR levels and a low UVB dose, UVR may contribute to the enhancement of primary production in our study. Nevertheless, it is crucial to consider that the relationship and slope of IPP (or surface PP) and UVR may differ under conditions of high PAR intensity.

Furthermore, the environmental conditions, particularly nutrient conditions, may play a favorable role in the production rates of phytoplankton under UVR exposure. During this study, we observed high ambient nutrient concentrations in the water column (Table 1). These elevated nutrient levels were previously reported by Park et al. (2014) [70], who noted abundant nutrient supply from sea-ice-melted waters during the spring season in the East/Japan Sea. It is noteworthy that nutrient limitation can heighten the sensitivity of phytoplankton to UVR levels [71]. Consistently, Litchman et al. (2002) [72] found a greater UVR inhibition in nutrient-limited cultures of dinoflagellates compared to nitrogen-replete conditions. Moreover, the decline in growth rates of chlorophyte species can occur more rapidly after phosphorus depletion in the presence of UVR [73]. Conversely, nutrient addition can lead to the increased synthesis of UV-absorbing compounds in a dinoflagellate, thus facilitating better photosynthetic performance compared to non-enriched samples [74]. Therefore, the high nutrient concentrations observed during this study could support the utilization of UVR as an additional energy source by phytoplankton, ultimately resulting in increased PP during UVR exposure. According to Erga et al. (2005) [41], CDOM content could significantly impact UVR attenuation and the consequent inhibition of primary

production, since high CDOM concentration at the surface can reduce UVR penetration and enhance phytoplankton productivity within the euphotic zone. A previous study has observed high CDOM concentrations in the southwestern area of the East/Japan Sea [75]. Although CDOM concentration was not measured during our study period, we can anticipate high CDOM levels based on the location of our sampling sites, primarily situated in the southwestern area. If this holds true, the high CDOM concentration might mitigate UVR inhibition on primary production, thereby contributing to the observed increase in primary production within the euphotic zone during this study. Nevertheless, comprehensive examination of various environmental factors, including optical properties in the water column, is necessary to gain a better understanding of the changes in primary production under conditions where UVR is anticipated to increase in the future. Moreover, it is important to monitor seasonal variations in UVR effects on primary production in the region, as the underwater transmission of UVR and environmental conditions vary throughout different seasons [32,76,77], potentially leading to different responses of phytoplankton to UVR.

4.2. Phytoplankton Size-Differential Response to UVR

The response of phytoplankton to UVR exposure may vary depending on their different cell sizes as the light availability, UVR tolerance or sensitivity, and carbon fixation can differ among size fractions [19,33,78,79]. In this study, UVR exposure led to a two-fold increase in primary production in large cells ($>2\ \mu\text{m}$) compared to the exposure of solely photosynthetically active radiation (PAR) (Table 3). In addition, UVR resulted in an increased proportion of large cells the proportion in terms of community contribution to primary production. These findings demonstrate the advantage of large cells over small cells in terms of primary production enhancement during UVR exposure.

Previous studies have indicated that large-size phytoplankton cells are more effective in biosynthesizing and accumulating UV-absorbing compounds such as mycosporine-like amino acids [33,35,80,81]. These compounds can protect cells from UVR damage and facilitate the transfer of UV energy to chl *a* for photosynthetic carbon fixation [67,77]. In fact, Taguchi et al. (2016) [47] revealed that the attenuation of UVR was positively correlated with the concentration of mycosporine-like amino acids. Unlike large cells, small cells are sensitive to UVR due to their high surface-to-volume ratios, limited self-shading, and less effective screening pigments [14,55,80]. Li and Gao (2013) [33] demonstrated that large cells ($>20\ \mu\text{m}$) can utilize most of the UV spectral energy during photosynthesis, while small cells ($<5\ \mu\text{m}$) are unable to effectively utilize UVR when PAR is limited. Consistently, Wrona et al. (2006) [82] observed a decrease in the relative contribution of picoplankton ($<2\ \mu\text{m}$) to primary production, while the contribution of large cells ($>20\ \mu\text{m}$) increased with UVR exposure. Wu et al. (2010) [32] reported that the differential effects of solar UV on primary production could be closely related to dominant species composition. Therefore, our study highlighted the importance of phytoplankton cell size in determining primary production change and size contributions to total phytoplankton production in the presence of UVR in the region. Nonetheless, it is important to note that phytoplankton exhibit significant interspecific variability in UVR sensitivity and tolerance [83]. Generally, diatoms (larger size) are less affected by solar UVB radiation, while cyanobacteria and small eukaryotes are more susceptible to UVR-induced damage [5]. Interestingly, contrary to expectations, some studies have shown that diatoms can be sensitive to UV light [84]. Laurion and Vincent (1998) [36] demonstrated the UVR resistance of cyanobacteria due to effective UV-protective mechanisms. Kaczmarek et al. (2000) [85] also observed low UVR damages in a picocyanobacteria-dominated phytoplankton assemblage.

These contrasting results make it challenging to predict phytoplankton responses to UVR based on short-term measurements. Furthermore, Häder et al. (2015) [5] emphasized that phytoplankton of the same taxonomic groups can exhibit significantly different sensitivities to UVR exposure depending on their geographical origin, such as tropical, temperate, and Antarctic habitats. Further studies in various ocean conditions are necessary to better understand the responses of phytoplankton to UVR. Particularly, examining

species-specific sensitivity in conjunction with the size-differential response would be crucial in determining primary production change in the presence of UVR.

4.3. Methodological Limitations

Since this study is based on a controlled comparison in the absence and presence of UVR, some methodological limitations should be acknowledged. According to a previous study [86], polycarbonate bottles can penetrate some UVA radiation. Consequently, the data from these bottles may inherently include some effects of UVR. An alternative approach could involve using quartz bottles covered with UV-cut filters to distinguish UVR-induced primary production and to separately evaluate the effects of UVA and UVB on primary production. Our experimental design does not replicate the exact underwater UVR environment. Using neutral density filters to attenuate solar radiation does not accurately reproduce the differential attenuation of UVR and PAR at depth. This limitation suggests that calculating primary production integrated with global radiation may lead to an overestimation of the impact of UV at greater depths. Future studies should include direct measurements of UVR attenuation within the water column to quantify primary production under natural UVR exposure conditions. The logistical constraints of our expedition significantly influenced the limited number of replicates in our treatments with and without UVR. While the limited replication is not ideal for robust statistical analysis, we observed consistent patterns of primary productivity response to UVR penetration across different seasons (unpublished data). These consistent patterns suggest that, despite the low replication, the observed trends are reliable and indicative of the general response of phytoplankton in the study area.

5. Conclusions

In conclusion, despite some limitations, this study provides valuable insights into the impacts of solar UVR on the primary production of phytoplankton in the East/Japan Sea, an area with limited research on this topic. These results highlight the critical effects of UVR penetration on phytoplankton primary production, leading to a substantial increase in carbon uptake rates. The presence of abundant nutrient conditions during the study period likely contributed to enhanced primary production by stimulating the synthesis of UV-absorbing compounds and/or improving photosynthetic performance. The low dose of UVB (mainly related to damage) during the study period may have resulted in weak inhibition on primary production, suggesting that the difference in light dose or balance between UVR damage and repair, particularly UVA, plays an important role in controlling primary production [41]. Furthermore, this study demonstrates a size-differential response among phytoplankton groups, with large cells exhibiting higher photosynthetic efficiency compared to small cells, indicating their effective utilization of UVR energy for photosynthesis. This highlights the influence of phytoplankton size composition on their response to UVR in terms of primary production.

Recently, some studies have reported the effects of UVR on phytoplankton under conditions of ocean acidification or global warming [18,68,87,88]. In the context of global warming, the projected increase in surface temperatures is expected to intensify stratification, resulting in changes to the depth of the mixed layer and reduced nutrient availability within the euphotic zone. Additionally, warming is likely to lead to higher doses of underwater UVR in the future [11]. These combined environmental changes will not only impact the composition of phytoplankton communities but also influence the species-specific sensitivities and vulnerabilities to UVR, including those related to cell size, as demonstrated in this study. While this study reveals a positive effect of UVR on total primary production in the East/Japan Sea, it remains challenging to anticipate whether phytoplankton will exhibit synergistic or antagonistic interactions with UVR under rapidly changing ocean conditions. Therefore, there is a need for further experimental field studies that specifically investigate the interactive effects of UVR and environmental factors. These studies will

contribute to advancing our understanding of the effects of UVR on phytoplankton and enable more comprehensive assessments of its impacts.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse12081258/s1>, Figure S1: Schematic representation of the experimental design, including treatments in which phytoplankton received full solar radiation (quartz bottles), UVR was removed (polycarbonate bottles).

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