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ORIGINAL ARTICLE

Effect of ultraviolet irradiation on the production and composition of fatty acids in plankton in a sub-Antarctic environment

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Abstract We investigated the effects of ultraviolet-B (UV-B) radiation on the natural phytoplankton assemblage in Marine Cove on King George Island, Antarctica, in December 2005. The amount of newly synthesized phytoplankton polyunsaturated fatty acids (PUFAs) was lower with exposure to full irradiation (PAR+UV-A+UV-B) than without such exposure (exposed instead to PAR+UV-A radiation) in an in situ incubation under the light conditions in two different types of incubation bottles: quartz bottles transmitting all light wavelengths including UV-B and polycarbonate bottles with no UV-B transmission and 20 % reduced PAR compared to the quartz bottle. However, the amount of newly synthesized saturated fatty acids was greater with than without UV-B radiation. Thus, UV-B radiation may have a significant influence on fatty acid synthesis in phytoplankton. In particular, the production of eicosapentaenoic acid [20:5(n-3)] and docosahexaenoic acid [22:6(n-3)] was reduced during incubation under the natural solar radiation including UV-B. To understand the indirect influence of UV-B on herbivores (the secondary producer), we conducted feeding experiments with amphipods fed in situ on the natural phytoplankton assemblage. The amphipods fed on the phytoplankton with the low PUFA values also exhibited a low PUFA accumulation rate, which could negatively affect their growth, development, and reproduction. Consequently, the diminished rate of essential fatty acid synthesis [especially 20:5(n-3) and 22:6(n-3)] in primary producers caused by UV-B exposure could affect the structure and function of the Antarctic marine ecosystem.

Keywords UV-B radiation · Carbon stable isotope · Fatty acids · Antarctica · Food web

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1 Introduction

The exposure of the Earth's surface to ultraviolet (UV) radiation (280–400 nm) has increased due to the destruction of the ozone layer, and has particularly affected the Antarctic and its surrounding seas (Smith et al. 1992; Newman et al. 2001; Solomon et al. 2007). Direct exposure to natural sunlight, particularly UV-B radiation (280–320 nm), has been shown to damage aquatic organisms (Williamson et al. 2001; Rozema et al. 2002), and UV-B radiation affects the survival, growth, and production of phytoplankton (Skerratt et al. 1998; Vincent and Neale 2000). The primary production of the water column is reduced by 25–76 % in response to UV-B radiation during phytoplankton blooms in the ice marginal zone of the Southern Ocean (Smith and Nelson 1986). Within the ultraviolet radiation (UVR) spectrum reaching ground level, the wavelengths in the UV-B band are the most detrimental to biological systems (Häder et al. 2003). UV-B radiation can limit primary production by reducing the ATP content in natural assemblages of marine phytoplankton (Vosjan et al. 1990), and it is possible that increasing UV-B radiation may suppress not only algal carbon fixation but also carbon transfer to higher trophic levels (Worrest et al. 1978; Häder et al. 2007). Additionally, UV-B radiation negatively affects several cellular

enzymes and biochemical processes (Döhler et al. 1991; Häder et al. 2003). Subsequently, changes in cellular biochemicals, such as fatty acids and amino acids in phytoplanktonic cells, can directly influence the quality of food available for organisms at higher trophic levels (Watanabe et al. 1983; Goes et al. 1994) and significantly affect the development and survival of copepods (Huntley et al. 1987). Kouwenberg and Lantoine (2007) reported that a reduced egg production and high frequency of naupliar abnormalities in the copepod, *Calanus helgolandicus*, could be explained by a deficiency of essential components in the maternal diet induced by the stress of UV-B exposure.

Polyunsaturated fatty acids (PUFAs) play an important role in the food web because they affect key physiological processes and are precursors to many hormones (Jónasdóttir et al. 2009; De Troch et al. 2012). Heterotrophic organisms do not synthesize these compounds de novo at a sufficient rate to satisfy their physiological needs and thus must acquire them from their diet (Sargent et al. 1997). Several studies have reported negative effects of UV-B radiation on PUFA production in marine phytoplankton species (Goes et al. 1994; Wang and Chai 1994; Skerratt et al. 1998). UV radiation may affect the nutritional quality of phytoplankton by the disruption of fatty acid synthesis and/or the oxidation of PUFAs (Döhler and Biermann 1994; Goes et al. 1994; Wang and Chai 1994; Skerratt et al. 1998). In addition, the effects of UV-B radiation varied among marine phytoplankton species (Hessen et al. 1997; Obermüller et al. 2007; Thomson et al. 2008) and zooplankton (Nahon et al. 2009, 2010; Pruski et al. 2009).

The purposes of this study are to clarify the changes in fatty acid synthesis that occur in phytoplankton cells and zooplankton (Amphipoda) exposed to natural UV-B radiation, and to discuss the potential effects of UV-B radiation on trophic interactions between primary producers and primary consumers within the Antarctic marine pelagic food chain.

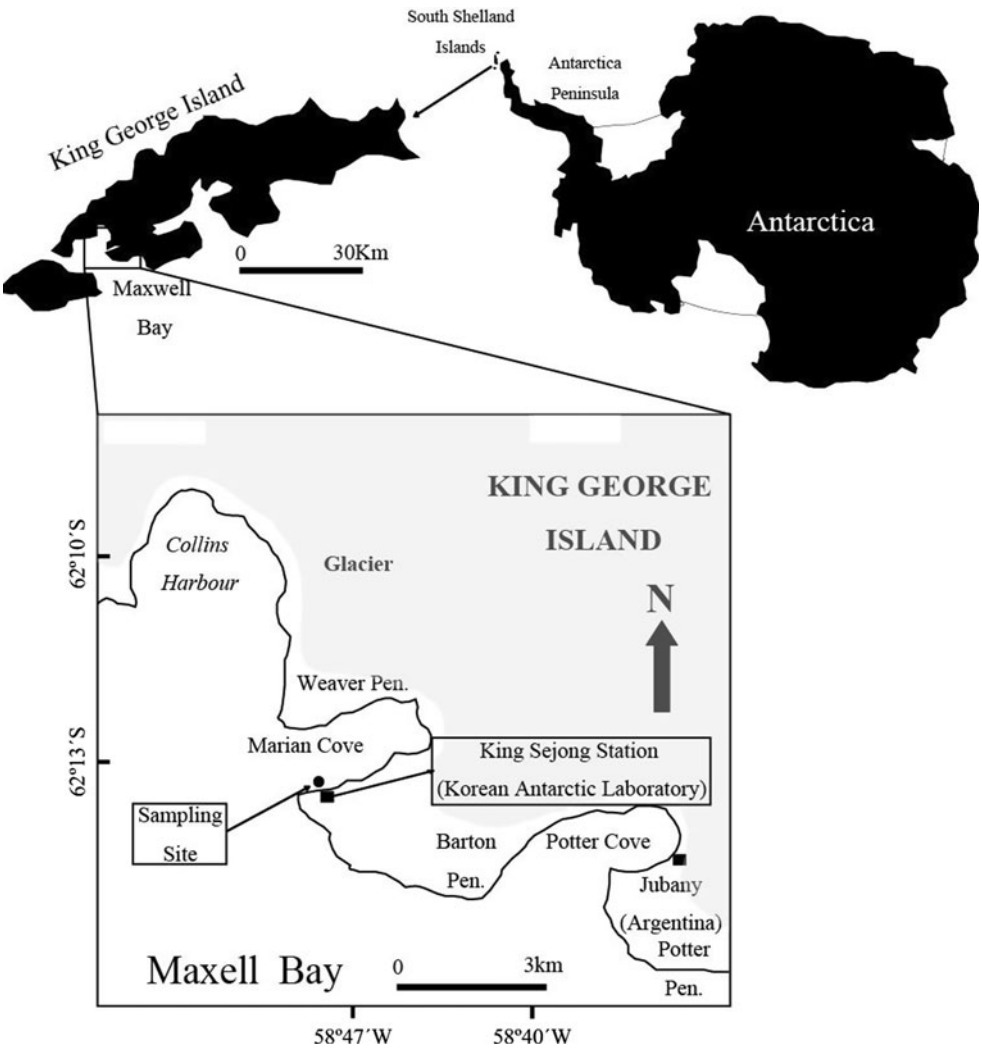

Fig. 1 Location of the study sampling and incubation site

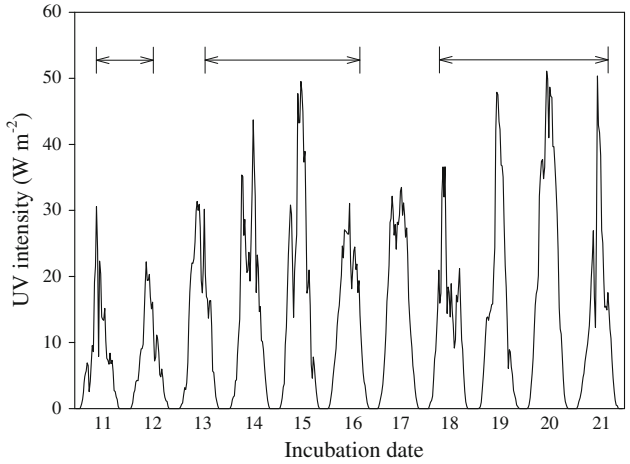

Fig. 2 Daily UV-B irradiation intensity (W m^{-2}) of King George Island during the incubation period (December 2005). *Arrows* indicate the incubation periods

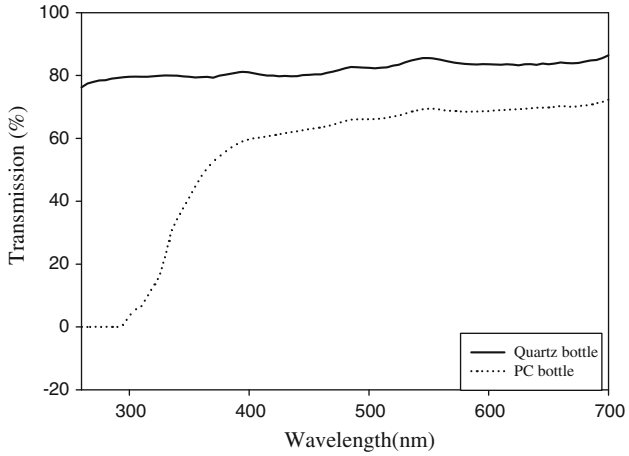

Fig. 3 Light transmission of polycarbonate (*PC*) and quartz bottles used for the in situ incubations, measured by spectrophotometer

2 Materials and methods

Surface seawater was obtained from a sampling site (near a port) in Marian Cove (62°13′S, 58°47′W) on King George Island near Antarctica from 11 to 21 December 2005 (Fig. 1). A phytoplankton species composition analysis, including identification and quantification, was performed at each incubation time. The distribution of the phytoplankton species composition was determined using a microscope (BX53TR-32FB3F0; Olympus, Japan) under a combination of light and epifluorescence microscopy at ×400 for microplankton and at ×1,000 for autotrophic pico- and nano-plankton (Booth 1993).

2.1 Experimental design

Samples of surface seawater were collected using a Van Dorn sampler which may not be enough for a clean technique, but we just collected surface seawater and the micronutrient availability for phytoplankton assemblage might not be critical in the coastal seawater of Antarctica in this study. Before the experiment, the seawater samples were filtered through a 100-μm mesh to remove large zooplankton and detritus. The samples were incubated for 24 h (from 0900 hours, on 11 and 12 December) and for 72 h (from 13 to 16 December) in situ (with the bottles moored to a corner side of a port deck) to evaluate the effect of UV-B on the natural phytoplankton assemblage in the surface seawater. The feeding experiment was performed simultaneously by adding amphipods to the natural phytoplankton assemblage and incubating the combination for 72 h (from 18 to 21 December) (Fig. 2).

The seawater samples were poured into four 500-ml quartz bottles (HanJin Quartz) and into 1,000-ml polycarbonate bottles (PC; Nalgene Labware). The quartz bottles were used as controls, including for the UV-B irradiation (Fig. 3). We measure the spectral distribution of each materials piece (PC and quartz) by spectrophotometer (Varian cary 50; Agilent, USA) as shown in Fig. 3. As a tracer, ^{13}C $NaHCO_3$ (99 at.% of ^{13}C) was added to the bottles. To achieve an increase in the isotopic ratio of a particulate organic carbon, the ^{13}C level was increased up to 15 at.% in the dissolved inorganic carbon (DIC) pool, which resulted in an increase of 110–115 % in the concentration of the DIC (Fig. 4). However, this level of increase of the DIC has little effect on the uptake rate in oceanic environments (Hama et al. 1983; Shin et al. 2000), although the CO_2 availability can affect carbon fixation and the elemental composition of algal cells (Riebesell et al. 1993; Burkhardt and Riebesell 1997). After incubation, the samples were collected by filtration through precombusted (450 °C, 4 h) GF/F glass fiber filters (nominal pore size, 0.7 mm; Whatman™) and stored at −80 °C until analysis.

In addition, the gammarid amphipod, *Gondogeneia antarctica* (Calliopiidae, Eusiroidea), was collected from the intertidal shore of Marian Cove, King George Island, using a hand net. Animals between 0.5 and 1 cm in size were taken at water depths of 10–50 cm. The amphipods swam freely near the surface, receiving full natural radiation. For the experiment, the *G. antarctica* were collected from the surface using a 100-μm mesh net, and five of the sampled individuals were added to each incubation bottle which contained the ^{13}C-$NaHCO_3$ (99 at.% of ^{13}C) added to determine the effects on the amphipoda of a diet containing UV-B-exposed phytoplankton. After 72 h (from 18 to 21 December) of incubation, the amphipods were recollected using the 100-μm mesh net and stored at −80 °C until analysis to measure ^{13}C-enriched fatty acids via their grazing on the ^{13}C-labeled diet.

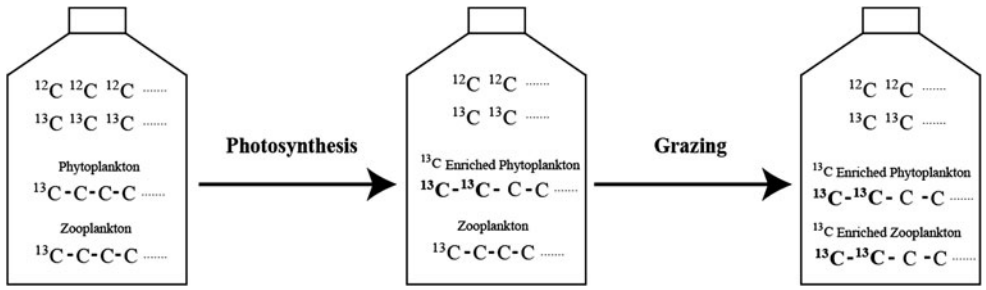

Fig. 4 Description of the in situ incubation experiment for phytoplankton photosynthesis and the grazing of the gammarid amphipod, *Gondogeneia antarctica* (Calliopiidae, Eusiroidea), using a ^{13}C tracer

2.2 Fatty acid analysis

Lipids were extracted with dichloromethane:methanol (2:1 v/v) after the addition of a C_{21} saturated fatty acid (21:0) as an internal standard according to the method described in Hama and Handa (1987).

The extraction was repeated three times under sonification for 20 min at <20 °C. After removal of the filter debris, the extracted lipids in the dichloromethane phase were separated from the water–methanol phase, saponified using 0.5 M KOH in methanol, and then methylated with BF_3 in methanol (80 °C for 30 min).

The concentrations of the fatty acid methyl esters (FAMEs) were determined using a gas chromatograph (HP 6890 GC system; Agilent) equipped with a flame ionization detector and a fused-silica capillary column (INNOWAX, 30 m × 0.25 mm i.d.; Agilent). Helium was used as the carrier gas. The injection and detection port temperatures were set at 300 °C, and the oven temperature was programmed to start at 40 °C for 1 min before increasing to 200 °C at a rate of 10 °C min^{-1}, and then to 250 at a rate of 2 °C min^{-1}. Finally, the oven temperature was increased to 300 °C at a rate of 10 °C min^{-1} and subsequently left at 300 °C for 5 min. The fatty acids were identified from the retention times of standards (37 component FAME mixture; Supelco, USA) and from mass spectra acquired using a combined gas chromatograph-mass spectrometer (GCMS-QP2010; Shimadzu, Japan). The GCMS was equipped with a fused-silica capillary column (VB-5, 30 m × 0.25 mm i.d.;Valco Bond, USA), and a temperature program identical to that used for the GC was employed. Chemical ionization spectra were obtained using isobutane as the reagent gas. The chemical ionization spectra were obtained under the following conditions: an ion source temperature of 200 °C, a repeat scanning speed of 0.5 s, and an *m/z* (mass to charge ratio) range of 100–400.

After the in situ incubation, a set of each treatment (POM and zooplankton) was pooled for the analysis of the fatty acid concentration and the enriched ^{13}C at.% because the amount of sample in each bottle replicate was insufficient for analysis; thus, the samples from all replicates were pooled, and the analytical results indicate average values for all measurements in this study. The ^{13}C at.% of each fatty acid was estimated by using the relative intensities of ions corresponding to both isotopes for the quasimolecular ion measured by the chromatographic peak maximum (Kouchi 1982; Hama and Handa 1987; Shin et al. 2003). The accuracy of this method for the estimation of ^{13}C at.% has been discussed earlier by Hama (1991) and Hama et al. (1993), who demonstrated an accuracy of ±3 % using GCMS analysis of the fatty acids and less than ±3 % with repeated analysis ($n = 3$).

The production rates of the individual fatty acids were calculated using a modified equation (Hama 1991).

$$\Delta\mathrm{FAC}(t) = \mathrm{FAC} \times \frac{a_{\mathrm{is}} - a_{\mathrm{ns}}}{a_{\mathrm{ic}} - a_{\mathrm{ns}}},$$

where $\Delta\mathrm{FAC}(t)$ is the amount of each fatty acid carbon photosynthetically produced during the incubation, a_{is} is the ^{13}C at.% in each fatty acid of the incubated sample, a_{ns} is the ^{13}C at.% in each fatty acid of the natural sample, a_{ic} is the ^{13}C at.% in the ^{13}C enriched inorganic carbon, and FAC is the concentration of each fatty acid carbon at the end of the incubation.

The possible isotopic discrimination against ^{13}C during photosynthetic uptake was not considered in our study because the correction for this discrimination has little significant effect on the uptake rate (Hama 1991; Shin et al. 2003). The production of FA in zooplankton is probably underestimated, because the isotopic ratio of food (particulate matter) is lower than that in inorganic carbon. However, this issue does not influence the relative compositional change in individual FA production rates of zooplankton in quartz and PC bottles through the in situ incubation experiment in this study.

3 Results

UV-B radiation was measured with a precision spectral pyranometer (model PSP, 295–385 nm; Eppley) at King

Sejong Station on King George Island. The average UVR value was 12.1 W m^{-2} during the in situ incubation experiments (from 11 to 21 December 2005) (Fig. 2). The ozone layer over the South Shetland Islands reached its minimum in September 2002 (159 Dobson Units, DU). The mean column ozone was 281 DU (minimum 198 DU) in November 2002 and 324 DU (minimum 300 DU) in December 2002 (source, AWI-Physics Department based on NASA TOMS data, http://ozoneaq.gsfc.nasa.gov/) (Thomson et al. 2008). The mean column ozone during our experimental period was 292 DU (minimum 269 DU) in December 2005.

During the incubation, the most abundant phytoplankton were *Phaeocystis* spp., with a relative abundance of 50.4–61.7 %. *Cryptomonas* spp. were second in abundance, at approximately 3–30 %. Bacillariophyceae and dinophyceae were present in small quantities (Table 1).

For the phytoplankton incubated in the quartz bottle, the percentage of fatty acids declined as the incubation time increased because of the UV-B effects (Table 2). The net fatty acid production rate of the phytoplankton cultured for 24 h varied from 11 to 14 μg C l^{-1} day^{-1} incubated in the PC and quartz bottles. With even longer incubation periods, the fatty acid production rates were 15 μg C l^{-1} day^{-1} in the PC bottle and 9.2 μg C l^{-1} day^{-1} for the phytoplankton incubated in the quartz bottle (Table 2). The low production rate due to UV-B radiation was accompanied by a difference in the percentage distribution of the newly assimilated carbon into fatty acids (Table 2). The production of PUFAs, in particular, was reduced in the quartz bottle (Table 2). With 24 h of incubation, there was little difference between the group incubated in the PC bottle and the single incubation in the quartz bottle. After 72 h, however, the relative percentage of production increased from 33 to 42 % for the SAFAs and from 16 to 19 % for the MUFAs incubated in the quartz bottle, and the corresponding percentage for PUFA production represented <39 % incubated in the quartz bottle whereas it was 51 % in the PC bottle (Table 2).

The incubation in the quartz bottle lowered the production rate of each fatty acid in the *G. antarctica* zooplankton incubated in situ with the phytoplankton (Table 3). The production rate of fatty acids was also low at the higher trophic level among the *G. antarctica* cultured with the phytoplankton incubated in the quartz bottle. The net fatty acid production rate of the phytoplankton cultured for 72 h with *G. antarctica* was 19 μg C l^{-1} day^{-1} in the PC bottle, but the rate was reduced to 13 μg C l^{-1} day^{-1} in the quartz bottle. The net fatty acid accumulation rate of the *G. antarctica* that consumed the phytoplankton cultured in situ as their main dietary component was 6.9 μg C l^{-1} day^{-1} in the PC bottle and 4.1 μg C l^{-1} day^{-1} in the quartz bottle (Table 3). The pattern of change in the fatty acid production rates due to UV-B radiation was similar to that of the phytoplankton cultured without *G. antarctica*. The UV-B radiation had a significant effect, in particular on the PUFA production rates of the phytoplankton and the *G. antarctica* cultured simultaneously under natural conditions. The PUFA production rate of the phytoplankton decreased from 52 % with the PAR exposure to 38 % in the quartz bottle (Fig. 5).

Table 1 The composition of the phytoplankton assemblage through in situ incubations

Date species	Incubation 1	Incubation 2	Incubation 3
Dinophyceae			
Gymnodinium spp. (<20 μm)			1.91 %
Bacillariophyceae			
Achnanthes sp.		0.01 %	
Chaetoceros spp.	0.02 %		
Cocconeis costata	0.02 %		
Fragilaria sp.	0.02 %	0.01 %	
Fragilariopsis cylindrus			0.38 %
Navicula glaciei		0.01 %	
Navicula sp.	0.01 %		0.02 %
Nitzschia sp.	0.17 %		
Thalassiosira spp.	0.01 %		
Cryptophyceae			
Cryptomonas sp.	29.60 %	15.89 %	8.01 %
Prymnesiophyceae			
Phaeocystis sp.	61.71 %	55.09 %	50.37 %
Unidentified sp. (micro-size)		0.02 %	
Unidentified sp. (nano-size)	3.51 %	5.38 %	15.64 %
Unidentified sp. (pico-size)	4.92 %	23.58 %	23.66 %
Number of species	10	8	7

Incubation 1 POM incubated for 24 h; *Incubation 2* POM incubated for 72 h; *Incubation 3* POM with zooplankton incubated for 72 h

4 Discussion

4.1 Effect of UV-B radiation on PUFA production rate in the natural phytoplankton assemblage of Antarctica

Our results confirm those of previous reports demonstrating that UV-B radiation may decrease the PUFA concentration in phytoplankton (Wang and Chai 1994; Goes et al. 1994; Skerratt et al. 1998). The production of PUFAs by phytoplankton may be preferentially affected by UV radiation

Table 2 Production rates (μg C l^{-1} day^{-1}) of individual fatty acids and their relative contribution to total fatty acid production rates on natural phytoplankton assemblage based on the PC bottle and the quartz bottle during in situ incubation for 24 and 72 h

	24 h				72 h			
	PC bottle		Quartz bottle		PC bottle		Quartz bottle	
	Production rate	Percentage	Production rate	Percentage	Production rate	Percentage	Production rate	Percentage
C12:0	ND	ND	ND	ND	ND	ND	ND	ND
C14:0	1.8	13	1.3	13	1.5	10	1.2	13
C15:0	ND	ND	0.02	0.14	0.2	0.93	0.2	1.8
C16:0	4.3	32	4.0	38	2.9	19	2.2	24
C16:1	1.4	11	1.1	11	1.8	12	1.2	13
C18:0	1.1	8.2	0.7	6.8	0.4	2.6	0.4	3.8
C18:1	1.2	8.6	0.9	8.2	0.7	4.7	0.6	6.4
C18:2	ND	ND	ND	ND	0.6	4.1	0.4	4.8
C18:3	1.6	12	1.2	11	1.0	6.6	0.6	6.9
C18:4	2.2	16	1.3	13	1.6	11	1.1	12
C18:5	ND	ND	ND	ND	1.1	7.6	ND	ND
C20:5	0.04	0.3	ND	ND	2.3	16	1.4	15
C22.6	ND	ND	ND	ND	0.9	6.3	ND	ND
SAFAs	7.2	53	6.1	58	5.0	33	3.9	42
MUFAs	2.6	19	2.0	19	2.4	16	1.8	19
PUFAs	3.9	28	2.5	24	7.5	51	3.6	39
Net production rate	14		11		15		9.2	

PC bottle polycarbonate bottle, *SAFAs* saturated fatty acids, *MUFAs* monounsaturated fatty acids, *PUFAs* polyunsaturated fatty acids, *ND* not detected

for several reasons. Intracellular reactive oxygen species created by UV-B radiation may generate harmful chemical species capable of lipid peroxidation, such as hydroxyl radicals (OH• or HO−), superoxide radicals (O_2^-), or their protonated form (HO_2), or hydrogen peroxide (H_2O_2) (Hessen et al. 1997). These chemical oxidants have detrimental effects on PUFAs because of their oxidative properties. Therefore, UV-B radiation may cause a decrease in the long-chain PUFAs in algal cells, although the membranes and organelles of the cells continuously defend against the oxidative deterioration of polyunsaturated lipids (Hessen et al. 1997). The oxidizability of simple PUFA esters is directly related to the number of doubly allylic positions present in the molecule (Gosgrove et al. 1987). Another inhibitory effect of UV-B radiation on PUFA synthesis may occur because UV-B radiation restricts ATP production in algal cells (Vosjan et al. 1990). This reduction in the supply of ATP could selectively reduce the cellular production of PUFAs (Goes et al. 1994). Because UV radiation affects the cellular stoichiometry of phytoplankton (Fauchot et al. 2000; Mousseau et al. 2000; Tank et al. 2003; Leu et al. 2007), such effects also inhibited for P-uptake in the green algae *Chlamydomonas reinhardtii* at low UV doses (Hessen et al. 1995). The initial stimulation was supposed to reflect a stress response with increased P-demands for photorepair (Hessen et al. 1997). Reduced ATP content in UV-stressed phytoplankton cells (Vosjan et al. 1990) also indicates the effect on the intracellular P metabolism.

In the present study, the production of long-chain fatty acids such as 20:5(n-3) and 22:6(n-3) was considerably lower when the plankton were exposed to UV-B radiation than when they were shielded from UV-B by the PC bottles. Although PUFAs make up a small fraction of the total amount of fatty acids within the lipid pool of phytoplankton cells, they are vital components of the cell (Hama 1988; Goes et al. 1997). The highly unsaturated fatty acids of the n-3 series [particularly 20:5(n-3) and 22:6(n-3)] are generally required and known to be essential nutrients for the growth, reproduction, and larval development of marine invertebrates (Harrison 1990, Jónasdóttir et al. 2009). A deficiency in the proportion of PUFAs within the cell wall membranes of phytoplankton can reduce membrane permeability and the ability of phytoplankton to assimilate nutrients. As a result, phytoplankton growth can be diminished (Goes et al. 1994, 1997). Our results were similar to those reported previously (Goes et al. 1994; Wang and Chai 1994). However, the inhibitory effect of

Table 3 Production rates (μg C l^{-1} d^{-1}) of individual fatty acid and their relative contribution to total fatty acid production rates of phytoplankton assemblage and amphipods incubated in the PC bottle and in the quartz bottle for 72 h

	POM (μg C l^{-1} day^{-1})				Amphipod (μg C $ind.^{-1}$ day^{-1})			
	PC bottle		Quartz bottle		PC bottle		Quartz bottle	
	Production rate	Percentage	Production rate	Percentage	Production rate	Percentage	Production rate	Percentage
C12:0	ND	ND	0.3	2.3	0.3	4.1	ND	ND
C14:0	1.8	9.7	1.6	12	0.3	4.0	0.1	2.8
C15:0	0.2	1.2	0.3	2.1	ND	ND	ND	ND
C16:0	3.3	17	2.9	22	0.7	10	1.3	30
C16:1	3.0	16	2.0	16	0.5	7.1	0.2	6.0
C16:2	0.8	4.5	0.6	4.8	ND	ND	ND	ND
C16:4	3.8	20	2.1	16	ND	ND	ND	ND
C18:0	0.3	1.7	0.4	2.9	0.3	4.4	0.2	5.3
C18:1	0.6	3.0	0.7	5.3	0.6	8.8	0.7	17
C18:2	1.2	6.4	ND	ND	ND	ND	0.1	2.6
C18:3	0.3	1.4	ND	ND	0.3	4.3	0.1	1.2
C18:4	ND	ND	0.4	3.0	0.3	3.7	ND	ND
C20:1	ND	ND	ND	ND	0.1	1.3	0.1	1.8
C20:4	ND	ND	ND	ND	0.1	1.3	0.04	0.9
C20:3	ND	ND	ND	ND	0.3	4.8	0.2	3.9
C20:5	3.6	19	1.8	14	2.2	32	0.4	9.1
C22:6	ND	ND	ND	ND	1.0	14	0.8	19
SAFAs	5.7	30	5.4	42	1.6	23	1.6	39
MUFAs	3.5	19	2.7	21	1.2	17	1.0	25
PUFAs	9.8	52	4.9	38	4.1	60	1.5	37
Net production rate	19		13		6.9		4.1	

PC bottle polycarbonate bottle, *SAFAs* saturated fatty acids, *MUFAs* monounsaturated fatty acids, *PUFAs* polyunsaturated fatty acids, *indi* individual, *ND* not detected

UV-B radiation on PUFA production in the natural phytoplankton assemblage of the Antarctic was elucidated by the culture experiment performed in situ in our study.

Phaeocystis spp. were the dominant species in the seawater collected for the in situ experiment on the intertidal shore of Marian Cove, King George Island. Skerratt et al. (1998) reported that 18:3(n-3) and 18:4(n-3) were increased in *Phaeocystis antarctica* when this species was exposed to low-level UV-B radiation (0.37 W m^{-2}). But our study exhibited that the newly assimilated carbon in 18:3(n-3) and 18:4(n-3) were similar in the phytoplankton with or without UV-B radiation. The production rate of newly produced 18:1 was also maintained in the both PC bottle and quartz bottle (Table 2). Our results indicated that the effect of UV-B radiation showed the less assimilated carbon in 18:1, 18:3(n-3), and 18:4(n-3) on *Phaeocystis* spp. The reason might be *Phaeocystis* spp. have been known to contain UV-absorbing compounds and to have greater tolerance to UV-B radiation exposure compared with diatoms and green algal flagellates, which contain relatively small amounts of UV-absorbing compounds (Yentsch and Yentsch 1982; Marchant et al. 1991). Consequently, *Phaeocystis* spp. could be the dominant phytoplankton species in the marine environment of the Antarctic under the increasing UV radiation intensity.

However, both UV-A and UV-B radiation may act to reduce the photochemical yield and growth rate on *Phaeocystis globosa* under high levels of solar radiation (Chen and Gao 2011). Our results also represented the UV-B radiation reduce the newly synthesized PUFA on the *Phaeocystis* spp.-dominant phytoplankton assemblage incubated in the quartz bottle.

4.2 Effect of UV-B radiation on PUFA assimilation by amphipods in the Antarctic and implications for food quality deterioration in the Antarctic pelagic ecosystem

UV-B radiation may have profound effects not only on primary consumers but also on the entire food web (Hessen et al. 1997). Increased UV-B radiation reduces the production (or synthesis) of PUFAs in phytoplankton cells.

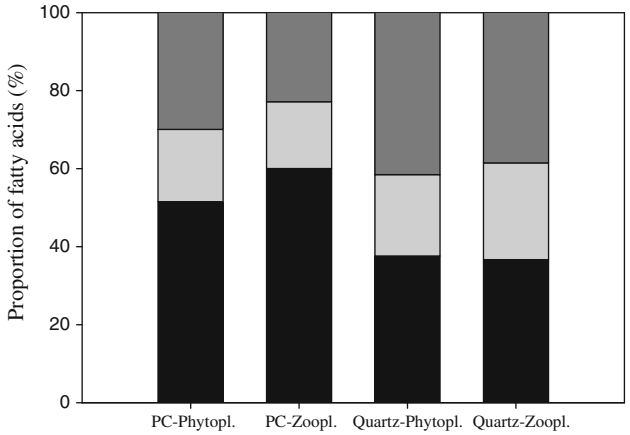

Fig. 5 Relative contributions of SAFA (*dark gray*), MUFA (*gray*), and PUFA (*black*) production rates in zooplankton and phytoplankton (*PC-Phytopl*. and *PC-Zoopl*. incubated in the PC bottle; *Quartz-Phytopl*. and *Quartz-Zoopl*. incubated in the quartz bottle). *SAFA* saturated fatty acid, *MUFA* monounsaturated fatty acid, *PUFA* polyunsaturated fatty acid

Therefore, UV-B radiation may affect the quality of the nutrients available to higher trophic organisms though the UV-B vulnerability of their food supplies (Thompson et al. 1993; Goes et al. 1994; Wang and Chai 1994). The levels of newly assimilated fatty acids in the omnivorous amphipod, *G. antarctica*, may be influenced by the fatty acid composition of phytoplankton exposed in situ to UV-B radiation. The low production rate of the PUFAs in the phytoplankton was proportionally reflected in their predator, *G. antarctica* (Fig. 5). These results indicate that an increased intensity of UV radiation affects not only phytoplankton physiology but also the population of herbivorous zooplankton. The intensity of UV radiation may play a major role in the food web by affecting the fatty acid composition, especially by reducing the amounts of PUFAs (Hessen et al. 1997). A dietary PUFA deficiency can limit the growth of herbivores (Watanabe et al. 1983; Lubzens et al. 1985). In particular, the rate of production of 20:5(n-3), an essential fatty acid, was significantly inhibited in phytoplankton cells exposed to UV radiation (Goes et al. 1994; Wang and Chai 1994). The UV-exposed phytoplankton could be associated with the lowest rate of 20:5 (n-3) production in *G. antarctica* (0.4 μg C indi^{-1} day^{-1}) because of the UV effects on the food sources (1.8 μg C l^{-1} day^{-1}) of *G. antarctica*. These values of phytoplankton (3.6 μg C l^{-1} day^{-1}) were higher in the PC bottle than in the quartz bottle. In addition, the absolute concentrations and rates of production of new 22:6(n-3) in the amphipods less produced under the high UV-B radiation (0.8 μg C indi^{-1} day^{-1}) than without UV-B conditions (1 μg C indi^{-1} day^{-1}) (Table 3). However, in the POM that included *Phaeocystis* spp. as the dominant species, no photosynthesized 22:6(n-3) was detected under the natural UV-B exposure, and the *G. antarctica* had a low 22:6(n-3) content. It is possible that *G. antarctica* accumulates tiny amounts of 22:6(n-3) from its phytoplankton food source or biosynthesizes 22:6(n-3) from precursors such as 18:3(n-3) and 18:4(n-3) obtained from phytoplankton (De Troch et al. 2012). Our results showed the negative effect of UV-B radiation on the biosynthesis of 20:5(n-3) by *G. antarctica* after assimilating photosynthetically produced fatty acids (Table 3).

Another reason for the decrease in PUFAs might be that toxic photochemical products, such as hydrogen peroxide and hydroxyl radicals produced by UV radiation, affect membrane phospholipids in amphipods (Clarke et al. 1985; Kawashima et al. 1999). When *G. antarctica* are exposed to UV radiation in an aquatic environment, the PUFA content in the cell membranes may decrease not only because of direct damage but also because of the low dietary PUFA content produced by UV-exposed phytoplankton. Zooplankton lipids are derived primarily from dietary sources, and little de novo synthesis occurs (Goulden and Place 1990; Phleger et al. 1998). In the case of *Daphnia*, de novo fatty acid synthesis contributed <2 % of the total fatty acids (Goulden and Place 1990), and most fatty acids were incorporated from dietary sources (Sundbom and Vrede 1997; Weers et al. 1997).

The effect of UV-B radiation on phytoplankton and the amphipod, *G. antarctica*, was tested through in situ incubation in the Antarctic using a ^{13}C tracer. The negative effects of UV-B radiation on PUFA production in phytoplankton were found in the intertidal environment of the Antarctic, demonstrating a decrease in the nutritional quality of both the phytoplankton and *G. antarctica* tested in situ. These results provide evidence supporting the hypothesis that UV-B radiation affects the carbon flow at low trophic levels that include phytoplankton and zooplankton in the coastal region of Antarctica.

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