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Growth, DMS and DMSP production in *Emiliania huxleyi* under elevated CO_2 and UV radiation☆

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ABSTRACT

The effects of ocean acidification and solar radiation on marine organisms have received increasing attention. Coccolithophores are a major producer of dimethylsulfoniopropionate (DMSP), which is a precursor of dimethylsulfide (DMS), a volatile biogenic active gas related to climate. Here, we investigated the individual and combined effects of elevated CO_2 and ultraviolet radiation (UVR) on growth, DMS, and DMSP production of *Emiliania huxleyi*. Elevated CO_2 (1000 μatm, HC) decreased the cell concentration, DMS, and particulate DMSP ($DMSP_p$) concentrations by 17%, 20%, and 13%, respectively, compared with ambient CO_2 (400 μatm, LC) in the semi-continuous culture. The addition of UVA to photosynthetically active radiation (PAR) increased cell concentration of *E. huxleyi* by 16% on day 4, which may be due to the photorepair effects induced by UVA, and the effect was time-dependent. PAR + UVA and PAR + UVA + UVB exposure decreased cellular DMS by 25%–56%, and increased cellular $DMSP_p$ by 60%–130% compared with PAR on days 3–4. Cellular $DMSP_p$ followed the order: PAR + UVA > PAR + UVA + UVB > PAR, and HC had no significant effects on cellular $DMSP_p$ compared with LC in the combined experiment. These results aid our understanding of the effects of ocean acidification and UV radiation on the production of methyl sulfur compounds in the ocean.

1. Introduction

The atmospheric CO_2 concentration has increased since industrialization began in the 1850s. The ocean is the major sink for atmospheric CO_2, and about one-third of the atmospheric CO_2 is incorporated in seawater, leading to ocean acidification (OA) (Sabine et al., 2004). OA changes the seawater carbonate chemistry and decreases seawater pH (Caldeira and Wickett, 2003). The atmospheric CO_2 concentration is predicted to reach 1000 μatm and 1900–2300 μatm by the years 2100 and 2300, respectively, which will decrease pH by 0.3–0.5 and 0.77 units, respectively (Caldeira and Wickett, 2003, 2005). The effects of OA on marine organisms (Huang et al., 2018; Hutchins and Fu, 2017; Kurihara and Ishimatsu, 2008; Müller et al., 2017; Riebesell et al., 2017), particularly calcifying phytoplankton, zooplankton, and other animals with calcium carbonate in their bodies, have been documented by many studies (Albright et al., 2016; Hofmann et al., 2010; Li et al., 2017; Tong et al., 2018). Coccolithophores, diatoms, and cyanobacteria have been the focus to study changes in the phytoplankton community structure and the physiology induced by OA (Dutkiewicz et al., 2015; Li et al., 2019; Tong et al., 2018). Elevated CO_2 has negative (Gao et al., 2009; Gao and Zheng, 2010), neutral (Feng et al., 2008), and positive (Iglesias-Rodriguez et al., 2008) effects on photosynthesis and the growth rates and calcification in *Emiliania huxleyi* and *Corallina sessilis*. The algal growth and photosynthesis rate changes were a net result of the balance of the positive effects caused by elevated CO_2 and negative effects caused by decreased pH (Gao et al., 2009). Different abilities of using bicarbonate or CO_2 concentrating mechanisms at different elevated CO_2 levels and other experimental conditions (i.e., irradiance) may be the

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reasons for the contradictory results (Gao and Zheng, 2010). In addition to short-term (ca. 10 generations) culture (Li et al., 2020), long-term (e.g., 1000 generations) experiments of *Gephyrocapsa oceanica* under elevated CO_2 (1000 μatm) have been performed to evaluate the effect of future CO_2, and showed a decline in growth rate under elevated CO_2 compared with that under atmospheric CO_2 (400 μatm) (Tong et al., 2018).

Solar ultraviolet radiation (UVR, 280–400 nm) due to ozone depletion is a major environmental threat to marine biota (Kataria et al., 2014). UVR has negative effects on primary production (Guan and Gao, 2010), bacterial communities (Hernández et al., 2009), coral chlorophyll *a* (Chl *a*) (Zhou et al., 2017), and copepod feeding (Yu et al., 2009). UVB (280–315 nm) radiation induces DNA damage (Buma et al., 2000), inhibits photosynthesis and growth (Guan and Gao, 2010), and changes the ultrastructure and antioxidant system (Tian and Yu, 2009) in phytoplankton. In addition, the positive effects induced by UVA (315–400 nm), i.e., enhanced photosynthetic rates, photosynthetic carbon fixation and activity of CO_2 concentrating mechanisms in phytoplankton (Gao et al., 2007; Gao et al., 2021; Helbling et al., 2003), and less breakage of filaments in the cyanobacterium *Arthrospira platensis* (Wu et al., 2005), have also been documented. DNA damage caused by UVB is photorepaired by UVA (Karentz et al., 1991), yet the repair mechanism induced by UVA is unknown.

Dimethylsulfide (DMS), an enzymatic cleavage product of dimethylsulfoniopropionate (DMSP), is a volatile biogenic active gas related to the formation of cloud condensation nuclei and thereby global climate (Charlson et al., 1987). DMSP is mainly produced by phytoplankton, phototrophic prokaryotes (Keller et al., 1989), higher plants (Dacey and Blough, 1987), and Alphaproteobacteria (Curson et al., 2017). Dinophyceae and Prymnesiophyceae (i.e., coccolithophorids) are the main DMSP producers among phytoplankton (Keller et al., 1989). *E. huxleyi* is a dominant coccolithophore on the surface seawater of the Yellow Sea and the East China Sea in summer, with its abundances ranged from 0 to 7.35 cells mL^{-1} (average: 0.90 cells mL^{-1}) (Sun et al., 2014). *E. huxleyi* is being affected by OA and have presented declining calcification and growth rates (Riebesell et al., 2000). As the most abundant extant coccolithophore morphospecies, *E. huxleyi* is an important DMS and DMSP producer (Holligan et al., 1993). Consequently, changes in DMS production in *E. huxleyi* due to OA may have important effects on the global sulfur biogeochemical cycle and the global climate (Hopkins et al., 2010).

Changes in DMS and DMSP concentrations under elevated CO_2 have been investigated in previous studies but different results have been reported (Hopkins et al., 2010; Hopkins and Archer, 2014; Vogt et al., 2008). Elevated CO_2 increases (Hopkins and Archer, 2014), decreases (Archer et al., 2013; Avgoustidi et al., 2012; Hopkins et al., 2010; Six et al., 2013; Zhang et al., 2018), or has no significant effect on DMS concentration (Vogt et al., 2008), compared with ambient CO_2. In parallel, DMSP is increased (Archer et al., 2013), decreased (Avgoustidi et al., 2012; Hopkins et al., 2010; Hopkins and Archer, 2014), or not affected by elevated CO_2 (Vogt et al., 2008; Zhang et al., 2018). Several factors, i.e., phytoplankton composition and biomass, algal DMSP lyase activity (DLA), zooplankton grazing, bacterial metabolism of DMSP and DMS, result in the different variations of DMS and DMSP production under elevated CO_2 (Archer et al., 2013; Archer, 2007; Kim et al., 2010; Kiene et al., 2000). Yet, the OA mechanisms that affect coccolithophore growth, and DMS and DMSP production have not been clearly clarified.

Many studies have demonstrated that UVR negatively affects marine microalgae, i.e., declining rates of growth, photosynthesis, and calcification in *E. huxleyi* (Guan and Gao, 2010; Van Rijssel and Buma, 2002). However, although some studies show that enhanced UVR inhibits DMSP production in *Phaeocystis antarctica* (Hefu and Kirst, 1997), or increases cellular DMSP content accompanying a decrease in growth rate of *E. huxleyi* (Van Rijssel and Buma, 2002), the effects of UVR on DMS and DMSP production of *E. huxleyi* have not been clarified.

Here, the individual and combined effects of elevated CO_2 (1000 μatm) and UVR on growth, DMS, and DMSP production were evaluated in *E. huxleyi*. The results will be helpful in the understanding of cycles of methyl sulfur compounds under elevated CO_2 and UVR.

2. Materials and methods

2.1. Algal culture

E. huxleyi (PML B92/11) was isolated from the coastal waters off Bergen, Norway. The algae were cultured at the exponential growth phase in Aquil medium (Sunda et al., 2005) at 20 °C and a 12 h: 12 h light: dark cycle with irradiance of 120 μmol m^{-2} s^{-1} photon flux density. Axenic algae were cultured in 2 L polycarbonate bottles sealed with polytetrafluoroethylene (PTFE) septum lids with minimal headspace (<5%). Seawater was filtered through a GF/F filter (Whatman, 0.7 μm pore size) and sterilized by autoclaving for 20 min at 121 °C.

2.2. Semi-continuous culture under elevated CO_2

Ambient CO_2 (400 μatm, LC) and elevated CO_2 (1000 μatm, HC) were used to evaluate the effects of OA on algal growth and DMS and DMSP production. HC and LC media were obtained by pre-bubbling sterilized seawater with CO_2-enriched air in a CO_2 chamber (HP1000G-D, Wuhan, China) and ambient air to equilibrium for 12 h at 20 °C. A portable CO_2 meter (M170, Vaisala Oyj, Finland) was used to monitor pCO_2 in the CO_2 chambers. Semi-continuous cultures were obtained to maintain *E. huxleyi* cell concentration $<1 \times 10^6$ cells mL^{-1} by diluting every 4 days with pre-equilibrated HC and LC medium at 20 °C to maintain stability of the carbonate chemistry and pH variations (<0.05 pH). The dilution rates for LC and HC were 1: 51 and 1: 46, respectively, based on the cell concentrations at day 4 and day 0. The pH values under LC and HC were 8.03/8.07 and 7.72/7.76 at the beginning/end of the experiment, respectively. Algal media were siphoned into glass-stoppered bottles, and cell concentration, specific growth rate (μ), cell size, pH value, Chl *a* content, and DMS and DMSP concentrations were determined at day 8 when the algal cells had acclimated for at least eight generations. There were three biological replicates for each CO_2 level.

2.3. UV radiation experiment

E. huxleyi suspensions in each of three replicates were placed in quartz tubes and exposed to a solar simulator (Hönle, UV Tech., Martinsried, Germany). The suspensions were exposed to three different solar radiation treatments by covering the quartz tubes with different cutoff films. Photosynthetically active radiation (PAR), PAR + UVA (PA), and PAR + UVA + UVB (PAB), where the quartz tubes were covered with 395-nm cutoff film (Ultraphan UV Opak, Digefra, Munich, Germany), 320-nm cutoff film (Montagefolie, Folex, Dreieich, Germany), and 295-nm cutoff film (Ultraphan, Digefra, Munich, Germany), and the wavelengths of >395 nm, > 320 nm, and >295 nm were transmitted, respectively. A filter radiometer (ELDONET, Real Time Computer Inc., Germany) was utilized to measure PAR, UVA, and UVB. The irradiance levels of PAR, UVA, and UVB were 97.8 W m^{-2} (450 μmol photons m^{-2} s^{-1}), 21.6 W m^{-2}, and 0.94 W m^{-2}, respectively. The algal suspensions were transferred to the illuminating incubator (GXZ380, Ningbo Jiangnan Instrument Factory, China) at 120 μmol m^{-2} s^{-1} photon flux density and cultured under a 12 L: 12D photoperiod after 2 h of radiation exposure daily.

2.4. Combined elevated CO_2 and UVR experiment

In addition to elevated CO_2 or UVR alone, the effects of elevated CO_2+UVR were also investigated to evaluate the interaction between OA and solar radiation. Semi-continuous cultures of *E. huxleyi* under elevated CO_2 (1000 μatm, HC) and ambient CO_2 (400 μatm, LC) were set

up to determine the response of phytoplankton acclimating to a stable OA environment. The concentration of *E. huxleyi* cells was diluted every 3 days with pre-equilibrated HC and LC medium. The dilution rates for different treatments (LC + PAR, HC + PAR, LC + PA, HC + PA, LC + PAB, and HC + PAB) ranged from 1: 34 to 1: 41, based on the cell concentrations at day 3 and day 0. Then the cultures were exposed to solar radiation (PAR, PA, and PAB) with the irradiance levels described above. After exposure, the algae were placed in the illuminating incubator. The pH values under LC and HC were 8.00/8.03 and 7.73/7.77 at the beginning/end of the experiment, respectively. Cell concentration, specific growth rate, cell size, pH, Chl *a* content, and DMS and DMSP concentrations were determined at day 6 when the algal cells had acclimated for at least eight generations. Three replicates of each treatment were run.

2.5. Cell concentration, cell size, and specific growth rate measurements

Cell concentration and cell size were determined with a Z2 Coulter Particle Counter and Size Analyzer (Beckman, Buckinghamshire, UK), and the aperture of 3–7 μm was used. Specific growth rate (μ) was calculated by the equation: $\mu = (\ln C_1 - \ln C_0)/(t_1 - t_0)$, where C_1 and C_0 are the cell concentrations at time t_1 and t_0, respectively (Zhang et al., 2015).

2.6. pH measurements

The pH meter (Mettler Toledo DL15 Titrator, Sweden) was calibrated before each pH measurement.

2.7. Chl a analysis

Algal suspensions to determine Chl *a* contents were filtered with GF/F filters and extracted at 4 °C overnight with absolute methanol, and then the extract was centrifuged (5000×*g*, 10 min) (Universal 320 R, Hettich, Germany) at 4 °C. The absorbance values at 665 nm, 750 nm, and 652 nm were measured using a spectrophotometer (DU800, Beckman, Fullerton, California, USA). Chl *a* was calculated following the equation in Ryckebosch et al. (2011).

2.8. DMS and DMSP measurements

DMS concentrations were separated and detected by a gas chromatography (Shimadzu GC-2014, Japan) equipped with a flame photometric detector. To separate sulfur gases, a chromatographic column which was a glass column packed with 10% DEGS on Chromosorb –AWDMCS was used. DMS concentration was analyzed by directly introducing a 2 mL sample of algal media into a glass purge chamber. The analytical conditions were followed as Yu et al. (2015). A volume of 10 mL algal medium was gravity filtered through a Whatman GF/F filter (0.7 μm) using a magnetic filter funnel (PN 4242, Pall Corporation, USA). Volumes of 4 mL dissolved DMSP ($DMSP_d$) and 10 mL total DMSP ($DMSP_t$) samples from the filtrate and unfiltered seawater were fixed using 40 μL and 100 μL of 9 mol L^{-1} H_2SO_4 for storage respectively (Zhang et al., 2014). $DMSP_d$ and $DMSP_t$ were measured after cleavage using KOH solution (10 mol L^{-1}) for ≥24 h at 4 °C. Particulate DMSP ($DMSP_p$) was obtained by subtracting $DMSP_d$ from $DMSP_t$. DMS, $DMSP_d$, and $DMSP_p$ divided by the cell concentrations and the cellular DMS, cellular $DMSP_d$, and cellular $DMSP_p$ were obtained.

2.9. Data analysis

Homogeneity of variance was assessed using SPSS version 11.5 software (SPSS Inc., Chicago, IL, USA) before the analysis. One-way analysis of variance (ANOVA) was used to determine differences between the treatments in the HC and LC, and PAR, PA, and PAB treatments. The interaction between HC/LC and PAR/PA/PAB was analyzed by two-way ANOVA.

3. Results

3.1. Semi-continuous culture with elevated CO_2

3.1.1. Cell concentration, specific growth rate, cell size, and Chl a contents

The cell concentration and the specific growth rate (μ) of *E. huxleyi* under HC decreased by 17% and 5%, respectively, compared with the corresponding values under LC. The cell concentration and μ of *E. huxleyi* under HC were significantly lower than those of the corresponding values under LC ($P < 0.05$) (Fig. 1a and b). HC significantly increased the cell size of *E. huxleyi* compared with the corresponding size under LC ($P < 0.05$) (Fig. 1c). HC did not significantly affect the total and cellular Chl *a* contents ($P > 0.05$) (Fig. 1d and S1a).

3.1.2. DMS, $DMSP_d$, and $DMSP_p$ concentration

HC decreased the total DMS and $DMSP_p$ concentrations by 20% and 13%, respectively. The total DMS and $DMSP_p$ concentrations under HC were significantly lower than those under LC ($P < 0.05$) (Fig. 1e and g). HC did not significantly affect the $DMSP_d$, cellular DMS, cellular $DMSP_d$, and cellular $DMSP_p$ concentrations compared with those of the corresponding values under LC ($P > 0.05$) (Fig. 1f, S1b–d).

3.2. UV radiation experiment

3.2.1. Cell concentration, specific growth rate, cell size, and Chl a contents

Exposure to PA and PAB did not significantly affect the cell concentrations and μ of *E. huxleyi* on day 3 ($P > 0.05$). In contrast, exposure to PA on day 4 increased cell concentrations and μ by 16% and 9% respectively, relative to their corresponding cell concentrations and μ under PAR (Fig. 2a and b), and the cell concentration and μ under PA were significantly higher than those under PAR or PAB ($P < 0.01$) on day 4. The size of cells exposed to PA on day 3 was larger than that of cells under PAR ($P < 0.05$), and the size of cells exposed to PA and PAB on day 4 was larger than that of cells exposed to PAR ($P < 0.05$) (Fig. 2c). Total Chl *a* content under PAB was significantly lower than that under PAR on day 3 or day 4 ($P < 0.01$). In contrast, total Chl *a* content under PA was significantly higher than that under PAR on day 4 ($P < 0.01$) (Fig. 2d). No significant differences were found among the cellular Chl *a* contents under PAR, PA, PAB (Fig. S2a, $P > 0.05$).

3.2.2. DMS, $DMSP_d$, and $DMSP_p$ concentration

Total DMS of PA/PAB decreased by 14%–58% and total $DMSP_p$ increased by 54%–144% during days 3–4 compared with the corresponding DMS and $DMSP_p$ under PAR (Fig. 2e and g). PA increased total $DMSP_d$ by 8%–9% and PAB decreased by 35%–56% compared with the corresponding $DMSP_d$ under PAR during days 3–4 (Fig. 2f). Total DMS (or $DMSP_d$) under PAB was significantly lower than the corresponding DMS (or $DMSP_d$) under PAR ($P < 0.01$) (Fig. 2e and f). Total $DMSP_p$ concentrations in the treatments were in the following order: PA > PAB > PAR. Significant differences were presented among them ($P < 0.01$) (Fig. 2g).

Cellular DMS under PA/PAB decreased by 25%–56% and cellular $DMSP_p$ under PA/PAB increased by 60%–130% during days 3–4 compared with the corresponding values under PAR (Fig. S2b and S2d). Cellular $DMSP_d$ under PA/PAB decreased by 7%/55% on day 4 compared with the corresponding values under PAR (Fig. S2c). Cellular DMS (or $DMSP_d$) under PAB was significantly lower than that of the corresponding DMS (or $DMSP_d$) under PAR (cellular DMS: $P < 0.05$; cellular $DMSP_d$: $P < 0.01$) (Fig. S2b–c). Cellular $DMSP_p$ under PAR, PA, and PAB presented in the following order: PA > PAB > PAR, and significant differences were displayed among them ($P < 0.01$) on days 3 or 4 (Fig. S2d).

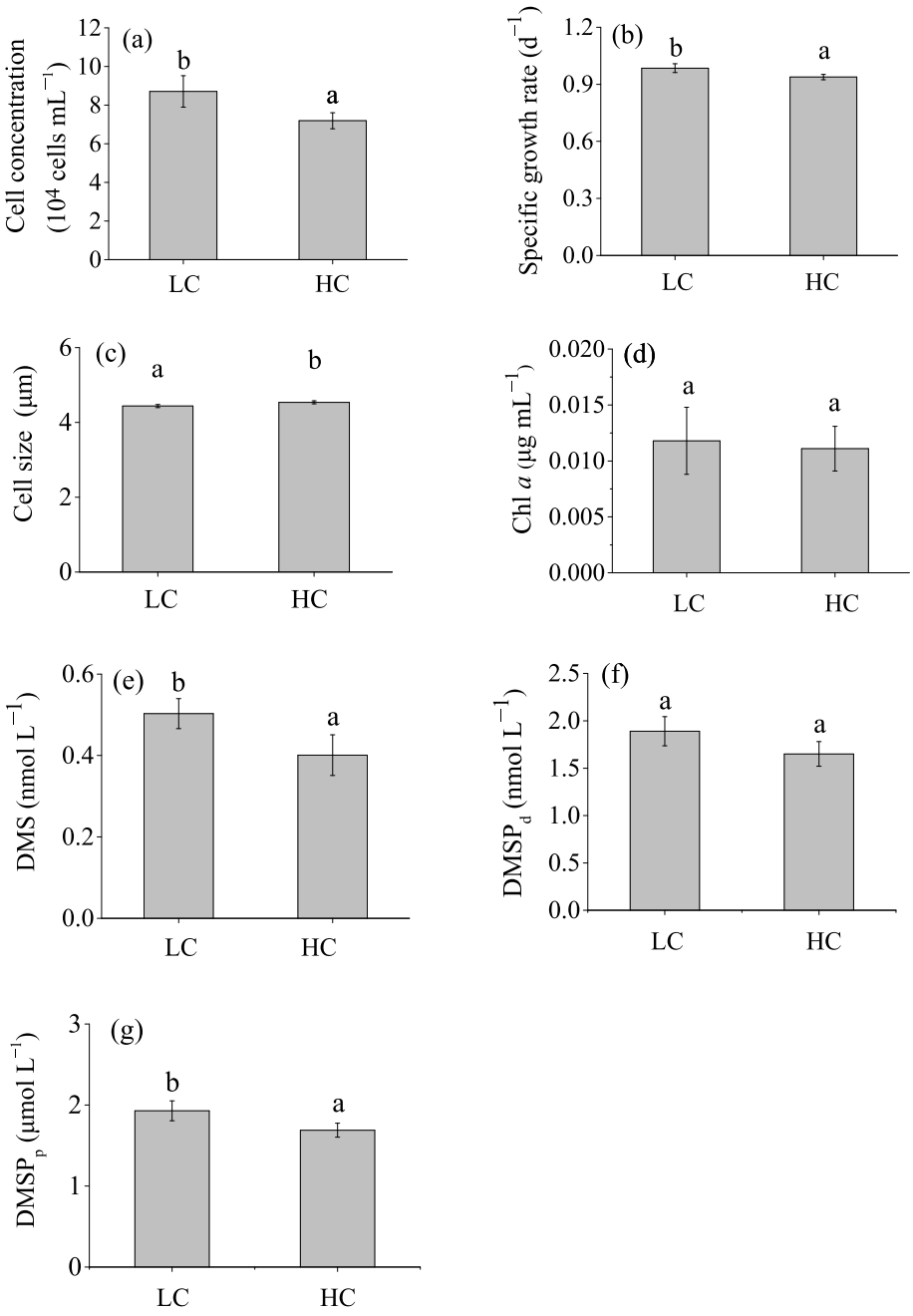

Fig. 1. Effects of ambient CO_2 (400 μatm, LC) and elevated CO_2 (1000 μatm, HC) on cell concentration (a), specific growth rate (μ) (b), cell size (c), Chl *a* concentration (d), DMS (e), $DMSP_d$ (f), and $DMSP_p$ (g) in *E. huxleyi* at day 8. Different letters above the bars indicate significant differences ($P < 0.05$).

3.3. Combined effects of elevated CO_2 and UVR

3.3.1. Cell concentration, specific growth rate, cell size, and Chl a contents

HC did not significantly affect the cell concentration and μ under PAR/PA/PAB compared with those of the corresponding values under LC ($P > 0.05$) (Fig. 3a and b). UVA increased cell concentration, and cell concentration under PA was higher than that of the corresponding value under PAR ($P < 0.05$), regardless of LC or HC. In comparison, UVB reduced cell concentration, and cell concentration under PAB was lower than that of the corresponding value under PAR ($P > 0.05$), regardless of LC or HC. μ under PA was higher than that of the corresponding value under PAR or PAB ($P < 0.01$), regardless of LC or HC (Fig. 3b). Cell size under PAR/PA/PAB increased by 2%–3% compared with that under HC with the corresponding LC cell size (Fig. 3c). Cell size under PA or PAB was significantly higher than that of the corresponding value under PAR in the LC or HC treatments ($P = 0.000$) (Fig. 3c). No significant difference was found among total Chl *a* contents of PAR, PA, and PAB ($P > 0.05$), regardless of LC or HC (Fig. 3d). Cellular Chl *a* contents of PAR/PA/PAB increased by 1%–4% compared HC with those of the corresponding value under of LC (Fig. S3a). Cellular Chl *a* contents of PA or PAB were lower than those of PAR under both HC and LC (HC + PA, HC + PAB, LC + PA: $P < 0.05$; LC + PAB: $P > 0.05$) (Fig. S3a).

3.3.2. DMS, $DMSP_d$, and $DMSP_p$ concentration

Total DMS, $DMSP_d$, and $DMSP_p$ under PAR/PA/PAB decreased by 1%–2%, 5%–11%, and 7%–11% respectively in HC compared with LC (Fig. 3e–g). Cellular DMS and $DMSP_p$ under PAR/PA/PAB were not significantly affected compared HC with LC ($P > 0.05$), while cellular $DMSP_d$ under PAR/PA/PAB decreased by 2%–9% (Fig. S3b–d). Total DMS and $DMSP_d$ under PAB were significantly lower than those of the

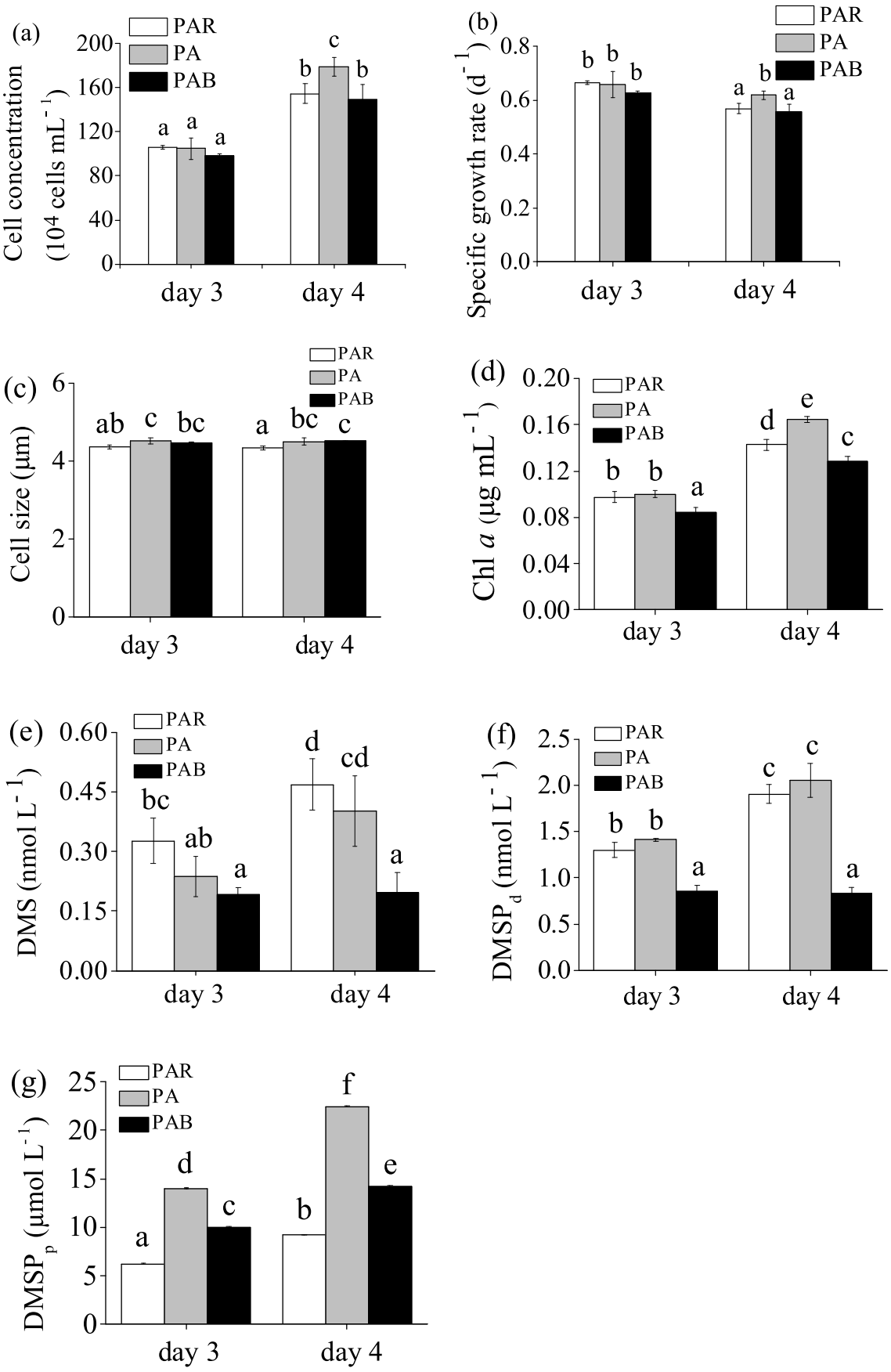

Fig. 2. Effects of PAR, PAR + UVA (PA), and PAR + UVA + UVB (PAB) on cell concentration (a), specific growth rate (μ) (b), cell size (c), Chl *a* concentration (d), DMS (e), $DMSP_d$ (f), and $DMSP_p$ (g) in *E. huxleyi*. Different letters above the bars indicate significant differences ($P < 0.05$ or $P < 0.01$).

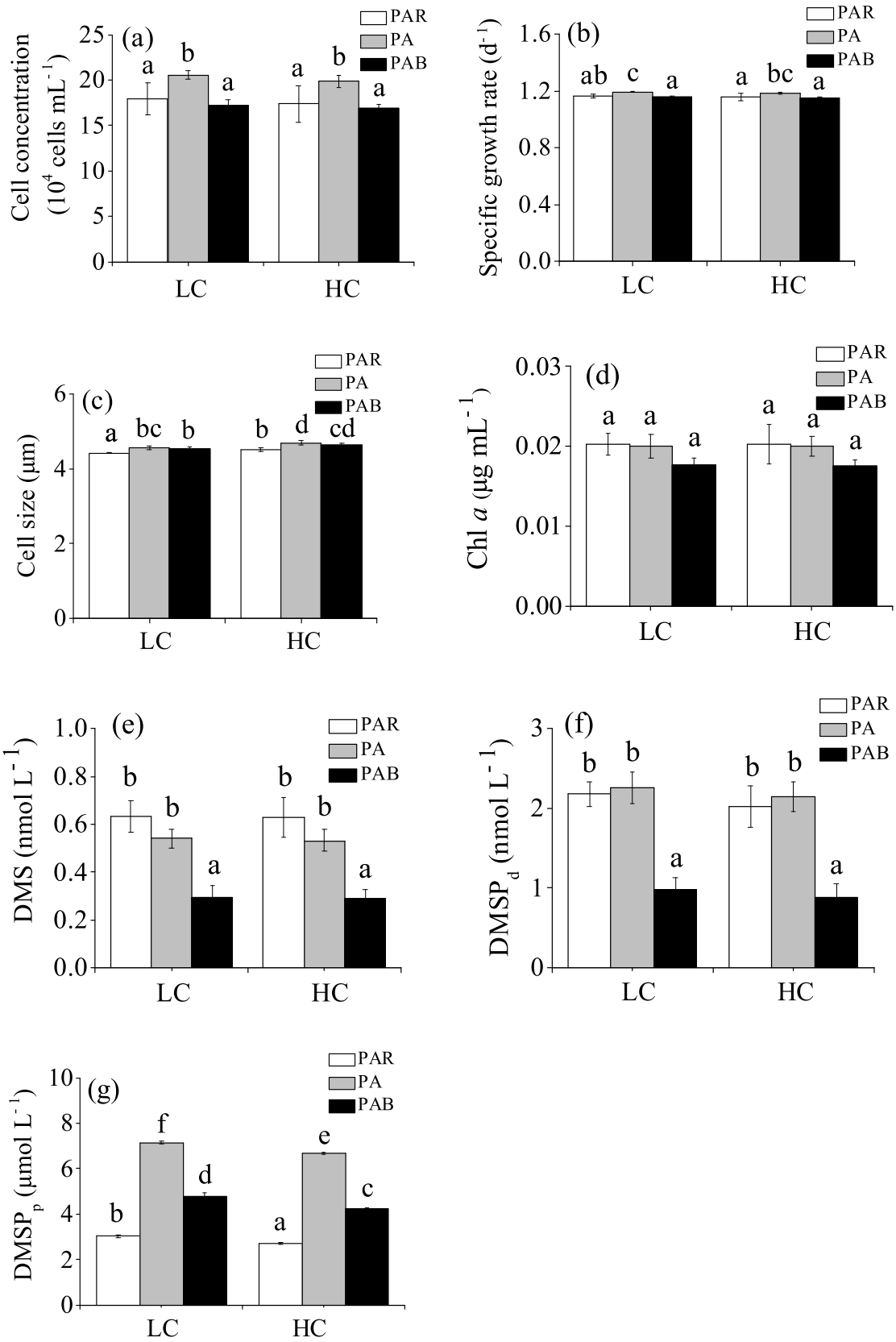

Fig. 3. Combined effects of ambient CO_2 (400 μatm, LC)/elevated CO_2 (1000 μatm, HC) and PAR/PAR + UVA (PA)/PAR + UVA + UVB (PAB) on cell concentration (a), specific growth rate (μ) (b), cell size (c), Chl *a* concentration (d), DMS (e), $DMSP_d$ (f), and $DMSP_p$ (g) in *E. huxleyi* at day 6. Different letters above the bars indicate significant differences ($P < 0.05$ or $P < 0.01$).

corresponding values under PAR or PA in LC and HC ($P < 0.01$) (Fig. 3e and f). Total $DMSP_p$ took the following order: PA > PAB > PAR, and significant differences were observed among them in LC or HC ($P < 0.01$) (Fig. 3g).

No interactive effects of pCO_2 and UVR were found on cell concentration, μ, Chl *a* content, cell size, $DMS/DMSP_d$, cellular Chl *a* content, or cellular $DMS/DMSP_d/DMSP_p$ (two-way ANOVA, $P > 0.05$). pCO_2 and UVR interacted with $DMSP_p$ (two-way ANOVA, $P < 0.05$).

Cellular DMS and $DMSP_p$ followed the order: PAR > PA > PAB and PA > PAB > PAR respectively, and there were significant differences among cellular $DMSP_p$ of PAR, PA, and PAB under LC and HC ($P < 0.01$) (Fig. S3b and S3d). UVB decreased cellular $DMSP_d$, and cellular $DMSP_d$ under PAB was significantly lower than that of PAR or PA under LC or HC ($P < 0.01$) (Fig. S3c).

4. Discussion

4.1. Effects of OA on phytoplankton growth, DMS and DMSP production

Studies about the effects of OA on phytoplankton growth have been reported in semi-continuous culture (Tong et al., 2018) and batch culture (e.g., algal bloom in a mesocosm experiment) (Zhang et al., 2018). Semi-continuous culture has revealed that growth of *G. oceanica* is inhibited by elevated CO_2 (Tong et al., 2018). However, the effects of elevated CO_2 on algal growth in batch culture depend on the growth phase (Liu et al., 2017). Our semi-continuous culture results showed that elevated CO_2 inhibited growth of *E. huxleyi* (Fig. 1). The combined effects of elevated CO_2 and UVR showed the different results, and HC + PAR did not significantly affect the growth compared with the corresponding values under LC + PAR (Fig. 3a and b). The differences may be due to the addition of PAR. Elevated CO_2 in the present study increased cell size in the semi-continuous cultures (Figs. 1 and 3), which was consistent with previous results (Li et al., 2017; Li et al., 2020). No significant difference was observed in Chl *a* content of HC or LC in our combined UVR and pCO_2 experiment (Fig. 3), which was similar with the results of Li et al. (2017) who reported that Chl *a* is not significantly different between LC (400 μatm) and HC (1000 μatm) under constant or variable light treatments in semi-continuous culture.

Results from natural waters have confirmed that elevated CO_2 resulted in a decrease of DMS production in a Norwegian coastal mesocosm (40–54%) (Avgoustidi et al., 2012; Hopkins et al., 2010) and an Arctic coastal pelagic mesocosm (35%) (Archer et al., 2013). Low DLA activity degradation, elevated DMSP demand of high bacterial production, high bacterial DMS metabolism accounted for the declined DMS at elevated CO_2 (Archer et al., 2013). HC decreased the total DMS (20%) and $DMSP_p$ (13%) in the present study (Fig. 1), and the decrease in DMS might be due to decreased DLA caused by elevated CO_2. The effect of elevated CO_2 on total $DMSP_p$ in this study was a consequence of a change in algal biomass. Inconsistent with our results, increased $DMSP_t$ concentrations were found in a mesocosm experiment off Spitzbergen which were due to phytoplankton composition changes, low DLA, and increased primary production at elevated CO_2 (Archer et al., 2013). The changes in DMS were similar with previous results in a mesocosm experiment (Zhang et al., 2018), in which HC significantly reduced mean DMS concentration by 28%. Inconsistent with the above observations, Kim et al. (2010) reported increased DMS (~80%) at elevated CO_2 in a mesocosm experiment in Korean waters, which may be due to increased grazing rate of microzooplankton. Hopkins and Archer (2014) reported increased DMS and decreased DMSP at high CO_2 in a shipboard bioassay experiment possibly because of decreased small phytoplankton (<10 μm) and DMSP synthesis rates, decreased bacterial consumption and increased bacterial production of DMS, differing sensitivity of phytoplankton and bacterial community to high CO_2.

4.2. Effects of UVR on phytoplankton growth, DMS and DMSP production

The cell concentration, μ, and Chl *a* content of *E. huxleyi* decreased compared PAB with PA (Fig. 2), demonstrating that UVB has detrimental effects on algal cells. The negative effects of UVB on phytoplankton have been documented in many studies (Gao et al., 2009; Guan and Gao, 2010). DNA and protein damage caused by UVB are the mechanisms of the harmful effects (Buma et al., 2000). UVA has negative and positive effects on marine organisms (Gao et al., 2009; Wu et al., 2005). PA exposure on day 4 increased cell concentration, μ, and Chl *a* content (Fig. 2), which may have been due to UVA dark repair (Karentz et al., 1991). Consistent with our results about time-dependent dark repair, Wu et al. (2005) reported that UVA significantly increases trichome length of the filamentous cyanobacterium *Arthrospira platensis* after 6 d of exposure, and that length recovered to the original length on day 10. Exposure to UVA and UVB increased cell sizes (Fig. 2), which agrees with the results of Guan and Gao (2010), in which *E. huxleyi* cells induced by UVR became bigger because of enhanced calcification and slower cell division.

Both UVA and UVB exposure decreased total and cellular DMS, and increased total and cellular $DMSP_p$ (Fig. 2 and S2). Consistent with our results, Slezak and Herndl (2003) showed that enhanced UVR increases cellular DMSP in *E. huxleyi*. Darroch et al. (2015) also reported increased intercellular DMSP in *E. huxleyi* (ca. 30%) and decreased DLA per volume (~45%) under UVR stress. Therefore, short-term UVR exposure stimulates DMSP biosynthesis in phytoplankton. In our study, the decreases in total DMS and cellular DMS for PAB were higher than those for PA, and the increases in total $DMSP_p$ and cellular $DMSP_p$ for PAB were lower than those for PA (Fig. 2 and S2). Consistent with our results, Sunda et al. (2002) showed a greater increase in intracellular DMSP concentration caused by UVA (98%) than that caused by UVA + UVB (59%). In addition, environmental stress (i.e., OA, UVR, microplastics) induces the production of reactive oxygen species (ROS), which are harmful to marine organisms (Jeong et al., 2016; Ma and Gao, 2010; Mostofa et al., 2013; Vega and Pizarro, 2000). Antioxidant systems including antioxidant enzymes and antioxidants can scavenge ROS produced due to environmental stress. DMS and DMSP also have a protective function in the antioxidant system and scavenge ROS induced by stress (Sunda et al., 2002). The high levels of DMSP have a protective function in the antioxidant system and scavenge ROS induced by UVR stress (Darroch et al., 2015). Increased cellular $DMSP_p$ under PA/PAB might indicate that $DMSP_p$ concentration increased to scavenge ROS induced by UVA and UVB.

4.3. Combined effects of CO_2 and UVR

In the present study, the addition of UVA stimulated algal growth compared with PAR and the addition of UVB inhibited algal growth compared with PA, regardless of CO_2 level (Fig. 3). The combined effects of elevated CO_2 and UVR on the calcification and photosynthetic rates show that elevated CO_2 enhances the detrimental effects of UVR in *E. huxleyi* (Gao et al., 2009). Inconsistent with the results of Gao et al. (2009), our results indicated that HC did not significantly affect the detrimental effects of PAR/PA/PAB on *E. huxleyi* (i.e., cell concentration, μ, Chl *a* content, cellular $DMSP_p$) compared with LC (Fig. 3 and S3). The combined of OA and UVB resulted in interactive effects on the production of $DMSP_p$. Jian et al. (2017) showed that low pH (7.7) exacerbates the UVB-induced DMS degradation rate from 40% to 61%, which coincided with the decrease in DMS in our study. Different from the effects of UVB, low pH (7.7) decreases the DMS degradation rate caused by UVA (Jian et al., 2017), suggesting different mechanisms for the coupling effect of UVB + pH and UVA + pH.

5. Conclusions

The individual and combined effects of UVR and elevated CO_2 on growth, DMS and DMSP production in *E. huxleyi* were evaluated in this present work. The adaptive mechanisms of growth, DMS and DMSP production in *E. huxleyi* under UVA and UVB were different. UVA and UVB exposure had positive and negative effects on cell growth of *E. huxleyi*, respectively. Our results indicate that the total DMS concentration under HC decreased by 20% compared with that under LC in the semi-continuous culture. In addition, research on long-term exposure should be intensified to reveal the transformation of the increased $DMSP_p$ caused by UVR exposure and the mechanisms involved in the changes in DLA, ROS, and the antioxidant system.

Credit author statement

Juan Yu, Ji-Yuan Tian: Conceptualization, Methodology, Investigation, Writing-original draft, Writing-Reviewing and Editing, Data curation. Guang Gao: Writing-Reviewing and Editing. Rui Xu, Jing-Guang Lai: Investigation. Gui-Peng Yang: Writing-Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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