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RESEARCH NOTE

Warming exacerbates the impacts of ultraviolet radiation in temperate diatoms but alleviates the effect on polar species

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Abstract

Under global change scenarios, the sea surface temperature is increasing steadily along with other changes to oceanic environments. Consequently, marine diatoms are influenced by multiple ocean global change drivers. We hypothesized that temperature rise mediates the responses of polar and temperate diatoms to UV radiation (UVR) to different extents, and exposed the temperate centric diatoms, *Thalassiosira weissflogii* and *Skeletonema costatum*, and a polar pennate diatom *Entomoneis* sp., to warming (+5°C) for 10 days, then performed short-term incubations under different radiation treatments with or without UVR. The effective quantum yields of the three diatoms were stable during exposure to PAR, but decreased when exposed to PAR + UVR, leading to significant UV-induced inhibition, which was 3% and 9%, respectively, for *T. weissflogii* and *S. costatum* under ambient temperature but increased to 12% and 17%, respectively, in the cells acclimated to the warming treatment. In contrast, UVR induced much higher inhibition, by about 45%, in the polar diatom *Entomoneis* sp. at ambient temperature, and the warming treatment alleviated the UV-induced inhibition, which dropped to 36%. The growth rates were significantly inhibited by UVR in *S. costatum* under the warming treatment and in *Entomoneis* sp. under ambient temperature, while there was no significant effect for *T. weissflogii*. Our results indicate that the polar diatom was more sensitive to UVR though warming could alleviate its impact, whereas the temperate diatoms were less sensitive to UVR but warming exacerbated its impacts, implying that diatoms living in different regions may exhibit differential responses to global changes.

KEYWORDS

diatoms, global warming, polar regions, stressor, UV radiation

INTRODUCTION

Phytoplankton play important roles in marine ecosystems and biogeochemical cycles,[1] and exhibit a rich diversity due to their flexibility in response to unfavorable environmental changes, such as UV radiation, extreme temperature, and pollutants.[2] In polar areas, where the sea ice melts seasonally, phytoplankton cells are able to thrive and

Abbreviations: PAR, photosynthetically active radiation; PSII, photosystem II; QY, quantum yield; UVR, ultraviolet radiation.

drive massive blooms, which undoubtedly enhance the regional primary production.[3,4] However, the phytoplankton productivity of the temperate zone varies regionally.[5]

The sea surface temperature varies diurnally and seasonally and is increasing gradually due to global warming.[6] As a basic physical parameter influencing life processes, temperature can influence the enzyme activities, and the fluidity and permeability of the cell membrane, thereby influencing physiological features such as nutrients, photosynthesis, respiration, and growth of phytoplankton.[7] Since the effects of temperature on phytoplankton are species-specific, the species competition can also be modulated by temperature changes.[8,9] Under global warming, it has been postulated that the responses of phytoplankton to ocean climate changes depend on latitude, with decreased diversity of phytoplankton in the tropical ocean, but increased values in polar oceans.[5] In addition to direct effects, temperature could also interact with other factors such as UV radiation,[10] ocean acidification,[11] nitrogen and CO_2 availability, which in turn affect the photophysiology of phytoplankton.[2]

Under a global warming scenario, the upper mixed layer of the ocean will become shallower and phytoplankton cells within it are then expected to be exposed to higher average levels of ultraviolet radiation (UVR), which is one of the most important environmental factors for phytoplankton in the euphotic zone.[12] UVR can affect multiple biological processes, causing inhibition of enzyme activity, damage to DNA, and changes to cell membrane permeability,[13] though some wavelengths of UVR can also drive photosynthetic carbon fixation of both macro- and micro-algae.[14–16] Though UVR fluxes are higher in equatorial regions, in high latitude areas, where significant ozone loss has been observed, polar species are likely to be exposed to a greater proportional change in UVR as the sea ice melts.[17,18] In addition to biochemical strategies to cope with harmful UV radiation, the regularly distributed pores of diatom silica frustules could diffract UVR, and allow frequency down-conversion of the incoming radiation, resulting in detrimental UVR being converted to the longer wavelengths of photosynthetically active radiation (PAR, 400–700 nm).[19,20]

Photosystem II catalyzes the photo-oxidation of water using light energy and plays a central role in the conversion of energy from photons trapped by pigments into electron flow to generate chemical energy used to drive the fixation of carbon dioxide.[21] In contrast to Photosystem I (PSI), PSII has been reported to be extremely sensitive to physical stressors, especially UVR and high-intensity PAR,[22,23] and can be damaged by UVR.[24] To maintain efficient photosynthetic performance, the damaged PSII subunits need to be replaced by de-novo-synthesized proteins,[25] which involves a series of enzyme-catalyzed reactions, and thus is also sensitive to temperature changes.[26] These two factors associated with climate change can interact to affect organisms to different extents. The damage to DNA caused by UVR is temperature-dependent, with fewer photoproducts produced at lower temperatures,[27] though warming can mitigate the inhibitory effect of UVR on diatoms by stimulating the repair rate of PSII.[28] However, beneficial effects of warming are not always observed, as reported for the dinoflagellate species *Prorocentrum micans* when exposed to UVR, as revealed in a comparative study on three phytoplankton species.[29]

Considering the multiple pressures encountered by phytoplankton, we speculate that phytoplankton species from temperate and tropical regions would naturally be exposed to higher UVR than polar species and might thus have evolved to be less affected by UVR exposure. We also hypothesize that warming, due to its greater effect on enzyme-catalyzed repair processes than on photodamage, might ameliorate negative effects of UVR on the physiology of phytoplankton. In particular, given that Photosystem II is a primary site of UVR-induced damage, we might expect any effect of warming to be reflected in the effective quantum yield of PSII. We tested these hypotheses by investigating the effects of UV and warming on growth and photophysiology (PSII yield) in 2 temperate diatoms and one polar species.

MATERIALS AND METHODS

Species and culture conditions

In this study, we selected three diatoms, namely two temperate species, *Thalassiosira weissflogii* (CCMA102), and *Skeletonema costatum* (JOUP006) that were isolated from the Daya Bay (N 22°42′10″, E114°39′36″) and Yellow Sea (N 34°41′24″, E119°30′15″), respectively, and a polar species *Entomoneis* sp. (JOUP008) that was originally isolated from the Bering Strait (N 64°30′15″, E190°18′20″). The temperate and polar species were stored in F/2 medium and maintained, respectively, at 20 and 5°C for about 3 years in our lab.

For precultures, the diatom cells were inoculated into sterilized natural seawater that was enriched to F/2 medium, which contained 882 μmol L^{-1} nitrate, 36.2 μmol L^{-1} phosphate, and 106 μmol L^{-1} silicate,[30] and semi-continuously grown (with dilution every 2–5 days) in triplicate 1 L polycarbonate bottles for 10 days in growth chambers at a light intensity of 120 μmol photons $m^{-2}s^{-1}$ (GXZ, Ningbo Jiangnan Instrument Co). Though the photoperiods for the 3 species would be different in the latitudes from which they were isolated, for a better comparison of photochemical responses, a

standard 12:12 h light–dark cycle was applied for all 3 species. The temperature was controlled at 20°C for the temperate diatoms, and 5°C for the polar species, while a 5°C increase for all three species mimics the likely rise from extreme events such as marine heatwaves under global warming scenarios.[31] The culture volume was replaced with ~60% fresh medium once every 2 days, and bottles were shaken by hand 4–5 times during the day-time and were then randomly placed in the growth chamber.

Experimental setup

After the acclimation at different temperatures for at least 10 days, sub-cultures were collected and dispensed into quartz tubes (100 mL) for determination of growth rate and quantum yield measured by chlorophyll fluorescence. Prior to the exposures, each of the tubes was maintained under the growth condition for 10 min, then they were placed into a water bath at 30 s intervals under homogeneous illumination conditions PAR or PAR + UVR (PAB). A fluorescent lamp was employed for PAR, and a Q-Panel UVA-340 lamp was used to provide UVR. Cut-off filters (ZJB280 or ZJB400) were placed on top of the quartz tubes to create PAB treatment or PAR alone treatment.

By adjusting the distance between lamps and the quartz tubes, and confirmed by a portable radiometer (PMA2100, Solar Light), the exposure light intensity was 120 μmol photons $m^{-2} s^{-1}$ for PAR, 4.2 W m^{-2} for UVR (comprising 4.0 W m^{-2} UVA and 0.2 W m^{-2} UVB). During the exposure, the temperature was controlled by a recirculating chiller (CTP3000).

Determination of growth rate and chlorophyll fluorescence

For growth rate measurements, cells were dispensed into quartz tubes and incubated for 24 h with a 12: 12 light: dark cycle under the respective treatments as described above. Sub-samples were taken before and after incubation and fixed with Lugol's solution, then cell concentrations were determined under a microscope. During the culturing, the quartz tubes were shaken 3–4 times to minimize shelf shading between cells.

For chlorophyll fluorescence measurement, cells were dispensed into quartz tubes and incubated under PAR or PAB conditions, then sub-samples (~2 mL) were taken from each tube regularly and measured within 10 s by an AquaPen fluorometer (Photon Systems Instruments, Czech Republic) with a saturating light pulse of 3000 μmol photons $m^{-2} s^{-1}$. The time interval between measurements was 6 min for the first 30 min and 10–15 min for the rest of measurements.[32]

Data analysis

The growth rate was calculated as follows.

$$\mu = \left(\ln C_1 - \ln C_0\right) / T,$$

where C_0 and C_1 represent the cell concentrations before and after incubation under PAR or PAB conditions, respectively, and T represents days of incubation.[28]

In this experiment, effective quantum yields (QY) were measured within 10 s after sampling while the actinic light was set to the growth light intensity. QY was calculated from the fluorescence values measured with the Aquapen fluorometer.[33]

$$\text{Effective quantum yield (QY)} = \left(F_m' - F\right) / F_m'$$

where F_m' represents the maximal fluorescence, and F represents the steady-state fluorescence under actinic light.

The relative inhibition of PSII induced by UVR was calculated as follows:

$$\text{Relative UVR inhibition}\,(\%) = \left(Y_{PAR} - Y_{PAB}\right) / Y_{PAR} \times 100\,\%.$$

Under UV stress in algae, photosystem II activity decreases until the damage and repair of PSII reach a balance, thereafter, remaining at a quasi-steady state.[34] In the present study, this occurred after 60 min exposure to UVR, thus Y_{PAR} and Y_{PAB} represent the averaged quantum yields from 60 to 120 min exposure under PAR and PAB, respectively.

The individual effects of temperature, UVR, and interactive effects of temperature + UVR on growth rates and photochemical quantum yields during exposure were analyzed by two-way ANVOA or two-way RM-ANOVA after verifying the assumptions of homoscedasticity for each data group by Levene's test, and a Greenhouse–Geisser correction was applied if needed. A post hoc analysis with Tukey's test was used for means comparisons. The significant ($p < 0.05$) difference in relative inhibition between radiation treatments were analyzed by two-sample t-tests (SPSS Statistics 25, IBM).

RESULTS

The specific growth rates of *T. weissflogii* were within the range of 1.00–1.18 d^{-1}, and no significant differences were observed between PAR and PAB under ambient

($p = 0.48$) or warming ($p = 0.09$) conditions (Figure 1A). For *S. costatum*, the growth rates were 1.82 to 2.07 d^{-1}, with a significant difference observed between PAR and PAB under warming ($p = 0.038$), while the difference was insignificant under ambient temperature ($p = 0.09$) (Figure 1B). Growth rates for *Entomoneis* sp. were 0.24–0.53 d^{-1}, with a significant difference between PAR and PAB under ambient temperature ($p = 0.024$), while the difference was insignificant under warming ($p = 0.26$) (Figure 1C). Furthermore, the warming resulted in a significant stimulation of growth in *Entomoneis* sp. ($p < 0.05$) (Figure 1C), while the effect on growth was insignificant for the temperate species under both PAR and PAB conditions (Figure 1A,B).

The QY of *T. weissflogii* under PAR remained stable during the exposure, being about 0.55–0.60 (Figure 2A,B), but was slightly lower under exposure to PAB treatment but stayed at a stable value during the whole exposure period. The presence of UVR reduced the steady-state QY values by up to 0.027 at the ambient temperature and by up to 0.077 under the warming treatment (Figure 2A,B, Table S1). The QY of *S. costatum* showed a similar pattern to that of *T. weissflogii*, with the maximal UV-induced decrease of 0.067 and 0.097, respectively, for the ambient and warming treatments during exposure (Figure 2C,D). For the polar species, *Entomoneis* sp., the QY increased slightly after exposure under PAR and then remained stable at 5°C, 0.51 ± 0.02, while the stable values at 10°C, were 0.56 ± 0.008. After exposure to UVR, QY decreased by up to 0.27 and 0.21 under the ambient and warming temperatures, respectively (Figure 2E,F). On average, the relative UV inhibition determined from 60 to 120 min of exposure where QY was stable, was around 3% for *T. weissflogii*, and around 9% for *S. costatum* at ambient temperature (Figure 3), and were both increased significantly under warming conditions, to 12% and 17%, respectively. For *Entomoneis* sp., the mean UV inhibition was around 45% at ambient temperature but decreased significantly to 36% under the warming condition ($p < 0.05$) (Figure 3).

DISCUSSION

In the context of ocean global changes, how phytoplankton respond and adapt is an essential determinant for estimating the carbon sink capacity of the oceans.[35] In the present study, our results clearly showed that the physiological responses of diatoms to warming are largely species-dependent, enhanced growth rate was more prominently observed for polar species, which has been also revealed by a meta-analysis study.[5] As one of the major detrimental factors for PSII, UVR generally reduced the PSII quantum yield, with a much stronger impact observed

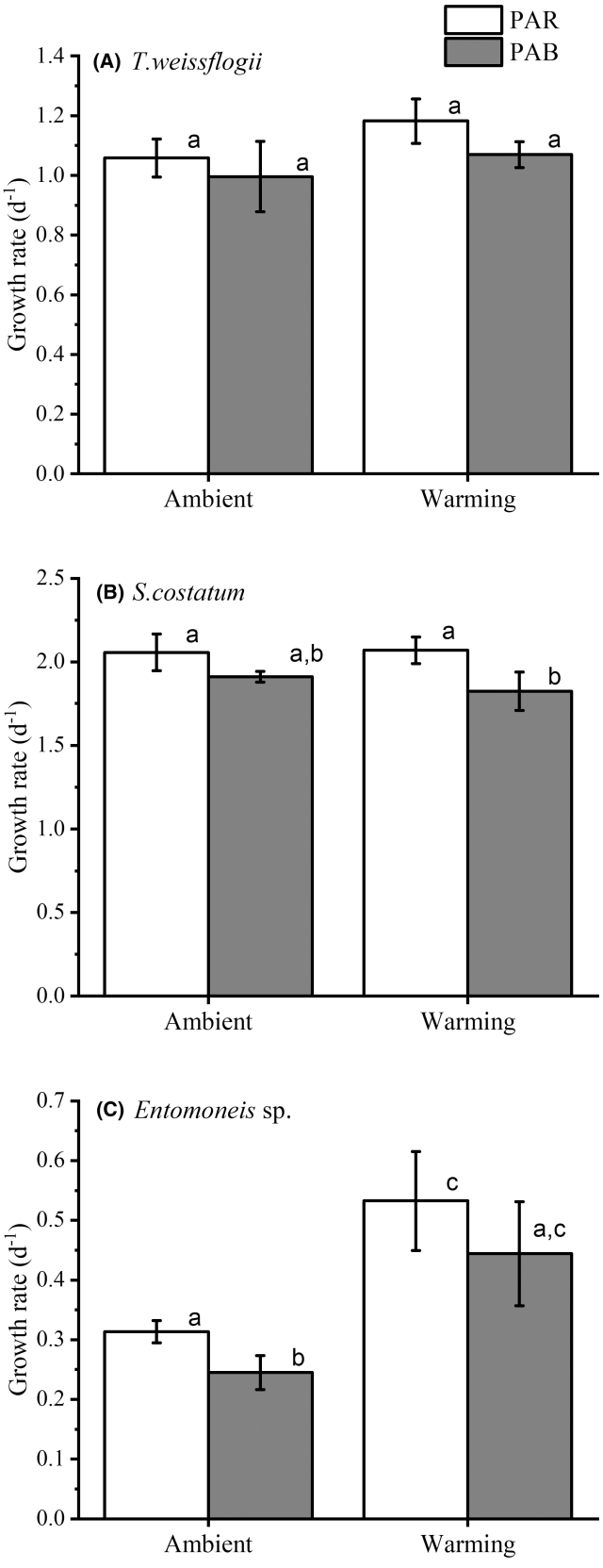

FIGURE 1 The specific growth rates of *Thalassiosira weissflogii* (A), *Skeletonema costatum* (B), and *Entomoneis* sp. (C) during 24 h exposure to PAR and PAB under ambient and warming conditions. Vertical lines represent standard deviations, $n = 3$, different letters above the bars indicate significant differences between treatments.

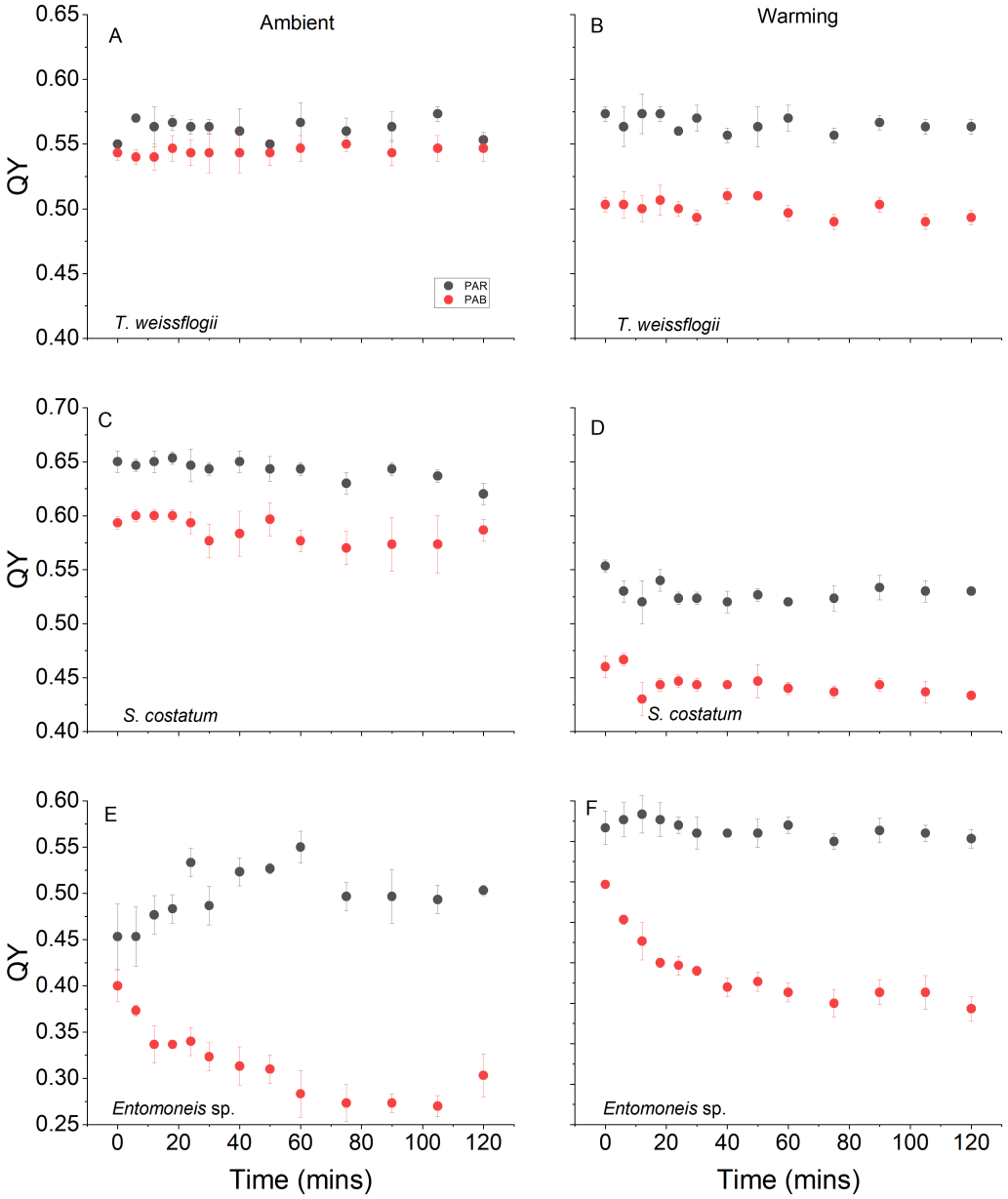

FIGURE 2 The quantum yields (QY) of photosystem II of *Thalassiosira weissflogii* (A, B), *Skeletonema costatum* (C, D), and *Entomoneis* sp. (E, F) exposed to two radiation treatments (PAR, black; PAB, red), cells were grown under ambient and warming treatments for 10 days before the experiment. Vertical lines represent standard deviations, $n = 3$.

in polar species, which could be attributed to a possible lower capacity for enzyme-catalyzed repair processes.[26] In addition, significant reductions in growth rate were also observed for *Entomoneis* sp. and *S. costatum* under UVR exposure. The UV-induced inhibition of PSII was generally lower for the temperate species studied, but higher for the polar species, though the UVR effect was alleviated by warming in the polar diatom, but exacerbated in the temperate species. The hypothesis we put forward, that warming would alleviate UVR-induced inhibition, was found to be valid only for the polar diatom, while the opposite was observed for the temperate species. This suggests that diatoms species from high latitudes could benefit from warming, whereas temperate species might be negatively affected by progressive ocean global changes.

UVR is known to cause major damage to the photosynthetic apparatus, carbon fixation, DNA, and other metabolic pathways.[36,37] In the present work, exposure under the relatively low light level used for growth would not induce significant nonphotochemical quenching, while UVR caused a significant decrease in the photochemical quantum yields of all species, probably due to damage to PSII, which can be inactivated even at relatively low levels of UVR.[2] Interestingly, the UV inhibition was correlated with the latitude where the species was isolated, *T. weissflogii* (isolated from the lowest latitude) was less sensitive

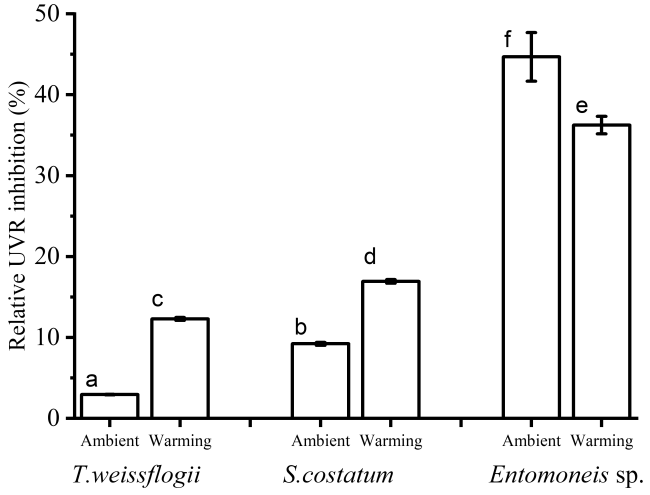

FIGURE 3 Relative UVR inhibition on temperate and polar species grown under ambient and warming conditions. Vertical lines represent standard deviations, $n = 3$, different letters above bars indicate significant differences between temperature treatments and species, and the order of relative UVR inhibition is consistent with the alphabetical order above bars.

to UVR compared with the other two species, while the polar species showed the greatest sensitivity, indicating that the light history might play a role in the differences in their UV resistance.[38]

Other short-term incubation experiments have shown that increasing temperature counteracts the negative effect of UV radiation on morphology and photosynthetic efficiency of three cyanobacteria,[39] and decreased UVR effects by enhancing repair of the damage.[40] However, our study showed that elevated temperature significantly exacerbated the impacts of UVR on the photochemical in the temperate diatoms, though it alleviated that in the polar species, suggesting that the warming could differentially affect the photosynthetic performances of diatoms in different regions.[41] Under a global change scenario, the loss of ozone in polar regions would increase the intensity of UVB reaching the sea surface, and this may counteract the benefits of warming to polar species.[17,18]

Diatoms in different waters are exposed to different levels of multiple environmental pressures, such as rising temperature, organic pollutants, enhanced UVR, and ocean acidification, and the interactions among these environmental factors are very complicated.[38,42] Thus, it is hard to predict the overall impact of multiple pressures on primary production because of the limited datasets on the interaction of multiple environmental factors.[43] However, our findings indicated that although temperate species showed less UVR effects on growth and photophysiology than the polar species tested, warming exacerbated the impact of UVR in temperate diatoms but alleviated it in the polar diatom and enhanced its growth. This study is the first report that rising temperature not only alleviated the magnitude of environment stress for a polar diatom but also could enhance the extent of UV inhibition of temperate species. Under an ocean global warming scenario, our results imply that UV radiation is likely to have more severe effects on temperate diatoms, while polar diatoms may benefit in terms of UV-induced harms. However, the species and experimental temperature range tested were limited in the present study, and a far greater range of species needs to be investigated to see if there are truly biogeographical correlates with the sensitivity of phytoplankton to combined warming and UVR.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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