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Differential photosynthetic response of marine planktonic and benthic diatoms to ultraviolet radiation under various temperature regimes

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Abstract:

We studied the photophysiological response to ultraviolet radiation (UVR) of two diatoms, isolated from different environmental niches. Both species showed the highest sensitivity to UV radiation under relatively low temperature, while they were less inhibited under moderately increased temperature. Under the highest temperature applied in this study, the benthic diatom *Nitzschia sp.* showed minimal sensitivity to UV radiation, while inhibition of the planktonic species, *Skeletonema sp.*, increased further compared with that at the growth temperature. These photochemical responses were linked to values for the repair and damage processes within the cell; higher damage rates and lower repair rates were observed for *Skeletonema sp.* under suboptimal temperature, while for *Nitzschia sp.*, repair rates increased and damage rates were stable within the applied temperature range. Our results suggested that the response of phytoplankton to UV radiation correlated with their niche environments, the periodic exposure to extreme temperature promote the resistance of benthic species to the combination of high temperature and UV radiation. Furthermore, the temperature-mediated UV sensitivities might also have implications for phytoplankton in the future warming oceans.

Keywords: Diatom, Photosynthetic performance, Temperature, UV radiation

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35 **Introduction**

36 As the most abundant group of phytoplankton, and one that plays an important
37 role in marine ecosystem function and biogeochemical cycles, diatoms are traditionally
38 divided into centric and pennate species on the basis of their valve symmetry (Round
39 et al., 1990). Centric diatoms are usually, though not invariably, planktonic and pennate
40 species are benthic, and are often found living in different niches (Irwin et al.,
41 2012;Keithan et al., 1988). The distribution of centric diatoms is more widespread, with
42 records for the open ocean as well as coastal water, and they maintain position in the
43 upper mixing layer by maintaining buoyancy with elaborated spines or excretion of
44 heavy ions (Lavoie et al., 2016;Villareal, 1988). In contrast, pennate diatoms are often
45 found in the intertidal zone (Stevenson, 1983). Therefore, the 2 groups of diatom are
46 likely to have evolved different strategies to cope with their niche environments
47 (Barnett et al., 2015;Lavaud et al., 2016;Lavaud et al., 2007).

48 Temperature affects almost all biochemical reactions in living cells, and is one of
49 the most important factors that determines the biogeography, as well as the temporal
50 variation of phytoplankton (Levasseur et al., 1984). Under global change scenarios,
51 increases in sea surface temperature would re-structure the phytoplankton assemblages
52 in the future ocean (Thomas et al., 2012). At small spatial scales, e.g. the coastal zone,
53 diurnal cycle of tides or meteorological events could expose benthic diatoms to extreme
54 environments, including high PAR and UV exposure as well as larger variations in
55 temperature than found for planktonic species. Hence organisms in such exposed areas
56 should potentially possess highly efficient mechanisms to adapt such environment
57 (Souffreau et al., 2010;Weisse et al., 2016).

58 In the intertidal zone, UV radiation (UVR) is another driving force. UVR is a
59 component of the solar spectrum, along with photosynthetically active radiation (PAR),
60 and has wide reaching effects on organisms, especially photoautotrophs due to their
61 demands for light energy (Williamson et al., 2014). The penetration of effective UVR
62 in coastal waters is mainly dependent on the properties of the seawater (Tedetti and
63 Sempere, 2006). Previous studies have found that UVR significantly inhibited carbon

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64 fixation by phytoplankton in the surface layer, with less inhibition or even stimulation
65 in deep water due to low UVR and limiting levels of PAR (Gao et al., 2007).
66 Detrimental effects, however, varied seasonally, with less inhibition observed for
67 planktonic assemblages during summer, though UV radiation was the highest. This may
68 be attributable to the higher water temperature which facilitated enzyme-catalyzed
69 repair processes within the cell (Wu et al., 2010). There are few documented studies on
70 benthic species, which actually are potentially more resistant to UVR as they are
71 periodically exposed to high solar radiation during low tide (Barnett et al., 2015).

72 Photosystem II (PSII) initiates the first step of photosynthesis, converting photons
73 to electrons efficiently, but this complex is very sensitive to light (Campbell and
74 Tyystjarvi, 2012). The subunits of PSII are broken down under UVR or high PAR while
75 repaired by insertion of de-novo synthesized protein (Aro et al., 1993); the repair
76 process eventually reaches a dynamic balance with damage (Heraud and Beardall,
77 2000). However, these two processes are independent from each other. The
78 photochemical damage is mainly determined by the intensity and spectrum of light
79 (Heraud and Beardall, 2000) and is temperature insensitive, while the repair process is
80 driven by a series of enzyme-catalyzed reactions, and is thus potentially sensitive to
81 temperature changes (Melis, 1999). Previous studies revealed that high temperature
82 alleviated UV inhibition of photosystem II in green algae (Wong et al., 2015), while it
83 interactively decreased photosynthetic activity in microphytobenthos under excessive
84 PAR conditions (Laviale et al., 2015).

85 Coastal water is a highly productive zone, with most of primary productivity
86 attributed to diatoms (Carstensen et al., 2015). Hence, how diatoms respond to
87 environmental factors, e.g. UV radiation, nutrient pulses or temperature, has been
88 extensively studied (Häder et al., 2011). These responses were often shown to be
89 species-specific, and could correlate with cell size, geometry or distinct mechanisms
90 operated by different species (Halac et al., 2014;Wu et al., 2015). Considering the
91 niches in which diatoms are living, physical and chemical factors are quite different
92 between planktonic and benthic species (Souffreau et al., 2010). In this study, we will

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use two isolated species to test the hypothesis that benthic diatoms have a stronger ability to adapt to potentially stressful solar UV radiation under high temperature regimes.

Materials and methods

1. Species and culture conditions

We collected samples from offshore water and intertidal sediments in the coastal area of the Yellow Sea. These were re-suspended in seawater, and enriched with Aquil medium and incubated in a growth chamber for 3 days (Morel et al., 1979). Then a sub-sample was examined under a microscope, and single cells were picked up with a micro pipette. *Skeletonema sp.* and *Nitzschia sp.* were chosen for the present study, and were maintained in Aquil medium in a growth chamber at 15 °C. Prior to the experiment, both species were inoculated into enriched seawater and cultured semi-continuously in 500 mL polycarbonate bottles, illuminated with cool fluorescent tubes at a photon flux density of ~200 μmol m^{-2} s^{-1}, with a 12:12 light/dark cycle. While temperature was set at 15, 20 or 25 °C with variation less than 0.5 °C, and culture bottles (triplicates for each temperature) were manually shaken 2–3 times during light period and randomly distributed in the growth chamber.

2. Determination of spectra and growth rate

50 mL of culture was filtered onto a GF/F filter, and extracted in 5 mL absolute methanol for 2 h at room temperature in a 10 mL centrifuging tube, then centrifuged at 4000 rpm for 15 min (TDZ4-WS, Luxiang Inc.). The supernatant was scanned with a spectrophotometer (Lambda 35, PerkinElmer) in the range of 280nm-750 nm. The cut-off filters were scanned in the same wavelength range against air as a blank. Specific growth rate was estimated from the changes of dark adapted chlorophyll fluorescence, and calculated as: $\mu = (\ln F_2 - \ln F_1) / (T_2 - T_1)$, where F_1 and F_2 represent the steady-state fluorescence intensity at T_1 or T_2, respectively.

3. Experimental set up

The experiments were performed under a customized solar simulator with a 1,000 W xenon arc lamp as the light source. The incident irradiances of UV-B light (280–315

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nm), UV-A (315–400 nm), and PAR (400–700 nm) were measured using a broadband radiometer (SOLAR-2UV, TINEL Inc.).

In the middle of the light period, samples of both species in the exponential phase were harvested and directly transferred to quartz tubes (35 mL) at a density of less than 20 µg chl *a* L^{-1}, dark-adapted for 15 min, and milli-Q water (as a control) or lincomycin (final concentration, 0.5 mg mL^{-1}, for the determination of damage rate in the absence of repair) were added. The tubes were then placed into a water bath one after another at 1 minute intervals while covered with cut-off filters (ZJB280, ZJB400) that block radiation below 280 or 400 nm, respectively (50% transmission at 280 nm or 400 nm, see Figure A1), to create PAR + UV-A + UV-B (PAB) and PAR (P) treatments respectively. The light levels applied were PAR =440 µmol photons m^{-2} s^{-1} and UVR = 41.6 W m^{-2}, while temperature was controlled with a cooling system (CTP3000, Eyela) and was set as the incubation level (termed "acclimated") or incubation temperature +10 °C (termed "short term"), the latter mimicking a moderate increase in temperature in the intertidal zone during a low tide period. After the light exposure, samples were moved into a water bath at the same temperature as light exposure, but under dim light (~30 µmol photons m^{-2} s^{-1}), for recovery, effective quantum yields were then measured at 12 min intervals.

4. Chlorophyll fluorescence measurements

A total of 12 tubes (2 species and 2 radiation treatments) were dark-adapted for 15 min, then each tube was moved into water bath one by one with 1 minute interval for light exposure, and sub-samples were taken to measure the initial chlorophyll fluorescence with an Aquapen fluorometer (AP-C 100, PSI). During the subsequent light exposure, sub-samples were withdrawn every 12 minutes from the quartz tubes for fluorescence measurement, this procedure ensured that every sample was exposed to radiation with exact the same time duration. After five rounds of measurements (60 min), samples that were without lincomycin were transferred into the low light condition under the same temperature for recovery, and chlorophyll fluorescence was measured as above for 60 min.

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151 5. Data analysis

152 Effective quantum yields were measured with the AquaPen and calculated
153 according to the following equations:

154 Effective quantum yield = $(F_m' - F_t) / F_m'$

155 where F_m' is the effective maximal fluorescence, and F_t is the steady-state fluorescence
156 under actinic light.

157 The relative inhibition of effective quantum yield by UV was estimated according
158 to the following equation:

159 Relative inhibition (%) = $(P_P - P_{PAB}) / P_P \times 100$,

160 where P_P and P_{PAB} represent the effective quantum yield under P and PAB treatments,
161 respectively. Relative inhibition was calculated when P_P and P_{PAB} were significantly
162 different.

163 The rates of UVR-induced damage to photosystem II (PSII) (k, min^{-1}) were
164 calculated from lincomycin treated samples assuming repair (r) under these conditions
165 was zero. Repair rates (r, min^{-1}) were calculated using non-lincomycin-treated
166 samples with the fixed k values obtained from the parallel experiments with lincomycin.
167 Both calculation were according to the Kok equation (Heraud and Beardall, 2000):

168 $$\frac{P_t}{P_0} = \frac{r}{k+r} + \frac{k}{k+r} e^{-(k+r)t},$$

169 where P_0 and P_t represent the initial effective quantum yield and yield at time zero
170 and t (minutes), respectively.

171 The recovery rates under dim light were calculated with a simple exponential rise
172 equation (Heraud and Beardall, 2000) :

173 $$y = y_0 + c\,(1 - e^{-\alpha t})$$

174 where y represents the effective quantum yield at time t (minutes) during the dim
175 light incubation, α was the recovery rate, while y_0 and c are constants.

176 Statistical differences among treatments were analyzed with a one-way analysis of
177 variance (ANOVA) and Tukey HSD was conducted for *post hoc* investigation. A
178 confidence interval of 95% was set for all tests.

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179

180 **Results**

181 *Skeletonema sp.* had a lower growth rate under 15 and 20 °C (p<0.05), while
182 growth increased significantly and was 23% higher than that of *Nitzschia sp.* under
183 25 °C (Fig 1) (p<0.01). The spectra of methanol extracts of both species had a similar
184 pattern, *Nitzschia sp.* showed relatively higher absorption in the range of 410-480 nm
185 under 15 or 20 °C (Fig 2 A, B), and this further increased significantly under 25 °C (Fig
186 2C). While no obvious peak in the UV range for both species.

187 The initial photochemical quantum yield of 15 °C grown *Skeletonema sp.* was
188 around 0.50 during light exposure (incubated under 15 °C), but decreased gradually
189 toward the end of the radiation treatments, with lower values under PAB than the P
190 condition (Fig 3A). During the dim light exposure period, the quantum yield recovered
191 to its initial value within 24 min under P treatment, while PAB treated cells only
192 recovered partially to ~70% by the end of the dim light incubation (Fig 3A). For 15 °C
193 grown cells that were incubated under 25 °C, the general patterns were similar as under
194 15 °C, though with smaller differences between the P and PAB treatments (Fig 3B).
195 Under dim light, quantum yield of both radiation treatments recovered to near initial
196 values (Fig 3B). For 15 °C grown *Nitzschia sp.* that was measured at 15 °C, the
197 decreasing pattern under P or PAB was similar to that of *Skeletonema sp.*, while for
198 PAB exposed cells, *Nitzschia sp.* could only recover to ~50% of initial value under dim
199 light (Fig 3C). However, when 15 °C grown *Nitzschia sp.* were incubated at 25 °C for
200 light exposure, both P and PAB treated cells had higher quantum yields, with less UVR
201 suppression of photosystem II compared with 15 °C, and PAB exposed cells could
202 recover to 75% of the initial value when subsequently incubated under dim light (Fig
203 3D).

204 The 20 °C grown *Skeletonema sp.*, independent of incubation temperatures (20 or
205 30 °C), showed insignificant UV inhibition for most of time points during radiation
206 exposure, and recovered more quickly under dim light, especially for PAB treated cells
207 compared with samples under 15 °C (Fig 4 A, B). For *Nitzschia sp.* that were grown at

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20 °C, cells showed moderate UV inhibition during radiation exposure, and the quantum yield under PAB treatment only recovered to ~80% at the end of the dim light incubation at 20 °C, while quantum yield recovered to the initial value in cells measured under 30 °C (Fig 4 C, D).

Skeletonema sp. that was grown and measured at 25 °C showed a similar pattern to that grown under 20 °C during both radiation exposure and subsequent dim light (Fig 5A). However, quantum yields decreased significantly once cells were moved into 35 °C, with much lower values observed under PAB and P treatment (p<0.001) than under 25 °C. During the dim light period, *Skeletonema sp.* only recovered to ~30% for P treatment, while there was no recovery after the PAB treatment (Fig 5B). For *Nitzschia sp.* measured under 25 or 35 °C, both treatments showed a similar response, with lower values under PAB than P during the radiation exposure (p<0.001 at 25 °C, p<0.01 at 35 °C), while cells could recover to near initial values at the end of the dim light incubation (Fig 5 C, D).

In the presence of lincomycin, changes in effective quantum yield showed a similar pattern for most of treatments (Figure A2-4), except for *Skeletonema sp.* incubated under 35 °C, which had relatively lower values compared with samples under 25 °C (Figure A4).

The relative inhibition induced by UV radiation at the end of radiation exposure is shown in Fig 6. Both species had the greatest sensitivities under 15 °C, with 80% and 70% relative inhibition of photochemical quantum yield for *Skeletonema sp.* and *Nitzschia sp.*, respectively. In the range of acclimated temperature, relative UV inhibition decreasing with increase of temperature for both species. While in the range of short term incubation with a 10 °C increase, UV inhibition of *Skeletonema sp.* was comparable at 25 °C and 30 °C, but increased significantly to ~50% at 35 °C (p<0.01). For *Nitzschia sp.*, relative UV inhibition during short term incubation reached a plateau, in the range of 25 – 35 °C, of around 25%.

During radiation exposure, the repair rates for photosystem II in *Skeletonema sp.* varied among different temperatures, with highest values observed at 25 °C, and lowest

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values at 35 °C for both radiation treatments (Fig 7A). The damage rates gradually decreased from 15 to 25 °C, then increased significantly toward 35 °C (Fig 7B) (p<0.001). The ratio of repair rate to damage rate (r : k) showed a unimodal pattern with peak values at 25 °C, and with lowest values under 15 or 35 °C, especially for the PAB treatment (Fig 7C).

The repair rate during light exposure for *Nitzschia sp.*, increased significantly in the temperature range of 15 to 25 °C (p<0.001), while kept relatively stable from 25 to 35 °C (Fig 8A). The damage rates were quite stable for all temperatures tested, whether cells were acclimated or exposed to short term elevation of temperature, with mean values around 0.075 for PAB and 0.032 for P treatment (Fig 8B). The r : k ratio increased with temperature in the range of 15-25 °C, reaching relatively stable values of around 1.50 for PAR, and around 1.0 for the PAB treatment (Fig 8C).

Under dim light, the rate constant for recovery of PAR-exposed *Skeletonema sp.* were around 0.10-0.15 min^{-1} in the range of 15-30 °C, while increased significantly to around 0.30 at 35 °C (p<0.01) (Fig 9A). The rate constant for recovery of P exposed *Nitzschia sp.* was relatively stable, around 0.25 min^{-1}, in the range of applied temperature (Fig 9B). The rate constant for recovery of PAB exposed *Skeletonema sp.* showed an increasing pattern from 0.05 to 0.17 min^{-1} in the range of 15-25 °C, but decreased significantly at 30 °C (p<0.05); at 35° values were unable to be estimated due to poor fitting of data points (Fig 9C). No consistent trend was found for the rate constant for recovery of PAB exposed *Nitzschia sp.,* around 0.10-0.15 min^{-1}, in the range of applied temperature (Fig 9D).

Discussion

The natural variation of physical and chemical factors, including nutrients, salinity, temperature, light etc., provide major controls that determine the distribution, succession and composition of phytoplankton (Levasseur et al., 1984). In response to these variables, phytoplankton have evolved different strategies of acclimation or adaptation (Irwin et al., 2015;Padfield et al., 2016). In this study, we found that both benthic and planktonic diatoms were less inhibited by UVR under moderately increased

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266 temperature, while the benthic species was more resistant to UVR under the extreme
267 temperature. These findings imply that temperature is a key factor that mediates the
268 response of diatoms to UVR, while different species have developed distinct
269 mechanisms in response to their particular niche environments (Laviale et al., 2015).
270 As a basic environmental factor, temperature affects all metabolic pathways, and
271 extreme or sub-optimal conditions are often encountered by various organisms in nature
272 (Mosby and Smith, 2015). The growth response of phytoplankton to temperature varies
273 from species to species, but often shows a unimodal pattern (Brown et al., 2004;Chen,
274 2015). For the applied temperature range in the present study, the growth rate of benthic
275 species showed a slight response, while growth increased with temperature to a greater
276 extent in the planktonic species, particularly above 25 ºC. However, life forms in the
277 natural environment are affected by multiple stressors concomitantly (Boyd et al., 2015).
278 For instance, a recent studies have demonstrated that increased temperature would
279 interactively affect phytoplankton with light intensity (Edwards et al., 2016), and could
280 alleviate UV direct inhibition on some sensitive species (Halac et al., 2014). When
281 species were acclimated under sub-optimal temperature (15 °C), both showed obvious
282 sensitivity to UVR (Fig 3). During the recovery period, the effective quantum yield of
283 the benthic diatom could rapidly reach the highest values within 12 min irrespective of
284 the incubation temperature. The planktonic diatom, however, only performed better
285 under short term elevated temperature. This suggests that the benthic species could have
286 broader adaptability in cope with the highly varied temperature environment they
287 frequently experience (Laviale et al., 2015).
288 The operation of Photosystem II is sensitive to light intensity as well as quality.
289 High P and UVR can usually induce significant damage to this complex, while the de
290 novo synthesis of protein can replace the damaged subunit (Aro et al., 1993;Lavaud et
291 al., 2016). The damage rate (k), which represents the efficiency of detrimental effects,
292 showed a different response for the 2 species in this study; in the planktonic species, k
293 was sensitive to temperature change with the lowest value at the medium temperature,
294 but was quite stable in the benthic species at all temperatures tested. This could be

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attributed to a decrease in electron transport, or changes in ultra-structure which resulted in higher intracellular light exposure for planktonic species (Melis, 1999;Nitta et al., 2005). The repair rates (r) and the ratio of r to k further demonstrated that the planktonic species had a relatively lower optimal temperature in response to UVR, with the highest r:k and lowest UV inhibition at 25 °C. In contrast, in the benthic species r and r:k increased steadily and reached relatively stable values at the highest temperature, and this coincided with lower UV inhibition, implying that although acclimated in lab condition for weeks, this species still had an active mechanism to respond to high temperature and UVR, as might occur in its natural niche environment (Laviale et al., 2015).

In addition to repair process that are initiated after damage, UV absorbing compounds could directly screen out part of the detrimental radiation, protecting cellular organelles from UV damage (Garcia-Pichel and Castenholz, 1993). In diatoms, however, the spectra of methanol extracts showed only a small absorbance peak in the UVR. Unlike xanthophyll cycle related pigments, UV-absorbing compounds (UVAC) are inducible and only synthesized under long-term UV exposure, indicating that UVAC are not a major protecting mechanism for lab cultured diatoms (Helbling et al., 1996). However, the xanthophyll cycle could respond quickly under photo-inhibition, and has been shown to be a major mechanism in diatoms in response to high light or UV (Cartaxana et al., 2013;Zudaire and Roy, 2001). Therefore, the relatively higher absorption in the blue range for benthic species, might indicate that temperature enhances the synthesis of xanthophyll related pigments (Havaux and Tardy, 1996).

The temperature dependent response to UVR has major implications for phytoplankton. With the continuing emission of greenhouse gases, the surface seawater temperature is predicted to increase by up to 4 °C by the end of this century (New et al., 2011), and this could potentially re-shape the phytoplankton assemblages (Thomas et al., 2012). While the situation might be more complex in the natural environment with the consideration of interaction of UVR with other factors (Beardall et al., 2009), for unicellular green algae, an increase of temperature could mitigate UVR harm for

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temperate species, while exacerbating UV inhibition for polar species (Wong et al., 2015). Moreover, the tolerance of phytoplankton to extreme temperature would be latitude dependent; for tropical areas where the temperature is already high, an increase of temperature reduced the richness of phytoplankton (Thomas et al., 2012).

The present study showed a differential response to UV radiation for two diatoms from contrasting niches. As predicted, the benthic species had a higher tolerance to the combination of extreme temperature and UV radiation, which can be attributed to the environment in which were living. Below the optimal temperature, both species performed better in response to UV radiation under elevated temperature, suggesting that the natural variation of temperature due to changes in the heat flux from the sun or meteorological events would alter the extent of UV effects on primary producers, and therefore the aquatic ecosystem (Häder et al., 2011). Furthermore, considering the projected global warming scenarios, UV radiation could impose different impacts on phytoplankton with respect to the regional differences (Beardall et al., 2009;Xie et al., 2010).

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468 **Fig legends:**

469 Fig 1 The specific growth rates of both species under different temperature levels, vertical lines
470 represent SD, n=3.

471 Fig 2 The absorption spectra of methanol extracts of *Skeletonema sp.* and *Nitzschia sp.* cultured
472 under different temperature, spectra were normalized with value set as 1.0 at wavelength of 665nm,
473 vertical lines represent SD, n=3.

474 Fig 3 The quantum yields of 15 °C grown *Skeletonema sp.* and *Nitzschia sp.* under P or P+UVR for
475 1 hour exposure and subsequent recovery under dim light (gray area) for 1 hour, that were incubated
476 and measured at 15 °C (A: *Skeletonema sp.*, C: *Nitzschia sp.*) or 25 °C (B: *Skeletonema sp.*, D:
477 *Nitzschia sp.*) , vertical lines represent SD, n=3.

478 Fig 4 The quantum yields of 20 °C grown *Skeletonema sp.* and *Nitzschia sp.* under P or P+UVR for
479 1 hour exposure and subsequent recovery under dim light (gray area) for 1 hour, that were incubated
480 and measured at 20 °C (A: *Skeletonema sp.*, C: *Nitzschia sp.*) or 30 °C (B: *Skeletonema sp.*, D:
481 *Nitzschia sp.*) , vertical lines represent SD, n=3.

482 Fig 5 The quantum yields of 25 °C grown *Skeletonema sp.* and *Nitzschia sp.* under P or P+UVR for
483 1 hour exposure and subsequent recovery under dim light (gray area) for 1 hour, that were incubated
484 and measured at 25 °C (A: *Skeletonema sp.*, C: *Nitzschia sp.*) or 35 °C (B: *Skeletonema sp.*, D:
485 *Nitzschia sp.*) , vertical lines represent SD, n=3.

486 Fig 6 The relative inhibition induced by UVR on the photosystem II of *Skeletonema sp.* (A) and
487 *Nitzschia sp.* (B) under grown or short term elevated temperature, vertical lines represent SD, n=3.

488 Fig 7 The repair rate (A) and damage rate (B) of photosystem II in *Skeletonema sp.* during P or
489 P+UVR exposure under grown temperature (acclimated) or short term elevated temperature
490 (short_term), and the ratio of repair to damage rate (C), vertical lines represent SD, n=3.

491 Fig 8 The repair rate (A) and damage rate (B) of photosystem II in *Nitzschia sp.* during P or P+UVR
492 exposure under grown temperature (acclimated) or short term elevated temperature(short_term),
493 and the ratio of repair to damage rate (C), vertical lines represent SD, n=3.

494

495 Fig 9 The rate constants for recovery of P exposed *Skeletonema sp.* (A) and *Nitzschia sp.* (B), and
496 rate constants for recovery of PAB exposed *Skeletonema sp.* (C) and *Nitzschia sp.* (D) under dim

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497 light, samples were incubated under grown temperature (acclimated) or short term elevated
498 temperature (short_term), vertical lines represent SD, n=3.

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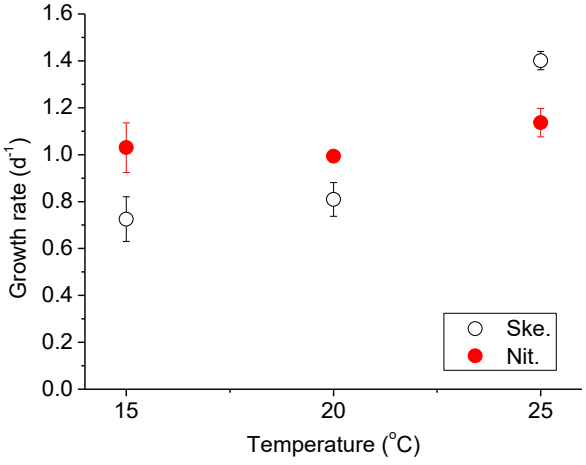

Fig 1

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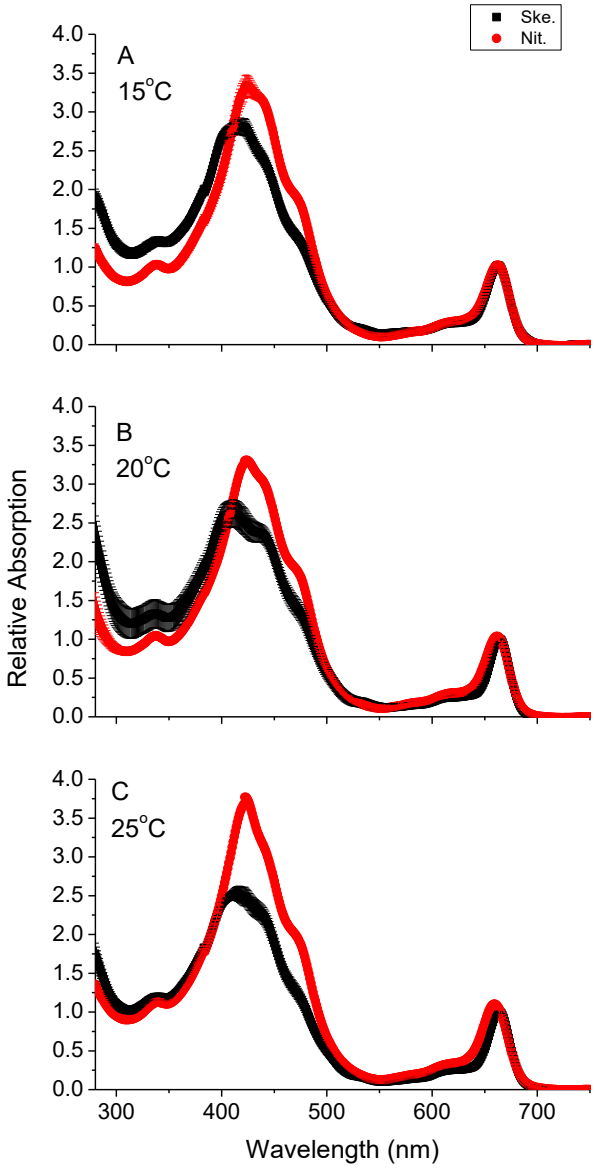

Fig 2

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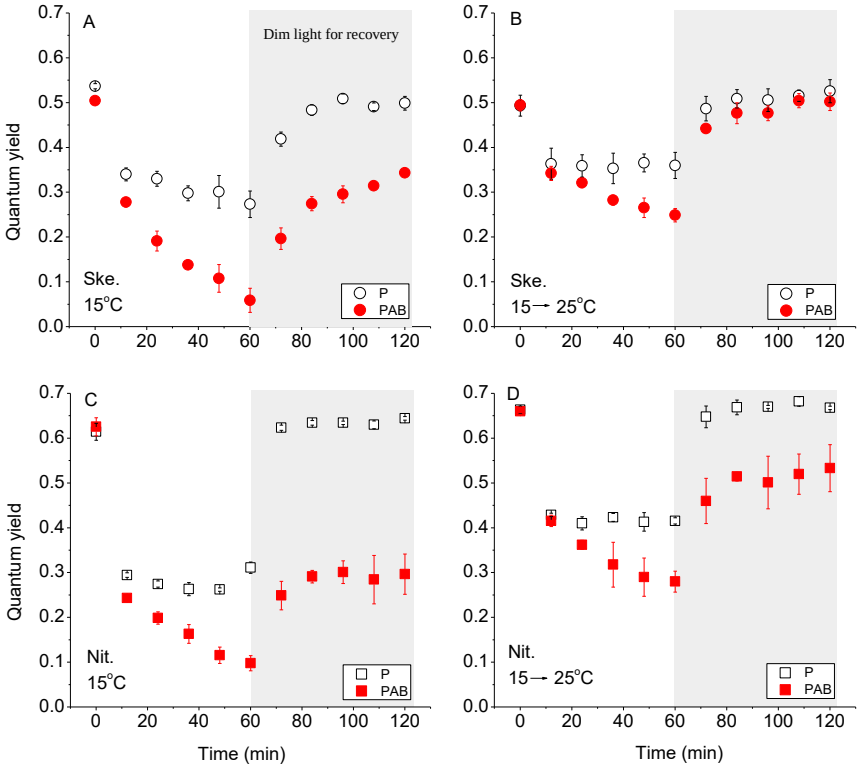

Fig 3

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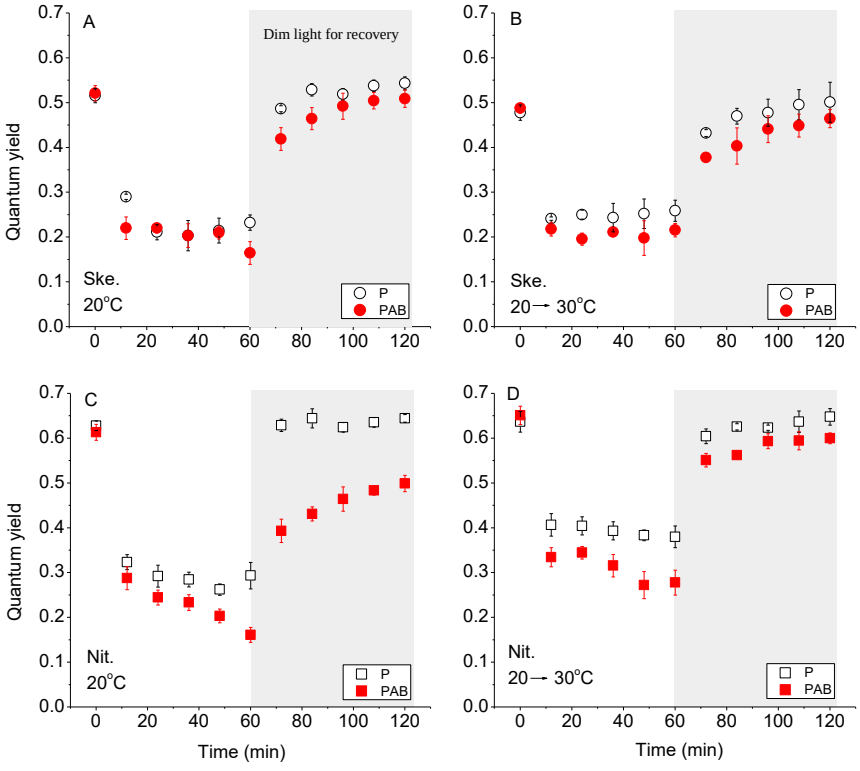

Fig 4

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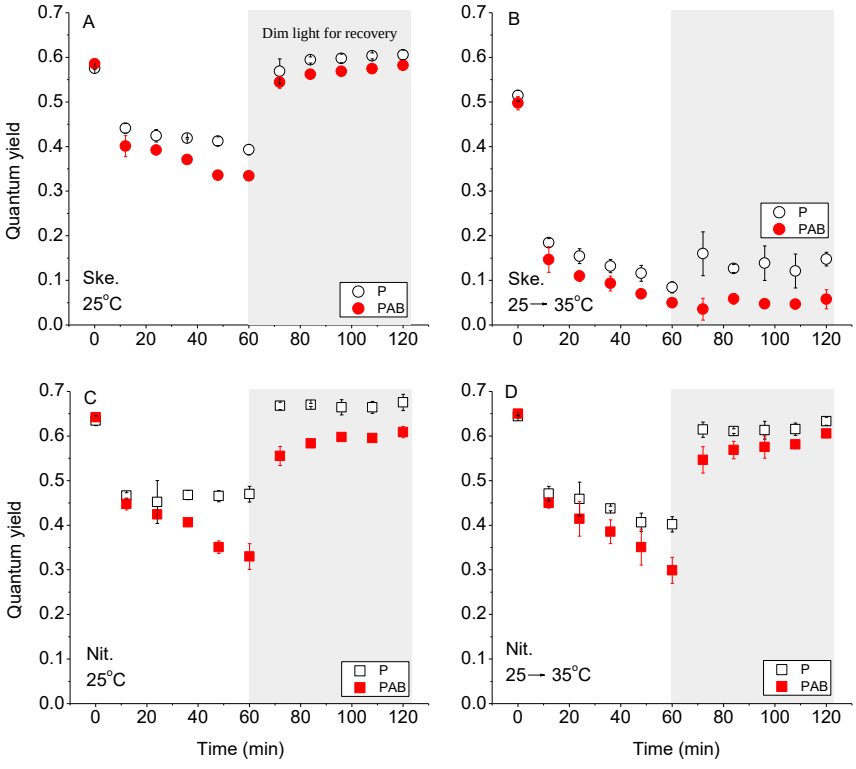

Fig 5

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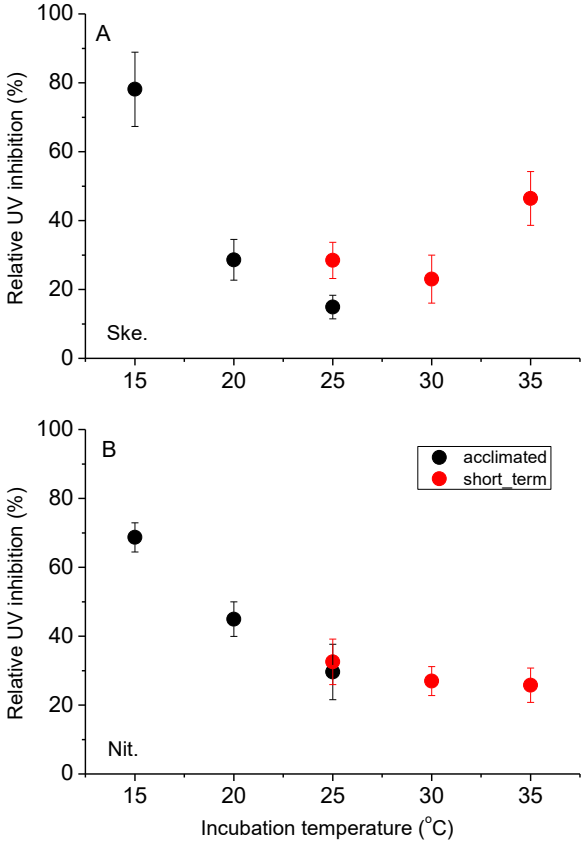

Fig 6

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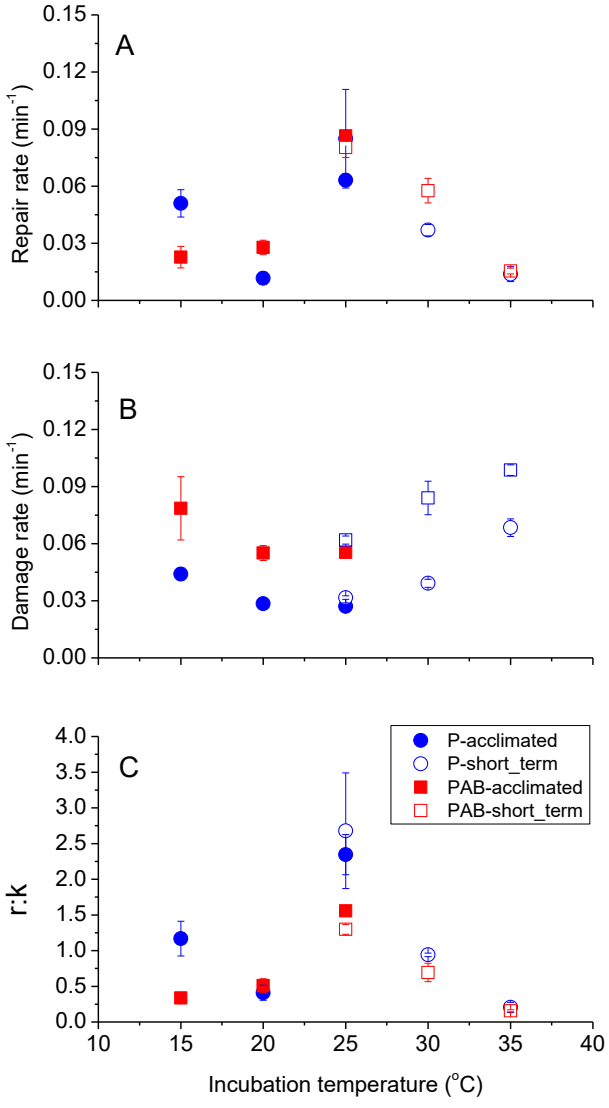

Fig 7

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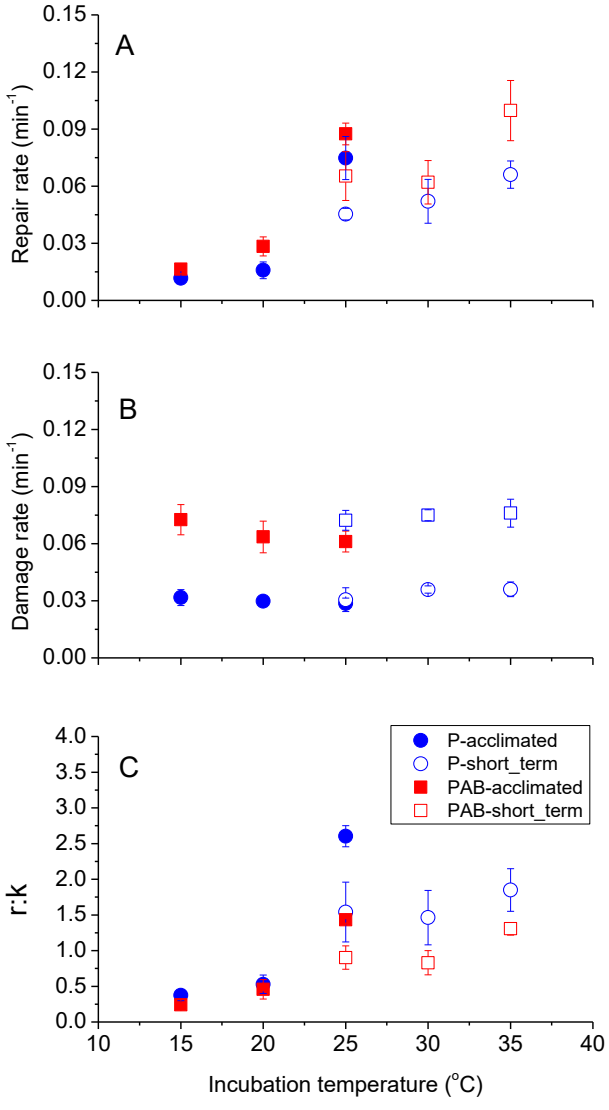

Fig 8

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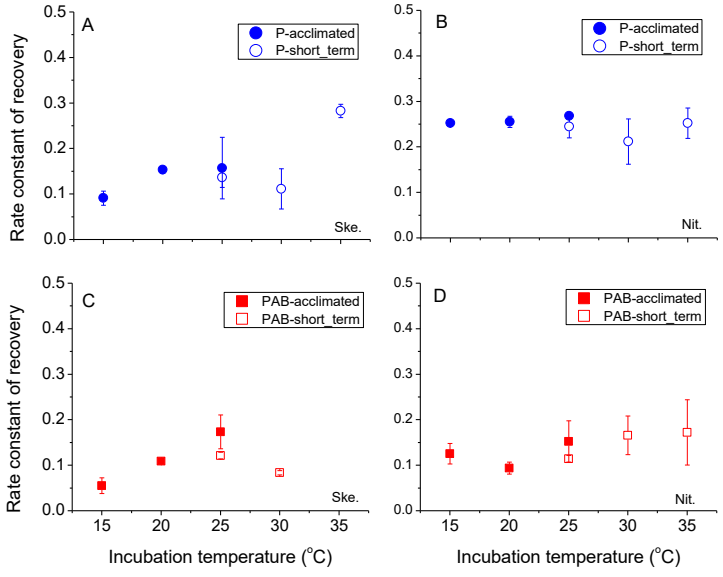

Fig 9

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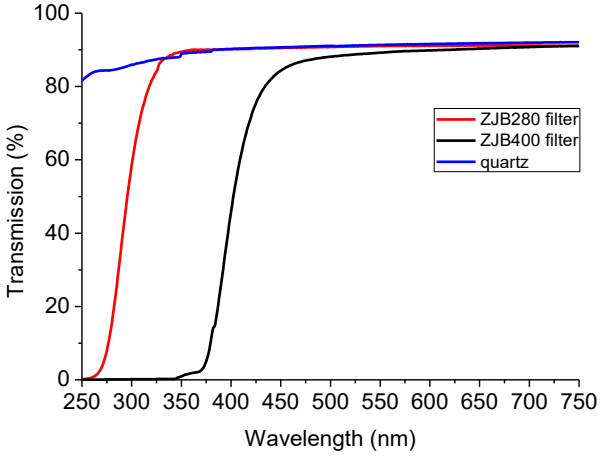

Figure A1The transmission spectra (in percentage) of different cut-off filters (ZJB280, ZJB400) and the quartz tube between 280 and 750 nm.

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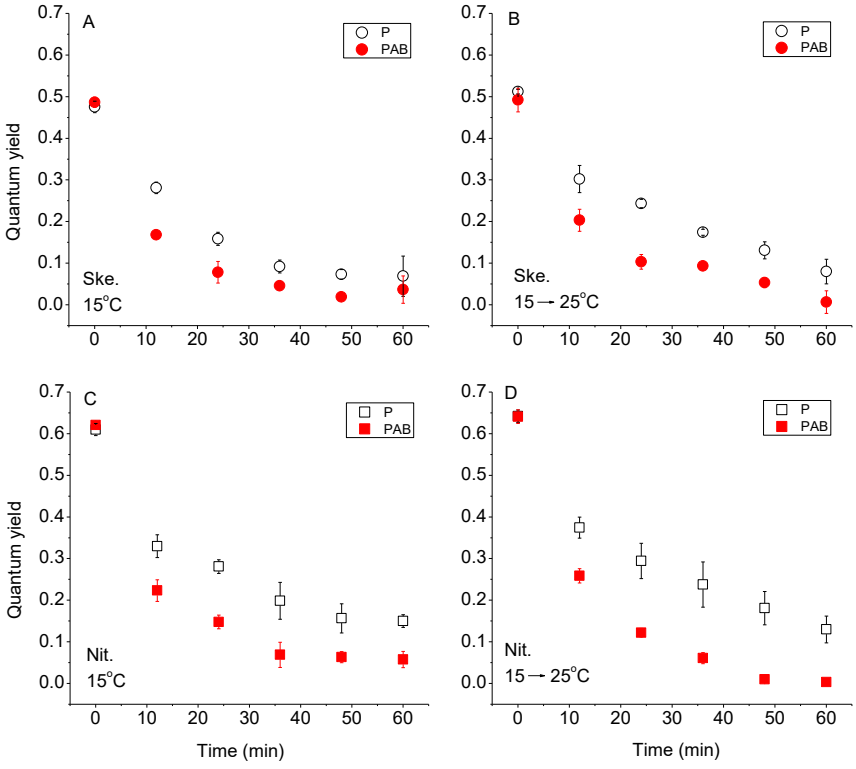

Figure A2 The quantum yields of 15 °C grown *Skeletonema sp.* and *Nitzschia sp.* under P or P+UVR for 1 hour exposure in the presence of lincomycin, that were incubated and measured at 15 °C (A, C) or 25 °C (B, D) , vertical lines represent SD, n=3.

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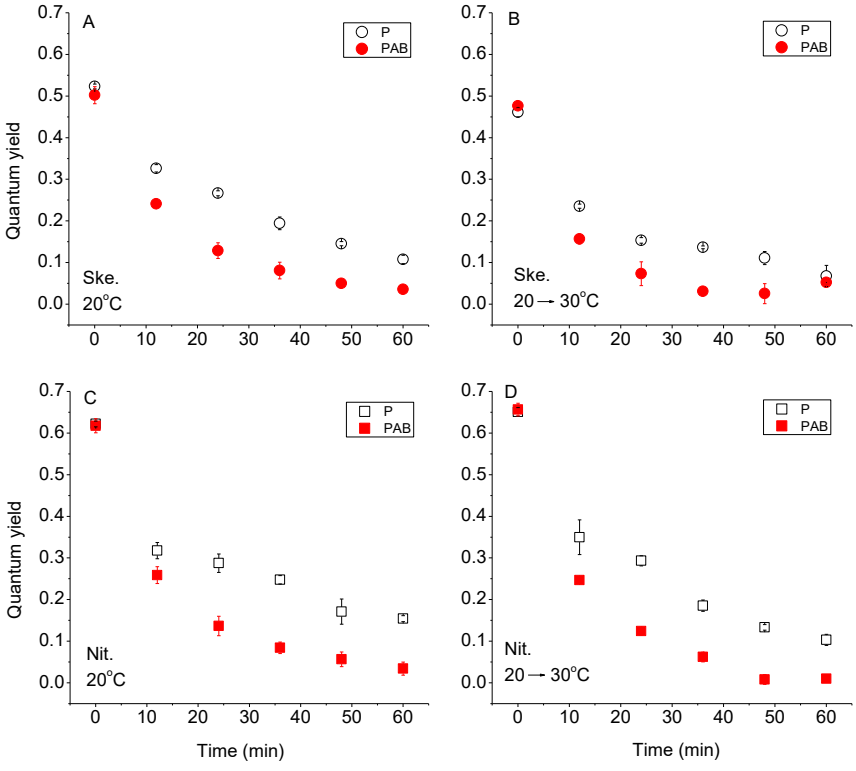

Figure A3 The quantum yields of 20 °C grown *Skeletonema sp.* and *Nitzschia sp.* under P or P+UVR for 1 hour exposure in the presence of lincomycin, that were incubated and measured at 20 °C (A, C) or 30 °C (B, D) , vertical lines represent SD, n=3.

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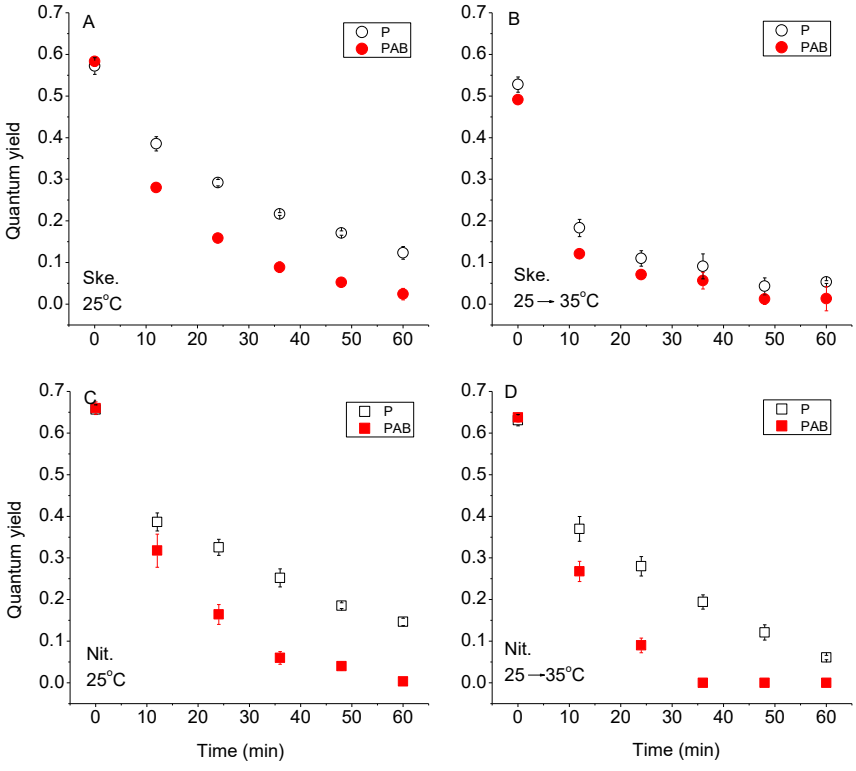

Figure A4 The quantum yields of 25 °C grown *Skeletonema sp.* and *Nitzschia sp.* under P or P+UVR for 1 hour exposure in the presence of lincomycin, that were incubated and measured at 25 °C (A, C) or 35 °C (B, D) , vertical lines represent SD, n=3.