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Differential susceptibility of Red Sea *Pocilloporidae* corals to UVB highlights photoacclimation potential

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Despite being exposed to extreme water temperatures and solar irradiances, Red Sea corals are relatively resistant to bleaching. While their thermal tolerance is well described, little is known about their resistance to ultraviolet-B radiation (UVB). Here, we performed a short-term (2 days) UVB-removal incubation with *Stylophora pistillata*, and *in situ* measurements with *Pocillopora verrucosa* complemented by a long-term (46 days) transplantation and UVB-removal experiment. Using a suite of physiological parameters (effective quantum yield (F_v'/F_m'), oxidative stress (lipid peroxidation, LPO), and primary production), we assessed the impacts of UVB on the physiology and acclimation capacity of Red Sea corals. Shielding *S. pistillata* from UVB did not change the gross primary production or F_v'/F_m', and respiration and LPO in the host remained unaffected. In situ, *P. verrucosa* exhibited less varying and significantly higher F_v'/F_m' in 8 m depth (0.61 ± 0.04) than in 4 m (0.52 ± 0.06), 2 m (0.51 ± 0.09), and 0.5 m (0.50 ± 0.11), where water temperatures ranged from 30.5−33.4, 30.6−34.0, 30.8−34.5, 30.6−37.3°C and daily UVB exposures averaged 0.9, 2.9, 11.8 and 21.4 kJ m^{-2}, respectively. F_v'/F_m' correlated the strongest with UVB (-0.57), followed by PAR (-0.54) and temperature (-0.40), suggesting that UVB is a key determinant of photosynthetic efficiency. F_v'/F_m' of upward transplanted specimens (T 1m) was initially decreased but gradually increased and reached the same values as shallow corals (1 m) after 44 days. UVB removal significantly increased the F_v'/F_m' of transplanted corals in the first 20 days. Oxidative stress was initially highest in T 1m samples under full sunlight but equalized with 1 m specimens by day 46, whereas oxidative stress was significantly reduced by day 4 in T 1m corals sheltered from UVB. Overall, UVB-removal generally had little impact on the physiology of shallow-water *S. pistillata* and *P. verrucosa* but considerably accelerated the acclimation of upward transplanted corals. Our study highlights that UVB is a crucial stressor governing the photoacclimation capacity of these Red Sea coral species.

1 Introduction

To preserve biodiversity and for coral reef management to be successful, it is crucial to understand ecosystem functioning in general, and the effects of environmental conditions on the physiology and health status of the coral holobiont (Hughes et al., 2017a).

Ecophysiology-focused reef studies have traditionally investigated the biological responses of corals to individual environmental stresses, such as temperature- (Yakovleva et al., 2009; Oliver and Palumbi, 2011; Sawall et al., 2015) and salinity-extremes (Gardner et al., 2016; Gegner et al., 2019), ocean acidification (Hoegh-Guldberg et al., 2007; Grinblat et al., 2018), and deoxygenation (Altieri et al., 2017; Johnson et al., 2018; Hughes et al., 2020). However, in recent years, an increasing number of studies have pointed out that a broader understanding of coral functioning can only be gained by including the complex interactions between various ecosystem stressors (Dunne, 2010; Ban et al., 2014; Cote et al., 2016; Ellis et al., 2019; Jin et al., 2019). In the context of coral reef science, obtaining a better understanding of the interplay between different stresses could aid to disentangle the mechanisms responsible for the phenomenon of coral bleaching, i.e., the loss of photosymbionts and photosynthetic pigments, which presently threatens coral reefs worldwide (Hoegh-Guldberg, 1999; Hughes et al., 2003; Hoegh-Guldberg and Bruno, 2010).

Several studies have concluded that the onset of coral bleaching is predominantly attributed to prolonged or closely recurring periods of extreme water temperatures (Fitt et al., 2001; Krueger et al., 2015; Hughes et al., 2017b). Yet, some reports have suggested that the concurrence of thermal stress and extreme irradiance can further deteriorate the corals' health or intensify the thermally induced bleaching response (Lesser et al., 1990; Anthony et al., 2007; Brown and Dunne, 2008; Nesa et al., 2012; Courtial et al., 2017). Detrimental impacts of light on scleractinian corals, however, have mainly been studied for solar radiation as a whole (Brown et al., 1994; Lesser and Farrell, 2004; Anthony and Kerswell, 2007; Richier et al., 2008; Bellworthy and Fine, 2017) or the photosynthetically active part of the solar spectrum (i.e., PAR, 400–700 nm) (Fitt et al., 2000; Warner et al., 2002; Ulstrup et al., 2008), although some studies have acknowledged the importance of spectral composition (Mass et al., 2010), particularly ultraviolet radiation (UVR, 280–400 nm).

UVR may affect a broad array of functional levels in marine organisms such as corals, ranging from molecular to behavioral responses (Banaszak and Lesser, 2009), such as disrupted reproduction and larvae recruitment (Kuffner, 2001; Gleason et al., 2006; Torres et al., 2008; Zhou et al., 2016), reduced growth rates (Torres-Perez and Armstrong, 2012) and symbiont densities (Zhou et al., 2017), increased accumulation of mycosporine-like amino acids (MAAs) (Shick et al., 2003; Shick et al., 2005), impaired photosynthetic efficiency (Kinzie, 1993; Ferrier-Pages et al., 2007), damage to the genetic material (Anderson et al., 2001; Baruch et al., 2005; Torregiani and Lesser, 2007), while, the responses of coral holobionts to UV remain understudied and consequently not well understood (van de Water et al., 2018).

A further effect of UVR exposure is an increased production of reactive oxygen species (ROS) (Lesser, 1996). ROS, which include superoxide anion (O_2^-), hydroxyl radicals ($\bullet$OH), and hydrogen peroxide (H_2O_2), are produced by organisms in low to moderate concentrations due to normal cellular metabolism and physiological cell processes (Birben et al., 2012). Under environmental stress, however, ROS production is enhanced, leading to adverse modifications to the corals' cell components, such as lipids, proteins, and DNA (Downs et al., 2002). Reported impacts include elevated lipid peroxidation levels, increased antioxidant enzyme activity, and the breakdown of the corals' photo-symbiosis (Levy et al., 2006; Csaszar et al., 2009; Linan-Cabello et al., 2010). To protect against ROS-induced damage, organisms can produce enzymatic ROS scavengers (e.g. superoxide dismutase, catalase) or non-enzymatic antioxidants (e.g. vitamins, β-carotene) (Birben et al., 2012).

The severity of UV impacts depends on the intensity and duration of solar UV exposure. Daily UV exposure ranges greatly between seasons at sea level due to the variation in the intensity of incoming solar radiation and the number of daylight hours. For example, daily UVB exposure in the central Red Sea was reported to range from 21.6 kJ m^{-2} d^{-1} in December to 48.3 kJ m^{-2} d^{-1} in June (Overmans and Agusti, 2020). In the water column, daily UV exposure is also governed by the depth at which an organism resides and the bio-optical properties of the water column. Due to the proximity of coral reefs to the equator and the high transparency of oligotrophic tropical waters (e.g. Red Sea min. K_d (305nm): ~0.16 m^{-1}) (Overmans and Agusti, 2019), corals in shallow parts of tropical reefs are typically exposed to extreme UV irradiances of > 30 kJ UVB m^{-2} d^{-1} in 1 m depth (Zepp et al., 2008; Downs et al., 2013; Overmans and Agusti, 2020).

The Red Sea is known to receive intense solar UV radiation (~ 50 kJ m^{-2} d^{-1}) (McKenzie et al., 2007; Smyth, 2011), while the UVB attenuation coefficient is exceptionally low (min. K_d(305nm): 0.168 m^{-1}) due to negligible UVB absorption by chromophoric dissolved organic matter (min. a_{CDOM}(305 nm): 0.128 m^{-1}) and minimal chlorophyll-a concentrations (0.07 mg m^{-3}), characteristic of ultraoligotrophic waters (Stambler, 2005; Overmans and Agusti, 2019; Overmans and Agusti, 2020).

Most of the existing studies that aimed to elucidate the ecological effects of UVB have examined the stress responses of corals in the laboratory using artificially supplied PAR and UVB without providing UVA (315–400 nm), despite the latter being known to have beneficial effects (Häder et al., 2015). The few in situ studies mostly tested stress responses of corals following upward transplantations without any additional manipulation of the light conditions, which makes it challenging to disentangle the impacts of increased UVB from those of increased PAR and UVA. Upward transplanted corals exhibited reduced fecundity, symbiosis breakdown, or died within 20 days of transplantation (Vareschi and Fricke, 1986; Richier et al., 2008; Torres et al., 2008; Cohen et al., 2013).

Due to the intense levels of incident UV and the high transparency of reef waters, we hypothesize that UV, and
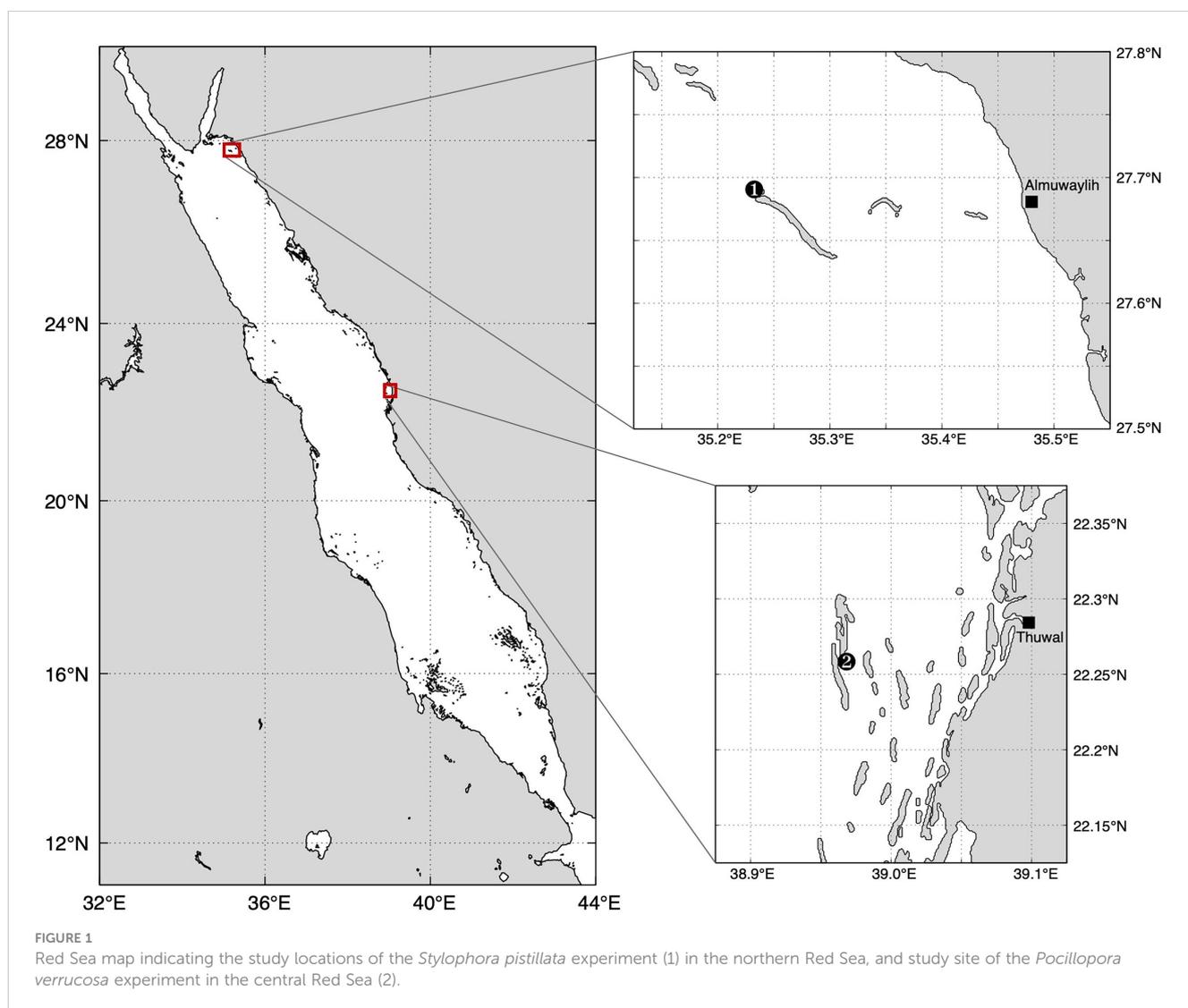
especially the highly energetic wavelengths of the UVB spectrum (280–315 nm), can induce severe stress on Red Sea corals and select for resistant organisms, as previously suggested (Agusti et al., 2015). We further hypothesize that these corals have developed acclimation responses to natural solar UVB.

We tested this hypothesis by determining the acclimation potential to natural solar UVB radiation and measuring physiological stress on the host and symbiont metabolism (oxidative stress, photochemical efficiency, and net primary production) of the two Pocilloporidae coral species, *Pocillopora verrucosa* and *Stylophora pistillata*, which are common in the Red Sea. We did so as part of a short-term (2 days) incubation experiment with *S. pistillata*, as well as *in situ* measurements with *P. verrucosa*. Subsequently, we performed a long-term (46 days) transplant experiment to test the acclimation capacity of *P. verrucosa* to increased UVB irradiances following transplantation from subsurface (5 m) to surface (1 m) waters.

2 Materials and methods

2.1 *Stylophora pistillata* incubation experiment (short-term)

Immediate effects of a short-term reduction or removal of solar UVB on the coral *S. pistillata* were investigated by performing a 2-day UVB-removal experiment onboard R/V Thuwal as part of the *Threats* oceanographic cruise (Overmans and Agusti, 2019). On 5th October 2016, *S. pistillata* specimens were sampled at an offshore reef in the far north of the Red Sea (27.686162° N, 35.231405° E) close to Almuwaylih (Figure 1). A total of 40 broken off coral fragments (~10–15 cm length) of >15 recently storm-damaged shallow water colonies were collected from the reef flat zone (~ 1.5 m depth) in the early morning and immediately transported back to the vessel in shaded 10 L containers filled with seawater. The specimens were transferred into an open-top incubator (LxWxH:

FIGURE 1
Red Sea map indicating the study locations of the *Stylophora pistillata* experiment (1) in the northern Red Sea, and study site of the *Pocillopora verrucosa* experiment in the central Red Sea (2).

150x80x50 cm) supplied with flow-through seawater to maintain *in situ* water temperature (29.0–30.8°C; see experimental setup Supplementary Figure 1). Incident PAR and UVB irradiances inside the incubator were monitored during the incubations with a PMA2100 data-logging radiometer (Solar Light, USA) fitted with a PAR (400–700 nm, model PMA2132-WP) and a UVB sensor (model PMA2106-WP). The coral fragments remained under those conditions for 20 h to allow some recovery time from sampling-induced stress.

The following morning, 12 fragments were transferred into 12 individual 2-L quartz glass Erlenmeyer flasks (UVB transmission: 88%, one fragment per flask) (Supplementary Figure 1) containing filtered (0.2 µm) seawater to prevent interference of microorganisms with metabolism measurements. The flasks were sealed and kept in the incubator at *in situ* temperatures. The samples were subdivided into three treatment groups (n=4 per treatment): PAR+UVA+full UVB, PAR+UVA+medium UVB, and PAR+UVA only, termed high UVB (H-UVB), medium UVB (M-UVB), and UVB removal (0-UVB), respectively. The three treatments were achieved by covering the flasks with different optical plastic screens. The M-UVB and 0-UVB treatment flasks were wrapped in foils that transmitted 54% (PE foil) and < 1% (Mylar foil) of the total UVB irradiance, respectively. The H-UVB flasks were covered in a coarse shade cloth (75% transmission) to create similar PAR conditions to the other two treatments (see Table 1; Supplementary Figure 2).

The oxygen evolution inside the flasks was monitored for 35 h (see section 2.4). Afterwards, the samples were shock-frozen in liquid nitrogen and stored at -80°C until analysis of lipid peroxidation (MDA) and total protein content (see 2.6).

The remaining coral fragments (n=24) were kept in an open-top incubator with sea water flow-through for 31 h (9 am–4 pm) at the three light treatments mentioned above (n=8 per treatment) by installing the optical screens directly above the fragments. The effective quantum yield (F_v'/F_m') of fragments was determined at the onset of the experiment, and after 3 h, 7 h, and 31 h (see section 2.5).

2.2 *Pocillopora verrucosa in situ* measurements and UVB dosimeter calibration

The photosynthetic efficiency of Red Sea *Pocillopora verrucosa* in different depths (0.5, 2, 4, 8 m) during summer (22nd July and 09th August 2018) was investigated by determining their F_v'/F_m' ratios using a Diving PAM fluorometer (Supplementary Figure 1, see section 2.5). *P. verrucosa* colonies were located on the inshore side of *Al Fahal* reef (22.254232 N, 38.960779 E) in the central Red Sea, ~10 km offshore from Thuwal, Saudi Arabia (Figure 1).

In each of the four sampling depths, one waterproofed and pre-calibrated UVB dosimeter (Scienterra, Oamaru, New Zealand) and one HOBO Pendant® data logger (Onset Computer Corporation, USA) were installed to record UVB (280–315 nm) irradiances, and water temperature (accuracy at 0–50°C: ± 0.53°C) and lux, respectively, in 10-minute intervals between 5th July and 12th August 2018. Lux values were converted to PAR using a

previously described conversion factor (1 µmol quanta m^{-2} s^{-1} = 52.0 lux) (Tilstra et al., 2018). The loggers were visited every 2-3 days to remove biofouling or to be replaced.

The UVB dosimeters were calibrated against spectrally-integrated, unweighted UVB (280–315 nm) irradiance data measured with a stationary UVB radiometer (model SUV-B, Kipp & Zonen, Netherlands). For the calibration, the dosimeters and radiometer recorded data in 60-second intervals from dawn until mid-day at the KAUST CMOR pier (22.304639°N, 39.102167°E) on a cloudless day (10th June 2018). Each dosimeter data set was plotted against the radiometer data, and a second-order polynomial curve in the form $y = A*x^2 + B*x + C$ was fitted, which provided a high coefficient of determination ($R^2 > 0.99$). The coefficients A, B, and C were subsequently used to convert raw dosimeter data to calibrated UVB values (in W m^{-2}).

In situ temperature data were used to identify periods when the coral bleaching thermal threshold of the Jeddah region (i.e., 32.1°C) was exceeded (Osman et al., 2018).

2.3 *Pocillopora verrucosa* transplant experiment (long-term)

To determine UVB exposure effects on the coral *Pocillopora verrucosa*, a long-term (46 days) *in situ* transplantation experiment was performed. Specimens were either kept at natural UVB irradiances, under UVB removal conditions, or exposed to elevated UVB irradiances (fragments transplanted from 5 m to 1 m depth). The study site was the inshore side of *Al Fahal* reef (22.254232 N, 38.960779 E), located in the central Red Sea ~10 km offshore from Thuwal, Saudi Arabia (Figure 1). On 28th April 2019, four *P. verrucosa* colonies were collected from the reef flat (0.5–1 m depth), and a further four colonies were sampled in ~ 4.5–5 m on the inshore side of the reef. Each colony was fragmented into 24 similarly sized (~ 10 cm long) nubbins (n= 96 fragments per sampling depth). Fragments from the same depth were randomized (to minimize colony effects) and attached to ~2 m long cords (8 cords, 12 fragments per cord) using small cable ties. Subsequently, the coral samples were returned to their original sampling depth for a fragmentation recovery period of 4 days.

On 2nd May 2019, the coral nubbins were recovered and equally distributed between two experimental treatments, for which two stainless steel frames (height: 1 m, base area: 1.58 m^2, top area: 5.62 m^2) were installed in the lagoon zone of the reef in 2 ± 0.1 m depth (tide-dependent) (see experimental setup in Supplementary Figures 1, 3). One frame, used for the full-sunlight (FS) treatment, was covered with a wire mesh fence on all sides to prevent predators from entering. The second fence, used for the UVB-removal treatment (-UVB), was secured with fencing at the sides, however, the top was covered with Mylar foil (UVB transmission: < 1%) (Supplementary Figure 2).

In each frame, 48 fragments from each of the two sampling depths (1 m and 5 m) were kept immediately below the top of the frames (1.0 ± 0.1 m depth), thereby generating four experimental groups: corals collected from 1 m depth under full sunlight (1 m FS) or UVB-removal conditions (1 m -UVB), and corals from 5 m

depth transplanted to 1 m depth kept in full sunlight (T 1m FS) or with UVB removed (T 1m -UVB). As such, samples that were collected in 1 m were either exposed to the same PAR and UVB conditions or the same PAR but without UVB while corals originating from 5 m depth were exposed to either increased PAR and UVB levels or elevated PAR but without UVB (see 3.2.1 for details).

In each sampling depth (1 m and 5 m), one HOBO Pendant[®] data logger (Onset Computer Corporation, USA) was installed to record water temperature and PAR conditions in 10-minute intervals. A waterproofed and pre-calibrated UVB dosimeter (Scienterra, Oamaru, New Zealand) was deployed to record UVB (280–315 nm) irradiances every 10 minutes. The frames were visited every 2-3 days to remove biofouling and replace the loggers.

During the experimental phase (2nd May–16th June), the effective quantum yield (F_v'/F_m') of the fragments was measured at the onset of the experiment and after 4, 7, 11, 14, 17, 20, and 24 days (see 2.5.). Additional F_v'/F_m' measurements were recorded for the FS fragments after 46 days.

At the start of the experiment and after 4, 11, and 20 days, 12 coral fragments per treatment (1m FS, 1m -UVB, T 1m FS, T 1m -UVB) were collected, plus an additional 12 fragments from the two FS groups after 46 days. The samples were shock-frozen in liquid nitrogen and stored at -80°C until further analysis of lipid peroxidation and total protein content (see 2.6.).

2.4 Primary production measurements

As part of the UVB-removal experiment with *Stylophora pistillata*, the oxygen evolution inside the sample flasks was assessed using a non-intrusive fluorescence-based method. A fiber optic Witrox Oxygen meter with oxygen mini-sensors (optodes) (Loligo Systems, Tjele, Denmark) fixed to the flasks were used to measure oxygen concentrations. In the mornings, a two-point calibration of the oxygen meter was performed according to the manufacturer's instructions. Oxygen concentrations (in μmol O_2 l^{-1}) inside each flask were measured on 6th October at 10 am and at 3 pm, 5 pm, and 6 pm. After the 6 pm measurement, the water inside the flasks was replaced with freshly filtered seawater to remove metabolic waste products. Further oxygen measurements were performed at 8 pm and on the following day at 6 am, 10.30 am, 3.30 pm, 6 pm, and 9.30 pm. Oxygen data were recorded, and salinity- and temperature-corrected (based on the SeaBird CTD measurements of the cruise stations; see Lopez-Sandoval et al. (2021)) using the software WitroxView (v.2.0.1). The changes in oxygen concentration (in μmol O_2 l^{-1} h^{-1}) during the light (10 am–6 pm) and dark periods (8 pm–6 am on day 1; 6 pm–9.9.30 pm on day 2) were used to calculate gross primary production (GPP), respiration (R), and net primary production (NPP). The change in oxygen concentration during the day informed about the NPP rate, while the rate of oxygen decrease during the night represents the respiration rate. GPP was calculated as GPP = NPP + R. Each of the three parameters was normalized by the coral fragments' surface area and reported as μmol O_2 cm^{-2} h^{-1}. To quantify the surface area, three photos per fragment were taken from different angles, the main dimensions were

measured with the image processing software ImageJ2 (v. 2.0.0) and the total surface area (in cm^{-2}) was calculated using the surface area formula of a cylinder (A = 2πr(r + h)).

2.5 Diving PAM measurements

UVB-induced damage to the photosynthetic apparatus of the corals' symbionts was evaluated by measuring the variable chlorophyll fluorescence of photosystem II (PSII) with a Diving Pulse Amplitude Modulation (Diving PAM) fluorometer (Heinz Walz GmbH, Germany). The effective quantum yield of coral samples (F_v'/F_m') was determined as the ratio of variable fluorescence (F_v') to maximal fluorescence (F_m') under actinic light (Genty et al., 1989; Baker, 2008). For the *Stylophora pistillata* experiment, fluorescence measurements (MI: 9–11, SI: 8, Sat width: 0.8 s, Gain 2–4, Damp: 2) were performed on eight fragments (n=8) per light treatment at the abovementioned sampling points. For the *in situ* measurements on *Pocillopora verrucosa*, ten fluorescence measurements (n = 10) per depth were recorded on each sampling day. During the long-term experiment with *P. verrucosa*, fluorescence measurements of ten fragments per light treatment were recorded per day. All measurements were recorded between 08:15 am and 10:45 am.

2.6 Lipid peroxidation (MDA), *in vivo* absorbance & total protein

Samples were processed according to standard protocols, with slight modifications (Krueger et al., 2015) (see Supplementary Figure 4). Each coral fragment was airbrushed and the tissue collected in 5 mL of ice-cold Phosphate buffer (50mM). The resulting tissue slurry was blended on ice for 30 s (3 x 10 s) and centrifuged at 3000 g and 4°C for 15 min to separate host tissue from symbiont cells. The resulting supernatant, containing enriched host cells, was analyzed for its malondialdehyde (MDA) content and absorbance in the UV and PAR spectra.

MDA was determined colorimetrically with an assay kit (Sigma-Aldrich, cat. # MAK085). Briefly, the samples were centrifuged at 13,000 g for 10 min to remove insoluble material. 200 μL of the supernatant from each homogenized sample was placed into a microcentrifuge tube, and 600 μL of TBA (thiobarbituric acid) solution was added to each standard or sample vial to form the MDA-TBA adduct. The mixtures were incubated (95°C for 60 min) and cooled to room temperature on ice for 10 min before the absorbances of samples at 532 nm (A532) were measured with a microplate reader (SpectraMax[®] Paradigm[®], Molecular Devices, USA). Absorbances were converted to MDA concentrations using a standard curve.

To compare the relative contribution of MAAs to UVB absorption, the absorbance spectra of coral tissues were measured (Rossbach et al., 2020). Briefly, 2 mL of the supernatant containing coral tissue were added to 2 mL 100% HPLC grade methanol, kept in the dark at 4°C for 24 h and subsequently centrifuged at 3000 g and 16°C for 5 min. The samples were transferred into a 1-mL

quartz cuvette and their absorbance between 280–750 nm was assessed against a methanol blank, using a UV/Vis/NIR Spectrophotometer (Lambda 1050, PerkinElmer, USA), and normalized by subtracting the absorbance at 750 nm, where absorbance was minimal.

Lipid peroxidation and absorbance were normalized by the total protein content. Protein contents were determined using a Micro-BCA™ Protein Assay Kit (Thermo Fisher, cat. # 23235). MDA concentrations were expressed as nmol MDA mg⁻¹ protein, while absorbances were presented as absorption coefficients (m⁻¹ mg⁻¹ protein).

2.7 Statistical analysis

To test for normal distribution of the data and equal variances, Shapiro–Wilk tests and Levene's tests were performed, respectively. For the *S. pistillata* experiment, one-way ANOVAs followed by Tukey's *post hoc* tests were performed to identify if mean gross primary production (GPP), respiration (R), net primary production (NPP), quantum yields (F_v'/F_m'), MDA concentrations and absorption coefficients at 330 nm varied significantly ($p < 0.05$) between radiation treatments. For the *P. verrucosa in situ* measurements, correlation analyses were performed using the F_v'/F_m' values of *P. verrucosa* colonies and the environmental parameters water temperature, PAR, and UVB measured in 0.5–8.0 m at Al Fahal reef between 15th July–09th August 2018. For temperature, PAR, and UVB, average values of the 10 min before each F_v'/F_m' measurement were used. For the *P. verrucosa* transplantation experiment, Student's t-tests were performed to identify whether mean temperatures in 1 m and 5 m were significantly different and test whether F_v'/F_m' and MDA concentrations differed significantly between the *P. verrucosa* fragments from the two sampling depths and radiation treatments. To establish at what rate (in % per day) MDA concentrations and F_v'/F_m' of the *P. verrucosa* corals from the three manipulative treatments (1 m -UVB, T 1m FS, T 1m -UVB) changed compared to the 1 m FS samples, a linear regression analysis was performed, whereby the slope of the regression line informed about the change in F_v'/F_m' and MDA concentration day⁻¹. All data were analyzed and visualized using either JMP Pro 15.1.0 (SAS Institute Inc., Cary, North Carolina, USA) or GraphPad Prism 8.4.2 (GraphPad Software Inc., CA, USA).

3 Results

3.1 *Stylophora pistillata* incubation experiment (short-term)

3.1.1 Light conditions and primary production

Across the three treatments, mean PAR irradiances varied from 710–784 µmol m⁻² s⁻¹ on 6th Oct and from 1005–1108 on 7th Oct, reaching maximum midday PAR values of 2210–2409 µmol m⁻² s⁻¹ (6th Oct) and 2078–2292 µmol m⁻² s⁻¹ (7th Oct) (Table 1; Supplementary Figure 5). UVB irradiances reached maxima of 1.34 W m⁻² and 1.29 W m⁻² in the full sunlight treatment on the first and second day of the experiment, while we measured UVB irradiances of up to 0.96 and 0.92 W m⁻² in the M-UVB treatment during the two days. UVB irradiances in the UVB-removal treatment were negligible (0.01 W m⁻²).

The pattern and absolute change in oxygen concentration showed no significant differences between the three radiation treatments (Supplementary Figure 6). On the first day, gross primary production (GPP) was on average lowest in the H-UVB treatment and highest in the M-UVB treatment, with GPP rates (mean ± SD) of 0.377 ± 0.021 µmol O₂ cm⁻² h⁻¹ (H-UVB), 0.406 ± 0.091 µmol O₂ cm⁻² h⁻¹ (0-UVB), and 0.455 ± 0.094 µmol O₂ cm⁻² h⁻¹ (M-UVB) (Figure 2). The respiration (R) rates did not differ significantly between the three treatments (H-UVB: -0.186 ± 0.014 µmol O₂ cm⁻² h⁻¹, M-UVB: -0.194 ± 0.041 µmol O₂ cm⁻² h⁻¹, 0-UVB: -0.190 ± 0.035 µmol O₂ cm⁻² h⁻¹). Mean NPP rates were very similar between the H-UVB (0.190 ± 0.026 µmol O₂ cm⁻² h⁻¹) and 0-UVB (0.216 ± 0.066 µmol O₂ cm⁻² h⁻¹) treatments and highest in the M-UVB treatment samples (0.261 ± 0.066 µmol O₂ cm⁻² h⁻¹), although neither treatment exhibited a significantly different NPP. On the second day, the average GPP was higher in all three treatments, and more similar between groups (H-UVB: 0.535 ± 0.090 µmol O₂ cm⁻² h⁻¹, M-UVB: 0.531 ± 0.027 µmol O₂ cm⁻² h⁻¹, 0-UVB: 0.511 ± 0.132 µmol O₂ cm⁻² h⁻¹) compared to the previous day. The same pattern could be observed for the respiration rates, with mean rates varying from -0.256 ± 0.038 µmol O₂ cm⁻² h⁻¹ (M-UVB) to -0.275 ± 0.072 µmol O₂ cm⁻² h⁻¹ (0-UVB), and a higher variability in respiration of H-UVB fragments (-0.272 ± 0.079 µmol O₂ cm⁻² h⁻¹) compared to day 1 (Figure 2). The mean NPP rates were highly similar between the corals of all three light treatments (H-UVB: 0.263 ± 0.024 µmol O₂ cm⁻² h⁻¹, M-UVB: 0.276 ± 0.064 µmol O₂ cm⁻² h⁻¹, 0-UVB: 0.236 ± 0.091 µmol O₂ cm⁻² h⁻¹).

TABLE 1   Water temperature, and PAR and UVB conditions during the *Stylophora pistillata* UV-experiment, conducted in October 2016 in the northern Red Sea as part of the THREATS cruise.

| | | | | PAR (400–700 nm) | | | | | | | | | UVB (280–320 nm) | | | | | | | | |
| | Temperature (°C) | | | Mean irradiance (µmol m⁻² s⁻¹) | | | Max. irradiance (µmol m⁻² s⁻¹) | | | Daily integr. irradiance (mol m⁻² d⁻¹) | | | Mean irradiance (W m⁻²) | | | Max. irradiance (W m⁻²) | | | Daily exposure (kJ m⁻² d⁻¹) | | |
Date	Min.	Mean	Max.	H-UV	M-UV	0-UV	H-UV	M-UV	0-UV	H-UV	M-UV	0-UV	H-UV	M-UV	0-UV	H-UV	M-UV	0-UV	H-UV	M-UV	0-UV
6th Oct	29.2	29.5	30.2	719	710	784	2210	2184	2409	29.25	28.90	31.88	0.30	0.22	0.00	1.34	0.96	0.01	12.40	8.87	0.11
7th Oct	30.7	31.0	31.8	1017	1005	1108	2103	2078	2292	41.37	40.88	45.09	0.43	0.31	0.00	1.29	0.92	0.01	17.41	12.45	0.16

Light conditions are presented for corals kept in different treatments: high UVB (H-UV), medium UVB (M-UV), and UVB-removal (0-UV) conditions.
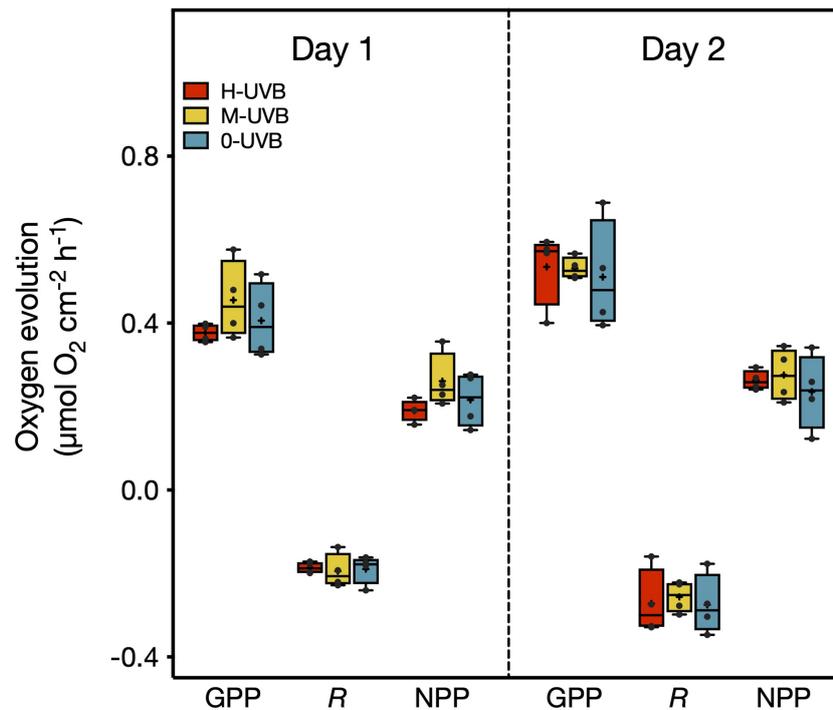
FIGURE 2
Oxygen evolution/consumption ($\mu mol\ O_2\ cm^{-2}\ h^{-1}$) measured during the incubations as part of the *Stylophora pistillata* experiment on 6th (Day 1) and 7th October 2016 (Day 2). Displayed are the gross primary production (GPP), respiration (*R*), and net primary production (NPP). Samples were incubated in either full UVB (red), medium UVB (yellow), or under UVB-removal (blue) conditions. Horizontal lines inside the boxplots indicate median values, and crosses the means. Black dots represent individual data points. One-way ANOVAs and subsequent Tukey's *post hoc* tests identified no significant differences (*p* < 0.05) between treatments for any of the three parameters on either day.

3.1.2 Effective quantum yield (F_v'/F_m')

Effective quantum yields (F_v'/F_m') of *Stylophora pistillata* ranged broadly from 0.11–0.51 (Figure 3). The Diving PAM measurements revealed that on day 1, the coral fragments from the two treatments where UVB was either reduced or removed, showed on average the lowest F_v'/F_m' values at midday (M-UVB: 0.22 ± 0.10 (mean ± SD), 0-UVB: 0.20 ± 0.09), while the fragments of the full sunlight, i.e., H-UVB, group had the highest F_v'/F_m' at that time (0.27 ± 0.09) (Figure 3). Towards the afternoon, F_v'/F_m' of the M-UVB fragments increased on average by 0.04 (mean: 0.25 ± 0.06), whereas in the 0-UVB corals, the mean F_v'/F_m' increased by 0.11 (mean: 0.31 ± 0.12) compared to 12 pm.

On both days, the highest recorded F_v'/F_m' at 4 pm were from fragments of the 0-UVB treatment (day 1: 0.51, day 2: 0.47), while the F_v'/F_m' values of the H-UVB corals did not exceed 0.33 and 0.42 on days 1 and 2, respectively. On the other hand, F_v'/F_m' ratios were the most similar between groups at the last measurement on day 2, with mean F_v'/F_m' of 0.33 ± 0.11, 0.34 ± 0.05, and 0.31 ± 0.08 for the 0-UVB, M-UVB, and H-UVB treatment, respectively.

3.1.3 Lipid peroxidation (MDA)

MDA concentrations in the *Stylophora pistillata* coral tissues varied from 199.2 to 241.9 nmol mg^{-1} protein, depending on the radiation treatment (Figure 4). The highest recorded concentration was found in a fragment from the H-UVB treatment, whereas a
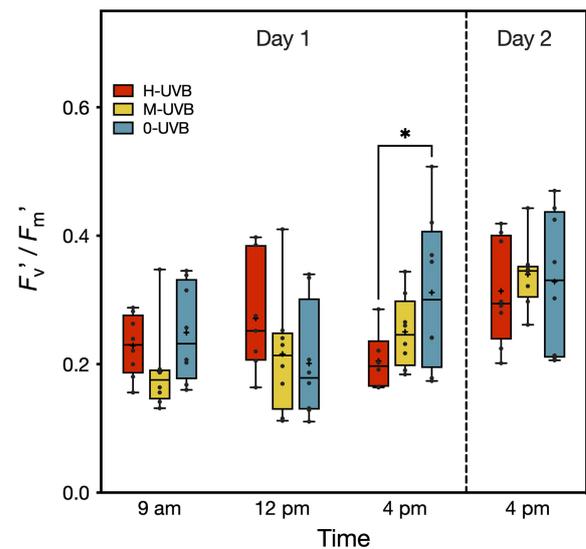
FIGURE 3
Effective quantum yield (F_v'/F_m') of *Stylophora pistillata* fragments, measured during the experiment on 6th (Day 1) and 7th October 2016 (Day 2). Coral fragments were incubated in either full UVB (red), medium UVB (yellow), or UVB removal (blue) conditions. Boxplots indicate 95% CIs. The horizontal lines inside the boxplots represent medians, while crosses indicate means (n=8). Tukey's pairwise comparison results are shown above boxplots (* indicates *p* < 0.05).

FIGURE 4
MDA concentrations (in nmol mg^{-1} protein) in *Stylophora pistillata* fragments at the end of the experiment performed on 6−7th October 2016. Coral fragments were incubated in either full UVB (red), medium UVB (yellow), or UVB removal (blue) conditions. Boxplots indicate 95% CIs. Horizontal lines inside the boxplots represent medians, while crosses indicate means (n=4). Tukey's pairwise comparison results are indicated above boxplots (ns = non-significant).

sample from the 0-UVB treatment exhibited the lowest degree of lipid peroxidation. Mean MDA concentrations gradually decreased from samples of the full sunlight treatment to those that were not exposed to UVB, with mean ± SD values of 229.4 ± 12.9, 220.5 ± 10.1, and 213.0 ± 14.9 nmol mg^{-1} protein for the H-UVB, M-UVB, and 0-UVB treatment, respectively.

3.2 *Pocillopora verrucosa in situ* measurements

3.2.1 Temperature and solar radiation

Between 5th July and 12th August 2018, the temperature at Al Fahal reef varied considerably between depths, and daily fluctuations were most pronounced in the shallows. Specifically, water

temperatures ranged from 30.6–37.3°C (0.5 m), 30.8–34.5°C (2 m), 30.6–34.0°C (4 m), and 30.5–33.4°C (8 m) (Supplementary Figure 7A; Table 2), which indicates that minimum temperatures were almost identical between the four depths, whereas maximum temperatures varied greatly. Overall, we determined that daily average temperatures in 0.5, 2, 4, and 8 m depth were 33.1 ± 1.2°C, 32.6 ± 0.7°C, 32.4 ± 0.6°C, and 32.3 ± 0.6°C, respectively. We did not detect any apparent signs of coral bleaching during our measurements, even though the bleaching threshold temperature of 32.1°C was exceeded during the daytime for the entire duration of the measurement period (5th July–12th August) in 0.5 and 2 m depth. In 4 m and 8 m depth, daytime temperatures exceeded the threshold after the 7th and 14th July, respectively. In 0.5 m, temperatures generally fell below the threshold temperature during the night, except between 31st July and 3rd August. In 4 m depth, the longest time that temperatures consistently remained above the critical threshold was from 31st July until 2nd August and from 4th–6th August. In contrast, the bleaching threshold temperature was exceeded in 2 m and 8 m depth for a prolonged period, i.e., from 30th July and 3rd August, respectively, until 15th August.

PAR irradiances reached midday maxima of 2569, 2283, 999, and 428 µmol m^{-2} s^{-1} in 0.5, 2, 4, and 8 m depth, respectively, while the average integrated PAR irradiances received in those depths per day were 26.81, 13.55, 6.68, and 3.82 mol m^{-2} d^{-1} (Table 2; Supplementary Figure 7B).
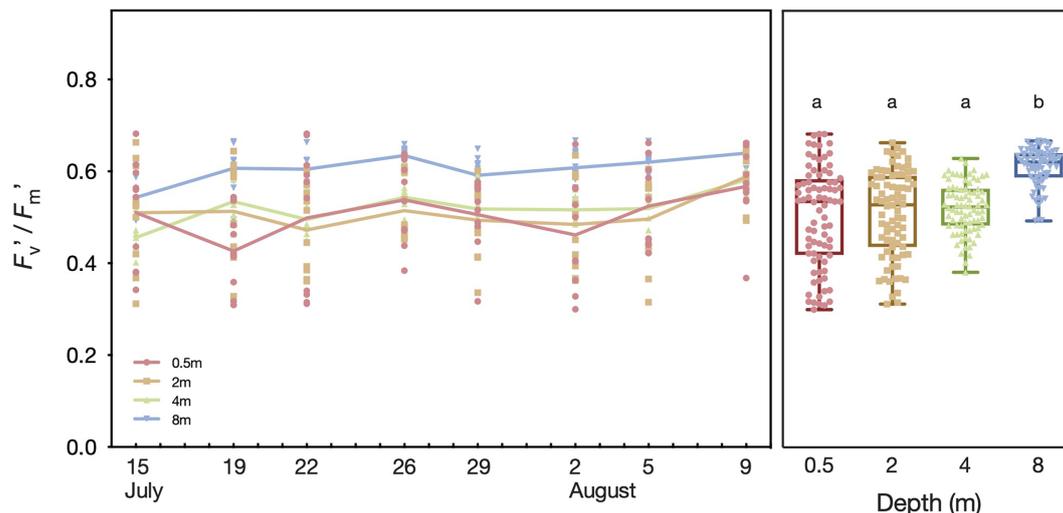
The maximum recorded UVB (280–315 nm) irradiances at noon were 2.06, 1.73, 0.96, and 0.11 W m^{-2} in 0.5, 2, 4, and 8 m, respectively (Table 2; Supplementary Figure 7C). The average daily UVB exposure measured in 2, 4, and 8 m was 11.82, 2.94, and 0.94 kJ m^{-2}, approximately 55, 14, and 4% of the daily UVB exposure received in 0.5 m depth (21.44 kJ m^{-2}) (Table 2).

3.2.2 Effective quantum yield (F_v'/F_m') *in situ*

The range of effective quantum yields (F_v'/F_m') was greatest in the shallows (0.5 m) and less variable towards the deepest sampling depth (8 m), with F_v'/F_m' ranging from 0.30–0.68, 0.31–0.66, 0.38–0.63, and 0.49–0.67 in colonies from 0.5, 2, 4, and 8 m depth, respectively (Figure 5). Overall, F_v'/F_m' varied significantly between the *P. verrucosa* coral fragments from the four sampling depths (F

TABLE 2 Water temperature and solar radiation (PAR and UVB) in different depths at Al Fahal reef in the central Red Sea between 5th July–12th August 2018, and during the *Pocillopora verrucosa* transplant experiment from 28th April–16th June 2019.

Date (year)	Depth (m)	Temperature (°C)			PAR (400–700 nm)			UVB (280–315 nm)		
		min.	mean	max.	mean irradiance (µmol m^{-2} s^{-1})	max. irradiance (µmol m^{-2} s^{-1})	mean integr. irradiance (mol m^{-2} d^{-1})	mean irradiance (W m^{-2})	max. irradiance (W m^{-2})	mean exposure (kJ m^{-2} d^{-1})
2018	0.5	30.6	33.1	37.3	562	2569	26.81	0.59	2.06	21.44
	2	30.8	32.6	34.5	284	2283	13.55	0.32	1.73	11.82
	4	30.6	32.4	34.0	140	999	6.68	0.08	0.96	2.94
	8	30.5	32.3	33.4	80	428	3.82	0.03	0.11	0.94
2019	1	26.3	30.0	33.7	328	2447	15.65	0.33	1.27	12.08
	5	26.2	29.9	32.6	198	1376	9.42	0.09	0.40	3.37

FIGURE 5
Effective quantum yield (F_v'/F_m') of *Pocillopora verrucosa* colonies in different depths at Al Fahal reef in the central Red Sea between 15th July−09th August 2018 on individual days (left panel) and combined for all days (right panel). The colored lines connect mean F_v'/F_m' values. Letters above the boxplots show the results of the Tukey's *post hoc* test, whereby plots that do not share the same letter had significantly different means at a level of $p < 0.05$.

(3, 312) = 29.55, $p < 0.0001$), with the mean F_v'/F_m' of the corals at 8 m depth (Mean ± SD = 0.61 ± 0.04) being significantly higher than the means of the corals in shallower depths, including those at 4 m (0.52 ± 0.06, $p< 0.0001$), 2 m (0.51 ± 0.09, $p< 0.0001$), and 0.5 m (0.50 ± 0.11, $p< 0.0001$).

We found a negative correlation between water temperature and F_v'/F_m' ($r = -0.40$), although the lowest and highest F_v'/F_m' were both recorded at intermediate temperatures (Figure 6). For PAR, we found an even stronger correlation with F_v'/F_m' ($r = -0.54$), and the highest F_v'/F_m' were recorded when PAR was only ~100 μmol m^{-2} s^{-1}, while the lowest F_v'/F_m' was determined when PAR was ~ 800 μmol m^{-2} s^{-1}. However, the strongest correlation was found between UVB and F_v'/F_m' ($r = -0.57$). It was evident that the maximum F_v'/F_m' ratios were all measured in the near absence of UVB while the minimum ratio was recorded when UVB was 0.52 W m^{-2}.

3.3 *Pocillopora verrucosa* transplant experiment (long-term)

3.3.1 Temperature and solar radiation

During the experimental period, water temperatures gradually increased from 02nd May until 3rd June, after which temperatures started to decrease again (Supplementary Figure 8A). Overall, mean water temperatures were significantly higher in 1 m (30.0 ± 1.6°C) than in 5 m depth (29.8 ± 1.6°C) (t(27401)= -8.62, $p < 0.0001$) (Table 2). Corals that were upward transplanted experienced an average temperature increase of 0.1°C. However, the maximum temperature was 1.1°C higher in 1 m (33.7°C) than in 5 m depth (32.6°C). In both depths, the critical bleaching threshold temperature of 32.1°C was only exceeded during the daytime. Specifically, this threshold temperature was surpassed between

26th May and 8th June (in 1 m depth) and from 29th May–3rd June and 5th–8th June (in 5 m).

Between 28th April and 16th June, PAR irradiance reached midday maxima of 2447 μmol m^{-2} s^{-1} in 1 m, and 1376 μmol m^{-2} s^{-1} in 5 m (Table 2; Supplementary Figure 8B), while the integrated PAR irradiance received per day was on average 66% higher in 1 m (15.65 mol m^{-2} d^{-1}) than in 5 m (9.42 mol m^{-2} d^{-1}). At midday, the maximum recorded UVB (280–315 nm) irradiances were 1.27 and 0.40 W m^{-2} in 1 and 5 m, respectively (Table 2; Supplementary Figure 8C). Daily UVB exposure was over 3.5-fold higher in the shallows (12.08 kJ m^{-2}) than in 5 m depth (3.37 kJ m^{-2}).

3.3.2 Effective quantum yield (F_v'/F_m')

Overall, the effective quantum yields (F_v'/F_m') of the 1 m *P. verrucosa* coral fragments had a significantly higher mean F_v'/F_m' ratio (0.62 ± 0.03) than the 5 m fragments (0.59 ± 0.03) (t(283)= -7.52, $p < 0.0001$), and varied significantly between the four different treatment groups (F(3, 280) = 29.64, $p < 0.0001$) (Figure 7A). F_v'/F_m' of the T 1m FS corals (Mean ± SD, 0.58 ± 0.04) was significantly lower compared to any other treatment group, including the T 1m -UVB fragments (0.61 ± 0.03) ($p < 0.0001$). Yet, the discrepancy in F_v'/F_m' between those two groups increased over time. On day 4 of the experiment, there was a marginal (< 2%) difference between the mean F_v'/F_m' of the 1 m FS (0.61 ± 0.02) and 1 m -UVB corals (0.60 ± 0.03). On day 14 there was a sharp decrease in F_v'/F_m' across all treatments. After 20 days, the F_v'/F_m' of the 1 m -UVB corals (0.65 ± 0.01) was significantly higher than that of the 1 m FS specimens (0.63 ± 0.02) ($p = 0.0115$).

Furthermore, the time required by the T 1m corals to reach the same F_v'/F_m' as the 1 m corals was shortened under UVB-removal conditions. The mean F_v'/F_m' of the 1 m FS and T 1 m FS corals was significantly different at each sampling point during the first 24
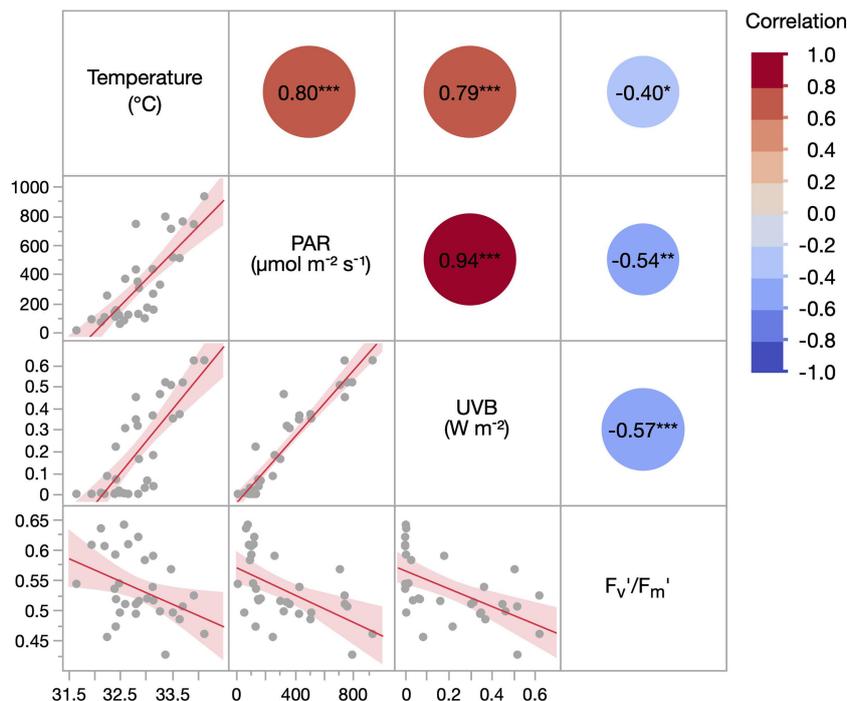
FIGURE 6
Correlation matrix of the environmental parameters water temperature, PAR, and UVB, as well as the effective quantum yield (F_v'/F_m') of *Pocillopora verrucosa* colonies. Measurements were performed in 0.5–8.0m at Al Fahal reef in the central Red Sea between 15th July–09th August 2018. Temperature, PAR, and UVB values are averages of the 10 minutes before each F_v'/F_m' measurement. The red line and shaded area represent the correlation line and 95% CIs, respectively. Values in the circles indicate the Pearson correlation coefficient (r). Asterisks show $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).

days. At the onset of the experiment, F_v'/F_m' of the corals from the T 1 m FS treatment was approximately 9.9% lower than of the 1 m FS fragments, but this difference decreased by 0.226% per day (y = 0.226x + 90.1, $p = 0.011$) (Figure 7B), which means the two treatments should have the same F_v'/F_m' after ~44 days. Indeed, after 46 days the mean F_v'/F_m' of the 1 m FS group (0.61 ± 0.05) was very similar to that of the T 1 m FS group (0.62 ± 0.02) (t(17)= 0.97, $p > 0.05$). In comparison, UVB removal significantly increased F_v'/F_m' in the T 1 m corals so that by day 4, there was no difference between the T 1 m -UVB corals and those from the 1 m FS treatment.

3.3.3 Lipid peroxidation (MDA)

The malondialdehyde (MDA) concentration inside the coral tissue ranged from 37.1–140.0 nmol mg^{-1} protein (Figure 8) and varied significantly between the four treatment groups (F(3, 116) = 26.29, p < 0.0001). Overall, T 1m FS corals had significantly higher MDA concentrations (86.7 ± 23.4 nmol mg^{-1} protein (mean ± SD) than 1m FS corals (55.5 ± 23.5 nmol mg^{-1} protein) ($p< 0.0001$), although this was not the case on day 46. However, when upward transplanted corals were kept under UVB removal conditions, mean MDA concentrations were significantly reduced (T 1m -UVB: 48.0 ± 6.6 nmol mg^{-1} protein) ($p< 0.0001$), and the concentrations were similar to those determined in the 1m FS samples.

The difference in mean MDA concentrations between the two upward transplanted coral treatments decreased during the experiment, i.e., on day 4, MDA levels in the T 1m -UVB

fragments (44.8 ± 26.2 nmol mg^{-1} protein) were significantly lower than in the T 1m FS corals (101.9 ± 26.2 nmol mg^{-1} protein) ($p< 0.0001$) (Figure 8). The concentrations were no longer significantly different between the T 1m -UVB (52.3 ± 26.2 nmol mg^{-1} protein) and the T 1m -FS corals (67.9 ± 6.9 nmol mg^{-1} protein) on day 20 ($p > 0.05$). Also, on day 46, mean MDA concentrations did no longer differ between the shallow and the transplanted corals (t(18)= -0.30, $p > 0.05$).

3.3.4 *In vivo* UV absorption

All absorbance spectra of the coral tissue samples showed the highest absorbance in the wavelength range 320–340 nm (Supplementary Figure 9). However, while the absorbance determined for *S. pistillata* had a distinct peak at 330 nm which decreases from 330 nm to 290 nm, the absorbance by *P. verrucosa* was relatively constant in the range 330–290 nm. The absorption coefficient at 330 nm i.e., a(330), was approximately 2–3 orders higher in *S. pistillata* than in *P. verrucosa* (Figure 9). The ANOVA found no difference in mean absorption at 330 nm between *S. pistillata* from the three radiation treatments. *P. verrucosa* 1m FS fragments initially had a significantly higher mean a(330) (33.2 ± 5.0 m^{-1} mg^{-1} protein) than corals that were upward transplanted from 5 m depth (17.9 ± 2.3 m^{-1} mg^{-1} protein) (t(8)= -2.79, $p < 0.05$). The opposite pattern could be observed on day 46, with corals from 1 m exhibiting a significantly lower a(330) (9.5 ± 0.6 m^{-1} mg^{-1} protein) than 5 m corals (14.8 ± 2.0 m^{-1} mg^{-1} protein) (t(8)= 2.60, $p < 0.05$).
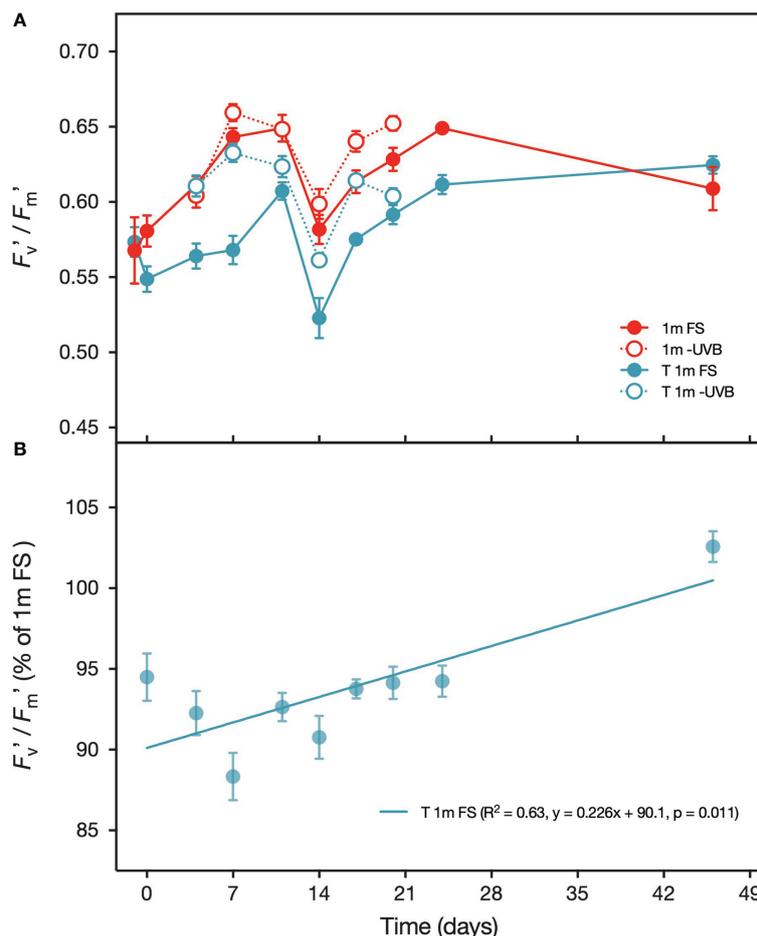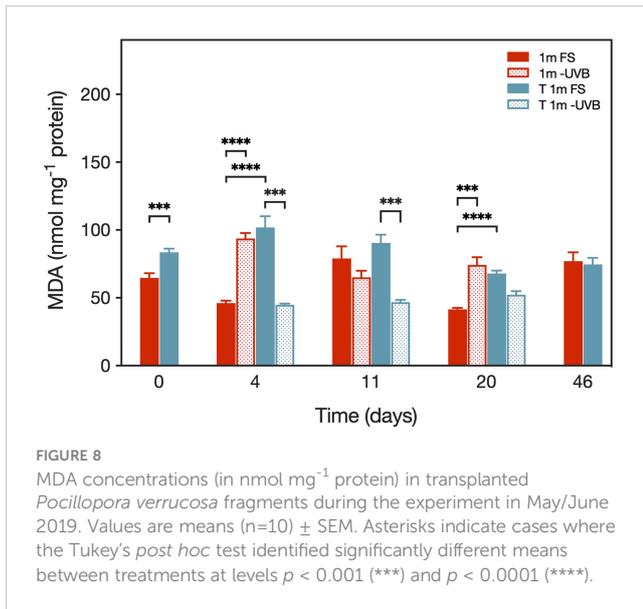
FIGURE 7
(A) Effective quantum yield (F_v'/F_m') of *Pocillopora verrucosa* fragments from 1 m (red) and T 1m (transplanted from 5 m) (blue) exposed to either full sunlight (filled circles) or with UVB-removed (open circles) during the transplantation experiment performed between 2nd May – 16th June 2019. Also displayed is the F_v'/F_m' of colonies *in situ* on the day before the experiment (T = -1 days). **(B)** Effective quantum yield (F_v'/F_m') of T 1 m (transplanted from 5 m) *Pocillopora verrucosa* specimens under FS, displayed as percentage of the F_v'/F_m' of the FS corals kept at their original sampling depth (1 m). Values are means (n=10) $\pm$ SEM.

4 Discussion

We observed that shallow specimens of the Red Sea coral *Pocillopora verrucosa* showed fast responses in their physiology while the LPO in *Stylophora pistillata* changed under UVB reduction, suggesting both corals were well acclimated to the high UVB in situ. However, *in situ* data from *Pocillopora verrucosa* indicated that deeper (8 m) specimens showed significantly higher and more constant effective quantum yields (F_v'/F_m') values than specimens at shallow depths, and the strong correlation between F_v'/F_m' and UVB irradiances suggests a considerable decrease of UVB stress with depth. We identified photo-physiological changes and the requirement of long-term acclimation responses of *Pocillopora verrucosa* specimens after their transplantation to shallower depths, suggesting that these corals optimize their photon capture and photochemical processes in response to new solar radiation conditions.

During the short-term UVB removal experiment with *S. pistillata* fragments, the reduction or removal of UVB did not result in an immediate, significant increase in effective quantum

yields (F_v'/F_m') of the algal symbionts nor enhance gross primary production (GPP) of the holobiont. Instead, both photosynthetic parameters remained equal between the three treatments during the experiment. In contrast, distinct signs of coral symbiont photoinhibition were reported from other manipulative experiments, following either a transplantation of the corals to shallower waters (Masuda et al., 1993; Shick et al., 1995; Lesser, 2000; Tamir et al., 2020) or the exposure of corals specimens to elevated levels of (solar) radiation (Gorbunov et al., 2001; Jones and Hoegh-Guldberg, 2001; Yakovleva and Hidaka, 2004; Brown and Dunne, 2008; Bellworthy and Fine, 2017) (Table 3). For example, *S. pistillata* fragments exposed to UV radiation had a significantly lower F_v/F_m than specimens exposed to PAR-only after 5 h of incubation irrespective of the incubation temperature; and F_v/F_m in the UV treatment was still significantly reduced after three days (Ferrier-Pages et al., 2007). Even after 17 days of incubation, F_v/F_m had not recovered to its initial value. However, it is noteworthy that the UV treatment in the before-mentioned experiment consisted of exposure to total UV, i.e., UVA and UVB, while the control samples were only exposed to PAR. In contrast, we either reduced or

FIGURE 8
MDA concentrations (in nmol mg^{-1} protein) in transplanted *Pocillopora verrucosa* fragments during the experiment in May/June 2019. Values are means (n=10) $\pm$ SEM. Asterisks indicate cases where the Tukey's *post hoc* test identified significantly different means between treatments at levels $p < 0.001$ (***) and $p < 0.0001$ (****).

removed UVB radiation in the present study, whereas UVA was always present.

Therefore, our result that neither GPP nor effective quantum yields were affected upon UVB reduction/removal is perhaps due to the presence of UVA in all treatments. Whereas UVA can have positive effects when received in moderate doses, extreme UVA exposure can have detrimental effects (Häder et al., 2015). For example, UVA exposure had a major impact on the quantum yields of *Montipora verrucosa* but the addition of UVB did not result in a further reduction of the quantum yield, highlighting the strong impact of UVA on the photophysiology (Torregiani and Lesser, 2007).

Regarding the corals' respiration, we found that reduced UVB exposure during the day, or the complete absence thereof, did not

result in a significant change in the respiration rates of *S. pistillata*. This result was surprising since previous studies found that corals exposed to bright sunlight would have higher respiration rates than corals exposed to low light or only PAR because of the increased metabolic costs entailed in maintaining the array of UV-protection and repair mechanisms (Anthony and Hoegh-Guldberg, 2003). However, we found no difference in respiration between coral from those two treatments, which is in line with reports on *Montipora verrucosa* where dark respiration of the corals was not affected by the light conditions (PAR or PAR+UV) immediately before the dark period (Kinzie, 1993). Similarly, respiration rates of intact corals collected at 1 m and 30 m depth did not change after exposure to UVB radiation (Masuda et al., 1993). In contrast, the same authors established that the respiration rates of isolated zooxanthellae were significantly reduced by UVB, indicating that zooxanthellae are protected against UVB damage when living in symbiosis. In contrast, UVB irradiation likely damages the mitochondria of zooxanthellae in isolation (Masuda et al., 1993).

We established that the concentrations of malondialdehyde (MDA), i.e., a product of lipid peroxidation and thus a proxy for oxidative stress, varied only marginally in *S. pistillata* between the radiation treatments. While we found that mean MDA concentrations gradually increased with increasing UVB exposure (0-UVB: 213.0, M-UVB 220.5, H-UVB: 229.4 nmol mg^{-1} protein), the concentrations were not significantly different, suggesting that UVB exposure had only minor effects on the coral host.

In comparison, lipid peroxidation in *P. verrucosa* colonies from the western Indian Ocean (11°30 S', 47°20 E') was unchanged after 5 days of enhanced or reduced irradiance levels, following an upward- (from 20 m to 5 m depth) or downward transplantation (5 m to 20 m), respectively (Richier et al., 2008). However, Richier et al. (2008) reported ~ 15 to 35-fold higher mean MDA concentrations than the concentrations measured in the present study, suggesting a higher resistance of *P. verrucosa* from the Red Sea. MDA

FIGURE 9
Absorption coefficient at 330 nm (m^{-1} per mg protein) of coral host tissue from *Stylophora pistillata* **(A)** and *Pocillopora verrucosa* **(B)**. Values are means (n=5) $\pm$ SEM. Asterisks indicate cases where the Tukey's *post hoc* test identified significantly different means between treatments at a level of $p < 0.05$.
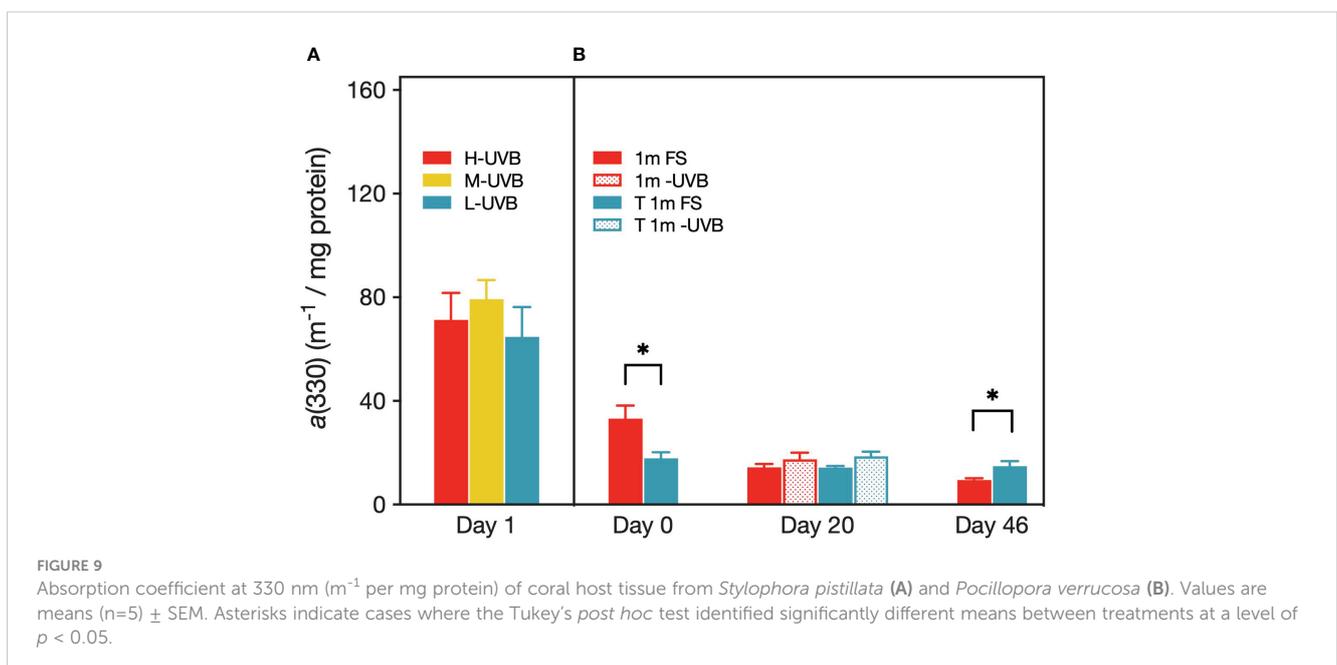
TABLE 3 Physiological parameters of *Stylophora pistillata* and *Pocillopora verrucosa* measured in the present study in comparison to previously reported values from the same species as well as other coral species.

Parameter	Species	Condition	Value	Reference
F_v'/F_m'	S. pistillata	H-UVB (12pm)	0.27 ± 0.09	present study
	P. verrucosa	transplanted from 5m to 1m	0.58 ± 0.04	present study
F_v/F_m	S. pistillata	27°C +UV (for 5 h)	~ 0.57	Ferrier-Pages et al. (2007)
	S. pistillata	5 m depth, 1000 W m^{-2}	~ 0.57	Winters et al. (2006)
	S. pistillata	Midday irradiance	~ 0.35	Jones and Hoegh-Guldberg (2001)
	S. pistillata	5 d at 24°C, 140 µmol photons m^{-2} s^{-1}	0.68 ± 0.02	Yakovleva and Hidaka (2004)
	S. pistillata	5 d at 31°C, 140 µmol photons m^{-2} s^{-1}	0.71 ± 0.015	Yakovleva and Hidaka (2004)
	Favia favus	5 m depth, 1000 W m^{-2}	~ 0.59	Winters et al. (2006)
	Paramontastrea peresi	10 m depth, 1 h dark acclimation	~ 0.69	Tamir et al. (2020)
	Paramontastrea lobata	10 m depth, 1 h dark acclimation	~ 0.65	Tamir et al. (2020)
	Goniastrea aspera	full sunlight (Feb), 10 cm depth	~ 0.53	Brown & Dunne (2008)
GPP	S. pistillata	H-UVB (on day 2)	0.535 ± 0.090 µmol O$_2$ cm^{-2} h^{-1}	present study
	S. pistillata	5 d at 24°C, 140 µmol photons m^{-2} s^{-1}	1.26 ± 0.06 µmol O$_2$ cm^{-2} h^{-1}	Yakovleva and Hidaka (2004)
	S. pistillata	5 d at 31°C, 140 µmol photons m^{-2} s^{-1}	2.19 ± 0.30 µmol O$_2$ cm^{-2} h^{-1}	Yakovleva and Hidaka (2004)
R	S. pistillata	H-UVB (on day 2)	-0.272 ± 0.079 µmol O$_2$ cm^{-2} h^{-1}	present study
	S. pistillata	5 d at 24°C, 140 µmol photons m^{-2} s^{-1}	–0.41 ± 0.01 µmol O$_2$ cm^{-2} h^{-1}	Yakovleva and Hidaka (2004)
	S. pistillata	5 d at 31°C, 140 µmol photons m^{-2} s^{-1}	–1.05 ± 0.23 µmol O$_2$ cm^{-2} h^{-1}	Yakovleva and Hidaka (2004)
	Montipora monasteriata	After exposure to 1300 µmol photons m^{-2} s^{-1}	-1.65 ± 0.12 µmol O$_2$ cm^{-2} h^{-1}	Anthony & Hoegh-Guldberg (2003)
	Montipora verrucosa	Acclimated and measured in PAR+ UV	-1.55 ± 0.25 µmol O$_2$ cm^{-2} h^{-1}	Kinzie (1993)
	Fungia spp.	1m corals after 1h UVB exposure	~ -0.65 (relative PS rate)	Masuda et al. (1993)
	isolated Symbiodinium	from 1m Fungia sp., after 1h UVB exposure	~ -0.20 (relative PS rate)	Masuda et al. (1993)
	Montastraea faveolata	5 m depth	-0.06 ± 0.16 µmol O$_2$ cm^{-2} h^{-1}	Lesser (2000)
	Acropora microphthalma	2 m (+UV)	-0.098 ± 0.022 µmol O$_2$ µg Chl a^{-1} h^{-1}	Shick et al. (1995)
Lipid PO	S. pistillata	H-UVB	229.4 ± 12.9 nmol mg^{-1} protein	present study
	P. verrucosa	transplanted from 5m to 1m	86.7 ± 23.4 nmol mg^{-1} protein	present study
	P. verrucosa	upward-transplanted (20 m to 5m) after 5 d	~6200 nmol mg^{-1} protein	Richier et al. (2008)
	Pocillopora capitata	32 h exposure to PAR+UVA+UVB	4.5 ± 1.3 nmol mg^{-1} protein	Linan-Cabello et al. (2010)

concentrations of *Pocillopora capitata* specimens exposed to PAR and those exposed to PAR+UVB+UVA (predominantly UVB, λmax: 310 nm) for 32 h were not significantly different (Linan-Cabello et al., 2010). However, when the data from all sampling points were pooled, UV-treated corals had significantly higher levels of lipid peroxidative damage (4.5 ± 1.3 nmol mg^{-1} protein) than PAR-treated specimens (3.4 ± 0.8 nmol mg^{-1} protein), which in our study was not evident for *S. pistillata*, but significant differences were observed for transplanted *P. verrucosa* after four days.

It is well known that corals possess specific physiological characteristics that allow them to cope with variations in solar radiation, one of these being the expression of green fluorescent proteins (GFPs) (Richier et al., 2008). The accumulation of GFPs

has been described as a photoprotective mechanism in shallow-water corals that dissipates highly energetic wavelengths, thereby providing photoprotection to both the coral host and its symbiotic algae (Salih et al., 2000; Scucchia et al., 2020). Additionally, corals can synthesize another group of UV-absorbing compounds, known as mycosporine-like amino acids (MAAs) (Shick et al., 1995; Dunlap and Shick, 1998). Shallow-water colonies of the coral *S. pistillata* were found to contain unusually large amounts of MAAs (Shick, 2004; Ferrier-Pages et al., 2007), which is in line with the high UV absorption we found and the high UV resistance observed during our short-term experiment with this coral species.

It has previously been reported that *S. pistillata* is exceptionally thermotolerant (Bellworthy and Fine, 2017; Krueger et al., 2017),

which could explain the relatively minor physiological changes in both the host and the endosymbionts upon UVB reduction or removal. We did not identify the symbionts associated with *S. pistillata* or *P. verrucosa* as part of our study. However, it is widely reported that shallow-water specimens of both species in the Red Sea are predominantly associated with *Symbiodinium* sp. clade A (Arrigoni et al., 2016; Ziegler et al., 2017; Bednarz et al., 2018), which is known to be thermotolerant (Sawall et al., 2014). The coral specimens were sampled from a shallow depth (~ 1 m) characterized by high solar irradiances, suggesting that the specimens were exceptionally well adapted or acclimated to extreme UV irradiances. Indeed, we identified a distinct peak in absorption by the coral at 320–340 nm, so it may be that the existing UV-protection strategies of shallow-water *S. pistillata* are so well developed that even under ambient UVB, the symbionts can photosynthesize at the highest possible rate. Consequently, reducing or removing UVB exposure could not further enhance their photosynthetic capacity.

The *in situ* measurements with *Pocillopora verrucosa* identified that the F_v'/F_m' of colonies between 0.5 and 4 m depths were very similar. In contrast, colonies at 8 m depth had a significantly higher F_v'/F_m' (Figure 5). This result might be due to the reduced PAR or UVA, the near-absence of UVB in 8 m depths, or due to the lower and more stable temperatures in deeper depths (Supplementary Figure 7). The strong correlation between these three environmental parameters in natural waters (see Figure 6) presents a challenge when trying to disentangle the effects of individual stressors. However, the correlation analysis strongly suggests that UVB ($r = -0.57$) is a crucial determinant for the photosynthetic efficiency of coral symbionts in situ; and possibly more so than PAR ($r = -0.54$) or water temperature ($r = -0.40$), which is in line with the finding that high solar irradiances reduce F_v/F_m in corals at least as much as high temperatures (Winters et al., 2006).

We did not observe any bleaching or mortality in any of the depths during our experiment. The critical bleaching threshold temperature of 32.1°C was frequently exceeded in the extreme shallows during the daytime. However, rapid cooling in the evening meant that temperatures quickly dropped again below the threshold, alleviating the corals from thermal stress, which may explain their high bleaching resistance (Safaie et al., 2018). Additionally, our findings confirm the observation that shallow-water corals on the wave-sheltered side of central Red Sea reefs experience extreme diurnal temperature variations in summer (> 5°C) (Davis et al., 2011), which may further contribute to their high bleaching resistance (Sammarco et al., 2006; Oliver and Palumbi, 2011).

Our transplantation experiment with *P. verrucosa* found that low-light adapted corals, i.e., those from deeper depths, have a lower initial tolerance to high irradiance conditions, particularly UVB. Specifically, we found that *P. verrucosa* fragments transplanted from 5 m to 1 m and kept under full sunlight conditions initially had significantly lower F_v'/F_m' than their shallow-water conspecifics adapted to high irradiance. Besides experiencing higher PAR (Δ mean: + 131 μmol m^{-2} s^{-1}, Δ max: +1071 μmol m^{-2} s^{-1}) and UVB (Δ mean: + 0.24 W m^{-2}, Δ max: +0.87 W m^{-2}) irradiances, the upward transplanted corals were also exposed to increased temperatures

(Table 2). The latter is important since several studies have described that the photosynthetic efficiency of corals can be severely reduced under elevated temperatures (Lesser, 1996; Bellworthy and Fine, 2017; Voolstra et al., 2020). However, the temperature increase due to the upward transplantation was relatively minor in the present study (Δ mean: + 0.1°C, Δ max: +1.1°C), so that the temperature increase did probably not contribute significantly to the observed inhibition of the photosynthetic efficiency. This hypothesis is further supported by the fact that a few days after the upward transplantation, there was no significant difference between the F_v'/F_m' of corals from 1 m and 5 m when UVB was removed, indicating that UVB rather than temperature or PAR is the key determinant. Four days after their transplantation, the removal of UVB in corals originating from 5 m depth also led to a significantly higher F_v'/F_m' compared to their full sunlight conspecifics, which lasted until day 20. In fact, for the entire experiment duration, the F_v'/F_m' of the UVB-removal specimens originating from 5 m was the same as that of the 1 m samples, which highlights the importance of UVB as photoinhibitor. This finding is in line with the report that *Montipora verrucosa* corals acclimated to PAR + UV displayed higher photosynthesis under full sunlight conditions than corals acclimated to PAR-only (Kinzie, 1993). However, no difference in the photosynthetic parameters was found when photosynthesis was measured in the light regime to which the corals had been acclimated, which agrees with our F_v'/F_m' results of corals *in situ*, from extreme shallows down to at least 4 m depth (see Figure 5).

The discrepancy in F_v'/F_m' between full sunlight samples from 1 m and those upward transplanted from 5 m gradually decreased throughout the experiment, and both groups performed equally well by the end of the experiment. Although differences in F_v'/F_m' values were small, this equalization suggests a slow acclimation potential of *Pocillopora verrucosa* from deeper waters to changes in solar UVB conditions. In contrast, the fast adaptation of transplanted *P. verrucosa* fragments when UVB was removed, highlights that elevated UVB was a primary factor limiting the acclimation response, as opposed to other changes such as increased temperature or PAR. This hypothesis is further supported by our findings that F_v'/F_m' exhibited the strongest correlation ($r = -0.57$) with the factor UVB, and that the highest F_v'/F_m' were measured when UVB irradiances were negligible (Figure 6).

The upward transplantation of 5 m corals to shallower waters may have initially caused an enhanced accumulation of intracellular oxygen that could have led to 1) damage to photosystem II and ultimately photoinhibition in the first few days because of the higher PAR and UVB photon flux in shallower waters, and 2) to the production of reactive oxygen species (ROS), which can damage chloroplasts (Finelli et al., 2006; Mass et al., 2010) and result in programmed cell-death and degradation (LeTissier and Brown, 1996; Franklin et al., 2004). ROS can also impact cellular adhesive proteins (Davies, 1987) leading to the expulsion of endosymbionts (Dunn et al., 2002). Therefore, the production of ROS initiates negative feedback by reducing the concentration of symbiont cells, thereby lowering the evolution rate of oxygen molecules that could become toxic. We, therefore, expect that the exposure of the 5 m corals to elevated UVB invoked by the transplantation triggered the

abovementioned ROS-induced photoacclimation, which supports the conclusion that UVB radiation acts as a photoacclimatory enhancer (Cohen et al., 2013).

The presence of MAAs is particularly prominent in shallow-water specimens (Banaszak et al., 1998; Shick and Dunlap, 2002), which agrees with our finding that *P. verrucosa* from 1m exhibited a higher absorption at 330 nm than corals from 5 m. Torres et al. (2007) reported a 40-fold increase in total MAA concentration in transplanted *Acropora cervicornis* corals (from 20 m to 1 m depth) after one month of enhanced UV exposure and an 88-fold increase in MAAs after a further three months. However, in the present study, *in vivo* absorption at 330 nm in upward transplanted corals did not change over 46 days. Therefore, the drastic improvement in the photosynthetic efficiency of transplanted corals in full sunlight after ~5 weeks was likely not linked to a change in MAAs concentrations. In the T 1 m FS corals, the acclimation of the symbionts' photosynthetic apparatus and the equilibration of MDA levels in the coral host occurred within a similar time frame of 1–1.5 months. While several studies have reported that high temperatures can cause an increased occurrence of lipid peroxidation (LPO) in corals (Flores-Ramirez and Linan-Cabello, 2007; Yakovleva et al., 2009), in our upward transplanted corals, the average temperature increase was only marginal (mean ΔT = + 0.1°C) compared to temperature increments of ≥2°C in previous reports, which suggest that other factors such as elevated solar irradiances likely caused the increased peroxidation of host lipids.

When we compared LPO between our experiments, we found that mean MDA concentrations in the full sunlight treated *S. pistillata* were approximately four-fold higher than in *P. verrucosa* despite the near-identical UVB conditions. This finding may suggest that 1) *S. pistillata* suffered more damage to lipids due to the stress of transferring the corals and keeping them in shallow incubators, or 2) that *P. verrucosa* possesses exceptionally well-developed, species-specific UVB coping-mechanisms. Also, the sensitivity of corals to UVB was found to be strongly dependent on the corals' prior history of UV exposure (Siebeck, 1981; Torregiani and Lesser, 2007). For example, when *Plerogyra sinuosa* specimens were upward transplanted from 25 m (where UVB was almost non-detectable) to 5 m depth, the mortality rate of UV-unshielded samples was 90% after one month (Vareschi and Fricke, 1986). In comparison, we did not detect any mortality nor signs of coral bleaching during our transplantation experiment, which is likely linked to the fact that corals in 5 m depth are already exposed to relatively high levels of UV and therefore possess a reasonably well baseline protection against UVB.

Additionally, it has been suggested that the ability to contend with substantial light variations is strongly species-specific (Nakamura and Yamasaki, 2008). For example, the discrepancy in mortality rates between the study of Vareschi and Fricke (1986) and ours might stem from the morphological differences between the two coral species. *Plerogyra sinuosa* has large vesicle-like polyps that often protrude from the skeleton structure, whereas *P. verrucosa* consists of small polyps that are mostly retracted into the corallites (Veron, 2000). This difference is of relevance since coral skeletons can 1) absorb UV radiation and dissipate excess energy as yellow fluorescence, resulting in less DNA damage in the coral tissue, and 2)

reflect PAR wavelengths to the overlying tissue, which benefits the photosynthesis of the endosymbionts and might be another factor contributing to the reasonably quick acclimation of *P. verrucosa* to enhanced UVB without any mortality incidences (Reef et al., 2009).

A recent study found that maximum incident UVB irradiances in the central Red Sea can be observed earlier in the year (May/June) than peak water temperatures (July/August) (Overmans and Agusti, 2020). However, it remains to be seen how *S. pistillata*, *P. verrucosa*, and other shallow-water Red Sea corals will fare in the near future since both temperature (Chaidez et al., 2017; Osman et al., 2018) and UVB (Watanabe et al., 2011; Meul et al., 2016; Bais et al., 2019) are predicted to increase over the next few decades, which will likely result in longer periods when both environmental parameters are above their critical threshold for corals (Overmans and Agusti, 2020). This prognosis is of particular relevance for specimens in shallow waters, where UVB exposure was already extreme (> 20 kJ m^{-2}) and water temperatures surpassed the bleaching threshold temperature during the daytime for > 5 weeks. We could observe that shallow-water *P. verrucosa* showed a stronger inhibition of F_v'/F_m', indicative of higher stress, possibly due to the combination of both environmental stressors. Similarly, the high UVB exposure in 1 m reduced the acclimation response to changing environmental conditions, suggesting that the acclimation response could be further decelerated in future climates under enhanced temperatures and UVB. Protecting *S. pistillata* from UVB did not change the gross primary production or F_v'/F_m', and respiration and LPO in the host remained unaffected, highlighting that *S. pistillata* possesses well-developed UVB coping mechanisms and hints that this species might have a high capacity to tolerate the predicted elevated UVB.

Previous studies have identified that elevated temperature and extreme ultraviolet can act synergistically, thereby leading to impacts of multiplicative magnitude (Ban et al., 2014; Jin et al., 2019). For instance, elevated temperature and UVB irradiances were found to act synergistically on the symbiont density (Drohan et al., 2005) and the survival and photosynthetic efficiency (Ferrier-Pages et al., 2007; Zeevi Ben-Yosef and Benayahu, 2008) of tropical reef cnidarians, which bears the question if Red Sea scleractinian corals will be able to acclimate to the increased temperatures and UVB exposure in future environmental conditions.

5 Conclusion

In summary, our study demonstrated that, overall, Red Sea corals showed a large acclimation capacity and resistance to UVB radiation, although we could observe species-specific tolerance capacities. Shielding shallow-water specimens from UVB did neither change their respiration nor enhance their photosynthetic efficiency, suggesting that shallow-water specimens can maximize photon capture and their photosynthetic activity, even when UVB irradiances are high. *P. verrucosa* in deeper waters (8 m) exhibited less varying and higher F_v'/F_m' than those in 4 m depth and above, where water temperatures, PAR and UVB were considerably higher. Upward transplanted corals exhibited slow acclimation under full sunlight and required 2-4 weeks to acclimate while under UVB

removal conditions the acclimation took ≤ 4 d, which highlights that UVB, besides temperature, is indeed a crucial stressor governing the physiology of *P. verrucosa*. Overall, however, *P. verrucosa* from 5 m were well protected against elevated UVB and temperature since neither bleaching nor mortality was detected after transplantation.

We conclude that elevated UVB exposure may serve as a trigger for corals to enhance their photoacclimation when exposed to increased solar irradiances. Furthermore, it would be interesting to test if a reduction or removal of UVB can help alleviate thermally induced stress in corals and ultimately lead to a higher resistance against coral bleaching or an accelerated recovery thereof.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

SA and SO conceptualized the study. SO collected the data. SO and SA analyzed the data. SO generated tables and figures. SO wrote the manuscript with a substantial contribution from SA. Both authors contributed to the article and approved the final version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.847559/full#supplementary-material

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