Journal of Photochemistry & Photobiology, B: Biology 167 (2017) 249–255

Contents lists available at ScienceDirect

Journal of Photochemistry & Photobiology, B: Biology

journal homepage: www.elsevier.com/locate/jphotobiol

UV-A induced delayed development in the larvae of coral *Seriatopora caliendrum*

Jie Zhou [a], Tung-Yung Fan [b,c], John Beardall [a,d], Kunshan Gao [a,*]

[a] State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen, Fujian, Republic of China
[b] National Museum of Marine Biology and Aquarium, Pingtung, Taiwan, ROC
[c] Institute of Marine Biology, National Dong Hwa University, Pingtung, Taiwan, ROC
[d] School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

ARTICLE INFO

Article history:
Received 9 November 2016
Received in revised form 26 December 2016
Accepted 3 January 2017
Available online 04 January 2017

Keywords:
Ultraviolet radiation
Coral larvae
Settlement
Symbiodinium

ABSTRACT

Coral reefs are vulnerable to ultraviolet radiation (UVR, 280–400 nm). Not only do the fluxes of UVR fluctuate daily, they are also increasing due to global ocean and atmospheric changes. The deleterious effects of UVR on scleractinian corals have been intensively studied, but much less is known about the response of corals in the early pre-settlement phase. In this study, we tested how UVR exposure affects survival and development of *Seriatopora caliendrum* larvae and examined the photophysiological changes induced in the symbiotic dinoflagellate *Symbiodinium*. Results showed that the contents of chl *c* and carotenoids normalized to the number of algae cells in the larvae decreased significantly when larvae were exposed to UVR compared to those protected from UVR, while the cell density of *Symbiodinium* was higher in UVR-exposed larvae. The effective photochemical efficiency of the symbiotic algae increased when cultured under PAR plus UV-A (here taken as 320–395 nm). We further present the novel finding that during the development experiment, presence of UV-A induced a decline in the rates of metamorphosis and settlement, which disappeared when the larvae were also exposed to UV-B (here defined as 295–320 nm). However, UVR had no distinguishable effect on the numbers of larvae that either survived, metamorphosed or settled by the end of the culture period. Therefore, it is concluded from this study that UV-A radiation may extend the planktonic duration of coral larvae, but not have an overall inhibitory effect on developmental outcomes.

1. Introduction

Ultraviolet radiation (UVR, 280–400 nm) can be a major threat to living organisms, especially photoautotrophic species. It is well known that the high-energy spectrum band of UVR can be absorbed by a number of biomolecules such as nucleic acids, proteins and lipids, thus leading to DNA mutation and damage to cellular structures, as well as blocking of enzymatic reactions and other physiological processes and inducing the formation of reactive oxygen species (ROS) [1]. The implementation of Montreal Protocol has indeed lowered the concentrations of ozone-depleting substances, and the ozone layer is predicted to return to 1980 levels by the middle of this century [2]. However, in low latitude regions, the flux of UV-B may be enhanced by 2–3% [3] due to effects of global climate change such as the presence or absence of trace gases and changes in atmospheric circulation patterns [4]. A 10-year solar radiation climatology study [5] revealed that in the Great Barrier Reef region of Australia, the level of solar radiation has increased slightly by nearly 1%, from the period 1995–2005, which corresponds closely with coral bleaching events. Model simulations [6] predicted that UVR will, by the end of the 21st century, increase by 3–8% in tropical areas due to the decrease in clouds and ozone depletion caused by the increase in greenhouse gases.

There is broader concern about the detrimental exposure of corals to UVR, especially those dwelling in the reef flats or lagoons with high clarity water, which is shallow, calm and sometimes exposed at low tide. For example, it has been found that UVR is an agent in coral bleaching, and may contribute to the worldwide bleaching events interacting with ocean warming [7–9]. In addition, the skeleton density, and fecundity of the coral and the photosynthetic efficiency of the symbiotic algae have also been shown to be inhibited under UVR exposure [10,11]. Comparatively, reports on research into the effect of UVR on coral larvae are scarce. Since the planula larvae or gametes released by the adult corals have to float in the shallow water for hours to days, they are likely to experience high levels of UVR before settling on the substratum. To date, it has been recognized that UVR would inhibit the survivorship and development of coral larvae, as well as leading to DNA lesions [12–16]. In addition, the expression of some genes, such as those

* Corresponding author.
E-mail address: ksgao@xmu.edu.cn (K. Gao).

http://dx.doi.org/10.1016/j.jphotobiol.2017.01.007
1011-1344/

associated with Ca^{2+} homoeostasis, stress response, neurogenesis and apoptosis, would also be affected by UVR [17].

Some coral planula larvae have the symbiotic dinoflagellate *Symbiodinium* inherited from the parental colony. Though little is known about the role of symbiotic algae in the development of coral larvae, the existence of symbiotic algae has been shown to extend larval longevity under light conditions [18–20], indicating that the coral larvae could derive considerable amounts of energy from the symbiotic algae, and the symbiosis between planula larvae and *Symbiodinium* may thus be similar to that in the adult corals. If the symbiotic algae provide energy to the host through photosynthesis as hypothesized, then the photoinhibition induced by UVR may disrupt the balance between larvae and symbiont. Surprisingly, our previous study on the effects of UVR on the larvae of *Pocillopora damicornis* showed that the development of larvae was severely inhibited by UV-A (315–400 nm), while the photosynthetic performance of the symbiotic algae was only lowered in the presence of both UV-A and UV-B (280–315 nm). Here we chose another brooding coral *Seriatopora caliendrum*, which is typically distributed on Indo-Pacific reef flats and reef slopes, and releases planula larvae monthly throughout the year in southern Taiwan [21]. Previous work has shown that *S. caliendrum* is sensitive to thermal stress [22], and its larvae have no substrate selectivity, thus settling quickly [21]. The present study focuses on the effects of UVR exposure on the development of rapidly settled larvae and on the photophysiology of the endosymbiont *Symbiodinium*, in order to better understand the potential significance of symbiotic algae in coral larvae.

2. Materials and Methods

2.1. Colony Sampling and Coral Larvae Collection

The *Seriatopora caliendrum* colonies were collected from 8 to 10 m depth, prior to the new moon, from Nanwan Bay, Southern Taiwan (21°56.290′N, 120°44.761′E). Colonies were kept in separate, partially shaded (maximum intensity of photosynthetically active radiation (PAR, 400–700 nm) ~736 μmol m^{-2} s^{-1}, and UV-A < 1.27 W m^{-2}, without UV-B), flow-through outdoor aquaria in the National Museum of Marine Biology and Aquarium (NMMBA, Checheng, Taiwan) for larvae collection. The larvae collection set-up was the same as in a previous study [16], i.e. a catcher fitted with 110-μm plankton mesh was positioned to receive the gentle seawater outflow from each aquarium. The catchers were checked at 07:30 h each day, and the larvae were collected and gently rinsed with 0.22 μm filtered seawater (FSW). Given the limited release number of larvae every day, and to ensure that each physiological parameter was obtained from the same cohort of larvae on the same day, the *S. caliendrum* colonies were collected on three occasions (May, November and December 2014). Sampling of corals for research use was carried out under permit from Kenting National Park Headquarters (No. 1030002637).

2.2. Experimental Setup

The experiment was conducted between May and December of 2014. Five cohorts of larvae were collected and used for different purposes as detailed in Table 1. To investigate the influence of UVR, three solar radiation treatments were carried out as follows: [1] larvae receiving only PAR (P treatment) with containers covered with 395-nm cutoff foil (Ultraphan UV Opak, Digefra, Munich, Germany), transmitting the irradiance above 395 nm; [2] larvae receiving PAR and UV-A (PA treatment) covered with Folex 320 filters (Montagefolie, Folex, Dreieich, Germany), transmitting the irradiances above 320 nm; [3] and containers covered with Ultraphan Film 295-nm cutoff filter (Digefra, Munich, Germany), which block radiation below 295 nm, to create PAR + UV-A + UV-B (PAB treatment). Triplicate samples were used for each radiation treatment. The incubation containers with larvae were placed in an outdoor water bath (45 L), exposed to natural solar radiation, and the temperature was controlled at ~27.5 °C by running seawater pumped from an indoor aquarium to the tank. And the temperature of outdoor tank was recorded at 5 min intervals using a submersible data logger (RBR concerto, Canada). Irradiance was also logged each 5 min by a PMA2100 data logging radiometer (Solar Light Co., Inc., Glenside, PA, USA).

Two kinds of containers were employed in the experiment, depending on the measurements made. [1] To investigate the short-term effects of UVR exposure on the photophysiological performance of symbiotic algae in the larvae, 15 mL quartz tubes were used. Exposure time was 3 h for the May cohort, and 6 h for the November and December cohorts. [2] To observe larval development, the larvae were incubated in a 45 mL plastic box, which was large enough to contain the clay tiles used for settlement. Specifically, two sides of each box were replaced with 110 μm plankton mesh to allow for water exchange. In addition, the top of each box was covered with polyethylene (PE) cling wrap, which transmits the full solar radiation spectrum, to prevent larvae getting lost if the containers turned over or water overflowed. The incubation lasted for 7 days.

2.3. Survivorship, Settlement and Metamorphosis

To assess the effect of UVR on the development of coral larvae, 30 freshly released larvae were added to each plastic box with settlement tiles, which had been maintained in the aquarium for two weeks prior to use, and allowed to settle for 7 days. The numbers of larvae in each of the following three development stages were identified at 17:00 h each day: [1] metamorphosed, larvae that had developed a basal disc; [2] settled, larvae that had metamorphosed and attached to the substrate; [3] survived, as the coral larvae would lyse within 24 h after death [23], thus all the larvae that remained in the container could be counted as survived. The survivorship, settlement and metamorphosis were expressed as the percentages of the number of larvae added at the start of the experiment.

Table 1
Temperature, total dose and maximum irradiance of PAR (400–700 nm), UV-A (315–400 nm) and UV-B (280–315 nm) for each cohort of *Seriatopora caliendrum* larvae. Values are means ± SD throughout the incubation period.

Experiment date	Temperature (°C)	Total dose (MJ m^{-2})			Maximum irradiance			Parameters
		PAR	UV-A	UV-B	PAR(μmol m^{-2} s^{-1})	UV-A (W m^{-2})	UV-B (W m^{-2})	
May 11[a]	26.71 ± 0.55	1.37	0.22	0.004	1260	36.3	0.88	*Symbiodinium* density, pigment contents, Fv/Fm, Fv′/Fm′
Nov 29	26.99 ± 0.15	4.41	0.64	0.017	1665	49.0	1.41	Fv/Fm, Fv′/Fm′
Nov 30	27.21 ± 0.14	4.20	0.71	0.017	1776	55.2	1.45	*Symbiodinium* density, pigment contents
Dec 8	24.82 ± 0.09	3.98	0.68	0.016	1610	46.2	1.30	Respiration, photosynthetic oxygen evolution
Dec 3 to 9	24.67 ± 0.45	3.50 ± 1.38	0.65 ± 0.15	0.015 ± 0.004	1215 ± 375	44.4 ± 8.1	1.12 ± 0.24	Survivorship, settlement, metamorphosis

[a] Exposure time was 3 h. The irradiance was partly shaded, and the data shown here are after shading.

2.4. Pigment Contents and UVACs

After short-term UVR exposure, 20 larvae were randomly sampled from each quartz tube to assess concentrations of pigments and UV-absorbing compounds (UVACs). The larvae were first filtered onto Whatman GF/F glass fiber filter (0.22 μm, 25 mm), and then extracted in 4 mL absolute methanol and maintained in darkness at 4 °C overnight. Following extraction, samples were centrifuged (10 min at 4, 000*g*; Eppendorf 5810 R, Germany), and absorbance of the supernatant was scanned between 250 and 750 nm with a spectrophotometer (BioMate 5, Thermo Spectonic, USA). The concentrations of chlorophyll *a* and chlorophyll *c* were determined following the equations of Ritchie [24] which are specific to dinoflagellates, and that of carotenoids was calculated according to Strickland and Parsons [25]. Quantification of the UVACs with absorption peaks around 320 nm in the corals was estimated using the peak height ratio between UVACs with chl *a* [26]. The contents of both pigments and UVACs were normalized to the sample size (μg larva^{-1}) and symbiont density (pg cell^{-1}).

2.5. Symbiodinium Density

To enumerate *Symbiodinium* cells per planula larva, ten to twenty-five *S. caliendrum* larvae were randomly sampled at the conclusion of the incubations, and fixed with 1 mL of 4% paraformaldehyde in FSW. To release *Symbiodinium* cells from coral tissue, a glass grinder was used gently until no visible tissue remained. The tissue homogenate was then centrifuged (10 min at 4, 000*g*), and the algae pellet was re-suspended in 2 mL FSW and needle sheared by passage 3 or 4 times through a 10 mL syringe with 24G needle. The algae number was counted manually with a hemocytometer, and the algae population was expressed as the number of symbiont cells per larva (cell larva^{-1}).

2.6. Photosynthetic Oxygen Evolution and Respiration

The coral respirometry assay was the same as that used in a previous study [16]. Briefly, dark respiration of a group of about twenty-five larvae, which had been dark-adapted for 1 h, was measured as oxygen flux with a fiber-optic oxygen meter (Fibox 3, PreSens GmbH, Germany) in 1.5 mL glass vials in the dark. The planar oxygen-sensitive foil (SP-PSt3, 5 mm), which was glued on the inside of the vials, was calibrated with a zero O_2 solution (nitrogen-bubbled distilled water) and an air-equilibrated distilled water prior to use. The dark respiration (R_{dark}) was determined by dividing the 10-min oxygen depletion rate by the number of coral larvae (nmol O_2 larva^{-1} min^{-1}).

Net photosynthetic productivity (P_{net}) and resulting gross productivity (P_{gross}) were determined by larvae acclimated at a light intensity of 552 μmol m^{-2} s^{-1} for 20 min. And light enhanced dark respiration (LEDR) was determined by monitoring the 10-min O_2 consumption after 1 min post-illumination. P_{gross} was the total amount of O_2 released in the light plus the R_{dark}, while the gross productivity in the light (P_{gross}′) was obtained by adding P_{net} to LEDR. The photosynthetic rates were expressed as nmol O_2 larva^{-1} min^{-1} and pmol O_2 cell^{-1} min^{-1}.

Photosynthetic efficiency of the *Symbiodinium* was assessed by measuring maximum quantum yield (F_v/F_m) and effective quantum yield (F_v'/F_m') using a Phyto-PAM (Walz, Germany). Prior to fluorescence measurement, one group of ca. 15 larvae were randomly selected and transferred into a quartz tube. F_v'/F_m' measurements were performed by applying 5 min actinic illumination with an intensity of 280 μmol m^{-2} s^{-1} (~310 μmol m^{-2} s^{-1} at the end of incubations), with terminal application of a saturation pulse. F_v/F_m measurements were taken after the larvae were dark-adapted for 40 min.

2.7. Data Analysis

The inhibition of photosynthetic efficiency induced by UVR was calculated as follows:

$$\text{Inh}-\text{UV}-\text{A}\ (\%) = (P_P - P_{PA})/P_P \times 100\%$$

$$\text{Inh}-\text{UV}-\text{B}\ (\%) = (P_{PA} - P_{PAB})/P_P \times 100\%$$

where Inh-UV-A and Inh-UV-B is the inhibition caused by UV-A or UV-B; P_P, P_{PA} and P_{PAB} are the quantum yield under P, PA and PAB treatments, respectively.

A two-sample *t*-test was used to determine the significance of differences between Inh-UV-A and Inh-UV-B. The effects of UV radiation on larval condition were tested by one-way ANOVA; post hoc Fisher's least significant difference (LSD) tests ($\alpha = 0.05$) were used to determine differences between individual groups. The prerequisite normality and homoscedasticity for the ANOVAs were carried out using a Shapiro-Wilk test and Levene's test, respectively. All the data were shown as means ± SD ($n = 3$).

3. Results

3.1. Development of Coral Larvae

During the 7-day exposure, it was cloudy on the first two days and the last day, resulting in a lower irradiance intensity on those three days (Fig. 1A). Specifically, the maximum PAR for the three days was between 690 and 903 μmol m^{-2} s^{-1}, while the values for the other four days all exceeded 1400 μmol m^{-2} s^{-1}. As for the UVR, the daytime doses for UV-A and UV-B during the middle four days were above 0.72 and 0.017 MJ m^{-2}, respectively, while the corresponding doses for the cloudy days fell to 0.52 and 0.012 MJ m^{-2} respectively. The average temperature during the incubation was 24.67 ± 0.45 °C.

After exposure to UVR for two days, fewer larvae metamorphosed and settled under the PA treatment compared to the P and PAB treatments (Metamorphosis: Fisher's LSD, $p < 0.05$; Settlement: $F_{2,6} = 6.93$, $p = 0.03$). With the extension of exposure time, on the fifth day, there were no differences in larval settlement between treatments ($F_{2,6} = 2.69$, $p = 0.15$), with the percentage ranging between 88 ± 5% and 96 ± 4%. On the last day, there appeared to be no difference in larval survival between treatments ($F_{2,6} = 0.25$, $p = 0.78$, Fig. 1B), and the percentage of larvae still alive was >87%. As for the final metamorphosis and settlement success, neither of these parameters were influenced by UVR (Metamorphosis: $F_{2,6} = 1.5$, $p = 0.29$, Fig. 1C; Settlement: $F_{2,6} = 1.5$, $p = 0.30$, Fig. 1D), with over 91% larvae settled on the substrate.

3.2. Symbiodinium Density and Pigment Contents

Following 3 h exposure to UVR (May cohort), the *Symbiodinium* density in coral larvae exposed to PAR + UV-A + UV-B (PAB) was significantly higher than in those exposed only to PAR + UV-A (PA; Fisher's LSD, $p = 0.03$). Similarly, the result of 6 h exposure (November cohort) also showed higher symbiont density in PAB-treated larvae, while the larvae incubated without UVR had the fewest *Symbiodinium* cells ($F_{2,6} = 18.94$, $p = 0.002$, Fig. 2A). Thus, the average *Symbiodinium* density in the PAB treatment was 1.68 ± 0.09 × 10^4 cells larva^{-1}, which was higher than that in the P treatment by 28%. Because the two exposure experiments were not conducted on the same day, and the *S. caliendrum* larvae were not from the same colony, the effects of exposure time under the same treatment were not compared here.

The chl *a*, chl *c* and carotenoids contents of algal cells were not influenced by the 3 h UVR exposure ($p > 0.05$, Table 2). However, the 6 h UVR exposure of the November cohort (when UVR and PAR were higher) resulted in a decrease of chl *c* from 4.46 ± 0.52 pg cell^{-1} to 3.29 ± 0.46 pg cell^{-1} (Fisher's LSD, $p = 0.02$), while the chl *c* content normalized to coral larvae stabilized between 0.05 and 0.06 μg larva^{-1} ($F_{2,6} = 0.03$, $p = 0.97$). The carotenoid concentration in larvae also showed obvious reduction under UVR stress (μg larva^{-1}: $F_{2,6} = 9.05$, $p = 0.01$; pg cell^{-1}: $F_{2,6} = 25.14$, $p = 0.001$), and the carotenoids per algal cell in the P treatment was about 1.78 fold higher compared to the PAB treatment. Correspondingly, the ratio of carotenoid to chl *a* reduced from 0.67 ± 0.05 in the P treatment to 0.50 ± 0.03 in the PAB treatment ($F_{2,6} = 19.51$, $p =$

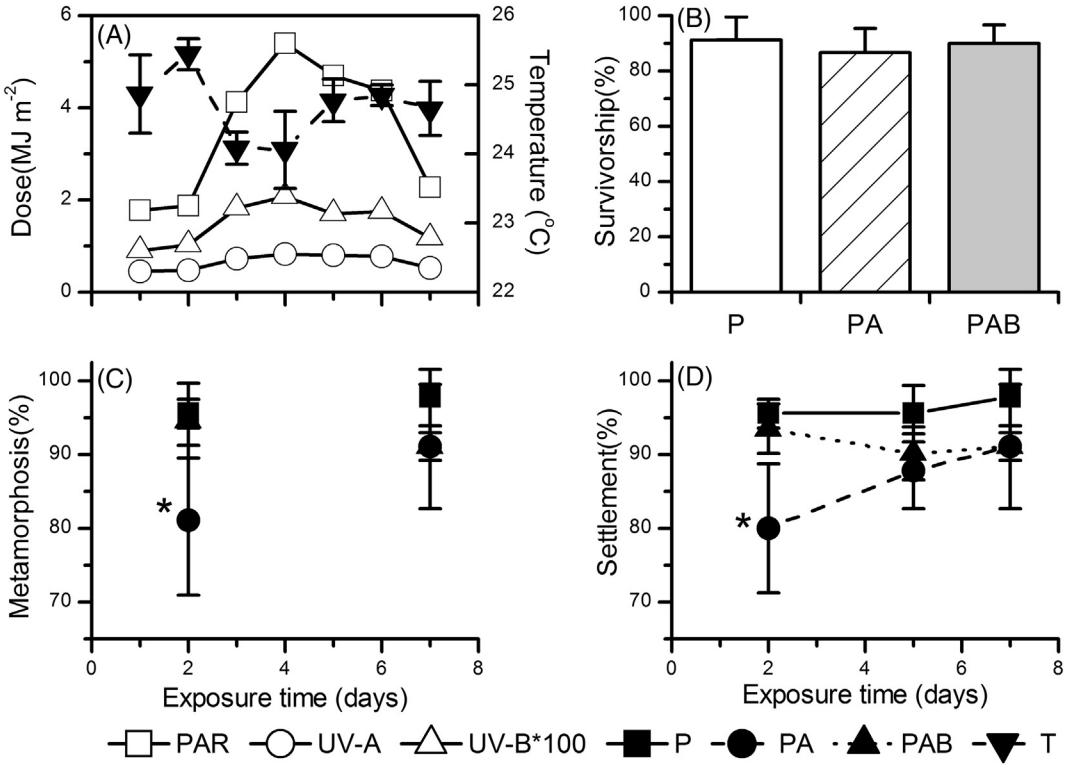

Fig. 1. The temperature and irradiance variations during the 7-day exposure (A), and the effect of UVR treatments on the percentage of *Seriatopora caliendrum* larvae that either survived (B), metamorphosed (C) or settled (D). Means ± SD ($n = 3$ for all treatments with 30 larvae each) are shown; treatment means marked with asterisks differ significantly (Fisher's LSD, $p < 0.05$).

0.002). The cell content of chl *a* showed an insignificant decrease under UV-A or UV-B ($p > 0.05$).

The content of UVACs in coral larvae was not affected by UVR exposure in both exposure times ($p > 0.05$, Table 2). Nevertheless, the 3 h UV-A and UV-B exposure led to an evident reduction of the UVAC:Chl *a* ratio compared to the control (Fisher's LSD, $p = 0.03$), which did not show in the 6 h experiment.

3.3. Photosynthetic Rate and Respiration

Following short term UVR exposure (both 1 h and 6 h), the effective quantum yield (Fv′/Fm′) displayed a significant increase under UV-A radiation (1 h: $F_{2,6} = 11.27$, $p = 0.01$; 6 h: $F_{2,6} = 9.42$, $p = 0.01$, Fig. 3A), while the effect of UV-B offset the increase, with the Inh-UV-B ranging from 28 ± 8% to 88 ± 21%. However, there was no significant variation in the maximum quantum yield (Fv/Fm), which stabilized between 0.46 ± 0.05 and 0.57 ± 0.09 ($F_{2,6} = 2.58$, $p = 0.15$, data not shown). Similar to the trend of Fv′/Fm′, the highest photosynthetic rates, including P_{net}, P_{gross} and P_{gross}', were observed in the PA treatment, though the result of one-way ANOVA showed insignificant differences between treatments ($p > 0.05$, Fig. 3B and C). In addition, neither the R_{dark} nor the LEDR responded obviously to radiation treatments ($p > 0.05$, Fig. 3D).

4. Discussion

The results showed that UVR exposure had negative effects on the cellular contents of chl *c* and carotenoids, whereas the *Symbiodinium* density in the larvae exposed to UV-A or UV-B was higher than that in the control larvae. We further present the novel finding that during the 7-day experiment, the presence of UV-A decreased the larval rates of metamorphosis and settlement, though this effect disappeared when the larvae were also exposed to UV-B, while the effective photochemical efficiency of the symbiotic algae increased when cultured under PAR and UV-A. However, at the end of development experiment, UVR had no effect on the numbers of larvae that either survived, metamorphosed or settled.

The positive effects of UV-A on the growth or photosynthesis of phytoplankton cells have been reported in several studies [27–31]. Here, we found that the effective quantum yield, Fv′/Fm′, of the algae in symbiosis with *S. caliendrum* larva was markedly modulated by UVR, in which the UV-A acted as a stimulation factor, while UV-B offset the enhancement of UV-A. A similar effect was also shown to occur in the photosynthetic oxygen evolution rate of the symbiotic algae within *Pocillopora damicornis* larvae upon UVR exposure [16]. Though the oxygen evolution rate of the algae within *S. caliendrum* larva in this study had a similar trend, the difference between treatments was not statistically significant. Given that the positive effects of UV-A on phytoplankton generally occurred under the conditions of low light dose (cloudy) or fast mixing in coastal regions where the nutrient state is rather high [31], it can be speculated that the coral symbiont may play a role in attenuating the incident UV-A radiation by UVACs.

Considering that *S. caliendrum* larvae generally settle fast and have no specialization in terms of substrate choice, we can eliminate the possibility that UV-A delayed larval development by damaging the substrate. The delayed development of larvae has seldom been reported in coral under stress. However, the phenomenon has been documented among a number of different organisms, such as bryozoans, gastropods, polychaetes, crustaceans, echinoids, urochordates, and amphibians [32]. The causes for delayed development include nutritional stress, salinity stress, exposure to UVR, and exposure to sublethal concentrations of pollutants. Pechenik et al. [33] found that the lack of food stimulated the larvae of gastropod *Crepidula fornicate* to metamorphose, but that this process was delayed when the food was in excess. Similar to our results, the fertilized eggs of an amphibian *Rana temporaria*, when exposed to UV-B before hatching, showed lengthened metamorphosis time and increased incidence of developmental abnormalities [34]. In this process, it is suggested that a trade-off of the energy allocation

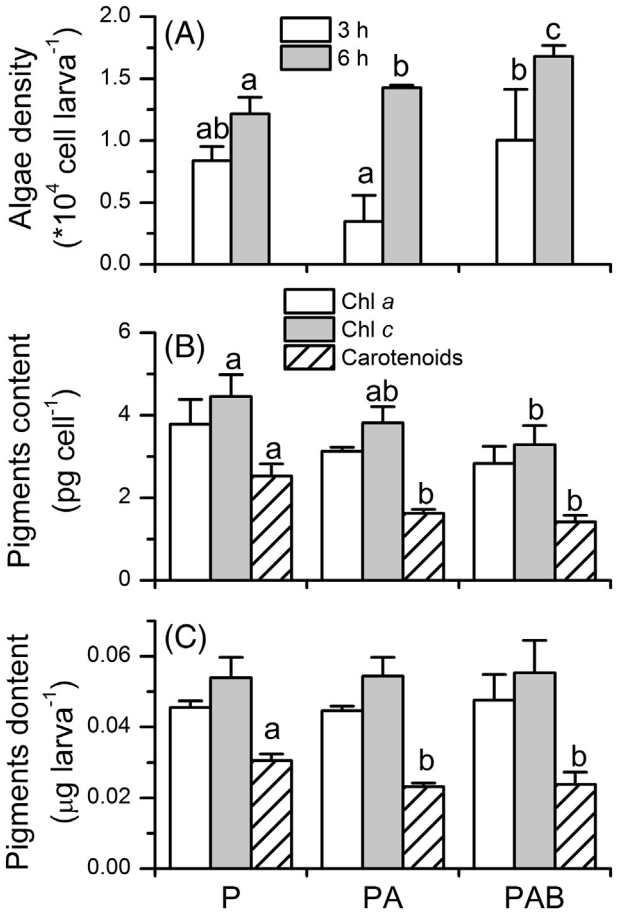

Fig. 2. Algae density in the larvae of *Seriatopora caliendrum* following 3 h (white, May cohort) and 6 h (grey, November cohort) UVR exposure (A), and the content of pigments per algae cell (B, November cohort) and per larva (C) following 6 h exposure, including Chl *a* (white), Chl *c* (grey) and carotenoids (grid). The different letters indicate significant differences among the radiation treatments at $p < 0.05$ (Fisher's LSD). Values are means ± SD ($n = 3$ for all treatments with 20 larvae each).

may exist between the repair of UVR-induced damage and larval development. However, there was no sign of obvious UVR damage to the larvae in our study compared to the control group, except that the concentration of chl *c* and carotenoids per algae cell was reduced under UV-A and UV-B exposure. However, the relatively high density of *Symbiodinium* in *S. caliendrum* larvae exposed to UVR possibly offset the reduction in pigment per cell, resulting in the lack of effect of UVR exposure on the pigment contents per larva.

Recently, Graham et al. [23] studied the temporal changes in metabolic rates of larvae without symbiotic algae from four coral species. The highly consistent dynamics of larval respiration rates showed that the rates were low prior to fertilization, then rapidly peaked and remained high in early development until the larvae became competent to metamorphose. After that, the rates quickly declined and larvae remained in a low metabolic activity state thereafter. Accordingly, these findings may shed light on our results. In the first two days, relatively more larvae under UV-A exposure stayed in the pre-metamorphic stage compared to those in the other two treatments. By analogy with the study of Grahams et al. [23], the coral larvae in this stage would have had higher metabolic activity in contrast to those that had metamorphosed. This is consistent with the higher photochemical efficiency of symbiotic algae under UV-A exposure. Therefore, the UV-A level in this study may potentially increase the energy reserves for the coral larvae through stimulating the photophsiological performance of *Symbiodinium*.

The delayed development of *S. caliendrum* larvae extended the dispersal period of the planula stage, which is of particular importance for the ecology and evolution of the coral species. For example, the extended dispersal is beneficial for the population to escape from an unfit environment and enhance population connectivity [35]. Nevertheless, dispersal depends on larvae having a sufficient energy store. Coral planulae that cannot feed in the planktonic stage have no external energy resource except material from the symbiotic algae. Thus, the increased energy expenditure during dispersal means that less energy would be left for post-settlement development. If the recruits cannot capture zooplankton within days of settlement, their survivorship would be threatened. Several studies have documented that delayed development caused a severe decrease in post-settlement survival, growth and adult fitness, especially for non-feeding species, and made them potentially more vulnerable to predators and physical stresses [36–39]. In contrast, the effects of delayed settlement seemed less applicable to coral larvae as expected. Graham et al. [40] found that although the initial sizes of *Acropora tenuis* larvae were negatively affected, the 4-week settlers budded more quickly than the 2-week and 6-week settlers. At the same time, the *Symbiodinium* acquisition rates increased in both the 4 and 6 weeks cohorts, while the survival of settlers was not affected [40]. Given that the observation of a UV-A induced delay of larval development was not reported in earlier studies on coral larvae [12,41,14,13], the details of these studies were examined. There could be three reasons for this discrepancy: 1) Less attention was paid to the

Table 2
Concentration of the different pigments and UVACs in the larvae of *Seriatopora caliendrum* following UVR treatments. The different letters indicate significant differences among the irradiance treatments at $p < 0.05$ (Fisher's LSD). Values are means ± SD ($n = 3$). *P* values are given (one-way ANOVA). The significant differences were marked in bold.

Pigment	unit	Exposure time (h)	P	PA	PAB	*p*
Chl *a*	μg larva^{-1}	3	0.06 ± 0.01	0.07 ± 0.01	0.07 ± 0.01	0.18
		6	0.05 ± 0.00	0.04 ± 0.00	0.05 ± 0.01	0.70
	pg cell^{-1}	6	3.78 ± 0.60	3.13 ± 0.10	2.83 ± 0.41	0.08
Chl *c*	μg larva^{-1}	3	0.06 ± 0.00	0.05 ± 0.00	0.06 ± 0.01	0.19
		6	0.05 ± 0.01	0.05 ± 0.01	0.06 ± 0.01	0.97
	pg cell^{-1}	6	4.46 ± 0.52^{a}	3.82 ± 0.39^{ab}	3.29 ± 0.46^{b}	0.06
Carotenoid	μg larva^{-1}	3	0.02 ± 0.00	0.02 ± 0.00	0.02 ± 0.00	0.45
		6	0.03 ± 0.00^{a}	0.02 ± 0.00^{b}	0.02 ± 0.00^{b}	**0.01**
	pg cell^{-1}	6	2.53 ± 0.30^{a}	1.63 ± 0.09^{b}	1.42 ± 0.16^{b}	**0.001**
UVACs	μg larva^{-1}	3	0.10 ± 0.00	0.10 ± 0.00	0.09 ± 0.01	0.11
		6	0.04 ± 0.01	0.04 ± 0.01	0.05 ± 0.02	0.90
UVAC:Chl *a*		3	1.67 ± 0.19^{a}	1.38 ± 0.17^{ab}	1.30 ± 0.10^{b}	0.07
		6	0.96 ± 0.13	0.98 ± 0.23	1.00 ± 0.29	0.98
Chl *c*:Chl *a*		3	0.89 ± 0.06	0.71 ± 0.09	0.86 ± 0.19	0.24
		6	1.19 ± 0.16	1.22 ± 0.09	1.16 ± 0.05	0.83
Carotenoid:Chl *a*		3	0.34 ± 0.07	0.32 ± 0.06	0.34 ± 0.05	0.89
		6	0.67 ± 0.05^{a}	0.52 ± 0.03^{b}	0.50 ± 0.03^{b}	**0.002**

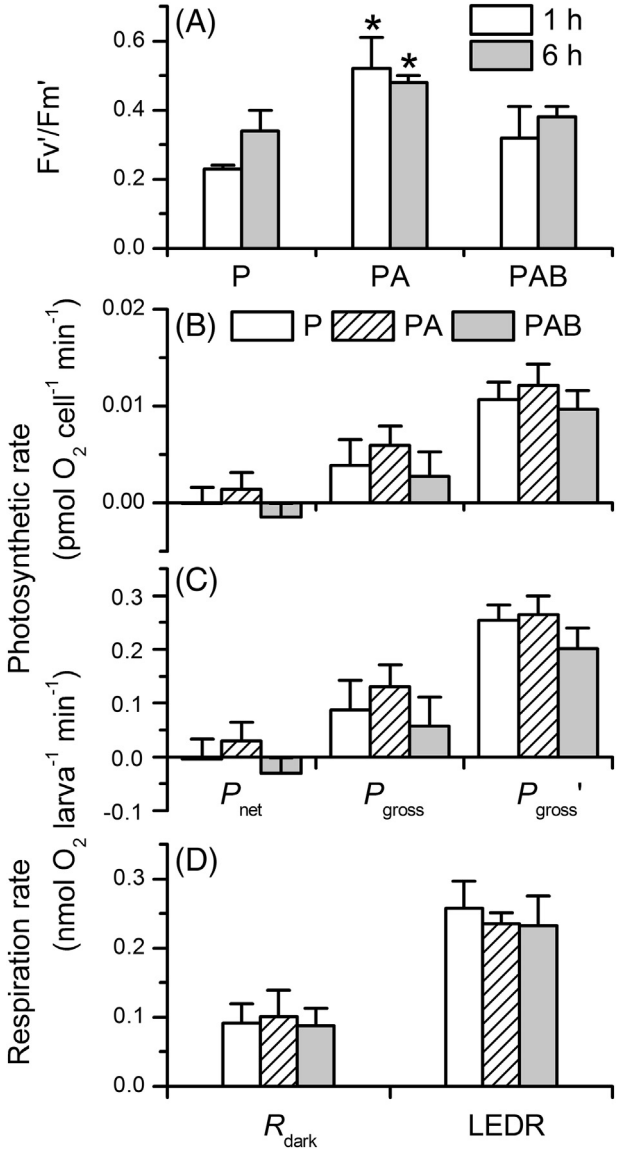

Fig. 3. Effective photochemical yield of *PSII* (F_v'/F_m', A) in symbiotic algae following 1 h (white, May cohort) and 6 h (grey, November cohort), photosynthetic oxygen evolution rate (B, C) and respiration rate (D) of *Seriatopora caliendrum* larva after exposure to PAR (P, white), PAR + UV-A (PA, grid) and PAR + UV-A + UV-B (PAB, grey) treatments for 6 h. B: pmol O_2 $cell^{-1}$ min^{-1}; C and D: nmol O_2 $larva^{-1}$ min^{-1}. Asterisks indicate significant differences among treatments at $p < 0.05$ (Fisher's LSD). Values are means ± SD ($n = 3$ for all treatments with ~25 larvae each).

effects of UV-A radiation; 2) most of the coral species studied had preferences for their settlement substratum, which would be affected under UVR exposure through the changes such as crustose coralline algae (CCA) cover and the composition of microbial communities on the CCA, both of which have been found to alter in response to other climate stressors [42–44]; 3) the experimental time may not have been long enough to fully trace the time course of larval development. By inference, our results suggest that these earlier studies may have overestimated the potential consequences of UV-A radiation on coral larvae. Future studies to ascertain if the larvae of other coral species that have no preference for specialized substrates exhibit a similar response to UV-A radiation would be instructive. Unraveling the complex relationship between corals and their symbiotic algae will help us in understanding the adaptive strategies that coral symbionts use to against various climate stressors.

Acknowledgement

This study was supported by the national key research programs 2016YFA0601400, the National Natural Science Foundation (41430967; 41120164007), the State Oceanic Administration (National Programme on Global Change and Air-Sea Interaction, GASI-03-01-02-04), the Joint project of National Natural Science Foundation of China and Shandong province (No. U1406403), the Strategic Priority Research Program of Chinese Academy of Sciences (No. XDA1102030204). We thank Chih-Jui Tan, Chia-Kuei Lin, Jiawei Liu for their help of coral collection at NMMBA in Taiwan. We are also grateful to Yahe Li, Fuwen Kuo, Li-Hsueh Wang and Yuechen Shi for technical assistance and experimental set-up, and to Xianglan Zen and Wenyan Zhao for the logistics. JB's visit to Xiamen was supported by Xiamen University.

References

[1] D.-P. Häder, C.E. Williamson, S.-A. Wangberg, M. Rautio, K.C. Rose, K. Gao, E.W. Helbling, R.P. Sinha, R. Worrest, Effects of UV radiation on aquatic ecosystems and interactions with other environmental factors, Photochem. Photobiol. Sci. 14 (2015) 108–126.
[2] R.L. McKenzie, P.J. Aucamp, A.F. Bais, L.O. Bjorn, M. Ilyas, Changes in biologically-active ultraviolet radiation reaching the Earth's surface, Photochem. Photobiol. Sci. 6 (2007) 218–231.
[3] R.L. McKenzie, P.J. Aucamp, A.F. Bais, L.O. Bjorn, M. Ilyas, S. Madronich, Ozone depletion and climate change: impacts on UV radiation, Photochem. Photobiol. Sci. 10 (2011) 182–198.
[4] E.C. Weatherhead, S.B. Andersen, The search for signs of recovery of the ozone layer, Nature 441 (2006) 39–45.
[5] I. Masiri, M. Nunez, E. Weller, A 10-year climatology of solar radiation for the Great Barrier Reef: implications for recent mass coral bleaching events, Int. J. Remote Sens. 29 (2008) 4443–4462.
[6] A.F. Bais, K. Tourpali, A. Kazantzidis, H. Akiyoshi, S. Bekki, P. Braesicke, M.P. Chipperfield, M. Dameris, V. Eyring, H. Garny, D. Iachetti, P. Jöckel, A. Kubin, U. Langematz, E. Mancini, M. Michou, O. Morgenstern, T. Nakamura, P.A. Newman, G. Pitari, D.A. Plummer, E. Rozanov, T.G. Shepherd, K. Shibata, W. Tian, Y. Yamashita, Projections of UV radiation changes in the 21st century: impact of ozone recovery and cloud effects, Atmos. Chem. Phys. 11 (2011) 7533–7545.
[7] D.F. Gleason, G.M. Wellington, Ultraviolet radiation and coral bleaching, Nature 365 (1993) 836–838.
[8] J.H. Drollet, M. Faucon, P.M. Martin, Elevated sea-water temperature and solar UV-B flux associated with two successive coral mass bleaching events in Tahiti, Mar. Freshw. Res. 46 (1995) 1153–1157.
[9] P.L. Jokiel, R.H. York Jr., Solar ultraviolet photobiology of the reef coral *Pocillopora damicornis* and symbiotic zooxanthellae, Bull. Mar. Sci. 32 (1982) 301–315.
[10] J.L. Torres-Pérez, R.A. Armstrong, Effects of UV radiation on the growth, photosynthetic and photoprotective components, and reproduction of the Caribbean shallow-water coral *Porites furcata*, Coral Reefs 31 (2012) 1077–1091.
[11] J.H. Torregiani, M.P. Lesser, The effects of short-term exposures to ultraviolet radiation in the Hawaiian Coral *Montipora verrucosa*, J. Exp. Mar. Biol. Ecol. 340 (2007) 194–203.
[12] D.F. Gleason, G.M. Wellington, Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient, Mar. Biol. 123 (1995) 693–703.
[13] G.M. Wellington, W.K. Fitt, Influence of UV radiation on the survival of larvae from broadcast-spawning reef corals, Mar. Biol. 143 (2003) 1185–1192.
[14] I.B. Kuffner, Effects of ultraviolet (UV) radiation on larval settlement of the reef coral *Pocillopora damicornis*, Mar. Ecol. Prog. Ser. 217 (2001) 251–261.
[15] B. Nesa, A.H. Baird, S. Harii, I.M. Yakovleva, M. Hidaka, Algal symbionts increase DNA damage in coral planulae exposed to sunlight, Zool. Stud. 51 (2009) 12–17.
[16] J. Zhou, T.-Y. Fan, J. Beardall, K. Gao, Incident ultraviolet irradiances influence physiology, development and settlement of larva in the coral *Pocillopora damicornis*, Photochem. Photobiol. 92 (2016) 293–300.
[17] M. Aranda, A.T. Banaszak, T. Bayer, J.R. Luyten, M. Medina, C.R. Voolstra, Differential sensitivity of coral larvae to natural levels of ultraviolet radiation during the onset of larval competence, Mol. Ecol. 20 (2011) 2955–2972.
[18] S. Harii, M. Yamamoto, O. Hoegh-Guldberg, The relative contribution of dinoflagellate photosynthesis and stored lipids to the survivorship of symbiotic larvae of the reef-building corals, Mar. Biol. 157 (2010) 1215–1224.
[19] R.H. Richmond, Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*, Mar. Biol. 93 (1987) 527–533.
[20] N. Isomura, M. Nishihira, Size variation of planulae and its effect on the lifetime of planulae in three pocilloporid corals, Coral Reefs 20 (2001) 309–315.
[21] V.R. Cumbo, T.Y. Fan, P.J. Edmunds, Physiological development of brooded larvae from two pocilloporid corals in Taiwan, Mar. Biol. 159 (2012) 2853–2866.
[22] Y. Loya, K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, R. van Woesik, Coral bleaching: the winners and the losers, Ecol. Lett. 4 (2001) 122–131.
[23] E.M. Graham, A.H. Baird, S.R. Connolly, M.A. Sewell, B.L. Willis, Rapid declines in metabolism explain extended coral larval longevity, Coral Reefs 32 (2013) 539–549.
[24] R.J. Ritchie, Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents, Photosynth. Res. 89 (2006) 27–41.
[25] J.D.H. Strickland, T.R. Parsons, A Practical Handbook of Seawater Analysis, Fisheries Research Board of Canada, Ottawa, Canada, 1972.

[26] W.C. Dunlap, G.A. Rae, E.W. Helbling, V.E. Villafañe, O. Holm-Hansen, Ultraviolet-absorbing compounds in natural assemblages of Antarctic phytoplankton, Antarct. J. US 30 (1995) 323–326.
[27] G. Li, K. Gao, Variation in UV irradiance related to stratospheric ozone levels affects photosynthetic carbon fixation of winter phytoplankton assemblages from surface coastal water of the South China Sea, Mar. Biol. Res. 8 (2012) 670–676.
[28] G. Li, K. Gao, G. Gao, Differential impacts of solar UV radiation on photosynthetic carbon fixation from the coastal to offshore surface waters in the South China Sea, Photochem. Photobiol. 87 (2011) 329–334.
[29] G. Li, K. Gao, Cell size-dependent effects of solar UV radiation on primary production in coastal waters of the South China Sea, 2Estuar. Coasts 36 (2013) 728–736.
[30] E.S. Barbieri, V.E. Villafanñ, E.W. Helbling, Experimental assessment of UV effects on temperate marine phytoplankton when exposed to variable radiation regimes, Limnol. Oceanogr. 47 (2002) 1648–1655.
[31] E.W. Helbling, K. Gao, R.J. Gonçalves, H. Wu, V.E. Villafañe, Utilization of solar UV radiation by coastal phytoplankton assemblages off SE China when exposed to fast mixing, Mar. Ecol. Prog. Ser. 259 (2003) 59–66.
[32] J.A. Pechenik, Larval experience and latent effects—metamorphosis is not a new beginning, Integr. Comp. Biol. 46 (2006) 323–333.
[33] J.A. Pechenik, M.S. Estrella, K. Hammer, Food limitation stimulates metamorphosis of competent larvae and alters postmetamorphic growth rate in the marine prosobranch gastropod *Crepidula fornicata*, Mar. Biol. 127 (1996) 267–275.
[34] M. Pahkala, A. Laurila, J. Merilä, Carry-over effects of ultraviolet-B radiation on larval fitness in *Rana temporaria*, Proc. R. Soc. Lond. B Biol. Sci. 268 (2001) 1699–1706.
[35] J.A. Pechenik, On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles, Mar. Ecol. Prog. Ser. 177 (1999) 269–297.
[36] D. Vaitilingon, R. Morgan, P. Grosjean, P. Gosselin, M. Jangoux, Effects of delayed metamorphosis and food rations on the perimetamorphic events in the echinoid *Paracentrotus lividus* (Lamarck, 1816) (Echinodermata), J. Exp. Mar. Biol. Ecol. 262 (2001) 41–60.
[37] M.A. Sams, F. Warren-Myers, M.J. Keough, Increased larval planktonic duration and post-recruitment competition influence survival and growth of the bryozoan *Watersipora subtorquata*, Mar. Ecol. Prog. Ser. 531 (2015) 179–191.
[38] J.A. Pechenik, M.E. Rice, Influence of delayed metamorphosis on postsettlement survival and growth in the sipunculan *Apionsoma misakianum*, Invertebr. Biol. 120 (2001) 50–57.
[39] J.A. Montory, O.R. Chaparro, J.A. Pechenik, C.M. Diederich, V.M. Cubillos, Impact of short-term salinity stress on larval development of the marine gastropod *Crepipatella fecunda* (Calyptraeidae), J. Exp. Mar. Biol. Ecol. 458 (2014) 39–45.
[40] E.M. Graham, A.H. Baird, B.L. Willis, S.R. Connolly, Effects of delayed settlement on post-settlement growth and survival of scleractinian coral larvae, Oecologia 173 (2013) 431–438.
[41] D.F. Gleason, P.J. Edmunds, R.D. Gates, Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral *Porites astreoides*, Mar. Biol. 148 (2006) 503–512.
[42] I.B. Kuffner, A.J. Andersson, P.L. Jokiel, K.u.S Rodgers, F.T. Mackenzie, Decreased abundance of crustose coralline algae due to ocean acidification, Nat. Geosci. 1 (2008) 114–117.
[43] K.E. Fabricius, A. Kluibenschedl, L. Harrington, S. Noonan, G. De'ath, *In situ* changes of tropical crustose coralline algae along carbon dioxide gradients, Sci. Rep. 5 (2015) 9537.
[44] N.S. Webster, A.P. Negri, E.S. Botté, P.W. Laffy, F. Flores, S. Noonan, C. Schmidt, S. Uthicke, Host-associated coral reef microbes respond to the cumulative pressures of ocean warming and ocean acidification, Sci. Rep. 6 (2016) 19324.