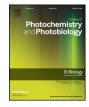
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UV-A induced delayed development in the larvae of coral *Seriatopora caliendrum*



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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.

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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

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

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 μ mol 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 \pm SD throughout the incubation period.

Experiment date	Temperature (°C)	Total dose (MJ m^{-2})			Maximum irradiance			Parameters
		PAR	UV-A	UV-B	PAR(μ mol 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	$0.65~\pm~0.15$	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.

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