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EDITED BY

Christophe Brunet,
Anton Dohrn Zoological Station
Naples, Italy

REVIEWED BY

Milan Szabo,
Eötvös Loránd Research Network
(ELKH), Hungary
Pau Loke Show,
University of Nottingham Malaysia
Campus, Malaysia

*CORRESPONDENCE

Holger Kühnhold
✉ holger.kuehnhold@leibniz-zmt.de

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Light intensity changes and UVB radiation affect peridinin content and antioxidant activity in the *Cassiopea andromeda* holobiont

Holger Kühnhold^{1,2*}, Monika Schreiner^{2,3}, Andreas Kunzmann^{1,2} and Karin Springer⁴

¹Department Ecology, Working Group Experimental Aquaculture, Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany, ²Food4Future (F4F), c/o Leibniz Institute of Vegetables and Ornamental Crops (IGZ), Großbeeren, Germany, ³Department Plant Quality & Food Security, Leibniz Institute of Vegetables and Ornamental Crops (IGZ), Großbeeren, Germany, ⁴Marine Botany, Faculty Biology/Chemistry, University Bremen, Bremen, Germany

Introduction: The up-side down jellyfish *Cassiopea andromeda* represents a yet untapped marine species that could be targeted as a new source for functional ingredients, such as natural pigments and antioxidants. Since *C. andromeda* hosts endosymbiotic dinoflagellates, this jellyfish contains peridinin pigments, which are linked with high antioxidant capacities and many other health-promoting properties. This study investigates the potential to specifically increase the content of peridinin and overall antioxidant activity in *C. andromeda*, through the targeted application of different photosynthetic active radiation (PAR) intensities and ultraviolet radiation, cultured in fully controlled indoor aquaculture systems.

Materials and Methods: Indoor bred *C. andromeda* specimens were exposed to five different PAR intensities (50, 100, 200, 400 and 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and a combined treatment of narrow-band UVB ($\lambda = 285 \pm 10 \text{ nm}$) radiation and intermediate (200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) PAR intensity over a period of four weeks. Before the treatment and after two- and four-week treatment intervals, pigment concentrations and antioxidant activity levels were measured using high-performance liquid chromatography (HPLC) and the Trolox Equivalent Antioxidant Capacity (TEAC) assay, respectively. In addition, relative growth rate, umbrella pulsation and photosynthetic efficiency (measured by pulse amplitude modulated fluorometry) of *C. andromeda* individuals were also monitored throughout the experiment.

Results: Chlorophyll a (Chl a) and peridinin (Per) dominated overall pigment content in *C. andromeda* endosymbionts, chlorophyll c2 and diadinoxanthin were detected in minor amounts. Over the treatment time, Chl a and Per concentrations, measured as $\mu\text{g g}^{-1}$ jellyfish dry weight and $\text{pg microalgae-cell}^{-1}$, decreased sharply at higher PAR intensities (200 – 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) compared to the control treatment (100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). After four weeks Chl a and Per concentrations were lowest at the highest PAR intensity (800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and highest at the lowest PAR intensity (50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). Moreover, the ratio of Chl a and Per showed a relative decrease of Per with increasing PAR intensity. The combined treatment of

narrow-band UVB ($\lambda = 285 \pm 10$ nm) radiation and intermediate ($200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) PAR intensity led to significantly elevated Chl *a* and Per concentrations compared to the $200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ PAR treatment without UVB. Significantly elevated antioxidant activity levels, measured as Trolox Equivalents mmol g^{-1} jellyfish dry weight, were only detected in UVB exposed *C. andromeda*, indicating that Chl *a* and Per did not determine overall antioxidant capacity. The photosynthetic efficiency of *C. andromeda* endosymbionts was not affected by elevated antioxidant activity. Opposing that, the jellyfish hosts that were exposed to the UVB treatment shrunk drastically, indicating a strong stress response.

Discussion: With this study, we demonstrate for the first time the application potential of PAR intensity manipulations and UVB irradiation, to increase the content of valuable pigments and antioxidants in *C. andromeda* jellyfish and their endosymbiotic dinoflagellates that live *in hospite* within the host tissue. Based on these findings, we propose the culture of *C. andromeda* under fully controlled and light-optimized conditions as new pathway to harness bioproducts and functional ingredients.

KEYWORDS

Light-harvesting pigments, carotenoids, endosymbiotic dinoflagellates, symbiodiniaceae, up-side down jellyfish, ultraviolet radiation (UVR) LEDs, health-promoting ingredients, new marine food

Introduction

The interest in jellyfish biomass as potential resource for bioproducts such as functional ingredients to enhance food, feed, cosmetic and pharmaceutical items is globally on the rise. While sustainable practices for the utilization of wild jellyfish stocks are being initiated (Edelist et al., 2021), a vast array of culture techniques enable the controlled indoor aquaculture of many species (Duarte et al., 2022). However, the resources (i.e. labor and energy) required to cultivate jellyfish in land-based aquaculture systems narrows the scope for species that contain high-value products, such as functional bioactive compounds. Moreover, detailed knowledge about the content of target compounds is essential for the economic viability of controlled production systems. Recent studies on the nutritional and pharmacological properties of several jellyfish (Leone et al., 2013; Leone et al., 2015; De Domenico et al., 2019; Leone et al., 2019; De Rinaldis et al., 2021) showed promising characteristics and revealed that jellyfish, which host endosymbiotic microalgae exhibit particularly prospective functional assets, as the proteinaceous animal tissue is enriched with value-adding algae components (Leone et al., 2015). In this regard, the upside-down jellyfish *Cassiopea andromeda* is a particularly auspicious candidate species for controlled captivity culture, as members of the genus *Cassiopea* harbor densely packed microalgal symbionts belonging to the dinoflagellate family Symbiodiniaceae (*Symbiodinium* spp.) (Lampert et al., 2012). In *C. andromeda*, dinoflagellates are endosymbionts that reside in the jellyfish mantle tissue, primarily in the appendages. The resultant

strongly interdependent organism-unit is referred to as a 'holobiont'. As the *C. andromeda* holobiont is specialized to provide optimal growing conditions and protection for the dinoflagellates, these microalgae can readily proliferate in this host habitat (Lampert, 2016; Djeghri et al., 2019).

Dinoflagellates are a major source of bioactive molecules in marine environments, producing a wide range of chemically diverse compounds (Gallardo-Rodríguez et al., 2012; Camacho-Muñoz et al., 2021). Among others, microalgal dinoflagellates contain peridinin (Per), which is known as their signature pigment (Barlow et al., 1993; Begum et al., 2016; Jeffrey et al., 2011). In previous studies Per has shown antioxidant, antitumor, and anti-inflammatory activities (Sugawara et al., 2007; Onodera et al., 2014; Supasri et al., 2021a). Like the accessory pigment fucoxanthin, Per is a xanthophyll with unique allenic bond, which enables strong antioxidant properties (Miyashita et al., 2011; Torregrosa-Crespo et al., 2018). Due to its remarkable structure, Per is among the very few carotenoids that can exhibit high antioxidant potential, even under anoxic conditions (Nomura et al., 1997; Sachindra et al., 2007; Supasri et al., 2021a). As for most of the functional substances that are discovered in dinoflagellates, the sourcing of Per is challenged by limited natural availabilities and difficulties to culture target species in captivity. The targeted production of Per has been tested through the long-term culture of free-living dinoflagellates (*Amphidinium carterae*) (Fuentes-Grünwald et al., 2016) and isolated endosymbiotic dinoflagellates (*Symbiodinium tridacnidorum* CS-73) (Supasri et al., 2021a; Supasri et al., 2021b). However, targeting valuable compounds such as Per in endosymbiotic *Symbiodinium*

spp., grown *in hospite* in a host species such as *C. andromeda*, has not been tested so far.

In dinoflagellates, the majority of Per occurs in two constellations: 1) in the thylakoid membrane-bound chlorophyll *a*-chlorophyll *c*₂-peridinin-protein complex (acpPC) (Iglesias-Prieto et al., 1993) and 2) in a water-soluble light-harvesting complex, namely peridinin-chlorophyll *a*-protein (PCP) (Iglesias-Prieto et al., 1991), where Per belongs to the primary components for light-harvesting (LH). The unique structure and LH properties of PCP has been extensively studied (Song et al., 1976; Koka and Song, 1977; Polivka et al., 2007; Carbonera et al., 2014) and revealed the function of Per as carbonyl-containing carotenoid in the antenna complex, which captures light outside the absorption spectra of chlorophyll. Next to that Per plays a crucial role as photo-protectant, which prevents the formation of reactive oxygen species (ROS) by quickly and efficiently quenching the chlorophyll *a* triplet state that can form under photic stress (Carbonera et al., 2014). These functional characteristics make LH pigments like Per also valuable ingredients for natural healthcare items, such as food supplements (Leong et al., 2018). The growing global interest in such products requires sophisticated tools for the extraction and recovery of pigment-protein complexes (Chia et al., 2020) and makes the exploration of new sources for the sustainable supply of valuable pigments such as Per a prime interest. Like all photoactive organisms, dinoflagellates are capable to continuously optimize their LH capacity by altering the number and ratio of photosynthetic pigments (Hennige et al., 2011), in order to respond to ambient light changes. Next to LH optimization, pigment alterations can also reflect photic stress e.g. due to high intensities of photosynthetically active radiation (PAR) and ultraviolet radiation (UVR), which are both linked with the formation of cell-damaging molecules such as ROS. The targeted manipulation of algae photosystems, through controlled light changes, has been broadly studied. Several studies have suggested that lower PAR intensities lead to the increased synthesis of LH pigments (Wyman and Fay, 1987; Grossman et al., 1993), whereas higher PAR intensities result in the enhanced expression of phycocyanin, phycoerythrin (Madhyastha and Vatsala, 2007), astaxanthin (Imamoglu et al., 2009), and β -carotene (Pisal and Lele, 2005) in microalgae and cyanobacteria. In similar studies, the exposure of microalgae and cyanobacteria to varying light spectra and UVB radiation proved feasible to enhance the synthesis of phycobiliproteins (Fatma, 2009) and the production of vitamin D₃ (Ljubic et al., 2020). In macroalgae, AOA levels could be significantly enhanced through elevated PAR intensities (Magnusson et al., 2015; Sommer et al., 2022). Such knowledge about the optimization of ambient light factors to enhance the production of target compounds in macroalgae and free-living microalgae, can also be considered as refinement key to enable the economic exploitation of photoactive holobionts, such as *C. andromeda*. Yet, information about the application of light manipulations to enhance the production of target compounds, such as Per, in *C. andromeda* endosymbionts cultured *in hospite* is scarce. Given that *C. andromeda* provides optimal growing conditions and protection for its endosymbionts, the *in hospite* culture approach may provide a more robust culture habitat

compared to the culture of free-living dinoflagellates. However, a crucial aspect of the symbiosis between host species and endosymbiotic dinoflagellates is the capacity of the host tissue to optimize the incoming light through absorption and scattering. Since the quantity and quality of light that reaches the endosymbionts within the host tissue is crucial for photosynthetic activity, host species developed specific tissue characteristics, with permeability for beneficial light and impermeability for harmful light radiation, to enhance the habitat for the endosymbionts. The medusa tissue of the endosymbiotic jellyfish *Cotylorhiza tuberculata* showed strong properties to absorb UVR and to attenuate high light intensities (Enrique-Navarro et al., 2022). In studies with corals, different Symbiodinium strains showed adjustments of pigments, due to photic changes, only outside the host environment (Roth et al., 2010). This raises the question whether the concentration of light-harvesting pigments (LHP) can be specifically triggered in *C. andromeda* endosymbionts growing *in hospite*, through the application of LED lighting.

At present, considerable knowledge gaps remain regarding the impact of the targeted application of PAR intensity changes and UVR on the *C. andromeda* holobiont, particularly in the context of health-promoting properties such as Per content and AOA levels. Therefore, the aim of this study was to elucidate the effects of a broad range of PAR intensities (50–800 photons $\mu\text{mol m}^{-2} \text{s}^{-1}$) and a low dose (1.3 KJ $\text{m}^{-2} \text{day}^{-1}$) of narrow-band UVR within the UVB spectrum ($\lambda = 285 \pm 10 \text{ nm}$) in combination with a mild PAR intensity (200 photons $\mu\text{mol m}^{-2} \text{s}^{-1}$) on (1) the content and ratio of the dominant LHPs in *C. andromeda* endosymbionts cultured *in hospite* and on (2) the AOA levels in the overall tissue of the *C. andromeda* holobiont cultured in land based, fully-controlled aquaculture systems.

Materials and methods

Jellyfish culture

Adult *Cassiopea andromeda* medusae were sourced from an established jellyfish culture bred from polyps (origin: Aquarium Berlin) within the aquaria facilities of the Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany. Incubation experiments were conducted in experimental tanks (ETs) in the Marine Experimental Ecology unit (MAREE) of ZMT. The individual ETs function as recirculating aquaculture systems with a water volume of ~120 L, with an upper culture unit and a sump tank equipped with a biofilter system and a protein skimmer below. The temperature and salinity were set at 26°C and 35 S_A (Red Sea Salt, Red Sea Fish, Israel), respectively, these conditions were controlled and regulated automatically through submerged sensors. The ETs were each illuminated with an Aquillumination Hydra FiftyTwo HD (AI Hydra 52 HyperDrive, USA) lamp with seven types of LEDs, emitting the full spectrum (380–680 nm) of photoactive radiation (PAR) with a photon flux density of 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$.

In total, 52 visually healthy (i.e. no injured bells or lost oral arms etc.) *Cassiopea andromeda* specimens with initial body weights of

111.4 ± 35.7 g and diameters of 10.3 ± 1.3 cm were randomly allocated into 6 ETs. Within these ETs, the animals were individually housed in plastic containers (length 16 cm, width 12 cm, height 12 cm). These containers were fixed just below the water surface, to maintain the same horizontal position and vertical distance under the lamps. This setup allowed for the recognition of individual jellyfish and the precise control of PAR emission on a per-animal basis. Slits on the sides of these plastic containers allowed the exchange of water within the container and the surrounding tank. Over the acclimation and experimental phase, the ETs were cleaned once per week. This included the scratching off of biofilms and the siphoning of feed residues and other particles. During cleaning, approximately one-third of the water volume was exchanged with filtered seawater. In addition, the bacterial film that accumulated at the surface of the water was removed daily with a fine mesh, to prevent the refraction of light through this layer. *C. andromeda* individuals were target fed daily with 1 mL of dense freshly hatched brine shrimp *Artemia* nauplii solution using a plastic pipette. One hour after feeding, remaining food residues and any faecal matter were removed from the plastic containers via siphoning with a small plastic pipette. The small plastic boxes were regularly rotated in order to exclude any potential confounding effects associated with different positioning within these tanks. For acclimation purposes, the jellyfish were kept for three weeks in the ETs at a constant PAR intensity of 100 μmol photons m⁻² s⁻¹ with 12:12 h light/dark cycle. Light intensities (Li-250A, LI-COR, USA) and spectra (RAMSES ACC-VIS spectroradiometer, TriOS, Germany) were determined at the bottom of the plastic containers.

Light treatment conditions

After the acclimation phase, four animals (n = 4) were collected for initial sampling. Subsequently, the PAR intensities in five ETs were changed in steps of no more than 100 μmol photons m⁻² s⁻¹ per day, until the desired PAR intensities of 50, 200, 400, and 800 μmol photons m⁻² s⁻¹ were reached. For the UVR-treatment, UVB-LEDs (λ=285 ± 10 nm) emitting a dose of 1.3 KJ m⁻² day⁻¹ were installed above second ET that reached a final PAR intensity of 200 μmol photons m⁻² s⁻¹. Once the target treatment conditions had been reached, these five different light manipulations remained constant over a four-week period. The sixth ET kept a constant PAR intensity of 100 μmol photons m⁻² s⁻¹ throughout the acclimation and experimental phase and served as control treatment.

Physiological parameter measurements

The umbrella pulsation rate, chlorophyll *a* fluorescence and wet biomass were quantified for each individual *C. andromeda* medusa initially, after the acclimation phase (day 0) and at the end (day 28) of the different PAR intensity treatments and the exposure to UVB radiation. Umbrella pulsations were counted over 15 s, this number was then extrapolated to determine the number of umbrella pulses per minute and served as proxy for overall organism activity. To exclude the effect of potential handling stress, umbrella pulsations

were counted before taking the organisms out of the tanks for further analyses. Chlorophyll *a* fluorescence was measured using a portable pulse amplitude modulated fluorometer (Diving-PAM, Walz, Effeltrich, Germany). Immediately before the fluorescence measurements, randomly selected *C. andromeda* specimens (n = 4 per treatment) were collected from the ETs and placed into small glass containers filled with seawater derived from their tanks. In these containers, the animals were kept in darkness for 8 min, to dark-adapt the endosymbiotic dinoflagellates. The subsequent fluorescence measurements included the following steps: 1) a probe with a low-intensity modulated measuring light was placed in close distance to the oral arms and tentacles of each *C. andromeda* specimen to detect minimal fluorescence (F₀) of the dark-adapted endosymbionts. 2) A saturating pulse of light (2700 μmol photons m⁻² s⁻¹) was applied (0.8 s) to obtain the maximum fluorescence (F_m) of the endosymbiotic dinoflagellates. On the basis of F₀ and F_m the ratio F_v/F_m was calculated using the formula (Schreiber et al., 1995; Maxwell and Johnson, 2000):

$$F_v/F_m = (F_m - F_0)/F_m$$

The ratio F_v/F_m quantifies the maximum quantum efficiency of photosystem II and can serve as a proxy for photosynthetic performance. Right after the fluorescence measurements, the *C. andromeda* medusa were placed on absorbent tissues for 5 s to remove excess water before determining the wet weight of the jellyfish on a digital scale (Sartorius, Germany). The relative growth rate (RGR) was calculated based on wet biomass weight using the formula (Connolly and Wayne, 1996):

$$RGR = \frac{\ln \frac{W_2}{W_1}}{\Delta T}$$

Where ln is the natural log, W₁ is the starting wet weight of one individual jellyfish, W₂ is the total jellyfish wet weight after four weeks experimental time and ΔT is the length of the experiment.

Sampling and preparation for biochemical analyses

For the analyses of pigments and AOA, four *C. andromeda* were sampled after the acclimation phase, after two weeks, and after four weeks (at the end of the experimental period). At each of these time points, whole animals were snap-frozen in liquid N₂ and stored at -80°C. Prior to lab-based analyses, the sampled organisms were lyophilized for 72 h at 1 mbar (ALPHA 1-4 LD plus; Christ GmbH, Osterode, Germany). After lyophilization the dry weight of individual organisms were documented before the whole jellyfish were ground to powder for 20 s, using a benchtop homogenizer (FastPrep-24, MP Biomedicals, Germany). For the counting of endosymbiotic algae cells, the protocol from Mammonne et al. (2021) was adapted and applied. From each sample, a quantity of ~20 mg lyophilized powder was resuspended in 500 μl of distilled water. For homogenization, the suspension was shaken for 16 h at 60 rpm (Intelli-Mixer RM-2L; ELMI SIA, Riga, Latvia). To prevent cellular clumping, resuspended sample solutions were ultrasonicated twice for 30 s (HD 2070.2; Brandelin electronic

GmbH & Co KG, Berlin, Germany) using a Sonotrode (MS 72; 20 KHz, 70 Watt, 285 μ m = 100%) with a low amplitude of 20% prior to cell counting. The sample solutions were then pipetted into a Neubauer Hemocytometer (0.1 mm depth), to count the microalgae cells in triplicate under an optical microscope (20x). The total amount of microalgae cells per individual jellyfish, was calculated based on the cell concentration per dry weight of the resuspended jellyfish sub-sample.

Pigment analyses

For pigment analyses, 140 mg of lyophilized sample material was weighed into Eppendorf tubes, after which the pigments therein were extracted in 1 mL of cold 90% acetone for 24 h at 4°C in the dark. After centrifugation (2500g, 4°C, 5 min) and filtration (0.45 μ m nylon syringe filters, Nalgene, USA), pigment analyses were performed using reversed-phase high-performance liquid chromatography (HPLC). Pigments (chlorophyll *a*, peridinin, chlorophyll *c*2, diadinoxanthin, and β -carotene) were separated on a LaChromElite system equipped with a chilled autosampler L-2200 and a DAD detector L-2450 (VWR-Hitachi, Germany) with a LiChropher 100-RP-18 guard cartridge, applying a gradient according to Wright et al. (1991). Peaks were detected at 440 nm, identified, and quantified *via* co-chromatography with appropriate standards (obtained from DHI Lab Products, Denmark). Pigment concentrations were expressed as μ g g⁻¹ *C. andromeda* dry weight and as pg cell⁻¹ of endosymbiotic microalgae.

Antioxidant activity measurements

To measure AOA, 200 mg of lyophilized sample was dissolved in 1 mL ethanol (70%) and extracted in a water bath (47°C) for 4 h, vortexing hourly. Prior to this analysis, samples were centrifuged (2500 g, 20°C) for 5 min. The AOA was determined using a modified version of the ABTS⁺ assay described by Re et al. (1999), also known as the Trolox Equivalent Antioxidant Capacity (TEAC) assay, with Trolox (6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid) serving as a standard. A 2.45 mM ABTS⁺ stock solution was

obtained by oxidizing 7.0 mM of ABTS⁺ with potassium disulfate (K₂S₂O₈) for 16 h. A working solution with a consistent photometrically measured absorption of 0.7 \pm 0.02 at a wavelength of 734 nm (UV/VIS-spectrophotometer, Thermo Scientific Genesys 140/150, Fisher Scientific GmbH, Schwerte, Germany) was obtained *via* dilution with absolute ethanol. For the AOA analysis, 1 mL of this ABTS⁺ working solution was added to 10 μ L of sample extract, and deradicalization was measured after 6 min. AOA of the samples was expressed as Trolox Equivalents (mmol TE 100 g⁻¹ DW) after adjusting for the appropriate dilution factor. All chemicals were purchased from Sigma (Aldrich/Merck KGaA, Darmstadt, Germany).

Statistical analysis

To compare potential changes in the measured parameters over time, the four *C. andromeda* specimens that were analyzed and sampled initially (following the acclimation phase) served as a reference. To determine the effects of the different PAR intensities and UVB radiation, the different treatments (50–800 μ mol photons m⁻² s⁻¹ and 200 μ mol photons m⁻² s⁻¹ + UVB) were compared with one another (n = 4 per treatment), with the treatment that was the continuation of the acclimation condition (100 μ mol photons m⁻² s⁻¹) serving as the control for these analyses. Statistical analyses were conducted using R (version 3.4.3; R Core Team, 2019). After confirming that data conformed to a normal distribution, differences over time and between treatments were compared using analyses of variance (ANOVAs). A p-value < 0.05 was the threshold for statistical significance. *Post-hoc* Tukey tests were used for pairwise comparisons among treatment groups.

Results

Analyses of *C. andromeda* physiological and photosynthetic performance

Initially, the relative growth rate (RGR), umbrella pulsation rates, and photosynthetic efficiency (F_v/F_m) values for the medusae

TABLE 1 Relative growth rate (RGR), umbrella pulsation rate, and photosynthetic efficiency (F_v/F_m) values for *Cassiopea andromeda* specimens treated with different levels of PAR intensities (50–800 μ mol photons m⁻² s⁻¹) and UVB radiation (1.3 KJ m⁻² day⁻¹).

Light Treatment	100 (initial)	50	100 (control)	200	200 + UVB	400	800
Parameter							
RGR (x10 ⁻³)		2.3 \pm 2.8	0.8 \pm 5	0.65 \pm 0.9	- 33.9* \pm 15.2	-0.07 \pm 6.7	0.8 \pm 3.5
Umbrella pulsation (min ⁻¹)	25.5 \pm 3	23 \pm 3.5	27 \pm 4	34.5 \pm 4.5	34.5 \pm 4.2	35.5 \pm 8.7	43* \pm 6.7
F _v /F _m	0.68 \pm 0.02	0.67 \pm 0.009	0.67 \pm 0.01	0.66 \pm 0.01	0.67 \pm 0.02	0.62 \pm 0.02	0.58* \pm 0.02

Values are given for the initial sampling and for the different treatments after four weeks of exposure and are expressed as means \pm SD from four medusae. Asterisks (*) denote significant differences based on one-way ANOVAs (n = 4; p < 0.05) followed by Tukey's HSD.

in different treatment groups were analyzed (Table 1). No significant differences in RGR were observed for *C. andromeda* treated with varying levels of PAR intensity (50–800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). In contrast, 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ PAR intensity with additional UVB ($\lambda=285 \pm 10 \text{ nm}$) radiation ($1.3 \text{ KJ m}^{-2} \text{ day}^{-1}$) exposure resulted in a significant reduction in RGR ($p < 0.01$; $n = 4$). The umbrella pulsation rate of *C. andromeda* revealed a clear positive correlation with PAR intensities. Compared to the initial values the pulsation rates increased significantly ($p < 0.05$; $n = 4$) for all specimens that were exposed to elevated PAR intensities (200–800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) for four weeks. *C. andromeda* specimens that adapted to 800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ almost doubled their pulsation rates ($p < 0.01$; $n = 4$) relative to the specimens raised under the lowest PAR intensity (50 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). The UVB radiation did not affect umbrella pulsation rates. After four weeks, the photosynthetic performance, measured as F_v/F_m remained in a very narrow range (mean values: 0.66–0.67) for *C. andromeda* endosymbionts treated with relatively low PAR intensities (50–200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and with additional UVB radiation, exhibiting no significant changes from the mean initial F_v/F_m values (0.68 ± 0.02). In contrast, at relatively high PAR intensities of 400–800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, F_v/F_m tended to decrease after a four-week exposure period. At 400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ the mean F_v/F_m dropped to 0.62 ± 0.02 , while the lowest mean F_v/F_m value (0.58 ± 0.02) was reached at the highest PAR intensity of 800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. This latter F_v/F_m value was significantly lower ($p < 0.05$; $n = 4$) compared to the initial mean and the values in all other treatment groups other than the 400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ group, following a four-week treatment period.

Detection of light-harvesting pigments

Analyses of light-harvesting pigments (LHP) in *C. andromeda* endosymbionts revealed the presence of chlorophyll *a*, (Chl *a*) chlorophyll *c2*, and the two carotenoids peridinin (Per) and diadinoxanthin (Table 2). β -carotene and diatoxanthin were also detected, but only in negligible amounts. Pigment quantification revealed Chl *a* and Per as the dominant LHPs in *C. andromeda* endosymbionts, both on a per jellyfish dry weight and a per microalgal cell basis.

The effects of PAR intensity and UVB exposure on chlorophyll *a*, peridinin, and AOA

Relative to the initial Chl *a* concentrations (per jellyfish dry weight), these levels only rose in *C. andromeda* endosymbionts

exposed to the 50 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ or UVB + 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ after a two-week exposure period (Figure 1). Chl *a* levels in the other treatment groups decreased below the initial values with increasing PAR intensity. After two weeks, the control (100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and elevated PAR intensity treatments (200–800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) exhibited significantly lower Chl *a* levels compared to the 50 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and UVB + 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ treatment groups ($p < 0.01$). After four weeks, the mean Chl *a* concentration had more than doubled at the lowest level of PAR intensity as compared to initial levels, with this group exhibiting the highest Chl *a* content ($p < 0.01$) compared to all other treatments with the exception of UVB + 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Chl *a* concentrations in all elevated PAR intensity groups (200–800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) dropped significantly ($p < 0.01$) below initial and control levels after four weeks, reaching the lowest concentrations at the highest levels of PAR intensity (800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). Throughout the experiment, jellyfish endosymbionts that were exposed to UVB + 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ exhibited significantly higher ($p < 0.01$) Chl *a* concentrations relative to endosymbionts in the 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ treatment group. The comparison of Chl *a* concentrations per cell of endosymbiotic microalgae revealed a very similar pattern as compared to the changes in Chl *a* content per jellyfish dry weight. But, the increase in Chl *a* was less pronounced on a per microalgal cell basis. An overall decrease ($p < 0.01$ – 0.05) in Chl *a* concentrations per microalgal cell was, however, measured at PAR levels above the control intensity (100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). Moreover, a significant ($p < 0.01$) increase in Chl *a* content per microalgal cell was detected in the endosymbionts treated with UVB + 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, compared to the endosymbionts that were treated only with the lowest PAR intensity elevation (200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$).

The overall changes in Per concentrations strongly paralleled those for Chl *a* concentrations, both on a per jellyfish dry weight and per microalgal cell basis (Figure 2). Specifically, Per concentrations dropped after two weeks ($p < 0.01$) in those jellyfish endosymbionts that were treated with elevated PAR intensities (200 – 800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), compared to all other treatment groups. After four weeks, Per concentrations under elevated PAR intensities remained significantly lower ($p < 0.01$), continuously decreasing with rising PAR intensity. Conversely, Per levels increased ($p < 0.01$) at the lowest PAR intensity (50 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), reaching significantly higher levels as compared to the control treatment. Throughout the experiment (after 2 and 4 weeks), the Per concentrations (per jellyfish dry weight and per microalgal cell) were significantly higher ($p < 0.01$) in *C. andromeda* endosymbionts treated with 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ + UVB as compared to those treated with 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in the absence of UVB exposure.

TABLE 2 Concentrations of chlorophyll *a*, peridinin, chlorophyll *c2*, and diadinoxanthin detected in initially sampled *Cassiopea andromeda* specimens.

Pigment	Chlorophyll <i>a</i>	Peridinin	Chlorophyll <i>c2</i>	Diadinoxanthin
$\mu\text{g g}^{-1} \text{ DW}$	104 ± 18.3	70.3 ± 43.5	53.2 ± 3.1	16 ± 17.3
$\text{pg cell}^{-1} \text{ algae}$	2.7 ± 0.1	1.5 ± 0.3	1.2 ± 0.2	0.27 ± 0.25

Values are expressed as means \pm SD from four medusae ($n = 4$).

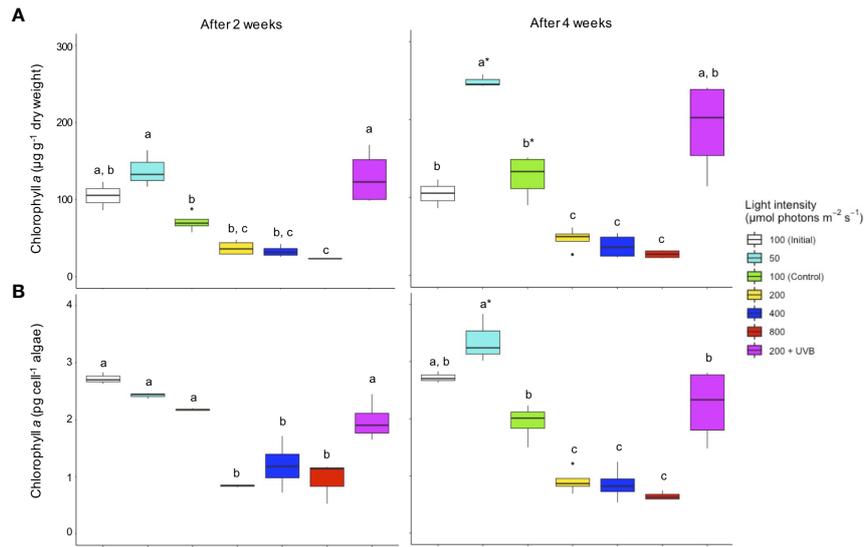


FIGURE 1 Chlorophyll *a* concentrations in *Cassiopea andromeda* specimens treated with different PAR intensities (50–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ + UVB ($1.3 \text{ KJ m}^{-2} \text{ day}^{-1}$). White boxes show the values upon initial sampling, while colored boxes show the values for these different light treatments after an exposure time of two weeks (left) and four weeks (right). Chlorophyll *a* concentrations are presented on a **(A)** per jellyfish dry weight and **(B)** per endosymbiotic microalgal cell basis. Boxes represent the interquartile range with lowest and highest percentiles (lines), while dots indicate outliers. Lowercase letters indicate significant differences between treatments and asterisk denote significant differences over time (between 2 and 4 weeks) within treatments. Significant differences are based on one-way ANOVAs ($n = 4$; $p < 0.05$) followed by Tukey's HSD test.

The Chl *a* to Per ratio (CPR) trended upwards when PAR intensities exceeded the control level of 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Figure 3A). After two weeks, the CPR was significantly higher in the endosymbiotic microalgae receiving 400 and 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ compared to those receiving 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. After

four weeks, *C. andromeda* endosymbionts treated with the highest PAR intensity exhibited a peaking CPR level, with significant ($p < 0.01$) differences compared to the initial, control, and lowest PAR treatment. UVB radiation did not affect CPR. No significant changes in overall AOA, as measured in Trolox equivalents (TE;

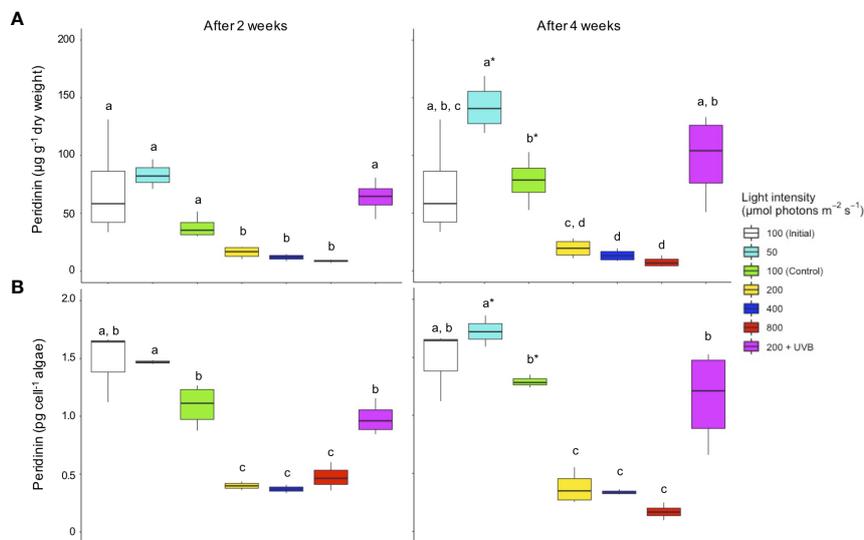


FIGURE 2 Peridinin concentrations in *Cassiopea andromeda* specimens treated with different PAR intensities (50–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ + UVB ($1.3 \text{ KJ m}^{-2} \text{ day}^{-1}$). White boxes show the values upon initial sampling, while colored boxes show the values for the different light treatments after two weeks (left) and four weeks (right) of exposure. Peridinin concentrations are presented on a **(A)** per jellyfish dry weight and **(B)** per endosymbiotic microalgal cell basis. Boxes represent the interquartile range with lowest and highest percentiles (lines), while dots indicate outliers. Lowercase letters indicate significant differences between treatments and asterisk denote significant differences over time (between 2 and 4 weeks) within treatments. Significant differences are based on one-way ANOVAs ($n = 4$; $p < 0.05$) followed by Tukey's HSD test.

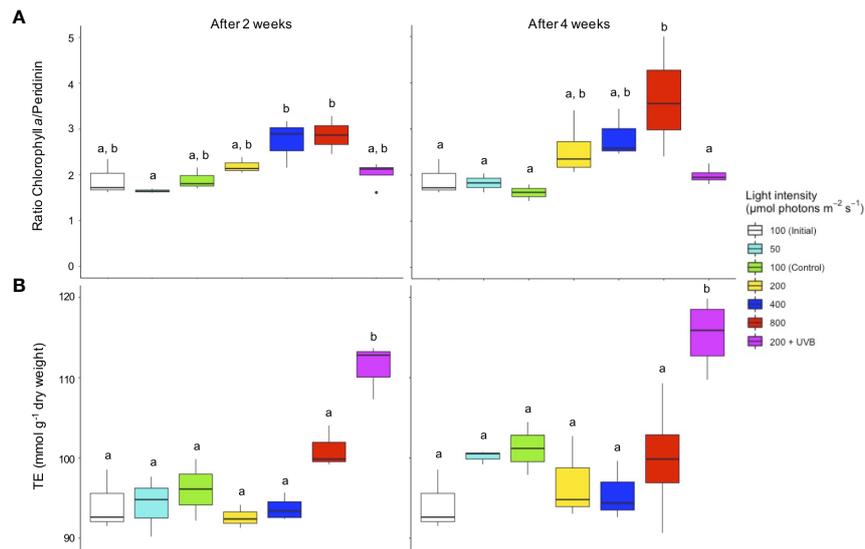


FIGURE 3

(A) The ratio of chlorophyll *a*/peridinin based on the concentrations per microalgal cells (pg cell^{-1}) and (B) antioxidant activity expressed in Trolox Equivalents (TE mmol g^{-1} dry weight) in *Cassiopea andromeda* treated with different levels of PAR intensity (50–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ + UVB ($1.3 \text{ KJ m}^{-2} \text{ day}^{-1}$). White boxes show the values upon initial sampling, while colored boxes display the values for the different light treatments after two weeks (left) and four weeks (right) of exposure. Boxes represent interquartile ranges with lowest and highest percentiles (lines), dots indicate outliers. Lowercase letters indicate significant differences between treatments. Significant differences are based on one-way ANOVAs ($n = 4$; $p < 0.05$) followed by Tukey's HSD test.

$\text{mmol per } 100 \text{ g}$ dried *C. andromeda*), were observed between any of the tested PAR intensities (50–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) nor over time (Figure 3B). Only those jellyfish that were exposed to 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ + UVB exhibited significantly elevated AOA after two and after four weeks.

Discussion

The effects of PAR intensity and UVB radiation on *C. andromeda* performance

In this study, the photosynthetic efficiency quantified as F_v/F_m was used as indicator for photosynthetic fitness of *C. andromeda* endosymbionts, which can also be considered as important vitality marker for the overall holobiont (Arossa et al., 2021). Based on this approach, the F_v/F_m ratio was measured to evaluate potential stress effects caused by the different PAR intensity treatments (50–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and the exposure to narrow-band UVB ($\lambda = 285 \pm 10 \text{ nm}$) radiation ($1.3 \text{ KJ m}^{-2} \text{ day}^{-1}$). Although the F_v/F_m values dropped clearly at elevated PAR intensities of 400 and 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, the maximum quantum yield of photosystem II was always within a photosynthetically active range ($F_v/F_m = 0.58\text{--}0.68$). This suggests that the endosymbionts of these indoor-raised *C. andromeda* holobionts were readily able to cope with changing PAR conditions. Similarly, wild *C. andromeda* holobionts exhibited a high degree of photosynthetic plasticity, with photosynthetic saturation reportedly being reached at 800 and 400 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and photosynthetic compensation occurring around 200 and 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ PAR in studies published by Mamme et al. (2021) and Welsh et al. (2009),

respectively. With respect to umbrella pulsation, *C. andromeda* showed a clear trend towards increased activity with rising PAR intensity. Faster bell contractions may indicate a growing energy demand of *C. andromeda* with increasing PAR intensities. This view is supported by a study from Battista et al. (2022), in which the jet stream generated by *C. andromeda* umbrella pulsation was linked to feeding, nutrient and gas exchange as well as with the removal of excreta. While RGR would be expected to reflect changes in energy turnover, the RGR of the jellyfish exposed to 50–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ did not differ. Overall, the mean RGRs observed in the tested range of PAR intensity manipulations were rather low and exhibited very large standard deviations. The poor growth performance of the medusa during this experiment may be a repercussion of spatial containment in the culture system. Hence, the measured RGRs cannot be considered as representative parameter for potential light effects, due to the applied PAR intensity changes. However, compared to all other treatments, the jellyfish that were exposed to narrow-band UVB radiation in addition to 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ shrank significantly over the experimental period. These UVB-treated jellyfish produced notably more mucus than the jellyfish that were only exposed to PAR intensity changes, suggesting that the applied UVB dose led to harmful effects on the *C. andromeda* host tissue, causing the disintegration of mantle tissue.

Quantification of pigments and antioxidants in *C. andromeda*

In this study, the primary photosynthetic pigments detected in *C. andromeda* endosymbionts were chlorophyll *a* (Chl *a*) and *c*₂ as well as the carotenoids peridinin (Per) and diadinoxanthin. This

finding is consistent with the pigment profile reported in other endosymbiotic dinoflagellates (Hennige et al., 2009; Roth, 2014) and has also been identified in other jellyfish holobionts, including *Cotylorhiza tuberculata* (Enrique-Navarro et al., 2022). Overall, the pigments Chl *a* and Per dominated the light-harvesting complex (LHC) of *C. andromeda* endosymbionts. Under control conditions (100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) the mean concentration of Chl *a* and Per in the endosymbiotic microalgae ranged from 2–2.7 pg cell^{-1} and 1–1.5 pg cell^{-1} , respectively. Chl *a* levels measured in other jellyfish holobionts were slightly lower than those reported in this study, including 1.33 pg cell^{-1} in *C. tuberculata* (Enrique-Navarro et al., 2022), 1–2.21 pg cell^{-1} in *Cassiopea xamachana* (Vodenichar, 1995; Verde and McCloskey, 1998; Estes et al., 2003), 2–2.1 pg cell^{-1} in *Linuche unguiculata* (Kremer et al., 1990; Wilkerson and Kremer, 1993), and 2 pg cell^{-1} in *Mastigias* sp. (McCloskey et al., 1994). When calculated as pigment concentration per *C. andromeda* dry weight, mean Chl *a* and Per contents ranged from 71–127 $\mu\text{g g}^{-1}$ dry weight (DW) and from 38–78 $\mu\text{g g}^{-1}$ DW, respectively, under control conditions in this study. Leone et al. (2013) reported much higher Per levels of $385 \pm 49.6 \mu\text{g g}^{-1}$ DW in the *C. tuberculata* holobiont. However, it should be considered that comparisons of total pigment concentrations are difficult because differences in sample processing and handling can lead to marked variations in the final data.

Overall, *C. andromeda* proved to be a robust medium for the biosynthesis and accumulation of health-promoting pigments through its endosymbiotic microalgae, implying strong utilization potential. Pigments are exclusively synthesized by plants and algae, this means that sufficient levels of pigments such as carotenoids need to be obtained exogenously for conversion into functional metabolites that are indispensable for human cells (Chuyen and Eun, 2017). With respect to AOA, *C. andromeda* exhibited considerable mean levels thereof under control conditions (from 92–94 TE mmol 100 g^{-1} DW). The AOA levels measured in this study are substantially higher than the mean AOA levels of 1.63 ± 0.125 and 2.94 ± 0.28 TE mmol 100 g^{-1} measured recently by De Rinaldis et al. (2021) in dried *C. andromeda* umbrella and oral arms, respectively. However, the AOA levels of *C. andromeda* found in the current study are in a similar range to the AOA levels reported for different microalgae such as *Haematococcus pluvialis* (up to 197.4 TE mmol 100 g^{-1} dried supercritical H_2O extract) (Rodríguez-Meizoso et al., 2010), *Dunaliella salina* (up to 111.8 TE mmol 100 g^{-1} dried hexane extract) (Herrero et al., 2006), and *Chaetoceros* sp. (102.9 TE mmol 100 g^{-1} dried dichloromethane extract) in terms of superoxide radical neutralization capacity (Guzman et al., 2001). The present data highlight the great potential of *C. andromeda* as a novel source of antioxidants for biofunctional purposes. Given that antioxidants are key mediators of endogenous ROS removal, a diet rich in antioxidants has been linked with many health benefits (Halliwell, 2000; Zampelas and Micha, 2015; Coulombier et al., 2021).

Triggering pigment content and AOA with different PAR intensities and UVB exposure

This study was developed to explore whether the synthesis of pigments, in particular Per can be specifically triggered in

C. andromeda endosymbionts through ambient light manipulations, including PAR intensity changes and UVB exposure. Moreover, it was tested whether the concentration of pigments in the endosymbionts correlate positively with AOA in the overall tissue of *C. andromeda* holobionts. The results of these analyses indicated that the endosymbiotic microalgae, growing *in hospite* in adult *C. andromeda* medusae exhibited significantly higher concentrations of the dominant light-harvesting pigments Chl *a* and Per at lower PAR intensities (50–100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) compared to elevated PAR intensities (200–800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). Similar results were also found in a study by Supasri et al. (2021b), in which the synthesis of the valuable Per-chlorophyll *a*-protein (PCP) complex was brought to a peak, in an isolated culture of endosymbiotic *Symbiodinium* (*S. tridacnidorum* CS-73), through the lowest PAR intensity treatment (30 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). The significantly highest concentrations of Per and Chl *a* pigments that were measured at the lowest PAR intensity (50 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in the present study, provide first evidence that pigment content can be triggered also in endosymbionts that grow *in hospite* in *C. andromeda*. Also low-dose UVB exposure (1.3 $\text{KJ m}^{-2} \text{ day}^{-1}$) in combination with 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ led to significantly increased pigment levels in *C. andromeda* endosymbionts, compared to the control treatment without UVB. This discovery contradicts the generally accepted assumption that UVR exposure leads to photoinhibition in endosymbiotic cnidaria as a result of damage to the photosynthetic apparatus (e.g. Weis, 2008; Enrique-Navarro et al., 2022). Similarly, in the microalgae *Nannochloropsis oceanica* the concentrations of chlorophylls and carotenoids decreased significantly with increasing UVB (312 nm) dose, ranging from 3–22 $\text{KJ m}^{-2} \text{ day}^{-1}$ (Ljubic et al., 2020).

To clarify whether the measured changes in $\mu\text{g pigment per C. andromeda}$ dry weight were triggered *via* PAR intensity- and UVB-induced pigment synthesis, within individual endosymbiont-cells, and not by variations in microalgae cell density in the *C. andromeda* tissue, the measured concentration of Chl *a* and Per were also quantified on a per microalgal-cell basis ($\text{pg microalgal cell}^{-1}$). Although less pronounced, the effects of PAR intensity and UVB on the amounts of Chl *a* and Per per microalgal-cell, followed the same significant trend of increasing pigment concentration with decreasing PAR intensity and UVB exposure, which was also detectable in total pigment quantities per jellyfish dry weight. Thus, it can be concluded that the measured differences in pigment quantities resulted from LHC adjustments within the endosymbiotic microalgae, in response to the targeted PAR and UVB manipulations, growing *in hospite* in the *C. andromeda* mantle tissue.

Moreover, a significant shift in the ratio of Chl *a* and Per in the endosymbiotic microalgae due to PAR intensity changes was observed, which indicated that targeted PAR intensity exposure changed not only total pigment concentrations but also relative pigment composition. Overall, the present study provides new significant insights, which demonstrates for the first time that the synthesis of LHC pigments can be drastically manipulated in endosymbiotic dinoflagellates, growing *in hospite*, through PAR intensity changes and UVB exposure. These pioneering results shed new light on the debate regarding the extent to which ambient light changes can affect Symbiodiniaceae in cnidaria holobionts, despite

protection through the host tissue. Previous studies have provided evidence for the assumption that optical properties of cnidarian tissue, in terms of scattering and absorption of the ambient light, shelter the endosymbionts from sub-optimal light conditions (Kühl et al., 1995; Roth, 2014). In these studies, only isolated endosymbiotic microalgae that were cultured *ex hospite* showed responses at the level of LHC pigment adjustments, due to ambient light changes. On the contrary, the present study shows that *in hospite* growing *C. andromeda* endosymbionts exhibited a clear pattern to adjust the concentration and composition of LHC pigments according to ambient PAR intensity changes. The decreased pigment synthesis at high PAR intensities observed in the current study might be a response of the microalgae to reduce the light-energy yield. For the same reason, the decrease of the Per/Chl *a* ratio with increasing PAR intensity may indicate a reduction of the overall LHC absorption spectrum, to prevent harmful effects due to excessive light energy. This assumption is strengthened by the measured F_v/F_m values, which indicated decreasing photosynthetic efficiency with increasing PAR intensity. The significantly enhanced pigment synthesis observed in response to UVB exposure presumably reflects the initiation of a protective response. However, given that the UVB-treated *C. andromeda* endosymbionts exhibited no photoinhibition in form of decreased F_v/F_m values, it can be assumed that the increased pigment synthesis was not yet a sign for photic stress, but rather a triggered form of UVB protection as has been demonstrated in terrestrial plants (Schreiner et al., 2017). Recent studies of UVB exposure in various terrestrial plant species have highlighted the regulatory properties of ecologically-relevant UVB radiation, which can trigger distinct changes in the levels of secondary plant metabolites such as carotenoids, chlorophylls, and flavonoids, ultimately leading to the desirable accumulation of these protective compounds for human dietary intake (Schreiner et al., 2009; Schreiner et al., 2012). In this line of research, the results of the present work are highly significant as they give a first indication that targeted low-dose UVB radiation can be used as an emerging technology to generate pigment-enriched food sources not only in terrestrial organisms but also in phototrophic marine organisms. Opposed to the mild UVB effects on *C. andromeda* endosymbionts, the UVB-exposed jellyfish host exhibited a strong stress response in the form of mucus production and drastic reduction of overall biomass. This suggests that most of the severe UVB stress was absorbed by the jellyfish tissue, raising the question to what extent the emitted UVB dose actually reached the endosymbionts in the jellyfish host tissue. The tissue of cnidarian holobionts is known to possess UVR-absorbing properties that can protect the endosymbionts therein (Higuchi et al., 2010; Enrique-Navarro et al., 2022). Moreover, mycosporine-like amino acids (MAA), which can be considered as functional UVR screen, were found in cnidarian holobionts (Banaszak and Lesser, 2009). In the endosymbiotic jellyfish *Cassiopea xamachana*, MAAs were synthesized by its own symbionts under UV (280–400 nm) exposure (Banaszak and Trench, 1995). Accounting for the different UVR-protection strategies of cnidaria holobionts, it can be assumed that only a fraction of the actual $1.3 \text{ KJ m}^{-2} \text{ day}^{-1}$ UVB

dose reached the endosymbionts in this experiment. This underlines that only a very mild UVB exposure is required to create pigment-promoting conditions in the studied *C. andromeda* endosymbionts. Future studies should determine the optimal UVB dose for the *C. andromeda* holobiont, which increases the synthesis of Per without harmfully affecting the host tissue.

Since only the jellyfish host showed significant stress symptoms in response to UVB exposure, whereas F_v/F_m values indicated no sign of photoinhibition in the endosymbionts, it can be assumed that the significantly enhanced AOA levels in UVB-treated *C. andromeda* primarily reflect damage to the host tissue. The fact that overall AOA levels did not correlate positively with changes in light-harvesting pigment concentrations suggests that the LHC of the endosymbionts was not the dominant driver of AOA levels in the *C. andromeda* holobiont.

Conclusions

This is the first study, which reveals that *C. andromeda* endosymbionts growing *in hospite* adjust the total content and relative composition of light-harvesting pigments (LHP) as response to ambient PAR intensity changes. Moreover, we provided first evidence that narrow-band UVB exposure leads to elevated LHP content and increased antioxidant activity (AOA) in the *C. andromeda* holobiont. With these new findings, we also provide practical information to systematically valorize the yet underutilized *C. andromeda* biomass by specifically enhancing the content of LHPs and AOA. The so enriched *C. andromeda* jellyfish, with increased functional and health-promoting properties possesses diverse utilization potentials for new food and healthcare items. Given that the inclusion of antioxidants, chlorophyll, and carotenoid-based formulations in human diets is emerging as a new focus for the promotion of a healthy lifestyle, *C. andromeda* enriched in peridinin, chlorophyll *a*, and overall AOA may represent a promising source of antioxidant and anti-lipoperoxidant compounds with utilization potential as innovative food ingredients to supplement dietary formulations such as functional foods and nutraceuticals. Moreover, the implementation of LED-light optimized, modular *C. andromeda* cultivation systems may present an innovative and resource-saving opportunity to exploit this marine biomass also in urban and suburban surroundings. However, the current results represent only the very first insights into the potential of *C. andromeda* as prolific source of high-value bioproducts. In future studies the ambient light conditions, which trigger the optimal balance between *C. andromeda* biomass yield, LHP content (mainly peridinin) and overall AOA needs to be narrowed down further. This is particularly relevant for the treatment with UVB, which led in the current study to significantly increased LHP and AOA levels, but caused also a major reduction in overall *C. andromeda* biomass. Next to that, protocols for the extraction of pigment-protein complexes need to be established and evaluated for *C. andromeda*, to generate practical information on total LHP yields from light-optimized cultures.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://issues.pangaea.de/browse/PDI-32852>.

Author contributions

HK planned and conducted the experiment. This included the experimental setup, the design of light treatments, monitoring/measuring of physiological parameters and sampling of the organisms. Moreover, HK did the analysis and statistical exploration of the data. Finally, HK wrote the manuscript and directed its continuous revisions, consisting of the remarks from the co-authors, until he submitted the final version. MS provided crucial expertise in terms of the application of UVB radiation as tool to enhance health-promoting properties in photoactive organisms. MS was also taking the lead with revising the manuscript content and structure. AK secured the funding for this work and contributed proof-reading of the final manuscript. KS assisted HK with the design of the light treatments and gave guidance, concerning methods to determine photosynthetic efficiency. KS took also full responsibility of sample processing and analyses, with regards to the measurement of pigments and antioxidants. During the writing phase KS assisted HK with the interpretation of the obtained results. All authors contributed to the article and approved the submitted 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.2023.1048346/full#supplementary-material>

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