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The Effects of Different Light Spectra, UV and Extreme Temperature on the Physiology of Endosymbiotic Jellyfish *Cassiopea andromeda*

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ABSTRACT

The endosymbiotic jellyfish *Cassiopea andromeda* represents a yet untapped marine species that could be targeted as a new source for bioproducts, including food and feed. Also, the potential use of contained valuable ingredients, such as carotenoids and other antioxidants, under controlled aquaculture conditions might be a particularly promising pathway. However, this requires close knowledge about physiology and culture conditions. In this study, the effects of different stress parameters such as different light spectra, light intensities, UV and extreme temperatures on *C. andromeda* were investigated. The following response parameters were measured: pigments, photosynthetic efficiency, bell pulsation rate, antioxidant activity (AOA) and respiration. The carotenoid peridinin and chlorophyll *a* were detected as dominant light-harvesting pigments. Three different experiments were performed. Over a four week treatment interval under four different light conditions, *C. andromeda* that were exposed to light spectra lacking blue color ($\lambda = 400–500$ nm) showed a decreasing content of chlorophyll, peridinin and all other detected pigments, while photosynthetic efficiency and AOA were not affected by any light spectra changes. Critical thresholds for both photosynthetic efficiency and respiration were detected beyond 39°C. UV seemed to have a similar effect on respiration as low temperatures, while UV did not seem to significantly affect bell pulsation rate and symbiont density. This study contributes to the development of an environmentally controlled *C. andromeda* indoor aquaculture system, revealing optimal temperature and light regimes. Accordingly, *C. andromeda* holds promise as a resource for pigment production that may offer value as a supplement for functional foods and nutraceuticals.

1 | Introduction

Headlines such as "Blue Growth Sectors, Blue Growth Strategies" or "Cultivating Blue Food Proteins" are becoming more and more popular. This is due to a rising global population, which has significantly decreased available land and freshwater. As a consequence, sustainable sources such as aquatic food(s) are becoming increasingly important. Therefore, effective utilization of aquatic food sources is vital to global food security and nutrition, particularly in countries of the Global South, where the risk of malnutrition is highest (Ahern et al. 2021). Many marine resources have the potential to provide health-promoting nutrients without a concomitant risk of reducing key resources such as arable land or freshwater (Duarte et al. 2009; Béné et al. 2015; Hilborn et al. 2018; Troell et al. 2019), offering an opportunity to improve the resilience of global food systems (Troell et al. 2014; Béné et al. 2019).

Jellyfish are a biomass source that may be amenable to sustainable exploitation as a novel food source (Edelist et al. 2021).

Worldwide increasing jellyfish biomass (Pauly et al. 1998, 2009) may represent an exploitable novel resource to coastal communities, with reference to its potential use in the pharmaceutical, nutritional, and nutraceutical Blue Growth sectors. While certain scyphozoan jellyfish, with unequalled developmental potential in the animal kingdom (Schmich et al. 2007), can have large seasonal biomass outbreaks. This currently represents a problematic issue in many coastal areas. On the other hand they could also represent a valuable source of protein and bioactive compounds (Leone et al. 2013, 2015; D'Amico et al. 2017).

Jellyfish possess a variety of macromolecules and compounds such as proteins, phenols, and enzymes with antioxidative properties (e.g., Leone et al. 2013, 2019; De Domenico et al. 2019, 2025). Some are novel bioactive compounds with strong utilization potential, which could be harnessed for dietary purposes such as supplementing functional foods and nutraceuticals.

Studies on the nutritional and pharmacological properties of several jellyfish (Leone et al. 2013, 2015; De Rinaldis et al. 2021) showed valuable characteristics and revealed that jellyfish that host symbiotic microalgae exhibit particularly rich nutritional profiles, as the proteinaceous animal tissue is enriched with nutritive algal components (Leone et al. 2015). In this regard, the upside-down jellyfish *Cassiopea andromeda* is a particularly promising candidate species, as representatives of this species harbor densely packed microalgal symbionts belonging to the dinoflagellate family Symbiodiniaceae (Lampert et al. 2012). These dinoflagellates are considered a potential source of pigments, including peridinin carotenoids, one of many factors that determine antioxidative activity (AOA) in *C. andromeda* (Kühnhold et al. 2023).

Thus, the utilization of *C. andromeda* jellyfish may not only lead to a new carotenoid source, but it could also provide a supplementary ingredient to contribute to a diet with enhanced endogenous antioxidant capacity, which has been linked to many health benefits (Zampelas and Micha 2015).

In order to fully exploit the potential of *C. andromeda* for antioxidant production, enhancing the concentrations of these target compounds is the key refinement strategy to substantially valorize this largely untapped marine biomass. In photosynthetically active organisms such as symbiotic jellyfish, the probability of ROS (reactive oxygen species) production in chloroplasts is increased during light stress in the saturation region of photosynthesis. As a physiological response, the production of antioxidative compounds is expected to increase under stress conditions (e.g., Kühnhold et al. 2023). One method commonly used in scientific studies to investigate and quantify the total antioxidant capacity of food sources is the 2,2′-azinobis-(3-ethylbenzothiazoline-6-sulphonic acid) $ABTS^{\bullet+}$ assay (Gülçin 2012). The ABTS-assay is a well-known method for higher plants, for example for fruits (Thaipong et al. 2006) and shows several strengths compared to other antioxidant tests. The assay is applicable to both lipophilic and hydrophilic antioxidants and can thus be used to measure the antioxidant activity of carotenoids, vitamins, phenolics and some plasma antioxidants. Meanwhile, this assay is also successfully used for edible algae (Stuthmann et al. 2022, 2023) and also applied to *Cassiopea* jellyfish (Kühnhold et al. 2023; De Domenico et al. 2025).

Like all photoactive organisms, *Symbiodinium* spp. alter the number and ratio of photosynthetic pigments to adjust their capacity for light harvesting (Hennige et al. 2011). Given that peridinin and chlorophyll *a* pigments dominate in endosymbiotic dinoflagellates, particular wavelengths of ambient light may trigger the synthesis of target pigments for example, carotenoids in *C. andromeda*. In the field of microalgal aquaculture, different light treatments including variations in PAR (photosynthetically active radiation) intensity, spectral composition, light flashing, and UV-B exposure are utilized to enhance the production of targeted photosynthetic active compounds (Begum et al. 2016; Ljubic et al. 2020). However, a matter of active research remains to what extend endosymbiotic microalgae that live *in hospite* can be manipulated through targeted light changes. Kühnhold et al. (2023) showed the feasibility to enhance the content of peridinin carotenoids in *C. andromeda* through light intensity changes and exposure to UV-B radiation. Whether light spectra manipulations can also induce changes in the overall content of carotenoids in dinoflagellates living *in hospite* in the *C. andromeda* host tissue has not been studied so far.

At present, considerable knowledge gaps remain regarding the impact of light spectra changes on *C. andromeda*, particularly in the context of health-promoting properties such as carotenoid content and AOA levels. On the other hand, the holobiont (the jellyfish plus its endosymbionts) is subject to changing climatic conditions. Studies should not just focus on light stress or different light spectra but also take into account stress caused by temperature and UV changes. Previous research has revealed that specific secondary metabolites can be induced by a variety of stressors.

Therefore, the aims of this study were on one hand to assess the effects of different light spectra compositions within the range of photosynthetically active radiation (PAR = 400–700 nm) at a constant intensity level (100 μmol photons $m^{-2} s^{-1}$). On the other hand we wanted to assess acute and moderate change of environmental temperature, on both the content of pigments including peridinin carotenoids and chlorophyll *a*, as well as on the overall AOA levels. Finally we wanted to assess stress effects on physiological parameters such as bell pulsation rate, respiration and photosynthetic efficiency in adult *C. andromeda* medusa cultured indoors in recirculating aquaculture systems.

2 | Materials and Methods

2.1 | Jellyfish Culture

Adult *Cassiopea andromeda* medusae were sourced from an established jellyfish culture bred from polyps within the aquaria facilities of the Leibniz Centre of Tropical Marine Research (ZMT), Bremen, Germany. Incubation experiments were conducted in experimental tanks (ETs) in the Marine Experimental Ecology unit (MAREE) of the 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 25°C ± 1°C and 35 S_A, respectively, with these conditions being controlled and regulated automatically through submerged sensors. The ETs were each illuminated with an Aquaillumination Hydra FiftyTwo HD (AI Hydra 52 HyperDrive, USA) lamp with seven types of LEDs, emitting the full spectrum of photoactive radiation (400–700 nm).

2.2 | Experiment 1: Effect of Different Light Spectra

In total, 52 visually healthy (i.e., no signs of pitched 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 and excretion residues 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 (see also RAMSES wavelengths profiles in Figures A1–A4 in the Appendix).

2.3 | Light Treatment Conditions

After three weeks of acclimation, the light spectra were changed to four different treatments, while keeping the light intensity constant at 100 μmol photons $m^{-2} s^{-1}$ and the light/dark cycle at 12:12 h. The light treatments were set as follows (Table 1): (1) full spectrum acclimation conditions (FS, Figure A1), (2) 50% green and 50% red light (GR, Figure A2), (3) 50% blue and 50% red light (BR, Figure A3) and (4) 50% blue and 50% green light (BG, Figure A4). Black foil was used to cover the tanks to prevent cross illumination between ETs.

TABLE 1 | Light treatments, indicating the proportions of the different wavelengths: Blue (B), green (G), red (R) and the program settings of the Aquaillumination Hydra FiftyTwo HD (AI Hydra 52 HyperDrive, USA) lamp. Irradiance was always kept at 100 μmol photons $m^{-2} s^{-1}$.

Treatment	% Of intensity (photon flux)	Program settings
Full spectrum (FS)	16.7% each	8% all channels (except UV)
Green + red (GR)	50% G + 50% R	361% G; 140% R
Blue + red (BR)	25% RB + 25% B + 50% R	8% RB, 7% B, 140% R
Blue + green (BG)	25% RB + 25% B + 50% G	8% RB, 7% B, 361% G

2.4 | Experiment 2: Effects of Acute Cold and Warm Treatments

In total, 48 visually healthy (i.e., no signs of pitched bells or lost oral arms, etc.) *Cassiopea andromeda* specimens were used for the temperature and respiration experiments. Groups of four animals accounting for a biomass of about 50 g were placed into gas-tight Acrylic chambers (AC; V = ca. 880 mL) and acclimatized to AC conditions with an open lid overnight at baseline environment conditions.

In order to test *C. andromeda*'s response to acute temperature changes, two runs were designed with one run assigned to gradual temperature increase (T1 = 25°C–41°C) and one to gradual temperature decrease (T2 = 25°C–11°C). Two temperature-controlled tanks (each containing 70 L aerated and filtered artificial seawater; 25°C; 34.8 S_A) were set up and equipped with one respiration chamber in the control tank and four respiration chambers in the treatment tank, each chamber containing four jellyfish. Depending on the treatment, a heater or a cooler was installed to regulate the increasing or decreasing temperatures in the treatment tank. In the first 30 min, initial oxygen measurements were carried out at 25°C, subsequently the temperature in the treatment tank was changed by 1°C every half an hour, whereas the temperature in the control tank was kept constant. This experimental design was repeated twice with four replicates (four chambers; $n = 4$) for each temperature treatment and one replicate (one chamber; $n = 1$), which was kept constantly at 25°C, served as control for each degree of temperature change.

The measurements were always conducted at the same daytime. The temperature-compensated oxygen concentration (mg L^{-1}) over time (in 20 s intervals) was continuously recorded throughout the experiment by an optic oxygen meter (FireSting-O2, PyroScience, Germany).

The respiration rate (μg $g^{-1} h^{-1}$) was calculated for each degree of temperature change (1°C every 30 min). According to Kühnhold et al. (2023), in the "linear correlation between temperature and O_2 consumption, peak and minimum respiration was defined as the temperature-induced maximum

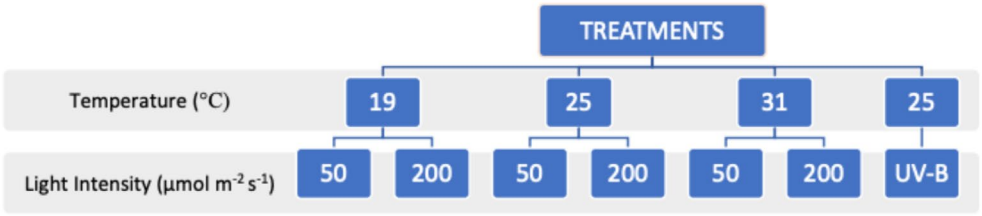

FIGURE 1 | Schematic diagram of seven treatments (plus one control treatment at 25°C and 100 µmol photons $m^{-2} s^{-1}$ photosynthetically active radiation/PAR; UV-B 290–315 nm).

(TMMR) and standard (TSMR) metabolic rates", referring to the critical warm (WT_{crit}) and cold (CT_{crit}) temperatures. Hence, the difference between TMMR and TSMR portrays the temperature-induced aerobic scope (TAS) (Kühnhold et al. 2023): TAS = TMMR − TSMR.

2.5 | Experiment 3: Effects of Cold and Warm Treatments and Different Light Intensities (Photon Flux) After Acclimatization

In total, 24 visually healthy (i.e., no signs of pitched bells or lost oral arms, etc.) *Cassiopea andromeda* specimens were used for the temperature and light treatments. The 24 specimen were randomly assigned to 8 different experimental tanks (control = 25°C and 100 µmol photons $m^{-2} s^{-1}$, three temperatures 19°C, 25°C and 31°C and two light treatments 50 and 200 µmol photons $m^{-2} s^{-1}$, plus one UV treatment). The experiment lasted three weeks, the temperature treatments (6°C) warmer and colder than control were reached in small steps of 2°C per day, that is, the final temperatures of 19°C and 31°C were reached after three days. The same acrylic chambers and respiration equipment was used, as described in experiment 3 below. Figure 1 shows a schematic diagram of the treatments.

2.6 | Physiological Parameter Measurements

The bell pulsation rate (BPR), photosynthetic efficiency (PE, maximum quantum yield of photosystem II), and wet weight (WW) were quantified for each individual *C. andromeda* medusa at the beginning (after the acclimation phase) and end of the experiment. Umbrella pulsations were counted over 15 s, and this number was extrapolated to determine the number of umbrella pulses per minute. To exclude potential stress reactions, umbrella pulsations were counted before taking the organisms out of the tanks for further analyses. *C. andromeda* were then removed by hand 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 before the variable chlorophyll *a* fluorescence measurements (Schreiber et al. 1995; Maxwell and Johnson 2000). In this way, the photosynthetic performance of the endosymbiotic dinoflagellates was determined by measuring the maximum quantum yield of photosystem II (photosynthetic efficiency; Fv/Fm), using a portable pulse amplitude modulation (PAM) chlorophyll fluorometer (Diving-PAM, Walz, Effeltrich, Germany). Subsequently, the organisms 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).

2.7 | Sampling and Preparation for Chemical Analyses

For the analyses of pigments and AOA, four *C. andromeda* were sampled after the acclimation phase, after two weeks, and after 4 weeks (at the end of the experimental period). At each of these time points, whole animals were snap-frozen in liquid N_2 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) and then ground to powder for 20 s using a benchtop homogenizer (FastPrep-24, MP Biomedicals, Germany). For the counting of endosymbiotic algae cells, ~20 mg of the lyophilized samples were resuspended in 50 µL of distilled water. For homogenization purposes, 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 (Sonotrode MS 72; SONOTRONIC Nagel GmbH, Karlsbad-Ittersbach, Germany) prior to cell counting. From each sample, a suspension volume of 1.5 mL was pipetted in a Neubauer Hemocytometer (0.1 mm depth), to count the microalgae cells in triplicate under an optical microscope (20×).

2.8 | 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 (2500 ***g***, 4°C, 5 min) and filtration (0.45 µm 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, diatoxanthin, 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 µg g^{-1} *C. andromeda* dry weight of endosymbiotic microalgae.

2.9 | 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 $ABTS^{\bullet+}$ stock solution was obtained by oxidizing 7.0 mM of $ABTS^{\bullet+}$ with potassium disulfate ($K_2S_2O_8$) for 16 h. A working solution with a consistent photometrically measured absorption of 0.7 ± 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 µL 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).

2.10 | 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 light irradiances, the different light spectra treatments were compared with one another ($n = 4$ per treatment), with the treatment that was the continuation of the acclimation condition (100 µmol photons $m^{-2}\,s^{-1}$) serving as the control for these analyses.

All 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. Figure generation was performed using ggplot 2.

3 | Results

3.1 | Effects of Different Light Spectra

3.1.1 | Detection of Light-Harvesting Pigments

The identification and quantification of the main characteristic pigments (chlorophyll *a*, chlorophyll *c2*, and the two carotenoids, peridinin and diadinoxanthin (Figure 2)) in *C. andromeda* also revealed the presence of β-carotene and diatoxanthin, but only in negligible amounts. Chlorophyll *a* and peridinin were clearly the dominant pigments in *C. andromeda* on a per jellyfish dry weight basis (between 200 and 300 µg g^{-1} DW). After four weeks of treatment with different light spectra, the green-red (GR) treatment resulted in lower concentrations of all detected pigments (Figure 2) in the jellyfish, specifically the Chl *a* and peridinin concentrations were significantly different from the other treatments.

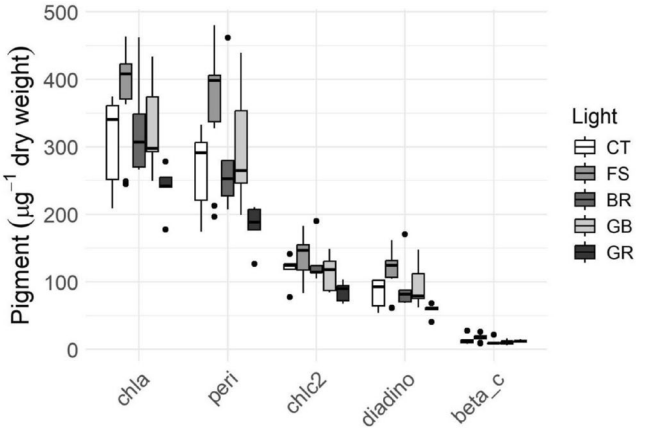

FIGURE 2 | Pigment concentration in *Cassiopea andromeda* (µg g^{-1} DW) after four weeks of treatment. beta_c = β-carotene; BR = blue-red; chla = chlorophyll *a*; chlc2 = chlorophyll c2; CT = control; diadino = diadinoxanthin; FS = full spectrum; GB = green-blue; GR = green-red; peri = peridinin.

3.1.2 | Physiological Response Parameters

The photosynthetic efficiency (PE, Fv/Fm, maximum quantum yield of photosystem II) of *C. andromeda* was in the range of 0.65–0.67 for all spectra treatments (Figure 3a). Fv/Fm values displayed a slightly higher variability for the blue-red (BR) and green-blue (GB) treatments. On the other hand, the counting of bell pulsations (bp min^{-1}) showed a clear decrease in *C. andromeda* species under the BR and green-red (GR) treatments (Figure 3b). A similar decrease was visible for the antioxidant activity AOA (TE mmol $100\,g^{-1}$ DW) in specimens under the BR and GR treatments, while the GB treatment caused a similar antioxidant performance of *C. andromeda* compared to the control (Figure 3c).

3.2 | Effects of Acute Cold and Warm Treatments

The bell pulsation rate BPR was used as a marker for the viability of *C. andromeda* (Figure 4) in acute treatments. In two experiments, three initial samples were measured once at 25°C, then temperatures were either increased or decreased, with measurements every hour.

In both experiments, one-way ANOVA analyses showed significant differences in the two treatments (Appendix A); cold experiment: $F = 101.3$, $p < 0.001$; warm experiment: $F = 64.6$, $p < 0.001$. In both experiments, the Post hoc Tukey-tests confirmed the trends apparent in Figure 4a,b: in the warm treatment, increased temperatures led to continuously significant ($p < 0.001$) reductions of bell pulsation rate in *C. andromeda* from 27°C to 41°C compared to the initial 25°C. The bell pulsation rate values (mean ± SD) of the warm treatment dropped significantly from 48.6 ± 4.7 at 25°C to 10.9 ± 1.3 at 37°C and jellyfish stopped pulsating completely from 39°C on.

In the cold treatment, decreased temperatures induced continuously significant ($p < 0.001$) reductions of pulsation rate in *C. andromeda* at every temperature degree change (23°C–11°C) compared to the initial 25°C. The bell pulsation rate values of

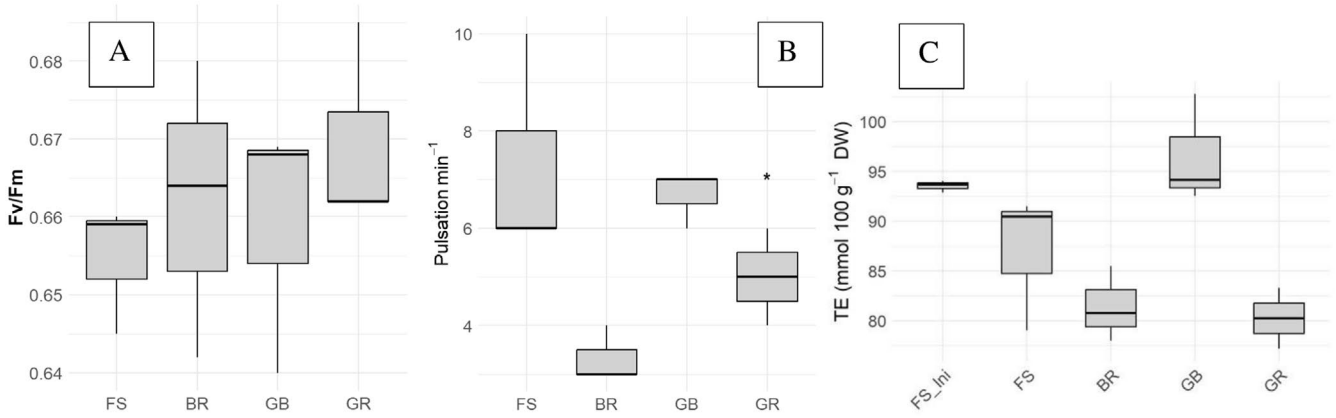

FIGURE 3 | (A) Photosynthetic efficiency (maximum quantum yield of photosystem II; Fv/Fm), (B) bell pulsations (pulsation min^{-1}) and (C) antioxidant activity (Trolox equivalents TE) of *Cassiopea andromeda* after four weeks under different treatments (BR = blue-red; CT = control; FS = full spectrum; GB = green-blue; GR = green-red).

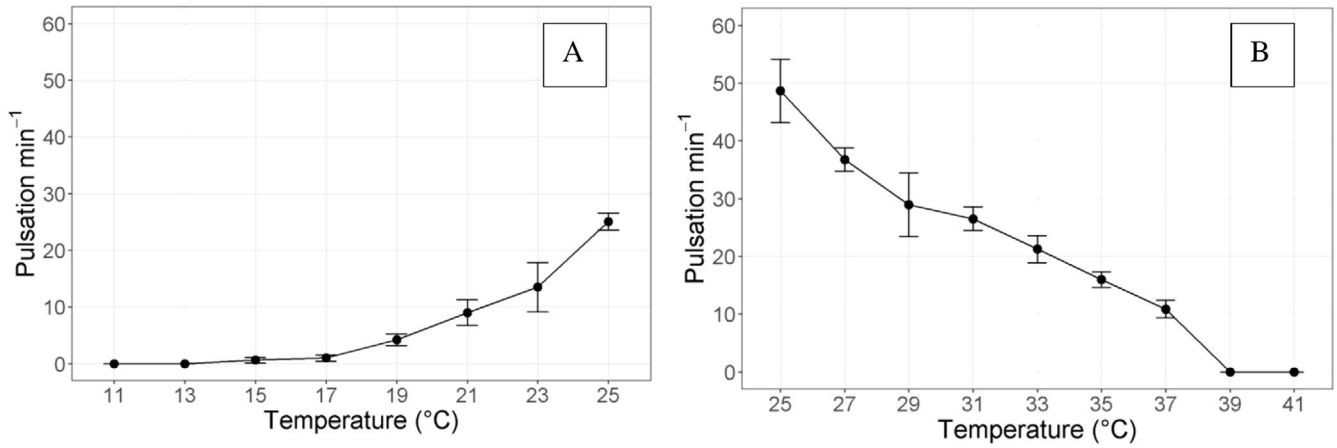

FIGURE 4 | Average (mean ± SD; $n = 4$) bell pulsation rate per minute (pulsation min^{-1}) of *Cassiopea andromeda* medusae exposed to two temperature treatments: (A) acute cold temperature decrease (25°C–11°C) and (B) acute warm temperature increase (25°C–41°C), with a 2°C change per hour.

the cold treatment dropped significantly from 25.1 ± 1.3 SD at 25°C to 1 ± 0.5 SD at 17°C and the jellyfish stopped pulsating completely from 15°C on. Overall, 15°C and 39°C, respectively, marked the lower and upper temperature thresholds of the measurements series, beyond which the animals stopped pulsating (Figure 4).

For determining the viability of algal symbionts associated with *C. andromeda*, the photo-synthetic efficiency (Fv/Fm) at acute treatments was measured (Figure 5). In two experiments (cold and warm), three initial samples were measured once at 25°C, then temperatures were either increased or decreased, with measurements every hour.

In both experiments, one-way ANOVA analyses showed significant differences in the treatments (Figure 5), cold experiment: $F = 7.1$, $p < 0.001$; warm experiment: $F = 60.4$, $p < 0.001$. From 27°C to 31°C, the maximum quantum yield values in *Cassiopea* species under the warm treatment were very similar to the value at 25°C (0.63 ± 0.005). Changes in Fv/Fm occurred beyond 31°C. The Post hoc Tukey-tests confirmed that increased temperatures led to significant ($p < 0.001$) reductions of Fv/Fm in the symbiotic algae at 39°C and 41°C compared to 25°C. After a slightly descending slope starting from ~31°C to 37°C, the Fv/Fm values dropped significantly to 0.46 ± 0.03 at 39°C and then even to 0.25 ± 0.08 at 41°C.

On the other hand, the cold treatment did not show significant changes in the range from 25°C to 17°C. Only beyond 17°C the Tukey-test exhibited a significant difference between the initial 25°C and all temperature degree changes from 17°C to 11°C ($p < 0.001$). Fv/Fm values in the cold exposed jellyfish ranged between 0.6 and 0.7 for the entire experiment.

Measurements of the respiration rate were used to determine the metabolic activity of *C. andromeda* in the acute cold and warm treatments. In two experiments (joined into one graph, Figure 6) the temperature ranged from 11°C to 41°C.

ANOVA analyses showed significant differences in the two treatments: cold experiment: $F = 32.9$, $p < 0.001$; warm experiment: $F = 17.36$, $p < 0.001$. The initial two measurements of jellyfish at 25°C revealed for both experiments a respiration rate of 14.1 to 16.2 $\mu g\, g^{-1}\, h^{-1}$. For the cold treatment, from 23°C to 15°C,

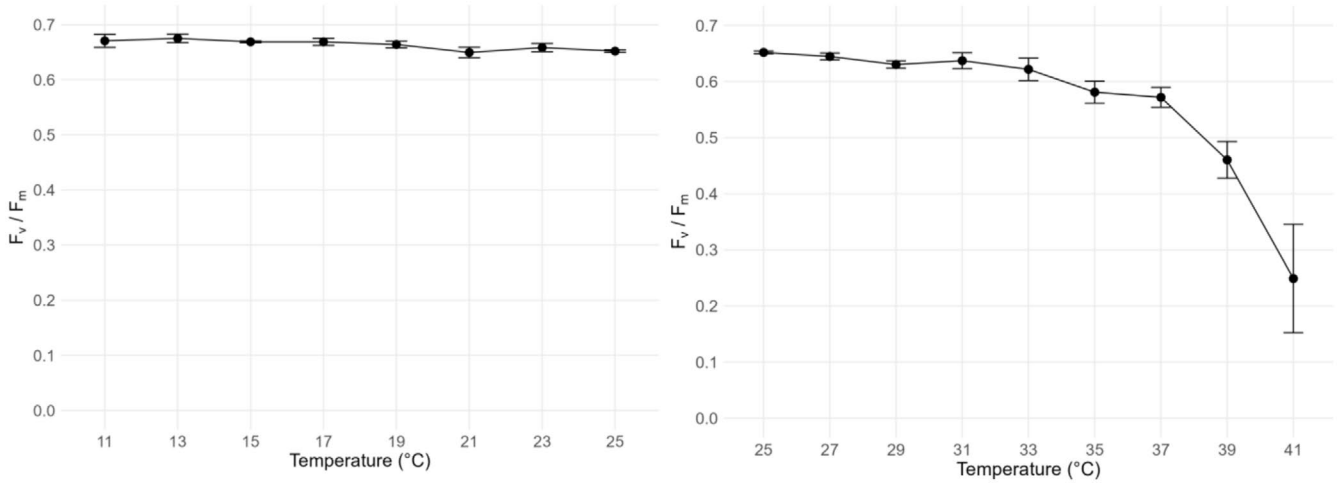

FIGURE 5 | Photosynthetic efficiency (maximum quantum yield of photosystem II; Fv/Fm, mean ± SD, $n = 4$) of the endosymbionts in *Cassiopea andromeda*, exposed to two temperature treatment experiments: Left acute cold temperature decrease (25°C–11°C) and right acute warm temperature increase (25°C–41°C), with a 2°C change per hour.

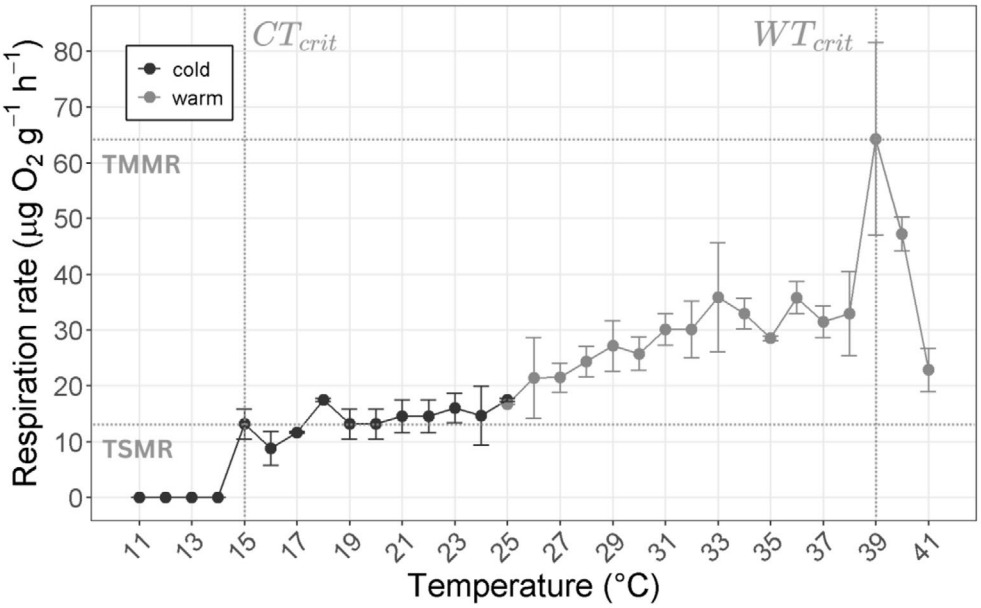

FIGURE 6 | Respiration rate (mean ± SD; $n = 4$) in *Cassiopea andromeda* exposed to two temperature treatment experiments: Left acute cold temperature decrease (25°C–11°C) and acute warm temperature increase (25°C–41°C), with a 2°C change per hour. TSMR = hypothetical temperature-induced standard and maximum metabolic rates (TMMR).

the respiration rate decreased steadily, beyond 15°C even more rapidly to values close to zero, pointing 15°C as the critical cold temperature (CTcrit) (Figure 6). At 15°C, *C. andromeda* reached its temperature-induced standard metabolic rate (TSMR) with $13.17 \pm 2.67\,\mu g\,g^{-1}\,h^{-1}$ (Table 2).

Similarly, temperature elevation led to an increasing respiration rate over the range of 27°C to 39°C. Beyond 39°C, the respiration rate dropped significantly. Temperature-induced maximal metabolic rate (TMMR) was therefore reached at 39°C at $64.30 \pm 17.3\,\mu g\,g^{-1}\,h^{-1}$, the corresponding critical warm temperature (WTcrit). The difference between mean TMMR and TSMR revealed a temperature-induced aerobic scope (TAS) of $51.13\,\mu g\,g^{-1}\,h^{-1}$ (Table 2).

3.3 | Effects of Medium-Term Temperature, Light Intensity and UV Treatments

Again, the bell pulsation rate BPR was used as a marker for the physical activity of *C. andromeda*, but this time after acclimation for three weeks. The pulsation rate increased with increasing temperature and *vice versa* (Figure 7). No statistically significant differences were noticed in the treatment of UV-B ($p = 0.188$) and at 25°C $200\,\mu mol\,m^{-2}\,s^{-1}$ ($p = 0.501$). All other treatments vs. the control at 25°C and $100\,\mu mol\,m^{-2}\,s^{-1}$ were found statistically significant ($p < 0.05$).

Again, measurements of the respiration rate were used to determine the metabolic activity of *C. andromeda* after acclimation

TABLE 2 | Respiration rates at control temperature, critical cold temperature (CT_{crit} = 15°C) and critical warm temperature (WT_{crit} = 39°C). Hypothetical temperature-induced standard (TSMR) and maximum metabolic rates (TMMR) indicate aerobic performance at CT_{crit} and WT_{crit}, respectively. The hypothetical temperature-induces aerobic scope (TAS) is calculated as the difference between TMMR and TSMR.

	Temperature (°C)	Respiration rate ($\mu g g^{-1} h^{-1}$)
Control cold	25	16.25
Control warm	25	14.10
TSMR	15	13.17 ± 2.67
TMMR	39	64 ± 17.3
TAS		51.13

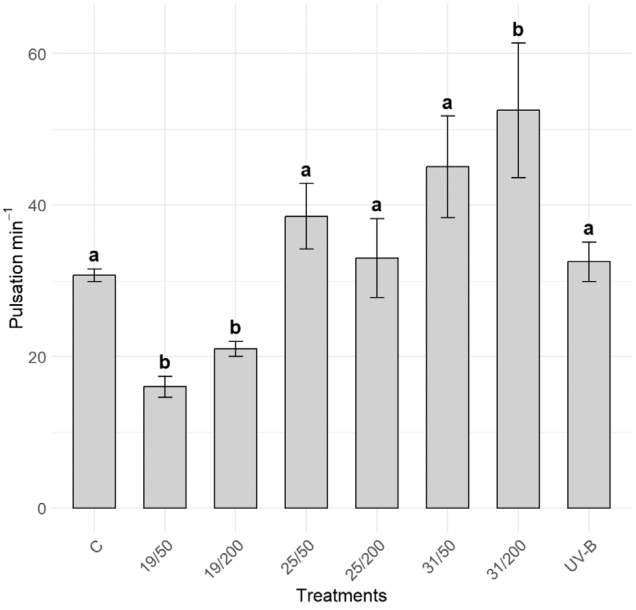

FIGURE 7 | Bell pulsation rate per minute (mean ± SD) of *Cassiopea andromeda* at different temperatures and PAR/UV treatments (n = 4). Different letters indicate significant difference ($p < 0.05$). C = control, 19, 25 and 31 refers to 19°C, 25°C and 31°C, respectively. 50, 200 refers to 50 and 200 μmol photons $m^{-2}s^{-1}$, UV-B refers to control conditions plus UV-B treatment, 280–315 nm.

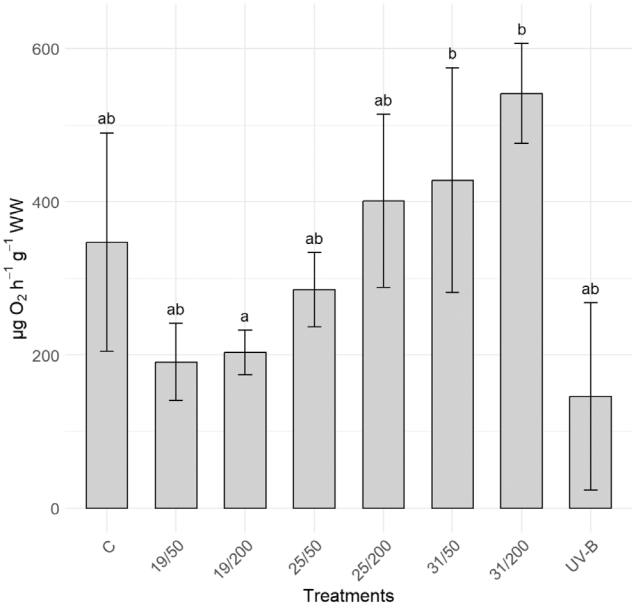

FIGURE 8 | The respiration rate (mean ± SD, n = 4) of *Cassiopea andromeda* exposed to different temperatures and photosynthetically active radiation (PAR) or UV-B radiation, respectively. Different letters indicate significant differences ($p < 0.05$) between treatments. C = control, 19, 25 and 31 refers to 19°C, 25°C and 31°C, respectively. 50, 200 refers to 50 and 200 μmol photons $m^{-2}s^{-1}$, UV-B refers to control conditions plus UV-B treatment, 280–315 nm.

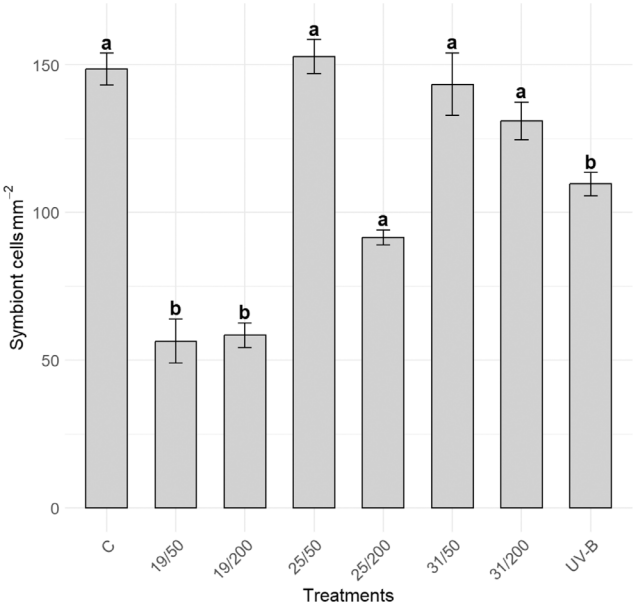

FIGURE 9 | The endosymbiont density (mean ± SD, n = 4) of *Cassiopea andromeda* under different stress treatments. C = control; 19, 25 and 31 refers to 19°C, 25°C and 31°C, respectively. 50, 200 refers to 50 and 200 μmol photons $m^{-2}s^{-1}$, UV-B refers to control conditions plus UV-B treatment, 280–315 nm.

for three weeks. The respiration rates were clearly lower in the colder (19°C) and the UV-B treatments (Figure 8). The highest respiration rate was found at the 31°C 200 μmol $m^{-2}s^{-1}$ treatment (541.15 μg O_2 $h^{-1}g^{-1}$ WW ± 65.088, mean ± SD). Only the 31°C 200 μmol $m^{-2}s^{-1}$ treatment was found statistically significant vs. control (p = 0.04). The respiration of other treatments vs. the control was not significantly different.

The endosymbionts were quantified at the end of the respiration measurements. The results showed the decrease in symbiont density for the treatments 25°C 200 μmol photons $m^{-2}s^{-1}$ and both 19°C treatments, compared to the control (Figure 9). Also, the UV treatment lowered the symbiont density. The lowest symbiont density (significantly different) was found in the 19°C treatments (both low and high PAR) treatment with 56–58 cells mm^{-2}. This is also confirmed by low photosynthetic activity at 19°C.

4 | Discussion

In this study we investigated the response of *Cassiopea andromeda* and its endosymbionts to a number of stress factors (different light spectra/wavelengths, different light intensities and different temperatures). Response parameters were photosynthetic efficiency (PE), bell pulsation rate (BPR), antioxidant activity (AOA), respiration rate, and symbiont density.

4.1 | The Effects of Different Light Spectra on *C. andromeda* Performance

In this study, the photosynthetic efficiency of *C. andromeda* symbionts confirmed the functionality of its light-harvesting pigments despite changes in light wavelengths. Pigment quantity and photosynthetic efficiency were nearly unchanged, except for green-red (GR) light. Chlorophyll *a* concentration, bell pulsation rate, and antioxidant activity (AOA) were clearly lowered under GR light conditions, compared to GB. Interestingly, the AOA under green-blue (GB) light was very similar (even slightly exceeding) the AOA of *Cassiopea* species under the full spectrum (FS) treatment.

4.2 | Pigment Composition and Antioxidants in *C. andromeda*

In the present study, the main photosynthetic pigments detected in *C. andromeda* were chlorophyll *a* and c_2 as well as the carotenoids peridinin and diadinoxanthin. This is consistent with the pigments reported from other endosymbiotic dinoflagellates (Hennige et al. 2009; Roth 2014). Also in other jellyfish holobionts, including *Cotylorhiza tuberculata* (Enrique-Navarro et al. 2022), the same pigment composition was described. Overall, the pigments chlorophyll *a* and peridinin dominated the light harvesting complex of *C. andromeda*, also confirmed by Kühnhold et al. (2023).

Overall, the biosynthesis of health-promoting pigments in *C. andromeda* is attractive, implying a strong utilization potential. As such health-promoting components are exclusively synthesized by plants and algae, the regular uptake of pigments is crucially important for the human diet. 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). Under control conditions, *C. andromeda* exhibited considerable mean levels of AOA (from 92 to 94 TE mmol $100\,g^{-1}$ DW). This is much more 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), but in a similar range to the AOA levels in different microalgae such as *Haematococcus pluvialis* (up to 197.4 TE mmol $100\,g^{-1}$; Rodríguez-Meizoso et al. 2010), *Dunaliella salina* (up to 111.8 TE mmol $100\,g^{-1}$; Herrero et al. 2006), and *Chaetoceros* spec. (102.9 TE mmol $100\,g^{-1}$), particularly in regard to superoxide radical neutralization capacity (Guzman et al. 2001). The present data highlight the great potential of *C. andromeda* as a novel source of pigments and antioxidants for biofunctional purposes. The fact that a diet rich in antioxidants has been linked with many health benefits (Halliwell 2000; Zampelas and Micha 2015) is due to the fact that antioxidants are key mediators of endogenous ROS removal. In a recent publication by De Domenico et al. (2025), where wild and reared *Cassiopea* species were compared, it was confirmed again that the most active bioactive compounds such as phenols and carotenoids, primarily derived from endosymbiotic microalgae, exhibited very strong antioxidant properties. Among those, particularly the carotenoids were highlighted for their antioxidant and anti-carcinogenic activities.

However, in the present study it was not possible to trigger the pigment synthesis with the help of different light spectra. The most energy-rich fraction of light is blue, but in the present study blue light (RB and GR) illumination led to similar pigment concentrations in *C. andromeda* specimens compared to the control.

4.3 | Acute Cold and Warm Treatments

Previous studies on endosymbiotic jellyfish have confirmed that they are less susceptible to thermal-induced bleaching and thrive in warm waters (Galil et al. 1990; AlJbour et al. 2017, 2018, 2019; Klein et al. 2019). However, the specific upper and lower temperature thresholds have not been defined yet. In addition, past experiments have rather applied long static, carefully controlled, and very slowly elevated temperature scenarios. However, based on Klein et al. (2019), the jellyfish's natural environments are often characterized by high temperature fluctuations. Therefore, in this study, acute extreme temperature stress over the course of 8 h was used to evaluate the minimum and maximum temperature thresholds of *C. andromeda*. This approach acknowledges that temperatures within coastal ecosystems can vary up to 10°C within diel cycles, i.e., in a very short time (Klein et al. 2019).

Our findings support the hypothesis that *C. andromeda* as an invasive species has a greater tolerance towards higher than lower temperatures. Specifically, 15°C and 39°C mark the lower and upper critical temperatures, which were indicated by a steep decline in the respiration rate and a stop in the bell pulsations of the jellyfish outside of the tolerated temperature range. A temperature range of 14°C between 25°C and 39°C compared to a mere 10°C difference between 25°C and 15°C supported previous studies that *C. andromeda* can withstand high thermal stress best (Klein et al. 2019).

4.4 | Combined Effects and Different Response Parameters

The high adaptability of *Cassiopea* sp. has already been described by several scientists (Mammone et al. 2021), but the combined effects of light intensity and UV in combination with temperature are not yet adequately documented. Therefore, it is necessary to look at different response parameters such as bell pulsation rate, respiration rate, pigment concentration, and symbiont density.

The bell pulsation rate as a response parameter was used as an indicator of jellyfish's health. The muscles of the bell contract and relax in a rhythm that generates the water flow around them. This movement is very vital for their oxygen

balancing, temperature regulation, and nutrition recirculation (Santhanakrishnan et al. 2012; AlJbour et al. 2017). In our results, higher temperatures increased bell pulsation, and lower temperatures significantly reduced bell pulsation. This corresponds also well with the response in respiration rates (see next paragraph). The same trend of pulsation rate was also found by AlJbour et al. (2017), in which *Cassiopea* sp. were acclimatized at 26°C and subjected to acute stress ±6°C. They found that the pulsation rate increased by 37% with the elevated temperatures and decreased by 46% at low temperatures, which is similar to our results although the acclimatization period was different. In another study by Béziat and Kunzmann (2022), an increase in the bell pulsation rate of *C. andromeda* was observed between 26°C and 32°C, but the pulsation rate decreased thereafter with increasing temperature and was lethal to the organisms at 36°C. The possible reason for the increasing bell pulsation could be the high metabolic activity and maintenance of photosynthetic symbionts (Béziat and Kunzmann 2022). Therefore, the range of 31°C–32°C may potentially serve as a marker for the point at which the photosynthetic machinery of *C. andromeda* algal symbionts gets out of balance.

All organisms need energy for their basic maintenance (Pörtner 2001), however, in elevated temperatures, the demand for energy increases and with lower temperatures the energy demand decreases. This is exactly confirmed by our study, where the lowest respiration rates (another response parameter) were observed at 19°C, while respiration rates at 31°C were slightly elevated. The wide distribution of *Cassiopea* sp., their invasive behaviour and high thermal tolerance are repeatedly confirmed (e.g., Galil et al. 1990), but their dispersion in the Mediterranean is restricted to the winter sea surface temperatures of 15°C-isotherm (Mammone et al. 2021). Also AlJbour et al. (2017) confirmed lower respiration rates at decreased temperatures.

In our study, the organisms lost pigments under both 200 μmol photons $m^{-2}s^{-1}$ treatments. In addition, C. *andromeda* specimens in the two 19°C treatments showed the lowest pigment concentrations of all treatments (significantly different).

In a study by Mammone et al. (2021) on *Cassiopea* sp. with the incubation at two different light intensities (200 and 500 μmol photons $m^{-2}s^{-1}$) no significant difference in symbiont density was found, which is contradictory to our findings. According to Wangpraseurt et al. (2017) bleaching and loss of pigments of cnidarians were mostly observed at high temperatures and light intensities, but no study of stress at lower temperatures has been reported so far.

With regard to UV treatment, it is interesting that respiration rates decreased under UV conditions, but bell pulsation rates did not seem to be affected. In this study we used UV radiation only as an additional factor, but this needs to be investigated in much more detail with modification of both intensity and duration.

5 | Conclusions

This study estimated acute temperature tolerance of the endosymbiotic jellyfish *Cassiopea andromeda* through defining critical cold (CTcrit) and critical warm (WTcrit) temperatures, at which the respiration rate discontinues and other response parameters such as bell pulsation rate cease. *C. andromeda* is a thermo-tolerant species in regards to heat stress that can withstand temperatures up to 33°C. The lower temperature limit is at 15°C, where both respiration rate and bell pulsations stop completely.

For the first time this study investigated the combined effect of temperature and light stress. As expected, bell pulsation rates and respiration rates decreased significantly with temperature. This was accompanied by a reduction of symbiont density.

The application of the latest LED lighting could be a key technology to target health-promoting ingredients derived from marine organisms, for example, through the pointed biosynthesis of functional compounds such as carotenoids. Unfortunately, we were neither able to significantly raise the pigment concentration nor the level of AOA. The potential of the utilization of LED-optimized, health-promoting food ingredients from new marine resources such as *C. andromeda* needs to be explored in more detail, particularly also with regard to the effects of soft UV treatments.

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Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Appendix A

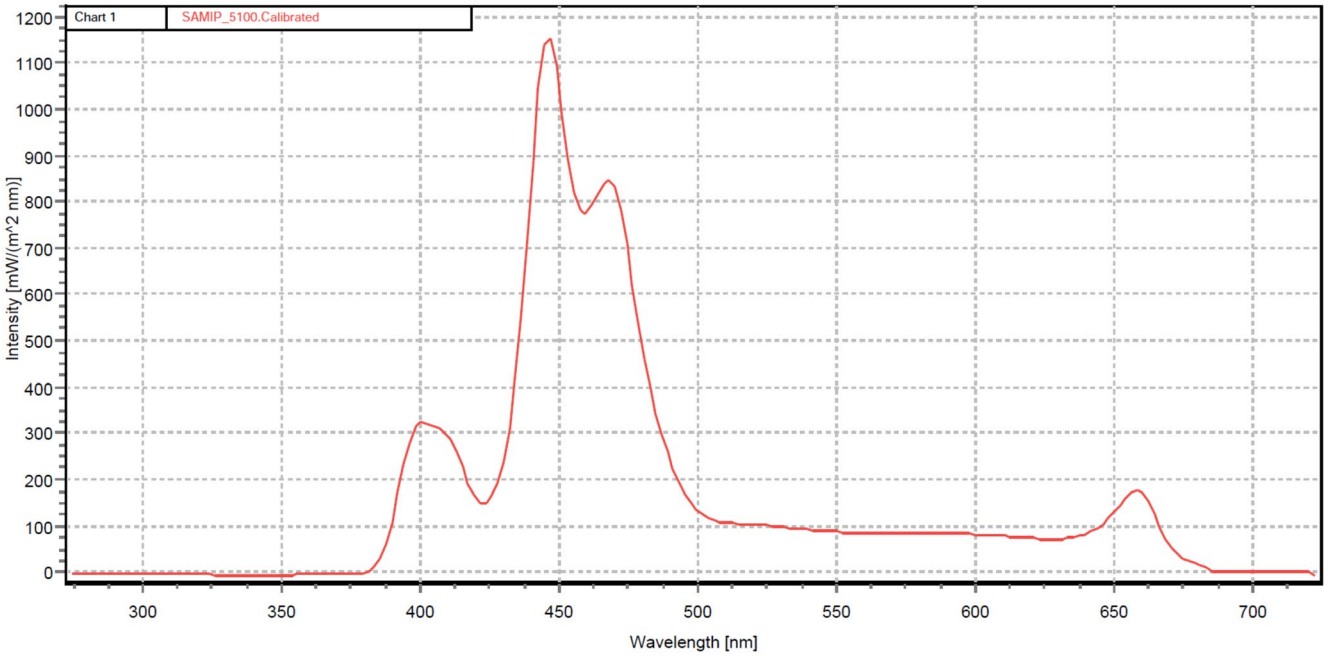

FIGURE A1 | Wavelengths profile of the full light spectrum (FS) measured by a RAMSES spectroradiometer.

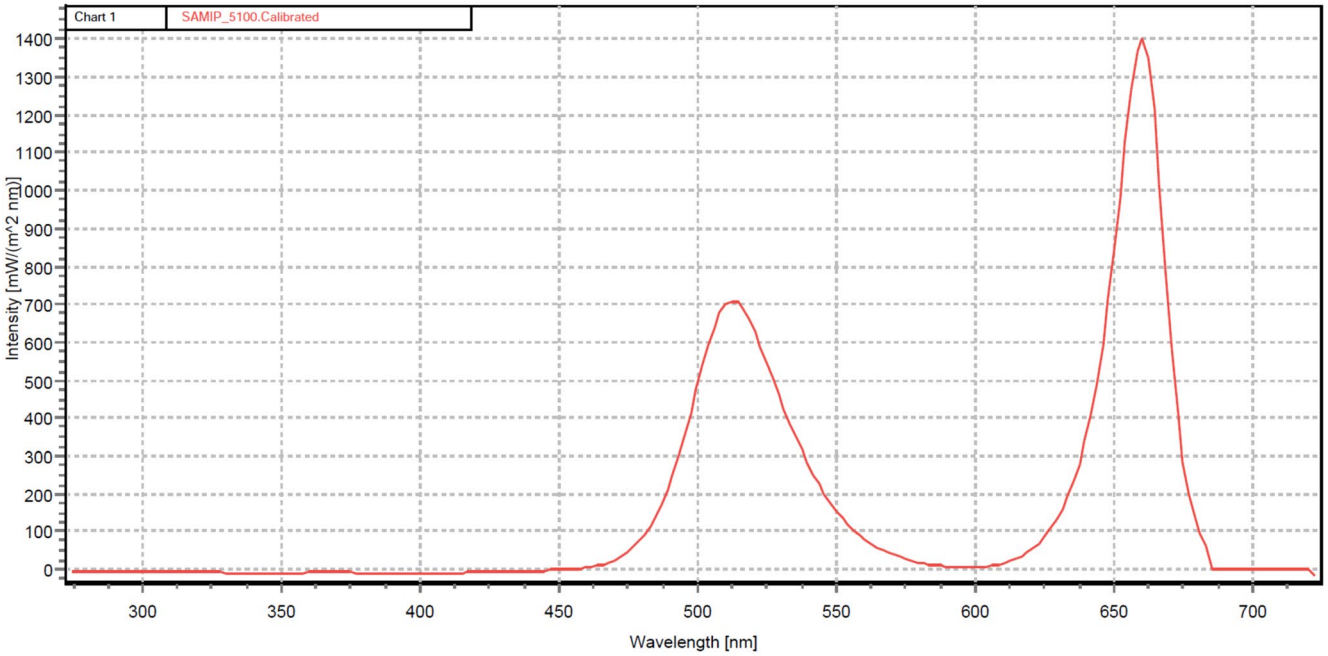

FIGURE A2 | Wavelengths profile of the GR (50% green and 50% red) spectrum measured by RAMSES.

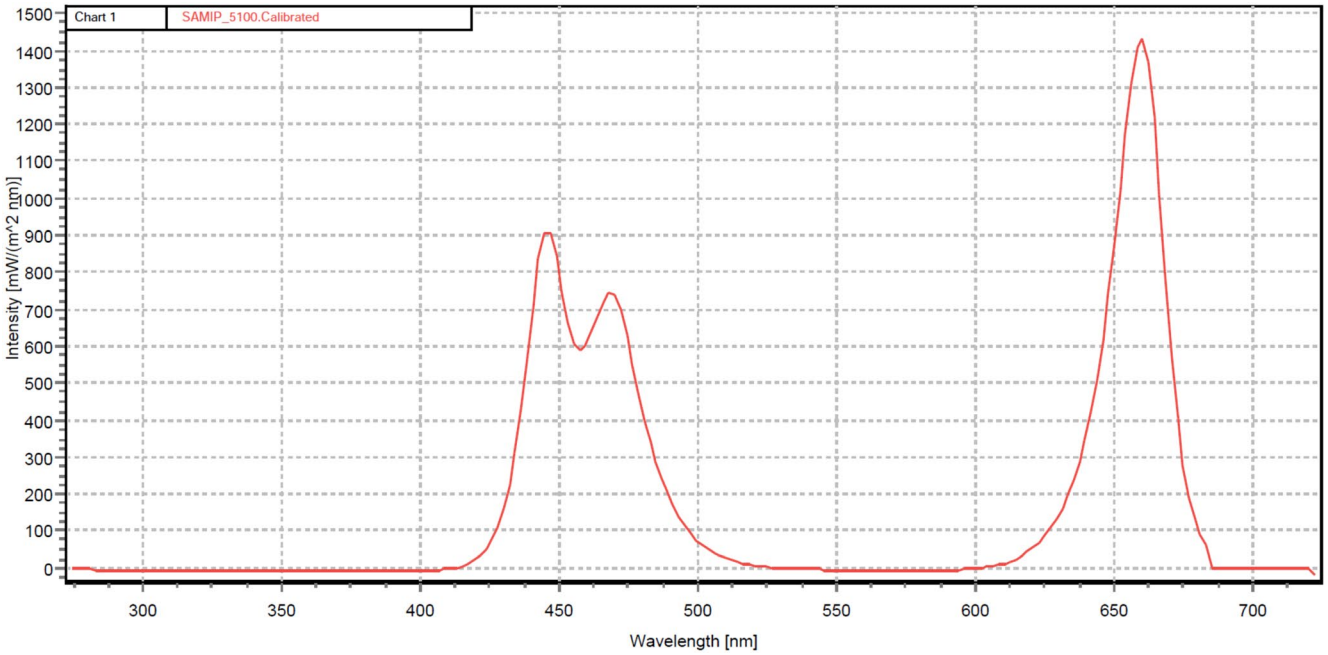

FIGURE A3 | Wavelengths profile of the BR (50% blue and 50% red) spectrum measured by RAMSES.

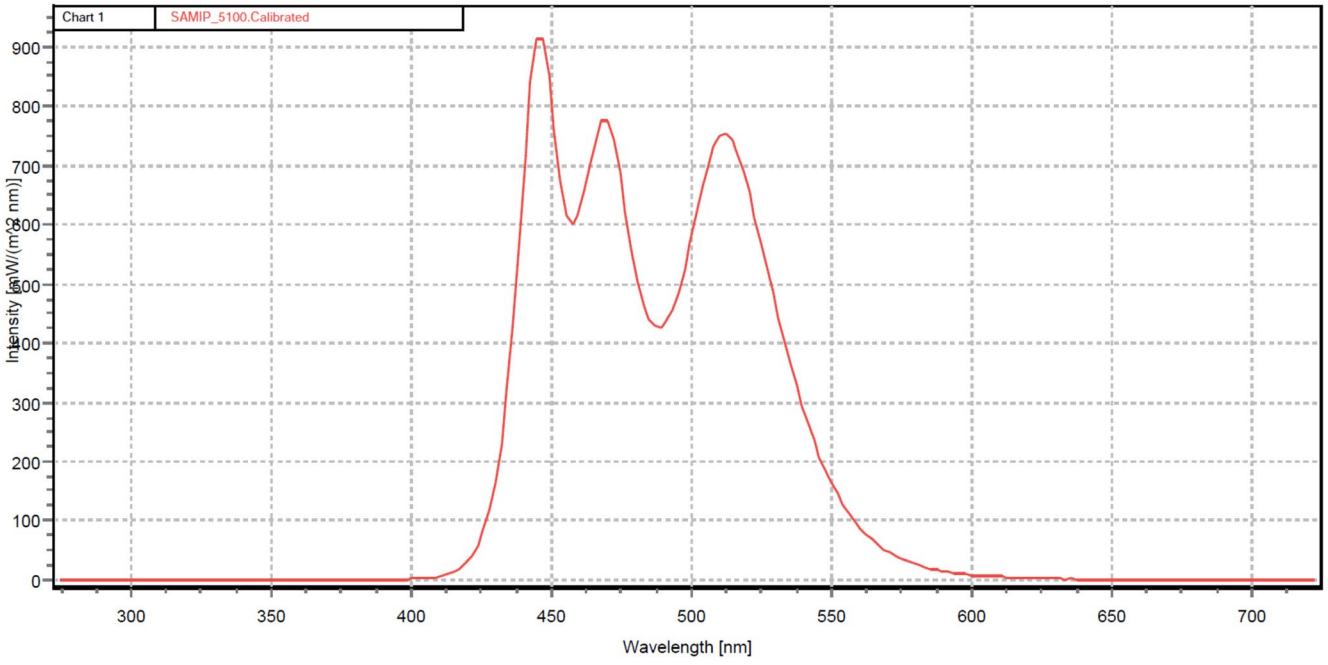

FIGURE A4 | Wavelengths profile of the BG (50% blue and 50% green) spectrum measured by RAMSES.