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Effects of light quality and temperature on the photosynthesis and pigment content of a subtidal edible red alga *Meristotheca papulosa* (Solieriaceae, Gigartinales) from Japan

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Abstract

This study investigated the effects of different light spectral qualities and temperature on the photosynthesis and pigment content of a subtidal edible red alga, *Meristotheca papulosa*. Photosynthesis–irradiance (*P–E*) experiments were carried out under red (660 nm), blue (450 nm), green (525 nm, light-emitting diodes), and white light (visible light, metal halide lamp), and at 12, 20, and 28 °C, respectively. Maximum net photosynthetic rates (NP_{max}) were highest under green light. Other *P–E* parameter estimates were similar among algae under red, blue, and green light, including their lower initial slope (α) and higher saturation irradiances (E_k) as compared to those under white light. Additionally, NP_{max} and E_k under white light were highest at 28 °C, and lowest at 12 °C with characteristic photoinhibition at irradiances greater than 150 μmol photons m^{-2} s^{-1}. Photosynthesis–temperature (*P–T*) experiment revealed that the maximum gross photosynthetic rate (GP_{max}) occurred at 22.1 °C, which was within the optimal temperature range of F_v/F_m (21.5–23.6 °C). Exposures to the different light qualities at 100 μmol photons m^{-2} s^{-1} for 7 days showed increased phycoerythrin (PE) concentration of algae under blue and green light, while chlorophyll-*a* and phycocyanin (PC) showed little variation in all light qualities. Therefore, considering future management prospects for *M. papulosa* mariculture, we suggest that green light could be utilized to enhance photosynthesis. Furthermore, if the aim is to achieve high PE content for an improved reddish-color fresh product, exposure to blue or green light could be a good alternative.

Keywords Algae · Light-emitting diode · Light quality · Photoacclimation · Photosynthesis · Photosynthetic pigment

Introduction

Meristotheca papulosa (Montagne) J. Agardh (Solieriaceae, Gigartinales) is a red alga that is widely distributed in the Indo-Pacific region, including the coastal waters of Madagascar (Silva et al. 1996), India (Rao and Gupta 2015), Australia (Watt et al. 2003), Philippines (Ang et al. 2014), Vietnam (Nguyen et al. 2013), China (Liu 2008), Korea (Lee 2008), and Japan (Yoshida et al. 2015). In Japan, this species can be found along the Pacific coast of central and southern Honshu, Shikoku, Kyushu, and Ryukyu islands, at depths of 3–30 m (Yoshida 1998; Faye et al. 2007; Lideman et al. 2012). Known as *tosaka-nori* in Japan, *M. papulosa* is a popular sea vegetable that is often used in seaweed salads and sashimi garnishes, although only natural populations have been exploited. This species has been harvested for commercial use and regional consumption in the prefectures of Kochi, Kumamoto, Miyazaki, and Kagoshima (Ohno 2004; Shinmura and Tanaka 2008); its annual production from Kagoshima alone reached 160–400 t of wet weight in 1995–

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2004 (approx. 2,000,000 US dollars; Shinmura and Tanaka 2008; Lideman et al. 2012). Because of the increasing demand for domestic *tosaka-nori* in Japan, there are concerns about overharvesting of this resource. For sustainable production of *M. papulosa*, appropriate management and the establishment of mariculture, based on an understanding of the ecophysiological characteristics of the species is essential. Initial field cultivation trials of this species were reported to be successful in Ehime Prefecture, Shikoku Island; however, commercial-scale cultivation remains elusive.

Indeed, several studies on *M. papulosa* have been conducted in Japan, concerning its vegetative and reproductive morphology (Faye et al. 2005), taxonomic features (Faye et al. 2007), callus induction, and thallus regeneration (Huang and Fujita 1997), as well as its phenology in growth and reproduction (Serisawa et al. 2000). Experimental tank culture studies (Ohno et al. 2002) and investigations related to photosynthesis and growth response of the species to ultraviolet radiation, irradiance, and temperature (Yokohama 1973; Murase et al. 1989; Maegawa et al. 1993; Lideman et al. 2011, 2012) have likewise been reported. For instance, photosynthesis experiments on *M. papulosa* using a pulse amplitude modulation (PAM)-chlorophyll fluorometer (Imaging-PAM) revealed its temperature optima for photosynthesis in the range of 18–28 °C (Lideman et al. 2012); such result was consistent with those obtained from oxygen evolution and growth experiments (Lideman et al. 2011). These studies have indeed contributed toward the elucidation of growth and photosynthesis characteristics of *M. papulosa* to establish effective techniques to conserve natural resources. However, there have been few reports of the effects of different light wavelengths on the photosynthetic efficiency, pigment content, and growth of this species (Murase et al. 2012).

Red, blue, and green light have special influence on regulating algae growth and photosynthetic pigments synthesis (Figueroa et al. 1995; Franklin et al. 2001; Tsekos et al. 2002; Godínez-Ortega et al. 2008; Wu 2016). Barufi et al. (2015) indicated red light as a possible reproductive inductor to produce tetraspores in the red alga *Gracilaria birdiae* Plastino et Oliveira (= *Crassiphycus birdiae* (Plastino et Oliveira) Gurgel, Norris et Fredericq; Gracilariaceae, Gracilariales), whereas green and blue light enhanced phycobiliprotein production. Phycobiliprotein is one important parameter to evaluate the quality of *M. papulosa* in the aspect of productivity and application. Aside from being accessory pigments that give the distinctive color and affect photosynthetic efficiency in red algae, phycobiliproteins have a variety of uses and offer interesting industrial perspectives (Sekar and Chandramohan 2008). Quality assessment of *tosaka-nori* is merely based on the appearance or color of the product, with a preference for dark-red thalli. Such alga growing subtidally at > 10 m depths was observed to have dark-red thalli, while those collected from shallow waters are yellowish-red, suggesting the influence of spectral composition on phycobiliprotein production. Understanding how the different light spectral qualities affect pigments synthesis of *M. papulosa* may assist in developing techniques to manipulate pigment composition of natural populations under controlled cultivation conditions.

The present study investigated the effects of different light spectral qualities and temperature on the photosynthetic performance, particularly on photosynthetic oxygen production and chlorophyll fluorescence of *M. papulosa*. Changes in the pigment content of the alga as subjected to the different light wavelengths were also examined.

Materials and methods

Specimen collection and maintenance

Individuals of *M. papulosa* (> 20 on each date) were collected by SCUBA from offshore of Cape Sata, Kagoshima Prefecture (31°0′ 11.5″ N, 130° 40′08″ E) at depths of 7–10 m on 13 June 2018 for oxygen evolution and chlorophyll fluorescence measurements, and from offshore of Nagashima, Kagoshima (32° 13′ 06″ N, 130° 10′ 59″ E) at same depths on 20 July 2018 for pigment analysis. Collected algae were transported to the laboratory of Kagoshima University in buckets filled with seawater at ambient temperature (c. 20 °C). Samples were held for 3 days prior to experiments in an aquarium tank (400 L) with a salinity of 33, pH of 8.0, seawater temperature of 20 °C and an irradiance of 200 μmol photons m^{-2} s^{-1} (14:10 light/dark cycle). Water motion was provided by aeration (c. 2.0 L min^{-1}). Only intact and healthy thalli were selected for the subsequent experimental treatments.

Underwater irradiance

Underwater irradiance was measured near the collection site, off the coast of Cape Sata (31° 30′ N, 130° 38′ E) between 13:34 and 13:48 on 14 July 2018 aboard the training vessel *T/S Nansei-Maru*, Kagoshima University. Measurements of downwelling irradiance below the seawater surface (1 m) and at depths of 3, 5, 10, 15, 20, 30, 40, and 50 m were taken using a 2π quantum data-logger (DEFI-L, JFE Advantech Co. Ltd., Hyogo, Japan) that was attached to a CTD. Irradiance was measured at 1 Hz, and the sampling duration was 1 min for each depth. Irradiance measurements were used to determine the extinction coefficient (K_u m^{-1}), according to Beer–Lambert equation:

$$E_{(Z)} = E_{(0)} \cdot \exp(-K_u \cdot Z) \quad (1)$$

where $E_{(Z)}$ is irradiance at the depth (Z) in meters, $E_{(0)}$ is the surface irradiance and K_u is the extinction coefficient (Cosgrove and Borowitzka 2011).

Photosynthesis–irradiance (*P–E*) experiments under different light spectral qualities

P–E experiments on *M. papulosa* were conducted under red, blue, green, and white light. The different light qualities were obtained using light-emitting diode (LED) arrays (CCS Inc., Kyoto, Japan) for red (646–664 nm [peak: 660 nm]; ISL-150X150-H4RR-SN), blue (444–467 nm [peak; 450 nm]; ISL-150X150-BB45), and green (510–543 nm [peak: 525 nm]; ISL-150X150-HGG) light, and a metal halide lamp (MHN-150D-S, Nichido Ind. Co. Ltd., Osaka, Japan) for white light. The wavelength ranges emitted by each LED array were measured with an illuminance spectrophotometer (CL-500A, Konica Minolta, Inc., Japan). Net photosynthesis (*NP*) rates were determined at 0, 30, 60, 100, 150, 200, 250, 500, and 1000 (800 in green light) μmol photons m^{-2} s^{-1} (n = 5 per irradiance level), which were obtained by appropriately layering neutral density screens between the reaction vessel and the light source. A spherical (4π) submersible quantum sensor (LI-192, LI-250A, LI-COR, USA) was used to measure irradiance. Water temperature in the reaction vessel was fixed at 20 °C using a recirculating water bath (Coolnit CL-600R, Taitec, Inc., Japan). Dissolved oxygen (DO) was measured using DO meters equipped with optical dissolved oxygen sensors (ProODO-BOD, YSI Inc., USA).

Thallus segments (c. 2–3 cm long, 1–2 cm wide) of *M. papulosa* were initially incubated overnight (12 h) with sterilized natural seawater at 20 °C in the dark. On the day of the experiment, four to five explants (0.51 ± 0.02 g SD fresh weight, g_{fw}) were randomly selected and placed in 100-mL biological oxygen demand (BOD) bottles (n = 5) containing sterilized natural seawater. The samples were acclimated to each experimental irradiance for 30 min before DO concentration (mg L^{-1}) readings were made every 5 min over a 30-min interval. Seawater medium was continuously stirred throughout the measurement to avoid boundary layer effects and was renewed after each irradiance exposure and measurement to avoid any effects that can be attributed to nutrient and dissolved carbon dioxide depletion.

The slope of the linear regression of the DO concentrations over a 30-min period was determined to estimate net photosynthesis and dark respiration rates, expressed in μg O_2 g_{fw}^{-1} min^{-1}. All rates were normalized to water volume of each BOD bottle and fresh weight of the sample.

P–E experiments at three different temperatures

P–E experiments were conducted at 12, 20, and 28 °C under white light. The three temperature treatments were assigned based on the mean seawater temperatures near the collection site (southern Kyushu–Shikoku islands) in mid-winter (February), spring or autumn (April–July/October–December), and summer (August–September; Terada et al. 2016). *Meristotheca papulosa* explants were acclimated overnight (12 h) in an incubator at each temperature treatment prior to the start of the experiment. Methods for *P–E* experiments were the same as previously described (Borlongan et al. 2017, 2018, 2019).

Photosynthesis–temperature (*P–T*) experiment

Net photosynthesis and dark respiration rates of *M. papulosa* were determined at 8 temperature treatments (i.e., 8, 12, 16, 20, 24, 28, 32, and 36 °C), with methods similar to those described in the *P–E* experiments.

Four to five thallus segments that were approximately 0.51 g_{fw} (SD ± 0.03) were placed into each BOD bottles (n = 5). They were acclimated to each temperature treatment under a constant saturating irradiance of 200 μmol photons m^{-2} s^{-1} for 30 min, followed by DO concentration measurements every 5 min for 30 min. Measurement of respiration rates (i.e., "post-illumination respiration"; Colombo-Pallotta et al. 2010; Vásquez-Elizondo and Enríquez 2016) were carried out after wrapping the BOD bottles with aluminum foil. Seawater was also renewed between temperature treatments.

Maximum quantum yield–temperature (F_v/F_m–*T*) experiment

The maximum quantum yields (maximum photochemical efficiency of photosystem II, F_v/F_m; Cosgrove and Borowitzka 2011) of *M. papulosa* were measured from 8 to 32 °C in 4 °C increments, with a Mini Imaging-PAM (Heinz Walz GmbH, Germany), as described in our recent articles (Terada et al. 2018, 2020). Sections of the thalli (c. 2–3 cm long, 1–2 cm wide) were previously incubated overnight (12 h) at 20 °C in the dark. Ten sections, which served as replicates, were then randomly assigned to each temperature treatment. F_v/F_m at 0 μmol photons m^{-2} s^{-1} was measured to provide initial values. Samples were subsequently placed in separate 500-mL flasks wrapped with aluminum foil, and were incubated in the dark at each temperature treatment for 72 h (EYELA MTI-201B, Tokyo Rikakikai Co., LTD., Japan). F_v/F_m (n = 10) at each temperature was measured every 24 h.

Photosynthetic pigment determination

To test the effect of the different light qualities on pigment content, *M. papulosa* explants were exposed to red, blue, green, and white light, respectively, for 7 days. Twenty to thirty thallus sections (c. 2–3 cm long, 1–2 cm wide) were placed in four separate 1000-mL beakers, which represent the four spectral light treatments. Irradiance was set at 100 μmol photons m^{-2} s^{-1}, while temperature was fixed at 20 °C in a water bath. Water in the beakers was continuously

stirred throughout the experimental period. Temperature and irradiance controls used were the same as previously described.

Pigment analysis was conducted upon completion of the experimental period. Ten replicates were derived from the samples exposed to each light treatment; five replicates were used for chlorophyll-*a* (chl-*a*) and phycobiliprotein measurements, respectively. Chl-*a* in the samples (0.49 ± 0.21 g_{fw}) were extracted under dark refrigeration using 10 mL of *N*,*N*-dimethylformamide (DMF) for 24 h. Phycobiliprotein pigments [phycoerythrin (PE) and phycocyanin (PC)] in samples (0.44 ± 0.16 g_{fw}) were likewise extracted under dark refrigeration using 10 mL extraction buffers (0.1 M phosphate buffer, pH = 6.8) for 24 h. Absorbance of the extracts was measured by UV-VIS spectrophotometer (DR5000, Hach Company, USA). Chl-*a* (mg g_{fw}^{-1}) was calculated according to Porra et al. (1989):

$$\text{chl}-a = \frac{12.00(Abs_{664}-Abs_{750})-3.11(Abs_{647}-Abs_{750})}{1000 \times FW} \quad (2)$$

PE and PC (mg g_{fw}^{-1}) were calculated according to Beer and Eshel (1985) and Ding et al. (2013):

$$\text{PE} = \frac{[(Abs_{564}-Abs_{592})-(Abs_{455}-Abs_{592}) \times 0.2] \times 0.12 \times 1000 \times 5}{1000 \times FW} \quad (3)$$

$$\text{PC} = \frac{[(Abs_{618}-Abs_{645})-(Abs_{592}-Abs_{645}) \times 0.15] \times 0.15 \times 1000 \times 5}{1000 \times FW} \quad (4)$$

Modeling the photosynthetic response to irradiance and temperature

Photosynthetic responses of *M. papulosa* under the different light qualities and temperatures were determined in the form of *P*–*E* curves. Calculations for photosynthetic parameters were made by fitting the data to an exponential equation (Webb et al. 1974; Jassby and Platt 1976; Platt et al. 1980; Henley 1993) that included a respiration term and a term to model the effects of photoinhibition:

$$NP = NP_{max}\left(1-exp\left(\frac{-\alpha}{NP_{max}}E\right)\right)exp\left(\frac{-\beta}{NP_{max}}E\right)-R_d \quad (5)$$

where NP is the net photosynthetic rate, NP_{max} is the maximum net photosynthetic rate, α is the initial slope of the *P*–*E* curve, R_d is the respiration rate, and E is the incident irradiance. β is a parameter to model the effects of photoinhibition and is set to 0 under conditions of no photoinhibition. Estimates for saturation irradiance (E_k) and compensation irradiance (E_c) were derived from the parameters, where $E_k = NP_{max}/\alpha$; and $E_c = NP_{max}ln\left(\frac{NP_{max}}{(NP_{max}-R_d)}\right)/\alpha$ when β is 0.

The responses of gross photosynthesis and F_v/F_m to temperature were analyzed by fitting the data to a peaked-Arrhenius model (Alexandrov and Yamagata 2007; Eq. 6), which had the form:

$$y = \frac{y_{max}\cdot H_d \cdot exp\left(\frac{H_a\cdot(K-K_{opt})}{K\cdot R\cdot K_{opt}}\right)}{\left(H_d-H_a\cdot\left(1-exp\left(H_d\cdot\frac{(K-K_{opt})}{(K\cdot R\cdot K_{opt})}\right)\right)\right)} \quad (6)$$

where y is the response variable, which can either be the gross photosynthetic rate or F_v/F_m, and K is temperature in Kelvin. There are four parameters in this model: y_{max} is a scaling parameter to fit the model to the range of y; K_{opt} is the absolute temperature where y is maximized; H_a is the activation energy in kJ mol^{-1}; and H_d is the deactivation energy in kJ mol^{-1}. R in this model is the ideal gas constant, with a value of 8.314 J mol^{-1}. The optimal value of y_{opt} at K_{opt} can be determined by substituting K_{opt} into the equation. The gross photosynthesis rate, which is assumed as a hidden state revealed by the model (Eq. 6), was estimated by simultaneously fitting the measured dark respiration rates to the Arrhenius equation (Eq. 7), and the observed net photosynthesis rates to the difference in Eq. 6 and Eq. 7. Gross photosynthesis rates were estimated by assuming that respiration rates after light pre-incubation were a good proxy for "kinetically limited" mitochondrial respiration, wherein oxygen is not a limiting factor in the process (Colombo-Pallotta et al. 2010). R_m is the respiration rate at the mean temperature (i.e., 22 °C; $K_m = 295.15$) and E_a is the activation energy. Simultaneous model fittings and determination of model parameters for Eq. 6 and 7 were carried out using a Bayesian approach, with appropriate prior probability distributions assigned to the parameters.

$$R_d = R_m exp\left(-\frac{E_a}{R}\left(\frac{1}{\mathrm{K}-K_m}\right)\right) \quad (7)$$

In the case of F_v/F_m, the expected values were assumed to be beta distributed, given that F_v/F_m is a ratio that is bounded by 0 and 1.

Statistical analysis

Statistical analyses were done using RStudio version 3.6.0 (R Development Core Team 2019), and Bayesian model fittings using RStan version 2.18.9 (Stan Development Team 2019). RStan primarily uses a variant of a Hamiltonian Monte Carlo sampler to construct the posterior distributions of the parameters; and four chains of at least 500,000 samples/ chain were

generated and assessed for convergence, which provided at least 1000 samples of each of the parameters of interest.

One-way ANOVA and Tukey's HSD test were used to analyze differences among spectral light treatments for each photosynthetic pigment, and the significance level was set at 0.05.

Results

Underwater irradiance in the habitat

On 2018 July 14, underwater irradiance measured offshore of Cape Sata ranged from 1382 ± 261 μmol photons m^{-2} s^{-1} (mean ± SD) at 1 m to 21 ± 1 μmol photons m^{-2} s^{-1} at 50 m (Supplementary Fig. 1). Meanwhile, irradiance at the seawater surface was 2046 ± 16 μmol photons m^{-2} s^{-1}. The skies were clear at the study site during measurement. The Beer–Lambert equation was fitted to the irradiance data using a linear regression on the log-transformed irradiances; the extinction coefficient (K_u m^{-1}) was 0.082 m^{-1}. Underwater irradiance at depths where *M. papulosa* samples are generally found were estimated based on these parameters. Estimated maximum irradiance in the habitat of this species ranged from 175 (at 30 m) to 1600 μmol photons m^{-2} s^{-1} (at 3 m).

P–E curves of *M. papulosa* under the different light spectral qualities

P–E curves under red, blue, green, and white light showed a typical hyperbolic shape with increases in *NP* rates at low irradiance until saturation at higher levels (Fig. 1). Photoinhibition was not observed on all light treatments; neither a decline in the convexity of the *P–E* curves nor a decrease in quantum yields of oxygen evolution (β) was found up to 1000 μmol photons m^{-2} s^{-1}. At 20 °C, *NP* rates of *M. papulosa* under red light rose from − 0.26 ± .016 μg O_2 g_{fw}^{-1} min^{-1} (mean ± SD) at 0 μmol photons m^{-2} s^{-1} to 6.58 ± 1.57 μg O_2 g_{fw}^{-1} min^{-1} at 1000 μmol photons m^{-2} s^{-1} (Fig. 1a), whereas *M. papulosa* under blue light had *NP* rates ranging from − 0.37 ± 0.15 to 5.77 ± 1.30 μg O_2 g_{fw}^{-1} min^{-1} (Fig. 1b). Highest *NP* rates were recorded for samples under green light, which reached 7.77 ± 0.46 μg O_2 g_{fw}^{-1} min^{-1} at 800 μmol photons m^{-2} s^{-1} (Fig. 1c). As for samples under white light, their *NP* rates increased from − 0.34 ± 0.06 at 0 μmol photons m^{-2} s^{-1} to 5.92 ± 0.62 μg O_2 g_{fw}^{-1} min^{-1} at 1000 μmol photons m^{-2} s^{-1} (Fig. 1d).

The parameter estimates which describe the significant features of each *P–E* curve are shown in Table 1. Maximum net photosynthetic rate (NP_{max}) was highest under green light (8.36 μg O_2 g_{fw}^{-1} min^{-1}). Other *P–E* parameter estimates were similar among algae under red, blue, and green light; their initial slopes (α) were 0.03, 0.02, and 0.04 μg O_2 g_{fw}^{-1} min^{-1} (μmol photons m^{-2} s^{-1}) $^{-1}$, respectively. As for *M. papulosa* under white light, α was slightly higher at 0.07 μg O_2 g_{fw}^{-1} min^{-1} (μmol photons m^{-2} s^{-1}) $^{-1}$. Thus, its saturation irradiance (E_k = 97 μmol photons m^{-2} s^{-1}) was lower compared to other spectral light treatments (208–316 μmol photons m^{-2} s^{-1}).

P–E curves of *M. papulosa* at three different temperatures

NP rates of *M. papulosa* at 12 °C were − 0.40 ± 0.10 μg O_2 g_{fw}^{-1} min^{-1} (mean ± SD) at 0 μmol photons m^{-2} s^{-1} and 1.80 ± 0.16 μg O_2 g_{fw}^{-1} min^{-1} at 150 μmol photons m^{-2} s^{-1}. Rates declined thereafter to 0.67 ± 0.15 μg O_2 g_{fw}^{-1} min^{-1} at 1000 μmol photons m^{-2} s^{-1} (Fig. 2a). On one hand, *NP* rates were highest at 28 °C, which ranged from − 1.18 ± 0.13 μg O_2 g_{fw}^{-1} min^{-1} at 0 μmol photons m^{-2} s^{-1} to 8.27 ± 1.54 μg O_2 g_{fw}^{-1} min^{-1} at 1000 μmol photons m^{-2} s^{-1} (Fig. 2c).

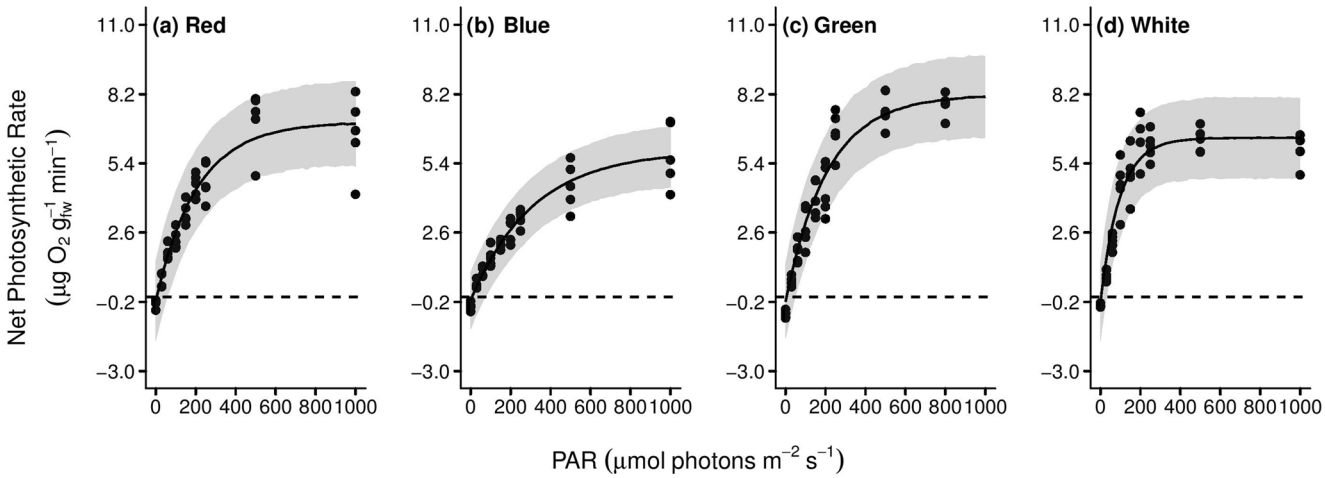

Fig. 1 Photosynthesis–irradiance (*P–E*) curves of *Meristotheca papulosa* under **a** red, **b** blue, **c** green, and **d** white light at 20 °C. Dots indicate measured rates (n = 5), and lines indicate expected values, and shaded regions indicate the 95% Bayesian prediction interval (BPI) of the model

Table 1 Mean and 95% Bayesian prediction intervals (95% BPI) of *P–E* parameters of *M. papulosa* under red, blue, green, and white light at 20 °C. NP_{max} = maximum net photosynthesis (μg O_2 g_{fw}^{-1} min^{-1}); α = initial slope [μg O_2 g_{fw}^{-1} min^{-1} (μmol photons m^{-2} s^{-1}) $^{-1}$]; R_d = respiration rate (μg O_2 g_{fw}^{-1} min^{-1}); E_c = compensation irradiance (μmol photons m^{-2} s^{-1}); E_k = saturation irradiance (μmol photons m^{-2} s^{-1}); β = photoinhibition constant

	Red		Blue		Green		White	
Parameter	Mean	95% BPI	Mean	95% BPI	Mean	95% BPI	Mean	95% BPI
NP_{max}	7.22	6.59–7.87	6.06	5.45–6.76	8.36	7.71–9.09	6.61	6.15–7.09
α	0.03	0.03–0.04	0.02	0.02–0.02	0.04	0.03–0.05	0.07	0.06–0.08
R_d	0.15	0.01–0.32	0.13	0.01–0.29	0.18	0.02–0.36	0.17	0.02–0.36
E_c	4	0–9	7	1–14	5	2–9	2	0–5
E_k	208	170–254	316	249–400	211	174–254	97	79–117
β	–	–	–	–	–	–	–	–

The *P–E* curves indicated that the lowest NP_{max} was observed at 12 °C (2.43 μg O_2 g_{fw}^{-1} min^{-1}), and the highest at 28 °C (9.58 μg O_2 g_{fw}^{-1} min^{-1}). *P–E* curve at 12 °C also depicted photoinhibition ($\beta = -0.002$), which occurred at irradiances greater than 150 μmol photons m^{-2} s^{-1}. α did not differ greatly among the three temperature treatments at 0.05–0.09 μg O_2 g_{fw}^{-1} min^{-1} (μmol photons m^{-2} s^{-1}) $^{-1}$. E_k levels increased with rise in temperature treatments, from 28 μmol photons m^{-2} s^{-1} at 12 °C to 212 μmol photons m^{-2} s^{-1} at 28 °C. Other model parameter estimates are presented in Table 2.

Effect of temperature on photosynthesis and dark respiration rates

Photosynthetic response of *M. papulosa* to temperature gradients depicted a characteristic bell-shaped curve (Fig. 3a); measured *NP* rates were low at 8 °C (0.61 ± 0.12 μg O_2 g_{fw}^{-1} min^{-1}), peaked at 20 °C (5.90 ± 1.69 μg O_2 g_{fw}^{-1} min^{-1}), and then declined with rising temperature to as low as − 2.11 ± 0.85 μg O_2 g_{fw}^{-1} min^{-1} at 36 °C.

Maximum gross photosynthetic rate (GP_{max}) was estimated to be 7.05 μg O_2 g_{fw}^{-1} min^{-1} [6.40–7.75 μg O_2 g_{fw}^{-1} min^{-1}, 95% Bayesian prediction interval (BPI)] at 22.1 °C (GPT_{opt}; Fig. 3b). The activation (H_a) and deactivation (H_d) energies were 107 (74–150, 95% BPI) and 279 kJ mol^{-1} (235–336, 95% BPI), respectively.

Dark respiration rates increased from 0.35 ± 0.19 μg O_2 g_{fw}^{-1} min^{-1} at 8 °C to 1.09 ± 0.13 μg O_2 g_{fw}^{-1} min^{-1} at 36 °C (Fig. 3c). The respiration rate at mean temperature of 22 °C (R_{22}) was 0.77 μg O_2 g_{fw}^{-1} min^{-1} (0.66–0.89, 95% BPI), with an activation energy (E_a) of 44 kJ mol^{-1} (33–56, 95% BPI).

Effect of temperature on F_v/F_m

Measured F_v/F_m of *M. papulosa* were relatively low (< 0.5) and variable across temperature gradients (8–32 °C)

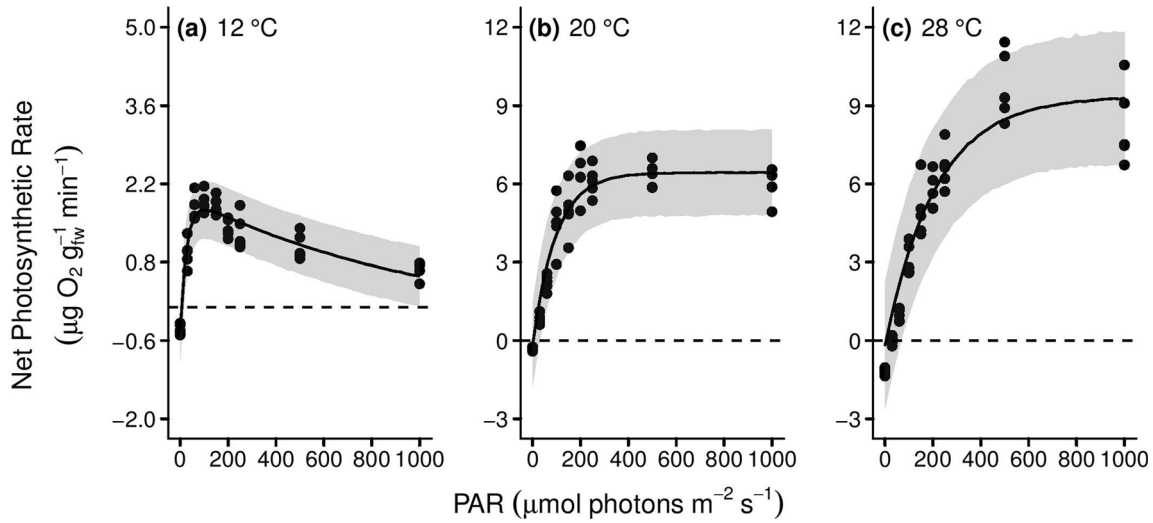

Fig. 2 *P–E* curves of *Meristotheca papulosa* at **a** 12, **b** 20, and **c** 28 °C. See the caption in Fig. 1 for the details

Table 2 Mean and 95% BPI of *P–E* parameters of *M. papulosa* at 12, 20, and 28 °C. See caption of Table 1 for the details

	12 °C		20 °C		28 °C	
Parameter	Mean	95% BPI	Mean	95% BPI	Mean	95% BPI
NP_{max}	2.43	2.15–2.71	6.61	6.15–7.07	9.58	8.66–10.55
α	0.09	0.07–0.12	0.07	0.06–0.08	0.05	0.04–0.05
R_d	0.41	0.18–0.64	0.17	0.02–0.35	0.20	0.04–0.38
E_c	5	2–7	2	0–5	4	1–8
E_k	28	21–36	97	79–116	212	170–263
β	0.002	0.001–0.003	–	–	–	–

throughout the 72-h exposure period. Nevertheless, its response pattern appears to be represented by a bell-shaped curve (Fig. 4), similar to net photosynthesis. Parameter estimates of the F_v/F_m–T model indicated the maximum F_v/F_m of 0.32 at 23.6 °C (T_{opt}), activation energy of 78 kJ mol^{-1}, and deactivation energy of 231 kJ mol^{-1} in samples exposed for 72 h. Model parameter estimates in *M. papulosa* after 24- and 48-h temperature exposures are presented in Table 3.

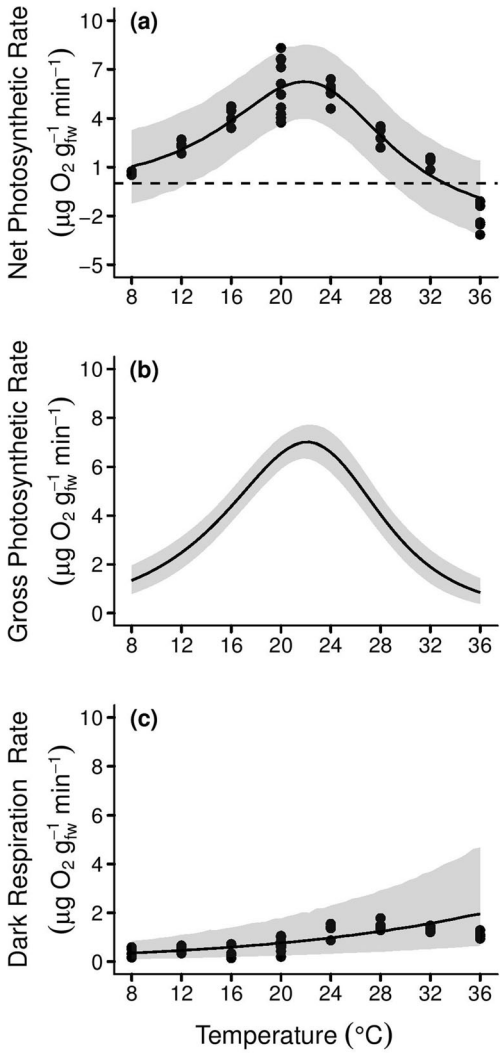

Fig. 3 Oxygenic photosynthesis and dark respiration responses of *Meristotheca papulosa* to temperature. **a** Net photosynthetic rates determined at 200 µmol photons m^{-2} s^{-1}. **b** Modeled gross photosynthetic rates at 200 µmol photons m^{-2} s^{-1}. Data were derived from the model curve of net photosynthesis and dark respiration. **c** Dark respiration rates determined at 0 µmol photons m^{-2} s^{-1}. See the caption in Fig. 1 for the details

Effect of different light qualities on pigment content of *M. papulosa*

Pigment contents of *M. papulosa* after exposure to the different spectral light treatments are summarized in Fig. 5. Results of the ANOVA for photosynthetic pigments are presented in Table 4. Higher PE contents were observed in thalli exposed to blue (0.048 ± 0.027 mg g_{fw}^{-1}) and green (0.049 ± 0.021 mg g_{fw}^{-1}) light. PE levels under red and white light were 0.003 ± 0.002 and 0.010 ± 0.003 mg g_{fw}^{-1}, respectively. Chl-*a* contents did not greatly differ among samples exposed to the four light treatments, with mean values ranging from 0.012 to 0.016 mg g_{fw}^{-1}. Slight increase in PC level was observed in blue (0.005 ± 0.002 mg g_{fw}^{-1}) and green (0.004 ± 0.001 mg g_{fw}^{-1}) light, when compared to red (0.002 ± 0.001 mg g_{fw}^{-1}) and white (0.002 ± 0.001 mg g_{fw}^{-1}) light.

Discussion

In this study, it is shown that *M. papulosa* were able to adjust their photosynthetic performance to accommodate various light spectra. *P–E* responses of this alga varied among the four light qualities; however, we interpreted these results with caution, as oxygen evolution experiments in the present study were conducted under short-term exposures (c. 1 h). Results revealed that a "stimulatory" effect was observed under green light, as shown by the higher *NP* rates compared to other light qualities. This response could have resulted from the absorption of green light by phycobiliproteins in phycobilisomes associated with *PSII*, which in turn transfer the collected energy to chlorophyll reaction centers for photosynthesis (Dumay et al. 2014). Although the minimum irradiance

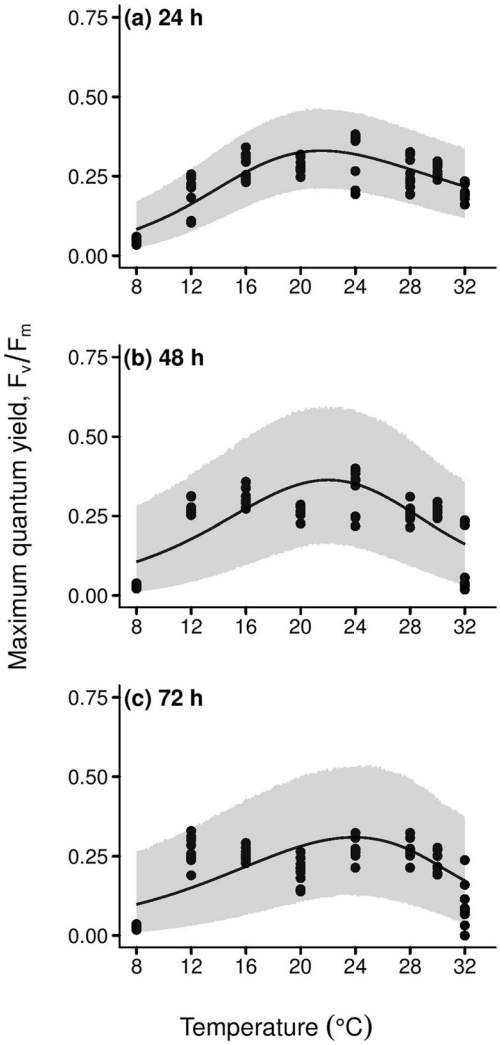

Fig. 4 Maximum quantum yield (F_v/F_m) responses of *Meristotheca papulosa* to seven different temperatures after **a** 24, **b** 48, and **c** 72 h without light. Dots indicate the measured values ($n = 10$), lines indicate the expected value, and shaded regions indicate the 95% BPI

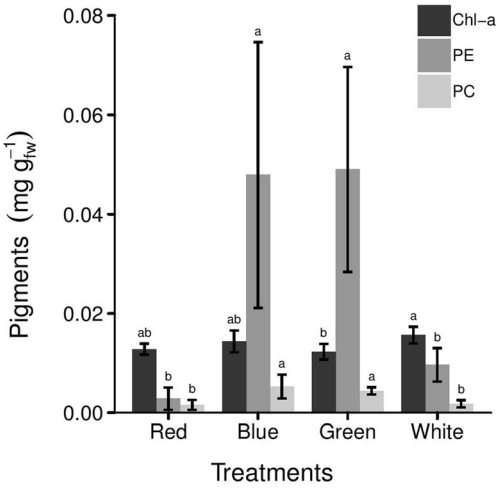

Fig. 5 Chlorophyll-*a* (chl-*a*), phycoerythrin (PE), and phycocyanin (PC) contents of *Meristotheca papulosa* after exposure to the different spectral light treatments for 7 days. Data are expressed as mean ± SD ($n = 5$). Error bars are standard deviations. Different letters indicate statistical significance between spectral light treatments ($P < 0.05$)

requirements (E_c) did not greatly differ among the spectral light treatments, α (quantum yield of oxygen evolution) was slightly lower under red, blue, and green light, resulting in higher saturation irradiances (E_k) when compared to white light. Such distinct light responses suggest the acclimation potential of the alga to spectral irradiance, corresponding to the spectrum distribution occurring in deep coastal waters. Indeed, *M. papulosa* occurs in the upper and middle subtidal zones between 3 and 30-m depths (Lideman et al. 2012), where blue and green light prevails. Photoacclimation of *M. papulosa* to green light may also be related to a change in the structure of its phycobilisomes. Ohki and Fujita (1992) reported that the phycobilisomes of a cyanobacterium, *Phormidium* sp. (Oscillatoriales) acclimated to green light were twice the size as those cells acclimated to red light; these changes in the phycobilisome structure occurred during chromatic adaptation of this marine cyanophyte. Other ways in which macroalgae can achieve acclimation include adjustment of the photosynthetic apparatus itself via changes of the reaction center ratio, or changes in the relative content of light

Table 3 Mean and 95% BPI of the parameters estimated for the F_v/F_m–temperature model in *M. papulosa* exposed for 24, 48, and 72 h. $F_v/F_{m\ (max)}$ = maximum quantum yield; H_a = activation energy for photosynthesis (kJ mol^{-1}); H_d = deactivation energy (kJ mol^{-1}); T_{opt} = optimum temperature (°C)

	24 h		48 h		72 h	
Parameter	Mean	95% BPI	Mean	95% BPI	Mean	95% BPI
$F_v/F_{m\ (max)}$	0.33	0.31–0.36	0.37	0.33–0.42	0.32	0.27–0.37
H_a	136	95–178	94	54–146	78	44–138
H_d	187	163–215	221	174–335	231	149–451
T_{opt}	21.5	20.2–22.9	21.9	19.6–24.7	23.6	20.5–26.6

Table 4 One-way ANOVA results for photosynthetic pigments in *M. papulosa* after exposure to the different light spectral qualities for 7 days

Source of variation	*df*	SS	*F* value	*P* value
Chl-*a*				
Between groups (light quality)	3	< 0.0001	4.06	< 0.05
Residual	16	< 0.0001		
PE				
Between groups (light quality)	3	0.00858	10.95	< 0.05
Residual	15	0.00392		
PC				
Between groups (light quality)	3	< 0.0001	9.45	< 0.05
Residual	15	< 0.0001		

protective pigments; all of these mechanisms influence primarily pigment ratios of the algae (Marquardt et al. 2010). On one hand, the higher growth rates of a red alga, *Pyropia haitanensis* (Chang et Zheng) Kikuch et Miyata (Bangiaceae, Bangiales), under blue, green, and white light were associated with increase in the photosynthetic efficiency of the alga, as evidenced by their higher $rETR_{max}$ (photochemical electron transport rate), qP (photochemical quenching), F_v/F_m, and α (Wu 2016). Studies on longer time-scales along with chlorophyll fluorescence measurements must be carried out for a more realistic assessment of how *M. papulosa* achieve "physiological" acclimation to the light climate (including irradiance and light quality) they are subjected to in nature. Implications of their physiological versus morphological photoacclimation strategies could provide insights for future management of mariculture of this species.

Nevertheless, the effects of the different light qualities on PE content of *M. papulosa* presented higher effect in blue and green light treatments, which was consistent with the results in *P–E* experiments, particularly under green light. Such increase in PE could be ascribed to acclimation in blue and green light spectra, as well as to improved energy absorption to make up for the absence of other light qualities that are usually absorbed by chlorophyll. Higher PE (and PC) contents were likewise found in several red algae under blue and green light [e.g., *Chondrus crispus* Stackhouse (Gigartinaceae, Gigartinales), *Corallina elongata* Ellis et Solander (Corallinaceae, Corallinales), *Plocamium cartilagineum* (Linnaeus) Dixon (Plocamiaceae, Plocamiales), *Porphyra umbilicalis* Kützing, *Pyropia leucosticta* (Thuret) Neefus et Brodie, *P. haitanensis* (Bangiaceae, Bangiales), and *G. birdiae*] (López-Figueroa and Niell 1989; Figueroa et al. 1995; Franklin et al. 2001; Tsekos et al. 2002; Barufi et al. 2015; Wu 2016). However, chl-*a* and PC contents of *M. papulosa* in the present study showed little variation in all light qualities. Our results differed from those of Kim et al. (2015) that showed increased chlorophyll concentration, hence superior growth rates in green and red + blue light-grown *Gracilaria tikvahiae* McLachlan (Gracilariaceae, Gracilariales); phycobiliprotein synthesis also seemed to be stimulated in parallel with chlorophyll synthesis. Higher chl-*a* were observed in *P. haitanensis* grown under blue and white light, but chl-*a* content decreased when the thalli were grown under red light; these results matched with their relative growth rates (Wu 2016). Nonetheless, the manifestation of the various types of photopigments, and their arrangement in the thylakoid membranes (Gantt 1981; Dumay et al. 2014) are responsible for the different photosynthetic efficiencies at various light spectra, which affect the overall photosynthetic performance of macroalgae. The high PE and PC contents in *M. papulosa* suggest enhanced production in pigment proteins by blue and green light. This response could also be considered as a photoprotection mechanism related to energy dissipation, similar to the elevated content of carotenoids and xanthophyll pigments in red algae *G. birdiae* (Ursi et al. 2003) and *Gracilaria tenuistipitata* var. *liui* Zhang et Xia (= *Agarophyton tenuistipitatum* (Chang et Xia) Gurgel, Norris et Fredericq; Gracilariaceae, Gracilariales) (Barufi et al. 2011). The sublittoral kelp *Laminaria saccharina* (Linnaeus) Lamouroux (= *Saccharina latissima* (Linnaeus) Lane, Mayes, Druehl et Saunders; Laminariaceae, Laminariales) was also shown to hold large amounts xanthophyll pigments to minimize photoinhibition during the high irradiance periods of spring (Gevaert et al. 2002). Several red algae including *M. papulosa* were found to have seasonal changes in thallus color, with "yellowing" being primarily dependent on nitrogen level as a material base of phycoerythrin, and secondarily on light condition in the sunlit bottom (Kobayashi and Fujita 2014). Pigment synthesis is driven by light, and is regulated by various photoreceptors for absorption of different light qualities (Rüdiger and López-Figueroa 1992). Green light effects on chlorophyll synthesis in red algae *C. crispus*, *Halymenia floresii* (Clemente) C. Agardh (Halymeniaceae, Halymeniales), and the brown alga *Desmarestia aculeata* (Linnaeus) Lamouroux (Desmarestiaceae, Desmarestiales), as well as on protein synthesis in the green alga *Ulva rigida* C. Agardh (Ulvaceae, Ulvales) were pointed to a possible coaction between a green photoreceptor and phytochrome (López-Figueroa 1991a, b; Rüdiger and López-Figueroa 1992; Godínez-Ortega et al. 2008). While blue and green light stimulate nitrogen assimilation and the accumulation of phycobiliproteins (Godínez-Ortega et al. 2008), red light blocks chlorophyll biosynthesis, which results in a decrease in the function of the light-harvesting system (Senger et al. 2002). Further investigations are required to elucidate how the different light spectral qualities regulate the biosynthesis process.

Net photosynthesis, dark respiration and chlorophyll fluorescence results of *M. papulosa* likewise revealed the sensitivity of the alga to temperature gradients. Their *P–E* curves and parameter estimates at 12, 20, and 28 °C were distinct from each other. *NP* rates were lowest at 12 °C, in parallel to the low *NP* rates and F_v/F_m in the temperature exposure experiments. A characteristic photoinhibition (i.e., decline in *NP* rates and quantum yield of oxygen evolution) was also observed at this critical temperature, thereby restricting the growth of this alga. Under these circumstances, low winter temperature could explain the absence of natural populations of *M. papulosa* in the cold-temperate regions of Hokkaido and northern Honshu islands. Perhaps, incident irradiance of more than 200 μmol photons m^{-2} s^{-1} at or below 12 °C in winter in the natural state would cause low temperature-induced photodamage to this species (Fukumoto et al. 2018). At the boundary of northern distribution of this alga (in northern Kyushu or in the Pacific coast of central Honshu), winter temperature could sometimes drop to 12 °C (Terada et al. 2016); however, low-temperature induced photodamage will probably not occur due to the low PAR environment at the subtidal habitat of this species at 3–30 m depths.

In contrast, NP_{max} was highest at 28 °C and so was E_k, allowing *M. papulosa* to utilize more light in photosynthesis. Such adjustment in photosynthetic response suggests efficient cultivation of the seaweed also in shallow waters during summer. While no indication of photoinhibition was detected after an hour of exposure to 1000 μmol photons m^{-2} s^{-1} at this temperature, the possibility of *PSII* inactivation under variable field conditions, particularly under circumstances in which temporarily supersaturating irradiances may hit the algae still needs to be tested. Indeed, a declining trend in dark-acclimated F_v/F_m (and *GP* rates) was already observed at 28 °C; photodamage to *PSII* in the alga will likely accelerate upon exposure to excessive irradiances (Terada et al. 2018; Borlongan et al. 2018, 2019). Maximum irradiance range in the depth distribution of this species was 175–1600 μmol photons m^{-2} s^{-1}. On one hand, F_v/F_m–*T* responses of *M. papulosa* showed peak values at temperature range of 21.5–23.6 °C; the temperature at which GP_{max} occurred (GPT_{opt} = 22.1 °C) was also within this range. These temperature optima for photosynthesis were in the same range as that for growth of *M. papulosa* (20–24 °C; Lideman et al., 2012). Dark respiration rates gradually increased from 8 to 28 °C; a temperature threshold in respiration was found above 28 °C, minimizing the impact of carbon and/or oxygen limitation at elevated temperatures (Vásquez-Elizondo and Enríquez 2016; Borlongan et al. 2017). *Meristotheca papulosa* is widely distributed along the Pacific coasts of southern Japan (Yoshida 1998), with seawater temperature range of 12–29 °C (Borlongan et al. 2017; Terada et al. 2016, 2018). They are abundant during spring and early summer (April–July), when temperatures rise to 18–26 °C (Shinmura 1974; Serisawa et al. 2000; Lideman et al. 2012; Kobayashi and Fujita 2014).

From the results obtained, the following conclusions can be drawn: green light has advantageous effects on the photosynthesis of *M. papulosa*. Blue or green light treatments in mariculture of this red alga can be used to stimulate phycobiliprotein production, thereby improving thallus color and product quality. Indeed, Japanese consumers generally prefer reddish-color product for this species. Exposure to blue or green light of yellow-colored individuals harvested from relatively shallow waters for a few days may be done prior to selling or shipment to buying centers. The ability of *M. papulosa* to adjust its *P–E* responses at different temperatures suggests its efficient cultivation under natural seawater temperatures within its natural distribution in Japan. Such information could provide significant contributions toward the advancement in cultivation of this edible resource, in addition to expanding upon existing scientific knowledge.

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