

# Thermal and PAR effects on the photosynthesis of *Eucheuma denticulatum* and *Kappaphycus striatus* (so-called *Sacol* strain) cultivated in shallow bottom of Bali, Indonesia

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Received: 8 April 2016 / Revised and accepted: 5 September 2016 / Published online: 27 September 2016  
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**Abstract** Photosynthetic responses to various temperature and PAR conditions of two carrageenophytes, *Eucheuma denticulatum* and *Kappaphycus striatus* (so-called *Sacol* strain), cultured in shallow areas of Bali, Indonesia, were examined using dissolved oxygen measurements and pulse–amplitude-modulated (PAM) fluorometry. Net photosynthesis–irradiance ( $P$ – $E$ ) curves at 26 °C revealed that the values of  $P_{\max}$  for *E. denticulatum* and *K. striatus* were 13.76 and 5.02  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$  (12.38–15.12 and 4.55–5.50  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ , 95 % Bayesian prediction interval (BPI)), respectively. Photoinhibition was not observed even at 1000  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Gross photosynthesis and respiration characteristics over a range of temperatures (8–36 °C) revealed optimum temperature for photosynthesis to be 31.1 °C for *E. denticulatum*, and 31.6 °C for *K. striatus*. These characteristics of photosynthesis indicate that both farmed seaweeds are well adapted to the light and temperature conditions of the cultivation site. However, studies on longer timescales for photochemical efficiency, photosynthesis, and respiration are still needed to determine their limits of tolerance. We also hypothesize that higher values of

photosynthetic parameters for *E. denticulatum* suggest that this species is relatively superior in productivity under optimal conditions, conditional on the farming method.

**Keywords** *Eucheuma denticulatum* · *Kappaphycus striatus* · Rhodophyta · Photosynthesis · PAM fluorometry · Seaweed cultivation

## Introduction

*Eucheuma* and *Kappaphycus* (Rhodophyta, Solieriaceae) are economically important red seaweeds, serving as raw materials for the production of iota and kappa–carrageenan, respectively. These algal genera are commercially cultivated in almost 30 countries, including Indonesia, Philippines, Malaysia (Neish 2013; Hurtado et al. 2014a, 2015), India (Krishnan and Narayanakumar 2013; Periyasamy et al. 2014), Tanzania (Msuya 2013; Msuya and Porter 2014), Latin America (Hayashi et al. 2013), and the Caribbean (Hurtado et al. 2014b). These seaweeds are grown in shallow to deep water farming areas, employing a variety of cultivation techniques, depending on species, site, and season. The fixed off-bottom, single floating-raft, and hanging long-lines are the most common methods adopted (Hurtado et al. 2014a).

Along with *Eucheuma denticulatum* (Burman) Collins et Hervey and *Kappaphycus alvarezii* (Doty) Doty ex Silva, *Kappaphycus striatus* (Doty) Doty ex Silva is one of the common carrageenophytes widely farmed in shallow areas of Bali beach, Indonesia, using the fixed off-bottom method (Adnan and Porse 1987; Luxton 1993). The *Sacol*-strain is characterized by its decumbent habit, dense, and thick cylindrical branches with blunt and forked tips of not more than 5 mm in diameter, which resemble a “cauliflower” shape (Trono 1993). This variety originated from *Sacol* Island,

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Zamboanga, Philippines, from which its name was derived (Hurtado et al. 2008). Regardless of species, these carrageenophytes have been subjects of numerous investigations in various countries with regard to their physiology, including growth, photosynthesis, and carrageenan yields (Glenn and Doty 1981; Collen et al. 1992; Dawes 1992; Ganzon-Fortes et al. 1993; Dawes et al. 1994; Aguirre von Wobeser et al. 2001; Granbom et al. 2001; Jacobsen et al. 2003; Hayashi et al. 2011).

For example, our recent studies using a pulse–amplitude-modulated (PAM) chlorophyll fluorometer revealed that the rapid light curves (RLCs) of the electron transport rate (ETR) of *E. denticulatum* and *Kappaphycus* sp. (Sumba strain) from South Sulawesi, Indonesia were temperature dependent, with optimal temperatures ranging from 23 to 32 °C and 22 to 33 °C, respectively (Lideman et al. 2013); whereas the highest maximum quantum yield ( $F_v/F_m$ ) of *K. alvarezii* from Vietnam occurred at 22.2 °C, with relatively high growth rates between 28 and 32 °C (Terada et al. 2016b). These species were found to be well adapted to the natural temperature environment of their corresponding cultivation sites. Moreover, a decline in effective quantum yield ( $\Phi_{PSII}$ ) as incident irradiance increased at noon, and subsequent recovery in the evening was also observed in Vietnamese-cultivated *K. alvarezii*, suggesting the possibility of photoadaptation, rather than of photoinhibition.

Despite these previous studies, we note that these two algal species from Bali, Indonesia, are cultivated differently by fixed, off-bottom monoline method, and little is known regarding their ecophysiology, particularly the photosynthetic characteristics of the sacol strain. Our former study on the Indonesian entity (Lideman et al. 2013) was also limited to rETRs from PAM measurements and lacked results from dissolved oxygen measurements. It is of great interest to evaluate and clarify site- and species-specific responses to environmental conditions. Indeed, PAM fluorometry has long been used as a rapid method to quantify the effects of changing environmental conditions on macroalgal photobiology (Renger and Schreiber 1986; Huppertz et al. 1990; Gévaert et al. 2002; Enriquez and Borowitzka 2011), providing greater detail, especially on their photosynthetic activity in response to temperature (Lideman et al. 2013; Fujimoto et al. 2014a, b, 2015; Kokubu et al. 2015; Vo et al. 2015; Terada et al. 2016a, b, c).

Hence, the present study was conducted to determine the photosynthetic responses of *E. denticulatum* and *K. striatus* (Sacol strain) cultivated in shallow beach areas of Bali, Indonesia to various temperature and light conditions, by PAM chlorophyll fluorometry and dissolved oxygen sensors. Knowledge on the photosynthetic characteristics, including temperature and irradiance optima of these species, is valuable for proper selection of carrageenophyte species and/or strains, relative to the cultivation site and method employed, for maximum crop yield and production.

## Materials and methods

### Sample collection and stock maintenance

*Eucheuma denticulatum* and *Kappaphycus striatus* were collected from a farming area along Geger Beach, Nusa Dua, Bali, Indonesia (08°48.915' S 115°13.580' E) on August 28, 2015. These seaweeds are cultivated by fixed off-bottom method, a farming technique practiced in shallow reef areas like the coastline, with the lowest mean tide level ranging from 25 to 100 cm (Doty 1973; Trono 1990). During collection, the actual depth of farmed seaweed was 85 cm below the water surface. Approximately 1 kg of each species was collected; wrapped with wet Kimtowel, moistened with seawater; separately stored in plastic bags; and transported to Japan via an overnight airline trip.

The algae were maintained for 1 to 3 days before examination at the Faculty of Fisheries, Kagoshima University, Japan, in an aquarium tank (1500 L) containing seawater at a salinity of 33 PSU, pH 8.0, seawater temperature of 26 °C (i.e., actual seawater temperature during collection), and under the irradiance of 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (14:10 light/dark cycle). Aeration ( $c. 2.0 \text{ L min}^{-1}$ ) was also provided to maintain saturated conditions of dissolved oxygen. Voucher herbarium specimens of the two taxa were deposited in the Herbarium of Kagoshima University Museum, Kagoshima.

### Effect of temperature on oxygenic photosynthesis

Detailed methods for measurement of photosynthesis were provided in previous studies (Fujimoto et al. 2015; Kokubu et al. 2015; Vo et al. 2015; Terada et al. 2016a, b, c). Briefly, seaweed samples were examined under eight temperature treatments (10, 14, 18, 22, 26, 30, 34, and 38 °C) with five replicates, at an irradiance of 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , which was higher than the saturation irradiances ( $E_k$ ) of the two carrageenophytes, as revealed by their photosynthesis–irradiance ( $P-E$ ) curves (detailed below). Light was provided by a metal-halide lamp and adjusted with neutral density screens (Nishihara et al. 2004), and temperature was controlled using a water bath.

Randomly cut segments (apical, mid, or basal) of *E. denticulatum* and *K. striatus* were approximately 0.98 g (SD  $\pm 0.13$  g) and 1.37 g (SD  $\pm 0.65$  g) fresh weight ( $g_{fw}$ ), respectively, and were acclimatized overnight with sterilized natural seawater in the incubator prior to experimentation (Serisawa et al. 2001). To begin the experiment, three to four explants were randomly selected and placed in biological oxygen demand (BOD) bottles containing approximately 100 mL sterilized natural seawater. The DO sensors were placed in sterilized seawater with utmost care so that no visible bubbles would be trapped. Net photosynthesis rates were determined by measuring the dissolved oxygen concentrations

(mg L<sup>-1</sup>) every 5 min for 30 min after a 30-min pre-incubation to acclimate the samples to each experimental condition. Respiration rates (i.e., “post-illumination respiration”; Colombo-Pallotta et al. 2010; Vásquez-Elizondo and Enríquez 2016) were determined following net photosynthesis measurements by wrapping the BOD bottles with aluminum foil. Water in the bottles was continuously stirred during the measurement. Sterile natural seawater was renewed after every measurement to avoid any effects that can be attributed to the depletion of nutrients and dissolved carbon dioxide.

A least squares linear regression model was fit to each of the concentrations with respect to time, and the slope estimated from the model was used as the photosynthetic rate. All rates were normalized to water volume of each BOD bottle and fresh weight of the sample. Dissolved O<sub>2</sub> (DO) was measured using DO meters equipped with optical dissolved oxygen sensors (ProODO-BOD; YSI Incorporated, USA).

### Effect of irradiance on oxygenic photosynthesis

Photosynthesis rates were determined at nine irradiance levels (0, 30, 60, 100, 150, 200, 250, 500, and 1000 μmol photons m<sup>-2</sup> s<sup>-1</sup>), with five replicates at 26 °C. Approximately 1.08 g (SD ± 0.18 g) and 1.27 g (SD ± 0.09 g) fresh weight (g<sub>fw</sub>) of *E. denticulatum* and *K. striatus* segments, respectively, were placed into each BOD bottle containing sterile natural seawater. Net photosynthetic rates were obtained by measuring the dissolved oxygen concentrations (mg L<sup>-1</sup>), using optical DO sensors (ProODO-BOD; YSI Incorporated, USA), every 5 min for 30 min, after a 30-min pre-incubation to the experimental irradiance. Methods used for this experiment follow those of the temperature experiment.

### Effect of temperature on PAM chlorophyll fluorometry

Detailed methodology on Maxi-imaging-PAM (IMAG-MAX/LR version, Heinz Walz GmbH, Germany) measurements has been provided in previous studies (Fujimoto et al. 2015; Vo et al. 2015; Terada et al. 2016a, b, c). Initially, approximately 5 to 8 cm-long portions (apical, mid, or basal combined) of thalli were cut and acclimated overnight. Sections were then placed in a stainless-steel tray (12 cm × 10 cm × 3 cm) with sterilized seawater, providing for 10 replicates for each temperature condition. Temperature was controlled by placing the stainless steel tray on the aluminum block of the incubator (BI-535A; Astec, Japan). Water temperature in the stainless steel tray was also measured with a thermocouple (model 925; Testo AG, Germany) to confirm that the appropriate temperature condition was achieved. Maximum quantum yields (maximum photochemical efficiency of photosystem II,  $F_v/F_m$ ; Cosgrove and Borowitzka 2011) of the alga were measured from 8 to 38 in 2 °C increments. Each increment in

temperature occurred over a 30 min period, with an additional 30 min for temperature and dark acclimation. One set of experiments typically took more than 8 h to complete.

### Modeling the photosynthetic response to temperature and irradiance

The responses of gross photosynthetic rates and maximum quantum yield ( $F_v/F_m$ ) to temperature were analyzed using a Bayesian approach. The model was based on a thermodynamic non-linear equation (Thornley and Johnson 2000; Alexandrov and Yamagata 2007; Eq. 1), where  $y$  is the response variable, which can either be the gross photosynthetic rate or the  $F_v/F_m$ ; and  $K$  is temperature expressed in Kelvin. The thermodynamic non-linear model (Eq. 1) assumes that photosynthesis enters a less active state beyond some optimal temperature. 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<sup>-1</sup>; and  $H_d$  is the deactivation energy in kJ mol<sup>-1</sup>.  $R$  in this model is the ideal gas constant and has a value of 8.314 J mol<sup>-1</sup>. The optimal value of  $y_{opt}$  at  $K_{opt}$  can be determined by substituting  $K_{opt}$  into the equation.

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

The gross photosynthesis rate, which is the sum of net photosynthesis rate and respiration rate, was estimated by simultaneously fitting the measured respiration rates to the Arrhenius equation (Eq. 2) and the net photosynthesis rates to the difference in Eq. 1 and Eq. 2. 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).  $R_{24}$  is the respiration rate at 24 °C and  $E_a$  is the activation energy. The constant 297.15 is 24 °C scaled in absolute temperature. Simultaneous model fittings and determination of model parameters for Eqs. 1 and 2 were done using a Bayesian approach, where the prior distributions for the parameters were determined by averaging the mean and variances of estimates from previous studies (Fujimoto et al. 2014a, b, 2015; Kokubu et al. 2015; Vo et al. 2015; Terada et al. 2016a, b, c).

$$R_d = R_{24} \exp\left(\frac{E_a}{R} \left(\frac{1}{K - 297.15}\right)\right) \quad (2)$$

The response of net photosynthetic rates to irradiance was examined by modeling the data using an exponential equation (Webb et al. 1974; Jassby and Platt 1976; Platt et al. 1980;

Henley 1993), which included a respiration term ( $R_d$ ) that had the form

$$P_{\text{net}} = P_{\text{max}} \left( 1 - \exp\left(\frac{-\alpha}{P_{\text{max}}} E\right) \right) - R_d \quad (3)$$

where  $P_{\text{net}}$  was the net  $\text{O}_2$  production rate,  $P_{\text{max}}$  was the maximum  $\text{O}_2$  production rate,  $\alpha$  was the initial slope of the photosynthesis versus irradiance curve,  $E$  was the incident irradiance, and  $R_d$  was the dark respiration rate. From this model, the saturation irradiance ( $E_k$ ) was calculated as  $P_{\text{max}}/\alpha$  and the compensation irradiance ( $E_c$ ) was  $P_{\text{max}} \ln\left(\frac{P_{\text{max}}}{(P_{\text{max}} - R_d)}\right) / \alpha$ .

### Statistical analysis

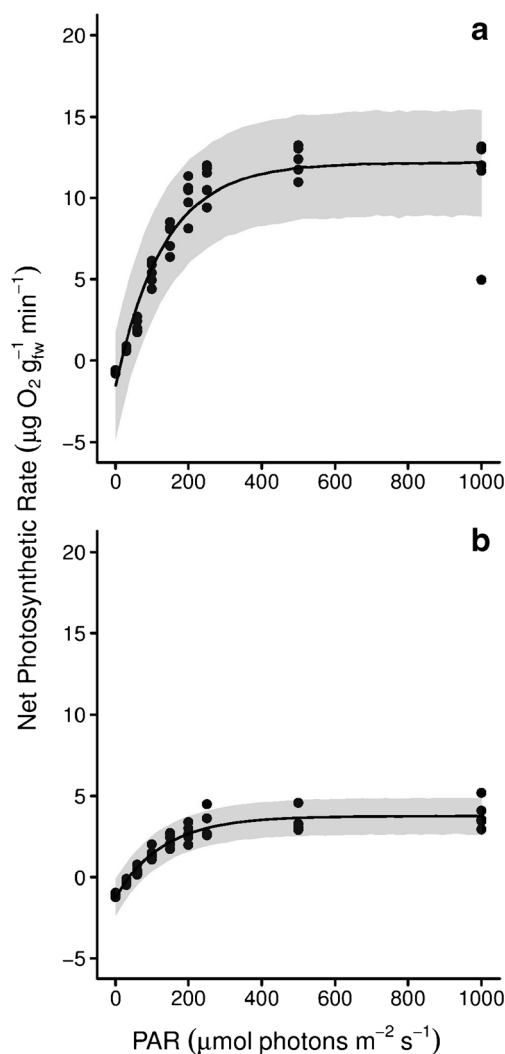
Statistical analyses were done using R version 3.3.0 (R Development Core Team 2015) and Bayesian model fitting was done using RStan version 2.9 (Stan Development Team 2015). RStan primarily uses a variant of a Hamiltonian Monte Carlo sampler to construct the posterior distributions of the parameters, and four chains of at least 500,000 samples per chain were generated and assessed for convergence, which provided at least 1000 effective samples of each of the parameters of interest.

## Results

### Effect of irradiance on the oxygenic net photosynthesis

Photosynthesis–irradiance ( $P$ – $E$ ) curves of *E. denticulatum* and *K. striatus* at 26 °C showed a characteristic hyperbolic shape, in which net photosynthesis rates increased linearly at low photosynthetically active radiation (PAR) and then become saturated to a constant rate at high PAR (Fig. 1a, b). No photoinhibition was also observed for both carragenophytes at high PAR up to 1000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . The measured net photosynthetic rates of *E. denticulatum* and *K. striatus* gradually increased from  $-0.64$  and  $-1.09 \mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1}$  [ $-0.72$  to  $-0.56$  and  $-1.18$  to  $-1.0 \mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1}$ , 95 % confidence interval (CI)] at 0  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  to a high of 10.97 and 3.85  $\mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1}$  (7.97–13.96 and 3.10–4.60  $\mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1}$ , 95 % CI) at 1000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , respectively.

The parameter estimates which describe the significant features of each  $P$ – $E$  curve are shown in Table 1. Maximum net photosynthetic rates ( $P_{\text{max}}$ ) of *E. denticulatum* and *K. striatus* at 26 °C were 13.76 and 5.02  $\mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1}$ , respectively. Respiration rate ( $R_d$ ) for *E. denticulatum* was 1.59  $\mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1}$ ; and 1.25  $\mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1}$  for *K. striatus*. Initial slopes ( $\alpha$ ) of the curve were 0.10 and 0.04  $\mu\text{g O}_2 \text{g}_{\text{fw}}^{-1} \text{min}^{-1} (\mu\text{mol photons m}^{-2} \text{s}^{-1})^{-1}$  for



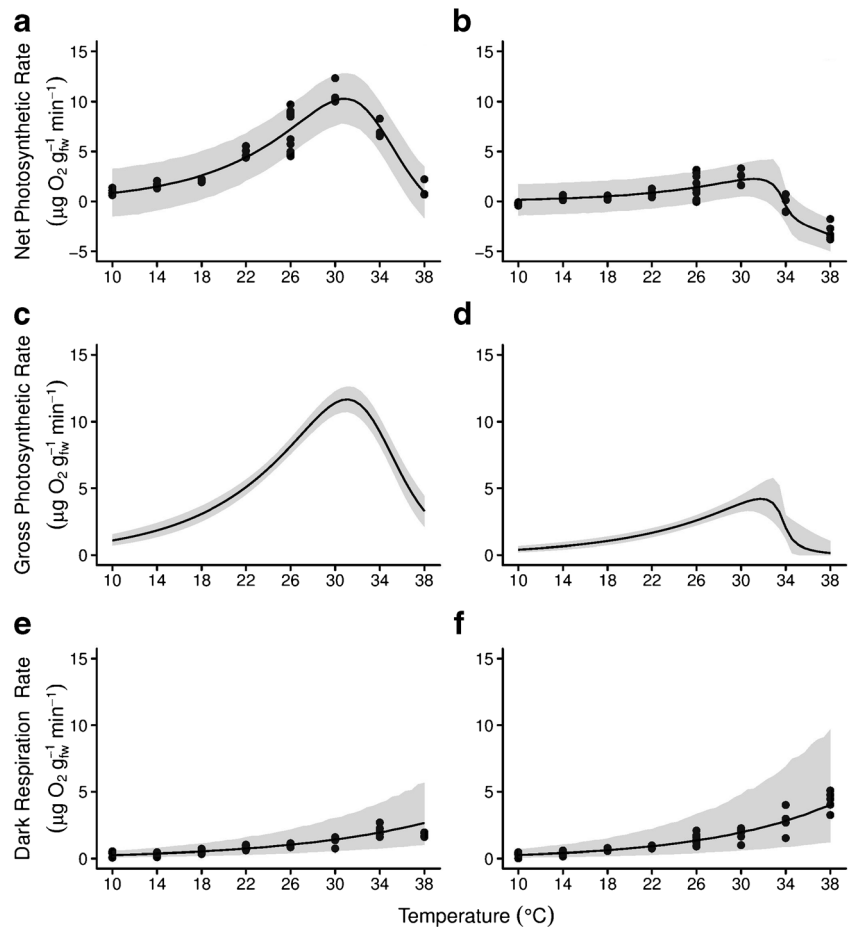
**Fig. 1** The response of the net photosynthetic rates of *Eucheuma denticulatum* (a) and *Kappaphycus striatus* (b) from Bali, Indonesia, to increasing photosynthetically active radiation measured at 26 °C. The dots indicate the measured rates ( $n = 5$ ), the line indicates the expected value, and the shaded region indicates the 95 % Bayesian prediction interval of the model

*E. denticulatum* and *K. striatus*, respectively. From these parameters, the saturation irradiances ( $E_k$ ) of *E. denticulatum* and *K. striatus* were 134 and 131  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ,

**Table 1** Mean and 95 % Bayesian prediction intervals (95 % BPI) of the parameters estimated for the net photosynthesis–irradiance model

Parameter	<i>E. denticulatum</i>		<i>K. striatus</i> (Sacol strain)	
	Mean	95 % BPI	Mean	95 % BPI
$P_{\text{max}}$	13.76	12.38–15.12	5.02	4.55–5.50
$\alpha$	0.10	0.08–0.13	0.04	0.03–0.05
$R_d$	1.59	0.52–2.63	1.25	0.88–1.64
$E_c$	16	7–24	37	29–45
$E_k$	134	109–162	131	105–162

**Fig. 2** The response of the oxygenic photosynthesis and dark respiration of *Eucheuma denticulatum* (a, c, e) and *Kappaphycus striatus* (b, d, f) from Bali, Indonesia. a, b The oxygenic net photosynthesis to temperature determined at 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . c, d The modeled gross photosynthetic rates determined at 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Data were derived from the model curve of net photosynthesis (a, b) and dark respiration (e, f). e, f The dark respiration rate to temperature at 0  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . The dots indicate the measured rates ( $n = 5$ ), the line indicates the expected value, and the shaded region indicates the 95 % Bayesian prediction interval of the model



respectively, with corresponding compensation irradiance ( $E_c$ ) values of 16 and 37  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ .

**Effect of temperature on photosynthesis and dark respiration rates**

Net photosynthetic rates of both *E. denticulatum* and *K. striatus* increased with rise in temperature from 10 to 30 °C and subsequently declined up to 38 °C (Fig. 2a, b). Peak net photosynthetic rates of *E. denticulatum* and *K. striatus* at 30 °C were 10.62 and 2.36  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$  (8.74–12.50 and 0.94–3.78  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ , 95 % CI), respectively.

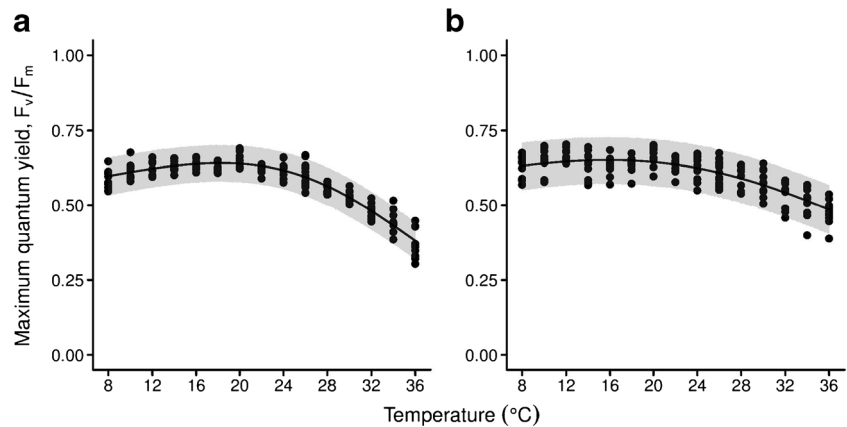
Meanwhile, dark respiration rates increased from 0.28  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$  (0.11–0.60  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ , 95 % BPI) at 10 °C to 2.6  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$  (0.96–5.56  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ , 95 % BPI) at 38 °C for *E. denticulatum*; and from 0.27  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$  (0.08–0.68  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ , 95 % BPI) at 10 °C to 4.33  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$  (1.32–10.49  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ , 95 % BPI) at 38 °C for *K. striatus* (Fig. 2e, f). The respiration rates at 26 °C ( $R_{26}$ ) for *E. denticulatum* and *K. striatus* were 0.79 and 0.96  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ , respectively.

Simultaneous model fittings (Eqs. 1 and 2) of net photosynthesis and dark respiration rates provided for estimates of gross photosynthesis rates (Fig. 2c, d) and model parameter values (Table 2). The optimum temperatures ( $T_{\text{opt}}$ ) of *E. denticulatum* and *K. striatus*, i.e., the temperature at which the maximum gross photosynthetic rates ( $\text{GP}_{\text{max}} = 11.71$  and 4.39  $\mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ ) would occur, were 31.1 and 31.6 °C, respectively.

**Table 2** Mean and 95 % Bayesian prediction intervals (95 % BPI) of the parameters estimated for the gross photosynthesis–temperature model

Parameter	<i>E. denticulatum</i>		<i>K. striatus</i> (Sacol strain)	
	Mean	95 % BPI	Mean	95 % BPI
$\text{GP}_{\text{max}}$	11.71	10.78–12.65	4.39	3.37–5.83
$H_a$	91	74–110	84	61–109
$H_d$	392	320–490	1390	361–3963
$T_{\text{opt}}$	31.1	30.4–31.7	31.6	29.9–33.1
$E_a$	61	50–72	71	60–82
$R_{26}$	0.79	0.69–0.90	0.96	0.83–1.11

**Fig. 3** The temperature response of the maximum quantum yield ( $F_v/F_m$ ) in *Eucheuma denticulatum* (a) and *Kappaphycus striatus* (b) from Bali, Indonesia. The dots indicate the measured values ( $n = 10$ ), the lines indicate the expected value, and the shaded regions indicate the 95 % Bayesian prediction interval of the model



### Effect of temperature on the maximum quantum yield ( $F_v/F_m$ )

Maximum quantum yield ( $F_v/F_m$ ) responses of *E. denticulatum* and *K. striatus* to temperature seemed different from their gross photosynthesis–temperature relationships.  $F_v/F_m$  of both seaweeds remained relatively stable at lower temperatures but gradually declined as temperature increased (Fig. 3). The maximum  $F_v/F_m$  for both *E. denticulatum* and *K. striatus* were estimated to be 0.65, which occurred at temperatures 18.2 and 15.7 °C, respectively.

### Discussion

Cultivation of *E. denticulatum* and *K. striatus* on shallow coasts of Bali beach, Indonesia employs the fixed off-bottom method; hence, these seaweeds are exposed to direct sunlight throughout the day. In this study, both *E. denticulatum* and *K. striatus* did not undergo photoinhibition, as net photosynthetic rates were saturated at  $E_k$  (i.e., at 134 and 131  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , respectively), and remained stable up to the highest irradiance level of 1000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. 1). Such observation corresponded well with previous reports, where robust circadian rhythm of oxygen evolution in seaweeds (Granbom et al. 2001) with no apparent photoinhibition based on RLCs (Lideman et al. 2013) was detected as PAR reached 1000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Exposure to such irradiance for 1 h under laboratory conditions in the present study may not have yet reduced the photosynthetic activity that can result into a negative  $\beta$  (i.e., quantum yield of oxygenic evolution) of the cultivated macroalgae. However, prolonged exposure to such PAR level or to even higher magnitudes, which can extend up to 2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , as recorded in cultivation sites in Tanzania (Collen et al. 1995) and Thailand (Terada et al. 2016b), may induce photoinhibition of photosynthesis rates. On the other

hand, a depression at noon but an upturn or recovery in  $\Phi_{\text{PSII}}$  by sunset was observed with Vietnamese-cultivated *K. alvarezii* (Terada et al. 2016b) and other macroalgae (Häder et al. 1996; Figueroa et al. 1997; Cabello-Pasini et al. 2000; Kokubu et al. 2015; Terada et al. 2016a), revealing their efficient protective response mechanism for downregulating photosynthesis to avoid chronic photodamage at high light stress levels (Beer et al. 2014). Regardless of whether photoinhibition and/or photoprotection affect the photosynthetic response to irradiance, measurements for both processes by oxygen evolution and PAM fluorometry are necessary to elucidate their threshold levels of PAR and to reveal the mechanisms that are involved in determining these levels. Furthermore,  $E_k$  determined in the present study was within the range of estimated  $E_k$  values of carrageenophytes from Indonesia (96–176  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Lideman et al. 2013), Vietnam (117–203  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Terada et al. 2016b), and Philippines (103–290  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Borlongan et al. 2016), which were all cultivated by hanging long-line method, adapted for deeper water areas with mild wave action (Hurtado et al. 2008). Despite the difference on how these seaweeds were planted in the sea, results of the present study show that these seaweeds are adapted to the same PAR conditions, with low irradiance requirement for oxygenic photosynthesis. Variations in growth performance of these carrageenophytes, relative to the farming method employed, can rather be attributed to nutrient availability and water movement (Glenn and Doty 1992), as these factors are also regarded as being crucial for the successful cultivation of these seaweeds in under natural conditions (Santelices 1999). Indeed, prolonged exposure to excessive PAR (and so as to high temperatures), especially in shallow areas with poor water movement, has been shown to reduce growth (Dawes et al. 1974), which is probably a result of carbon limitation, as observed in sheltered, shallow coral reef environments (Enríquez and Rodríguez-Román 2006). Adaptive strategies of these carrageenophytes to efficiently grow in their respective habitats would also be an interesting topic for further studies. However, we compared our results with the aforementioned studies with caution, taking into consideration the different

techniques and controlled conditions employed for estimation of photosynthesis.

Likewise, gross photosynthesis and respiration rates of *E. denticulatum* and *K. striatus* were strongly affected by temperature. The temperature responses of the gross photosynthetic rates (Fig. 2c, d) for both species were characteristically domelike in shape, with estimated maximum gross photosynthetic rates of *E. denticulatum* ( $11.71 \mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ ) and *K. striatus* ( $4.39 \mu\text{g O}_2 \text{ g}_{\text{fw}}^{-1} \text{ min}^{-1}$ ) occurring at 31.1 and 31.6 °C ( $T_{\text{opt}}$ ), respectively.

Results were favorably comparable with a previous study (Aguirre von Wobeser et al. 2001), where photosynthesis of *K. alvarezii* (red and green morphotypes from the Philippines) reached maximum at 30 °C. Moreover, these optimal temperatures are within the range of temperatures where  $r\text{ETR}_{\text{max}}$  of Indonesian *E. denticulatum* (23 to 32 °C) and *Kappaphycus* sp. (22 to 33 °C) was highest (Lideman et al. 2013). Meanwhile, dark respiration of both species increased exponentially with temperature when increased from 10 to 38 °C (Fig. 2e, f), with higher and more variable measured rates for *K. striatus* at higher temperatures. In contrast with the results of GP–temperature experiments, maximum quantum yields ( $F_v/F_m$ ) of both species appeared relatively stable from 8 to 24 °C, with a decrease thereafter (Fig. 3). The present study revealed that  $F_v/F_m$  of both species dropped as temperatures reached their threshold levels, as also observed with the Vietnamese entity (Terada et al. 2016b) and other macroalgae (Fujimoto et al. 2015; Vo et al. 2015; Terada et al. 2016a). Indeed, reduction of  $F_v/F_m$  (i.e., measured at  $<10 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ ) in coralline algae was revealed, with photodamage being enhanced at elevated temperatures (Vásquez-Elizondo and Enríquez 2016). Allakhverdiev et al. (2008) suggest that there are three major heat-sensitive sites in the photosynthetic apparatus: photosystem II (PSII) with its oxygen-evolving complex (OEC), the ATP-generating synthase, and the enzymes of the Calvin cycle. Additionally, thermal stress at high temperatures produces reactive oxygen species (ROS), which consequently inhibit de novo synthesis of the D1 protein in PSII, resulting in a reduction of  $F_v/F_m$ , and oxygen evolution. Seaweeds subjected to high temperatures in the present study were probably undergoing similar responses in their PSII reaction centers, hence the observed decline in  $F_v/F_m$  and GP rates. We recommend that quantum yield ( $F_v/F_m$ ,  $\Phi_{\text{PSII}}$ ) measurements over chronic PAR exposures at elevated temperatures be done in order to elucidate interactive effects of these environmental factors in the photochemical efficiency, thus in the photosynthesis of the farmed seaweeds. The severity of the impact of thermal stress on the physiology and performance of marine macrophytes will depend upon the presence and magnitude of additional limiting or disruptive stressors (e.g., light). We also acknowledge that further studies are needed to explain the mechanisms associated with  $F_v/F_m$ –temperature response of these carrageenophytes at low temperatures, given the distinct patterns from their GP–

temperature responses in the present study, as well as from the  $F_v/F_m$ –temperature responses of Vietnamese *K. alvarezii* (Terada et al. 2016b), and other Paleotropical red macroalgae (Fujimoto et al. 2014a, b, 2015; Vo et al. 2014; Vo et al. 2015). The discrepancy between  $F_v/F_m$  and GP–temperature response is probably due to the process being observed, where oxygen evolution represents net photosynthesis, which includes the oxygen-consuming process of respiration, whereas  $F_v/F_m$  reflects the efficiency of light harvesting and electron transport in PSII (Beer et al. 2014), which is only a part of several processes involved in photosynthesis. Results of the present study revealed that between the two photosynthetic measurements, GP seemed more sensitive to temperature than  $F_v/F_m$  in these carrageenophytes and so provides a better link between seaweed productivity and the thermal environment.

Nevertheless, the concurrent decline in gross photosynthetic rates and  $F_v/F_m$ , and rise in respiration rates above 31 °C indicate impairment of the seaweeds' photosynthetic process above this temperature threshold. Indeed, temperatures of up to 33–35 °C have caused seaweed pigment concentrations to drop, leading to loss of photosynthetic efficiency, poor growth rates, and finally to “ice–ice” whitening and loss of biomass due to fragmentation (Ganzon-Fortes et al. 1993; Largo et al. 1995). Seaweeds also became fragile and had retarded growth rates when seawater temperature exceeded 33 °C (Ohno et al. 1996) and even after prolonged periods at 30 °C (Mandal et al. 2015). More importantly,  $T_{\text{opt}}$  for GP in the present study is within the recorded annual seawater temperature that ranged from 28 to 34 °C (Amin et al. 2008; World Sea Temperatures 2016). Hence, seaweed production in the cultivation site would be greatly affected during the “dry” season, when temperatures are extreme. While the seaweeds' lower limits of temperature tolerance may not be of ecological importance in tropical areas, this information is valuable when we consider cultivation sites outside the tropics, in more temperate areas. For example, seawater temperatures drop to as low as 16 °C during winter along the southeastern coast of Brazil (Paula et al. 2002; Paula and Pereira 2003; Hayashi et al. 2011).

It is also important to note that at any given temperature, PAR, and net and gross photosynthetic rates of *E. denticulatum* tended to be higher than those of *K. striatus*. Given their higher values for  $P_{\text{max}}$  and  $\alpha$ , *E. denticulatum* exhibited more active photosynthesis and light utilization capacity than *K. striatus*, suggestive of their possible growth advantage over *K. striatus* under optimal conditions in commercial seaweed cultures. The difference in photosynthetic responses between the two species can be primarily attributed to the variation in pigment composition, given their similar filamentous morphology. Indeed, previous reports (Dawes et al. 1994; Hurtado-Ponce 1995; Muñoz et al. 2004; Hayashi et al. 2007) showed different growth rates among *E. denticulatum* and color morphotypes of *K. alvarezii*. Additional investigations including

photosynthetic pigment determination and  $P-E$  and temperature acclimation experiments (with longer timescale) are necessary in order to verify such disparity. Indeed, the posterior probability that  $E_k$  and  $T_{opt}$  were not different between *E. denticulatum* and *K. alvarezii* were 0.89 and 0.45, respectively, suggesting that both seaweeds are adapted to similar range of light and temperature conditions. A temperature threshold in respiration was found in *E. denticulatum*, depicted by a decrease in respiration rates above 34 °C (Fig. 2e). A respiration threshold at 32 °C was also observed in crustose coralline alga *Lithothamnion* sp., but not in the rhodolith *Neogoniolithon* sp. and the articulated coralline alga *Amphiroa tribulus* (Vásquez-Elizondo and Enríquez 2016). The reduction observed in respiration is probably a physiological response to minimize the impact of carbon and/or oxygen limitation at elevated temperatures. Therefore, such a species-specific physiological threshold may indicate an advantage for *E. denticulatum* over *K. striatus* at temperatures exceeding the upper limit. The apparent decrease of  $F_v/F_m$  and lower respiration rates at high temperatures in *E. denticulatum* indicates that such seaweeds were less susceptible to high temperature-induced impairment of the photosynthetic apparatus. These characteristic responses, however, are quite the opposite from findings obtained by Lideman et al. (2013). This is not unusual, given differences in farming technique, hence dissimilar acclimation response. If so, then farming of *E. denticulatum*, rather than of *K. striatus* by the off-bottom method may lead to greater crop yield. However, cultivation experiments are needed in order to confirm this hypothesis. Nonetheless, Luhan and Sollesta (2010) observed that *K. striatum* var. Green Sacol, planted in the shallow intertidal zone, decolorized, and died when seawater temperature reached 29 °C, due to their exposure to even higher air temperatures (i.e., 35.5 °C on April to May 2008) during low tide. Another study (Hurtado et al. 2008) also suggested that *K. striatus* are best grown at a depth of 50–100 cm by the floating raft method to maximize growth rates, carrageenan content, and molecular weight.

In conclusion, optimum temperature for maximum photosynthesis (i.e., growth) of *E. denticulatum* and *K. striatus*, based on oxygen evolution measurements, is between 31 and 32 °C. Although this temperature is within the range of seawater temperature in the cultivation site, it is likely close to the upper limit for thermal inhibition, given the decline in  $F_v/F_m$ . Higher photosynthetic parameter values of *E. denticulatum* also suggest that such species will probably be more superior in productivity under optimal conditions, while farmed in shallow shores by fixed-off bottom method.

**Acknowledgments** This research was sponsored in part by a CREST (no. JAJJ110062) from Japan Science and Technology Agency (SK) and Grant-in-Aid for Scientific Research (nos. 25340012, 25450260, and 16H02939) from the Japanese Ministry of Education, Culture, Sport,

and Technology (RT and GNN). All authors have provided consent. This research was part of the dissertation submitted by the first author in partial fulfillment of the PhD degree.

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