ORIGINAL ARTICLE

The effect of irradiance and temperature on the photosynthesis of two agarophytes *Gelidium elegans* and *Pterocladiella tenuis* (Gelidiales) from Kagoshima, Japan

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Abstract The effect of irradiance and temperature on the photosynthesis of two Japanese agarophytes, *Gelidium elegans* and *Pterocladiella tenuis* (Gelidiales), was determined using dissolved oxygen sensors and pulse amplitude modulated (PAM) fluorometry. Gross photosynthesis and dark respiration rates were determined over a range of temperatures (8–36 °C). The highest gross photosynthetic rates were 40.3 and 37.0 mg O_2 g_{ww}^{-1} min^{-1} and occurred at 24.3 and 25.5 °C [95 % Bayesian credible interval (BCI) 20.7–28.0 and 23.4–28.3 °C], respectively. The dark respiration rate in *G. elegans* and *P. tenuis* increased with increasing temperature at a rate of 0.10 and 0.31 mg O_2-g_{ww}^{-1} min^{-1} $°C^{-1}$, respectively. Modeling the net photosynthesis–irradiance (*P–E*) responses of *G. elegans* and *P. tenuis* at 20 °C revealed that the net photosynthetic rates quickly increased at irradiance levels below the estimated saturation irradiance of 88 and 83 μmol photons m^{-2} s^{-1}, with a compensation irradiance of 14 and 19 μmol photons m^{-2} s^{-1}, respectively. The highest value of the maximum effective quantum yield (Φ_{PSII}) occurred at 20.1 °C (BCI 18.9–21.5 °C) and 21.3 °C (BCI 20.2–22.5 °C) for *G. elegans* and *P. tenuis* and was 0.49 and 0.45, respectively. These optimal temperatures of Φ_{PSII} were relatively lower than those determined by the photosynthesis–temperature model of oxygen evolution. The temperature response of these species indicates that they are probably well adapted to the current range of seawater temperatures in the study site but that they are near the boundary of their tolerable limits.

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Introduction

Red algal species of the order Gelidiales (Rhodophyta) are both major sources of agar and an indispensable component of Japanese dietary culture. Until recently about 3,000 tons (dry weight) of Gelidiales species were harvested annually in Japan [1–3]. Of these, *Gelidium elegans* Kützing and *Pterocladiella tenuis* (Okamura) Shimada, Horiguchi et Masuda are regarded as major agarophytes in Japan, and of the many members of the order Gelidiales they provide most of the biomass harvested for processing and production [3].

G. elegans and *P. tenuis* are originally endemic to the temperate regions of the northwestern Pacific, including Japan [4–9]. They can be found on rocks in the lower intertidal to upper sublittoral zones and within Japan proper, in the temperate region, including Honshu, Shikoku and Kyushu Islands [6–8]. In 1991, the expanse of *Gelidium*/*Pterocladiella* habitat was estimated to be 19,000 ha in all of Japan [10]. However, degradation of natural coastal areas has led to the loss of much of the natural habitat of these two species. The highest annual

production/harvesting of the members of order Gelidiales (21,000 tons dry weight) was in 1967; however, it had decreased by nearly 85 % by the last decade [3].

In addition to loss of habitat, changes in regional water temperature are of some concern, especially with respect to the harvesting of *Gelidium/Pterocladiella* in southern Japan. It has been reported that water temperatures off the Kyushu and Shikoku Islands in the Pacific Ocean increased by an average of 1.24 °C during the period of 1900–2010 [11, 12]. This is in accordance with increases in coastal seawater temperature measurements off Kagoshima of 1–2 °C in the past four decades [13–15]. This increase in seawater temperature significantly impacts the harvesting of *Gelidium/Pterocladiella* because the southern part of Kyushu Island is known as a marginal region for both temperate and tropical species [1]. For example, many common temperate edible species, including *Undaria pinnatifida* (Harvey) Suringar (brown alga) and *Pyropia tenera* (Kjellman) Kikuchi et al. (red alga), can be observed in this region, which is their southern limit of distribution [16, 17]. Despite the relatively high latitude (31°N), a number of tropical species in this area has been observed incidentally in this region over the past decade [18]. Therefore, it is reasonable to presume that in this region the warming of local seawater may result in additional shifts in species composition.

Given the commercial importance of *G. elegans* and *P. tenuis*, numerous investigations on their physiology have been conducted. Studies of Japanese Gelidiales have generally relied on manometric and electro-chemical techniques [19–21] to investigate the evolution of oxygen from photosynthesis. These early studies provided with much insight into the changes in oxygen evolution rates, but information on their response to temperature and irradiance remains limited to coarse temperature gradients and relatively low irradiance levels [20–24]. By applying modern techniques in photobiology, such as pulse amplitude modulated (PAM)-chlorophyll fluorometry, we can further enhance our understanding of the ecophysiology of these two species.

PAM-chlorophyll fluorometry has been used in aquatic research to measure the photosynthetic responses of various species of order Gelidiales [25–28]. This method is advocated as a rapid method to quantify the effects of changing environmental conditions on macroalgal photobiology [29], thereby allowing the temperature response of photosynthesis to be routinely studied under high resolution.

Given the lack of high-resolution studies on the photobiology of Japanese marine macroalgae and the scarcity of chlorophyll fluorescence studies, the aim of our study was to update our understanding of how water temperature and irradiance affect the photosynthesis of *G. elegans* and *P. tenuis*.
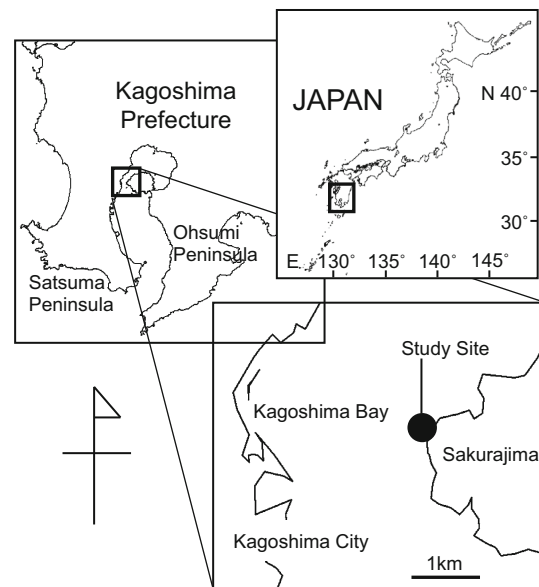

Fig. 1 Map showing the collecting site (*filled circle*) of *Gelidium elegans* and *Pterocladiella tenuis* in Sakurajima, Kagoshima, Japan

tenuis. More importantly, we sought to assess the response of specimens collected from Kagoshima Prefecture, which is known as the southern-most region where temperate *Gelidium/Pterocladiella* are harvested, using both PAM-chlorophyll fluorometry and dissolved oxygen sensors. Our results will most likely facilitate the sustainable utilization and conservation of these important agar resources.

Materials and methods

Specimen collection and stock maintenance

G. elegans and *P. tenuis* (approx. 30 individuals each) were collected from the intertidal to upper sublittoral zones at Sakurajima, Kagoshima, Kagoshima Prefecture (32°6′33″N, 130°18′21″E; Fig. 1) on May 11, 2012, and used for the measurement of oxygen evolution (both species) and PAM-chlorophyll fluorometry (only *G. elegans*). Additional *P. tenuis* specimens (approx. 30 individuals) were collected from the same site on April 10, 2013, for PAM-chlorophyll fluorometry measurements of photosynthesis.

Collected algae were stored in 1,000-ml plastic bottles filled with seawater and transported directly to the Laboratory of Fisheries Biology and Oceanography, Faculty of Fisheries, Kagoshima University in a cooler kept at about 20 °C, which is approximately the same temperature as on the sampling date. The samples were kept for 1–3 days prior to examination in 1,000-ml flasks containing sterile seawater at a salinity of 33 psu. For analysis, the flasks

were placed in an incubator (EYLA MTI-201B; Tokyo Rikakikai Co., Ltd., Tokyo, Japan) at a water temperature of 20 °C and under photosynthetic active radiation (PAR) of 100 μmol photons m^{-2} s^{-1} (12/12 h, light/dark). Voucher specimens were deposited in the Herbarium of Kagoshima University Museum, Kagoshima. The terminology and definition of each parameter in the text are based on Cosgrove and Borowitzka [30].

Effect of temperature on photosynthesis

The measurement methods are described in detail in our previous reports [16, 17, 31, 32]. Briefly, the materials were divided into eight temperature treatment groups (8, 12, 16, 20, 24, 28, 32, and 36 °C; $N = 5$ replicates/treatment) and maintained under 200 μmol photons m^{-2} s^{-1}, which is higher than the saturation irradiance (E_k), as revealed by the photosynthetic–irradiance (P–E) curve (as detailed below). Light was provided by a metal-halide lamp [33], and temperature was controlled using a water bath (Coolnit CL-600R; Taitec, Inc., Tokyo, Japan).

Dark respiration and net photosynthetic rates were determined by measuring the dissolved oxygen (DO) concentration (mg l^{-1}) every 5 min for 30 min after a 30-min pre-incubation to acclimate the samples to each experimental condition. The slope of a linear regression was determined from the data of the 30-min measurements to estimate rates. DO was measured using a polarographic sensor and a DO meter (Models 58 and 5100; YSI Incorporated, Yellow Springs, OH).

Explants used in this experiment weighed approximately 300 mg (wet weight, mg_{ww}) and were acclimated overnight with sterilized seawater in the incubator [34, 35]. To start the experiment, we randomly selected at least five explants and placed them in 100-ml BOD bottles containing sterilized natural seawater. The DO sensors were placed in the sterilized natural seawater so that no bubbles were trapped in the sensors and the seawater was continuously stirred during the measurement. The exact volume of the BOD bottles was determined after the experiments and was used in the estimates of photosynthesis and dark respiration rates. Seawater medium was renewed after each measurement to avoid any effects due to the depletion of nutrients and dissolved carbon dioxide.

Irradiance effect on the photosynthesis

The procedures are described in detail our previous reports [16, 17, 31, 32]. Photosynthetic rates were determined at 0, 30, 60, 100, 150, 200, 250, and 500 μmol photons m^{-2} s^{-1} ($N = 5$ replicates/level) at 20 °C, and the procedure is the same at that of the temperature experiment. The temperature for this experiment was determined based on that of

the natural habitat during the sampling date. This temperature generally corresponded with the temperature at which net photosynthesis was highest, as determined by the photosynthesis versus temperature experiment.

Temperature and irradiance effect on photosynthetic parameters

Maxi-imaging-PAM (Heinz Walz GmbH, Effeltrich, Germany) measurements were based on procedures described in detail in our previous studies [16, 17, 32, 36]. Ten whole algae from a population that was pre-incubated were randomly selected and placed in a stainless-steel tray (12 × 10 × 3 cm) containing sterilized seawater. The temperature of the tray was controlled with a block incubator (BI-535A; Astec, Fukuoka, Japan) by placing the tray on the aluminum block of the incubator. The temperature of the water in the tray was measured with a thermocouple to confirm that the appropriate temperature condition was achieved.

The maximum effective quantum yields (Φ_{PSII}; at 0 μmol photons m^{-2} s^{-1}) were measured at temperatures ranging from 8 to 36 °C in 2 °C increments. Each increment in temperature occurred over a 30-min period with an additional 30 min allowed for dark and temperature acclimation. One set of experiments typically took more than 6 h to complete.

Modeling the photosynthetic response to irradiance and temperature

The temperature response of gross photosynthesis (oxygen evolution) and the Φ_{PSII} (chlorophyll fluorescence) were assumed to follow a non-linear exponential function (Eq. 1), where y is the response variable, which is either the gross photosynthetic rate or Φ_{PSII}, and K is the temperature in Kelvin [37]. There are four parameters in this model: y_{max} is the maximal rate of y occurring when the temperature is K_{opt}, H_a is the activation energy (kJ mol^{-1}), and H_d is the deactivation energy (kJ mol^{-1}); R in this model is the ideal gas constant and has a value of 8.314 J K^{-1} mol^{-1}. The gross photosynthetic rates were calculated by summing up the dark respiration rates and the net photosynthetic rates, after assuming that the dark respiration rates approximated photorespiration.

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

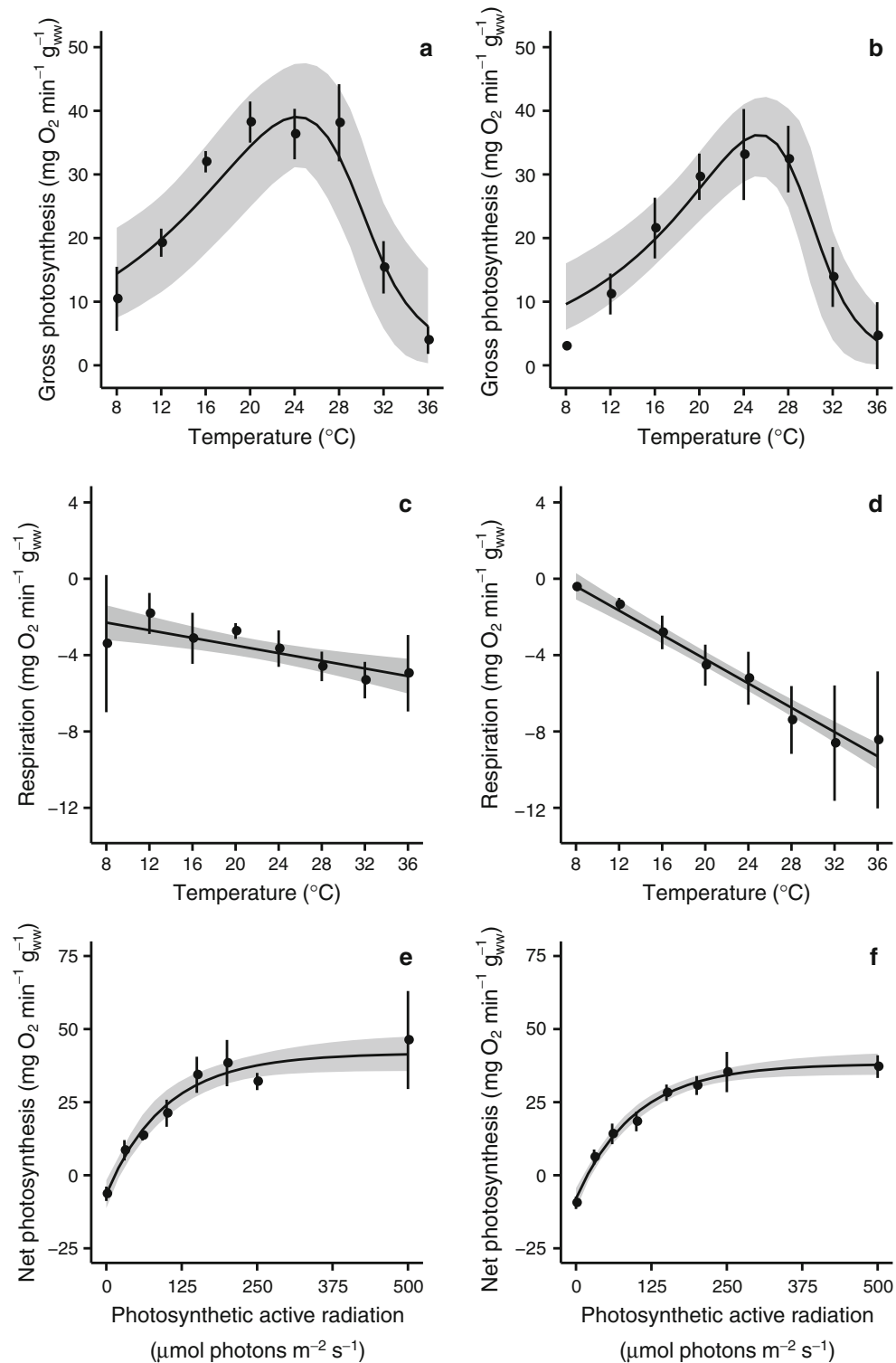The relationship between the dark respiration rate and temperature was assumed to follow a simple linear model.

Fig. 2 The response of oxygenic photosynthesis and dark respiration of *Gelidium elegans* (**a**, **c**, **e**) and *Pterocladiella tenuis* (**b**, **d**, **f**) to temperature and irradiance. **a**, **b** Gross photosynthetic rates along a temperature gradient determined at 200 μmol photons m^{-2} s^{-1}. **c**, **d** Dark respiration rates along a temperature gradient. **e**, **f** Net photosynthetic rates along an irradiance gradient determined at 20 °C.

Filled circles and *vertical lines* Mean and 95 % confidence interval (CI) of the mean ($N = 5$), respectively, *solid curved lines* expected value, *shaded region* in **a**, **b**, **e**, **f** 95 % Bayesian credible interval of the model, *shaded region* in **c**, **d**, 95 % CI of the generalized linear model. g_{ww} grams wet weight

The response of photosynthesis to irradiance was examined by modeling the data using an exponential equation [38–41] that includes a respiration term, which has the form:

$$P_{net} = P_{max}\left(1 - \exp\left(-\frac{\alpha}{P_{max}}E\right)\right) - R_d \qquad (2)$$

where P_{net} is the net O_2 production rate, P_{max} is the maximum O_2 production rate, α is the initial slope of the photosynthesis versus irradiance curve, E is the incident irradiance, and R_d is the dark respiration rate. From this model, the saturation irradiance (E_k) was calculated as P_{max}/α, and the compensation irradiance (E_c) was $P_{max} \ln\left(\frac{P_{max}}{(R_d - P_{max})}\right)/\alpha$.

Statistical analysis

Statistical analyses of all the models were performed using R version 3.0.1 [42], and model fitting was done using rstan version 2.1 [43]. The parameters were examined by fitting the relevant models (i.e. Eq. 1 or Eq. 2) using Bayesian inference. 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.

Weakly informative normal priors were placed on all of the parameters of the model, and a half-cauchy prior was placed on the scale parameter of the models [44, 45]. A generalized linear model was used to analyze the dark respiration–temperature relationship, assuming a normal error distribution.

Results

Effect of temperature on gross photosynthesis and dark respiration (oxygen evolution)

The measured gross photosynthetic rates of *G. elegans* and *P. tenuis* were generally higher at temperatures of between 20 and 28 °C. Maximum values of 38.2 and 33.1 mg O_2 g_{ww}^{-1} min^{-1} [95 % confidence interval (CI) 35.0–41.5 and 26.0–40.3], respectively, were obtained at 20 °C (*G. elegans*) and 24 °C (*P. tenuis*), and minimum values of 4.0 and 3.0 mg O_2 g_{ww}^{-1} min^{-1} (95 % CI 1.8–6.1 and 0.0–9.9 µmol O_2 mg$_{chl-a}^{-1}$ min^{-1}), respectively, were obtained at 36 °C (*G. elegans*) and 8 °C (*P. tenuis*) (Fig. 2a, b).

The model (Eq. 1) fit to the data indicated that the optimal temperature $\left(T_{opt}^{GP}\right)$ of *G. elegans* and *P. tenuis*, i.e. the temperature at which the maximal gross photosynthetic rates {GP_{max} = 40.3 and 37.0 mg O_2 g_{ww}^{-1} min^{-1} [95 % Bayesian credible interval (BCI) of 33.6–48.7 and 30.7–43.2 mg O_2 g_{ww}^{-1} min^{-1}], respectively} would occur, was 24.3 and 25.5 °C (95 % BCI 20.7–28.0 and 23.4–28.3 °C), respectively. The activation energy $\left(H_a^{GP}\right)$ of *G. elegans* and *P. tenuis* was determined to be 56.6 and 64.1 kJ mol^{-1} (95 % BCI 27.9–95.4 and 34.0–99.4 kJ mol^{-1}) and the deactivation energy $\left(H_d^{GP}\right)$ was 330 and 405 kJ mol^{-1} (95 % BCI 168–714 and 236–881 kJ mol^{-1}), respectively.

The measured [mean ± one standard error (SE)] dark respiration rates of *G. elegans* and *P. tenuis* increased from 3.4 ± 1.8 to 4.5 ± 1.0 and from 0.4 ± 0.03 to 8.4 ± 1.8 mg O_2 g_{ww}^{-1} min^{-1}, respectively, as experimental temperatures were increased from 8 to 36 °C (Fig. 2c, d). The generalized linear model of the dark respiration rates, with the temperature as a covariate and the species as discrete factors, indicated that there were statistically significant differences between the slopes of the fitted linear model ($F_{(1,81)} = 22.4$; $P < 0.0001$). The respiration rates increased at a rate of 0.10 ± 0.03 (mean ± SE) mg O_2 g_{ww}^{-1} min^{-1} °C for *G. elegans* and 0.32 ± 0.03 mg O_2 g_{ww}^{-1} min^{-1} °C for *P. tenuis*.

Effect of irradiance on net photosynthesis (oxygen evolution)

The measured net photosynthetic rates of *G. elegans* and *P. tenuis* at 20 °C steadily increased from −6.3 and −9.4 mg O_2 g_{ww}^{-1} min^{-1} (95 % CI −8.8 to −3.9 and −11.6 to −7.3 mg O_2 g_{ww}^{-1} min^{-1}), respectively, at 0 µmol photons m^{-2} s^{-1} to a high of 46.3 and 37.2 mg O_2 g_{ww}^{-1} min^{-1} (95 % CI 29.5–63.0 and 33.3–41.0 mg O_2 g_{ww}^{-1} min^{-1}), respectively, at 500 µmol photons m^{-2} s^{-1} (Fig. 2e, f).

Given the model (Eq. 2) and the data, the posterior distribution of the parameters of *G. elegans* and *P. tenuis* to describe the model was determined to be 48.3 and 46.1 mg O_2 g_{wwh}^{-1} min^{-1} (95 % BCI 42.3–56.0 and 46.7–50.9 mg O_2 g_{ww}^{-1} min^{-1}), respectively, for the maximum net photosynthetic rate (P_{max}), 6.5 and 8.0 mg O_2 g_{ww}^{-1} min^{-1} (95 % BCI 1.7–11.3 and 4.4–11.7 mg O_2 g_{ww}^{-1} min^{-1}), respectively, for the dark respiration rate (R_d), and 0.50 and 0.47 mg O_2 g_{ww}^{-1} min^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$ [95 % BCI 0.34–0.74 and 0.36–0.61 mg O_2 g_{ww}^{-1} min^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$, respectively] for the initial slope (α) of the model.

From these parameters, we estimated that the 95 % BCI of the compensation irradiance (E_c) of *G. elegans* and *P. tenuis* ranged from 4.5 to 23 and 12 to 25 µmol photons m^{-2} s^{-1}, with a mean value of 14 and 19 µmol photons m^{-2} s^{-1}, respectively, and that the 95 % BCI of the saturation irradiance (E_k) ranged from 51 to 135 and 59 to 116 µmol photons m^{-2} s^{-1}, with a mean value of 88 and 83 µmol photons m^{-2} s^{-1}, respectively.
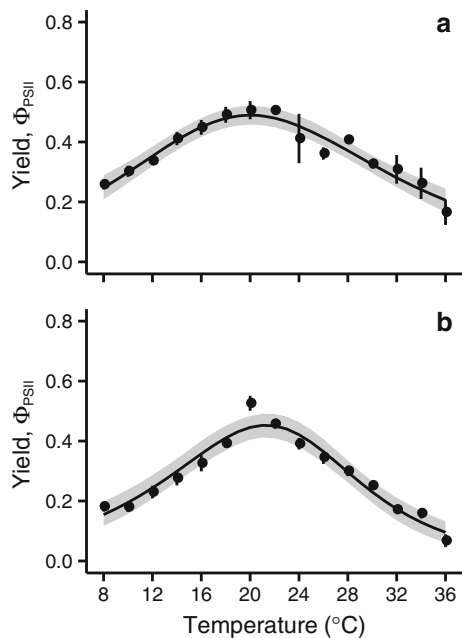
Fig. 3 Temperature response of the maximum effective quantum yield (Φ_{PSII}) in *Gelidium elegans* (**a**) and *Pterocladiella tenuis* (**b**). *Filled circles* and *vertical lines* Mean and 95 % CI of the mean ($N = 10$), respectively, *solid curved lines* expected value, *shaded region* 95 % Bayesian confidence interval of the model

Effect of temperature on the maximum Φ_{PSII} (chlorophyll fluorescence)

The temperature response of the measured maximum Φ_{PSII} at 0 µmol photons m^{-2} s^{-1} between the two species was almost similar (Fig. 3a, b). Indeed, the Φ_{PSII} of *G. elegans* and *P. tenuis* was low at low temperatures and was 0.26 and 0.18 (95 % CI 0.24–0.28 and 0.16–0.20), respectively, at 8 °C, reaching a peak of 0.51 and 0.53 (95 % CI 0.48–0.58 and 0.50–0.55), respectively, at 20 °C, then decreasing to 0.17 and 0.07 (95 % CI 0.12–0.21 and 0.05–0.09), respectively, at 36 °C.

Given the model (Eq. 1) and the data, there was little difference among Φ_{PSII} occurring at the optimal temperature $\left(T_{opt}^{\Phi_{PSII}}\right)$ between *G. elegans* and *P. tenuis*, which was 0.49 and 0.45 (95 % BCI 0.46–0.52 and 0.41–0.49), respectively, at a temperature $\left(T_{opt}^{\Phi_{PSII}}\right)$ of 20.0 and 21.3 °C (95 % BCI 18.8–21.5 and 20.2–22.4 °C), respectively. The values for $H_a^{\Phi_{II}}$ were 78.0 and 81.5 kJ mol^{-1} (95 % BCI 49.7–105.1 and 57.5–107.9 kJ mol^{-1}), respectively, and the values for $H_d^{\Phi_{II}}$ were 148 and 211 kJ mol^{-1} (95 % BCI of 129–169 and 180–247 kJ mol^{-1}), for *G. elegans* and *P. tenuis*, respectively.

Discussion

The results of this study demonstrate that temperature and irradiance strongly influenced both the photosynthetic and

respiratory rates of *G. elegans* and *P. tenuis* (Figs. 2, 3). These two algae species are found on the substrata throughout the year as a perennial species; however, they reach peak abundance in early summer (i.e., June and July in Kagoshima) [3]. Although we did not measure the seasonal changes in seawater temperature at the study site in our study, Tsuchiya et al. [15] reported that the seawater temperature at the study site and at the depth habitat (3 m) in 2010 ranged from 16 to 29 °C [15] and that, in particular, the seawater temperature in June and July fell within the range of 20–28 °C.

The optimal temperature for maximum photosynthetic activity was consistently higher in experiments conducted using oxygen sensors than PAM-chlorophyll fluorometry. The differences between optimal temperature that maximized Φ_{PSII} (PAM-chlorophyll fluorometry) and that which maximized gross photosynthesis (oxygen evolution) were 4.2 °C (95 % BCI 0.5–8.0 °C) for *G. elegans* and 4.2 °C (95 % BCI 1.6–6.8 °C) for *P. tenuis*. The upward shift in optimal temperature attributable to the gross photosynthesis experiment can be partly attributed to the effect caused by the addition of dark respiration to net photosynthesis. Therefore, it is reasonable to presume that there is a shift in the temperature optima to the right caused by the addition of dark respiration rates in the determination of gross photosynthetic rates. Nevertheless, the chlorophyll fluorescence experiment provides an approximate minimum and the dissolved oxygen sensor experiment provides an approximate maximum, and these can be used to indicate the most optimal range of temperatures for photosynthesis. By this definition, the optimal temperature range for *G. elegans* was estimated to be 20.0–24.3 °C and for *P. tenuis*, 21.3–25.5 °C. The mean water temperature in June/July (e.g., 20–28 °C) expected at the collection site and the aforementioned temperature range are remarkably similar. Furthermore, in the case of *G. elegans*, these ranges are comparable to those reported in earlier studies in which optimal growth temperatures of between 24 and 28 °C were indicated [22, 24]. Despite the lack of any information on the optimal temperature ranges for *P. tenuis*, we assumed that it is similar to that of *G. elegans*.

These two algal species can be found in the same habitat, and in Japan, their horizontal distribution tends to overlap, clearly indicating that two species share similar temperature characteristics. Similar to the study carried out on *Gracilariopsis chorda* (Holmes) Ohmi [31], comparison of the photosynthetic activities of these two species from geographically different locations will be needed to confirm these conclusions.

The maximum quantum yield (F_v/F_m) is typically temperature independent when determined after long periods of darkness. Nevertheless, the effective quantum yield (Φ_{PSII}) is temperature dependent in physiologically

appropriate temperature ranges and will vary with species [46, 47]. The reduction in gross photosynthesis at high temperatures is partly attributable to increased respiration rates, as demonstrated by the dark respiration experiments, and in part to reduced CO_2 uptake as Rubisco activity declines [47]. However, the mechanisms associated with the decline in Φ_{PSII} remain to be determined. Typically in higher plants, the drop in Φ_{PSII} at high temperatures can be associated with inactivation of photosystem II (PSII) reaction centers [48]. However, unlike higher plants and other orders of macroalgae, red algae possess a light harvesting antennae that include phycobilisomes (i.e., phycoerythrin, phycocyanin, and allophycocyanin), which captures a wide band (580–680 nm) of light energy [49–51]. Approximately half of the energy captured by phycobilisomes is then transferred to photosystem I (PSI), and when all the photochemical traps of PSII are closed, up to 100 % of this energy can be transferred to PSII [52].

Therefore, with respect to the high-temperature chlorophyll fluorescence experiments, the decreases in Φ_{PSII} may be due to changes in the state of PSII or to the proportion of energy transferred to PSI and PSII. It should be noted that the values of Φ_{PSII} determined for G. elegans and P. tenuis are lower than typical values observed for the red algae *Pyropia yezoensis* (Ueda) Hwang et Choi [53] and for the brown algae *Sargassum fusiforme* (Harvey) Setchell as (*Hizikia fsiformis*) (0.58) [54].

Only a few studies have been published on photosynthetic activity in species of order Gelidiales, especially with respect to chlorophyll fluorescence and oxygen evolution. Domínguez-Álvarez et al. [55] reported that the Φ_{PSII} of three species of Gelidiales [*Gelidium arbuscula* Bory de Saint-Vincent ex Børgesen, *G. canariense* (Grunow) Seoane Camba ex Haroun et al., and *Pterocladiella capillacea* (Gmelin) Santelices et Hommersand] from the Canary Islands was negatively correlated with incident irradiance and that Φ_{PSII} decreased as irradiance increased towards noon, subsequently recovering during the evening. These findings suggest that photoinhibition occurs at high irradiances. The photosynthetic capacity (relative electron transport rates and gross photosynthesis) of *Gelidium sesquipedale* (Clemente) Thuret from Portugal has also been reported to be irradiance dependent, decreasing with depth [27].

In our study, the net photosynthetic rate of G. elegans and P. tenuis at 20 °C was strongly dependent on irradiance when PAR was <88 and 83 µmol photons m^{-2} s^{-1}, respectively (Fig. 2e, f). We also detected no signs of photoinhibition, as was the case for a similar study on the agarophyte *Gracilariopsis chorda* [31]. However, in accordance with the suggestions of the authors of these earlier studies conducted on the Canary Islands and in Portugal [27, 55], we also suggest that further research is required on our two species. In particular, in situ

measurements of photosynthetic activity are needed to determine how these species adapt to irradiance in their natural habitat.

Despite being at the southern limit of distribution in Japan, G. elegans and P. tenuis can be considered to be well-adapted to the current range of seawater temperatures in this region; however, they do appear to be close to their range of tolerable temperatures and are likely sensitive to changes in environmental water temperature. Indeed, the relatively high seawater temperature caused by the arrival of the meandering Kuroshio Current has been associated with decreasing Gelidium/Pterocladiella production in the coastal areas of Hachijo-jima Island (Izu Islands) [56]. Therefore, if summer seawater temperatures continue to increase in this area, as has been shown in previous studies [13–15], it will become much more difficult, if not impossible to harvest this species in this region.

It should be noted that the results of this study are based on short-term laboratory measurements of photosynthesis and respiration using both dissolved oxygen and fluorescence measurements. As such, the temperature characteristics of these species have not yet been fully elucidated. Temperature acclimation has not been examined for photosynthesis and respiration, which was observed in higher plants [57]. Therefore, extrapolation of our results must be done with caution, and we acknowledge that studies of a longer time-scale are needed to verify our hypotheses, especially in terms of climate change-induced increases in temperature.

In conclusion, the natural seawater temperature conditions at the present time are most likely sub-optimal for G. elegans and P. tenuis growing in the Kagoshima area, and any significant upward shifts in temperature will most likely negatively affect the population of these species. The results can be detrimental to the productivity of this important fisheries resource, and diligent monitoring is essential to detect any changes in their distribution and population size.

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