



Ecotypic differentiation in populations of Brazilian coast: recognizing adaptation to temperature in *Gracilariopsis tenuifrons* (Gracilariales, Rhodophyta)

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Abstract

The Brazilian coast presents diverse abiotic characteristics, such as temperature, and we know that surface seawater temperatures are rising as a result of climate change. Therefore, to better interpret the effects of such changes, we chose to investigate *Gracilariopsis tenuifrons*, a species of red algae widely occurring on the Brazilian coast. We specifically evaluated the effect of different temperatures (18–35 °C) on growth rates (GRs), photosynthetic parameters, and pigment contents of female gametophytes from five different populations distributed along 7450 km of coastline, including Maranhão State (MA, 2.4°S), Rio Grande do Norte State (RN, 5.4°S), Bahia State (BA, 14.48°S), and São Paulo State (SP1, 23.5°S and SP2, 24.2°S). All samples tolerated temperatures between 18 and 33 °C, but none of them could tolerate temperatures of 35 °C, irrespective of the populations. However, the highest GRs varied among populations (MA, 23–30 °C; RN, 28–33 °C; BA, 23–28 °C; SP1, 25–28 °C; SP2, 28 °C). MA and BA populations showed the highest maximal measurement (μ_{\max}) of the thermal performance curve when compared to SP1 and SP2 populations. The RN population showed the worst μ_{\max} values, 5.6% day⁻¹; however, it was more resilient to stressful temperatures (33 °C) than the others. The BA population presented some physiological characteristics similar to populations from the northeastern and southeastern regions. Our data showed that *Gp. tenuifrons* presents latitudinal ecotypes associated with temperature. Northeastern populations could be more vulnerable in a drastic scenario of climate change (up to 4 °C); otherwise, this species could occupy regions further to the south of its current distribution.

Keywords Marginal populations · Ecotypes · Brazilian coast · Climate change · Sea surface temperature · Thermal adaptation

Introduction

The concept of ecotype is a precursor to speciation, and it is related to populations of species that have different physiological adaptations owing to environmental conditions or geographic barriers (Lowry 2012). The occurrence of ecotypes along a latitudinal distribution can bring advantages for the permanence of a species, even in the face of climate change, since some of them may present characteristics

that are more adaptable to the changes imposed. Among the red algae, ecotypes of some species have already been characterized relative to different abiotic factors, including temperature (Zanolla et al. 2015; Borlongan et al. 2017).

Marine heatwaves and increased sea surface temperatures (SST) have occurred with more frequency in the last 30 years compared to the early twentieth century (Smale et al. 2019; Turkington et al. 2019). This climatic change is related to anthropogenic activities, and it causes the redistribution and reorganization of species in natural habitats (Burrows et al. 2011; Chen et al. 2011). Therefore, range-edge populations are likely to be most vulnerable and may be affected by the increase of SST (Smale et al. 2019). The extinction of a species can be avoided if (i) individuals are able to physiologically acclimate, (ii) populations undergo evolutionary

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adaptations, or (iii) populations move to more favorable habitats (Hoffmann and Sgrò 2011; Jueterbock et al. 2013). Thus, if we know how marine species populations respond to changes in temperature, we can better predict changes in coastal ecosystems, according to IPCC forecast scenarios (optimistic 1.5–2 °C, intermediate 2.7–3.6 °C, and drastic 4 °C), related to gas emissions, such as aerosol, methane, nitrous oxide, carbon dioxide, and others (IPCC 2021).

Along the Brazilian coast, an extensive shore with a wide latitudinal variation of irradiance, temperature, and nutrients, ecotypic populations have been recognized in four species of algae, including *Gracilaria birdiae* Plastino and E.C. Oliveira (Ursi et al. 2013), *Gracilaria caudata* J. Agardh (Araujo et al. 2014; Faria et al. 2017), *Gracilaria domingensis* (Kützinger) Sonder ex Dickie (Castro and Yokoya 2018), and *Hypnea pseudomusciformis* (Nauer et al. 2020). These ecotypic populations could allow us to gain a better understanding of adaptation induced by different environmental conditions, as well as a perspective of how individual populations respond to environmental variations. Moreover, knowing the thermal tolerance of species can contribute to a better interpretation of their geographical distribution, as shown by McLachlan and Bird (1984) for different species of *Gracilaria*.

The genus *Gracilariopsis*, together with *Gracilaria*, produces 91% of the total agar value, and another 9% is produced by other red algae (Lim et al. 2017; Porse and Rudolph 2017). Phycocolloid industries use agar as a main resource for producing animal feed (Qi et al. 2010; Johnson et al. 2014), biomaterial for packing, thickener for foods, or skincare products (Leandro et al. 2020). According to FAO (2021), *Gracilariopsis* and *Gracilaria* have become the principal red algae cultivated in the world with 3.6 million tonnes of annual production. China (around 95%) followed

by Indonesia (around 3%) are the main cultivators for both genera in the world (FAO 2021).

Gracilariopsis tenuifrons (Fig. 1C) occurs from Mexico, Cuba, and Venezuela (Hernandez et al. 2020) to the Brazilian coast (Lyra et al. 2021) where it is found between Maranhão (2.4°S) and São Paulo States (24°S, southern limit). In Brazil, the distance between limit populations is around 7450 km. This species has a “*Polysiphonia*”-type life history (Brito and Silva 2005), and individuals of a single-studied population from Alagoas State (9°S) tolerates a wide range of salinity (15–40) and temperature (17–32 °C) under laboratory conditions (Plastino et al. 1998). Furthermore, *Gp. tenuifrons* has been considered economically important as an efficient biofilter for absorbing nutrients in integrated multi-trophic aquaculture, helping in the reduction of water usage and removal of metabolites produced by marine fishes (Hernández et al. 2006) and shrimps (Carneiro et al. 2021).

As noted, *Gp. tenuifrons* is economically important and has a wide geographical distribution along the Brazilian coast with a wide range of sea surface temperatures (27–29 °C, northeastern Brazil; and 20–26 °C, southeastern Brazil) (Fig. 1B). Nonetheless, few studies have reported on the putative thermal adaptations, considering different populations. Therefore, we aimed to elucidate and characterize putative ecotypes by evaluating the effects of temperatures (18, 20, 23, 25, 28, 30, 33, and 35 °C) on five populations, including those that occur at the extremes of their distribution (2.4°S and 24°S). At the higher range of SST, these results are expected to help in the interpretation of the effects of higher temperatures owing to climate change on these algal populations. This study should also advance a preliminary analysis of the performance of these populations for future mariculture in Brazil and for the development of effective conservation strategies in an environment subject to

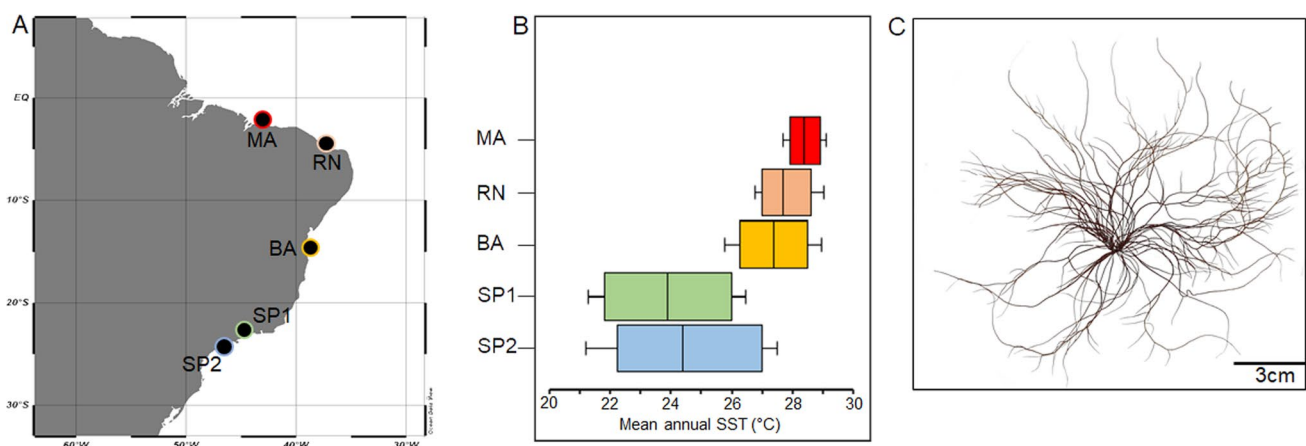


Fig. 1 A Map of the Brazilian coast showing five site places where *Gp. tenuifrons* was collected: São Luis-Maranhão State (MA), Macau-Rio Grande do Norte State (RN), Ilhéus-Bahia State (BA), Ubatuba-São Paulo State (SP1), and Itanhaém-São Paulo State (SP2);

B Mean annual (2015–2019) of sea surface temperature at each sampling location (MA, RN, BA, SP1, and SP2) based on satellite-obtained mean monthly SST datasets (<http://podaac-tools.jpl.nasa.gov/soto>); and **C** habit of *Gp. tenuifrons*, scale bar = 3 cm

abiotic and anthropogenic factors, such as habitat fragmentation, degradation, and overharvesting.

Materials and methods

Biological material

Five tetrasporophytes of *Gracilariopsis tenuifrons* were collected from each of five localities along the Brazilian coastline (Fig. 1A). Collections were made (i) in October 2018 at São Marcos Beach (2.4°S 44.28°W), São Luis, Maranhão State (MA), a marginal population of the northeastern Brazilian coast; (ii) in August 2018 at Diogo Lopes Mangrove (5.4°S 36.26°W), Macau, Rio Grande do Norte State (RN); (iii) in August 2016 at Me Ache Beach (14.48°S 39.01°W), Ilhéus, Bahia State (BA) (hereinafter considered an intermediate population between MA/RN and the following sites); (iv) in August 2017 at Dura Beach (23.5°S 45.1°W), Ubatuba, São Paulo State (SP1); and (v) in June 2018 at Cibratel Beach (24.2°S 46.8°W), Itanhaém, São Paulo State (SP2), the limit and marginal southeastern distribution of the species. Samples were collected in two different environments, i.e., rocky shores (i, iii, iv, and v) and mangrove (ii). Unialgal non-axenic cultures of unfertilized female gametophytes were established from tetraspores released and cultivated in control conditions (Plastino and Oliveira 1990). Tetraspores produced male and cystocarpic plants. Small apical branches of the latter were cultivated at the same cultural conditions for at least 2 months, assuring the absence of fertilized carpogonia prior to the start of experimentation. Experimental plants are hereinafter designated as female gametophytes from Maranhão State (MA); from Rio Grande do Norte State (RN); from Bahia State (BA); from Ubatuba, São Paulo State (SP1); and from Itanhaém, São Paulo State (SP2). Plants derived from spores were kept in the Gracilariaceae Germplasm Bank of the University of São Paulo (Costa et al. 2012). Voucher specimens were deposited in the herbarium of the Bioscience Institute at the University of São Paulo (MA, SPF-58489; RN, SPF-58286; BA, SPF-58287; SP1, SPF-58491; SP2, SPF-58940).

General culture conditions

Apical segments of strains were maintained in von Stosch-enriched seawater with modifications (Ursi and Plastino 2001) and diluted to 50% with sterile seawater (salinity at 32). The algae were kept in a temperature-controlled room at 25 ± 1 °C with a photoperiod of 14 (14:10, light:dark). Photosynthetically active radiation (PAR) was $70 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ provided by Osram 40 W Daylight fluorescent tubes and was measured by a quantameter (Li-COR

model L1-185). Cultures were aerated for 30 min h^{-1} , and the medium was renewed weekly.

Experimental design

One week before the start of experimentation (pretreatment in each temperature), 32 apical segments of *Gp. tenuifrons* 20 mm in length were obtained from one individual (total: five individuals and 160 tips) of unfertile female gametophytes derived from each of the five populations (MA, RN, BA, SP1, and SP2; total 800 apical segments). These tips of each individual (total of 32) were grouped into clusters of four and cultivated in eight Erlenmeyer flasks (total: 40 flasks per population), containing 400 mL of enriched seawater (four apical segments, and about 12 mg of algae per flask), under general culture conditions. According to our experimental design, plants received eight treatments: 18 and 20 °C (low temperatures); 23, 25, and 28 °C (intermediate temperatures); and 30, 33, and 35 °C (high temperatures) provided by BOD Incubator (Bio-Oxygen Demand) with accurate temperature control (EL141/3, Eletrolab). Five replicates per treatment were made for each population with cultivation over a period of 28 days. Each replicate was represented by one distinct individual. Growth was assessed weekly; in vivo chlorophyll fluorescence and pigment content were assessed at the end of the experiment.

Growth rates

Growth was assessed by measuring fresh mass. Growth rates were estimated as $\text{GR} = [(Fm_t/Fm_0)^{1/t} - 1] \times 100\%$, where Fm_t is final fresh mass, Fm_0 is initial fresh mass, and t is time (Yong et al. 2013).

In vivo chlorophyll fluorescence

Fluorescence measurements were performed after 28 days for all individuals ($n = 5$). The measurements were made from 11:00 to 14:00 after 4 h of exposure to light in the culture chamber. In vivo chlorophyll fluorescence was measured using an underwater Diving-PAM fluorometer (Walz, Germany). Apical segments were arranged on a magnetic sample holder to avoid overlap and acclimated in the dark for 10 min for PSII exposure. We used 8 levels of irradiance to construct electron transport rate (ETR) \times irradiance (PAR) curves: 8, 25, 50, 90, 132, 184, 276, and $378 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The exposure time of the apical segments in each irradiance was 20 s, interspersed with a saturation pulse of 0.8 s, approximately $6100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The maximum quantum yield (F_v/F_m) was provided by the Diving-PAM after an initial saturation pulse when the samples were at a low-intensity pulse of blue light (approximately $1.5 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). ETR was calculated

as $ETR = \Delta F/F_m' \times E_{PAR} \times A \times 0.15$, where $\Delta F/F_m'$ is the effective quantum yield measured; E_{PAR} is the incident irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); A , absorptance, is the fraction of incident light absorbed by algae; and 0.15 is the fraction of incident light absorbed by PSII, equivalent to red algae (Figueroa et al. 2003). Absorptance was calculated as $A = 1 - (E_{\lambda 0}/E_{\lambda})$, where $E_{\lambda 0}/E_{\lambda}$ is the transmittance (Enríquez and Borowitzka 2011). $ETR \times PAR$ curves were fitted using the KaleidaGraph software, according to the models of Webb et al. (1974), respectively: $ETR = ETR_{\max} \times [1 - \exp(-\alpha ETR \times E_{PAR}/ETR_{\max})]$, where ETR is the electron transport rate, ETR_{\max} is the maximum electron transport rate, αETR is the photosynthetic efficiency based on ETR data, and E_{PAR} is the irradiance. The following parameters were calculated and analyzed (Schreiber 2004): αETR , ETR_{\max} , and saturating irradiance from ETR data ($E_k - ETR = ETR_{\max}/\alpha ETR$).

Pigment analyses

Phycobiliprotein extractions were carried out at 4 °C according to Kursar et al. (1983) with modifications (Plastino and Guimarães 2001). Briefly, 100 mg FW of apical segments from each replicate ($n=5$) were ground in liquid nitrogen, followed by the addition of 1 mL of phosphate buffer 50 mM, pH 5.5. Crude extracts were centrifuged at $44,000 \times g$ for 20 min. The supernatant containing phycobiliproteins, including phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (APC), was removed, separated, and kept in sealed vials at 4 °C until read by spectrophotometry (HP 8452A). Chlorophyll *a* (Chlo-*a*) was extracted after dissolving the pellet from the previous procedure in methanol (addition of 1 mL) and then centrifuging at $12,000 \times g$ for 15 min. PE, PC, and APC concentration was calculated according to Kursar et al. (1983), and Chlo-*a* concentration was calculated according to Torres et al. (2014).

Sea surface temperature dataset

Sea surface temperature (SST) data were obtained from the PODAAC GHRSSST database (O'Carroll et al. 2019), which incorporates corrected estimates of temperature obtained from a high-resolution radiometer (AVHRR) at a temporal and spatial resolution of 1 day. Local SST estimates were taken at the same coordinates as the collection sites, namely MA, BA, SP1, and SP2. For the RN population, the SST estimate was performed closer to the mangrove's mouth owing to a lack of data at the coordinates of collection sites. SST datasets were plotted from January 2015 to December 2019. The highest SST values were observed from January to April, and the lowest SST values were observed from May to October. During summer, January to March, temperature ranges around 28 ± 0.3 °C in the northeastern region and

around 26 ± 0.6 °C in the southeastern region. In the middle of autumn to the end of winter, May to September, temperature ranges around 27 ± 1 °C in the northeastern region and around 22 ± 1 °C in the southeastern region (Fig. 1B).

Quantifying thermal performance curve

The nonlinear relationship between each of the five populations (MA, RN, BA, SP1, and SP2) and the range of temperatures noted above was analyzed according to Fernández et al. (2020). Briefly, a growth rate performance curve was constructed using a model-fitting approach (Gaitán-Espitia et al. 2014). The data were fitted for several mathematical models, e.g. Gaussian, modified Gaussian, Flinn, LRF, and quadratic, using the rTPC and nls.multstart R package (Padfield et al. 2021). Thermal performance curve (TPC) parameters, such as maximal measurement (μ_{\max}), thermal optimum (T_{opt}), thermal tolerance ($T_{\text{tolerance}}$), and critical thermal minimum and maximum at which population growth decreases (CT_{\min} and CT_{\max}) were derived from the best-fitted models. Overall, the quadratic_2008 model (Montagnes et al. 2008) was best-fitting according to the Akaike Information Criterion (AIC) (Angilletta 2006). Parameters of the curves were compared through confidence intervals (CI) computed from the likelihood profile and using AIC and the extra sum-of-square F test.

Statistics

The assumptions of normality and homogeneity of variances were tested using the Kolmogorov–Smirnov and Cochran test, respectively. When necessary, logarithmic transformation was employed ($x = \log(x + 1)$) and retested (Zar 1996). Growth rates, in vivo chlorophyll fluorescence (F_v/F_m , ETR_{\max} , E_k , and α), and pigment concentrations (PE, PC, APC, and Chlo-*a*) were analyzed by two-way factorial ANOVA (independent variables: temperature and population). Thermal performance curve (TPC) parameters related to GRs were analyzed by one-way ANOVA (μ_{\max} , T_{opt} , $T_{\text{tolerance}}$, CT_{\min} , and CT_{\max}) (Gaitán-Espitia et al. 2013). In all cases, the a posteriori Newman–Keuls test was used to establish statistical differences. Statistical analyses were done using the Statistica 12 program, considering $p < 0.05$. Raw data of GRs, photosynthesis, and pigment concentration are available as supplementary information (Table S2).

Results

Gracilariopsis tenuifrons cultivated at 35 °C did not survive after 1 week of treatment, regardless of population. In addition, all populations, excepted by the RN, showed the worst physiological performance at 33 °C. The populations

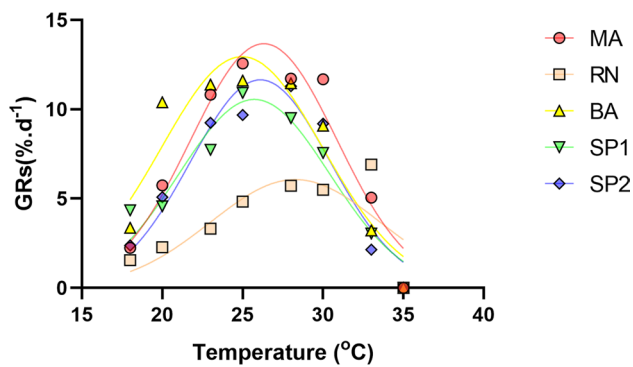


Fig. 2 Growth rate curves of *Gracilariopsis tenuifrons* from distinct populations (red circle=Maranhão State, MA; pink square=Rio Grande do Norte State, RN; yellow triangle=Bahia State, BA; green upside triangle=Ubatuba-São Paulo State, SP1; and blue diamond=Itanhaém-São Paulo State, SP2). Each point represents the mean growth ($n=5$) at each temperature treatment (18, 20, 23, 25, 28, 30, 33, and 35 °C)

Table 1 TPC traits (i.e., modeled data) for the growth rate of *Gracilariopsis tenuifrons* cultivated at different temperatures (18–35 °C)—maximal measurement (μ_{\max}), thermal optimum (T_{opt}), thermal tolerance ($T_{\text{tolerance}}$), and critical thermal maximum and minimum (CT_{\min} and CT_{\max}). Each emphasis used (regular, bold, italic, and underlined> on the different letters indicates a different statistical treatment

Population	μ_{\max}	CT_{\min} (°C)	T_{opt} (°C)	CT_{\max} (°C)	$T_{\text{tolerance}}$
MA	12.7 ^a	17.4 ^a	26.2 ^b	35.1 ^b	17.7 ^c
RN	5.6 ^c	17.4 ^a	27.4 ^a	37.4 ^a	20.0 ^a
BA	12.2 ^a	15.9 ^b	25.3 ^d	34.7 ^b	18.8 ^b
SP1	9.6 ^b	16.3 ^b	25.6 ^{cd}	34.9 ^b	18.6 ^b
SP2	10.6 ^b	17.2 ^a	25.7 ^{bc}	34.7 ^b	17.5 ^c

showed different thermal adaptation and the best GRs for each population varied according to the temperature (MA, 23–30 °C; RN, 28–33 °C; BA, 23–28 °C; SP1, 25–28 °C; SP2, 28 °C) (Figs. S1 and S2).

Thermal performance curves (TPCs)

Gracilariopsis tenuifrons from distinct populations exhibited the typical nonlinear relationship between temperatures and growth rates (Fig. 2, Table 1), according to the typical bell shape curve observed for ectothermic organisms (Angilletta et al. 2002). However, photosynthetic and pigment parameters exhibited negative and linear relationships, respectively, and it is making it impossible to evaluate the main traits of the TPCs.

MA and BA populations showed the highest μ_{\max} , around 12.2–12.7% day⁻¹, when compared to SP1 and SP2 populations that showed μ_{\max} around 9.6–10.6% day⁻¹. Furthermore, the RN population showed the worst μ_{\max} values, 5.6%

day⁻¹ (Table 1). However, the mangrove population (RN), showed the highest T_{opt} (27.4 °C), CT_{\max} (37.4 °C), and $T_{\text{tolerance}}$ (20.0 °C), when compared to rocky shore populations (MA, BA, SP1, and SP2) (Table 1). CT_{\max} values were about the same for rocky shore populations (34.7–35.1 °C). However, MA and SP2, as the species distribution limit, showed higher CT_{\min} (17.2–17.4 °C), when compared to BA and SP1 (15.9–16.3 °C) (Table 1). However, BA and SP1 showed higher $T_{\text{tolerance}}$ (18.6–18.8 °C), when compared to MA and SP2 (17.5–17.7 °C). For T_{opt} , MA showed higher optimum temperature (26.2 °C), when compared to BA and SP1 (25.3 and 25.6 °C, respectively). T_{opt} for SP2 (25.7 °C) was similar to that for MA (26.2 °C) and SP1 (25.6 °C) (Table 1).

In vivo chlorophyll fluorescence

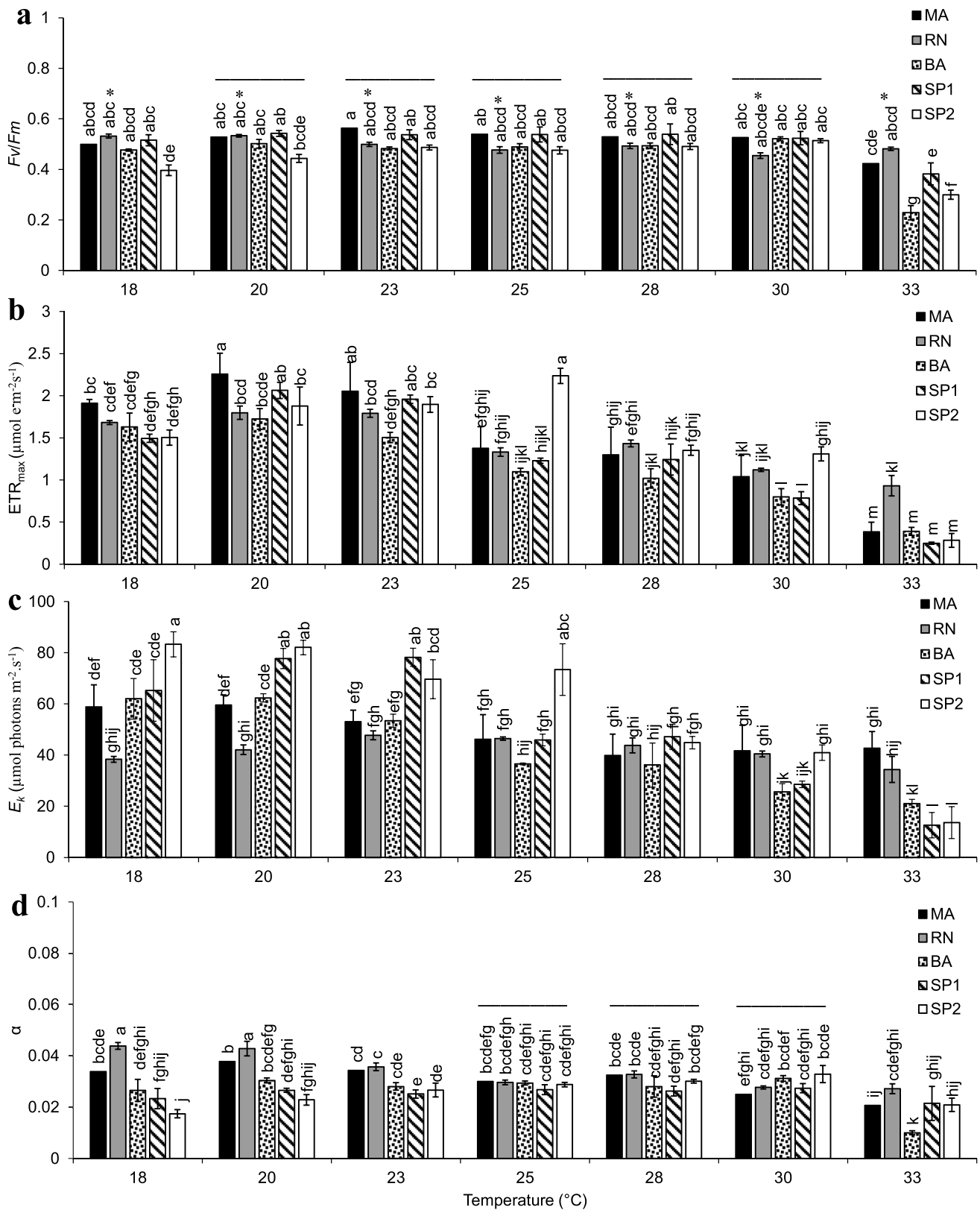
Maximum quantum yield (F_v/F_m), maximum electron transport rate (ETR_{\max}), saturating irradiance (E_k), and photosynthetic efficiency (α) of female gametophytes of *Gp. tenuifrons* cultivated for 28 days differed according to population (MA, RN, BA, SP1, and SP2) and temperature (18, 20, 23, 25, 28, 30, and 33 °C) (isolated and interactive effects) (Table S1).

Comparing the same population in different tested temperatures

Rocky shore (MA, BA, SP1, and SP2) and mangrove (RN) populations showed similar F_v/F_m (around 0.47) between 18 and 30 °C, whereas the populations occupying the highest latitudes of the Brazilian coast (SP1 and SP2) showed the lowest F_v/F_m at 33 °C (around 0.33) (Fig. 3a). In general, the intermediate population (BA) and populations occupying the lowest latitudes of the Brazilian coast (MA and RN) showed the highest ETR_{\max} at 18–23 °C (1.61 $\mu\text{mol e}^{-}\text{m}^{-2}\text{ s}^{-1}$), but the lowest ETR_{\max} between 25 and 33 °C (0.79 $\mu\text{mol e}^{-}\text{m}^{-2}\text{ s}^{-1}$) (Fig. 3b). In contrast, southeastern populations (SP1 and SP2) showed the lowest ETR_{\max} at 33 °C compared to other temperatures. Moreover, southeastern populations showed the lowest E_k values at 33 °C ($\pm 13 \mu\text{mol photons m}^{-2}\text{ s}^{-1}$) and the highest values at 18–23 °C ($\pm 75 \mu\text{mol photons m}^{-2}\text{ s}^{-1}$) (Fig. 3c).

Comparing different populations in each tested temperature

In general, temperatures promoted similar photosynthetic values as observed among the different populations tested between 20 and 30 °C for F_v/F_m , at 28 °C for E_k and between 25 and 30 °C for α (Fig. 3a, b, d).



Low temperatures At 18 $^{\circ}\text{C}$, SP2 showed the highest E_k value ($83 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), MA, BA, and SP1 showed intermediate E_k values ($\pm 62 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), and

RN showed the lowest E_k value ($42 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) (Fig. 3c). At 20 $^{\circ}\text{C}$, SP1 and SP2 showed the highest E_k values ($79 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), RN showed the lowest E_k

Fig. 3 In vivo chlorophyll fluorescence of *Gracilariopsis tenuifrons* from distinct populations (Maranhão State, MA; Rio Grande do Norte State, RN; Bahia State, BA; Ubatuba-São Paulo State, SP1; and Itanhaém-São Paulo State, SP2), cultivated at different temperatures (18, 20, 23, 25, 28, 30, and 33 °C): **a** F_v/F_m , maximum quantum yield; **b** ETR_{max} , maximum electron transport rate; **c** E_k , saturating irradiance; and **d** α , photosynthetic efficiency. Data presented as mean and standard deviation ($n=5$). Different letters represent significant differences among temperatures and populations ($p<0.05$). The extended line means a similar result among populations, and the asterisk means similar result among temperatures in a single population

value ($83 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), and MA and BA showed intermediate E_k values ($60 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), among all populations (Fig. 3c).

Middle temperatures At 23 °C, southeastern populations (SP1 and SP2) showed the highest E_k values ($\pm 73 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) in contrast to northeastern populations (MA, RN, and BA) ($\pm 51 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) (Fig. 3c). At 25 °C, SP2 showed the highest ETR_{max} and E_k values ($\pm 2.23 \mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$, ETR_{max} ; $\pm 73 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, E_k) in comparison to all other populations ($\pm 1.25 \mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$, ETR_{max} ; $\pm 44 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, E_k) (Fig. 3b, c). At 28 °C, all populations showed similar ETR_{max} values ($1.26 \mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$), except for BA, which showed lower values than RN ($1.43 \mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$) (Fig. 3b).

High temperatures At 33 °C, the worst photosynthetic performance was observed for SP2, followed by SP1, when compared to the others. Evaluating F_v/F_m , MA and RN showed higher values (± 0.45) when compared to SP2 (± 0.38), SP1 (± 0.29), and BA (± 0.22). Evaluating ETR_{max} , RN showed the highest value ($0.93 \mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$) in contrast to all other populations ($\pm 0.32 \mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$) (Fig. 3b). Evaluating E_k , MA and RN showed higher values ($\pm 39 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) than BA, SP1, and SP2 ($\pm 16 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) (Fig. 3c).

Pigments content

Phycocyanin (PE), phycocyanin (PC), allophycocyanin (APC), and chlorophyll-*a* (Chlo-*a*) contents of female gametophytes of *Gp. tenuifrons* cultivated for 28 days differed by population (MA, RN, BA, SP1, and SP2) and temperature (18, 20, 23, 25, 28, 30, 33, and 35 °C) (isolated and interactive effects) (Table S1).

Comparing the same population in different tested temperatures

For the mangrove population (RN), middle temperature (25 °C) promoted 1.88 times more PE and PC contents than all other temperatures. Otherwise, the lowest

temperature (18 °C) promoted the lowest PE and PC contents (Fig. 4a, b). Low, middle, and high temperatures (20–30 °C) promoted 2.10 times more Chlo-*a* contents than extreme temperatures (18 and 33 °C) (Fig. 4d).

For the intermediate population (BA), middle temperature (25 °C) promoted 1.71 times more PE content than high temperature (33 °C) (Fig. 4a). Furthermore, middle (25–28 °C) and high temperatures (only 33 °C) promoted 3.18 times more Chlo-*a* content than 18–23 and 30 °C (Fig. 4d).

Considering the southeastern populations, SP1 exposed to low temperature (20 °C) showed 2.64 times more PE content than when exposed to high temperature (33 °C) (Fig. 4a). Furthermore, SP1 exposed to low temperature (18 °C) promoted 3.13 times more Chlo-*a* content than when exposed to 23, 28, 30, and 33 °C (Fig. 4d).

For the southeastern marginal population (SP2), middle temperature (28 °C) promoted 3.65 times more PE content than low and high temperatures (18–20, and 33 °C), which showed the lowest PE contents (Fig. 4a). Furthermore, SP2 exposed to 20–30 °C showed 5.17 times more PC content than when exposed to 33 °C (Fig. 4b). SP2 exposed to low temperatures promoted 4.48 times more Chlo-*a* content than when exposed to middle and high temperatures (Fig. 4d).

Comparing different populations in each tested temperature

In general, the mangrove population (RN) presented higher chlorophyll-*a* content when compared to rocky shore populations (MA, BA, SP1, and SP2), as observed at 20, 23, and 30 °C (Fig. 4d). Furthermore, RN presented higher phycocyanin content at middle temperatures (23–28 °C) than that presented by other populations.

Low temperatures At 18 °C, MA, BA, and SP1 showed higher PE and PC contents than the southeastern marginal population (SP2) (Fig. 4a,b). RN, however, showed content similar to that among all populations (Fig. 4a, d); the BA population showed higher APC content than RN and SP2 (Fig. 4c). At 20 °C, the BA population showed higher phycocyanin content than both marginal populations (MA and SP2) (Fig. 4a).

Middle temperatures At 23 °C, the northeastern marginal population (MA) showed the highest PC content when compared to the southeastern populations (SP1 and SP2) (Fig. 4b). At 25–28 °C, the mangrove population (RN) showed the highest PE content when compared to all other populations (Fig. 4a). Considering chlorophyll-*a*, RN and BA showed the highest contents at 25–28 °C, when compared to all other populations (Fig. 4d).

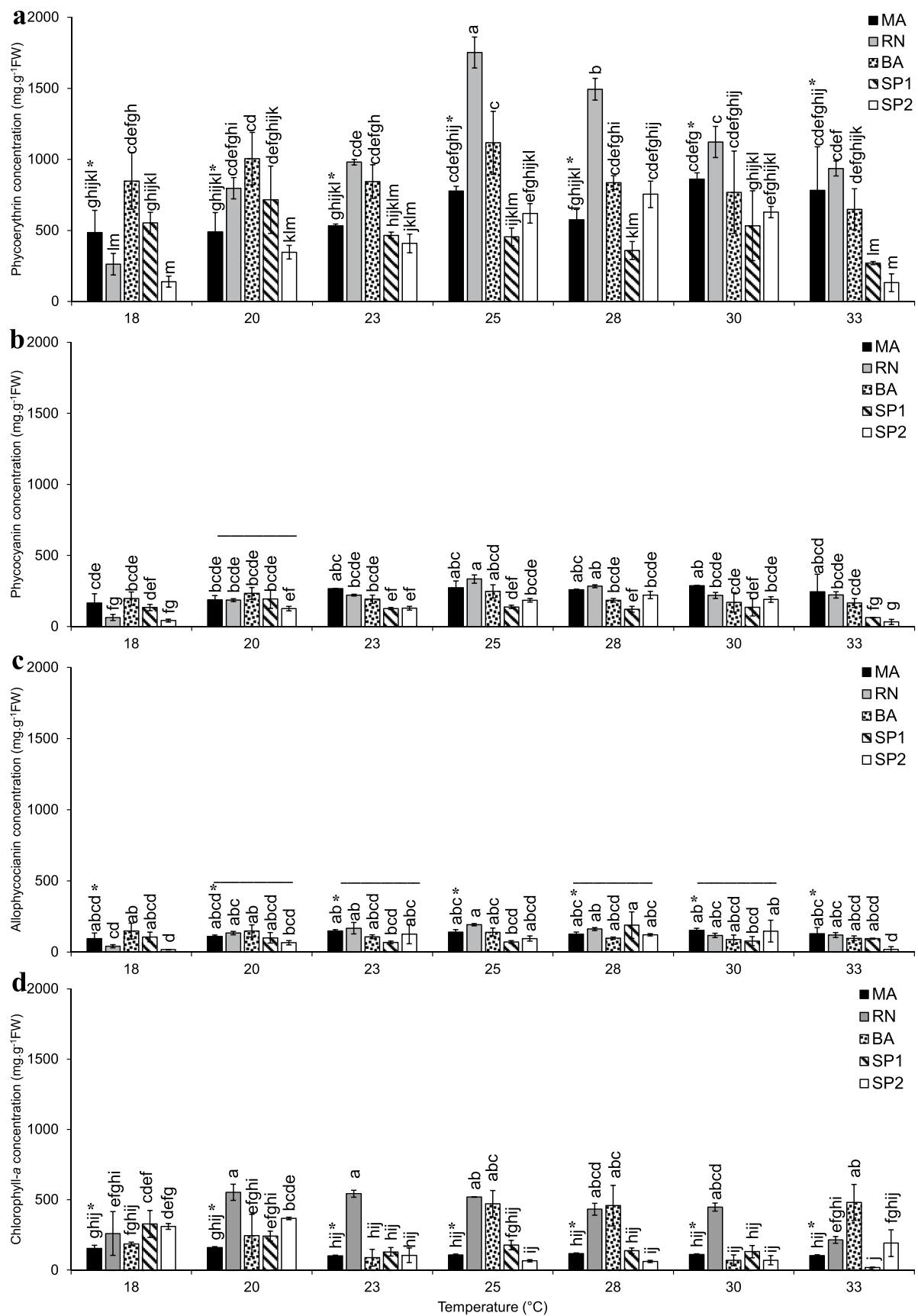


Fig. 4 Pigment concentration of *Gracilariopsis tenuifrons* from distinct populations (Maranhão State, MA; Rio Grande do Norte State, RN; Bahia State, BA; Ubatuba-São Paulo State, SP1; and Itanhaém-São Paulo State, SP2), cultivated at different temperatures (18, 20, 23, 25, 28, 30, and 33 °C): **a** phycoerythrin (PE); **b** phycocyanin (PC); **c** allophycocyanin (PC); and **d** chlorophyll *a* (Chlo-*a*). Data presented as mean and standard deviation ($n=5$). Different letters represent significant differences among temperatures and populations ($p<0.05$). The extended line means similar result among populations, and the asterisk means a similar result among temperatures in a single population

High temperatures At 30 °C, all populations showed similar PE contents, except the southeastern populations (SP1 and SP2) that showed lower contents than RN (Fig. 4a). At 33 °C, the northeastern populations (MA, RN, and BA) showed the highest PE and PC contents when compared to the southeastern populations (SP1 and SP2) (Fig. 4a, b).

Discussion

Female gametophytes of *Gracilariopsis tenuifrons* from five distinct populations (MA, RN, BA, SP1, and SP2), distributed along 7450 km of the Brazilian coast, tolerated temperatures between 18 and 33 °C but less tolerance at 35 °C, which was considered deleterious, irrespective of the analyzed population. However, populations showed different thermal adaptations as revealed by their physiological performance. Therefore, our data support the hypothesis that *Gp. tenuifrons* presents latitudinal ecotypes and that such ecotypes differ according to the temperature range and populations in which they occur.

The occurrence of ecotypes in a species of wide distribution on the Brazilian coast, such as *Gp. tenuifrons*, evidences the potential to house other species with adaptations already established according to the temperature gradient presented along this coast. Indeed, ecotypes related to temperature were reported in other red algae that occur along this same coastline, such as *Gracilaria birdiae* (Ursi et al. 2003) and *G. domingensis* (Castro and Yokoya 2018). However, other parameters were also used to recognize ecotypes along that coast, such as (i) photosynthetically active radiation in *Gracilaria caudata* (Faria et al. 2017) and *Hypnea pseudomusciformis* (Nauer et al. 2020); and (ii) ultraviolet radiation B in *G. caudata* (Araujo et al. 2014).

The intermediate population (BA) of *Gp. tenuifrons* and those populations occupying the lowest latitudes of the Brazilian coast (MA and RN) present some unique physiological characteristics. However, we further showed that they are better able to physiologically develop over higher (23–28 °C) and stressful (30–33 °C) temperatures when compared to southeastern populations (SP1 and SP2). Indeed, for most of the populations analyzed, it was possible to find a statistical

significance, either at the highest range, e.g., T_{opt} (MA at 26.2 °C; RN at 27.4 °C; BA and SP1 at 25.3–25.6 °C; SP1 and SP2 at 25.6–25.7 °C), or the lowest range, e.g., μ_{max} (RN, 5.6% day⁻¹; SP1 and SP2, 9.6–10.6% day⁻¹). BA and SP1 populations differed each other based on their μ_{max} (BA, 12.2% day⁻¹; SP1, 9.6% day⁻¹), the highest growth temperature range (BA, 23–28 °C; SP1, 28–30 °C), GRs (at 20–23 °C and 28–30 °C), and some photosynthetic parameters. SP1 and SP2 populations differed each other based on their CT_{min} , $T_{tolerance}$, the highest growth temperature range (SP1, 28–30 °C; SP2, 28 °C), GRs (at 18 °C and 30 °C), and some photosynthetic parameters. The physiological differences observed between the two southern populations (SP1 and SP2) showed that different adaptation patterns can also occur between close populations, even in the presence of putative gene flow, as already observed in other red algae (Ayres-Ostrock et al. 2019; Nauer et al. 2019).

Physiological differences between populations of *Gp. tenuifrons* were also evident in the analysis of the maximum quantum yield (F_v/F_m). Specifically, temperatures of 20–30 °C promoted higher F_v/F_m , but stressful temperature (33 °C) promoted lower F_v/F_m . Both MA and RN populations were exceptions as they showed similar values at 33 °C. It was difficult to compare our photosynthetic parameter results to other studies since different species adapt differently to different temperatures according to environmental conditions. However, the thermal influence on photosynthetic performance in other red algae was also evident, e.g., *Gp. lemaneiformis* (Liu et al. 2017), *Gelidiella acerosa* (Fujimoto et al. 2015), *Hydropuntia edulis* and *H. eucheumatoides* (Vo et al. 2015), *Kappaphycus alvarezii* (Terada et al. 2016), *Kappaphycus* sp. (Borlongan et al. 2017), *Pyropia tenera* (Watanabe et al. 2014), and *P. yezoensis* (Watanabe et al. 2016).

Particularly, the decreases in photosynthesis of *Gp. tenuifrons* may be related to changes in the state of PSII or in the proportion of energy transferred during the process of ATP production. Our study showed a significant negative effect of stressful temperature, 33 °C, on BA, SP1, and SP2 populations for which F_v/F_m , ETR_{max} , and E_k presented the lowest values, together with minimal physiological performance. Furthermore, lower PE and PC contents were observed (only southern populations). Thermal stress can rearrange the structures of the thylakoid membranes, deactivate PSII (Roleda 2009), or inhibit synthesis de novo of protein D1 in PSII owing to the accumulation of hydrogen peroxide (Allakhverdiev and Murata 2004; Allakhverdiev et al. 2008; Takahashi and Murata 2008).

Rocky shore × mangrove populations

Our results also highlighted the differences between populations of *Gp. tenuifrons* that occur in rocky shore (MA, BA,

SP1, and SP2) and mangrove (RN). At 33 °C, RN showed the highest values of GRs and ETR_{max} when compared to the others. Otherwise, rocky shore populations showed better μ_{max} on TPCs and higher GRs between 20 and 30 °C. However, even though RN showed the lowest growth than the other populations, it showed the highest T_{opt} , CT_{max} , and $T_{tolerance}$ on TPCs, and it produced the highest pigment contents (PE, PC, and Chlo-*a*) when compared to some, not all, rocky shore populations (SP1 and SP2). Although the mangrove population developed unique adaptive characteristics that allowed these individuals to establish themselves and survive in this environment, they also adapted to this site at the cost of metabolic losses, which ended up compromising growth. Comparing both environments, mangrove (RN) has a salinity that varies between 38 (near the mouth) to 50 (near the end of the system upstream) and temperature between 28 and 37 °C (Santiago et al. 2005; Lucena 2012). In contrast, rocky shore populations (MA, BA, SP1, and SP2) have stable salinity of 35 and temperatures between 20 and 26 °C at the southern coast and between 27 and 29 °C at the northeastern coast. These distinct environmental characteristics may explain the differences observed in terms of growth and other physiological parameters between the mangrove population and those of rocky shore. However, it is important to consider the laboratory conditions used in our experimental design to evaluate physiological responses, since these may have favored rocky shore populations over mangrove populations.

Northeastern (MA) × southeastern populations (SP1 and SP2)

The population located further toward the northeast (MA) of the country and those in the southeast (SP1 and SP2) have been influenced by different temperatures throughout the years, enabling *Gp. tenuifrons* to make a distinct thermal adaptation. As was expected, at stressful temperature, 33 °C, SP1 and SP2 populations showed the worst physiological developments, when compared to MA that showed a slightly better physiological development (F_v/F_m , E_k , PE, and PC). MA population also presented higher μ_{max} (12.7% day⁻¹) on TPCs when compared to southeastern populations. Moreover, SP1 and SP2 showed the lowest values of CT_{min} , according to the lowest temperatures that they are submitted. It is possible that populations of *Gp. tenuifrons* of the southeast would benefit from an increase of sea surface temperature, as predicted by IPCC (1.5–2.0 °C, until 2050 in an optimistic scenario; 2021) since their physiological performance was not so bad between 28 and 30 °C, as well as by the higher CT_{max} observed. Moreover, it is not expected for populations located closer to the equator (MA and RN) any change in an optimist scenario, since they are already subjected to more stable and higher temperatures throughout the year.

However, a synergy among local abiotic factors is expected, including radiation and nutrients, which could lead to different responses. Indeed, a study on the southern marginal population of *Laurencia catarinensis* (27.6°S, Santa Catarina State) showed the synergic effect of temperature and nutrients on its physiology (Gouvêa et al. 2018).

Intermediate population (BA)

The BA population showed some physiological characteristics similar to those observed in populations located further to the northeast and others more similar to those observed for populations located further to the southeast. According to some studies on red algae (Ayres-Ostrock et al. 2019; Nauer et al. 2019), Bahia State is considered an intermediate region on the Brazilian coast owing to the Vitória-Trindade Seamount Chain between northern Espírito Santo and the southern Bahia States. This chain was recognized as a barrier to gene flow, and it was responsible for the current genetic and floristic structure (Bard et al. 1990; Corrêa 1996; Lambeck et al. 2002). Thus, it was expected that BA would show some similar physiological characteristics in comparison to southeastern individuals, regardless of the temperature. Our results corroborate other studies that tested different irradiances on *Gracilaria caudata*. The BA population of this species showed some physiological characteristics similar to northeastern (Ceará State, closer to RN) and southeastern (SP1, same site) populations (Faria et al. 2017). Besides, molecular studies on other red algae showed that the BA region may correspond to a refugium and a contact zone between the highly differentiated northeastern and southeastern regions (Ayres-Ostrock et al. 2019; Nauer et al. 2019). Accordingly, a comparison of genetic diversity in *Gp. tenuifrons* will be necessary to better characterize the populations along the Brazilian coast.

Stressful temperature (33 °C)

The stressful temperature of 33 °C differentially affected the populations located closer to the equator (MA and RN) compared to the southeastern region (SP1 and SP2). Populations closer from the equator had higher photosynthesis (F_v/F_m ; E_k) and pigment contents (PE and PC) than SP1 and SP2 populations. It is possible that MA and RN populations produce more accessory pigments like PE and PC because they are already adapted to regions with higher irradiances and temperatures. Additional pigment content would contribute to increasing electron uptake, as well as ATP production, necessary for the acclimation of individuals. On the contrary, southeastern populations, in order to maintain their basic physiological functions at 33 °C, use their pigments, like PE, as a source of nitrogen,

as already demonstrated in previous studies on other red algae (Lapointe 1981; Talarico 1996; Faria and Plastino 2016).

Conclusion

Our data support the hypothesis that the five populations of *Gp. tenuifrons* are ecotypes. This result can be attributed to the wide distribution of the species on the Brazilian coast (2.4–24°S), which presents quite diverse environmental characteristics, for example, temperature. Rocky shore populations (MA, BA, SP1, and SP2) proved to be more adapted to low–high (18–30 °C) temperatures than the mangrove (RN) population. The latter is also more resilient to stressful temperatures (33 °C) than the others, although it showed the lowest GR in other temperatures. Furthermore, the BA population presented some physiological characteristics similar to populations located further northeast and southeast. None of the populations survived at 35 °C.

If the SST should rise to around 1.5–2.0 °C (optimistic scenario) in the next 30 years (IPCC 2021), *Gp. tenuifrons* populations could not be affected, especially the southeastern populations (SP1 and SP2). However, in a drastic scenario (up to 4 °C), especially MA and BA populations could be affected and may suffer a decline. In the present study, individuals did not show satisfactory physiological performances with temperatures above 28–30 °C (rocky shore) and 33 °C (mangrove). RN population showed the lowest growth in all temperatures, with exception of 33 °C, in which the other populations showed worst physiological performances. Timing of growth is considered an important response to global climate changes, and they could alter the composition of communities and the nature of species interactions (Hoffmann and Sgrò 2011). Based on physiological characteristics observed in our experiment, especially the lowest growth at almost all temperatures, we believe RN would also be affected in a future drastic scenario. However, the southeastern populations (SP1 and SP2) could benefit from such a rise, including in a drastic scenario, and this would allow the expansion of the species to regions further to the south of their current distribution.

Finally, since some northeastern states are now developing artisanal cultivation techniques of Gracilariales (Simioni et al. 2019), it is plausible to suggest that experimental mariculture tests of *Gp. tenuifrons* as a new species be exploited. Among studied populations, the MA and BA populations are highlighted because mariculture already exists in the northeast region of the country.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10811-022-02721-2>.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

References

- Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P (2008) Heat stress: an overview of molecular responses in photosynthesis. *Photosynth Res* 98:541–550
- Allakhverdiev SI, Murata N (2004) Environmental stress inhibits the synthesis de novo of proteins involved in the photodamage-repair cycle of photosystem II in *Synechocystis* sp. PCC 6803. *Biochim Biophys Acta* 1657:23–32
- Angilletta MJ (2006) Estimating and comparing thermal performance curves. *J Therm Biol* 31:541–545
- Angilletta MJ Jr, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology in ectotherms. *J Therm Biol* 27:249–268
- Araujo FO, Ursi S, Plastino EM (2014) Intraespecific variation in *Gracilaria caudata* (Gracilariales, Rhodophyta): growth, pigment content, and photosynthesis. *J Appl Phycol* 26:849–858
- Ayres-Ostrock LM, Valero M, Manger S, Oliveira MC, Plastino EM, Guillemain M, Destombe C (2019) Dual influence of terrestrial and marine historical processes on the phylogeography of the Brazilian intertidal red alga *Gracilaria caudata*. *J Phycol* 55:1096–1114
- Bard E, Hamelin B, Fairbanks RG (1990) U-Th ages obtained by mass spectrometry in corals from Barbados: sea level during the past 130,000 years. *Nature* 346:456–458
- Borlongan IA, Nishihara GN, Shimada S, Terada R (2017) Effects of temperature and PAR on the photosynthesis of *Kappaphycus* sp. (Solieriaceae, Rhodophyta) from Okinawa, Japan, at the northern limit of native *Kappaphycus* distribution in the western Pacific. *Phycologia* 56:444–453
- Brito L, Silva S (2005) Fenología y ciclo del alga *Gracilariopsis tenuifrons* (Gracilariaceae) em Sucre, Venezuela. *Ver Biol Trop* 53:67–73
- Burrows MT, Schoeman DS, Buckley LB et al (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334:652–655
- Carneiro MAA, Resende JFD, Oliveira SR et al (2021) Performance of the agarophyte *Gracilariopsis tenuifrons* in a multi-trophic aquaculture system with *Litopenaeus vannamei* using water recirculation. *J Appl Phycol* 33:481–490
- Castro JZ, Yokoya NS (2018) Growth and biochemical responses of tropical and subtropical strains of *Gracilaria domingensis* (Gracilariales, Rhodophyta) to temperature and irradiance variations. *J Appl Phycol* 31:607–613
- Chen I-C, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026
- Corrêa ICS (1996) Les variations du niveau de la mer durant les derniers 17.500 ans BP: l'exemple de la plateforme continentale du Rio Grande do Sul - Brésil. *Mar Geol* 130:163–178

- Costa E, Plastino EM, Petti R, Oliveira EC, Oliveira MC (2012) The Gracilariaceae Germplasm Bank of the University of São Paulo, Brazil - a DNA barcoding approach. *J Appl Phycol* 24:1643–1653
- Enriquez S, Borowitzka MA (2011) The use of the fluorescence signal in studies of seagrasses and macroalgae. In: Suggett DJ, Prásl O, Borowitzka MA (eds) *Chlorophyll a fluorescence in aquatic sciences: methods and applications*. Springer, Dordrecht, pp 187–208
- FAO (2021) Fishery and Aquaculture Statistics. Global Production Statistics 1950–2019. FAO Fisheries Division [online]. FishStaJ – Software for Fishery and Aquaculture Statistical Time Series. www.fao.org/fishery/statistics/software/fishstatj/en. Accessed 10 Jan 2022
- Faria AVF, Bonomi-Barufi J, Plastino EM (2017) Ecotypes of *Gracilaria caudata* (Gracilariales, Rhodophyta): physiological and morphological approaches considering life history phases. *J Appl Phycol* 29:707–719
- Faria AVF, Plastino EM (2016) Physiological assessment of the mariculture potential of a *Gracilaria caudata* (Gracilariales, Rhodophyta) variant. *J Appl Phycol* 28:2445–2452
- Fernández PA, Gaitán-Espitia JD, Leal PP, Schmid M, Revill AT, Hurd CL (2020) Nitrogen sufficiency enhances thermal tolerance in habitat-forming kelp: implications for acclimation under thermal stress. *Sci Rep* 10:3186
- Figueroa FL, Conde-Álvarez R, Gómez I (2003) Relations between electron transport rates determined by pulse amplitude modulated chlorophyll fluorescence and oxygen evolution in macroalgae under different light conditions. *Photosynth Res* 75:259–275
- Fujimoto M, Nishihara GN, Prathep A, Terada R (2015) The effect of irradiance and temperature on the photosynthesis of an agarophyte, *Gelidiella acerosa* (Gelidiales, Rhodophyta), from Krabi, Thailand. *J Appl Phycol* 27:1235–1242
- Gaitán-Espitia J, Belén Arias M, Lardies M, Nespolo R (2013) Variation in thermal sensitivity and thermal tolerances in an invasive species across a climatic gradient: lessons from the land snail *Cornu aspersum*. *PLoS One* 8:e70662
- Gaitán-Espitia JD, Bacigalupe LD, Opitz T, Lagos NA, Timmermann T, Lardies MA (2014) Geographic variation in thermal physiological performance of the intertidal crab *Petrolisthes violaceus* along a latitudinal gradient. *J Exp Biol* 217:4379–4386
- Gouvêa LP, Schubert N, Martins CDL, Sissini M, Ramlov F, Rodrigues ERdO, Bastos EO, Freire VC, Maraschin M, Carlos Simonassi J, Varela DA, Franco D, Cassano V, Fonseca AL, Barufi JB, Horta PA (2018) Interactive effects of marine heatwaves and eutrophication on the ecophysiology of a widespread and ecologically important macroalga. *Limnol Oceanogr* 62:2056–2075
- Hernández I, Pérez-Pastor A, Vergara JJ, Martínez-Aragón JF, Fernández-Engo MÁ, Pérez-Lloréns JL, al. (2006) Studies on the biofiltration capacity of *Gracilariopsis longissima*: from microscale to macroscale. *Aquaculture* 252:43–53
- Hernandez OE, Dreckmann KM, Núñez-Resendiz ML, Vilchis MI, Senties A (2020) *Gracilariopsis lemaneiformis* (Gracilariaceae, Rhodophyta) in the Mexican Coasts: a case of disjunct distribution? *Am J Plant Sci* 11:111–124
- Hoffmann A, Sgrò C (2011) Climate change and evolutionary adaptation. *Nature* 470:479–485
- IPCC (2021) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R, Zhou B (eds) *Climate Change 2021: the physical science basis Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press
- Johnson RB, Kim JK, Armbruster LC, Yarish C (2014) Nitrogen allocation of *Gracilaria tikvahiae* grown in urbanized estuaries of Long Island Sound and New York City, USA: a preliminary evaluation of ocean farmed *Gracilaria* for alternative fish feeds. *Algae* 29:227–235
- Jueterbock A, Tyberghein L, Verbruggen H, Coyer JA, Olsen JL, Hoarau G (2013) Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecol Evol* 3:1356–1373
- Kursar TA, van der Meer J, Alberte RS (1983) Light-harvesting system of the red alga *Gracilaria tikvahiae*: I. Biochemical analyses if pigment mutations. *Plant Physiol* 73:353–360
- Lambeck K, Esat TM, Potter E (2002) Links between climate and sea levels for the past three million years. *Nature* 419:199–206
- Lapointe BE (1981) The effects of light and nitrogen on growth, pigment content, and biochemical composition of *Gracilaria foliifera* v. *angustissima* (Gigartinales, Rhodophyta). *J Phycol* 17:90–95
- Liu C, Zou D, Yang Y, Chen B, Jiang H (2017) Temperature responses of pigment contents, chlorophyll fluorescence characteristics, and antioxidant defenses in *Gracilariopsis lemaneiformis* (Gracilariales, Rhodophyta) under different CO₂ levels. *J Appl Phycol* 29:983–991
- Leandro A, Pereira L, Gonçalves AMM (2020) diverse applications of marine macroalgae. *Mar Drugs* 18:17
- Lim PE, Yang LE, Tan J, Maggs CA, Brodie J (2017) Advancing the taxonomy of economically important red seaweeds (Rhodophyta). *Eur J Phycol* 52:438–451
- Lowry DB (2012) Ecotypes and the controversy over stages in the formation of new species. *Biol J Linn Soc* 106:241–325
- Lucena LAF (2012) Estrutura e composição de macroalgas de manguezais hipersalinos do Rio Grande do Norte, Brasil: diversidade e suas correlações com as variáveis ambientais. Thesis, Universidade Estadual da Paraíba
- Lyra GM, Nunes JMC, Pestana EM, de Matos JCG, Caires TA, de Jesus PB, Costa EdS, Oliveira MC (2021) Diversity of Gracilariaceae (Rhodophyta) in Brazil: integrating morphological and molecular data. *Phytotaxa* 496:1–53
- McLachlan J, Bird CJ (1984) Geographical and experimental assessment of the distribution of *Gracilaria* species (Rhodophyta: Gigartinales) in relation to temperature. *Helgol Meeresunters* 38:319–334
- Montagnes DJS, Morgan G, Bissinger JE, Atkinson D, Weisse T (2008) Short-term temperature change may impact freshwater carbon flux: a microbial perspective. *Glob Change Biol* 14:2823–2838
- Nauer F, Gurgel CFD, Ayres-Ostrock LM, Plastino EM, Oliveira MC (2019) Phylogeography of the *Hypnea musciformis* species complex (Gigartinales, Rhodophyta) with the recognition of cryptic species in the western Atlantic Ocean. *J Phycol* 55:676–687
- Nauer F, Naves M, Plastino EM, Oliveira MC, Fujii MT (2020) Ecotypes of *Hypnea pseudomusiformis* (Cystocloniaceae, Rhodophyta) revealed by physiological, morphological, and molecular data. *J Appl Phycol* 32:4399–4409
- O’Carroll AG, Armstrong EM, Beggs HM et al (2019) Observational needs of sea surface temperature. *Front Mar Sci* 6:420
- Padfield D, O’Sullivan H, Pawar S (2021) *rTPC* and *nls.mtstart*: a new pipeline to fit thermal performance curves in R. *Methods Ecol Evol* 12:1138–1143
- Plastino EM, Guimarães M (2001) Diversidad intraespecífica. In: Alveal KV, Antezana TJ (eds) *Sustentabilidad de la Biodiversidad. Universidad de Concepción, Concepción*, pp 19–27
- Plastino EM, Oliveira EC (1990) Crossing experiments as an aid to the taxonomic recognition of the agarophyte *Gracilaria*. In: Oliveira EC, Kautsky N (eds) *Cultivation of seaweeds in Latin America*. Universidade de São Paulo, São Paulo, pp 127–133
- Plastino EM, Ursi S, Heimbecker AMC (1998) Efeito da temperatura e salinidade no crescimento de *Gracilariopsis tenuifrons* (Gracilariales, Rhodophyta). In: IV Congresso Latinoamericano de Ficologia, 1998, Caxambú-MG. *Anais do IV Congresso Latinoamericano de Ficologia*. 2:359–369

- Porse H, Rudolph B (2017) The seaweed hydrocolloid industry: 2016 updates, requirements, and outlook. *J Appl Phycol* 29:2187–2200
- Qi Z, Liu H, Li B, Mao Y, Jiang Z, Zhang J, Fang J (2010) Suitability of two seaweeds, *Gracilaria lemaneiformis* and *Sargassum pallidum*, as feed for the abalone *Haliotis discus hannai* Ino. *Aquaculture* 300:189–193
- Roleda MY (2009) Photosynthetic response of Arctic kelp zoospores exposed to radiation and thermal stress. *Photobiol Sci* 8:1302–1312
- Santiago MF, Passavante JZO, Silva-Cunha MGG (2005) Caracterização de parâmetros físicos, químicos e biológico em ambiente hipersalino, estuário do rio Pisa Sal (Galinhos, Rio Grande do Norte, Brasil). *Trop Oceanogr* 33:39–55
- Simioni C, Hayashi L, Oliveira MC (2019) Seaweed resources of Brazil: what has changed in 20 years? *Bot Mar* 62:433–441
- Smale DA, Wernberg T, Oliver ECJ et al (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat Clim Chang* 9:306–312
- Schreiber U (2004) Pulse-amplitude-modulation (PAM) fluorometry and saturation pulse method: an overview. In: Papageorgiou GC, Govindjee (eds) *Chlorophyll a fluorescence: a signature of photosynthesis*. Kluwer, Dordrecht, pp 279–319
- Takahashi S, Murata N (2008) How do environmental stresses accelerate photoinhibition? *Trends Plant Sci* 13:178–182
- Talarico L (1996) Phycobiliproteins and phycobilisomes in red algae: adaptive responses to light. *Sci Mar* 60:205–222
- Terada R, Vo TD, Nishihara GN, Shioya K, Shimada S, Kawaguchi S (2016) The effect of irradiance and temperature on the photosynthesis and growth of a cultivated red alga *Kappaphycus alvarezii* (Solieriaceae) from Vietnam, based on in situ and in vitro measurements. *J Appl Phycol* 28:457–467
- Torres PB, Chow F, Furlan CM, Mandelli F, Mercadante A, Alves DY, Santos CD (2014) Standardization of a protocol to extract and analyze chlorophyll *a* and carotenoids in *Gracilaria tenuistipitata* Var. *liui* Zhang and Xia (Rhodophyta). *Braz J Chromatogr* 62:57–63
- Turkington T, Timbal B, Rahmat R (2019) The impact of global warming on sea surface temperature based El Niño–southern oscillation monitoring indices. *Int J Climatol* 39:1092–1103
- Ursi S, Costa VL, Hayashi L, Pereira RTL, Paula EJ, Plastino EM (2013) Intraspecific variation in *Gracilaria birdiae* (Gracilariaceae, Rhodophyta): growth, and agar yield and quality of color strains under aquaculture. *Bot Mar* 56:241–248
- Ursi S, Pedersen M, Plastino EM, Snoeijs P (2003) Intraspecific variation of photosynthesis, respiration and photoprotective carotenoids in *Gracilaria birdiae* (Gracilariaceae, Rhodophyta). *Mar Biol* 142:997–1007
- Ursi S, Plastino EM (2001) Crescimento *in vitro* de linhagens de coloração vermelha e verde clara de *Gracilaria* sp. (Gracilariaceae, Rhodophyta) em dois meios de cultura: análise de diferentes estádios reprodutivos. *Rev Bras Bot* 24:587–594
- Vo TD, Nishihara GN, Kotamura Y, Shimada S, Kawaguchi S, Terada R (2015) The effect of irradiance and temperature on the photosynthesis of *Hydropuntia edulis* and *Hydropuntia eucheumatoides* (Gracilariaceae, Rhodophyta) from Vietnam. *Phycologia* 54:24–31
- Watanabe Y, Nishihara GN, Tokunaga S, Terada R (2014) Effect of irradiance and temperature on the photosynthesis of a cultivated red alga, *Pyropia tenera* (= *Porphyra tenera*), at the southern limit of distribution in Japan. *Phycol Res* 62:187–196
- Watanabe Y, Yamada H, Mine Y, Kawamura Y, Nishihara GN, Terada R (2016) The response of photosynthesis of *Pyropia yezoensis* f. *narawaensis* to a thermal and PAR gradient varies with the life history stage. *Phycologia* 55:665–672
- Webb WL, Newton M, Starr D (1974) Carbon dioxide exchange of *Alnus rubra*. *Oecologia* 17:281–291
- Yong YS, Yong WTL, Anton A (2013) Analysis of formulae for determination of seaweed growth rate. *J Appl Phycol* 25:1831–1834
- Zanolla M, Altamirano M, Carmona R, De La Rosa AJ, Sherwood A, Andreakis N (2015) Photosynthetic plasticity of the genus *Asparagopsis* (Bonnemaisoniaceae, Rhodophyta) in response to temperature: implications for invasiveness. *Biol Invasions* 17:1341–1353
- Zar JH (1996) *Biostatistical analysis*. Prentice Hall, Upper Saddle River

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