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Responses of the macroalgae *Ulva lactuca* (Ulvales, Chlorophyta) and *Sargassum cymosum* (Fucales, Ochrophyta) to thermal stress evaluated by PAM fluorometry

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Abstract

There is growing concern regarding the thermal effects of global warming on benthic marine macroalgae, which are ecologically important ecosystem engineers on rocky shores. Metabolic responses to thermal stress vary among species and depend on their optimal temperature and tolerance range. Physiological studies using pulse amplitude modulated (PAM) fluorometry to assess photosystem II are essential for understanding macroalgal responses to temperature fluctuations. This study evaluated photosystem II response behavior under extreme temperature conditions in *Ulva lactuca* Linnaeus and *Sargassum cymosum* C. Agardh to detect the sensitivity of these species to temperature variation. Maximum and effective quantum efficiencies (*Fv/Fm* and *ΔF/Fm')* and photosystem II thermal tolerance were measured under 25°C (control) and 35°C (thermal stress) conditions in the laboratory. Both species showed reduced *Fv/Fm* and *ΔF/Fm'* values at 35°C, with *Ulva lactuca* being the most affected species. The thermal stability of photosystem II was not altered between the tested temperatures but was consistently lower in *Sargassum cymosum*. These results indicate that thermal stress resistance and exposure frequency in their natural habitats influence species-specific thermal tolerance. *Ulva lactuca*, which is typical of intertidal zones with frequent short-term thermal fluctuations, loses its photosystem II efficiency and biomass under prolonged thermal stress. In contrast, *Sargassum cymosum*, found in warm subtidal waters, exhibits greater tolerance and maintains growth despite its reduced photosystem II efficiency. Thus, photosystem II thermal stability and photosynthetic efficiency appeared to be independently selected.

Keywords: Ecophysiology - Global Warming - Photosystem II - Photosynthesis - Seaweeds - Thermal Tolerance

INTRODUCTION

Considering the importance of temperature as a crucial and determining factor for the survival, growth, reproduction, and biogeographic distribution of benthic marine macroalgae (Lünning 1990; Hurd et al. 2014; Bettignies et al. 2018; Lalegerie et al. 2020), there is a notable concern regarding the increasing changes that these organisms are exposed to as a result of the thermal effects of global warming (Quintano et al. 2019; Al et al. 2020). The effects of high temperatures on marine macroalgal communities have already been described worldwide, such as the displacement of species towards the poles, loss of species with more complex and perennial thallus structures, replacement by tolerant and opportunistic species, and even extinction (Harley et al. 2012; Pardal et al. 2023; Celis-Plá et al. 2017; Gouvea et al. 2017; Figueiroa

et al. 2019; Wang et al. 2021). The physiological mechanisms related to the effects of temperature variation, such as tolerance limits and adaptations in macroalgae, are not fully understood (Harley et al. 2012; Figueiroa et al. 2019). However, physiological responses to thermal stress are directly related to the optimal temperature and thermal tolerance range of the environment in which they live, and these responses can vary among species (Jueterbock et al. 2013; Wilson et al. 2015).

In this context, chlorophyll fluorescence-based approaches, using Pulse Amplitude Modulated (PAM) fluorometry, have proven valuable for investigating the ecophysiology of photosynthetic organisms by assessing photosystem II (PSII) activity under different environmental conditions (Oliveira et al. 2013; Zhong et al. 2021). Thermal stress, for instance, can trigger physiological and biochemical responses that impair PSII efficiency, which is reflected in the reduction of the maximum quantum yield (*Fv/Fm*), a sensitive parameter measured using this technique (Maxwell and Johnson 2000; Zou et al. 2018).

In this study, we sought to understand the physiological responses through growth rate and chlorophyll-α fluorescence parameters (*Fv/Fm* and *ΔF/Fm'*), and uniquely, the thermal tolerance of PSII in two frequent and contrasting marine macroalgal species from the northern coast of Rio de Janeiro State, *Ulva lactuca* Linnaeus (1753) (Chlorophyta, Ulvales), and *Sargassum cymosum* C. Agardh (1820) (Ochrophyta, Fucales) under high thermal stress.

Macroalgae of the genus *Sargassum* C. Agardh are abundant in tropical and subtropical regions and occur widely in both subtidal and intertidal zones. In intertidal habitats, they are commonly found in tide pools, where there is permanent submersion, as they do not tolerate prolonged exposure (Stiger-Pouvreau et al. 2023). Biogeographic evidence suggests their origin in the warm waters of the Central Indo-Pacific, followed by a recent colonization (<1.5 Ma) of the Atlantic Ocean (Yip et al. 2020; Álvarez-Canali et al. 2024). In Brazil, *Sargassum* species are widespread along the coast, particularly in the southeastern region where they form dense beds (Széchy and Paula 2000). These species provide critical ecosystem services, primarily by acting as habitat-forming engineers (Carneiro et al., 2023; Stiger-Pouvreau et al., 2023). However, ongoing environmental stressors have led to documented declines in *Sargassum* populations in various regions (Celis-Plá et al., 2017; Gorman et al., 2020; Carneiro et al., 2023).

In contrast, species of the genus *Ulva* Linnaeus, commonly found in intertidal zones and exhibiting a cosmopolitan distribution (Carneiro, V. et al. 2023), display traits characteristic of opportunistic macroalgae, such as rapid growth, short life cycles, and high phenotypic plasticity. These features confer

broad tolerance to environmental fluctuations (Hurd et al. 2014; Gao et al. 2018), enabling their proliferation in disturbed or eutrophic environments, where they function as effective bioindicator organisms (Hurd et al. 2014).

This decline in Sargassum populations reduces habitat availability for other species. Consequently, they pose a threat to the diversity, structure, function, and ecosystem services they provide (Bernal-Ibáñez et al. 2021; Gibbons and Quijón 2023). In contrast, more tolerant species, such as those from the genus *Ulva*, may dominate disturbed regions, thereby reducing environmental complexity (Umanzor et al. 2019). Thus, the following hypotheses were tested: (a) the increase in temperature in laboratory conditions affects PSII thermal tolerance and activity in both species, but (b) the way it affects is directly associated with their life habits. We discuss the relevance of our results in terms of how the global warming scenario can impact the biological processes and ecological importance of the studied species.

MATERIALS AND METHODS

Sample collection and treatment

Samples containing 10 specimens each of *U. lactuca* and *S. cymosum* were collected from Cavaleiros Beach, Macaé, Rio de Janeiro, Brazil, in November 2021. The samples were then transported to the laboratory in a thermal box containing filtered natural seawater. In the laboratory, the algae were cleaned to remove all epiphytes and associated fauna and then washed with filtered seawater. *Sargassum* and *Ulva* specimens were identified using morphological keys (Széchy 1987, Carneiro et al. 2023), and morphological identification was supported by molecular analysis. The nomenclature followed Algaebase (Guiry and Guiry 2025) and Wynne (2022).

After cleaning, approximately 2 g of fresh thallus mass from each individual was transferred to 1 L Erlenmeyer flasks containing filtered natural seawater enriched with $NaNO_3$, $Na_2HPO_4.12H_2O$, and Fe $(NH_4)_2(SO_4)_2.6H_2O$ in the concentration of the Von Stosch culture medium (Edwards 1970). For laboratory acclimation, the flasks were placed in environment-controlled rooms with air conditioning for 5 days at a temperature of 25°C, irradiance of ca. 30 µmol photons m^{-2} $s^{-1,}$ and a photoperiod of 12:12 h light:dark cycle with constant aeration through an aquarium air compressor.

Experimental design

To investigate the effects of temperature, specimens of *U. lactuca* and *S. cymosum* were transferred from acclimated conditions to two contrasting temperature conditions in different rooms for ten days: 25°C, which is the expected ideal condition for physiological performance of these macroalgae, and 35°C, which is a stressful condition. For each condition, 10 replicates of each species were used. All other experimental conditions were identical to those of the acclimatization process. The treatment group was subjected to a gradual increase in temperature at a rate of 2°C every 24 h until reaching 35°C, at which point it was maintained for five days. The entire experimental procedure was conducted for 10 days in acclimated chambers. Erlenmeyer flask positions were randomized daily to minimize the possible effects of light variability.

Growth rate measurements

The initial and final fresh weights were determined after carefully blotting the thalli between the tissue papers until all superficial water was absorbed. The relative growth rate (RGR) was determined at the end of the experiment and calculated as follows (Pérez-Mayorga et al*.,* 2011):

$$RGR\ (\%day^{-1}) = \left((lnX_2 - lnX_1)\ /\ T_2 - T_1\right) \times 100$$

where X_1 is the initial fresh weight, X_2 is the final fresh weight after 15 days, T_1 is the start period of the experiment, and T_2 is the final experiment period (15 days).

Chlorophyll fluorescence measurements

The chlorophyll *a* fluorescence parameters of PSII of *U. lactuca* and *S. cymosum* were measured using a portable Pulse Amplitude Modulation Fluorometer (Mini PAM, H. Walz, Effeltrich, Germany) in a temperature-controlled room on final the experiment.

Effective Quantum Yield of PSII

The effective quantum yield (Δ*F/Fm'*) of PSII in light-acclimated samples was used to quantify the photosynthetic performance of the macroalgae. Δ*F/Fm'* and rETR were measured during the illuminated period on the last day of the experiment, and two sub-samples were selected to obtain the parameters for each individual. The samples were acclimated to the same light conditions (PAR 30,37 µmol photons m^{-2} s^{-1}). The effective quantum yield was determined as follows:

$$\Delta F/Fm' = (Fm' - Ft)\ /\ Fm'$$

where *Fm'* is the maximal fluorescence after the saturating light pulse (800 ms, PAR > 4000 µmol photons m^{-2} s^{-1}) in the light-acclimated sample, and *Ft* is the basal fluorescence in the light-acclimated sample.

The relative electron transfer rate (rETR)

rETR is a parameter that relates the effective quantum yield of PSII to light absorption (μmol photons m^{-2} s^{-1}) and is used to estimate macroalgal primary production. The *rETR* was measured as follows:

$$rETR = \Delta F/Fm' \cdot PAR \cdot 0.5$$

where PAR is the photosynthetically active radiation absorbed by the plant surface and 0.5 is the relative distribution of absorbed energy to PSII.

Maximum PSII Quantum Yield (Fv/Fm)

This parameter represents the PSII quantum yield in samples after dark acclimation and is used to indicate the metabolism of photosynthetic stress. Thus, stressed macroalgae show lower *Fv/Fm* values than healthy macroalgae do. On the last day of the experiment, after dark adaptation, three sub-replicates were measured for each individual. *Fv/Fm* values were measured as follows.

$$Fv/Fm = (Fm - F_0) \,/\, Fm$$

where *Fm* is the maximal fluorescence after saturating the light pulse in the dark-acclimatized sample, and F_0 is the basal fluorescence after dark acclimation.

Thermal tolerance of PSII

The thermal tolerance of PSII was determined using the protocol developed by Borgo (2022). For each *U. lactuca* and *S. cymosum* individual, portions of the fronds or phylloids with an average diameter of approximately 1 cm were used for the measurements. Selected portions of the macroalgae were placed between two stainless steel plates (7 cm × 10 cm), one of which had perforations of 0.9 mm in diameter. The tissues were positioned to keep the piece of the stem exposed for the measurement of chlorophyll-*a* fluorescence. Filter paper moistened with filtered seawater was placed between the plates to prevent desiccation of the samples during measurement. The joined plates were placed in a transparent polyethylene zip-lock bag submerged in an ultra-thermostatic water bath with a circulator (Techne® RB-5A) (Neuner and Pramsohler, 2006).

In the dark, the samples were subjected to increasing temperature variations at intervals of 2°C, starting at an initial temperature of 25°C. The samples were kept at each temperature for two minutes, and chlorophyll *a* fluorescence was measured using Mini-Pam. When the values of *Fv/Fm* reached 0, indicating complete inactivation of PSII, the measurements were halted.

Borgo (2022) adopted the sigmoidal function to configure *Fv/Fm* values in response to temperature and thus defined the critical points of the graphical profile of the thermal tolerance of PSII. *Tmin* corresponds to the minimum temperature at which the process of inhibition of maximum potential quantum yield (*Fv/Fm*) begins; thus, *Tmin* is the initial point of thermal sensibility of PSII, from which its desactivation is triggered. *Tmax* indicates the complete deactivation of PSII, that is, the temperature at which *Fv/Fm* reaches zero. The temperature range between *Tmin* and *Tmax*, where the deactivation of PSII occurs, is called ΔT. Parameter *b* corresponds to the rate of decay of *Fv/Fm*, which is the slope of the line at IT_{50} represented in the sigmoidal model graph (Figure 1).

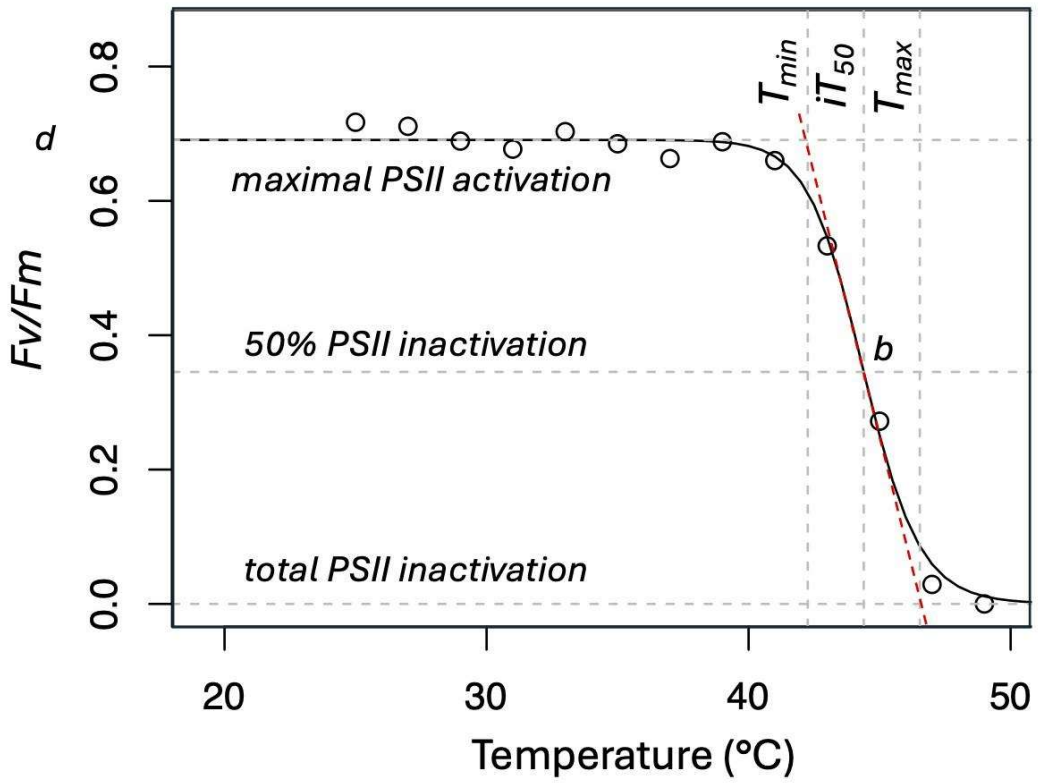

Figure 1. A graphical representation of the three-parameter sigmoidal logistic model (*d*, *b*, and IT_{50}) was adopted to model the response of *Fv/Fm* to temperature. Extracted critical points: *Tmin*, *Tmax*, and ΔT. The dashed red line corresponds to the slope of the line at the IT_{50}. Borgo (2022).

Statistical analysis

Means and standard deviations (SD) were calculated to assess the effects of temperature on the relative growth rates of *Ulva lactuca* and *Sargassum cymosum*. The Shapiro-Wilk test was applied to assess the normality of the data distributions for each treatment. For *S. cymosum*, because both thermal groups

followed a normal distribution, an unpaired two-tailed Student's t-test was used to compare the growth rates between 25°C and 35°C. For *U. lactuca*, the data from the 35°C group did not meet the normality assumption; therefore, a non-parametric Wilcoxon rank-sum test (Mann–Whitney U test) was applied. Statistical significance was set at $p < 0.05$. All statistical analyses were performed using RStudio software (version 2023.06.0+421; RStudio Team, 2023).

The mean and standard deviation of *Fv/Fm*, *Yield*, and *rETR* were explored and compared between species (*U. lactuca* and *S. cymosum*), treatments (25°C and 35°C), and interactions between these factors. Two-way analysis of variance (ANOVA) was used to determine statistically significant differences. A p-value of 0.05 represented a significant difference among treatments. To determine the thermal tolerance of PSII, the mean and standard deviation for each specimen were calculated using logistic regression models according to Borgo (2022), and the determination of its parameters and critical points of thermal tolerance was performed in RStudio software (version 2021.09.2+382) using the minpack.lm package (Elzhov et al. 2023).

Results & Discussion

The growth of *S. cymosum* and *U. lactuca* was affected by an increase in temperature. When exposed to 25°C for 10 days, both species showed a relative growth rate (RGR) of 4.58% day^{-1} ± 0.63% for *U. lactuca* and 3% day^{-1} ± 0.98% for *S. cymosum*, indicating that this thermal range is favorable for physiological performance, particularly for *U. lactuca* under tropical conditions. However, for the same period at 35°C, a reduction in growth rates was observed, 2.14% day^{-1} ± 0.59% for *U. lactuca* and 1.65% day^{-1} ± 0.74% for *S. cymosum,* demonstrating that the increase at ten degrees impaired the growth of both species (Figure 2).

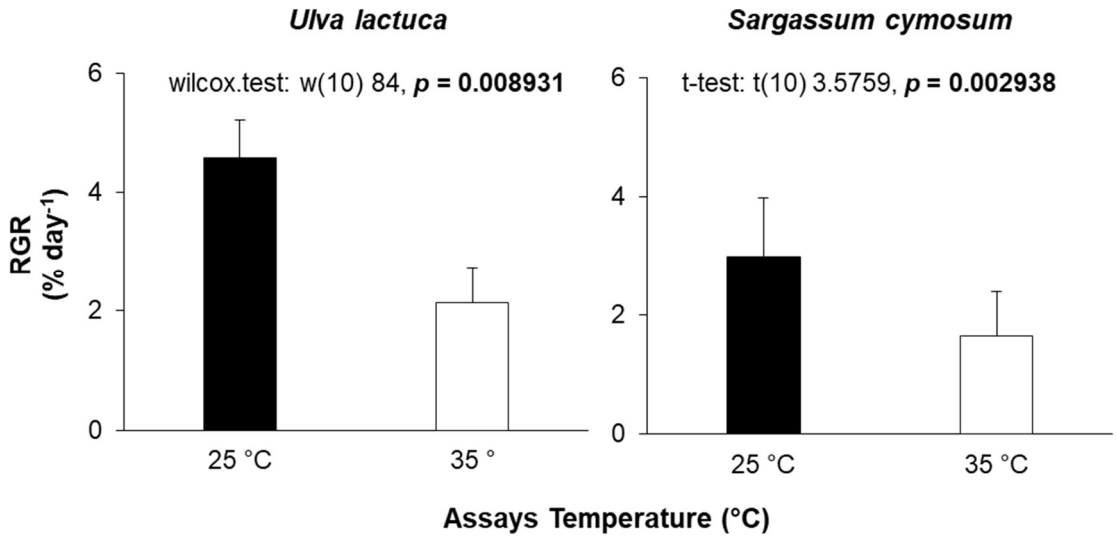

Figure 2. Relative growth rate (%s day^{-1}) of *U. lactuca and S. cymosum* under different temperature treatments. Columns represent means and error bars +SD (N = 10).

Growth performance to temperature is differently reported in the literature for *Ulva* and *Sargassum* species. Studies have shown optimal performance of *Ulva* species cultivated between 15°C and 30°C but with a decrease in growth observed at temperatures above 25°C in temperate regions (Taylor et al. 2001; Kang and Kim 2016). In contrast, Lee and Kang (2020) observed that the growth rates of *U. linza* were not altered under high temperatures in samples cultivated for 14 days (30°C). For *Sargassum*, favorable conditions were reported to be between 20°C and 25°C, whereas significant growth inhibition was observed at temperatures above 30°C (Zhang et al. 2014; Zou et al. 2012; Urrea-Victoria et al. 2020; Wang et al. 2021).

Our results, together with those from the literature, indicate that the negative effect of high temperature on growth depends on the species of *Ulva* and *Sargassum* and also on their local conditions. The greater phenotypic plasticity described for *Ulva* confers it a wider tolerance range to stress (Gao et al. 2016; Wan et al. 2017; Oliveira et al. 2019; Carneiro, V. et al. 2023), which could explain its higher growth rate compared to *Sargassum* at high temperatures.

Macroalgae have an optimal growth range, which, in combination with other factors, favors physiological performance. Therefore, for the species studied, a temperature of 25 °C represents a thermal range suitable for growth in tropical climates, particularly for *U. lactuca*.

Through *Fv/Fm*, it is possible to obtain responses regarding the thermal stability of photosystem II, indicating the sensitivity or thermal tolerance of PSII in marine macroalgae in response to temperature increases. In this context, differences were found in the effective and maximum quantum yields and in the relative electron transfer rate among species under the two temperature conditions to which the macroalgae were subjected, as well as in the interaction between species and temperature.

The rates of maximum and effective quantum yields of PSII at 25°C indicate that under these conditions, the plants are physiologically healthy (Figure 3). However, photosynthesis is easily affected by environmental stress caused by high temperatures. Although more affected in terms of growth, *S. cymosum* showed the highest effective quantum yield in both treatments. On the other hand, *U. lactuca* prioritized growth, being considered a fast-growing alga. However, in the long term and when subjected to thermal stress, the rates of maximum and effective quantum yield decreased. In contrast, *S. cymosum*, even though it does not invest in fast growth, maintained high photosynthetic rates in both thermal treatments compared to *U. lactuca* (Figure 3).

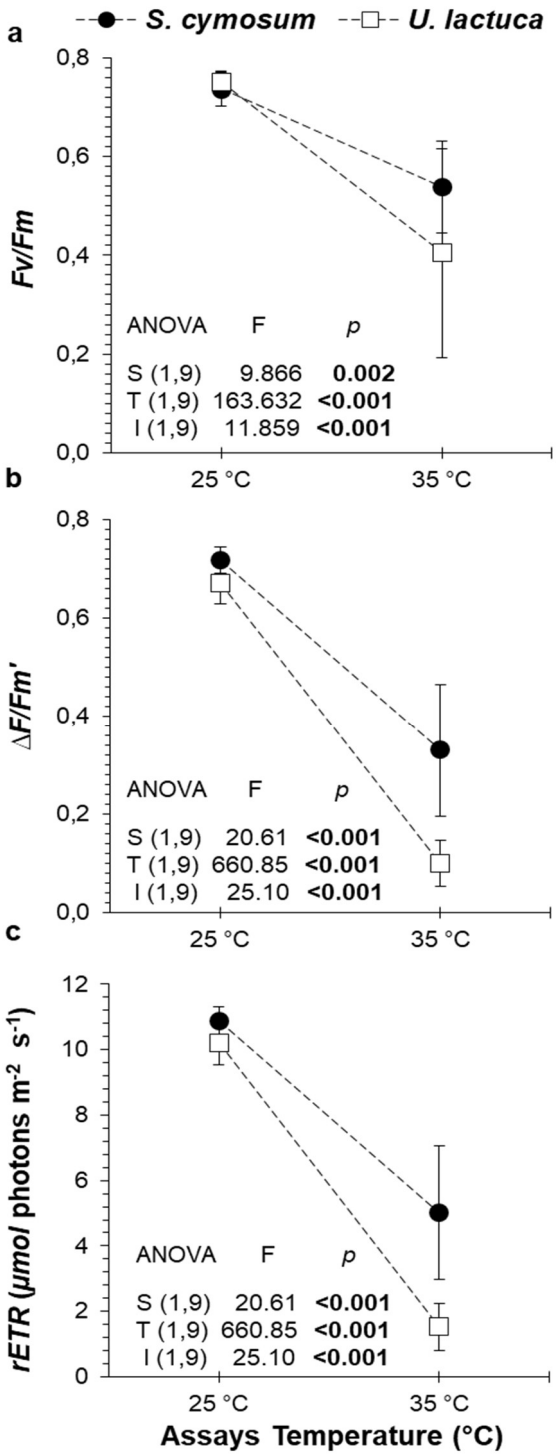

Fig 3 Photosynthetic rate of (**a**) maximum quantum yield (*Fv/Fm*); (**b**) effective (*ΔF/Fm'*); (**c**) the relative electron transfer rate (*rETR*) of photosystem II of *Sargassum cymosum* and *Ulva lactuca* under different temperature treatments (25°C and 35°C). Data are presented as the mean ± SD (n = 10). Two-Way ANOVA Effects for Species (S), Temperature (T), and their interaction (I) are given

Therefore, the thermal stability of PSII in *U. lactuca* and *S. cymosum* is associated with the origin and life conditions of the species. The origin of *Sargassum* is linked to high-temperature environments, and our results are consistent with those found for *S. fusiforme* (Zou et al. 2012; Kokubo et al. 2015), demonstrating that high *Fv/Fm* values can occur under relatively high thermal conditions.

Although considered a stress-resistant alga, the thermal stability of PSII in *Ulva* was significantly affected by a constant temperature increase, especially when compared to a more stress-sensitive species, such as *Sargassum*. This result suggests that the thermal stability of PSII in *Ulva* represents an adaptation that confers resistance to elevated temperatures in the short term but not to prolonged thermal exposure, which is consistent with the adaptive physiology of the species in environments with more challenging temperature variations (Carneiro, V. et al. 2023).

Unlike previous results concerning photosynthetic parameters, the thermal tolerance of PSII, as indicated by the minimum (*Tmin*) and maximum (*Tmax*) limits of the studied species, remained stable across the tested temperatures (Figure 4).

However, PSII in *S. cymosum* was less stable than that in *U. lactuca*, indicating a higher thermal tolerance in PSII for *U. lactuca* for the onset and complete deactivation of the photosystem compared to *S. cymosum*. Specifically, thermal sensitivity (*Tmin*), which marks the beginning of a decline in *Fv/Fm* yield and the start of PSII deactivation, occurred within the range of 41.1°C to 42.1°C for *U. lactuca* and between 39.5°C and 40.3°C for *S. cymosum* (Figure 4). Conversely, the maximum critical point (*Tmax*), signifying complete deactivation of PSII when *Fv/Fm* yield drops to zero, was reached at temperatures between 48.2°C and 48.4°C for *U. lactuca*, and between 46.2°C and 47.2°C for *S. cymosum* (Figure 4).

The range in which PSII is negatively affected by thermal stress until its complete deactivation. It was observed that both species subjected to the same temperature conditions had similar values (Figure 4): for *U. lactuca*, 6.3±1.8 °C (25 °C) and 7.1±2.1°C (35 °C), and for *S. cymosum*, 6.0±2.0 °C (25 °C) and 7.7±2.8 °C (35 °C). The same pattern was identified for parameter *b* (*ΔF/Fm*' $°C^{-1}$), representing the rate of decline of the potential quantum efficiency. The species recorded approximate values under the same conditions of temperature (Figure 4): *U. lactuca* showed values at 25 °C (31.4±10.4) and 35 °C (27.1±7.7), while *S. cymosum* recorded 25 °C (33±13.9) and 35 °C (25±7.8).

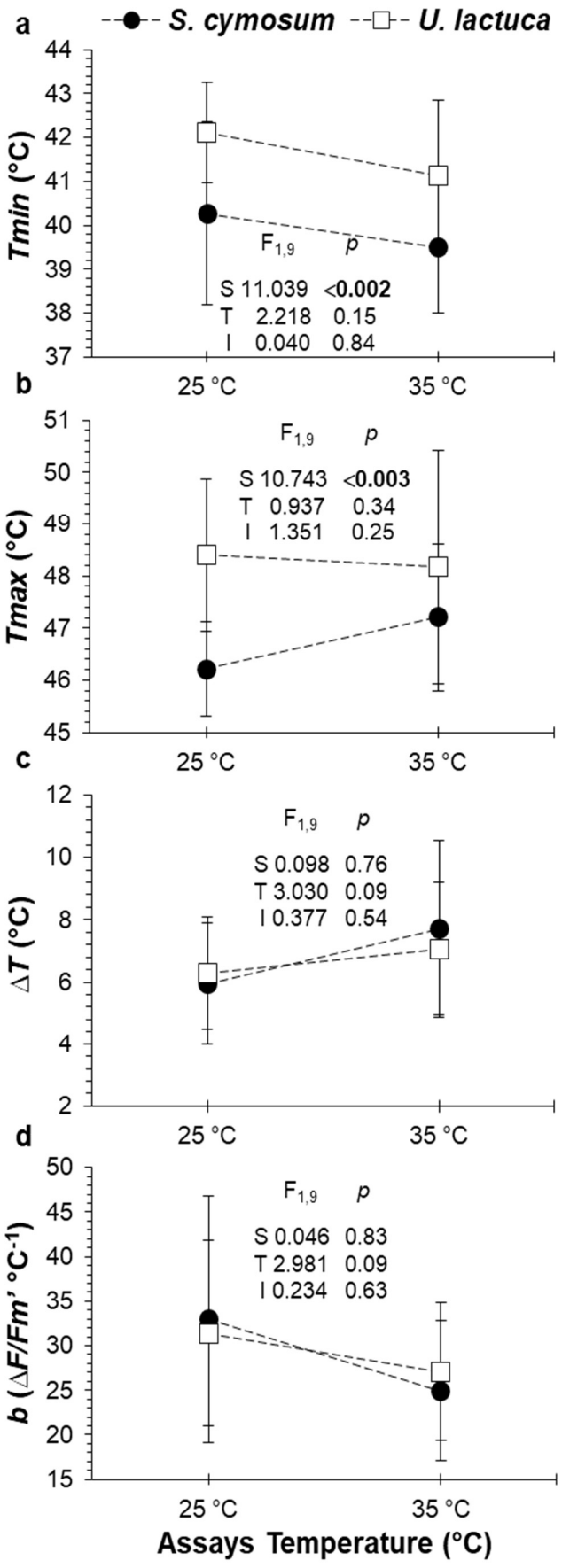
a
S. cymosum
U. lactuca
Tmin (°C)
F1,9 p
S 11.039 <0.002
T 2.218 0.15
I 0.040 0.84
25 °C
35 °C
b
Tmax (°C)
F1,9 p
S 10.743 <0.003
T 0.937 0.34
I 1.351 0.25
c
ΔT (°C)
F1,9 p
S 0.098 0.76
T 3.030 0.09
I 0.377 0.54
d
b (ΔF/Fm' °C-1)
F1,9 p
S 0.046 0.83
T 2.981 0.09
I 0.234 0.63
Assays Temperature (°C)

Fig 4 Critical points (**a**) minimum temperature (*Tmin*), (**b**) maximum temperature (*Tmax*), (**c**) *ΔT* and (**d**) *b* obtained by logistic analysis regression of the *Fv/Fm* response as a function of increasing temperature variation only for *S. cymosum* and *U. lactuca* under two thermal conditions (25°C and 35°C). Data are represented as means ± SD (n = 10). Two-Way ANOVA Effects for Species (S), temperature (T), and their interaction (I) are given.

Borgo (2022) also assessed the thermal stability of PSII, albeit using a different methodology, in which *Fv/Fm* measurements were taken immediately after the collection of macroalgae. Despite the different approaches, the results for *Tmin* and *Tmax* stability were similar. The *Tmin* values for *U. lactuca* and *S. filipendula* were 44.2 ± 0.7°C and 37.7 ± 2.4°C, respectively, whereas the *Tmax* values were 47 ± 0.8°C and 43.7 ± 1.2°C, respectively. These similarities were significant, especially when no differences were observed between the temperatures tested in this study, indicating that PSII stability is an intrinsic characteristic of the species and does not exhibit distinct behaviors in response to temperature variations. Therefore, it is possible to validate Borgo's results (2022), in which these temperatures represent the thermal tolerance range of PSII, which is a plastic characteristic of the photosystem and, in principle, intrinsic to each species.

For the parameters (*ΔT* and *b*), by not varying among species, this result may indicate that, despite the unique thermal tolerance limits for each species, the range in which the deactivation process occurs may be a conserved characteristic among macroalgae species. Compared to Borgo's results (2022), few differences are observed, especially for *Ulva*, between the parameters of the deactivation range (*ΔT*) and decay rate (*b*), where for *U. lactuca*, *ΔT* (2.9 ± 0.9°C) was lower and b much higher (71.5 ± 28 *Fv/Fm* $°C^{-1}$), while for *S. filipendula*, *ΔT* is similar, but *b* was higher (39.9 ± 29.4 *Fv/Fm* $°C^{-1}$). Differences in these rates may have been influenced by the methodology, with measurements taken in the field and in controlled environments. However, our results support those of other researchers, indicating that *ΔT* is directly influenced by *Tmin*, with a higher *Tmin* resulting in a narrower range of PSII deactivation, although a smaller *ΔT* leads to faster decay of *Fv/Fm*. Therefore, *Ulva* may be more tolerant, but PSII is deactivated quickly, whereas *Sargassum* is more sensitive to temperature, and the photosystem takes longer to be completely deactivated.

In conclusion, the stability of PSII may be related to the adaptation of the photosynthetic apparatus in response to lifestyle and external factors to which macroalgae are subjected daily. Therefore, in

predictions of temperature increases where variations are more hostile, populations of *Ulva* and *Sargassum* experience significant biomass losses, affecting the stocks of these species and habitat loss.

Regarding PSII stability, thermal acclimation in macroalgae can represent an efficient strategy for adjusting their responses to multiple environmental stresses, avoiding damage to the photosynthetic system. This process may be associated with the mechanisms for repairing PSII damage. The characteristics of maximum and effective quantum yield, as well as the thermal stability of PSII in scenarios of temperature changes caused by climate change, indicate that the *U. lactuca* PSII will withstand more frequent and intense heat waves. Additionally, it has been suggested that the ongoing increase in sea temperature affects *U. lactuca* more in terms of primary production. Consequently, the distribution of species on rocky shores may change in vertical pattern, abundance, and species composition, potentially leading to a dominance of opportunistic and tolerant species, affecting primary productivity and the ecosystem services that maintain coastal environments.

Changes will not be limited just to local beaches, but also to the global distribution of marine macroalgae, where species typical of temperate regions may move towards the poles, while tropical and subtropical species may expand their coverage, resulting in a loss of global diversity (Wernberg et al. 2013; Gouvea et al. 2017).

Contributions

All authors contributed to the study conception and design. Field experiments were conducted by Willian Costa (WC), Lisia Gestinari (LG) and Carlos Barboza (CB), and the experiments in the laboratory were conducted by WC, Vinicius Peruzzi (VP) and Heitor Duarte (HD). Data analysis was performed by all participants. WC wrote the first draft of the manuscript. Writing review and editing, resource acquisition, and supervision were provided by everyone. All authors have read and approved the final manuscript.

Declarations

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The authors declare that they have no conflicts of interest.

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