1   **Phenotypic plasticity in *Sargassum* forests may not counteract projected biomass losses along a**

2   **broad latitudinal gradient**

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15   **Highlights**

16   - Macroecological environments drive physiological and biomass changes of *S.*

17   *cymosum*

18   - Tropical individuals show higher thermal tolerance compared to temperate ones

19   - Future biomass losses might occur regardless of the higher thermal tolerance

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21

22   **Abstract**

23   Phenotypic plasticity and local adaptation can adjust individual responses to environmental

24   changes across species' ranges. Studies addressing the implications of such traits have been

25   underrepresented in the marine environment. *Sargassum cymosum* represents an ideal model

26   to test phenotypic plasticity, as populations along the southwestern Atlantic Ocean display a

27   sharp decrease in abundance towards distributional range limits. We (1) characterized the

28   macroecological environment of *S. cymosum* across a latitudinal gradient, (2) evaluated

29   potential differences in ecophysiological adjustments (biomass, photosynthetic pigments,

30   phenolic compounds, total soluble sugars and proteins, and carbon-nitrogen - CN - content),

31   and (3) tested for differences in thermal tolerance based on time series analyses produced from

32   the present to contrasting representative concentration pathways scenarios (RCP) of future

climate changes. Our results showed distinct macroecological environments, corresponding to tropical and warm temperate conditions, driving biomass and ecophysiological adjustments of *S. cymosum*. Populations from the two environments displayed contrasting thermal tolerances, with tropical individuals better coping with thermal stress when compared to more temperate ones (lethal temperatures of 33ºC vs. 30ºC); yet both populations lose biomass in response to increasing thermal stress while increasing secondary metabolites (e.g., carotenoids and phenolic compounds) and decrease chlorophyll's content, Fv/Fm, total soluble sugars concentration and CN ratio, owing to oxidative stress. Despite evidence for phenotypic plasticity, significant future losses might occur in both tropical and warm temperate populations, particularly under the no mitigation RCP scenario, also known as the business as usual (i.e., 8.5). In this context, broad compliance with the Paris Agreement might counteract projected impacts of climate change, safeguarding *Sargassum* forests in the years to come.

Keywords: *Sargassum cymosum*; climate change; centre-edge populations; experimental essays; global warming; marine heatwave; physiological performance.

Introduction

Higher population abundance is predicted in the center of species' geographic distributions due to the prevalence of more favorable conditions, while towards the edge, abundance is expected to decrease as conditions become less suitable (Brown 1984; Brussard 1984). However, this pattern may not be universal, and species may preserve performance along their ranges owing to phenotypic plasticity, which can be determined by acclimation (variations in responses of an individual, without genetic changes) and by local adaptation (selective genetic changes in allele frequencies in a population) (Sagarin and Gaines 2002; Ntuli and others 2020). Accordingly, populations of the same species may invest differently in reproduction, growth, and chemical composition under similar conditions due to potential differences in their niches (e.g., Ferreira and others 2014; King and others 2020). This has much relevance in the scope of climate change ecology as plasticity might ensure survival in the face of ongoing and projected environmental changes. Compared to terrestrial systems, the implications of phenotypic plasticity and adaptation have been underrepresented in the marine environment (but see King and others 2018).

Cellular mechanisms are expected to manifest different outcomes when populations from contrasting ranges (e.g., center vs. edges) are exposed to extreme conditions (Eggert 2012; Harley and others 2012). For instance, thermal stress can force biochemical and physiological adjustments in metabolic pathways, affect membrane-associated processes (e.g., stability and biochemical composition), and promote greater production of secondary metabolites (e.g., phenolic compounds and carotenoids) associated with protective strategies against oxidative stress (Balboa and others 2013; Mannino and others 2016; Hargrave and others 2017). When exposed to extreme thermal conditions, photosynthesis, resource utilization, and growth, as well as changes in carbon (C), nitrogen (N), proteins, and storage of carbohydrate content are straightforward indicators of cell's physiological status (Torres and others 1991; Wernberg and others 2016; Gouvêa and others 2017; Costa and others 2019). Ultimately, these indicators can be used to test for phenotypic plasticity between populations of contrasting ranges under increasing thermal stress.

Over the past decades, global climate change has increased ocean temperatures through marine heatwave events (MHWs). These events have been recorded globally, severely impacting biodiversity in the Mediterranean Sea, Northwest Atlantic, Northeast Pacific Ocean, West Australia, Tasman, and Tropical Australian Sea (Mills and others 2013; Smale and others 2019; Arafeh-Dalmau and other 2020). More frequent and intense MHWs are anticipated for the future, yet highly dependent on the representative concentration pathway (RCP) scenarios of greenhouse gas emissions (Oliver and others 2018; Oliver and others 2019). These can range from high mitigation strategies aligned with the Paris Agreement initiative, whereby atmospheric temperatures increase up to 2°C above pre-industrial levels by 2100 (e.g., RCP 2.6), to the no mitigation scenario, also known as the business as usual, with raising temperatures of up to 4.9 °C (e.g., RCP 8.5; IPCC, 2014). Accordingly, distinct biodiversity outcomes are expected when considering such contrasting RCP scenarios. For instance, the projected consequences of future climate changes to marine forests of large brown algae can vary between moderate losses at lower latitude range margins to severe range shifts, eroding unique biodiversity hotspots across taxa (Assis and others 2017).

Sargassum is a canopy-forming macroalga distributed in tropical and subtropical environments and known for its high biomass and carbon stock (Gouvêa and others 2020). It forms dominant communities with vital ecological roles in coastal marine ecosystems and offshore islands. Marine forests of *S. cymosum* represent an ideal model to address potential

1 phenotypic plasticity changes and adaptation across ranges, particularly in the southwestern

2 Atlantic Ocean, where populations follow the abundant-center hypothesis, with a sharp

3 decrease in abundance towards the distributional range limit of Brazilian coastlines.

4   The present study evaluated the physiological responses and phenotypic plasticity of

5 *S. cymosum* forests to increasing thermal stress. In particular, it (1) characterized the

6 macroecological environment of *S. cymosum* across a broad latitudinal gradient, (2) assessed

7 for differences in ecophysiological adjustments (biomass, photosynthetic pigments, phenolic

8 compounds, total soluble sugars and proteins, and CN), and (3) tested for thermal plasticity

9 based on time series analyses produced from the present to contrasting representative

10 concentration pathways scenarios (RCP) of future climate changes.

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12 **Materials and Methods**

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14 **Ecophysiological responses along a latitudinal gradient**

15   *Sargassum cymosum* (C. Agardh) is widely distributed in both hemispheres, occurring

16 in the Atlantic and Pacific Oceans, as well as in the Indian islands. Along the coastlines of

17 Brazil, the species presents a north (warmer region) to south (colder region) decline in

18 abundance, towards the edge of its distribution (Cardoso beach; SC). To analyze the

19 macroecological environment of the species along a broad latitudinal gradient (Brazil

20 coastline; Table S1), i.e., to understand the relationship between its distribution and the

21 environment, at large spatial scales, samples were collected in nine distinct populations (from

22 here on referred to as a population). Sampling was performed in the summers (December to

23 March) of 2016 and 2017 in the upper subtidal zone during low tides. On average, fifteen

24 0.0625 m² quadrats were randomly placed and scraped along a 20 m transect laid across *S.*

25 *cymosum* forests, in areas distancing 3 meters far apart (120 samples in total). Fresh and dry

26 weights were recorded using an analytical balance (Marte, AY 220). Epiphytes and epifauna

27 were removed, and species identification followed dichotomous keys and appropriate

28 literature (Ouriques 1997; Nunes 1998; Pedrini 2012).

29   Samples were dried at 60°C (± 2°C) for 48 hours for biomass measurements. Fresh

30 weight samples were stored in -80 °C for subsequent chemical analyses. Chemical analyses

31 for photosynthetic pigments, phenolic compounds, total soluble sugars and proteins, total

32 organic carbon and nitrogen (CN) were performed according to the protocols of Ritchie

(2008), Aman and others (2005), Costa and others (2019), Shannon (1968) and Bradford (1986). Detailed information on the methods used for each chemical analysis can be found in S4.

A Hierarchical clustering multivariate analysis (HCA) was performed with the biomass and chemical data (n=4, total of 36 samples) to assess distinct ecophysiological responses along the latitudinal gradient (nine sites). All variables were standardized and displayed in a heat map. This analysis used Euclidean distances to examine patterns between sampled regions and specimens' chemical compounds and biomass values. The analyses were performed in R (R Development Core Team, 2018).

Macroecological environment

To analyze the macroecological environment of the sampled populations (i.e., the nine sites along the latitudinal gradient), a cluster analysis was performed over a set of biologically meaningful environmental variables (temperature, nitrate, phosphate, salinity, and light at bottom) downloaded from Bio-ORACLE v2.0 (Assis and others 2018). The analysis inferred the environmental dissimilarity between paired samples by using Ward's method over the Euclidean distance of the normalized values of the five variables (averaged for each site; Hair and others 2009). Additionally, a distance-based redundancy analysis (dbRDA) was performed to show the relationship between environmental data (four replicates per site) and the macroecological clustering of sites. In this process, the environmental variables were standardized with square root transformation and a site-by-environment dissimilarity matrix was produced based on Bray–Curtis distance (Legendre and Legendre 2012). To test the significance of each testable component, an ANOVA-like permutation test for the dbRDA was performed. Because the correlation between variables was low (R < 0.6), no variables were excluded from both clustering and dbRDA analyses. This analyses were performed in R (R Development Core Team 2018).

Responses to thermal stress between the center and edge populations

Thermal stress responses were tested between the two sampled sites further apart, i.e., Coqueiro, a tropical population characterizing the center of the species distribution and

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Cardoso, a more temperate population characterizing the high latitude edge (Table S1). Environmental parameters (nutrients, salinity and temperature) were measured in the field and used as experimental control conditions (data according to Bio-ORACLE v2.0; see Table S2). Control temperatures (28ºC for center and 25ºC for the edge population) largely coincide with the average temperatures of the time series analyses (see Figure 1).

Seawater was sterilized by filtering (sand-filters 25 μm, 20 μm, and 5 μm; GF/F Whatman 0.45 μm filters) and exposure to ultraviolet light (UVC). Dissolved inorganic nutrients (NO_3^{-2}, NH_4^+, PO_4^{-3}) were determined colorimetrically according to Tréguer and Le Corre (1975) and Grasshoff (1983), using a spectrophotometer (UV-1100, Pro-Analise ISE Quımica e Diagnostica Ltda, Brazil). Seawater was changed every 48h, and nutrient levels were adjusted by adding $(NH_4)_2SO_4$, Na_2HPO_4, and $NaNO_3$. *Sargassum cymosum* fronds (~2.0 g, n=5, apical portions of approximately 7 cm) were placed in Erlenmeyer flasks of 250 mL with sterilized seawater and acclimated for 20 days at the control treatment temperatures of 28°C ± 1 ºC (tropical samples) and 25±1 ºC (warm temperate samples) at an irradiance of 110±10 μmol photons.m^{-2}. s^{-1} (fluorescent lamps, Osram 30 W DayLight), with continuous aeration, and 12 h photoperiod starting at 6 a.m. The cleaning, identification, and storage of samples are detailed in the above section of *Ecophysiological responses along a latitudinal gradient* as well as in S4.

Experimental treatments included the exposure of both populations to four temperatures (25 ºC, 28 ºC, 30 ºC and 33 ºC) for 30 days. Water temperature was manipulated using submersed heaters (Master, Brazil). Treatments were achieved by increasing temperatures by to 2ºC per hour, and monitored with data loggers (HOBO Pendant Temperature, Onset, Bourne, USA). These temperatures were chosen based on time-series analyses of covering the period 1993-2100 (Figure 1). This was produced with daily temperature data for the present (period 1993-2019) retrieved from the Global Ocean Physics Reanalysis gridded dataset (Global Monitoring and Forecasting Center; E.U. Copernicus Marine Service), and daily data for the future (period 2020-2100) produced for two contrasting RCP scenarios (2.6 and 8.5) by ensembling distinct models from Coupled Model Intercomparison Project Phase 5 (HadGEM2-ES, MIROC-ESM, IPSL-CM5A-LR) with the change factor approach, as detailed in Assis and others (2018). These data with daily temporal resolution allows estimating sharp

changes in temperature according to the patterns of MHW events (e.g., Oliver and others 2019).

Relative growth rate (RGR) changes were determined from the beginning to the end of the experiment according to the following equation (Lignell and Pedersén 1989):

Growth rate (GR) = $[(Wt/Wi)^{1/t} - 1] \times 100$

where Wi = initial fresh weight, Wt = final fresh weight, and t = experimental time results are expressed as a daily percentage [% day^{-1}] of biomass production.

Photosynthetic performance was evaluated *in vivo* (n=4) via pulse amplitude modulated (PAM) fluorometry of chlorophyll *a* in photosystem II (PSII) using a Jr-PAM (Walz, Germany). The parameters set before measuring were gain intensity = 2, measurement light = 8, light pulse = 0.8 s, n = 3 per replica. The maximum quantum yield (Fv/Fm) was determined after acclimating algae in the dark for 30 minutes. These are optimal parameters inferred in preliminary analyses testing a range of values. The final Fv/Fm values were calculated according to the equations from Schreiber and others (1986). In addition to relative growth rate and maximum quantum yield, we also tested the effect of increasing temperatures in the chemical composition of *S. cymosum,* as detailed in S4.

All analyses of ecophysiological performance (RGR; Fv/Fm) and chemical composition (n=4; carotenoids, phenolic compounds, Chl ac, total soluble sugars, and CN) at different temperatures (25℃, 28℃, 30℃, 33℃) were tested with two-way analysis of variance (ANOVA). Newman Keuls significant difference post hoc tests were used to identify the statistically different groups. Homogeneity of variance was tested a priori with the Cochran test. Variables were not standardized. All analyses were performed in R (R Development Core Team 2018).

Results

Macroecological characterization and ecophysiological adjustments

The cluster analysis using macroecological environmental variables divided the populations along the latitudinal gradient in two main clusters: tropical, comprising PI, RN,

PB BA, ES and warm temperate represented by RJ, SP and SC. The tropical cluster was further subdivided into two subclusters (Figure 2a).

The dbRDA analysis for macroecological clustering (Figure 3; $R^2 = 0.72$) showed temperature, light and dissolved nutrients strongly segregating data along the first axis (higher temperature and light levels in tropical regions and higher nutrients in more temperate regions). Salinity correlated with the second axis (Figure 3) and explained the differentiation of the two tropical subclusters, although this axis explained much less variability compared to the first (74.90% vs. 15.45%).

The ecophysiological responses along the latitudinal gradient also showed the existence of two main groups, which coincided with the tropical and warm temperate regions (Figure 2b). Phenolic compounds, biomass, CN (Table S5), and total soluble sugars presented higher concentrations in the tropics, while carotenoids, proteins and chlorophylls were higher in the warm temperate region.

Responses to thermal stress between center and edge populations

The two populations analyzed displayed contrasting thermal tolerances, with individuals from the tropical (center) region better coping with thermal stress, when compared to those from the temperate (edge) region (Figure 4; lethal temperatures of 33°C vs. 30°C); yet both lost biomass in response to increasing thermal stress, above control conditions. The center population lost biomass with temperatures > 30°C and the edge population with temperatures > 28°C. Future temperature analyses for RCP 2.6 show the center region frequently exposed to 30°C, especially after 2025, but not to the lethal threshold of 33°C. Under RCP 8.5 scenario, this region is expected to reach and remain permanently above the 30°C after 2030, and above 33°C by the end of the century (2080). For the edge population, future projections follow the same trend, with RCP 2.6 temperatures frequently overcoming the biomass loss threshold of 28°C, especially after 2025, and the RCP 8.5 temperatures reaching the lethal temperature of 30°C after 2050 (Figure 1).

The individuals of both center and edge populations produced higher carotenoids and phenolic compounds content with rising temperature (Figure 5a, b). The population of the center region showed 60% more chlorophyll concentration and 10% Fv/Fm higher values when compared to the edge population at 30°C (Figure 5c, d). On the other hand, total soluble

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sugars content was reduced with increasing temperatures; the population from the edge lost more than ~70% when exposed to 28°C and 30°C, when compared to the control treatment (i.e., 25°C; Figure 5e). This had consequences for the CN ratio, which showed more than ~50% decrease at these same temperatures (Figure 5f and Table S6). All analyzes showed significant differences (ANOVA p<0.001, Table S3).

Discussion

The present study shows marked ecophysiological adjustments of *S. cymosum* forests driven by distinct macroecological environmental conditions, which coincide with the previously defined biogeographical provinces (Spalding and others 2007). Tropical populations exposed to higher levels of irradiation, temperature and lower nutrient conditions were characterized by higher total soluble sugars content, CN ratio and biomass, while populations in more temperate environments tend to produce more photosynthetic pigments and proteins. When exposed to increasing thermal stress, populations lose biomass and change ecophysiological adjustments, but not to the same extent. Populations from contrasting ranges (i.e., center vs. edge) showed signs of phenotypic plasticity, with the individuals characterizing the center of the species' distribution tolerating up to 30ºC, a temperature leading individuals of the edge to perish. These results have much relevance in the scope of projected environmental changes, as plasticity might ensure long-term survival in the face of extreme conditions, yet future projections render high relevance to the RCP scenario chosen. While less demographic changes might occur in the RCP scenario aligned with the Paris Agreement (i.e., RCP 2.6), potential local extirpations are expected for both center and edge populations in the no mitigation scenario. Broad compliance with the Paris Agreement might therefore counteract such expectations, safeguarding *Sargassum* forests in the years to come.

Across a broad latitudinal gradient with more than 4000 km, *S. cymosum* forests inhabit two main macroecological environments, which largely coincided with the Tropical Atlantic and Warm Temperate Southwestern Atlantic marine provinces defined by Spalding and others (2007). At a macroecological level, analyses showed the expected general trend of higher irradiance and temperature levels in the tropics and nutrient enriched conditions

(phosphate and nitrate) in the more temperate region. Between these two regions, *S. cymosum* forests exhibited contrasting biomass and ecophysiological adjustments. In particular, biomass and carbon stocks were higher in the tropics, as the result of physiological trade-offs between potential growth and structural maintenance (Mauffrey and others 2020). This pattern is in the light of the abundant-center hypothesis (but see Sagarin and Gaines 2002; Ntuli and others 2020), which predicts higher fitness of individuals and more abundant populations at the center of the species distribution, owing to more favorable conditions (Brown 1984; Brussard 1984). There, populations might have increased photosynthetic capacity and fixed carbon available for growth, resulting in higher biomass, CN and total soluble sugars content (Manns and others 2017). Also, sugar content in macroalgae has been shown to be inversely related to nutrient conditions (Marinho-Soriano and others 2006) as a consequence of the reallocation of carbon skeletons necessary to reduce nitrate and form amino acids (Huppe and Turpin 1994). On the other hand, the populations from the temperate region produced more pigments and proteins. Previous findings also support these results, showing that pigment's response has been attributed to high nutrient concentration in *Sargassum* forests (Gaol and Nakahara 1990).

The tropical populations (i.e., center of distribution) also showed increased production of phenolic compounds content (Hargrave and others 2017), suggesting that *S. cymosum* may adjust chemical defensive barriers against oxidative stress (Costa and others 2015, 2019), in response to environments characterized by elevated solar radiation, as shown in the macroecological analysis. Previous studies with brown seaweeds along the same latitudinal gradient support the observed pattern of higher photoprotective compounds towards the tropics (Schmitz and others 2018). Higher herbivory pressure could also explain this (Poore and others 2012; Zarco-Perello and others 2017; Vasconcelos and others 2019). Despite the lack of data to test this, the general latitudinal herbivory-defense hypothesis predicts higher herbivore pressure toward the tropics, with tropical populations developing higher levels of defenses than those at higher latitudes (Gao and others 2019). Increasing thermal stress led to populations from both center and edge regions to increase carotenoid production, which acts in dissipating the excess light energy through the xanthophyll cycle and also as accessory pigments of photosynthesis, which together with chlorophylls, sustains photosynthetic activity (Takaichi 2011; Balboa and others 2013). Also, carotenoids can be degraded inversely to the chlorophyll content, i.e., in the treatments at higher temperatures,

reduced chlorophyll concentration was observed while carotenoids increased, indicating their potential role as an energy source for maintaining physiological integrity. The reduction in chlorophylls content observed in the edge population under thermal stress also impacted Fv/Fm, as a possible consequence of light-harvesting capacity modification affecting net carbon fixation and re-allocation of energy derived from photosynthesis (Lalegerie and others 2020). In general, the carbohydrates reserve is a ratio between accumulation from photosynthesis and consumption for energy production, biosynthesis, and growth. Therefore, CN imbalance can cause adverse effects to brown algae, impacting photosynthetic pigments, carbohydrates and proteins (Urrea-Victoria and others 2020).

S. cymosum populations from contrasting ranges (i.e., center vs. edge) showed different growth and physiological responses when exposed to increasing thermal stress. At control conditions, both populations exhibited maximum growth rates, as observed for additional *Sargassum* species (*S. vestitum* in Poore and others 2016; *S. polycystum* in Graba-Landry and others 2020), as well as increased photosynthesis, chlorophylls, CN ratio and total soluble sugars. However, thermal tolerances differed by up to 3ºC, with the individuals from the center of the species distribution more adapted to warmer conditions. This supports the idea of phenotypic plasticity, i.e., the ability of an individual to change the phenotype in response to environmental changes (king and others 2017). Yet, our data does not allow concluding whether local adaptation might also be implied, as this process acts through the selection and changing of allele frequencies towards a local optimum (king and others 2017). In such conditions, the species may have adapted to local temperature conditions, resulting in an ecotype with different optimal temperatures for photosynthesis and growth in center, compared to edge populations (Gerard and Du Bois 1988; Pakker and others 1996; Gouvêa and others 2017). Thermal tolerance differences between populations from contrasting ranges are widespread in marine macrophytes (King and others 2018), but the observed pattern of more warm-tolerant populations in the center, completely contrasts with previous studies, which were mostly performed with cold-temperate species with range edges typically exposed to warmer conditions than the center (e.g., Gerard and Du Bois 1988; Bennett and others 2015; Saada and others 2016).

Despite the evidence of phenotypic plasticity, significant future losses are anticipated for both center and edge populations, but severity depends on the future scenario. Under the mitigation scenario complying with the Paris agreement (RCP 2.6), global warming is not

expected to reach lethal thresholds, but biomass losses are anticipated for both populations. Such losses are already evident in field observations and are expected to further increase by 2025. *Sargassum* is already declining 2.6% per year in the last decades, and overall losses in biomass sum up to 52% (ranging from 20% to 89%) since systematic records began in 1969 on the Brazilian coastline (Gorman and others 2020). Potential loss of the *Sargassum* forests could trigger cascading ecosystem turnovers, impacting the local biodiversity and turning these rich and complex ecosystems to, e.g., sea urchin barrens, unable to support the ecological services of the previous forests (Arafeh-Dalmau and others 2020; Bernal-Ibáñez and others 2021). Under the no-mitigation scenario (RCP 8.5), global warming impacts on *S. cymosum* are anticipated to be more severe. Biomass loss thresholds are projected to be permanently crossed by 2050 and lethal thresholds by the end of the century, leading the *S. cymosum* populations of both center and edge ranges to perish. This may further contribute to the loss of genetic diversity due to population bottlenecks, as observed for additional macroalgal species (Gurgel and others 2020), possibly reducing the evolutionary capacity of the species as a whole (Hampe and Petit 2005). For instance, *Sargassum fallax* and *Scytothalia dorycarpa* have lost between 30% to 65% of their average genetic diversity due to population declines while exposed to a heatwave event (Gurgel and others 2020). Considering that *Sargassum* species can disperse over long distances (Mattio and others 2013), potential gene flow from more adapted tropical to warm-temperate populations could improve regional thermal fitness. This would depend on direction of ocean current transport (Molinos and others 2017), and on warming not exceeding the inferred critical thermal thresholds.

The knowledge about divergent ecophysiological responses between populations along species´ distributional ranges is crucial to estimate the potential impacts of climate change. Distributional and abundance changes have been reported and projected worldwide, both in the central and edge populations of marine and terrestrial species, beyond the *Sargassum* forests here addressed (Galaiduk and others 2013; Vergés and others 2014; Poloczanska and others 2016; Cavanaugh and others 2019; Osland and others 2021). Because phenotypic plasticity / local adaptation has been increasingly reported elsewhere (e.g., crustacean and echinoid; Paganini and others 2014), additional species could display the pattern of *S. cymosum*, of drastic climate-induced impacts, regardless of distinct population ecophysiological responses.

Overall, our findings represent a baseline to predict the survival of *S. cymosum* populations in the future, so coastal management strategies focused on this macroalgae may help maintaining ecosystem services at higher structural and functional levels. In this context, broad compliance with the Paris Agreement is critical to reducing the potential impacts of climate change, as it may be more important than plasticity in safeguarding biodiversity in the years to come.

Acknowledgements

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21 **Figure legends:**

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23 Figure 1: Time series of sea surface temperature for tropical and warm temperate regions for

24 present-day conditions (in grey) and contrasting scenarios of projected climate change (in

25 blue RCP 2.6, and in red RCP 8.5). Temperature data for the present (period 1993-2019) were

26 accessed from the Global Monitoring and Forecasting Center (Copernicus Marine Service),

27 while projected conditions were accessed from the Coupled Model Intercomparison Project

28 Phase 5 (models HadGEM2-ES, MIROC-ESM, IPSL-CM5A-LR).

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30 Figure 2: (a) Sites where *S. cymosum* samples were collected along a latitudinal gradient and

31 cluster analysis of environmental data (maximum temperature, nitrate, phosphate, light at

32 bottom and salinity) separating the sites into two main regions. Abbreviations correspond to

Piauí (PI), Rio Grande do Norte (RN), Paraíba (PB), Bahia (BA), Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP) and Santa Catarina (SC). (b) Relationship between environmental clustering and chemical composition and biomass inferred for 36 *S. cymosum* specimens sampled along the latitudinal gradient in Brazilian coastline (9 sites, n=4, two replicates in SC). Dendrograms depict hierarchical clustering between regions and samples. Gradient from blue to orange shows values from low to high chemical concentrations and biomass values (-3 and +3 are standardized values). The tropical province was characterized by the high content of phenolic compounds, total soluble sugars, CN and biomass while warm temperate by carotenoids, Chl ac and total soluble proteins.

Figure 3: Distance-based redundancy analysis (dbRDA) biplot of first and second axes depicting the multivariate dissimilarity of macroecological environment data of S. cymosum populations in association with tropical (i.e., central populations; gray circles) and warm temperate (i.e., edge populations; black circles) regions.

Figure 4: Relative growth rate (RGR, % d^{-1}) of warm temperate and tropical *S. cymosum* under the temperature stress experiment (30 days exposure under 25ºC, 28ºC, 30ºC and 33ºC). The temperatures of 25 ºC and 28 ºC were used as control treatment to warm temperate and tropical populations, respectively. Data are shown as mean ±SD (n = 5). Different letters indicate significant differences, $p < 0.05$ (Newman–Keuls test, two-way ANOVA).

Figure 5: Chemical composition of warm temperate and tropical *S. cymosum* samples under the temperature stress experiment (30 days exposure under 25ºC, 28ºC, 30ºC and 33ºC). The temperatures of 25 ºC and 28 ºC were used as control treatment to warm temperate and tropical populations, respectively. Data are shown as mean ±SD (n = 4). Different letters indicate significant differences, $p < 0.05$ (Newman–Keuls test, two-way ANOVA). (a) Carotenoids, (b) Phenolic compounds, (c) Chlorophylls a and c, (d) Fv/Fm, (e) Total soluble sugars and (f) CN ratio present in *S. cymosum.*

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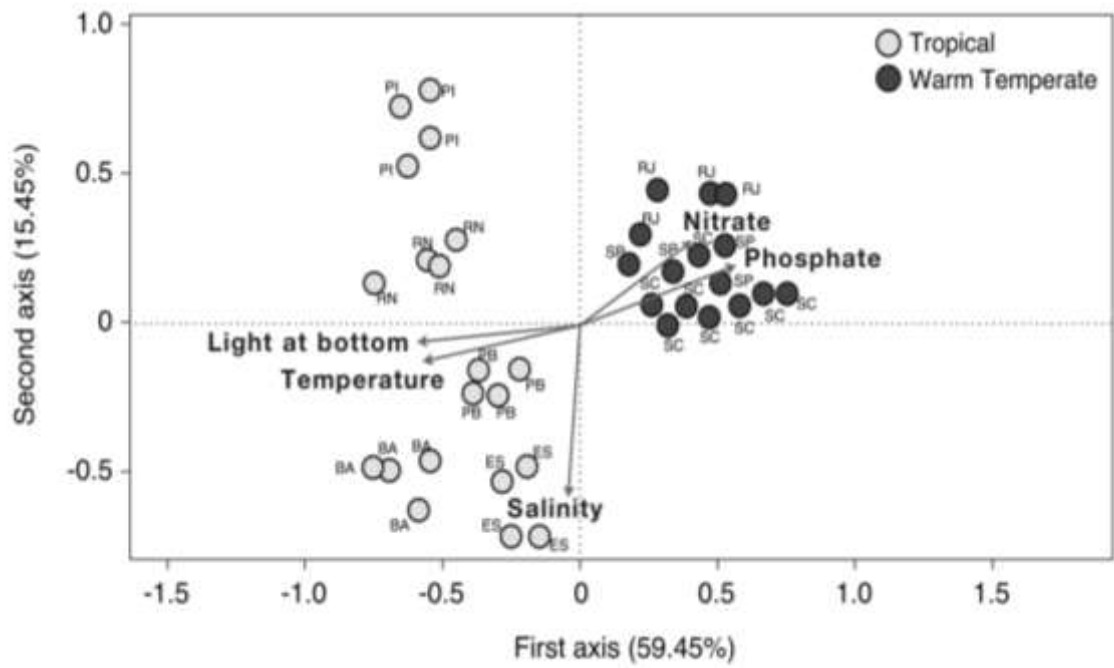
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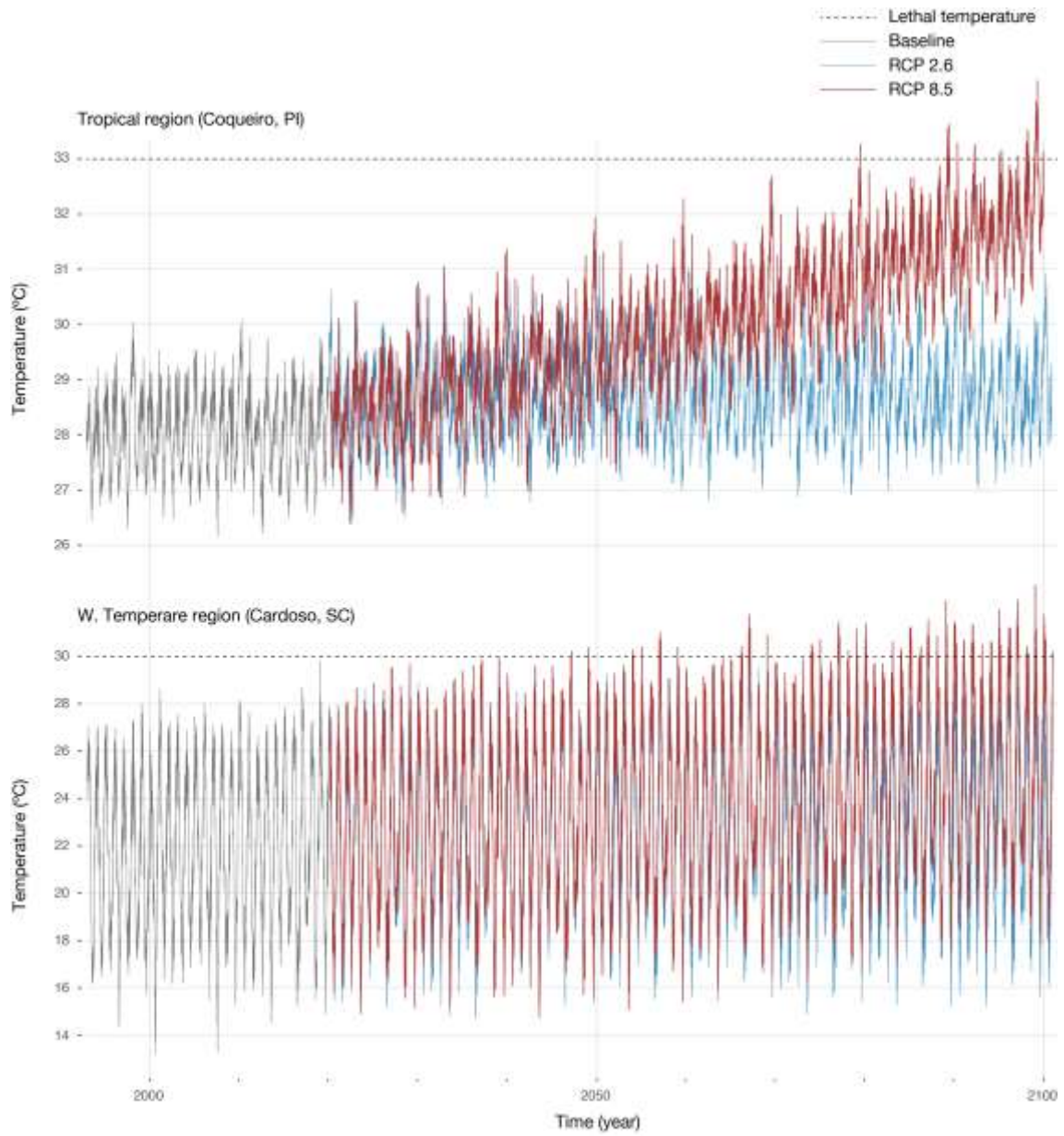
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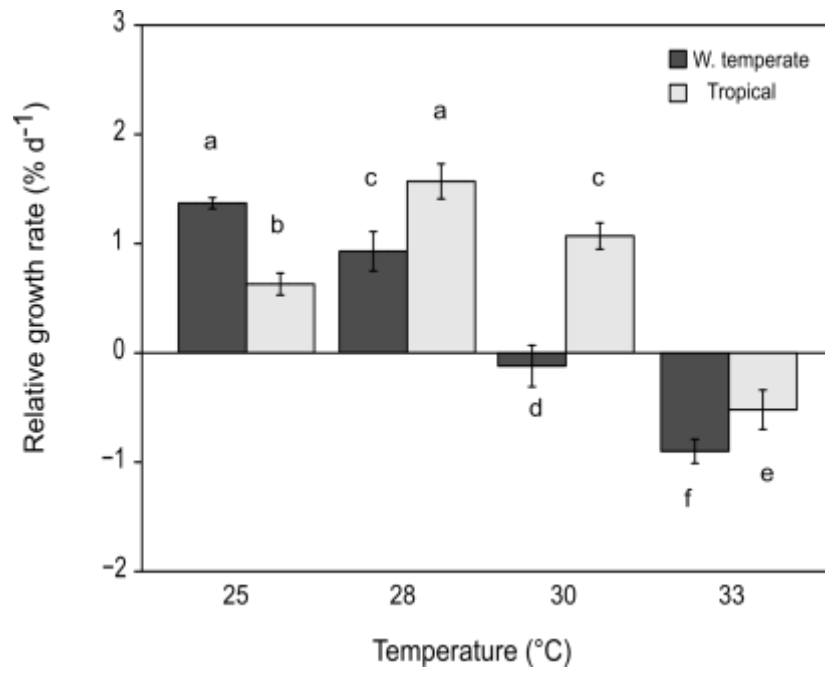7
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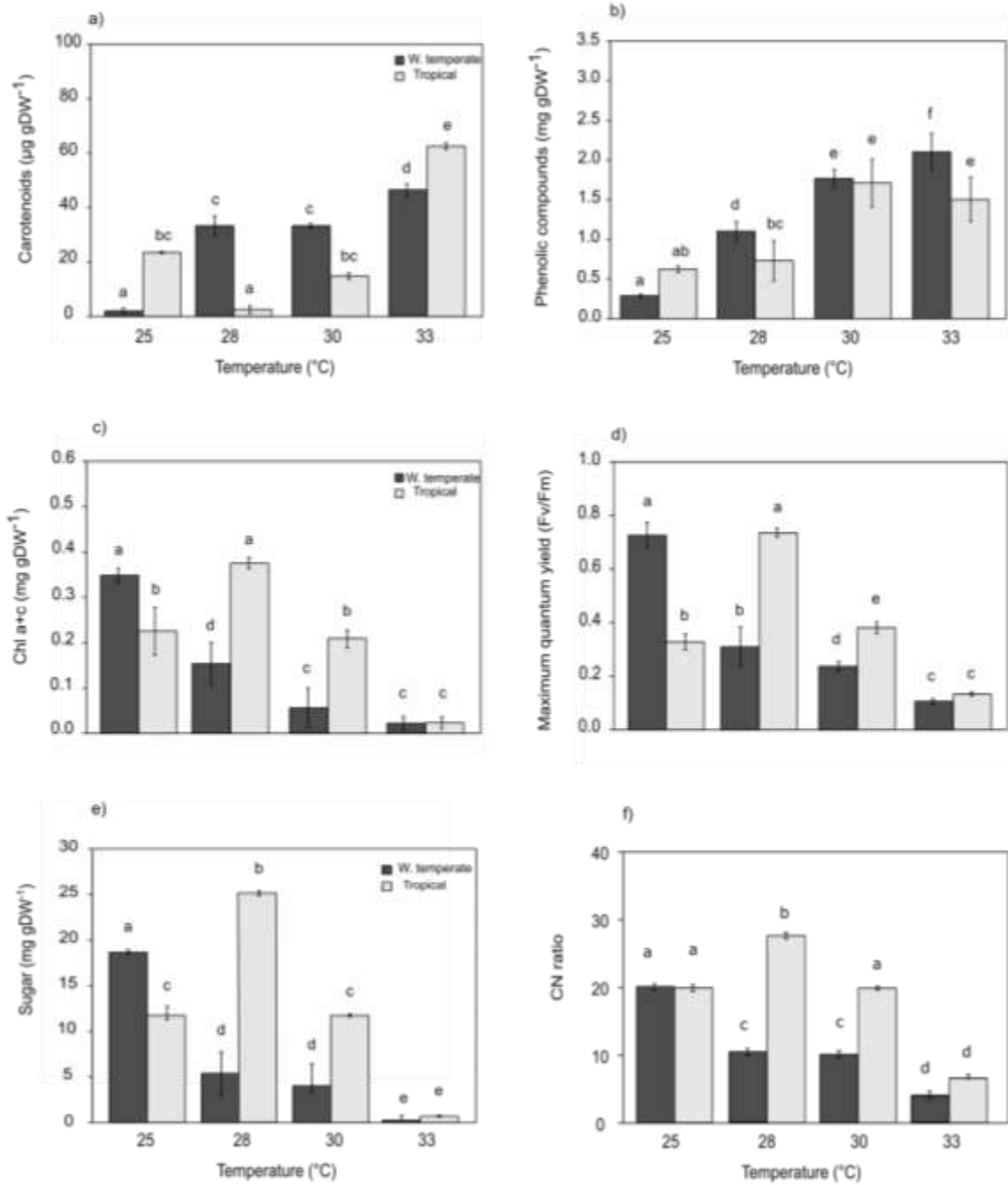20
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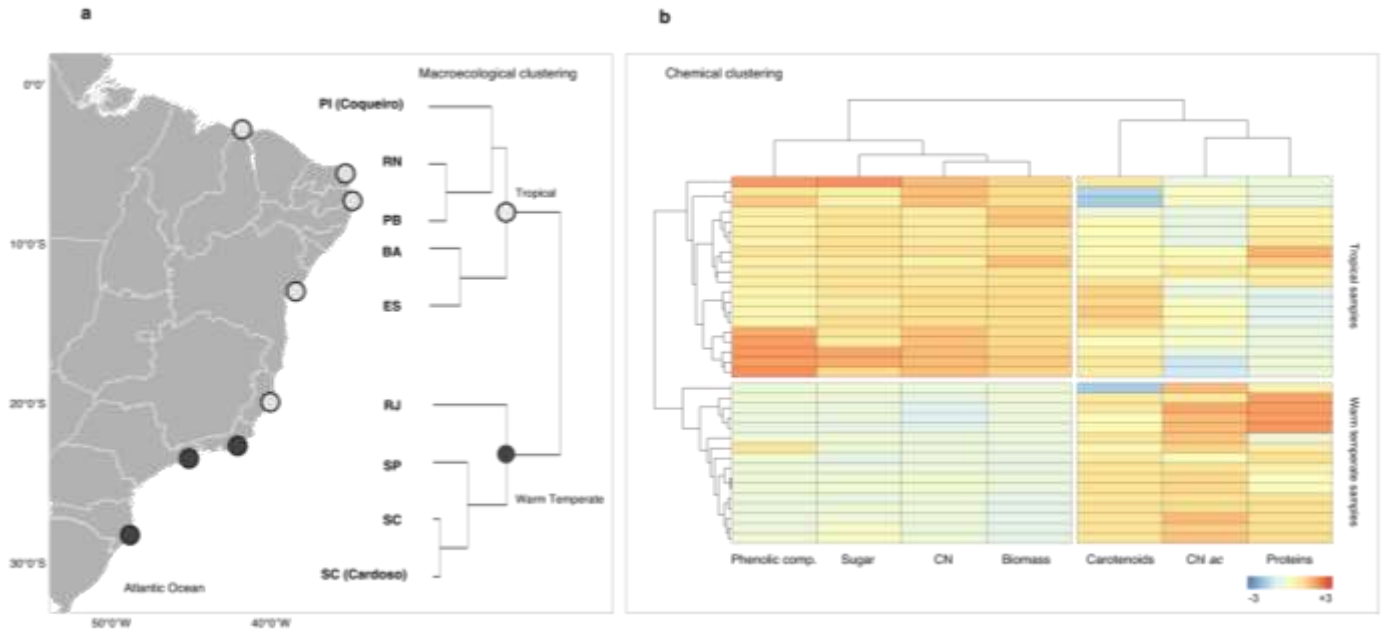
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