



Herbarium macroalgae specimens reveal a rapid reduction of thallus size and reproductive effort related with climate change

B. Alfonso^{a,*}, M. Sansón^a, C. Sangil^a, F.J. Expósito^b, J.P. Díaz^b, J.C. Hernández^c

^a Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, Canary Islands, Spain

^b Departamento de Física, Universidad de La Laguna, Canary Islands, Spain

^c Departamento de Biología Animal, Edafología y Geología, Universidad de La Laguna, Canary Islands, Spain

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ABSTRACT

Understanding and forecasting the effects of climate changes on vulnerable species are leading concerns for ecologists and conservation biologists. Herbaria are invaluable for use in long-term data series, and one of the few available methods for quantifying biodiversity changes over large periods of time. *Gelidium canariense* is an endemic and habitat-forming macroalga of the Canary Islands that coexists with two other habitat-forming Gelidiales: *G. arbuscula* and *Pterocladia capillacea*. This study assesses long-term changes in thallus size and reproductive effort of all specimens deposited in the Herbarium of Universidad de La Laguna of these three Gelidiales species. Also assessed were the effects of seawater temperature and increased incident light on net primary production (NPP), and the effects of extreme desiccation conditions on the relative water content and NPP of the three Gelidiales species. The length of the thallus of the endemic species *G. canariense* was halved during the past 40 years. The shortening of the thallus coincided with a significant decrease in the number of reproductive structures in both *Gelidium* species. These morphological changes coincide with a significant increase of the sea surface temperature, air temperature above sea surface and ultraviolet radiation in the studied area. The experiments have revealed the deleterious effects of extreme desiccation and extreme irradiance on all three species. Hence, these results suggest that air temperature and irradiance are related with these morphological changes over time in the habitat-forming *Gelidium* species and that are most likely compromising the survival of their populations which are already declining.

1. Introduction

The deleterious effects of anthropogenic climate change on marine ecosystems are well established (Doney et al., 2012). Understanding and forecasting these effects on the abundance and distribution of native and invasive species are leading goals of ecologists and conservation biologists (Parmesan and Galbraith 2004; Helmuth et al. 2006; Parmesan et al., 2005). Increasing temperatures and high levels of irradiance pose real threats to macroalgae, especially those exposed to emersion—and hence desiccation—during low tides (Contreras-Porcia et al., 2017; Fierro et al., 2017).

Several studies have revealed the negative impacts of ocean warming and high irradiance on macroalgae leading to growth reduction (Poore et al., 2013, 2016; Graba-Landry et al., 2018), decreased production of chemical defences (Sudatti et al., 2011), delayed maturation of spores and propagules (Lüning 1988; Agrawal, 2009; de Bettignies et al., 2018),

increased mortality during early life stages (Andrews et al., 2014; Wernberg et al., 2016; Capdevila et al., 2019; Kreusch et al., 2019) and even local extinctions of species (Smale and Wernberg 2013; Wernberg et al., 2013). Moreover, it has been demonstrated that climate change is likely to result in an increased frequency, intensity, and duration of extreme temperature events (e.g., heatwaves) (Meehl and Tebaldi 2004; IPCC et al., 2012; Frölicher and Laufkötter 2018; Oliver et al., 2018, 2019), with severe implications for macroalgae populations and the ecosystems they underpin (Smale et al., 2019; Straub et al., 2019).

The last few decades have seen a growing interest in the use of long-term data sets to delineate the effects of climate change on various organisms. Despite the difficulty in obtaining these data series, they are of utmost importance, as they can unravel changes in biological patterns (Wernberg et al., 2011; Meineke et al., 2018, 2019). Natural history collections (e.g., herbaria) are good examples of long-term data series that gather information dating back decades to centuries

* Corresponding author.

E-mail address: balfonso@ull.es (B. Alfonso).

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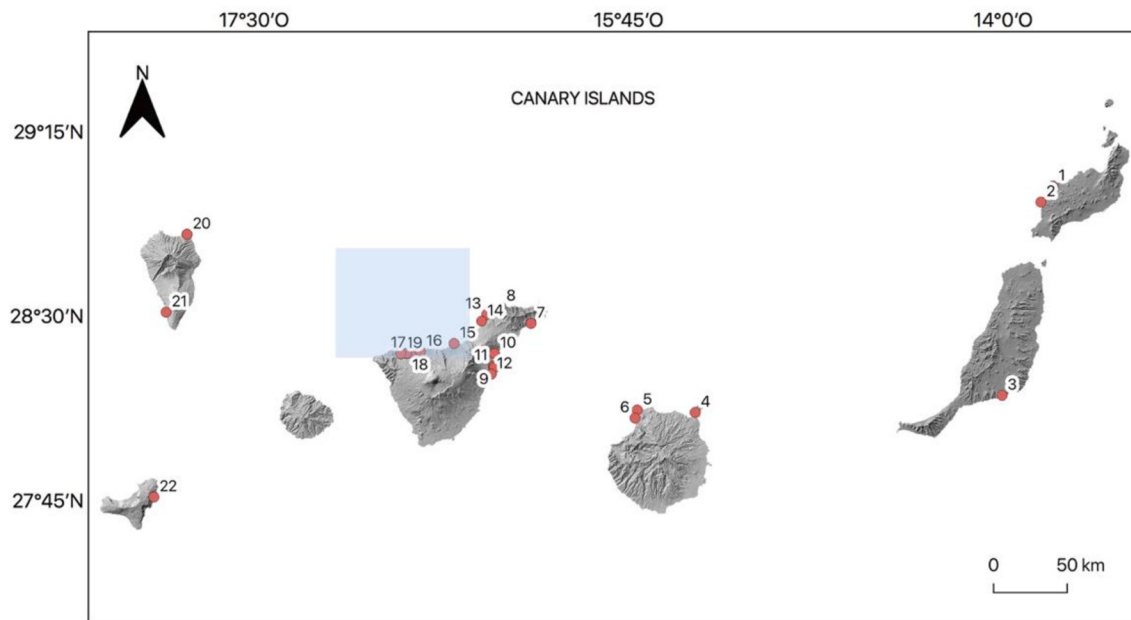


Fig. 1. Collection sites of the herbarium specimens from Universidad de La Laguna of *Gelidium canariense* (15, 16, 18, 19), *G. arbuscula* (1, 2, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 21) and *P. capillacea* (1, 2, 3, 4, 8, 9, 10, 11, 12, 15, 18, 19, 20, 22) in the Canary Islands. 1 = Playa de la madera, 2 = Morritos del perro, 3 = Gran Tarajal, 4 = Las Canteras, 5 = Puerto Sardina, 6 = punta de Agaete, 7 = San Andrés, 8 = Punta del Hidalgo, 9 = Punta de la Entrada, 10 = Caletillas, 11 = El Socorro, 12 = Puertito de Güfmar, 13 = La Barranquera, 14 = El Pris, 15 = Puerto de la Cruz, 16 = Playa moreno, 17 = Playa de la Consolación, 18 = Garachico, 19 = Caleta de Interián, 20 = La Fajana, 21 = Punta del Banco, 22 = Bahía de Tijimiriague. Climatic variables data were obtained for the blue square off the north coast of Tenerife. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(ThiersHerbaria, 2019). Thus, some authors have considered herbaria as real witnesses to biodiversity changes (Lang et al., 2019; Mannino et al., 2020). Others have documented changes in plant and animal morphology (Riera et al., 2015; McLean et al., 2016), species decline (Margules and Austin 1994), shifts in distribution (Thibaut et al., 2005; Wernberg et al., 2011), population structure (Rivers et al., 2010), and timing of life-history events, such as the evolution of flowering plants (Davis et al., 2015; Daru et al., 2018; Meineke et al., 2018).

These historical data allow us to reveal patterns not otherwise observable from other data sources (Meineke et al., 2018, 2019). For this reason, studies using information from herbaria have grown in number over the past decade (Wernberg et al., 2011; Lavoie 2013; Heberling and Isaac 2017; Nualart et al., 2017; Meineke et al., 2019). However, to establish the factor (natural or human) responsible of these morphological and distributional changes revealed by historical data is not an easy task. In fact, to accurately determine the causality of such historical changes, field and experimental studies are needed (Huisman and Millar 2013; Wernberg et al., 2014; Elmendorf et al., 2015).

Sea surface temperature, air temperature, irradiance, and ultraviolet radiation have been widely shown to strongly influence the structure and distribution of macroalgal populations (Fujimoto et al., 2014, 2015; Piñeiro-Corbeira et al., 2018; Wernberg et al., 2016; Quintano et al., 2017; Graba-Landry et al., 2018, 2020). According to Eggert (2012), temperature responses of species are often correlated with the local thermal environments, consequently, phenotypic plasticity allows these species to locally adapt. Three types of temperature responses can be differentiated: (1) genetic adaptation to local conditions; (2) phenotypic acclimation in response to changes in environmental conditions; and (3) short-term physiological regulation (King et al., 2018; Wernberg et al., 2018). Acute environmental changes (e.g., heatwaves), which species are exposed to more frequently over the past century (Oliver et al., 2018, 2019), pose threats to the health of marine ecosystems (Smale et al., 2019; Gurgel et al., 2020; Román et al., 2020; Verdura et al., 2021). Therefore, characterising the impacts of extreme environmental changes on habitat-forming macroalgae species should be of utmost importance.

The only endemic and habitat-forming macroalgae species on the

Canary Islands is *Gelidium canariense* (Grunow) Seoane Camba ex Haroun, Gil-Rodríguez, Díaz de Castro & Prud'homme. In this archipelago located northwest off the African continent, this red algal species co-exists with two other habitat-forming Gelidiales: *G. arbuscula* Bory de Saint-Vincent ex Borgesen and *Pterocladia capillacea* (S.G. Gmelin) Santelices & Hommersand. This macroalgal assemblage inhabits the upper sublittoral of the northern wave-exposed rocky shores of the central and western islands of the Canary Islands, leaving the upper limit of their populations exposed to the air during the most intense low tides. Throughout the past few decades, studies on the canopy-forming Gelidiales in the Canary Islands found an apparent reduction in the maximum thallus length of *G. canariense* and *G. arbuscula* specimens, whereas *P. capillacea* has exhibited similar length over the years (Sansón et al., 2013; Alfonso et al., 2019). This morphological trend coincides with the actual rising of sea surface temperatures registered both worldwide and in the Canary Islands (Hernández 2016). However, there remains a dearth of experimental studies on the effects of temperature on the growth of these species. Thus, the aim of this study is (1) to assess long-term changes in the size of the thallus and reproductive effort of the asexual individuals (sporophytes) of all specimens deposited in the Herbarium of Universidad de La Laguna, Tenerife (TFC Phyc. Herbarium) of *G. canariense*, *G. arbuscula*, and *P. capillacea*; (2) to study the effects of seawater temperature and increased incident light on net primary production (NPP); and (3) to examine the effects of desiccation on NPP and the relative water content (RWC) of the three species of Gelidiales.

2. Material and methods

2.1. Collection site

G. canariense, *G. arbuscula*, and *P. capillacea* are red perennial arborescent macroalgae species from the order Gelidiales. These are dioecious species with isomorphic sexual (male and female gametophytes) and asexual (sporophyte) life phases. Fertilization occurs at the female thallus, where a tiny spermatia (male gamete) reaches the trichogyne of

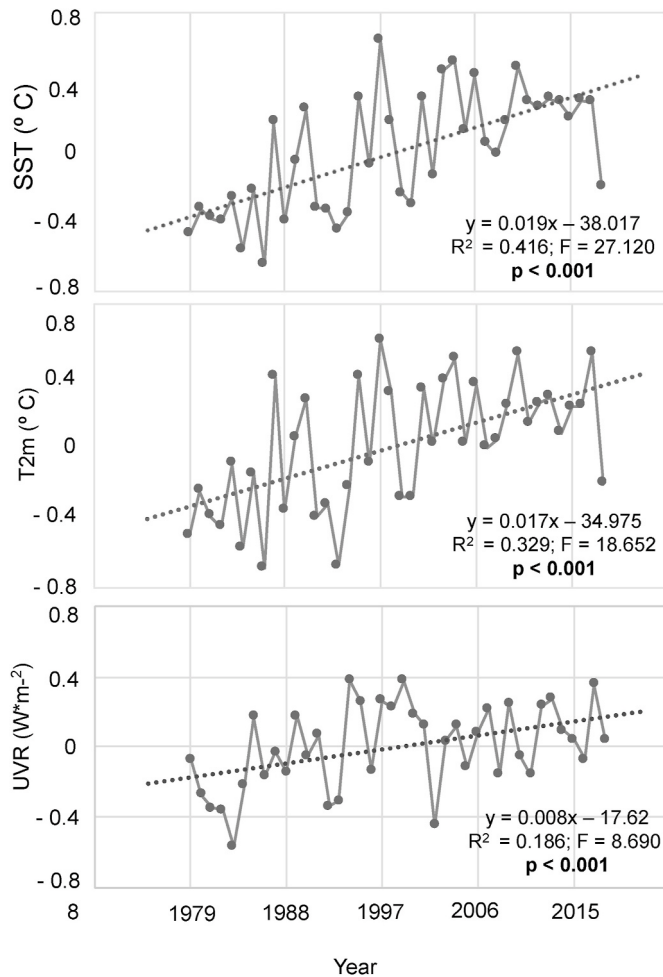


Fig. 2. Linear regression of SST (sea surface temperature), T2m (temperature 2 m above sea surface), UVR (downward ultraviolet radiation) anomalies with time for the period 1979–2018. The linear trend equation, R^2 , F-statistic and p-values are provided for each variable.

carpogonia (female gametangia), giving rise to sessile zygotes that develop into a new life phase -the carposporophyte- in the tips of female thallus. Release, attachment, and germination of the diploid carpospores result in sporophytes. Sporangia formed within the sori at the end of fertile sporophytes generally undergo meiosis to generate haploid tetraspores, which begin to germinate 2–6 h (depending on the species) following spore release (Hommersand and Fredericq 1988; Alfonso et al., 2018). As is characteristic of most Gelidiales species, the sporophytes are the dominant life cycle phase in natural populations of these species (Lindgren et al., 1998; Polifrone et al., 2012; Alfonso et al., 2017).

G. canariense, *G. arbuscula*, and *P. capillacea* are dominant and canopy-forming species of the rocky upper sublittoral of the marine flora of the Canary Islands. However, only *G. canariense* is endemic to this archipelago, and its distribution is restricted to the wave-exposed northern rocky shores of the La Palma, La Gomera, Tenerife, and Gran Canaria islands (Pinedo and Afonso-Carrillo 1994; Sangil et al., 2004; Alfonso et al., 2019); whereas, *G. arbuscula* and *P. capillacea* display a wider insular distribution and occupy a broader range of environments. *P. capillacea* and *G. arbuscula* typically inhabit the belt immediately above *G. canariense*, and together they constitute a unique assemblage of Gelidiales species.

Specimens for incubation and desiccation experiments were collected at Puerto de La Cruz (north of Tenerife, Canary Islands) in July 2020 and April 2018, respectively. To characterize temperature patterns

at the collection site, data were obtained with a HOBO sensor (Onset Computer Corporation, USA) placed at a depth of 2–3 m in the same locality from October 2012 to April 2015. The seawater temperature of the collection site was found to range from a minimum of 17.51 °C in March to a maximum of 25.55 °C in September, with an average annual temperature of 20.8 °C.

2.2. Historical study of climatic variables

Monthly averages for the period 1979–2018 of sea surface temperature (SST), air temperature at 2 m above the sea surface (T2m), downward UV radiation at the surface (UVR), the amount of ultraviolet radiation reaching the sea surface with a wavelength range of 0.20 nm–0.44 nm corresponding to the northern shore of Tenerife Island, were obtained from the Copernicus Climate Change Service (European Commission) with a resolution of 0.25° (Fig. 1). These data correspond to ERA5, the most recent climate reanalysis dataset produced by the European Centre for Medium Range Weather Forecasts (ECMWF, <https://www.ecmwf.int>). The reanalysis data combine observations from international sources with model data. This combination allows us to estimate biases between observations and produce data where *in situ* coverage is low.

One of the novelties in the ERA5 dataset is the estimation of uncertainty using the 10-member data assimilation (EDA) system. Although the reanalysis data from ERA5 are designed for global studies, the only meteorological station located at the study site is situated 2000 m above sea level (Izaña Atmospheric Research Centre–AEMET, Tenerife Island); hence, we considered the data from ERA5 quite useful in the absence of other available sources to obtain long-term climatic variables at sea level.

2.3. Historical morphological study

A total of 641 herbarium specimens of *G. canariense* ($n = 247$), *G. arbuscula* ($n = 200$) and *Pterocliadiella capillacea* ($n = 194$) from the TFC Phyc. Herbarium (Universidad de La Laguna) from the period 1970–2015 were used in the study (1970s $n = 32$, 1980s $n = 80$, 1990s $n = 243$ and 2000s $n = 286$) (Table S1, Fig. 1). Additionally, reproductive morphological characteristics of all tetrasporophyte specimens ($n = 385$) were measured and compared between decades. The morphological characteristics analysed were as follows: (1) length of the greatest primary branch per thallus, and (2) number of tetrasporangial sori in the primary branches, as described in Alfonso et al. (2017).

2.4. Samples for ex situ experiment

Specimens were collected at Puerto de la Cruz (Tenerife) in July 2020 and transported to the laboratory at ambient temperature (20 °C) in dark containers. Samples were meticulously cleaned of macroepiphytes and held in filtered seawater at 4 °C. Before initiating the experiments, the specimens were acclimated for 2 h at room temperature in a beaker with aeration. For each sample, surface water was blotted and 80–100 mg of fresh alga was used, always trying to sort a complete branch tip. Only a small fraction of cells were assumed to be damaged in the process of severing an apical section from a whole thallus; thus, any possible increased respiration due to cell wounding was assumed to be negligible.

2.5. Seawater temperature and incident PAR experiment

To analyse the effects of seawater temperature and incident PAR on the NPP of the three species, a combined experiment was performed with three different seawater temperatures: 18.8 °C $\pm$ 0.9 (SD) (actual winter temperature), 21.7 °C $\pm$ 0.8 (IPCC near-future prediction), and 27.5 °C $\pm$ 0.5 (extreme heat wave temperature), and three distinct natural PAR measures: low ($61.0 \pm 13.6 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, simulating a

Table 1

Permutational analysis of variance of morphological variables that characterize the morphotype of *Gelidium canariense*, *G. arbuscula* and *Pterocladia capillacea* (Length of the longest primary branch of all the individuals and number of tetrasporangial sori of the primary branch of the tetrasporophytes) with two factors “species” (fixed, 3 levels) and “decade” (fixed, 4 levels 70s, 80s, 90s, 00s). Data has been square root transformed. *A posteriori* analysis are done when needed.

Morphological variables	Source	df	SS	MS	Pseudo-F	P(perm)
Population						
<i>Length of 1st branch</i>						
	Species	2	620.79	310.4	115.04	0.000 ^a
	Decade	3	187.09	62.364	23.114	0.000 ^a
	Species x Decade	6	136.44	22.74	8.428	0.000 ^a
	Residual	629	1697.1	2.698		
	Total	640	3278			
PAIRWISE						
	Groups	t	P(perm)			
- <i>G. canariense</i>	1 × 2	1.081	0.283			
	1 × 3	5.762	0.000 ^a			
	1 × 4	4.474	0.000 ^a			
	2 × 3	9.614	0.000 ^a			
	2 × 4	7.783	0.000 ^a			
	3 × 4	2.065	0.039 ^a			
- <i>G. arbuscula</i>	1 × 2	0.217	0.823			
	1 × 3	3.018	0.004 ^a			
	1 × 4	0.342	0.736			
	2 × 3	4.050	0.000 ^a			
	2 × 4	0.791	0.420			
	3 × 4	5.662	0.000 ^a			
- <i>P. capillacea</i>	1 × 2	0.263	0.808			
	1 × 3	1.502	0.133			
	1 × 4	0.000	0.998			
	2 × 3	0.711	0.470			
	2 × 4	0.370	0.712			
	3 × 4	2.709	0.007 ^a			
Tetrasporophytes						
<i>Nº of tetrasporangial sori</i>						
	Source	df	SS	MS	Pseudo-F	P(perm)
	Species	2	1633.6	816.82	11.381	0.000 ^a
	Decade	3	1574.6	524.87	7.3131	0.001 ^a
	Species x Decade	6	1156.6	192.77	2.685	0.019 ^a
	Residual	297	21316	71.772		
	Total	308	26726			
PAIRWISE						
	Groups	t	P(perm)			
- <i>G. canariense</i>	1 × 2	0.975	0.338			
	1 × 3	1.871	0.074			
	1 × 4	2.176	0.030 ^a			
	2 × 3	1.348	0.175			
	2 × 4	1.598	0.123			
	3 × 4	0.129	0.899			
- <i>G. arbuscula</i>	1 × 2	0.365	0.181			
	1 × 3	2.047	0.048 ^a			
	1 × 4	1.965	0.05 ^a			
	2 × 3	3.732	0.002 ^a			
	2 × 4	3.425	0.004 ^a			
	3 × 4	0.243	0.808			
- <i>P. capillacea</i>	1 × 2	0.934	0.350			
	1 × 3	0.564	0.582			
	1 × 4	0.093	0.929			
	2 × 3	0.373	0.719			
	2 × 4	0.080	0.290			
	3 × 4	1.175	0.255			

^a Significant values.

cloudy day), medium ($570.3 \pm 100.0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, simulating intermediate light incidence with alternate cloudy and sunny days), and extreme PAR incidence ($1471.5 \pm 147.8 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, simulating a clear, sunny day). SST and PAR values were selected in order to broadly cover all actual and possible future climatic events. Each sample was incubated during 30 min and 5 replicates were used per treatment. All incubations were performed in 60 mL transparent syringes placed in transparent plastic containers kept in a bath. Syringes were sealed with parafilm to prevent oxygen and water exchange. The temperature was maintained using a thermostat for each container (EHEIM thermocontrol 50, EHEIM GmbH & Co. KG). NPP was measured by oxygen production after the incubation time and calculated as $\text{mgO}_2 \cdot \text{g Dry}$

$\text{Weight}^{-1} \cdot \text{hour}^{-1}$. Initial O₂ concentration was measured with an O₂ sensor before introducing the algae sample. After the incubation time samples were removed from the syringe and store for dry mass determination (i.e., dried oven at 60° for 48h), and final O₂ concentration was measured. This experimental design was used for each species. The oxygen and seawater temperature were measured with an oximeter (Phenomenal OXI4000, VWR). The seawater sample was continuously stirred during the measurement, as recommended by the sensor manufacturer. The PAR measurements were registered every 2–5 min during the experiment using a solar light sensor (SQ-212, PAR Sensor, Apogee).

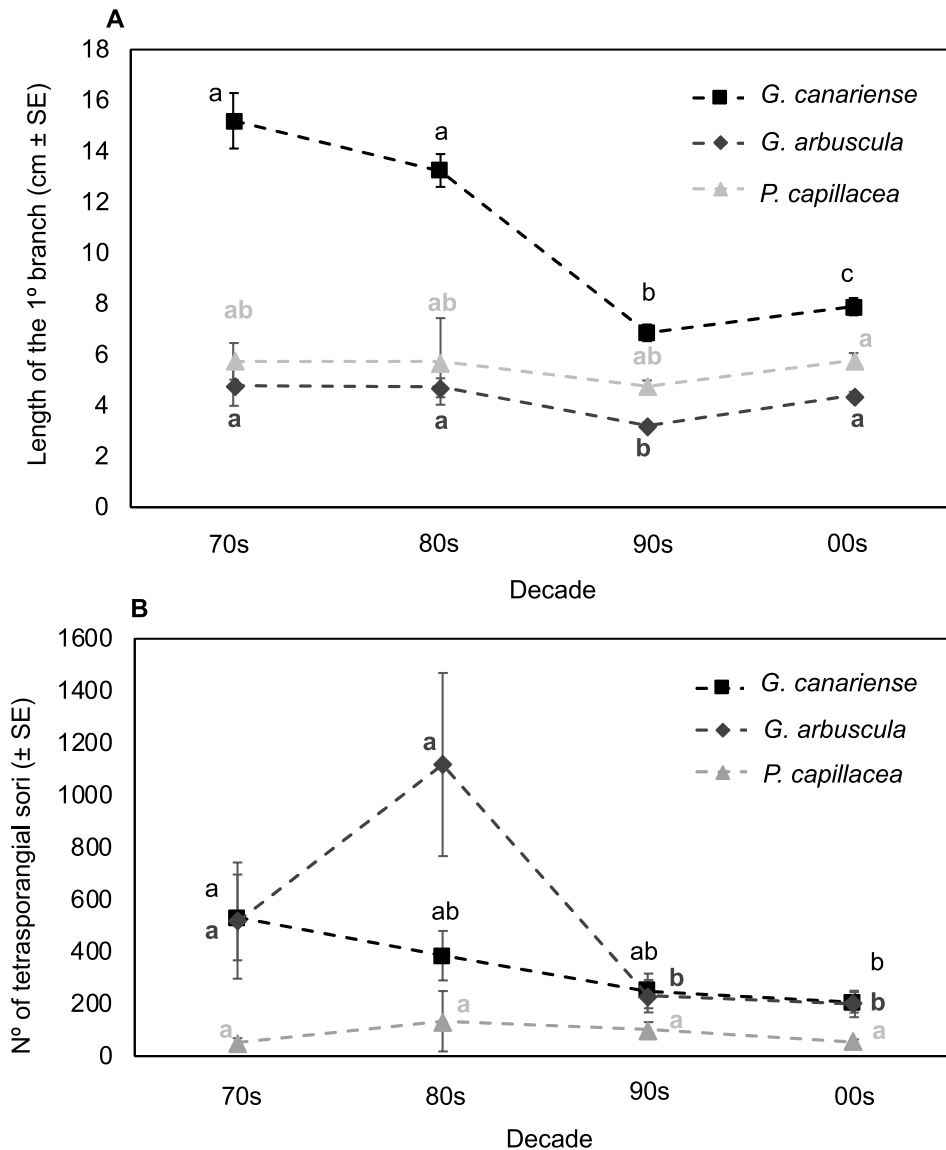


Fig. 3. Historical morphological changes of *G. canariense*, *G. arbuscula* and *P. capillacea*. (a) Length of the primary branch of total specimens deposited in the TFC Phyc Herbarium (Universidad de La Laguna) of the three species during the decades of 1970s, 1980s, 1990s and 2000s. Significant differences of the interaction factor ‘species x decade’ was obtained in the permutational ANOVA analysis. (b) Number of tetrasporangial sori in sporophytes during the decades of 1970s, 1980s, 1990s and 2000s. Significant differences of the interaction factor ‘species x decade’ was obtained in the permutational ANOVA analysis. Significant differences of the pairwise analysis are represented by lower-case letters.

2.6. Desiccation experiment

In order to determine the effect of desiccation during extreme air temperature conditions, the NPP after an emersion period of the three Gelidiales species was analysed. The experiment simulated the emersion of specimens under extreme conditions with no humidity during low tide; specimens were kept for 1 h under three different temperatures: 20 °C, 25 °C, and 30 °C. Following desiccation, samples were incubated at ambient temperature (20 °C) for 45 min and NPP was measured as previously explained. A control treatment with non-desiccated samples was also performed. Five replicates were used in each treatment, and all incubations were performed in 60 mL transparent syringes sealed with parafilm to avoid oxygen exchange. The magnitude of desiccation was calculated as the relative water content (RWC, in %), where $RWC = (\text{desiccated weight} - \text{dry weight}) / (\text{fresh weight} - \text{dry weight}) \times 100\%$. Fresh weight was determined by blotting surface water from fully hydrated samples, whereas dry weight was determined by drying for 48 h at 60 °C. The oxygen concentration and seawater temperature were measured with an oximeter immediately following incubation. The seawater sample was continuously stirred during the measurement, as recommended by the sensor manufacturer.

2.7. Statistical analysis

The temporal trend of each climatic variable was evaluated by calculating the linear regression of the anomalies of each variable *versus* the time for the total period per year. All analyses were performed with IBM SPSS Statistics 26.0.

Historical changes in the morphological variables (length of the primary branch and number of tetrasporangial sori) of the herbarium specimens of the three Gelidiales were analysed by performing a permutational analysis of variance (ANOVA) (Anderson et al., 2008) with a two-factor design that included “species” (fixed, 3 levels) and “decade” (fixed, 4 levels). The analysis of the length of the primary branch and the number of tetrasporangial sori were performed on a Euclidean similarity matrix calculated with square-root transformed data. To study the effects of seawater temperature and incident PAR on the NPP of each species, a permutational ANOVA with two factors was performed: “temperature” (fixed, 3 levels) and “PAR” (fixed, 3 levels). The effects of desiccation on the NPP and relative water content changes were analysed by performing a permutational ANOVA with two factors: “species” (fixed, 3 levels) and “temperature” (fixed, 4 levels), and a permutational ANOVA with two factors: “species” (fixed, 3 levels) and “temperature” (fixed, 3 levels), respectively. Both analyses were

Table 2

Permutational analysis of variance of the net primary production (NPP) with two factors “temperature” (fixed, 3 levels, 18.8, 21.7, 27.5 °C) and PAR (fixed, 3 levels 60, 500, 1400 $\mu\text{mol}^{\text{m}^{-2}}\text{s}^{-1}$) for each species. A *posteriori* analysis is included when needed.

<i>G. canariense</i>	Source	df	SS	MS	Pseudo-F	P(perm)
	Temperature	2	8.881	4.440	3.343	0.044 ^a
	PAR	2	142.91	71.454	53.804	0.002 ^a
	Temperature x PAR	4	2.109	0.527	0.397	0.801
	Residual	36	47.81	1.328		
	Total	44	201.71			
Pairwise - Temperature	Groups	t	P (perm)			
	18.8 °C x 21.7 °C	2.393	0.023 ^a			
	18.8 °C x 27.5 °C	2.115	0.043 ^a			
	21.7 °C x 27.5 °C	0.574	0.562			
- PAR	60 × 500	6.339	0.000 ^a			
	60 × 1400	2.956	0.006 ^a			
	500 × 1400	10.985	0.002 ^a			
<i>G. arbuscula</i>	Source	df	SS	MS	Pseudo-F	P(perm)
	Temperature	2	11.154	5.577	5.939	0.003 ^a
	PAR	2	20.155	10.077	10.731	0.000 ^a
	Temperature x PAR	4	7.214	1.803	1.920	0.129
	Residual	36	33.806	0.903		
	Total	44	72.329			
Pairwise - Temperature	Groups	t	P (perm)			
	18.8 °C x 21.7 °C	3.005	0.003 ^a			
	18.8 °C x 27.5 °C	4.057	0.000 ^a			
	21.7 °C x 27.5 °C	0.654	0.526			
- PAR	60 × 500	3.515	0.001 ^a			
	60 × 1400	1.617	0.120			
	500 × 1400	3.930	0.002 ^a			
<i>P. capillacea</i>	Source	df	SS	MS	Pseudo-F	P(perm)
	Temperature	2	30.042	15.021	10.814	0.000 ^a
	PAR	2	51.932	25.966	18.693	0.000 ^a
	Temperature x PAR	4	12.762	3.190	2.206	0.080
	Residual	36	50.007	1.389		
	Total	44	144.74			
Pairwise - Temperature	Groups	t	P (perm)			
	18.8 °C x 21.7 °C	2.680	0.015			
	18.8 °C x 27.5 °C	4.611	0.000 ^a			
	21.7 °C x 27.5 °C	1.987	0.061			
- PAR	60 × 500	5.191	0.000 ^a			
	60 × 1400	1.298	0.213			
	500 × 1400	4.239	0.000 ^a			

^a Significant values.

performed on a Euclidean similarity matrix, and all statistical analyses were performed using PRIMER 7 and PERMANOVA+ (Anderson et al., 2008).

3. Results

3.1. Importance of climatic variables

The SST, T2m, and UVR were found to have increased significantly over the last 40 years off the northern coast of Tenerife. SST and T2m rose 0.2 °C per decade, whereas UVR rose 0.1 $\text{W}\cdot\text{m}^{-2}$ per decade (Fig. 2).

3.2. Herbarium study: historical changes of thallus length and reproductive effort

The interaction term “species × decade” was significant for the length of the primary branch of the total specimens studied. The *a posteriori* analysis showed that the thallus length of *G. canariense* shortened

significantly as of the 1990s; the average length of 13.24 ± 0.6 (SE) cm in the preceding decade fell to 7.8 ± 0.3 cm. *G. arbuscula* thallus length shortened slightly, but only during the 1990s, whereas *P. capillacea* has maintained the same thallus length since the 1970s (Table 1, Fig. 3a).

With respect to the tetrasporophytes, the interaction term “species × decade” for the number of tetrasporangial sori from the primary branch was also significant. Thus, the number of sori for *G. canariense* fell significantly as of 1970, while a similarly significant reduction for *G. arbuscula* only occurred after 1980. The number of tetrasporangial sori of *P. capillacea* remained relatively constant over the past 40 years (Table 1, Fig. 3b).

3.3. SST and PAR experiment

For all three species, the factors “temperature” and “PAR” were significant (Table 2). The *a posteriori* analysis showed a significantly lower NPP at 18.8 °C relative to 21.7 °C or 27.5 °C (Fig. 4a,c,e). The second factor displayed a NPP in *G. canariense* that differed significantly for each PAR treatment. The lowest NPP was registered at extreme PAR

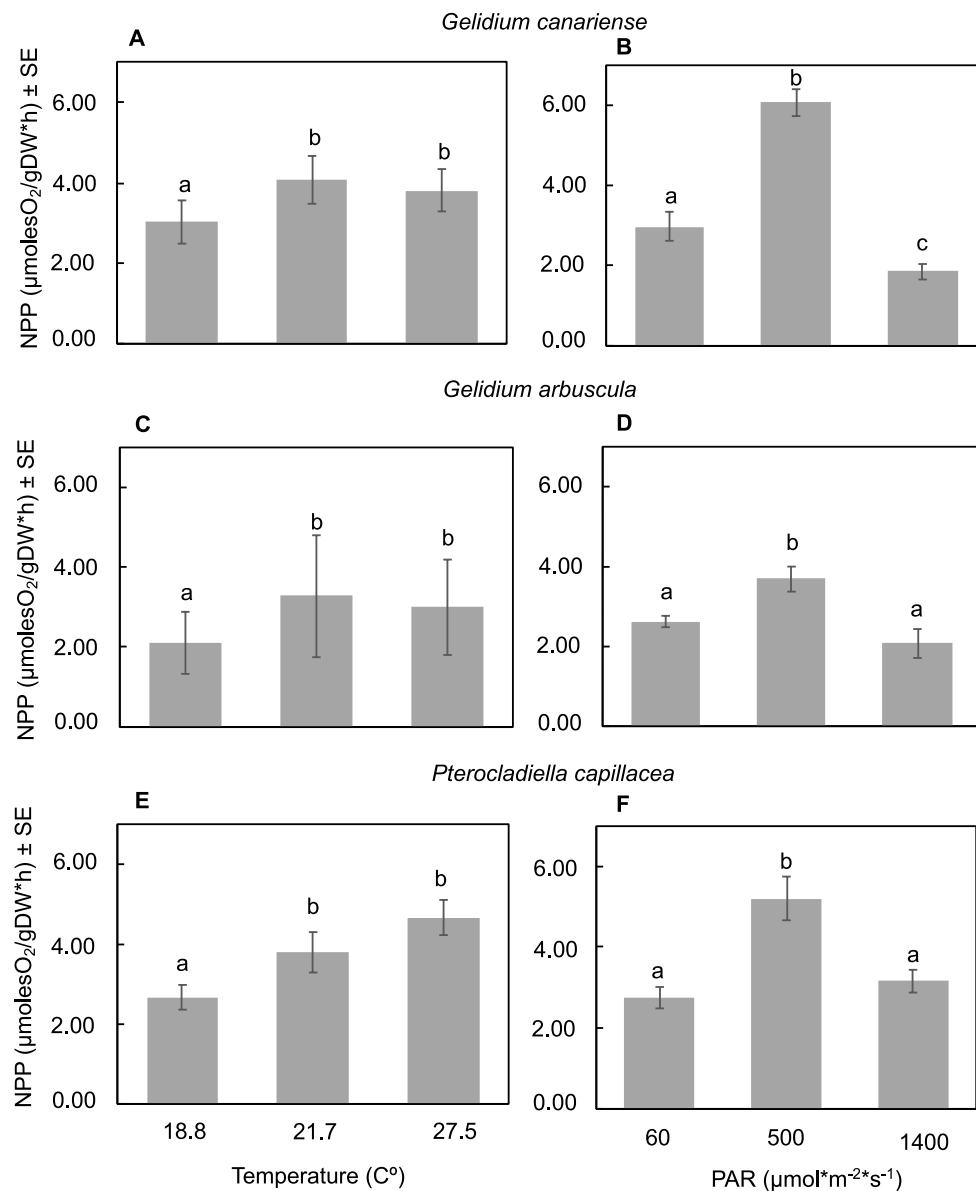


Fig. 4. SST and PAR experiment. Net primary production (NPP) obtained with three different temperatures treatments and three different PAR of irradiance for *G. canariense* (a, b), *G. arbuscula* (a, d) and *P. capillacea* (e, f). Significant differences of the pairwise analysis are represented by lowercase letters.

incidence, and the highest at intermediate PAR incidence. In *G. arbuscula* and *P. capillacea*, low and extreme PAR incidences were significantly different than intermediate ones in NPP (Fig. 4b,d,f).

3.4. Desiccation experiment

Desiccation temperature significantly affected the NPP and the RWC of the three species. The *a posteriori* analysis showed that the NPP of non-desiccated algae were significantly higher than the NPP of algae exposed to the desiccation treatments. Furthermore, the desiccation at ambient temperature differed significantly from desiccation at 25 °C and 30 °C in that it was the only condition in which any oxygen production was registered; all other treatments consumed oxygen (Table 3, Fig. 5a). A reduction of RWC of more than 80% was registered. Additionally, the reduction of RWC at 25 °C and 30 °C was significantly higher relative to the treatment at 20 °C in all three species (Fig. 5b).

4. Discussion

Our study of herbarium specimens of *G. canariense*, *G. arbuscula*, and *P. capillacea* in the Canary Islands revealed that the length of the thallus of the endemic macroalga *G. canariense* was halved over the last 40 years. The reduction of thallus size only coincided with the decrease in tetrasporangial sori in both *Gelidium* species. Hence, not only these Gelidiales have exhibited a significant shortened thallus length over the last four decades, but also their reproductive effort has significantly changed in the *Gelidium* species. Furthermore, our experiments revealed the deleterious effects of desiccation and extreme irradiance on the three species. Additionally, there was a significant increment in the northern coast of the island of 0.2 °C per decade in SST and T2m, respectively, and 0.1 W*m⁻² per decade in UVR probably linked to the thinning of the low-cloud layer registered in the Macaronesian region (Díaz et al., 2019). These results suggest that the air temperature and irradiance (UVR) are major contributors to the progressive morphological changes observed in *G. canariense*, *G. arbuscula*, and *P. capillacea*.

According to the *ex situ* experiments, thallus desiccation, which

Table 3

Permutational analysis of variance of the net primary production (NPP) after desiccation with factor “temperature” (fixed with 4 levels control, 20 °C, 25 °C, 30 °C) and species (fixed with 3 levels *Gelidium canariense*, *G. arbuscula*, *Pterocladia capillacea*) and Relative Water Content (RWC) with factor “temperature” (fixed with 3 levels, 20 °C, 25 °C, 30 °C) and species (fixed with 3 levels *Gelidium canariense*, *G. arbuscula*, *Pterocladia capillacea*). A *posteriori* analysis is included when needed.

NPP	Source	df	SS	MS	Pseudo-F	P(perm)
	Species	2	0.543	0.271	0.256	0.784
	Temperature	2	21.752	10.878	10.28	0.000 ^a
	Species x Temperature	4	7.494	1.873	1.770	0.154
	Residual	38	40.214	1.058		
	Total	46	71.129			
Pairwise Temperature	Groups	t	P (perm)			
	25 °C x 30 °C	1.091	0.311			
	25 °C x 20 °C	3.635	0.001			
	30 °C x 20 °C	3.680	0.001			
RCW	Source	df	SS	MS	Pseudo-F	P(perm)
	Species	2	35.098	17.549	0.516	0.593
	Temperature	2	1498.2	749.12	22.047	0.002 ^a
	Species x Temperature	4	196.35	49.087	1.444	0.239
	Residual	38	1291.2	33.978		
	Total	46	3112.5			
Pairwise Temperature	Groups	t	P (perm)			
	20 °C x 25 °C	4.939	0.000 ^a			
	20 °C x 30 °C	5.573	0.000 ^a			
	25 °C x 30 °C	0.834	0.413			

^a Significant values.

simulated the emersion conditions at low tides, produced the strongest deleterious effect on the NPP of the three studied species. These inhabitants of the upper level of the sublittoral can be exposed to emersion conditions lasting 1–2 h twice a day due to the semidiurnal regime of tides in the Canary Islands (Braun and Molina 1984). In our study, exposing the specimens to a simulated low tide with extreme heat conditions for a period of 1 h and a recovery period of 45 min resulted in the loss of more than 80% of the water content in *G. canariense*, *G. arbuscula*, and *P. capillacea*, causing harmful effects to these macroalgae on the basis that the NPP abruptly diminished relative to non-desiccated controls. Desiccation tolerance is a limiting factor for macroalgae and determines the vertical distribution of several macroalgae species (Davison and Pearson 1996; Hurd et al., 2014). Domínguez-Álvarez et al. (2011) also found a severe water loss after emersion in these species of Gelidiales; the authors suggested that the zonation of these species was strongly affected by the negative effects of desiccation on net photosynthesis, similar to some fucoids (Williams and Dethier 2005). Some intertidal species are able to maintain high rates of photosynthesis in air when they are fully hydrated, but this rate declines along with decreasing water content (Shafer et al., 2007), as observed in our study.

The effect of seawater temperature has been shown to be less of a determinant in the NPP of *G. canariense*, *G. arbuscula* and *P. capillacea* than was the irradiance level. The fact that responses to the temperature treatments of 21.7 °C and 27.5 °C did not differ significantly in any species may indicate that a higher temperature is required to reveal a deleterious effect on the NPP, as occurs with other Gelidiales species (Fujimoto et al., 2014, 2015). Nevertheless, a photoinhibition of the photosynthesis at extreme irradiance levels is seen in *G. canariense*. Temperature, irradiance, and desiccation have each been associated with the bleaching of some macroalgae, including *G. corneum*, *Calliarthron tuberculatum*, *Corallina officinalis*, and *Caulerpa taxifolia* (Latham 2008; Martone et al., 2010; Scrosati and DeWreede, 1998; Quintano et al., 2017). In some species of Gelidiales, bleaching has been linked not only to high irradiance levels, but also to the nutrient depletion and high temperatures characteristic of summer conditions (Santelices 1988; Borja 1994; Rico and Fernandez 1996; Quintano et al., 2017). *G. canariense*, *G. arbuscula*, and *P. capillacea* populations can usually be

seen depigmented during late summer or after long periods of extreme temperatures (authors pers. obs.), which aligns with data of other Gelidiales.

The study of natural history collections to detect morphological variation in relation to climate change is quite common with terrestrial plants (e.g., Guerin et al., 2012; Dalrymple et al., 2015; McAllister et al., 2019), yet only a few studies have been carried out with macroalgae (i. e., Riera et al., 2015; Álvarez-Canali et al., 2019). In the present study, we report for the first time the decrease in thallus length and in reproductive effort of a habitat-forming macroalgae endemic to an oceanic archipelago (*G. canariense*), and we discuss the possible contributing factors based on experimental data.

Depending on the species and the life history stage, desiccation has been shown to magnify or reduce the effects of high temperatures (Hunt and Denny 2008; Chu et al., 2012), and the results of our study show that desiccation under extreme conditions that exceed 20 °C is fatal to *G. canariense*, *G. arbuscula* and *P. capillacea*. This implies that heatwaves during low tides will be lethal to populations of these macroalgae in the Canary Islands, as recently stated for other habitat-forming macroalgae (Hereward et al., 2020; Román et al., 2020). The role of irradiance—UVB in particular—has also proven to be a determinant in the presence and growth of other *Gelidium* species (Gómez and Figueroa 1998; Quintano et al., 2014; Schmidt et al., 2015). In particular, spore germination, rather than growth, appeared to be the eco-physiological bottleneck for initiating mass development of algae (Agrawal, 2009), and for the resilience of habitat-forming macroalgae species (Kreusch et al., 2019).

Recently, it has been demonstrated a drastic decline in the distribution and cover of *G. canariense* and *G. arbuscula* related with the increment in SST, T2m and UVR in the archipelago. Particularly more than 90% of the former distribution of *G. canariense* has already disappeared in north coast of Tenerife Island, where the greatest populations of this species were found 30 years ago (Alfonso et al., 2021). Several environmental factors (e.g., air/seawater temperature, light availability, sedimentation, nutrient concentration, etc.) can hinder the development of macroalgae (e.g., Airolidi and Cinelli, 1997; Borja et al., 2018; Smale et al., 2020). Nevertheless, in this study we have determined a negative effect of high irradiances and the lethal consequences of

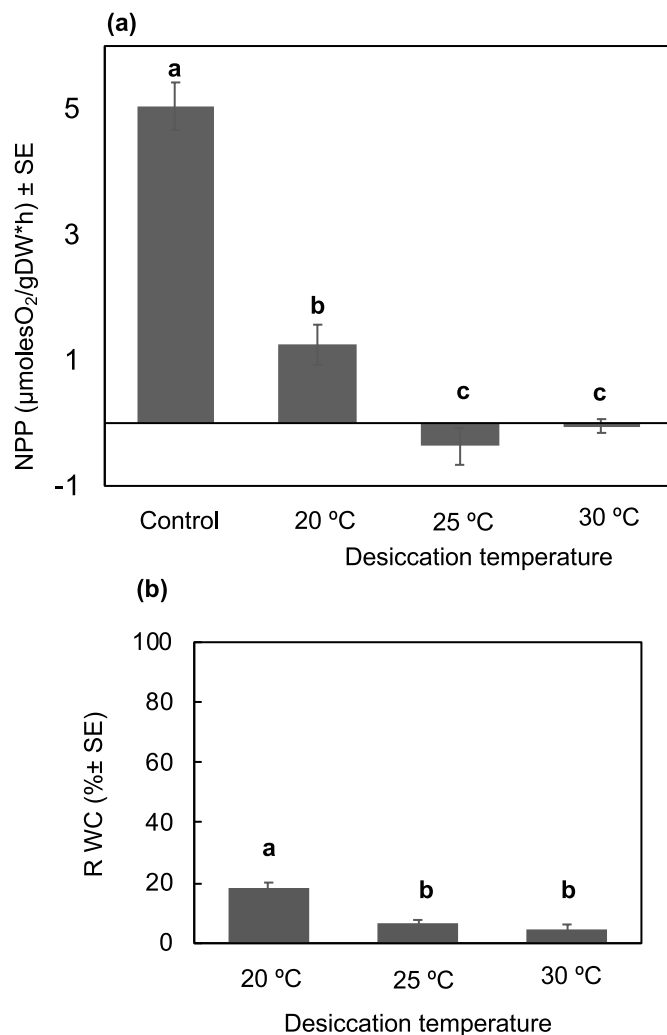


Fig. 5. Desiccation experiment. **A)** Net primary production (NPP ± SE) obtained with three different temperatures treatments for the three species. **B)** Percentage of relative water content (RWC ± SE) of the three species for the three temperatures. Significant differences of the pairwise analysis are represented by lowercase letters.

desiccation at high temperatures on the NPP of these habitat-forming macroalgae, hence, these factors are most likely related with the size reduction in the species over the last decades. Furthermore, the negative implications of climate change on their reproductive effort would compromise the survival of their populations in the near future as they are already in severe decline.

5. Conclusions

The individuals of the endemic and habitat-forming *G. canariense* have exhibited a significant shortening in thallus length over the last four decades. Also, the reproductive effort has significantly changed in both *Gelidium* species, *G. canariense* and *G. arbuscula*. The *ex situ* experiments revealed the deleterious effects of desiccation with the loss of more than 80% of the water content in *G. canariense*, *G. arbuscula* and *P. capillacea*, resulting in the abrupt reduction of the NPP relative to non-desiccated controls. Furthermore, extreme irradiance has shown to be more determinant in the NPP of these Gelidiales than was the seawater temperature. This study has highlighted the extreme vulnerability of two habitat-forming Gelidiales from the Canary Islands to the significant increase of environmental factors related with climate change.

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Author statement

Beatriz Alfonso: Investigation, Formal analysis, Writing – Original Draft, Visualization.

Marta Sansón: Conceptualization, Writing – Review & Editing.

Carlos Sangil: Conceptualization, Writing – Review & Editing.

Fracisco J. Expósito: Data Curation, Writing – Review & Editing.

Juan P. Díaz: Data Curation, Writing – Review & Editing.

José Carlos Hernández: Conceptualization, Methodology, Formal analysis, Writing - Review & Editing, Supervising.

Data availability

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

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2021.105546>.

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