



Local and global stressors as major drivers of the drastic regression of brown macroalgae forests in an oceanic island

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Received: 2 October 2023 / Accepted: 27 March 2024
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Abstract

Similar to other coastal regions worldwide, forests created by brown macroalgae have severely declined in recent decades across the Macaronesian oceanic archipelagos (northeastern Atlantic), eroding the provision of ecosystem services. However, the putative effects of natural and anthropogenic stressors (both local and global) on such declines across spatial and temporal scales remain unresolved. Our research endeavored to investigate the connection between local and global stressors and the distribution and extent of the brown macroalgae *Gongolaria abies-marina* in the rocky intertidal and adjacent subtidal zones of Gran Canaria over the past four decades. We also quantified the presence of populations at small scales, according to local micro-habitat topography (“open rock” versus “refuge”). Through herbarium records, we additionally analyzed the historical variation in the thallus size of the species. Finally, we experimentally assessed the thermotolerance of embryonic stages to warming. The main environmental drivers explaining the regression of *G. abies-marina* were the increasing number of marine heatwaves, while the number of local human impacts (quantified through the HAPI index) also accounted for further regression in the extent of marine forests. Warming experimentally reduced the survival and size of macroalgal embryos. A progressive miniaturization of the species, currently restricted to micro-habitat refuges as a survival strategy, seems likely to be the final stage in the progressive disappearance of this macroalgae from the island’s rocky shores.

Keywords Global change · Conservation · Atlantic · Macroalgal forests · Habitat-forming · Marine heatwaves

Introduction

Marine forests created by canopy-forming brown macroalgae (Laminariales, Tilopteriales, and Fucales) globally form highly productive ecosystems on rocky coastlines, increasing

structural complexity and providing habitats for associated species (Wernberg and Filbee-Dexter 2019). Macroalgal forests, because of their high primary productivity rates, are important contributors to the benthic carbon cycle of rocky coasts (Krause-Jensen and Duarte 2016), aside from other relevant ecosystem services provided, such as nutrient cycling, food production, nursery habitat and control of

Communicated by Wolfgang Cramer

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water quality (De La Fuente et al. 2019; Eger et al. 2023). In the past half-century, however, threats (i.e., ocean warming, thermal anomalies, overgrazing, species invasions, and eutrophication) to canopy-forming brown macroalgae have increased in number and severity, leading to a decline in their abundance in many temperate locations or latitudes (Mineur et al. 2015; Krumhansl et al. 2016). The loss of macroalgal forests implies a damage, or impoverishment, in the provision of ecosystem services (Smale et al. 2019). Thus, understanding the causes of declines in macroalgal forests is essential for implementing appropriate conservation and restoration schemes (Coleman and Wernberg 2017).

A combination of natural and anthropogenic stressors often explains the decay of macroalgal forests around the world (Strain et al. 2014; Mineur et al. 2015; Krumhansl et al. 2016). Among these stressors, climate change has become one of the most important drivers of such global ecological change (Wernberg et al. 2016). Currently, there is evidence that climate change has modified the distribution of species, which has altered the structure and functioning of ecosystems (Pecl et al. 2017). Many species have changed their geographic distribution, colonizing more favorable habitats (Vergés et al. 2014; Bevilacqua et al. 2019; Álvarez-Losada et al. 2020), while becoming locally extinct in areas previously occupied (Gouvêa et al. 2017; de Bettignies et al. 2018; Gurgel et al. 2020). Extreme thermal anomalies, in particular Marine Heat Waves (MHWs), have occurred with increasing intensity, frequency, and duration around the world (Hobday et al. 2016; Oliver et al. 2018; Thorat et al. 2022), which abruptly alter the structure and function of marine ecosystems, including brown macroalgal forests (Wernberg et al. 2016; Straub et al. 2019; Sen Gupta et al. 2020; Smale 2020; Pessarrodona et al. 2021). Concurrently, local human disturbances, such as habitat destruction, pollution, and eutrophication, act cumulatively and even synergistically, amplifying the effects of climate change on coastal habitats (Gouvêa et al. 2017; Orfanidis et al. 2021). From a conservation point of view, it is critical to ascertain, not only the nature of varying factors involved in the declines of macroalgal forests, but also their relative contributions, and how these factors alter processes across levels of organization, from physiological effects to ecological interactions (Côté et al. 2016; Duarte et al. 2018).

Chronic warming and MHWs affect the phenology and physiology of macroalgal species creating marine forests, harming their performance, growth, and size (Doney et al. 2012; Smith et al. 2023), increasing their vulnerability to other stressors, and eventually leading to population decline and local extinction (Wernberg et al. 2010, 2016). A large body of literature has evaluated thermal stress on the physiology and biology of brown algae, both for early and adult stages (Andrews et al. 2014; Capdevila et al. 2019; Falace et al. 2021; Verdura et al. 2021). Overall, the pattern that has

emerged is a high sensitivity for the early life stages and a relative ability of adults to survive over broader temperature ranges, physiologically compensating thermal stress (Falace et al. 2021; Verdura et al. 2021). The speed, extent, and magnitude of species' range shifts following MHWs, as well as their capacity to recover, are highly variable and may be dependent on species' traits and local and regional processes (Sunday et al. 2015; Smale et al. 2019; Smith et al. 2023). For example, corals, seaweeds, and seagrasses are more sensitive to MHWs than mobile species (Garrabou et al. 2009; Stipcich et al. 2022; Smith et al. 2023), often exhibiting sharp declines after exposure to anomalously high temperatures (Garrabou et al. 2009; Wernberg et al. 2016). However, at the same time, some species are favored by MHWs (Boudouresque et al. 2024). Often, due to warming and/or extreme events, species find refuge in cryptic habitats, as a survival strategy, allowing their persistence and recovery, or ultimately as a final stage before its disappearance (Franco et al. 2015; Shay et al. 2021; Verdura et al. 2021; Zarco-Perello et al. 2021; Grimaldi et al. 2023).

Brown macroalgae of the genera *Cystoseira*, *Ericaria*, *Gongolaria*, and *Sargassum* (family Sargassaceae) are key components of Mediterranean-Atlantic marine forests, essential for biodiversity and ecosystem functioning (Tuya and Haroun 2006), which have suffered severe declines in the last decades (Thibaut et al. 2005; Blanfuné et al. 2016; Valdazo et al. 2017; Bernal-Ibáñez et al. 2021b). Populations of these species are particularly vulnerable to anthropogenic impacts and, therefore, are indicators of good environmental status (Blanfuné et al. 2017). Across the coasts of the Macaronesian oceanic archipelagos (eastern Atlantic), a range of local human activities has altered coastal habitats (Tuya et al. 2014; Ferrer-Valero et al. 2017; Bernal-Ibáñez et al. 2021b). At the same time, ocean warming has been attributed to have negative effects on brown macroalgae (Sansón et al. 2013; Geppi and Riera 2022), and the occurrence of MHWs has become more frequent and intense in recent decades (Bernal-Ibáñez et al. 2022). In the NE Atlantic coast, the decline and even disappearance of these species have been reported (Friedlander et al. 2017; Valdazo et al. 2017; Bernal-Ibáñez et al. 2021b; Martín-García et al. 2022), and several processes, such as herbivory by sea-urchins, human development, extreme wave events and MHWs, have been pointed in this sense (Bernal-Ibáñez et al. 2021a, b; Martín-García et al. 2022).

In this study, we aimed to partition the effects of a range of environmental and anthropogenic drivers on the progressive disappearance of marine forests created by *G. abies-marina* at an island scale. We collected data in the oceanic island of Gran Canaria (Canary Islands, eastern Atlantic) through the last four decades, as a regional case study, to initially link time series of local (levels of local human activity) and global stressors (ocean warming, marine heatwaves, and

solar radiation) with spatio-temporal decreases in the distribution of the brown macroalgae *Gongolaria abies-marina* on the rocky intertidal and adjacent shallow subtidal. We also compared the presence of *G. abies-marina*, at small scales, according to local micro-habitat topography (“open rock” versus “refuge”). Through herbarium sheets, we also analyzed the historical variation in the thallus size of the species to assess whether miniaturization of the species occurs as a final stage in the regression of the macroalgae. This observational data was then complemented with an experimental assessment of the thermo-tolerance of early stages of this macroalgae to warming.

Material and methods

Target species

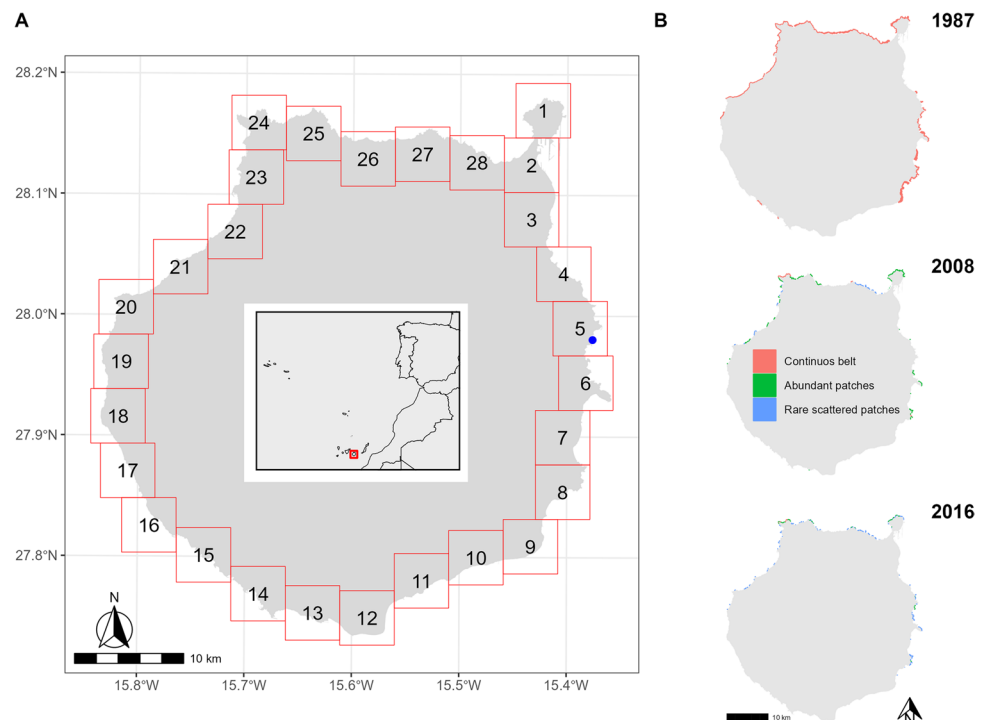
Gongolaria abies-marina (S.G. Gmelin) Kuntze is a species of *Cystoseira* s.l. that thrives almost exclusively in the NE Atlantic coasts (Macaronesia and adjacent coasts of north-western Africa) with marginal populations in the western Mediterranean Sea (Ribera et al. 1992). In the Canarian Archipelago, this is a habitat-forming species that created extensive marine forests from the lower intertidal to the shallow subtidal in coasts exposed to high wave action (Tuya and Haroun 2006; Sangil et al. 2011; Martín-García et al. 2022). This is a perennial caespitose macroalgae with no conspicuous holdfast and no stipe, attached to the substratum

by small discoid haptera (Gil-Rodríguez et al. 1988; Gomez Garreta et al. 2000). Individuals are monoecious, with male and female gametes housed within the same conceptacle, which are grouped in terminal (apical) receptacles (Gil-Rodríguez et al. 1988). Reproduction is oogamic (large non-motile eggs and biflagellate sperm), and fertilization is external (Guern 1963; Gómez-Garreta 2000). After fertilization, large and free-living zygotes (~70–100 µm) rapidly sink on the bottom, where they are fixed during the first 12–24 h (Verdura et al. 2021). This gives the species a low dispersal ability (<20 cm; Mangialajo et al. 2012), despite long dispersal also observed for different species of *Cystoseira* s.l. (Thibaut et al. 2016; Reynes et al. 2021). In the study area, the growth pattern is seasonal (Medina and Haroun 1994; Valdazo et al. 2020), and reproductive structures are present throughout the entire year but are more abundant from May to November (Valdazo et al. 2020).

Historical distribution

Valdazo et al. (2017) presented the historical distribution of *G. abies-marina* in Gran Canaria (Fig. 1A and B) from the 1980s to 2016, which included an up-to-date current distribution through field surveys between 2015 and 2016. Locally, the distribution of populations was categorized as rare, scattered patches (small patches normally thriving in crevices), abundant patches (large patches forming irregular belts), and continuous belts (wide and continuous belts irrespective of local topography). All *G. abies-marina*

Fig. 1 **A** Location of Gran Canaria Island in the eastern Atlantic and the distribution of the grid used to map the temporal distribution of *G. abies-marina*. The blue dot corresponds to the location of Salinetas, where sample collection of reproductive tissue took place. **B** Historical distribution of *G. abies-marina* around Gran Canaria



populations were geo-localized and recorded on A4 aerial photographs from the IGN (Instituto Geográfico Nacional, 1:2500 scale). Changes in the distribution (km de coastal perimeter) and extent (occupied area in ha) over time were analyzed with the open-source QGIS (<http://www.qgis.org>), using a 1:2500 scale and a WGS-84/UTM Zone 28N coordinate system.

In this study, to relate spatio-temporal changes in the distribution of populations with spatio-temporal changes in local and global stressors, the coast was divided into a grid of (5 × 5 km) 28 sectors (Fig. 1A), where several environmental drivers were estimated (see below). To operationally link changes in the temporal distribution of *G. abies-marina* with sets of local and global stressors, we finally considered three temporal frames: 1981–1986 (algal distribution data provided by Valdazo et al. 2017), 1987–2007 (Rodríguez et al. 2008), and 2008–2016 (Valdazo et al. 2017).

Local and global environmental drivers

To explain changes in the distribution of *G. abies-marina* over time, we used time series of potential environmental drivers affecting the distribution of the species, according to previous studies on this species (Tuya and Haroun 2006; Sangil et al. 2014; Martín-García et al. 2022) and other brown canopy-forming macroalgae (Álvarez-Losada et al. 2020). Local (small-scale) environmental drivers describe the population-level conditions throughout the study area, such as coastal geomorphology, exposure to waves, and anthropic pressures. Whereas global environmental drivers here refer to climatic conditions that account for global warming, extreme events, and variation in solar radiation.

Local geomorphology and wave energy

We used the digital terrain model from the eco-cartographic study of Gran Canaria Island (M.M.A. 2001, 2005), which delimitates the type of coastal substrates between 0 and 50 m depth, to obtain the surface and length of the rocky substrate, for each sector, as well as the slope and orientation (eastness and northness) along the island coastal perimeter. We calculated variables describing the structure of the shallow rocky bottom using QGIS and the R “sf” (Pebesma 2023) and “terra” (Hijmans 2023) packages. Data on wave energy were obtained from Losada et al. (2010); we used the average annual wave power (kW m^{-1}), for each of the 28 sectors, by using values at 20 m depth downscaled to a resolution of 0.05° .

Local anthropogenic drivers

Because local human activities may account for declines in the presence of brown macroalgae (Blanfuné et al. 2017;

Orfanidis et al. 2021), we used the Human Activities and Pressures Index (HAPI, Blanfuné et al. 2017), previously adapted by Valdazo et al. (2017) to the study area. The index includes three metrics for both terrestrial and marine human-related pressures (see Table S1 for sources and metrics). For terrestrial pressures (presence of urban, industrial, and agricultural areas), the three metrics were calculated as the percentage area covered in each 5 × 5 km sector (data from CORINE land cover, available at <https://land.copernicus.eu/pan-european/corine-land-cover>). For marine pressures, we calculated the level (percentage) of shoreline artificialization and the level of aquaculture facilities and sewage effluents to the sea, both calculated as the percentage of shoreline, by considering a 500 m radio circle around each facility within each 5 × 5 km sector. This information was obtained from the Spatial Data Infrastructure of the Canary Islands (<https://www.idecanarias.es/>). The HAPI index was calculated over the three time periods (1990, 2006, and 2018; Table S1 and Fig. S1), which approximately correspond to the historical distribution data of *G. abies-marina* here considered.

Climatic drivers

We collected long-term satellite-derived data from Copernicus Marine Environment Monitoring Service (CMEMS, <https://www.copernicus.eu/>) and the European Centre for Medium-Range Weather Forecast (ECMWF (<https://www.ecmwf.int/>)) for three climatic variables: sea surface temperature (SST), surface solar radiation downwards (SSRD), and ultraviolet radiation (UV) (see Table S2 for details). SST data were used, not only to describe spatiotemporal patterns in SST, but also to detect monthly SST anomalies and MHWs, which were defined as periods when daily mean temperatures exceeded the 90th percentile (relative to the baseline climatology) for at least five consecutive days (Hobday et al. 2016; Oliver et al. 2018). We calculated four metrics for each climatic driver: the slope, mean, standard deviation, and maximum value for each of the three time periods (1981–1986, 1987–2007, and 2008–2016) in each of the 28 sectors (Figs. S2 to S5). In addition, daily SST was used to quantify seven key MHW metrics: (a) the number of events in each period, (b) the duration of the events (number of days), (c) the variability (standard deviation) of the duration, (d) the mean intensity (the mean temperature anomaly relative to the climatological, seasonally-varying, mean, in $^\circ\text{C}$), (e) the variability (standard deviation) of the intensity, (f) the maximum intensity (the maximum temperature anomaly relative to the climatological, seasonally varying, mean, in $^\circ\text{C}$), and (g) the cumulative intensity (integrated temperature anomaly over the season/year, in $^\circ\text{C} \times \text{days}$) (Fig. S6). Metrics of MHWs were calculated using the R “heatwaveR” package (Schlegel and Smit 2018).

Effect of predictor variables on *G. abies-marina* distribution

We implemented generalized linear models (GLMs) to explore the relative contribution of predictor environmental drivers on spatio-temporal changes in the area (ha) covered by *G. abies-marina* across the 28 sectors around the island perimeter. To prevent collinearity among predictors, we selected those of a larger biological significance among those that were significantly correlated. A cutoff threshold of 0.7 was used in all cases (Zuur et al. 2009). Firstly, a correlation analysis was carried out between those geomorphological drivers consistent through time (Fig. S7). Northness and eastness were not included in further modelling, as both significantly correlated with wave power and slope. Then, separate correlation analyses were implemented for the metrics of each climatic predictor (Figs. S8 to S12) and uncorrelated metrics of climatic predictors (Fig. S13). A final correlation matrix between each pair of predictors including geomorphological and climatic was obtained (Fig. S14). Because mean values of UV and SSRD significantly correlated with wave power, these metrics were not considered in the model selection approach.

A model selection approach was implemented, through the R “MuMIn” package (Barton 2023), by considering those uncorrelated predictors (Table 1). Initially, all possible combinations were included using the “dredge” function (Tables S3). All models were subsequently ranked according to the Akaike information criterion corrected for small sample sizes (AICc) and importance weights (w_i) obtained for each model. Then, we estimated potential collinearity among predictors via variance inflation factors (VIF) using the “car” R package (Fox and Weisberg 2019). Finally, we performed a multimodel averaging to consider model selection uncertainty (Table S4). We also estimated the relative importance of each predictor variable, as the sum of the Akaike weights over all possible models. All models were fitted with a “Gaussian” error distribution

Table 1 Summary of environmental predictors, obtained for each of the 28 sectors across the island perimeter of Gran Canaria Island, finally implemented in the model selection statistical approach

Predictors	Type	Variation
Surface of the rocky shore	Geomorphological	Spatial
Length of the rocky shore		
Wave power	Local stressors	Spatio-temporal
Slope of the rocky shore		
HAPI Index		
N° of MHWs		
SD in the duration of MHWs		
Maximum values of SSRD	Global stressors	

family and a “log” link function. Model assumptions were checked via the R “performance” package (Lüdecke et al. 2021) and the Breusch-Pagan heteroscedasticity test.

Small-scale distribution patterns

To describe small-scale patterns in the distribution of *G. abies-marina*, populations (previously defined in Valdazo et al. (2017)), were classified into two different micro-habitat types: “open rock” (individuals living in open rocky areas) (Fig. 2A) and “refuge” (individuals living in topographical refuges, e.g., crevices, Fig. 2B), as reported for other brown macroalgae (Keppel et al. 2012; Franco et al. 2015).

To compare temporal patterns in the local-scale distribution of *G. abies-marina*, we used the proportion occupied in each micro-habitat (“open rock” vs “refuge”) in each sector around the island. A generalized mixed-effects linear model (GLMM) then tested whether the proportion differed between micro-habitats through times (two-way interaction, “time × micro-habitat”). The sector was included as a random effect. The model was implemented in the R “glmmTMB” package (Brooks et al. 2023), as a zero-inflated model with a “beta” error distribution family. Model assumptions were checked through the R “performance” package (Lüdecke et al. 2021). Also, we fitted a linear regression with local distribution data collected in 2016 to test whether the extent (area) occupied by *G. abies-marina* per sector predicted the local proportion of populations in “open rock” and “refuge.”

Temporal changes in frond size

We compiled a frond-size database from herbarium vouchers (Fig. 2D), deposited in the BCM (Depart. of Biology, University of Las Palmas, <http://www.geoportal.ulpgc.es/herbariobcm/>), from 1990 to 2021 (104 vouchers between 1990 and 2008 and 41 vouchers between 2008 and 2021), which included a total of 145 measured thallus ($4.67 \text{ thallus year}^{-1}$) at ten sites around Gran Canaria Island. Thallus length was measured from the base to the apex (Riera et al. 2015; Geppi and Riera 2022) of entire fronds with the help of the ImageJ software. Temporal changes in frond size were analyzed using a general additive model (GAM), fitted using “cubic regression” splines through the R “mgcv” package (Wood 2010), which captured strong non-linear temporal patterns. The basis dimensions “k” of the smoothers were limited to five, to avoid overfitting and ensure monotonic relationships. The model was visually inspected for residual patterns.



Fig. 2 **A** Large intertidal patch of *G. abies-marina* (“open rock” micro-habitat); **B** presence of *G. abies-marina* in a crevice (“refuge” micro-habitat); **C** experimental mesocosm where early-stages of the

macroalgae were subjected to varying thermal treatments; **D** herbarium sheets of two specimens of the studied macroalgae

Survival and growth of early stages

In October 2015, during the autumn reproductive peak of *G. abies-marina* (Valdazo et al. 2020), healthy apical fronds, including ca. 3–5 cm length of mature receptacles, were collected from the intertidal at Playa Salinetas, Gran Canaria (27°58'49.5"N, 15°22'34.6"O; Fig. 1). Receptacles were wrapped with seawater-wetted towels and placed in plastic bags without seawater and rapidly transported to the laboratory under cold and dark conditions. The bags were then stored in the fridge (at 4 °C and dark conditions) to promote subsequent gametes liberation (Irving et al. 2009). After 24 h, the same biomass of receptacles (~ 10 gr FW) was placed in fifteen 5-L aquaria, where ten microscope slides (75 × 26 mm) were set on the bottom, as a substrate for zygote settlement. At the start of the experiment, receptacles were suspended on the surface of each aquarium with a 1-mm plastic mesh for 24 h to induce the release of gametes; after this time, receptacles were discarded to avoid interference with zygote settlement. To examine the effects of temperature on survival and growth of early stages, five temperature treatments were established: 18, 20, 22, 24, and 25 °C, with three replicated 5-L aquaria for each treatment. Embryos were obtained under each of the experimental temperatures. Temperatures were chosen to reflect the annual temperature range and MHWs in the study area (Fig. S15). The photoperiod was set to a 12:12 h light to

dark cycle. The light was provided by two 20-W LED light bars (LD1034011, LEDBOX), supplying $125 \mu\text{mol m}^{-2} \text{s}^{-1}$. All aquaria contained filtered seawater, which was renewed every 2 days and was vigorously aerated using 200-mm air stones. All tanks were immersed in a “cool bath” held at 17–18 °C by a TECO TR10 chiller unit. Except for the 18 °C treatment, all aquaria kept their temperature stable using 50-W adjustable Jager aquarium heaters, calibrated using multi-parametric sensors. Temperature and salinity were daily monitored (Fig. S16 and S17).

After 1, 5, 11, 14, and 25 days, two randomly selected settlement slides were collected from each aquarium. Survival of embryos was then evaluated; i.e., each embryo was considered either dead or alive, and the size (μm^2) of ten random embryos from each slide was measured (Fig. S18). Embryos that had structurally collapsed, or failed to attach, were considered dead. The size of embryos was assessed via the “ImageJ” software (ImageJ, NIH US Department of Health and Human Services) after taking photographs through a microscope (Leica, DM1000, Berlin, Germany).

To quantify the effect of temperature on survival and growth of embryos, we fitted GLMMs, with a “binomial” family error distribution and a “logit” link function and a “Gamma” family error distribution and a “log” link function, respectively. We included the date as a random factor. Models were fitted through the R “glmmTMB” package (Brooks et al. 2023). We assessed the significance of model terms

using Wald chi-squared and F tests (Zuur et al. 2009); model assumptions were checked via the R “performance” package (Lüdtke et al. 2021). For multiple comparisons, we applied the Tukey test using “emmeans” package (Lenth et al. 2023).

Results

Historical distribution

Overall, populations of *G. abies-marina* have progressively disappeared during the last four decades around Gran Canaria Island (Fig. 1B). This alga dominated the intertidal and shallow rocky shores of the entire island in the 1980s, where a continuous belt extended along 120.5 km of the coastline and occupied 928 ha. In the first decade of the twenty-first century, fragmented populations were found along 52.2 km of the coastline and occupied 12.6 ha. Finally, in 2016, this species was found along 37.8 km of the coastline and occupied only 7.4 ha, mainly as scattered patches.

Drivers of decline

Results of the model selection (Table S4, $R^2 = 91.4\%$) initially identified that the surface (estimate = 0.0009, $P = 1e^{-07}$) and length (estimate = 0.0142, $P = 0.046$) (Table S4, Fig. 3) of the rocky coast positively influenced the area covered by *G. abies-marina*, i.e., the larger the presence of rocky habitat, the larger the area occupied. Wave power positively influenced the area covered by

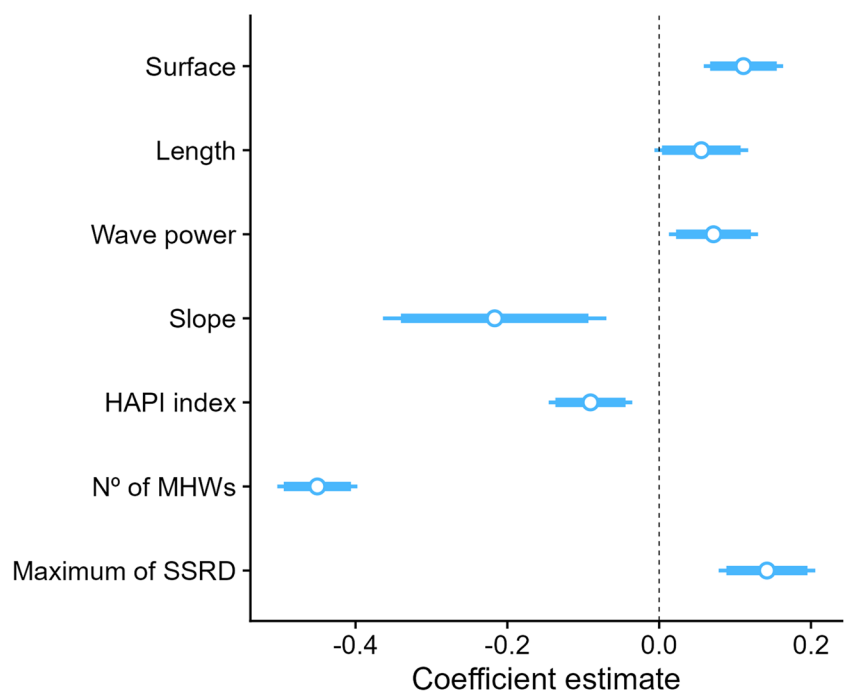
G. abies-marina (estimate = 0.02, $P = 0.079$), while the reverse was observed for the slope of the rocky coast (estimate = -0.214 , $P = 9e^{-05}$) (Table S4, Fig. 3).

The number of MHWs affected negatively the area covered by *G. abies-marina* (estimate = -0.027 , $P = 2e^{-16}$), while the maximum SSRD showed a positive effect on the area (estimate = 0.000003, $P = 0.0016$) (Table S4, Fig. 3). Both were selected as the most important environmental predictors driving variation in the area of *G. abies-marina* through scales of spatial (i.e., across sectors) and temporal (i.e., time periods) variation. The number of local human impacts (i.e., HAPI index) also significantly contributed to explaining the decay in the area covered by the macroalgae across scales of spatial and temporal variation (estimate = -0.052 , $P = 0.002$, Table S4, Fig. 3).

Small-scale distribution patterns

We observed a significant temporal change in the proportion of *G. abies-marina* (Fig. 4A, B) in each micro-habitat (“time period \times micro-habitat,” $P = 2.2e^{-16}$, Table S5). While in the 1980s and early 2000s, most individuals were locally present in “open rock,” individuals in 2016 were majorly in “refuge.” In 2016, the local presence of *G. abies-marina* in “open rock” increased with the extent (area) of the macroalgae in each sector (Fig. 4C, $P = 8e^{-4}$, Table S6), while a reversal pattern was observed for the presence of the macroalgae in “refuge” (Fig. 4D, $P = 8e^{-4}$, Table S6).

Fig. 3 Estimates for each predictor variable of the more parsimonious model explaining spatio-temporal variation in the area of *G. abies-marina* around Gran Canaria Island. Blue dots are means of coefficients and blue bars are $\pm 95\%$ confidence intervals



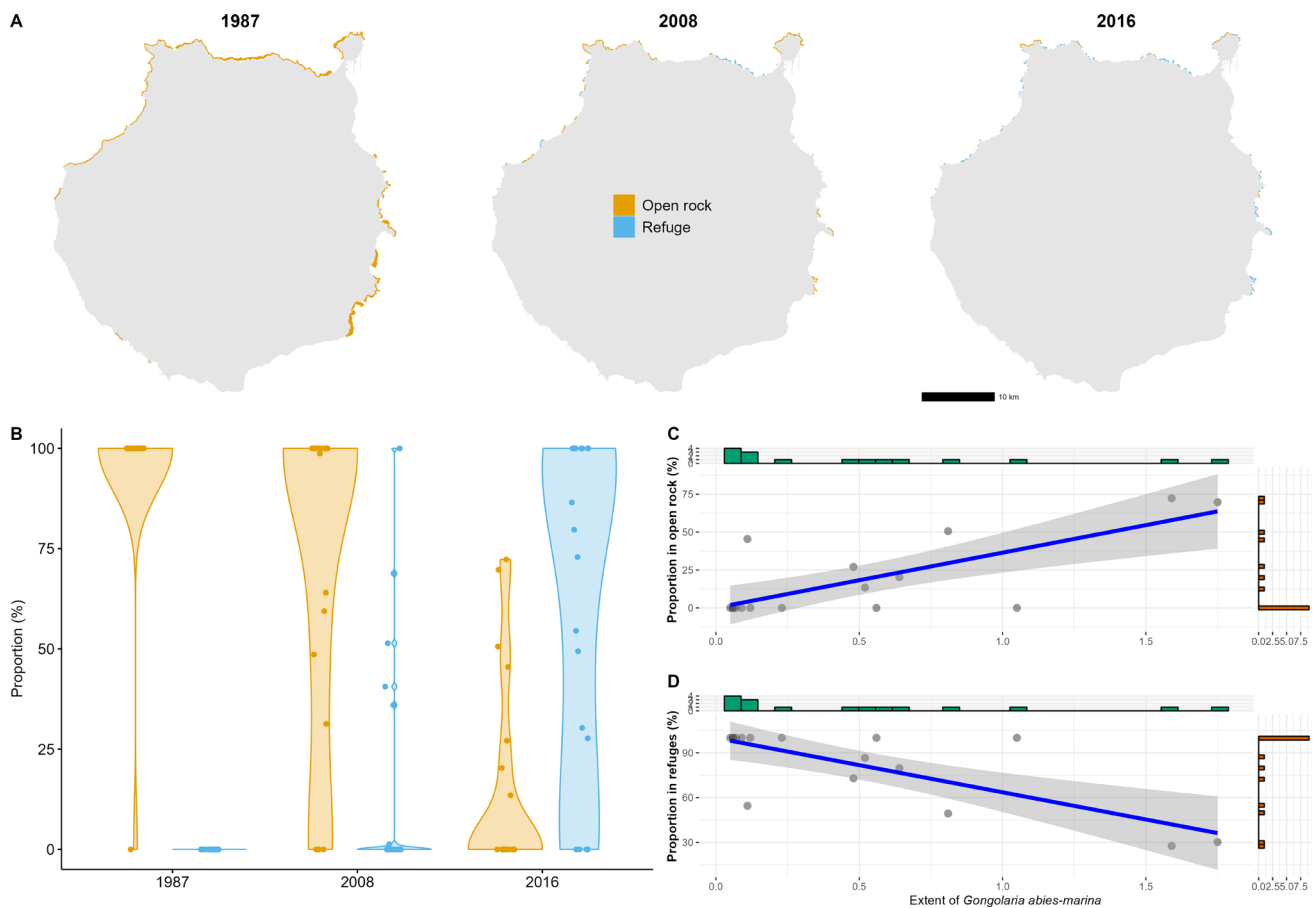


Fig. 4 **A** Distribution and **B** proportion of *G. abies-marina* at two local micro-habitat types (“open rock” and “refuge”) through time periods. The linear fit between the proportion of *G. abies-marina* in

(C) “open rock” and **D** “refuge” and the area (extent) occupied by the macroalgae in each of the 28 sectors around Gran Canaria in 2016

Temporal changes in frond size

The macroalgal frond size progressively decreased through time, with the fitted GAM depicting a sharp decrease since 2010 onwards (Table S7, Fig. 5; 9.35% of total explained deviance).

Survival and size of early stages

Both survival and size of algal embryos were significantly affected by sea-water temperatures ($P = 2.2e^{-16}$, Table S8, Fig. 6A, B). Although embryo survival progressively decreased throughout the experimental period for all treatments (Fig. 6A), a large reduction in survival (<25%) was observed for those treatments at 24 °C and 25 °C (Fig. 6A, Table S9). Similarly, embryos grown at 24 °C and 25 °C were smaller than those grown at 18 °C, 20 °C, and 22 °C (Table S10; Tukey tests, $P = 0.001$ for all pairwise comparisons).

Discussion

Results obtained by this study improve our knowledge on the causes of marine forests decline in the Northeast Atlantic, where only a few algal species have been adequately evaluated over decades, due to a lack of historical information (Blanfuné et al. 2016; Filbee-Dexter and Wernberg 2018). Our study is relevant because historical data on the distribution and extension of *G. abies-marina*, together with a time series of environmental stressors and human pressures, allowed us to elucidate the causes and their relative weights, on such historical changes. Our study showed that the area covered by *G. abies-marina* around Gran Canaria Island followed a declining trajectory over the last decades (1987–2016), which was mainly related to a combination of human-driven environmental stressors operating at both global and local scales. Results from the early stages thermo-tolerance-controlled condition experiment, together with the increased severity in MHWs, provide solid evidence to explain the declines of *G. abies-marina*, as reported for

Fig. 5 Changes in *G. abies-marina* frond size over the last three decades in Gran Canaria Island. The blue line represents the fitted (smooth) GAM function, and the gray shaded area has a 95% confidence interval

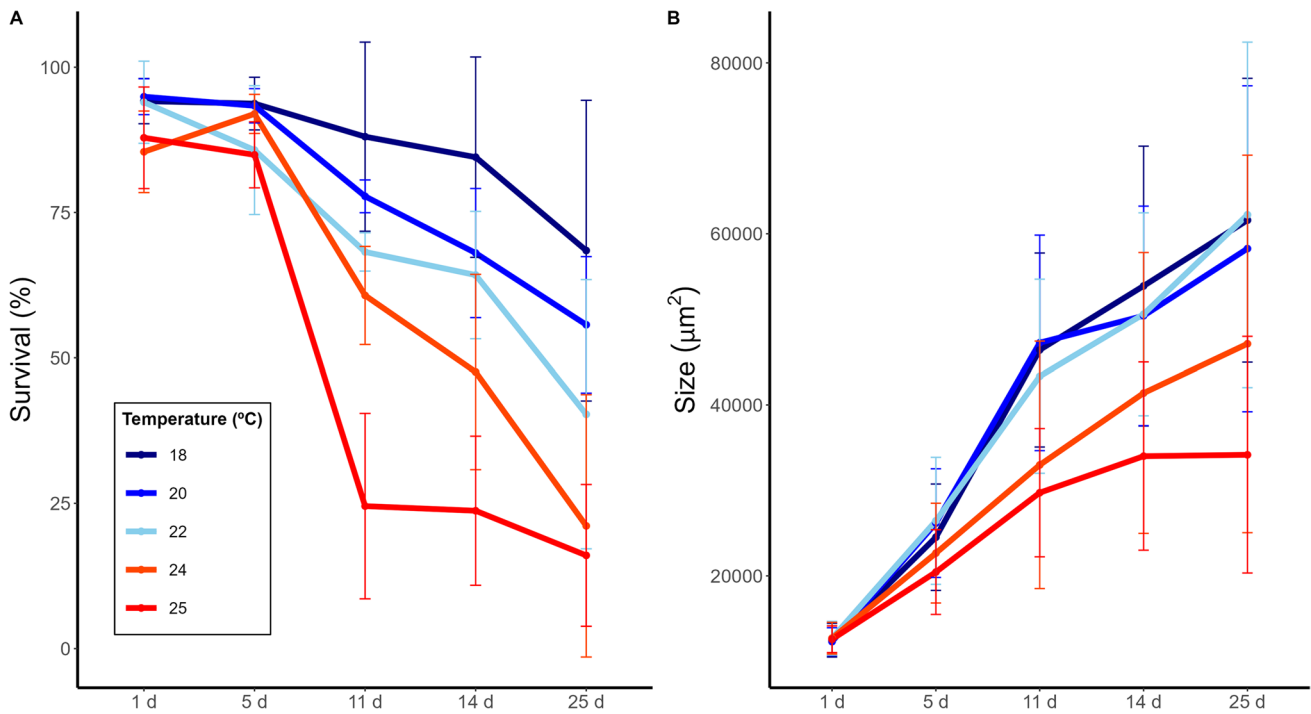
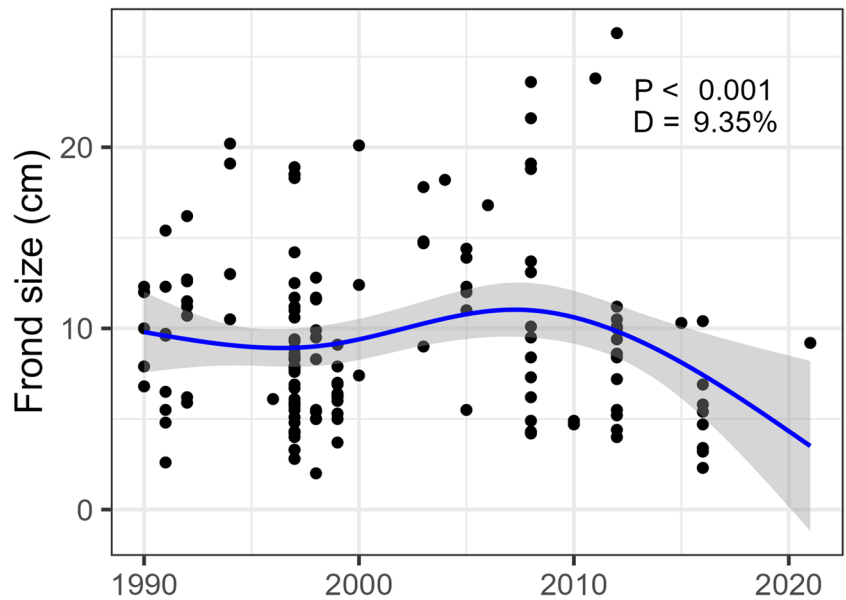


Fig. 6 **A** Survival and **B** size of algal embryos according to thermal treatments through the 25-day experiment. The error bars show confidence intervals (\pm SD) around means

sibling species from the Mediterranean (Falace et al. 2021; Verdura et al. 2021). Along most of the rocky coasts of Gran Canaria, there is a considerable probability that *G. abies-marina* is functionally near extinction, in accordance with what has occurred in other islands of the Canary (Martín-García et al. 2022) and Madeira archipelagos (Bernal-Ibañez et al. 2021b). These fragmented populations, in

Gran Canaria Island, mostly persist in topographic microhabitats, where they find small-scale refuge, as reported for other Fucales (Thibaut et al. 2015) and other large brown macroalgae (Franco et al. 2015; Shay et al. 2021; Grimaldi et al. 2023).

According to our modelling, the most extensive forests of *G. abies-marina* developed along the east and southeast

of Gran Canaria, where the large surface and length of the rocky coast (i.e., gently slopes) receive considerable solar irradiance (SSRD). However, current populations that persist are found in the north and northwest coast, under high wave energy regimens and low anthropogenic pressures. Our model selection approach showed that the main environmental predictor of temporal changes in the extent of *G. abies-marina* forests was the increase in the number of MHWs. Our best candidate model explained a considerable amount of spatio-temporal variability (91.4%), even without including biotic drivers. However, there is sufficient evidence that increased coastal impacts (habitat destruction, pollution, eutrophication, overfishing, etc.), coupled with ocean warming and MHWs, increase severity of biotic drivers on brown macroalgae, such as grazing by sea-urchins and fishes, and competition from massive turf development (Vergés et al. 2014; Filbee-Dexter and Wernberg 2018; Roma et al. 2021; Mancuso et al. 2022). It is possible that, in combination with those stressors included in our model selection approach, several biotic stressors not considered here (e.g., overgrazing, increased competition with invasive species and turfs) are concurrently involved with additive or even synergistic effects.

Superimposed to decadal-scale increases in mean coastal temperatures (Espino et al. 2019), MHWs are increasing in frequency, duration, and intensity in Gran Canaria Island, with a sharp increase in the number of events since the late 1980s (Fig. S6). In the first period (1981–1986), the mean number of events per sector was 0.32 (0.05 events per year); in the second period (1987–2007), the mean number of events was 37.11 (1.85 events per year); and in the last period (2008–2016), the average number of events was 26.67 (2.67 events per year). This pattern does not only occur for the number of MHWs, but also for their duration and intensity (Fig. S6), with likely effects on the physiology and phenology of *G. abies-marina*, impairing their performance and increasing their vulnerability to other stressors, as pointed out for similar species (Gouvea et al. 2017; de Bettignes et al. 2018; Bernal-Ibañez et al. 2021b). These trends are consistent with those observed globally (Oliver et al. 2018; Thorat et al. 2022) and in the Macaronesian region (Bernal-Ibañez et al. 2022). In addition, warming also influences the arrival of tropical herbivorous fish (Vergés et al. 2014; Zarco-Perello et al. 2021), invasive species (Occhipinti-Ambrogi and Galil 2010), the expansion of algal species with tropical affinities (Sangil et al. 2011), and the rise of turfs that compete for space with brown macroalgae (Filbee-Dexter and Wernberg 2018; Pessarrodona et al. 2021). In the study region, there is a relationship between large abundances of the key herbivorous sea-urchin *Diodema africanum* and overfishing of natural predators (Tuya et al. 2004a), which created large sea-urchin barrens (Tuya

et al. 2004b). In recent years, however, this herbivore has suffered massive mortalities (Hernández et al. 2020).

Although the HAPI index did not show significant temporal differences between the three temporal periods, human pressures on the coast were higher in the 2000s and 2010s (Fig. S1). Our model selection approach also included the HAPI index, mostly to explain spatial differences in the presence of *G. abies-marina*. In turn, current remaining populations persist in those sectors of the coast under less local anthropogenic pressures (north and northwest), but also where wave exposure is maximum. The value of the HAPI index in the 1980s was calculated with land use data corresponding to the 1990s and discharge censuses from 2003, so the value of the HAPI index, in this first period, may be overestimated; for this reason, there is no evidence of a temporary change in local anthropic pressures. In any case, as a result of the emergence and rapid rise of the tourist industry, urban expansion in Gran Canaria took place at a fast pace, with a more or less constant rate of construction since the 1960s–1970s (García-Romero et al. 2023). The first records of the disappearance of *G. abies-marina* subtidal forests begin in the early 1990s (Medina and Haroun 1994); at this time, anthropogenic pressures were already high in the Canary Islands, because of 20–30 years of intense urban development on the coast. The artificialization of the coast and concurrent increased organic pollution (sewage outfall) and eutrophication of nearshore waters, for example, due to wastewater discharges during that time, could have affected the resilience of *G. abies-marina* populations. This has been advocated to explain the erosion in the extent of other “foundation” species in the study area, such as the seagrass *Cymodocea nodosa* (Tuya et al. 2014).

We here determined the thermal tolerance thresholds of the early stages of *G. abies-marina*, showing that higher temperatures affected the performance of embryos. In particular, we found a tolerance threshold of 24 °C, from which the survival and size of the embryos notably decreased. These results agree with studies in similar shallow-water *Cystoseira* s.l. species from the Mediterranean Sea, such as *Ericaria aementacea* (Falace et al. 2018), *Ericaria selaginoides* (Campos-Cáliz et al. 2019), and *Ericaria crinita* (Verdura et al. 2021). For these species, the tolerance threshold was 28 °C; they are species adapted to higher temperatures than those from the NE Atlantic. On the contrary, our results contrast with the thermal optimum of *Ericaria giacconei*, which requires lower temperatures (12–15 °C) than other *Cystoseira* s.l. (Falace et al. 2021).

In general, adults of brown macroalgae are more tolerant to high temperatures than their early-life stages (Román et al. 2020; Verdura et al. 2021; Falace et al. 2021). However, these studies have also pointed to the presence of thermal thresholds for adults. In the case of *Ericaria crinita*, when a threshold of 28 °C is surpassed,

there is a sharp decline in the reproductive biomass, which seems more sensitive to thermal stress than other parts of the thallus (Verdura et al. 2021). This is particularly relevant for intertidal macroalgae under direct contact with the atmosphere at low tides because they can suffer simultaneous atmospheric and marine heatwaves (Román et al. 2020). Since *G. abies-marina* can thrive in the low intertidal, it is plausible that concurrent atmospheric and marine heatwaves can notoriously erode apical branches with receptacles, in particular, if this occurs in the reproductive season, as we here detected for MHWs (Fig. S15). This would lead to massive mortality of zygotes and embryos, thus defeating the reproductive efforts of the species. Furthermore, the negative effects of warming and MHWs on recruitment could be exacerbated by other stressors that have been shown to negatively affect the early developmental stages of *Cystoseira* s.l., such as herbicides, pollutants (de Caralt et al. 2020), and grazing (Monserrat et al. 2023). Successful recruitments of new individuals may be a critical bottleneck for the population persistence of large brown seaweeds (Schiel and Foster 2006). If the duration and intensity of MHWs exceed certain thresholds, it can lead to decreased population densities, fragmentation, and, ultimately, survival in the refuge, as our results seem to indicate. In this sense, the frond size of the species has been decreasing in recent decades. Because the size of the thallus determines the species' reproductive performance, i.e., the amount of biomass allocated to reproductive structures (Valdazo et al. 2020), a progressive decrease in the size (i.e., miniaturization) of *G. abies-marina* puts the viability of the populations at risk, due to a reduction in the reproductive efforts.

In conclusion, our results evidenced that increasing MHWs in a context of global warming, coupled with increasing human activities along the coastal zone, had major impacts on macroalgal forests created by *G. abies-marina*. This information is pertinent to identify appropriate management actions at local scales to halt losses of marine forests. Reducing local stressors (i.e., discharges, controlling herbivores), while maintaining favorable environmental conditions, and prioritizing cooler areas of ideal habitat availability (i.e., large rocky areas with gentle slopes) for conservation are useful management approaches. Such actions can, to some extent, reduce the susceptibility of this habitat-forming furoid species and their associated communities to MHW intensification in the upcoming decades.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10113-024-02228-1>.

Acknowledgements We thank Alejandro García, Tony Sánchez, and Fernando Espino for their help during the fieldwork. We would also thank Javier Martínez and Alejandro Moreno for their help with R

coding. We would also like to thank Francisco Otero-Ferrer for their support in preparing the experimental thermotolerant mesocosms.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This research was partly funded by the University of Las Palmas through a research technician contract with José Valdazo. In addition, analyses of the time series of environmental and anthropogenic data were carried out by elittoral enterprise within the framework of a project supported by the Government of the Canary Islands: "Study of the delimitation, characterization, and dissemination of the coralline community and the monitoring of the conservation status of protected algal species of the genera *Treptacantha*, *Carpodesmia*, and *Gelidium*," co-financed by the FEDER Canarias operational program (2014–2020).

Data Availability The data that support the findings of this research are available on request from the corresponding author.

Declarations

Competing interest The authors declare no competing interests.

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