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Responses of intertidal seaweeds to warming: A 38- year time series shows differences of sizes

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ABSTRACT

The increase of sea temperature is a key driver affecting marine organisms. The ongoing decline of cold-temperate macroalgae, e.g. kelp or fucoids, is pervasive. Edge populations of fucoids in subtropical latitudes are particularly sensitive to environmental changes. We here studied long-term variability (38-year period, 1978–2016) of morphological characters of three fucoid species using herbarium records from the subtropical archipelago of the Canaries (NE Atlantic Ocean). The study species were *Gongolaria abies-marina*, *Cystoseira compressa* and *Cystoseira humilis* that have been recently reported population decline. Rising temperatures had effects on the morphology of these species, probably due to an excess of thermal tolerance and this may be related to the algae size, ocean warming has been contrasted as a significant effect on the growth and distribution of the studied populations, and the tolerance temperature has key implications in the adaptive capacity of the studied species.

1. Introduction

Global warming is a major driver of marine biodiversity change (Poloczanska et al., 2013). Temperature is a key factor determining the spatial distribution and physiological rates of marine macrophytes (Clarke, 2003; Martínez et al., 2012; Mannino et al., 2016) and temperature tolerance may differ in marine species due to their characteristic ecosystems (Pakker et al., 1996). Organisms are responding to climate warming by either tolerating change (i.e., through phenotypic or genotypic plasticity; Somero, 2010), adapting (i.e., through genetic variation within the population; Somero, 2010) or migrating to more favourable environments (Pecl et al., 2017, Poloczanska et al., 2013). Species redistribution has been observed across the biosphere (Pecl et al., 2017; Sunday et al., 2012; Buonomo et al., 2018) and will be crucial to the survival of species on a global scale. Locally, warming has produced negative effects on marine organisms, even changing diets of organisms to force them to adopt the new environmental conditions (Vergés et al., 2014). The disappearance of native species from communities can have catastrophic impacts on the resilience and function of those ecosystems (Wernberg et al., 2011; Perry et al., 2005, Bennett et al., 2015, 2016). Also, high rates of warming, increasing frequency and magnitude of extreme temperature events, and long generation time of species may exceed their capacity to adapt to current shift rates of marine species beyond their native environments (Clarke, 2003).

The observed decrease of some cold and temperate intertidal macroalgal species has been attributed to ocean warming (Martínez et al., 2012). Therefore, it will expand warm water species to colder regions, while cold water species will be poleward shifting (Wernberg et al., 2016). Marine macroalgae in subtropical or temperate regions usually have optimal temperatures for metabolic processes that are much higher than cold regions (Müller et al., 2008). Metabolic pathways of seaweeds may acclimate to temperature changes and species growing under colder environments may achieve higher photosynthetic rates at lower temperatures compared to those growing under warmer regions (Staehr and Wernberg, 2009; Eggert et al., 2006). Thermal acclimation of photosynthesis and respiration is associated with temperature-induced changes in cellular biochemical composition that condition the algal growth (Staehr and Wernberg, 2009). This adaptation may benefit some species by increasing their metabolism activity, as reflected in studies where photosynthesis is more enhanced than respiration with warming on short-term scales (Zou and Gao, 2013). But the effects of global change have major drawbacks. Ocean warming and its associated excessive human pressure deteriorate coastal ecosystems further. Consequently, this affects the organisms that come from them in the

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same way (Pecl et al., 2017). For example, the loss of kelp forest as a consequence of the increased herbivory due to the tropicalization of fish communities (Vergés et al., 2016), changes in seaweed meadows distribution in the North Atlantic rocky intertidal (Jueterbock et al., 2013). Moreover, it has been reported the regression of *Fucus guiryi* (Riera et al., 2015), *Gelidium canariense* (Afonso et al., 2021) and variations in populations of endangered macroalgae in the Canary Islands (Valdazo et al., 2020).

Most fucoid species show regression in their distributions due to ocean warming (Martínez et al., 2018). Fucoids are characteristic of cold waters, and redistribution of their populations to colder environments show evidence of a lack of adaptation to stress emersion in the intertidal because of rising ocean temperature (Martínez et al., 2012). Ocean temperature is by far the strongest predictor of species distribution for habitat-forming temperate seaweeds in Australia, and that projected future warming is likely to cause widespread contraction of these seaweeds (Martínez et al., 2018). These climate driven changes in distribution could significantly impact ecosystem structure and function across large geographic areas (Bennett et al., 2016). Nine of the 15 ecosystem engineer species studied by Martínez et al. (2018) predicted to lose >70% of their current distribution by 2100, i.e., with the iconic giant kelp *Macrocystis pyrifera* (Linnaeus) Agardh, 1820, and three prominent fucoid species, *Durvillaea potatorum* (Labillardière), Areschoug, 1854, *Xiphophora chondrophylla* (R. Brown ex Turner) Montagne ex Harvey, 1855, and *Phyllospora comosa* (Labillardière) Agardh, 1839, predicted to become extinct in Australia under the estimated scenario of medium emission levels.

In the Canary Islands, there is evidence of population declines of *Gongolaria abies-marina* (S.G. Gemelin) G. Agardh (previously known as *Cystoseira abies-marina*) (Valdazo et al., 2017). This species forms a characteristic forest on the intertidal rocky shores (Medina and Haroun, 1993). *Cystoseira* species are the main groups of ecosystem engineer species in the region, together with *Sargassum* spp. (Tuya and Haroun, 2006). The regression of those species has the potential to jeopardize the ecological balance on the coasts of the Canary archipelago. All *Cystoseira* species, except *Cystoseira compressa,* i.e., *C. barbata, C. mauritanica, C. foeniculacea or C. mediterrana,* are included in Annex II of the Barcelona Convention (United Nations Environment Program/Mediterranean Action Plan [UNEP/MAP], 2013) and the Spanish Catalogue for Endangered Species (Decree 139/2011), to which they were added in 2014 by an amendment published in the BOE (n° 98 of April 23rd, 2014). Due to this situation, studies of possible regressions or adaptations to increased ocean temperature are essential to understand how certain species will evolve according to this stressor. For this purpose, data from herbaria are pivotal as historical data sets to assess recent changes in temperate macroalgal assemblages (Wernberg et al., 2011; Riera et al., 2015), and not only for taxonomic purposes as previously used. This study aims to use specimens available from Canarian localities in the herbaria dataset to check long-term differences (1978–2016) in various morphological characteristics of three fucoid species (*Cystoseira compressa, Cystoseira humilis and Gongolaria abies-marina)* (Fig. 1). Additionally, these data are analysed with sea surface temperatures to check any correlation between morpho-anatomical characters and ocean warming throughout the study period.

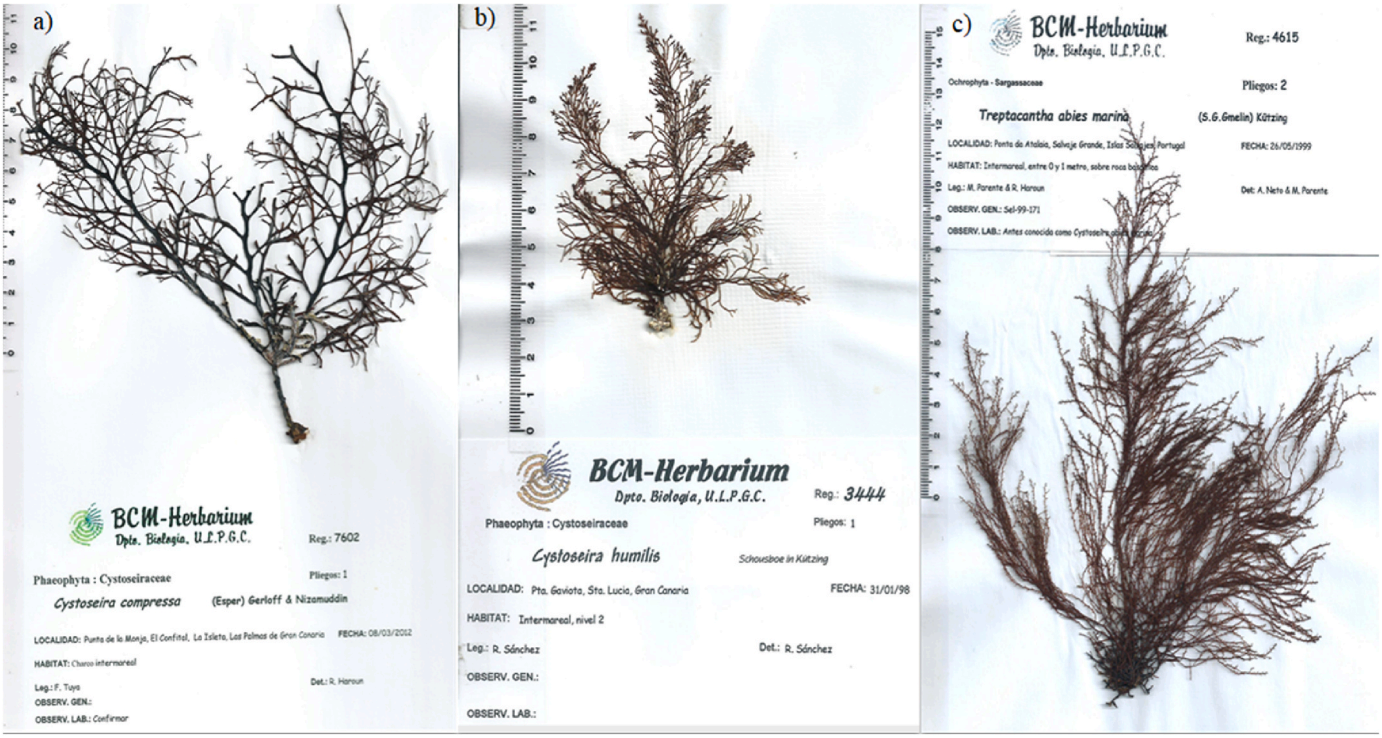
2. Material and methods

2.1. Herbarium data

For this study we have used a total of 460 specimens of three species of the order Fucales, 143 samples of *G. abies-marina*, 87 samples of *C. compressa* and 84 samples of *C. humilis*. Those specimens were from 72 locations of 7 islands (La Palma, El Hierro, Tenerife, Gran Canaria, Lanzarote, Fuerteventura, and La Graciosa), and were collected throughout the study period (1978–2016). The samples used were obtained from the record deposited in the BCM (Department of Biology, University of Las Palmas de Gran Canaria (ULPGC)) (Thiers, 2021).

2.2. Morphological features

Several morphological characteristics of each herbarium specimen were measured, following Riera et al. (2015) and including additional



BCM-Herbarium
Dpto. Biologia, U.L.P.G.C.
Reg.: 7602
Pliegos: 1
Phaeophyta : Cystoseiraceae
Cystoseira compressa (Esper) Gerloff & Nizamuddin
LOCALIDAD: Punta de la Monja, El Confital, La Isleta, Las Palmas de Gran Canaria
FECHA: 08/03/2012
HABITAT: Charco intermareal
Leg.: F. Tuya
Det.: R. Haroun
OBSERV. GEN.:
OBSERV. LAB.: Confirmar

BCM-Herbarium
Dpto. Biología, U.L.P.G.C.
Reg.: 3444
Phaeophyta : Cystoseiraceae
Pliegos: 1
Cystoseira humilis Schousboe in Kützing
LOCALIDAD: Pta. Gaviota, Sta. Lucia, Gran Canaria
FECHA: 31/01/98
HABITAT: Intermareal, nivel 2
Leg.: R. Sánchez
Det.: R. Sánchez
OBSERV. GEN.:
OBSERV. LAB.:

BCM-Herbarium
Dpto. Biologia, U.L.P.G.C.
Reg.: 4615
Ochrophyta - Sargassaceae
Pliegos: 2
Treptacantha abies marina (S.G.Gmelin) Kützing
LOCALIDAD: Ponta da Atalaia, Salvaje Grande, Islas [illegible] Portugal
FECHA: 26/05/1999
HABITAT: Intermareal, entre 0 y 1 metro, sobre roca [illegible]
Leg.: M. Parente & R. Haroun
Det: A. Neto & M. Parente
OBSERV. GEN.: Sel-99-171
OBSERV. LAB.: Antes conocida como [illegible]

Fig. 1. Herbarium sample showing specimens of the three studied species. a) *Cystoseira compressa,* b) *Cystoseira humilis and* c) *Gongolaria abies-marina.*

measures, such as the thallus basal length or the thallus mean length. Thallus length was measured of distance from the holdfast to the apex. The basal length was measured from the holdfast to the first branch, and thallus mean length was measured from the first branch to the apex of the specimen. Branch interval length represents the mean distance between secondary branches along the thallus and apical length is the distance between the last branch of the thallus to the apex. Measurements were collected using the "Unbend specimens" module Jim Rohlf's tpsUtil to create shape analysis from digitized samples as images (Haas and Orleans, 2011).

2.3. *Sea surface temperature*

Selected results on sea surface temperatures (SST) were compiled from a 38-year record of global atmospheric field analysis available online at the National Oceanic and Atmospheric Administration (NOAA/ESRL PSD from NASA-GISS, 2020). These outputs were treated with a monthly moving average filter to eliminate the seasonality of the time series and minimize noise that could make it difficult to analyse the temporal evolution of temperature, used as a descriptor of a long time and seasonal variations.

2.4. *Statistical analysis*

The islands were grouped into two categories (western and eastern) considering the oceanographic characteristics along the environmental gradient of the Canary Archipelago (Barton et al., 1998; Tuya et al., 2004). The western islands included La Palma, El Hierro and Tenerife. This group has high tropical affinities in their marine flora (Tuya et al., 2004). The eastern islands are made up of Gran Canaria, Lanzarote, Fuerteventura, and La Graciosa, characterized by a colder-temperature flora (Tuya et al., 2004).

The general trend of the SST temperature anomalies as a function of time was first estimated from a generalized linear model (GLM) (Table 2a). Subsequently, the temperature data were classified into intervals separated by years where changes in the mean and variance of the data were observed (Fig. 2). These years of change were obtained using the function 'cpt.meanvar:{changepoint}' (Killick et al., 2012). This function is based on approximation methods of the change points in the mean and the variance of a data record as a function of an independent variable (Killick et al., 2012; Chen and Gupta, 2000), in this case, they would be the SST anomalies as a function of time.

The hypothesis proposed to carry out the contrasts in the intervals is based on in years associated with the tipping points, there is a change in the mean and variance of the temperature. As change years are not equispaced with time, the rate of temperature change will be different between intervals. As a consequence, a quantification of the rate of change of temperature anomalies was conducted as a function of time for each interval defined from generalized linear models (GLM) (Table 2b).

To verify differences in the characteristics of the thallus as a function of SST anomalies, the records are grouped between the periods delimited by the tipping points calculated and selected based on the temporal covered by the studied algae species (cold period: before 1997 (1978–1997); intermediate period: 1997–2001; and warm period: after 2001 (2001–2016)) (Table 2c). The ANOVA analysis was necessary to estimate the differences of the measurements between fixed time intervals (Table 4).

Differences in morphological measures were also analysed using ANOVAs for the "island group" factor (western islands, eastern islands) and the "Species" factor (*Cystoseira compressa, Cystoseira humilis* and *Gongolaria abies-marina*) (Table 3). In this way, it is verified that morphological measurements are different according to the species and according to the orientation in the archipelago. The spatial descriptions of the variables were made from the distribution of size proportions for each species (Fig. 3). Temporal descriptions of morphology *vs.* time were performed in two ways, observing the total trend of each measure as a function of time for each species (point cloud diagram) and grouping the data in each time interval (box plots) to observe an appreciable differentiation between the morphological measures (Fig. 3).

The differences estimated from the ANOVAs were quantified using generalized linear models (GLM) of each variable and species for the spatial factor (group of islands) and the temporal factor (period). These estimates make it possible to quantify the differences between the groups associated with each fixed factor, taking one of them as a reference.

The reference group allows one data set to be compared with another one about an assigned characteristic, i.e. the temperature difference associated with space or time. This is necessary because it allows quantifying the differences in the characteristic studied for a sample group used as a control (the reference group). The oldest interval (before 1997) shows the changes variables could present due to warming to study the temporal variation. Therefore, the oldest interval will be used as the reference group or control group for the time contrast, since the differences of each interval will be according to the beginning. All statistical analysis were carried out using R software.

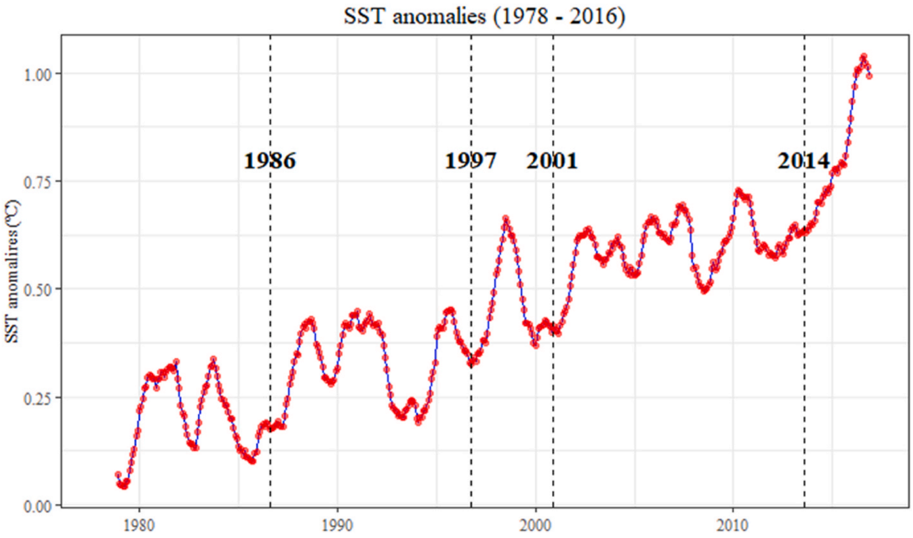


Fig. 2. Anomalies in SST (°C) (Sea Surface Temperatures) in the Canary Islands with an annual moving average filter. Year marks are the tipping points when the SST anomalies mean has changed significantly.

Fig. 3. Distribution of length frequencies of morphological measures percentage analysed for three species of macroalgae (*Cystoseira compressa, Cystoseira humilis and Gongolaria abies-marina*) and divided by the factor "Island groups" [two levels: blue for "Western islands" (El Hierro, Tenerife and La Palma); and red for "Eastern islands" (La Graciosa, Fuerteventura, Lanzarote, and Gran Canaria)]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3. Results

3.1. Sea surface temperature variations over time

SST anomalies showed the increasing trend in temperature becomes more relevant as time progresses ($5.29 \times 10\text{-}5 \pm 1.26 \times 10\text{-}6$ °C/month) (Table 2a). From 1978 to 2016, the SST anomaly mean has significantly changed four times (1986, 1997, 2001 and 2014) throughout the study period (Fig. 2), being in 2016 almost 3-fold higher than before 1986 (Table 2b). The contrast of period fixed for the study shows that SST anomalies showed a 2-fold increase (Before 1997, 0.275 ± 0.007 °C; 1997–2001, 0.189 ± 0.017 °C; and after 2001, 0.365 ± 0.011 °C) (Table 1c).

Table 1
Morphological variables studied for *Cystoseira compressa, Cystoseira humilis* and *Gongolaria abies-marina*. Mean (X), standard deviation (SD), median (Med), quantile 25% (Q25), quantile 75% (Q75), minimum (Min) and maximum (Max).

Variable	Species	X	SD	Med (Q25, Q75)	Min	Max
Thallus Length	*C. compressa*	7.86	3.8	6.73 (4.74, 10.82)	2.63	18.17
	C. humilis	8.11	3.45	6.93 (5.77, 9.61)	3.21	19.48
	G. abies-marina	13.8	6.75	12.17 (9.39, 16.14)	3.40	30.54
Basal Length	*C. compressa*	0.62	0.33	0.54 (0.40, 0.76)	0.21	1.90
	C. humilis	0.71	0.59	0.58 (0.42, 0.88)	0.23	3.56
	G. abies-marina	0.70	0.32	0.62 (0.51, 0.82)	0.24	1.53
Medium Thallus Length	*C. compressa*	7.11	3.83	6.16 (4.18, 9.56)	0.33	17.27
	C. humilis	7.41	3.11	6.33 (5.14, 8.94)	2.88	15.91
	G. abies-marina	13.1	3.63	11.4 (8.88, 15.45)	3.08	29.67
Branch Interval Length	*C. compressa*	0.38	0.13	0.38 (0.29, 0.43)	0.15	0.69
	C. humilis	0.33	0.10	0.32 (0.25, 0.37)	0.16	0.61
	G. abies-marina	1.01	0.23	0.94 (0.83, 1.16)	0.49	2.00
Apical Length	*C. compressa*	0.22	0.07	0.20 (0.18, 0.25)	0.13	0.42
	C. humilis	0.24	0.07	0.24 (0.19, 0.29)	0.13	0.44
	G. abies-marina	0.54	0.17	0.52 (0.43, 0.64)	0.18	1.10

Table 2
a) General linear model estimating the dependency between SST anomaly (°C) and time (years) along 38 years from 1978 to 2016. b) Differences estimated between time intervals defined by SST mean change years (1976–1986; 1986–1997; 1997–2001; 2001–2014; 2014–2016). c) Differences estimated between time intervals defined to contrast herbarium database (before 1997; from 1997 to 2001; and after 2001). Significant differences ($p < 0.05$) are highlighted in bold.

Source	Estimate	Std. Error	t-value	Pr(>$\vert t\vert$)	Significance
a) Dependency estimated					
SST anomaly (°C)	−1.561E-02	1.195E-02	−1.493	0.192	ns
Month	**5.288E-05**	**1.264E-06**	**41.832**	**< 2e-16**	***
b) Intervals of Change					
1978–1986	**0.204409**	**0.009074**	**22.53**	**2.00E-16**	***
1986–1997	**0.125667**	**0.012045**	**10.43**	**2.00E-16**	***
1997–2001	**0.260125**	**0.015345**	**16.95**	**2.00E-16**	***
2001–2014	**0.392801**	**0.011520**	**34.10**	**2.00E-16**	***
2014–2016	**0.607942**	**0.016693**	**36.42**	**2.00E-16**	***
c) Period					
<1997	**0.275717**	**0.007666**	**35.97**	**2.00E-16**	***
1997–2001	**0.188816**	**0.017648**	**10.70**	**2.00E-16**	***
>2001	**0.365422**	**0.011176**	**32.70**	**2.00E-16**	***

3.2. Morphological differences and variation

Significant differences were detected in morphological measures between island groups and among species (Table 3). Between species, *C. compressa* and *C. humilis* did not present significant differences between each other. But *G. abies-marina* is significantly larger than *C. compressa* and *C. humilis,* in thallus length (8.29 ± 1.76 cm), medium thallus length (8.49 ± 1.71 cm), branch interval length (0.74 ± 0.07 cm) and apical length (0.32 ± 0.04 cm). Between island groups, *C. humilis* and *G. abies-marina* were significantly different in one morphological variable (apical length and branch interval length, respectively) (Fig. 2). *Cystoseira humilis* had a smaller apical length in eastern islands (0.19 ± 0.05 cm) than western islands (0.28 ± 0.04 cm). *Gongolaria abies-marina* had a larger branch interval length in western islands (1.09 ± 0.07 cm) than eastern islands (0.93 ± 0.05 cm) (Fig. 3).

Because of the significant differences among species, the contrast of morphological measures was made for each species. General tendencies for each measure differed between species throughout all year (Fig. 4). *Gongolaria abies-marina* showed an apparent positive tendency on apical length (Fig. 4e) and an apparent negative tendency on medium thallus length (Fig. 4c). *Cystoseira compressa* presented apparent positive tendencies on thallus length (Fig. 4a) and medium thallus length (Fig. 3c). Also, it showed negative tendencies on apical length (Fig. 4e) and branch interval length (Fig. 4d). *Cystoseira humilis* had an apparent positive tendency on apical length (Fig. 4e) and an apparent negative tendency on basal length (Fig. 4b).

Significant differences were found between intervals of contrast in four morphological variables (Basal length, medium thallus length, branch interval length and apical length) for at least one of three species (Table 4). *Gongolaria abies-marina* decreased its medium thallus length by 4.49 ± 2.03 cm and increased its apical length by 0.11 ± 0.05 cm in the second interval (1997–2001). *Cystoseira compressa* and *C. humilis* presented significant changes in their morphology in the third interval (Table 4). *Cystoseira compressa* increased its medium thallus length 2.09 ± 0.89 cm and decreased its branch interval length 0.07 ± 0.03 cm and apical length 0.07 ± 0.02 cm after 2001. *Cystoseira humilis* on the contrary increased its apical length by 0.02 ± 0.04 cm and decreased its basal length by 0.38 ± 0.15 cm after 2001.

4. Discussion

The main result of this study reveals that variations of the structures of the studied algae occur heterogeneously spatially and temporally. The broad relationship between the western islands and the eastern islands is due to differences in temperature and nutrients (Tuya et al., 2004). The arrival of upwelling filaments to the eastern islands underpins higher primary production and lower surface water temperature, which does not occur in the western islands (Barton et al., 1998). This differentiation of oceanographic characteristics makes it possible to contrast the spatial variability of the species. But concerning long-term temporal variability, differences are more related to temperature than nutrients if the periods of nutrient input do not vary over time (Zou and Gao, 2013; Wernberg et al., 2012; Staehr and Wernberg, 2009; Pekker et al., 1996), because these contributions are directly related to the cold waters of the upwelling zone of north western Africa that reach the easternmost islands (Barton et al., 1998).

The ranges of marine species tend to closely follow their limit tolerance temperature and have responded directly to climate warming, allowing reliable predictions of the latitudinal contractions and expansion of the studied region (Sunday et al., 2012; Buonomo et al., 2016). For example, *Cystoseira tamariscifolia*, *C. amentacea* and *C. compressa*, are characterized by having a short propagule dispersal, potentially limiting the establishment of populations, and restricting the flow of variability (Buonomo et al., 2016). Therefore, ocean currents and habitat continuity play an important role in the dispersal and connectivity of some fucoid species (i.e., *Cystoseira tamarascifolia* and *Cystoseira compressa*)

Table 3

One-way ANOVAs of morphological characteristics of seaweeds for factor "Island group" [two levels: "Western islands" (El Hierro, Tenerife and La Palma); and "Eastern islands" ("La Graciosa", "Fuerteventura", "Lanzarote" and "Gran Canaria"] and factor Species (three levels: *Cystoseira compressa, Cystoseira humilis* and *Gongolaria abies-marina*). Significant differences ($p < 0.05$) are highlighted in bold.

Source	Morphological Variable	Df	SS	MS	F	Pr(>F)	Significance
Islands group	Thallus length	1	31	31.2	1.29	0.258	
	Basal length	1	0.525	0.5245	3.437	0.0655	
	Medium tallus length	1	46	45.6	1.884	0.171	
	Branch interval length	**1**	**1.78**	**1.779**	**41.7**	**4.17E-10**	***
	Apical length	**1**	**0.702**	**0.702**	**26.76**	**4.14E-07**	***
Species	**Thallus length**	**2**	**1350**	**675.2**	**27.89**	**3.55E-11**	***
	Basal length	2	0.385	0.1924	1.261	0.2862	
	Medium thallus length	**2**	**2616**	**1308**	**54.084**	**2.00E-16**	***
	Branch interval length	**2**	**17.491**	**17.491**	**409.9**	**2.00E-16**	***
	Apical length	**2**	**7.864**	**3.932**	**149.89**	**2.00E-16**	***
Residuals	Thallus length	167	4044	24.2			
	Basal length	165	25.18	0.1526			
	Medium thallus length	273	6602	24.2			
	Branch interval length	307	13.1	0.043			
	Apical length	310	8.133	0.026			

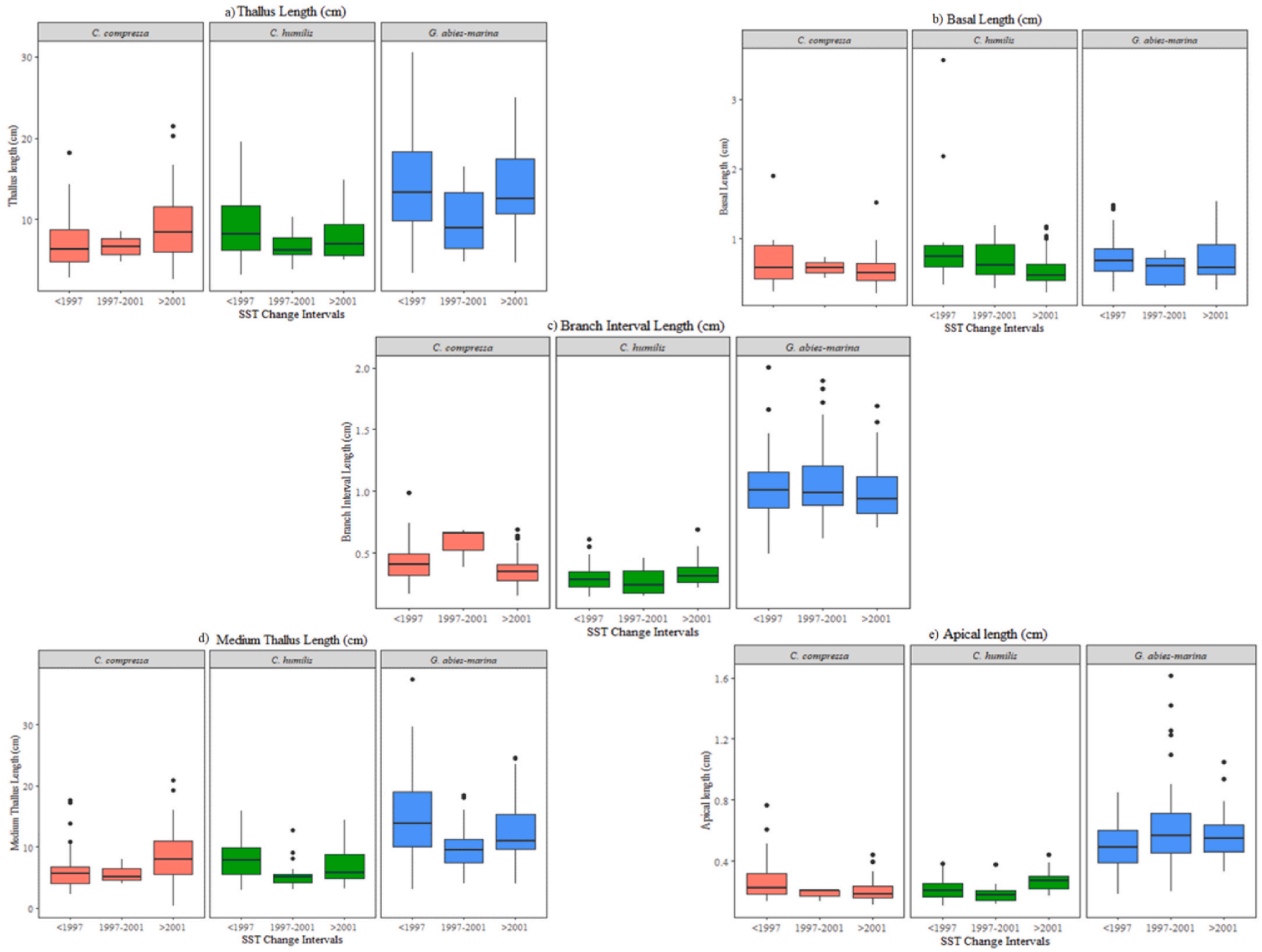


Fig. 4. Differentiation of morphological measurements for each species (red: *Cystoseira compressa*; green: *Cystoseira humilis*; and blue: *Gongolaria abies-marina*) between the three studied intervals (<1997, 1997–2001 and >2001). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Buonomo et al., 2016). Together with their sensitivity to environmental stressors, makes them particularly vulnerable (Sales et al., 2012). A rapid contraction of the distribution range could trigger a loss of diversity due to low dispersal rates (Buonomo et al., 2016), further reducing the resilience of populations (Wernberg et al., 2018). A regression of species driven by ocean warming could unleash cascading

Table 4
One-way ANOVAs of morphological characteristics of each seaweed species for the factor “Period” [three levels: “<1997” (from 1978 to 1997), “1997–2001” (from 1997 to 2001) and “>2001” (from 2001 to 2016)]. Significant differences ($p < 0.01$) are highlighted in bold.

Source	Morphological Variables	Species	Df	SS	MS	F	Pr(>F)	Significance
Periods	Thallus length	*C. compressa*	2	60.9	30.46	1.841	0.168	
		C. humilis	2	27.6	13.82	1.246	0.297	
		G. abies-marina	2	121	60.51	1.371	0.262	
	Basal length	*C. compressa*	2	0.116	0.05781	0.632	0.535	
		C. humilis	**2**	**1.812**	**0.9058**	**3.407**	**0.0417**	***
		G. abies-marina	2	0.085	0.04272	0.393	0.677	
	Medium thallus length	***C. compressa***	**2**	**106.2**	**53.1**	**3.255**	**0.0437**	***
		C. humilis	2	16.8	8.387	0.936	0.396	
		G. abies-marina	**2**	**216**	**107.86**	**2.617**	**0.00777**	***
	Branch interval length	***C. compressa***	**2**	**0.1385**	**0.06926**	**3.407**	**0.0379**	***
		C. humilis	2	0.039	0.0195	1.735	0.183	
		G. abies-marina	2	0.21	0.10517	1.451	0.238	
	Apical length	***C. compressa***	**2**	**0.1225**	**0.6124**	**5.536**	**0.00551**	***
		C. humilis	**2**	**0.0825**	**0.04127**	**9.91**	**0.00014**	***
		G. abies-marina	**2**	**0.22**	**0.11014**	**2.38**	**0.00963**	***
Residuals	Thallus length	*C. compressa*	60	922.7	16.55			
		C. humilis	47	521.4	11.09			
		G. abies-marina	55	2427	44.13			
	Basal length	*C. compressa*	59	5.396	0.09146			
		C. humilis	46	12.23	0.2659			
		G. abies-marina	55	5.974	0.10862			
	Medium thallus length	*C. compressa*	81	13213	16.31			
		C. humilis	79	707.8	8.959			
		G. abies-marina	108	4452	41.22			
	Branch interval length	*C. compressa*	82	1.6669	0.02033			
		C. humilis	80	0.8991	0.01124			
		G. abies-marina	10	10.15	0.07248			
	Apical length	*C. compressa*	84	0.9292	0.01106			
		C. humilis	81	0.3373	0.00416			
		G. abies-marina	140	6.48	0.04629			

effects on associated ecosystems, changing the diversity and interactions of communities, as well as key functions and services (Smale and Wernberg, 2013; Bracken et al., 2007). The climatic effects on the populations that structure ecosystems and their consequences for genetic diversity and evolutionary potential could be of great importance because many limited ecosystems contain populations with a unique large genetic diversity (Buonomo et al., 2018; Benedetti-Cecchi et al., 2001). This change in climatic conditions is expected to cause local extinction, since adaptation processes of the species could, hypothetically, be restricted by the loss of intraspecific genetic diversity (Pearson et al., 2009). *Cystoseira* species shows a high and unique diversity in the region’s most vulnerable to climate change, where each population has shown high levels of diversity distinction (Buonomo et al., 2018). The loss of populations of species such as these could be a permanent blow to the variability of the species genetic pool (Hampe and Petit, 2005).

The total lengths of the studied algae did not show a significant variation. But the fact that they showed increases and decreases in all the parts that make up the total structure could suggest a possible long-term adaptation to temperature. The fact that *G. abies-marina* triggered its changes before the other two species is a key point to consider. Therefore, the thermal sensitivity of *G. abies-marina* could be lower than *C. compressa* and *C. humilis*. A potential difference in thermal tolerance implies its macrophyte sensitivity and vulnerability to warming is higher (Bennett et al., 2018). By presenting morphological changes earlier than other species, *G. abies-marina* will have less tolerated to the stressor studied. In addition, the fact that the largest alga is the first to be affected could be an indication that the species have an inverse proportionality between the size of the structure and the limit of tolerance temperature (Bennett et al., 2018).

Consequently, ocean temperature rising can produce a stressful effect on species that change their morphological structure due to the physiological changes in their organisms. These changes could occur more rapidly when the tolerable temperature of the studied species is lower. The degree of stress applied to the algae will be higher than the environment temperature where it is found (Martínez et al., 2012; Bennett et al., 2018). Because of this, if the climate scenario evolves according to the predictions made by Chistensen et al. (2007) and Palmer et al. (2007), the adverse effects on morphology could produce migrations of algae species from temperate waters to colder regions (Wernberg et al., 2011; Riera et al., 2015), due to crossing the temperature tolerance limits and increased sensibility to warming (Bennett et al., 2018).

For future studies, a greater geographic range would allow checking how distributions of the species will change over time and to make more precise prediction models. In addition, the increase in climatic variables associated with ocean warming could provide more information about how warming is modifying the population of the affected species. A properly conserved and catalogued herbarium over time will therefore allow it to be a pivotal tool for future research on the effects of climate change on marine ecosystems. The use of an herbarium has made it possible to show results that explain the morphological variations of different fucoid species and reveal those responses could potentially be related to ocean warming. The high sensitivity associated with low tolerance temperature could imply more significant changes in the phenotypic structures of the algae. In addition, this limit temperature may be significantly related to the specific size of the studied species. Future studies would need to verify the genetic variations of the affected species to approximate the impact of warming on the diversity of ecosystems. Predicting the possible redistribution of populations to ecosystems with optimal temperatures would allow anticipating the places where the settlement of the ecosystem could cause the greatest impact. Also, it would be necessary to consider regressions of the current populations of algae can trigger a regional extinction of the affected species and a potential loss of the diversity associated with these ecosystems.

CRediT authorship contribution statement

Eros Fernando Geppi: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Rodrigo Riera:** Conceptualization, Supervision, Writing – original draft, Writing – review &

editing.

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.

The corresponding author (RR) on behalf of the remaining authors, declares no conflict of interest concerning this manuscript.

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