Long-term herbarium data reveal the decline of a temperate-water algae at its southern range

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ABSTRACT

Distributional shifts of marine species have recently received attention as a result of increasing man-induced pressures on coastal ecosystems and global climate change (i.e. ocean warming). The southernmost geographical limit of the fucoid *Fucus guiryi* is the Canarian archipelago (Northeastern Atlantic Ocean) where this species is currently forming scarce and low-dense populations. Studies on long-term herbarium data revealed the decrease in size of morphological features (length and width of thallus and receptacles), and recent surveys confirmed the sharp decline, or even extinction, of *F. guiryi* from most sites previously documented. The increase of mean seawater surface temperature consistently matches the regression of populations of *F. guiryi*. Other environmental variables, such as wave exposure, cloud cover and chlorophyll-a concentration, contributed to explain local-scale spatial variability detected in Canarian populations.

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1. Introduction

Rising global seawater temperatures have been noticed in the last decades. According to IPCC (2013), this global warming is projected to continue at a faster rate in the near future. Environmental characteristics determine the distribution of species (Clarke, 2003) and some taxa have responded to recent global warming by shifts in their geographic ranges (Hughes, 2000; Lima et al., 2007; Poloczanska et al., 2013). In the northern hemisphere, most marine species have exhibited poleward displacements in latitude (Zacherl et al., 2003), which has been observed for fishes (Perry et al., 2005), crustaceans (Southward et al., 2005), mollusks (Sagarin and Somero, 2006), corals (Yamano et al., 2011) and macroalgae (Airoldi and Beck, 2007).

Ocean warming may affect macroalgal assemblages in different physiological ways, such as decreasing primary productivity and increasing photoinhibition and respiration (Tait and Schiel, 2013). Different responses to rising seawater temperatures are expected depending on the adaptability of macroalgal species and the species composition of macroalgal assemblages (Wahl et al., 2011). Shifts are greater in polar and temperate regions, where cold-temperate species dominate macroalgal assemblages (i.e. kelp forests) (Wernberg et al., 2013). In recent decades, a steady loss of cold-water species from large coastal areas has been related to seawater warming (Lemos and Sansó, 2006; Smale and Wernberg, 2013). These species are characterized by their limited tolerance to high temperatures. A gradual change to sediment-covered algal turfs is occurring in several areas formerly dominated by kelp forests (Wernberg et al., 2013) or canopy-forming algae (Perkol-Finkel and Airoldi, 2010), as a consequence of rising temperatures in sheltered shallow bays. Intertidal species respond rapidly to temperature shifts since they are exposed to both seawater and air temperatures (Helmuth et al., 2002). Changes in ranges of species are particularly marked in geographical distribution limits where cold- and warm-water species coexist (Lima et al., 2007; Tuya et al., 2012).

Regressions of fucoids have been extensively documented during the last decades in temperate and polar regions (e.g. Tanaka et al., 2012; Smale and Wernberg, 2013; Nicastro et al., 2013). Ocean warming is considered a key factor in the ongoing decline of fucoid species (Martínez et al., 2012). Fucoids are displaced to colder waters, and polewards migrations are noticed in several geographical regions, e.g. *Fucus serratus* in the Cantabrian Sea (Martínez et al., 2012). These species are genetically adapted to tolerate stress emersion in the intertidal zone, but restricted gene flow could trigger isolation of populations and therefore possible

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speciation, as occurred with *Fucus guiryi*, previously identified as *Fucus spiralis* var. *platycarpus* (Zardi et al., 2011).

In the Canary Islands, there are recent field evidences that indicate the decline or disappearance of populations of *Fucus guiryi*, an engineering species that formed characteristic belts in the upper intertidal at semiexposed rocky shores. The phenology of these populations were studied in the past (Reyes and Sansón, 1999), and as a result of extensive floristic and taxonomic studies carried out by local and foreign researchers in these islands since the 1960s, an important stock of herbarium sheets of *F. guiryi* (most identified as *Fucus spiralis*) are deposited at TFC and BCM herbaria (Sansón et al., 2013). Data from herbaria have been traditionally used for taxonomic purposes; however, Wernberg et al. (2011) exhibited its importance as historical data sets to assess recent changes in temperate macroalgal assemblages. The aim of this study is precisely to use available *exsiccata* from numerous Canarian localities to check long-term (1970–2012) differences in several morphological features of *F. guiryi* and assess whether they match changes occurred in several environmental variables (seawater surface temperature, wave exposure, cloud cover and chlorophyll-a). Also, populations of *F. guiryi* were newly sampled for comparative analysis with populations studied by Reyes and Sansón (1999) at the same localities.

2. Material and methods

2.1. Herbaria data

Voucher specimens are deposited in TFC (Departamento de Biología Vegetal, University of La Laguna, ULL, Tenerife, Canary Islands) and BCM (Departamento de Biología, Ciencias del Mar, University of Las Palmas de Gran Canaria, ULPGC, Gran Canaria, Canary Islands). TFC was founded in 1969 and include 83,000 *exsiccata*, mostly of specimens from the Canary Islands and Macaronesian archipelagos but also from other parts of the world. About 15,000 *exsiccata* are of marine algae species. The collection of the phycologist R. Schnetter is deposited in the TFC Phyc (Phycology) section. BCM was founded in 1989 and include 8674 *exsiccata* of marine algae from Macaronesian archipelagos, especially the Canary Islands, and from Hawaii, Japan, Panama and Florida (Thiers, 2014). For this study, a total of 694 specimens of *Fucus guiryi* were examined, from 33 localities at 5 islands (La Palma, Tenerife, Gran Canaria, Lanzarote and La Graciosa), some of them were sampled several times throughout the study period. Details are shown in Appendix 1.

2.2. Morphological characteristics of Fucus guiryi

Several morphological characteristics were measured from each herbarium specimen, following the study of Reyes and Sansón (1999). Thallus length represents the longest distance from the holdfast to the apex. Thallus basal width was measured just above the holdfast, thallus medium width at the first branching, and thallus apical width at the tip. Length and width of receptacles were obtained from the most mature receptacle in each thallus.

2.3. Environmental data

Selected outputs on seawater surface temperatures (SST) were obtained from a 40-year record of global analyses of atmospheric fields available online at http://www.ncdc.noaa.gov. Anomalies in SST at the Canary Islands were calculated as positive or negative differences between the mean SST in each year and the average temperature of the whole data set (1948–2012). Temperature is used as a descriptor of long-time and seasonal variations. Data on

cloud cover and primary productivity (concentration of chlorophyll-a; mg m^{-3}) were obtained from the Bio-Oracle database (Ocean Rasters for Analysis of Climate and Environment; Tyberghein et al., 2012). Data on wave exposure, in terms of average wave power (kW/m), were obtained from an oceanic database (http://www.enola.ihcantabria.com) for Spanish coasts. Cloud cover, chlorophyll-a and wave exposure are used as descriptors of local spatial variation.

2.4. Statistical analysis

For analysis purposes, islands were grouped in two categories (Western and Eastern) taking into account the geographical location and oceanographic characteristics along the environmental gradient at the Canarian archipelago (Tuya et al., 2004; Sangil et al., 2012). One group is constituted by the westernmost islands (La Palma and Tenerife), which exhibited a marine flora with higher tropical affinities. The other group is composed of the easternmost islands (Gran Canaria, Lanzarote and La Graciosa), with a more cold-temperate flora (Fig. 1). Moreover, we classified temperature data in two groups, since according to Brito et al. (2005) and Sansón et al. (2013), SST at the Canary Islands has increased notably from the 1990s (Fig. 2). Therefore, analyses were conducted to check the variability of thalli size between two time periods [colder period before 1992 (1972–1992) *vs* warmer period after 1992 (1993–2012)]. To test the relationships between the morphology of *Fucus guiryi* and selected environmental variables, a distance-based linear model routine (DistLM) was applied (Legendre and Anderson, 1999). The following continuous environmental variables were included in this analysis: temperature of the month of collection, mean annual temperature, minimum annual temperature, maximum annual temperature, mean wave power, mean cloud cover and mean chlorophyll-a. This method does multivariate multiple regressions on the basis of any distance measure and does a forward selection of the predictor variables, either individually or in specified sets, with tests by permutation. In our study, this analysis, based on similarity matrices, used the Euclidean distance for the biological data. The method used was stepwise selection, an adjusted R^2 criterion and 4,999 permutations. Because the correlations between our variables were low in our case (R < 0.5), no variable was excluded. Following recommendations by Clarke and Gorley (2006), morphological characteristics of *F. guiryi* were square-root transformed and environmental variables were normalised. Morphological data were averaged from plants measured at each sampling location (33 in total) from each year of collection (Appendix 1). In those localities with a relative high number of sheets, a balanced number of individuals were randomly selected for measurement. The multivariate regression model and multidimensional space generated by DistLM analysis (McArdle and Anderson, 2001) was used to compare morphological characteristics with environmental variables. To retain variables with good explanatory power, a result of colinearity among variables, the AIC routine was used as a selection criterion (Legendre and Anderson, 1999).

Differences in morphological features (length and width of thallus and receptacles) were tested by means of a permutational analysis of variance (PERMANOVA; Anderson et al., 2008). The design consisted of a two-way analysis, with 'Island group' (two levels: easternmost islands and westernmost islands) treated as a fixed factor and 'Period' (two levels: 1972–1992 and 1993–2012) as a fixed factor. ANOVA, using the same model but in a univariate context, was tested for differences in morphological features of individuals throughout the study period. Multivariate data were square root transformed, and multivariate and univariate analyses were based on Bray–Curtis dissimilarities and Euclidean distances,
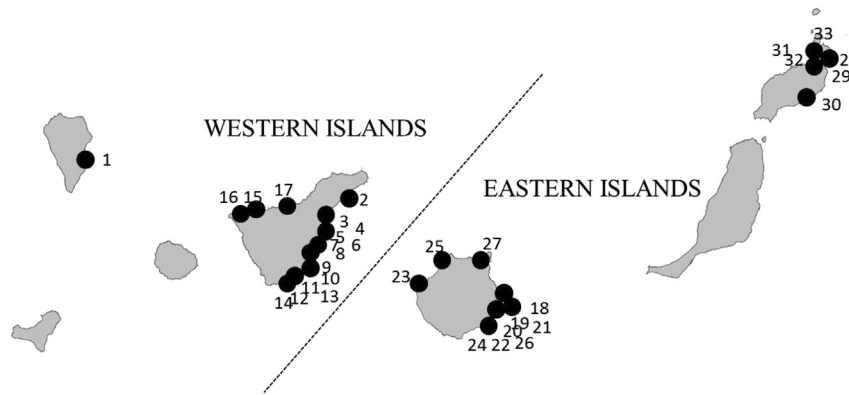
Fig. 1. Map of the Canary Islands showing all sampling localities listed in Appendix 1.
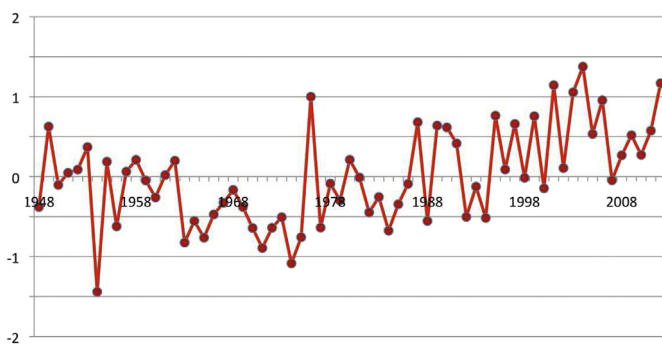

Fig. 2. Anomalies in SST (seawater surface temperature) at the Canary Islands represented as positive or negative differences between the mean SST in each year and the average temperature of the whole data set (1948–2012).

respectively. P-values were calculated from 4,999 unrestricted permutations of the raw data. Despite variances remained heterogeneous in all univariate cases, we avoided an increase in a type I error by reducing the α value to a 0.01 level (Underwood, 1991); ANOVA is robust to such departures for balanced studies. Pairwise comparisons (using 4,999 permutations) were used, when appropriate, to resolve differences among levels of significant factors. All multivariate procedures were carried out using PRIMER-E® v.6 + PERMANOVA+ (http://www.primer-e.com; Clarke and Gorley, 2006).

3. Results

3.1. Morphological characteristics of Fucus guiryi

A significant interaction between factors 'period × Island group' was detected in thallus length, and length and width of receptacles (Table 1), suggesting a temporal variability between the two time periods (1972–1992 vs 1993–2012) but was different in eastern and western islands. Other morphological features (thallus base width, thallus medium width and thallus apical width) exhibited highly significant differences for factor 'period', while thallus apical width was the only parameter significantly different for factor 'Island group' (Table 1).

A high variability of all morphological characteristics of Fucus guiryi is observed considering both factors (eastern vs western islands; and 1972–1992 vs 1993–2012) (Fig. 3). Thallus length is shorter in the second period (eastern islands: 9.73 ± 0.92 cm in 1972–1992, 6.58 ± 0.13 cm in 1993–2012; western islands: 10.44 ± 0.17 cm in 1972–1992, 4.87 ± 0.48 cm in 1993–2012) (Fig

3A). Thallus basal width is slightly shorter in 1993–2012 (0.13 ± 0.01 cm) than in 1972–1992 (0.14 ± 0.01 cm) in eastern islands (Fig. 3B). Thallus medium and apical width do not show significant variations at both levels (Fig. 3C and D). Length and width of receptacles decrease significantly from the first to second period, with greater differences in western islands. Receptacle length in the eastern islands varies from 0.75 ± 0.08 cm (1972–1992) to 0.53 ± 0.03 cm (1993–2012), while in the western islands from 1.29 ± 0.03 cm (1972–1992) to 0.37 ± 0.07 cm (1993–2012). Receptacle width decreased in the eastern islands from 0.57 ± 0.06 cm (1972–1992) to 0.4 ± 0.02 cm (1993–2012), while in the western islands decreased from 0.82 ± 0.02 cm (1972–1992) to 0.30 ± 0.06 cm (1993–2012) (Fig. 3E and F).

The percentage of fertile specimens decreased significantly in time (χ^2 = 20.88, p = 0.022), especially when Fucus thalli were <10 cm length. During 1972–1992 all specimens between 12.6 and 32.5 cm length were fertile, while in 1993–2012 all plants were fertile from 10.1 to 17.5 cm length (Fig. 4).

3.2. Environmental variables

Mean SST show high values in the last two decades, reaching in 2002, 2004, 2005 and 2012 more than 1 °C above the mean maximum annual temperature (23.7 °C) of the whole time series (1948–2012) (Fig. 2). Only in 2000 and 2007, mean SST anomalies are lower than this annual temperature. Highly significant differences were detected between the two time periods (1972–1992 vs 1993–2012), with consistent variations in all temperature parameters (Table 2).

3.3. Multivariate analyses

The DistLM analysis show that mean SST and wave exposure were the environmental variables that most contribute to the morphological variability of Fucus guiryi (see sequential tests, Table 3), as a result of colinearity among several variables, such as minimum and maximum SST and mean temperature of the month of collection. Percentages of variation explained by these variables are scarce. Thus, significant unique contributions of variables likely represent a greater influence than that observed in the present study. The first two axes from the db-RDA explain approx. 25% of total variation of morphological characteristics of F. guiryi (Fig. 5). Minimum and mean SST are positively correlated with the first axis, which explain approx. 24% of total variation. The second axis is positively correlated with the concentration of chlorophyll-a and negatively correlated with maximum SST.
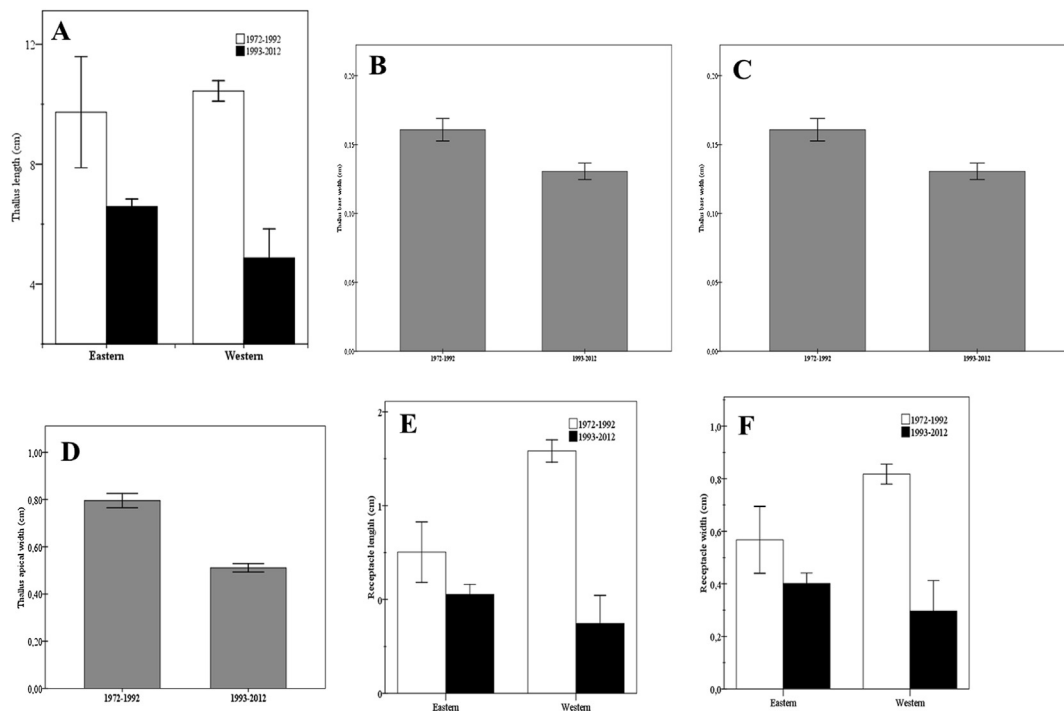
Table 1
Two-way ANOVAs of morphological characteristics of *Fucus guiryi*, for factor 'Island group' [two levels: westernmost islands (La Palma and Tenerife), easternmost islands (Gran Canaria, Lanzarote and La Graciosa)] and factor 'period' (two levels: 1972–1992 and 1993–2012). Significant differences (p < 0.01) are highlighted in bold (df = degrees of freedom, SS = sum of squares, MS = mean squares).

| Source	Variable	df	SS	MS	F	p
Period	Thallus length	1	1500.53	1,500,53	156.68	**<0.001**
	Thallus basal width	1	0.038	0.38	7.87	**0.005**
	Thallus medium width	1	2.36	2.36	30.20	**<0.001**
	Thallus tip width	1	3.08	3.08	51.76	**<0.001**
	Receptacle length	1	25.85	25.85	101.27	**<0.001**
	Receptacle width	1	9.34	9.34	75.89	**<0.001**
Island group	Thallus length	1	20.02	20.02	2.09	0.149
	Thallus basal width	1	0.01	0.01	1.55	0.214
	Thallus medium width	1	0.32	0.32	4.10	0.043
	Thallus tip width	1	1.17	1.17	19.68	**<0.001**
	Receptacle length	1	2.91	2.91	11.39	**0.001**
	Receptacle width	1	0.42	0.42	3.38	0.066
Period × Island group	Thallus length	1	115.93	115.93	12.11	**<0.001**
	Thallus basal width	1	0.02	0.02	5.11	0.024
	Thallus medium width	1	0.00	0.00	0.002	0.966
	Thallus tip width	1	0.01	0.01	0.14	0.710
	Receptacle length	1	9.50	9.50	37.21	**<0.001**
	Receptacle width	1	2.49	2.49	20.24	**<0.001**
Error	Thallus length	669	6407.14	9.58		
	Thallus basal width	669	3.22	0.01		
	Thallus medium width	669	52.23	0.08		
	Thallus tip width	669	39.76	0.06		
	Receptacle length	669	170.79	0.26		
	Receptacle width	669	82.29	0.12		
Total	Thallus length	672	9331.27			
	Thallus basal width	672	3.40			
	Thallus medium width	672	60.41			
	Thallus tip width	672	54.33			
	Receptacle length	672	271.82			
	Receptacle width	672	112.75			

4. Discussion

A high variability in the morphology of *Fucus guiryi* from the Canary Islands is detected, showing a consistent temporal trend.

The increase in SST during the recent decades matched with the decrease in all of the studied morphological characteristics, i.e. length and width of thalli and receptacles. *Fucus guiryi* is also losing reproductive capability, in terms of a reduction in the number of

Fig. 3. Morphological characteristics of *Fucus guiryi* (mean ± SD) comparing levels of factor 'Island group' (westernmost: La Palma and Tenerife; easternmost: Gran Canaria, Lanzarote and La Graciosa) and levels of factor 'period' (1972–1992 and 1993–2012). A. Thallus length. B. Thallus basal width. C. Thallus medium width. D. Thallus apical width. E. Receptacle length. F. Receptacle width. All measurements are in centimetres.
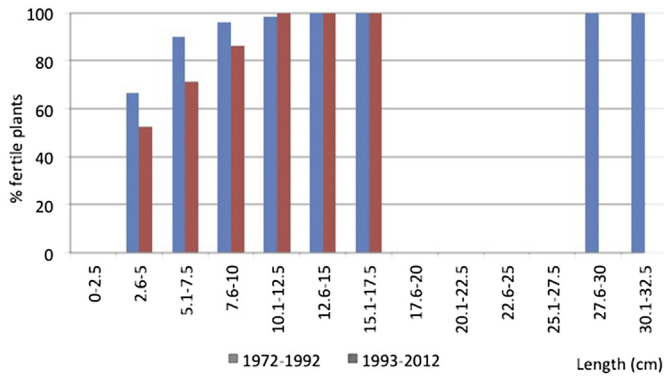
Fig. 4. Frequencies of fertile thalli of *Fucus guiryi* per classes of length (in cm). Data from the two periods (1972—1992 *vs* 1993—2012) are represented.

Table 2
T-test of environmental variables to test differences between two levels (1972—1992, 1993—2012) of factor 'period' (Tmonth = sea surface temperature of the month of collection; Tmean, Tmin and Tmax = mean, minimum and maximum annual sea surface temperature of the year of collection; wave exposure = mean wave power (kW/m) during the month of collection). Significant differences ($p < 0.01$) are highlighted in bold (df = degrees of freedom, SS = sum of squares, MS = mean squares).

Variables	df	SS	MS	F	p
Tmonth	1	17.86	17.86	7.58	**0.006**
Tmean	1	146.67	146.67	1236.3	**<0.001**
Tmin	1	59.68	59.68	132.7	**<0.001**
Tmax	1	93.24	93.24	416.5	**<0.001**
Wave exposure	1	237.03	237.03	2.05	0.153
Cloud cover	1	0.60	0.60	132.52	**<0.001**
Chlorophyll-a	1	0.25	0.25	229.86	**<0.001**

fertile thalli along the long-term study period. This reproductive loss is especially accentuated in small and medium-length individuals in the warmest recent decades. Seawater temperatures were correlated to the vegetative and reproductive success of *F. guiryi* at the Canary Islands, its southernmost limit of distribution (Zardi et al., 2011), as it has been previously documented in other intertidal fucales (Jueterbock et al., 2013).

Reproductive success sharply decreases if increases mortality of adults regardless the investment of reproduction (Karlsson and Méndez, 2005). The reproductive traits are highly dependent on individual size (e.g. Weiner et al., 2009), especially at distributional limits (Viejo et al., 2011). Long-term data of morphological characteristics are of great importance to determine reproductive success of macroalgae and thus to interpret the forecasted changes in local and regional scales (Connell et al., 2008). In the present study, Canarian thalli of *Fucus guiryi* show a reproductive decline in the last decades, as previously documented for populations in Garachico (North of Tenerife) and La Tejita (South of Tenerife), sites where long-term data (>20 years) are available (Reyes and Sansón, 1999; Sansón et al., 2013).

Some spatial differences in morphology of *Fucus guiryi* are also found along the archipelago, most of them highly correlated with oceanographic conditions. A well-known gradient in SST and concentration of chlorophyll-a occurs from the eastern to the western islands caused by the nearby northwest African coastal upwelling and the Canary Current (Barton et al., 1998), that affects the structure of intertidal assemblages (Tuya et al., 2006). The western islands are affected by warmer SST and lower concentration of chlorophyll-a, and *F. guiryi* seems to be currently at threat of extinction, showing populations with smaller-sized and less fertile thalli than in the eastern islands.

Wave exposure is found to be a key environmental variable at smaller scales since the best preserved populations with larger-sized specimens of *Fucus guiryi*, are currently found at exposed northernmost localities at the Canary Islands, where seawater spray reaches the upper shore level during low tides where this species grows, maintaining suitable conditions of humidity and moderate temperatures throughout the year. Together with wave exposure, concentration of chlorophyll-a are slightly higher in northern *vs* southern localities at the islands supporting this spatial variability. Additionally, cloud cover presents higher values in the same northern sites where it prevents thalli of *F. guiryi* from severe desiccation by higher air temperatures during daily emersion periods.

Strong declines of kelp and fucoid forests have been observed over recent decades worldwide (Thibaut et al., 2005; Jueterbock et al., 2013; Wernberg et al., 2013). Connell et al. (2008) considered that this trend could be partially explained by historical events and not only by human-mediated interactions, such as coastal occupation and pollution. However, Jueterbock et al. (2013) link global warming to the greatest impact on three foundational, macroalgal fucoids that occur along North-Atlantic shores: *Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum*. These authors point out that if these foundational species are unable to adapt to rising temperatures, they will lose their centers of genetic diversity and their loss will trigger an unpredictable shift in intertidal ecosystems. Consequently, studies on temporal and spatial variability of foundational, canopy-forming or engineering algae are important issues especially in marginal populations located at distributional limits where populations could be altered by unfavourable or highly variable environmental conditions (Viejo et al., 2011). *Fucus guiryi* is a clear example of this kind of endangered macroalgal species at the Canarian archipelago.

Studies on long-term herbarium records have become an attractive alternative to fill historical gaps of species distributions and to detect unregistered shifts (Wernberg et al., 2011), although there are some limitations, such as biased information due to partially or insufficiently recorded species (Miller-Rushing et al., 2004). The conspicuous fucoid *Fucus guiryi* has been consistently recorded and deposited in the Canarian herbaria (TFC and BCM) during the last four decades (see Table 1). Thus, herbarium specimens studied constituted a reliable source of materials collected from 1972 to present at different islands. This provided us with numerous *exsiccata* to study and analyze variations occurred

Table 3
Results of multivariate multiple regression testing the relationships between the measured set of environmental variables and the morphological characteristics of *Fucus guiryi*. To retain variables with explanatory power, the AIC criteria were used for the selection of explanatory variables (sequential tests, Legendre and Anderson, 1999). Significant differences ($p < 0.01$) are highlighted in bold.
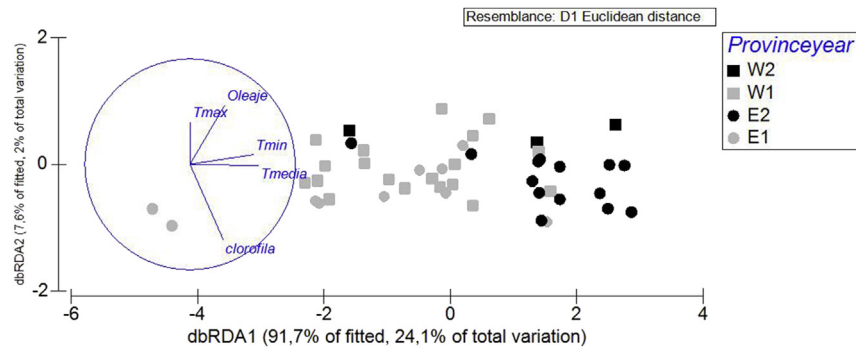
Variable	AIC	SS(trace)	Pseudo-F	p	% of explained variation
+Mean SST	182.57	125.15	11.626	**0.0006**	13.58
+Min SST	182.36	22.867	2.1574	0.1300	0.02
+Max SST	182.80	15.694	1.4906	0.2186	0.02
+Wave exposure	179.98	46.634	4.6541	0.0218	0.05
+Chlorophyll-a	178.48	31.978	3.2946	0.0604	0.03

Fig. 5. Distance-based redundancy analysis (db-RDA) biplot of first and second axes, with those environmental variables that affected significantly (see sequential tests in Table 3) the morphological characteristics of *Fucus guiryi*. Centroids for each distance are plotted. (W1 = western islands, 1972–1992; W2 = western islands, 1993–2012; E1 = eastern islands, 1972–1992; E2 = eastern islands, 1993–2012).

through time in selected morphological characteristics. This study has showed adverse effects on vegetative and reproductive morphology in current climate scenarios. Ocean warming is currently driving migrations of temperate species poleward (Wernberg et al., 2011), and future scenarios are likely to drive extinctions of populations at the southern range margin of the species.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2015.05.008.

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