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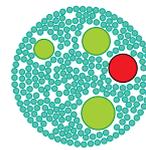
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Seasonality in the canopy structure of the endangered brown macroalga *Cystoseira abies-marina* at Gran Canaria Island (Canary Islands, eastern Atlantic)

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ABSTRACT

Cystoseira abies-marina is a canopy-forming brown seaweed distributed along the western Mediterranean and the adjacent Atlantic coasts, which has suffered massive declines in recent decades, particularly in the Canary Islands. Here, we describe seasonal variation in the canopy structure of this alga, addressing the role of environmental drivers. Four sites around the island of Gran Canaria were investigated monthly during an entire annual cycle. Annually, the non-fertile stage made up the majority of populations, in terms of frond density, while the fertile stage was comparatively sparser. This fertile stage, however, had the largest biomass and reached the longest lengths, showing significant seasonality. Best fitted GAM models included wave action, PAR and seawater temperature, but only accounted for a moderate variation in the seasonal frond structure of this alga. Total frond biomass, mostly fertile fronds, showed a bimodal pattern, with a peak in spring and a less accentuated peak in late summer–early autumn. This pattern was particularly obvious at sites with a wide annual variation in wave action, with lower biomass at times of high wave action. The frond size-structure was dominated, at all sites and times, by small fronds. The high frond density seems to promote intraspecific facilitation throughout the year. These results provide fundamental knowledge to improve the conservation and potential restoration actions for endangered populations of this alga.

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KEYWORDS Canopy-forming seaweed; conservation; environmental drivers; frond structure; intraspecific interactions; production; phenology

Introduction

Marine forests of large brown macroalgae, mostly belonging to the orders Fucales and Laminariales, are unique habitats which support a great variety of organisms in coastal zones worldwide and are comparable to terrestrial forests for the services they provide (Steneck *et al.*, 2002). These canopy-forming macroalgae are very important primary producers (Mann, 1973) and increase the structural complexity where they live, providing shelter and food for associated species (Schiel & Foster, 2006; Cheminée *et al.*, 2013), and increasing biodiversity (Chapman, 1995; Steneck *et al.*, 2002; Piazzini *et al.*, 2018). Thus, the conservation of these habitat-forming species is a crucial goal for ecologists and environmental managers. To achieve this, a better understanding of the structure and dynamics of canopies of algal forests in relation to environmental drivers and intraspecific interactions is crucial (Schiel & Foster, 2006; Bennett & Wernberg, 2014; Smale *et al.*, 2016).

Subtidal and intertidal algal forests experience large variations in their distribution, abundance and fitness at a range of spatial and temporal scales (Martínez *et al.*, 2012; Ferreira *et al.*, 2014; Yesson *et al.*, 2015). Their structure and extent are influenced by a variety of

environmental variables, including temperature (Tuya *et al.*, 2012), light availability (Creed *et al.*, 1998), nutrients (Piazzini & Ceccherelli, 2017) and wave intensity (Engelen *et al.*, 2005). Ecological processes, such as intraspecific and interspecific competition and facilitation, can also affect their structure and functioning (Bennett & Wernberg, 2014). Although macroalgae are important habitat-formers in temperate and subtropical rocky ecosystems, there are still few studies on their frond structure, particularly in terms of their temporal dynamics (Åberg, 1992; Schiel & Foster, 2006).

Seasonal changes in photoperiod are important in initiating the growth of macroalgae after the winter dormancy period. Likewise, an increase in water temperature is related to the beginning of growth and reproduction (Graiff *et al.*, 2015; de Bettignies *et al.*, 2018). Normally, in temperate seas, there is a mismatch between the period of maximum macroalgal growth and the concentration of nutrients in the water (Ballesteros, 1988; Delgado *et al.*, 1994). For example, Laminariales build up reserves of nitrogen (N) which are used to initiate growth in early spring, when light levels increase (Chapman & Craigie, 1977; Nielsen *et al.*, 2014). Many *Cystoseira* species can store reserves in their tophules, storage structures situated on the base of the branches (García-Fernández &

Bárbara, 2016), although some species such as *Cystoseira abies-marina* lack tophules or alternative structures to store reserves (González & Afonso-Carrillo, 1990). Wave action is one of the primary factors affecting canopy structure and dynamics (Engelen *et al.*, 2005; Kregting *et al.*, 2016), including local adaptation to hydrodynamic forces (de Bettignies *et al.*, 2015).

Subtidal and intertidal temperate reefs are characterized by a dense cover of perennial algal canopies (Schiel & Foster, 2006), which promote positive interactions through physical stress amelioration (Bennett & Wernberg, 2014). However, competition due to resource availability (light, nutrients, etc) can arise when living at high densities (Santelices, 2004; Scrosati, 2005). Both interactions can modulate frond dynamics, and consequently the size structure may exhibit seasonal variations. The shade effects on small individuals (or fronds) by large individuals, particularly in peak growth season, may limit their success due to low light, resource availability and wave action (Santelices, 2004; Rivera & Scrosati, 2008). The opposite effect can also occur, i.e. high-density canopies can favour the recruitment and survival of the smallest individuals in harsh environments, by buffering them against high radiation, temperature, desiccation and salinity (Bulleri, 2009; Bennett & Wernberg, 2014). In the Mediterranean Sea and the adjacent eastern Atlantic, brown algae of the genus *Cystoseira* are among the more important canopy-forming species (Giaccone *et al.*, 1994; García-Fernández & Bárbara, 2016). *Cystoseira* species occur from the intertidal down to the lower limit of the euphotic zone (García-Fernández & Bárbara, 2016). Losses of *Cystoseira* assemblages have been reported all around the Mediterranean and the Canary Islands, attributed to habitat destruction, eutrophication and overgrazing by herbivores (Thibaut *et al.*, 2005; Blanfuné *et al.*, 2016; Iveša *et al.*, 2016; Valdazo *et al.*, 2017).

Cystoseira abies-marina (S. G. Gmelin) C. Agardh is a habitat-forming species, living in shallow waters (0–20 m depth), particularly in places with high wave action and solar radiation. This alga is distributed throughout the Macaronesian region and reports from Morocco and Senegal require confirmation. In the Mediterranean Sea *C. abies-marina* is restricted to the western zone, where populations are reduced (González & Afonso-Carrillo, 1990; Ribera *et al.*, 1992). In the Canarian Archipelago, it used to be the most abundant and productive furoid species (Johnston, 1969), typically forming extensive stands in the lower intertidal to shallow subtidal zone of moderately exposed and exposed rocky reefs (Wildpret *et al.*, 1987; Medina, 1997). Morphologically, *C. abies-marina* is an atypical member of the genus (Gil-Rodríguez, 1978). With no conspicuous holdfast and no stipe, *C. abies-marina* is a caespitose macroalgae, attached to the substratum by small discoid haptera. The base is sympodial, formed by a creeping axis from

which multiple primary axes grow, often at points opposing the attachment structures. Branches can reach 50 cm in length and are replaced annually, while the creeping axis is perennial (Gil-Rodríguez, 1978; González & Afonso-Carrillo, 1990). During the reproductive season, receptacles (reproductive structures) develop from secondary and tertiary thorny branches, which can reach 10 cm in length, sprouting from the apical part of branches (González & Afonso-Carrillo, 1990). In previous studies, populations of *C. abies-marina* have shown seasonal patterns of growth and reproduction, with peaks of biomass in spring and summer and a period of dormancy in autumn and winter (González & Afonso-Carrillo, 1990; Medina, 1997). Although many fronds are lost after the reproductive peak, the thalli never go through a total rest phase, because branches from different seasons coexist (González & Afonso-Carrillo, 1990). This alga spreads through both vegetative (clonal) propagation and sexual reproduction (Medina, 1997). Similar to other species of the genus, thalli are negatively buoyant, and zygotes are heavy and tend to sink close to the parents (Guern, 1962), which gives the species/genus a low dispersal ability (< 20 cm; Mangialajo *et al.*, 2012).

In the 1990s, regressions of *C. abies-marina* forests were recorded in the Canary Islands (Medina & Haroun, 1994). Recent mapping of the distribution of *C. abies-marina* populations from Gran Canaria has shown a huge regression, despite a lack of consensus on the reason for such declines (Valdazo *et al.*, 2017). For this reason, this alga is included in the regional catalogue of endangered species (Canary Island Catalogue of Protected Species; Law 4/2010, 4 June 2010). Recently, the alga was also included in the Spanish national catalogue of endangered species (TEC/596/2019, 8 April 2019).

Identifying relevant environmental drivers affecting the structure of canopies of *C. abies-marina* is, therefore, of interest to quantify the ecosystem functions and services they provide (e.g. primary production and nurseries). In this study, we explicitly linked seasonal variation in environmental conditions with the frond structure and reproduction of this canopy-forming macroalga on the island of Gran Canaria through an annual cycle. We predicted that canopy descriptors (density, biomass, length and frond production) would vary seasonally, associated with environmental conditions, in particular sea surface temperature, light, nutrients and wave energy. Finally, we analysed variations in the frond size-structure of this alga to assess the prevalence of positive and/or negative frond interactions.

Materials and methods

Study sites and Cystoseira abies-marina canopy structure

Our study was performed at four sites on the island of Gran Canaria (Canary Islands, eastern Atlantic, Spain;

Fig. 1): two in the north, Playa Canaria (PLC) and El Confital (CON); and two in the east, Clavellinas (CLA) and Salinetas (SAL). These sites cover a large part of *C. abies-marina* distribution on the island, incorporating different types of environmental conditions, mainly in terms of wave action. The main environmental and anthropogenic characteristics for each site are summarized in Supplementary table 1.

Cystoseira abies-marina is a clonal seaweed with modular construction (Santelices, 2004) that forms monospecific stands (Fig. 2), made up of ramets or fronds arising from creeping axes, which are attached to the substratum by small haptera (Fig. 3). The entwinement of axes and branching of plants makes ramets difficult to distinguish from genets (Fig. 4). Moreover, it is difficult to accurately age individuals and ramets; in the absence of growth rings, no ageing method is currently available (Blanfuné *et al.*, 2016). For these reasons, we considered 'fronds' as the sample unit. We distinguished two stages in the macroscopic life history of *C. abies-marina*: non-fertile fronds (NF) (Fig. 5), and fertile fronds (F) (Fig. 6). We defined non-fertile fronds as any primary axis

without receptacles (reproductive structures). Fertile fronds, which are usually much branched, carry the receptacles in the distal part of branches (Fig. 7). In this study, we used the length of the primary axis of fronds, despite their deciduous character, to describe algal dynamics.

Sampling and sorting

At each site, sampling was carried out at the lower limit of the intertidal zone, where *C. abies-marina* forms dense monospecific stands. Subtidal populations have disappeared in Gran Canaria (Valdazo *et al.*, 2017). We decided to use a small sampling unit (25 cm²), because this alga is under protection by national and regional laws. Every month, from May 2014 to April 2015 (except January and March 2015, due to bad weather), at low tide, six samples were haphazardly collected by scraping the substrate to ensure that the creeping and erect fronds were collected complete and intact. Algal samples were placed in sealed bags and carried to the laboratory, where they were immediately frozen.

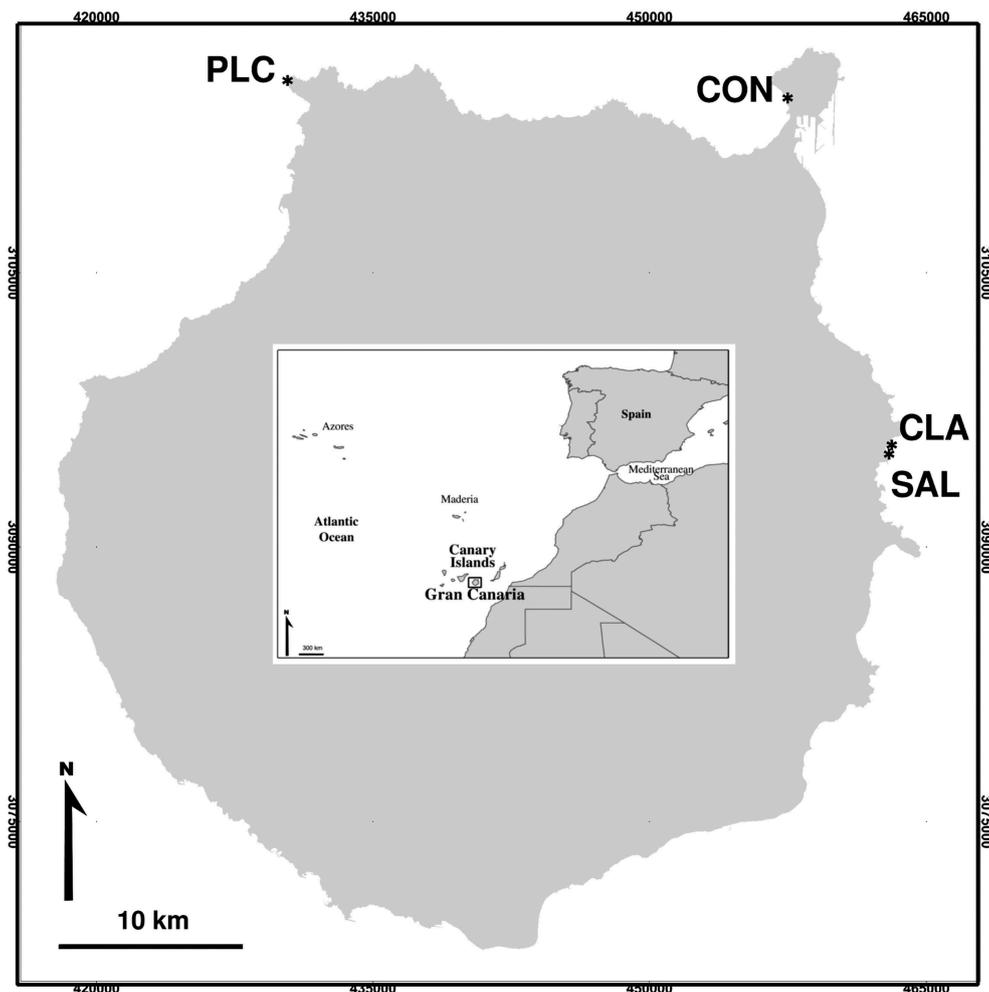
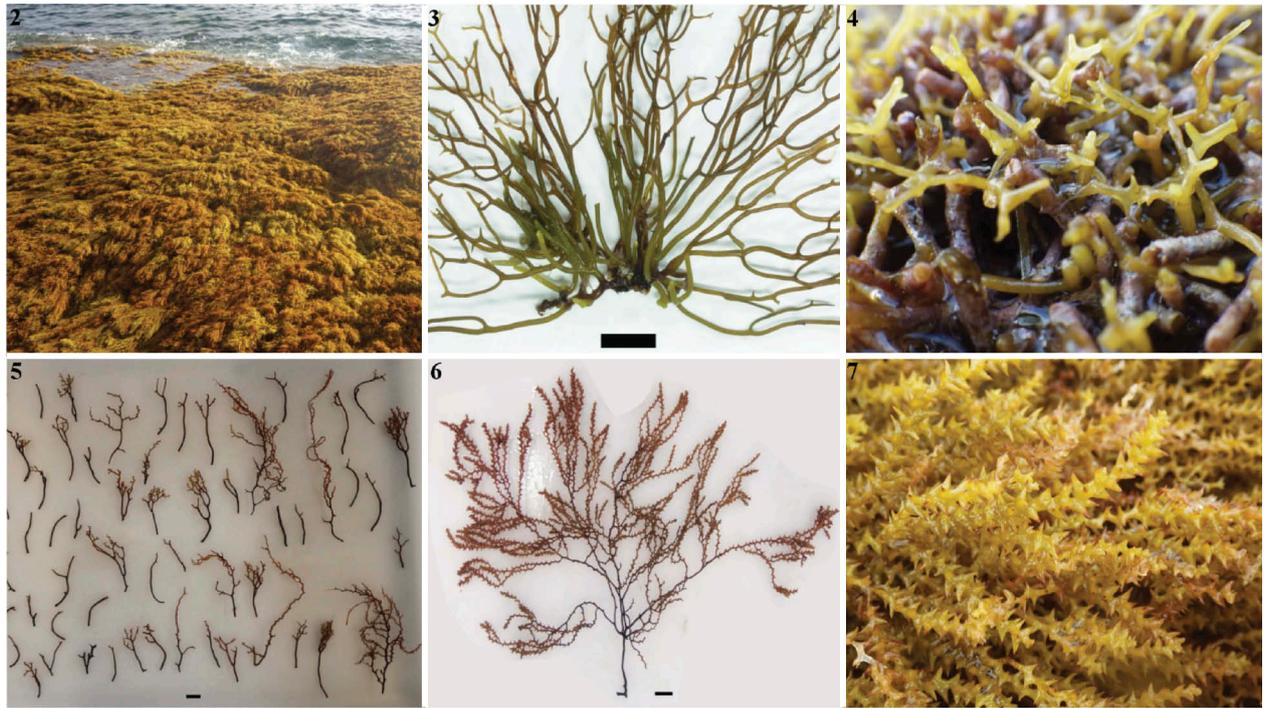


Fig. 1. Map of Gran Canaria Island, showing study sites Playa Canaria (PLC), El Confital (CON), Salinetas (SAL) and Clavellinas (CLA).



Figs 2–7. *Cystoseira abies-marina*, showing **Fig. 2.** monospecific stand; **Fig. 3.** fronds arising from creeping axes; **Fig. 4.** entwined creeping axes; **Figs 5, 6.** non-fertile fronds; **Fig. 7.** fertile fronds. Scale bars correspond to 1 cm.

Once defrosted, algal samples were rinsed, and all epiphytes and sandy and rocky debris eliminated. We first measured the length of the primary axis with a ruler. For each sample, fronds were classified into seven size classes: 0–3, 3.1–6, 6.1–9, 9.1–12, 12.1–15, 15.1–18, and >18 cm to describe their population size structure. The seven classes were established to describe population frond size-structure (Åberg, 1992), including non-fertile and fertile fronds. The number of non-fertile/fertile and the total number of fronds were subsequently determined for each sample. We obtained the mean length of non-fertile (>3cm) and fertile fronds by measuring at least 50% of fronds of each stage. The dry weight (dwt) of each stage was obtained after drying fronds for two days at 80°C. As a result, the stand density (fronds m⁻²) and the stand biomass (g dwt m⁻²) were estimated for each stage over time for each site. Lastly, we calculated the annual mean, including frond densities and biomasses across all sites.

Biomass production (P) was calculated, for each site, between each of two consecutive sampling times by considering all the stages. Fronds are not perennial, and so production of *C. abies-marina* was calculated using its annual biomass cycle. Then, we calculated the daily turnover ratio (r) of fronds, using the formula (Sales & Ballesteros, 2012):

$$r = \ln \left(\frac{P}{B_1} + 1 \right) \Delta t^{-1}$$

P is the production attained during a given time interval (g dwt), B₁ is the initial biomass (g dwt), and Δt is the time length of the interval (days). We calculated the average annual production of the four sites. Finally, we converted the biomass (g dwt) to carbon tissue content according to previous research on a range of *Cystoseira* species, which indicated that carbon content is ~34% of dwt (Ballesteros, 1990a; Delgado *et al.*, 1994).

Environmental drivers

Wave exposure, sea surface temperature, light availability and nutrient concentrations (chlorophyll *a*, used as a proxy) were obtained, on a monthly basis, for each site (Supplementary fig. 1). Data on wave energy were obtained from the Enola project (www.enola.ihcantabria.com). We used averaged monthly power (Kw m⁻¹) as a proxy for wave energy. Monthly sea surface temperature (SST, °C), chlorophyll *a* (Chla, mg m⁻³) and photosynthetically active radiation (PAR, μmol m⁻² d⁻¹) were obtained from the NASA Giovanni Data Portal (<http://giovanni.gsfc.nasa.gov/giovanni>). Temperature data were monthly means from May 2014 to April 2015, using 9-km² pixel resolution, from the Pathfinder AVHRR satellite. Chla concentration data were monthly means from May 2014 to April 2015, using 4-km² pixel resolution, from the MODIS Aqua satellite. Since there were no PAR data after 2010, we used, as a proxy for light

availability through the study period, monthly means from 1997 to 2010, using 9-km² pixel resolution, from the SeaWiFS satellite.

Statistical analysis

Differences in size-frequency distributions between sites and months were tested using the non-parametric Kolmogorov–Smirnov test (Legendre & Legendre, 1998). Regression analyses examined the relationship between densities, biomasses and length of each of the two stages and environmental predictors. We initially used the ‘chart.Correlation’ function in the ‘PerformanceAnalytics’ R package (Peterson & Carl, 2014) to explore collinearity in predictor variables, the relationship between response variables and environmental drivers, and relationships between response variables. We identified a strong negative correlation between Chla and SST ($R^2 = -0.77$), so Chla was removed. Data exploration revealed that relationships between predictor and response variables were non-linear and, therefore, a Generalized Additive Model (GAM) strategy was adopted (Zuur *et al.*, 2009). All models were fitted using the R ‘mgcv’ package (Wood, 2006, 2008), which uses the default method of a ‘thin-plate regression spline’ for smoothing and automatic selection of smoothing parameters by cross-validation. We fitted the models with a gamma error distribution for the non-fertile stage, and a Gaussian error distribution for the fertile stage. The GAM models were conceptualized as:

$$Y \sim Pw + s(\text{PAR}) + s(\text{SST})$$

Y is the density, biomass and length of each stage (response variables); s is the non-parametric smoothed functions of photosynthetically active radiation (PAR) and sea surface temperature (SST) and Pw is the parametric coefficient of wave energy. We built models with all possible combinations of explanatory variables, then we chose the models with the best fit using the AIC (Akaike Information Criterion) as an indicator of the best fitted model (the lower, the better). We assessed models performance using the ‘gam.check’ function, which produces graphical diagnostics (QQ-plots, residuals histograms, residuals versus fitted values and fitted values *versus* observed values). For the models of the fertile stage (biomass, density and length), the plots of residuals against linear predictors for the GAM model displayed some normality problems and, therefore, the dependent variables were square root transformed. We used partial residual plots of the models to contrast the relative influence of each predictor.

Results

Canopy structure: variation across sites

During the study, at all four sites, *C. abies-marina* populations were dominated by non-fertile fronds ($85\,911.8 \pm 34\,783.3$ fronds m⁻²; annual mean \pm SE, Fig. 8). Fertile fronds had a comparatively lower mean annual density (9984.4 ± 433.8 fronds m⁻², Fig. 8). Fertile fronds, however, carried the largest annual biomasses (2924.1 ± 175.4 gr dwt m⁻², Fig. 9). In terms of mean frond length, fertile fronds were longer (14.7 ± 0.1 cm) than non-fertile fronds (6.9 ± 0.04 cm) (Supplementary fig. 2).

Size structure: evidence of intraspecific relationships

Within sites, no significant changes in size-frequency distributions were observed through time (Fig. 10; Supplementary table 2). Across sites, and throughout the year, *C. abies-marina* stands were mostly dominated by small-sized fronds (classes 1 and 2), so there was no direct indication of negative interaction, even in the season when large-sized fronds increased (May to October, Fig. 10). Large fronds (classes 6 and 7), which were mostly fertile, were always sparse and disappeared during winter from most sites (PLC, CON and CLA) (Fig. 10).

Linking environmental variation with canopy structure

The best model explaining variation in the total density of fronds only included photosynthetically active radiation (PAR); the model only explained 8.33%

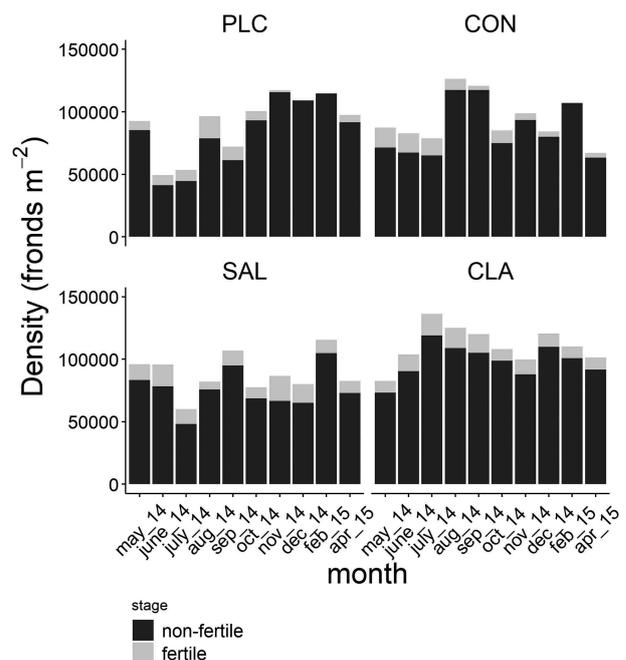


Fig. 8. Temporal variation in *Cystoseira abies-marina* frond densities for Playa Canaria (PLC), El Confital (CON), Salinetas (SAL) and Clavellinas (CLA).

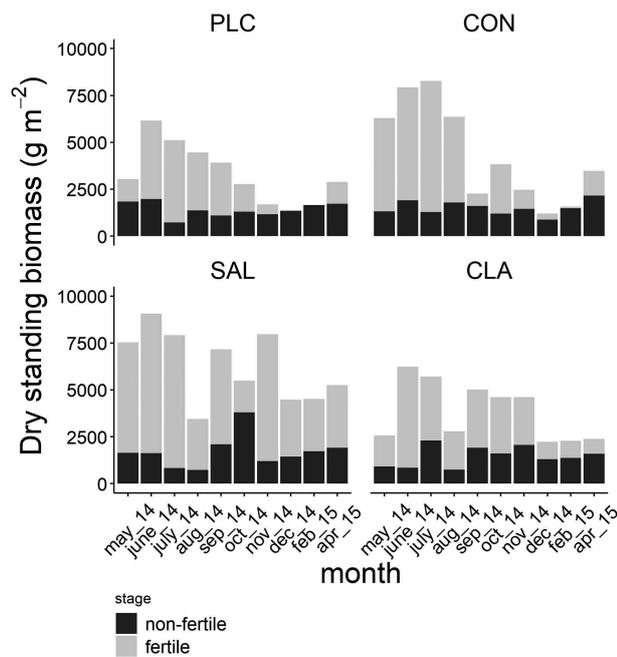


Fig. 9. Temporal variation in *Cystoseira abies-marina* frond biomass for Playa Canaria (PLC), El Confital (CON), Salinetas (SAL) and Clavellinas (CLA).

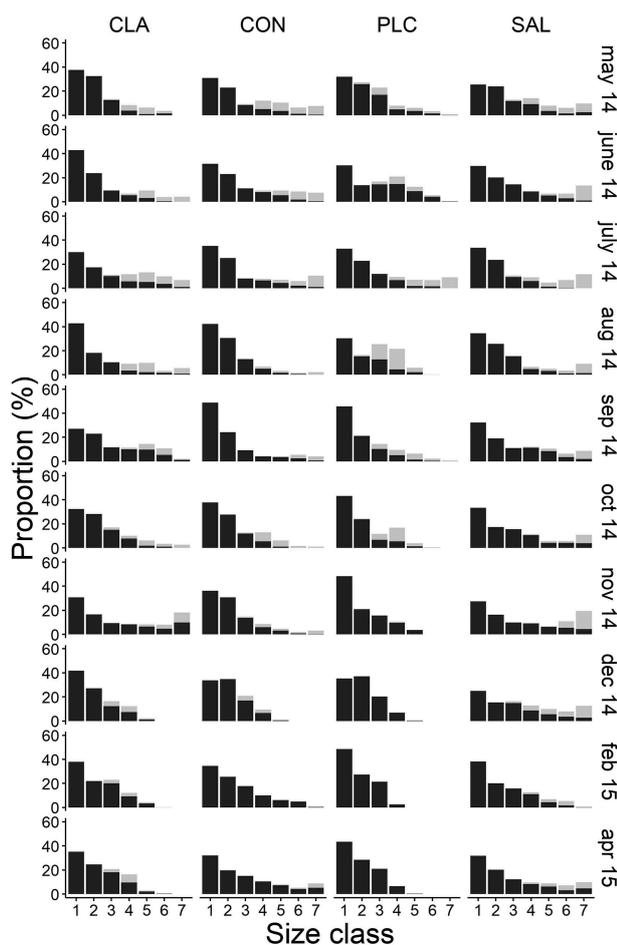


Fig. 10. Temporal changes in the size-frequency distribution of *Cystoseira abies-marina* fronds for Clavellinas (CLA), El Confital (CON), Playa Canaria (PLC) and Salinetas (SAL). Size classes are: 1 (0–3 cm), 2 (3.1–6 cm), 3 (6.1–9 cm), 4 (9.1–12 cm), 5 (12.1–15 cm), 6 (15.1–18 cm), 7 (>18 cm). The fertile stage is denoted in light grey, while the non-fertile stage is in dark grey.

(adjusted $R^2 = 0.07$) of the variance (Table 1 and Supplementary table 3). The models accounting for temporal variation in the density of non-fertile fronds only explained 10.9% (adjusted $R^2 = 0.09$) (Table 1 and Supplementary table 3). However, variation in the density of fertile fronds was explained by variation in photosynthetically active radiation (PAR), sea surface temperature (SST) and wave power (Pw) (Table 1 and Supplementary table 3). The model explained 55% (adjusted $R^2 = 0.51$) of the variance (Table 1). The residual plot of PAR showed a bimodal pattern (Fig. 11a) with a higher density of fertile fronds at high and low radiation levels, which correspond with spring (April, May, June) and autumn (October and November). SST showed a similar pattern of residuals with a higher density at low (< 18°C) and high (> 22°C) temperatures (Fig. 11b). Wave power was the most important predictor, revealing a general pattern of negative residuals (i.e. low frond density) with increasing wave power (Fig. 11c).

The best model explaining variation of the fertile biomass, which strongly correlated with the total biomass ($R^2 = 0.9$), included photosynthetically active radiation (PAR), sea surface temperature (SST) and wave power (Pw) (Table 1 and Supplementary table 4). The model explained 55.3% (adjusted $R^2 = 0.52$) of the variation (Table 1). The partial residual plots were similar to those of the density of fertile fronds, as both variables were moderately correlated ($R^2 = 0.63$). A clear relationship was evident for SST, with positive residuals for SST values >21°C (Fig. 11d). The residual plot of PAR showed a bimodal pattern (Fig. 11e) with a higher fertile biomass at low (< 27 $\mu\text{mol m}^{-2} \text{d}^{-1}$) and high (45–55 $\mu\text{mol m}^{-2} \text{d}^{-1}$) radiation levels, which correspond with autumn (October and November), spring and summer (April, May, June; July and August). Wave power was, again, the most important predictor, revealing a general pattern of negative residuals (i.e. low biomass) as it increased (Fig. 11f).

As for the density and biomass of fertile fronds, the models that best explained variation in the length of the non-fertile and fertile stages included photosynthetically active radiation (PAR), sea surface temperature (SST) and wave power (Pw) (Table 1 and Supplementary table 5). For the length of non-fertile fronds, the model explained 32% of the variance (adjusted $R^2 = 0.27$) (Table 1). The residual plot of PAR showed a bimodal pattern with the higher length at low (25–27 $\mu\text{mol m}^{-2} \text{d}^{-1}$) and high (> 45 $\mu\text{mol m}^{-2} \text{d}^{-1}$) levels of radiation (Fig. 12a). Similarly, a bimodal pattern was observed for SST, including positive residuals at low (SST values < 18°C) and high temperatures (> 23°C) (Fig. 12b). A weak pattern of positive residuals (i.e. higher length) was observed under increased wave power (Fig. 12c). In terms of the length of fertile fronds, the model explained 49% of the variance (adjusted $R^2 = 0.45$)

Table 1. GAMs explaining variation in the density and biomass of each stage of *Cystoseira abies-marina* according to sea surface temperature (SST), photosynthetically active radiation (PAR) and wave power (Pw).

Model	D ² (%)	Adj. R ²	AIC	GCV
B = Total biomass (Gamma(log))				
B1 ~ Pw	24.8%	0.174	-68.81	0.31
B2 ~ s(SST)	25.8%	0.241	-62.84	0.32
B3 ~ s(PAR)	25.4%	0.219	-55.48	0.33
B4 ~ s(PAR) + s(SST)	40.5%	0.326	-99.48	0.28
B5 ~ Pw + s(PAR)	42.5%	0.352	-118.77	0.26
B6 ~ Pw + s(SST)	40.8%	0.336	-119.3	0.26
B7 ~ Pw + s(PAR) + s(SST)	50.6%	0.415	-145.04	0.24
NFB = Non-fertile biomass (Gamma(log))				
NFB1 ~ Pw	1.03%	0.004	-553.26	0.33
NFB2 ~ s(SST)	1.4x10 ⁻⁵ %	4.3x10 ⁻⁷	-552.64	0.33
NFB3 ~ s(PAR)	5.01%	0.006	-550.5	0.33
NFB4 ~ s(PAR) + s(SST)	14.6%	0.052	-562.39	0.32
NFB5 ~ Pw + s(PAR)	6%	0.017	-551.95	0.33
NFB6 ~ Pw + s(SST)	1.03%	0.004	-553.26	0.33
NFB7 ~ Pw + s(PAR) + s(SST)	14.5%	0.053	-562.1	0.32
FB = Fertile biomass (Gaussian)				
FB1 ~ Pw	29.2%	0.29	-19.7	0.05
FB2 ~ s(SST)	32.9%	0.31	-19.7	0.05
FB3 ~ s(PAR)	30.6%	0.28	-9.14	0.06
FB4 ~ s(PAR) + s(SST)	44.1%	0.406	-49.94	0.05
FB5 ~ Pw + s(PAR)	47.3%	0.45	-73.01	0.043
FB6 ~ Pw + s(SST)	46.8%	0.454	-77.55	0.04
FB7 ~ Pw + s(PAR) + s(SST)	55.3%	0.52	-99.33	0.038
D = Total density (Gamma (log))				
D1 ~ Pw	0.008	-0.004	1258.4	0.133
D2 ~ s(SST)	6.24%	0.058	1245.2	0.127
D3 ~ s(PAR)	8.33%	0.07	1243.8	0.126
D4 ~ s(PAR) + s(SST)	8.48%	0.068	1245.1	0.127
D5 ~ Pw + s(PAR)	8.49%	0.067	1245.4	0.127
D6 ~ Pw + s(SST)	6.26%	0.054	1247.1	0.128
D7 ~ Pw + s(PAR) + s(SST)	7.27%	0.061	1245.7	0.127
NFD = Non-fertile density (Gamma (log))				
NFD1 ~ Pw	1.02%	0.007	1256.4	0.17
NFD2 ~ s(SST)	7.9%	0.076	1241.5	0.16
NFD3 ~ s(PAR)	10.9%	0.095	1238.4	0.158
NFD4 ~ s(PAR) + s(SST)	10.9%	0.092	1239.4	0.16
NFD5 ~ Pw + s(PAR)	11%	0.094	1239.9	0.16
NFD6 ~ Pw + s(SST)	8.34%	0.077	1242.3	0.16
NFD7 ~ Pw + s(PAR) + s(SST)	9.43%	0.085	1240.6	0.16
FD = Fertile density (Gaussian)				
FD1 ~ Pw	35.4%	0.351	174.45	0.120
FD2 ~ s(SST)	18.7%	0.165	240.10	0.158
FD3 ~ s(PAR)	19%	0.162	242.85	0.160
FD4 ~ s(PAR) + s(SST)	31.2%	0.269	215.20	0.143
FD5 ~ Pw + s(PAR)	43.8%	0.416	157.13	0.112
FD6 ~ Pw + s(SST)	45.1%	0.428	152.63	0.110
FD7 ~ Pw + s(PAR) + s(SST)	55%	0.514	120.83	0.097
NF = Non-fertile length (Gamma)				
NFL1 ~ Pw	14.8%	0.129	966.51	0.074
NFL2 ~ s(SST)	10.6%	0.066	993.29	0.082
NFL3 ~ s(PAR)	13%	0.097	985.80	0.080
NFL4 ~ s(PAR) + s(SST)	23.9%	0.179	969.68	0.075
NFL5 ~ Pw + s(PAR)	26.7%	0.229	945.70	0.068
NFL6 ~ Pw + s(SST)	26.5%	0.235	943.63	0.067
NFL7 ~ Pw + s(PAR) + s(SST)	32%	0.265	937.52	0.066
FL = Fertile length (Gaussian)				
FL1 ~ Pw	32.1%	0.318	726.86	1.2
FL2 ~ s(SST)	16.8%	0.156	780.33	1.5
FL3 ~ s(PAR)	20%	0.171	780.8	0.17
FL4 ~ s(SST) + s(PAR)	30.4%	0.257	760.74	1.39
FL5 ~ Pw + s(PAR)	41.9%	0.396	705.86	1.11
FL6 ~ Pw + s(SST)	43.3%	0.411	700.02	1.08
FL7 ~ Pw + s(PAR) + s(SST)	49%	0.453	688.93	1.03

The Akaike information criterion (AIC) and the GCV, measures of the relative quality of each statistical model, are provided. Selected models are in bold.

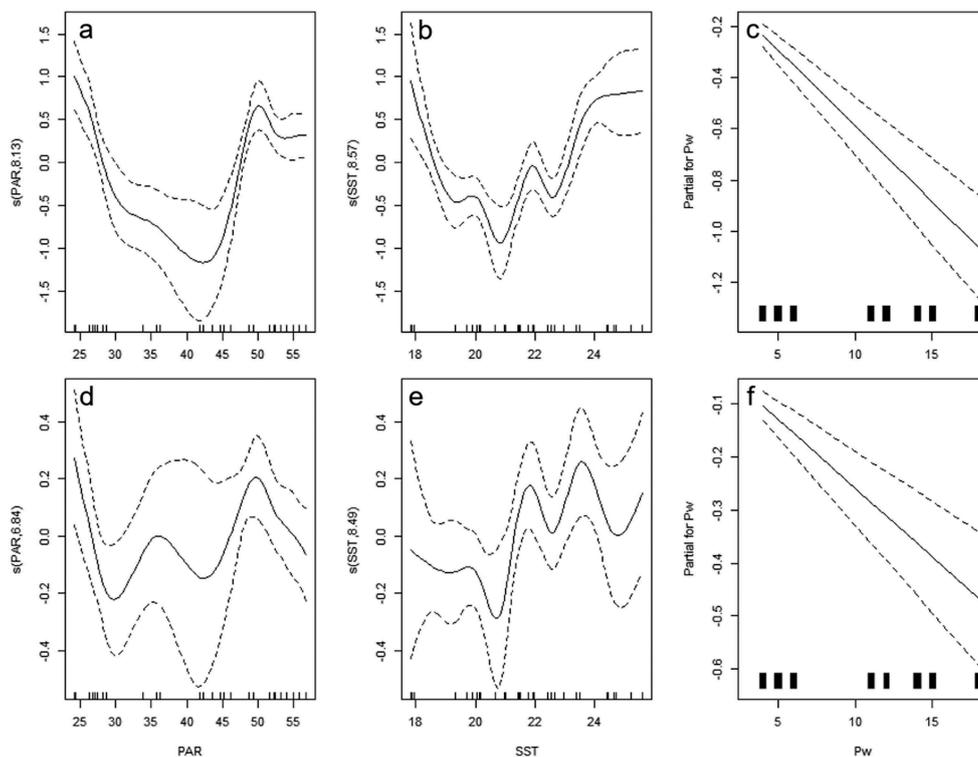


Fig. 11. Partial residual plots for the GAMs terms explaining variation in the density and biomass of fertile *Cystoseira abies-marina*. For fertile frond density: (a) photosynthetically active radiation (PAR), (b) sea surface temperature (SST), (c) wave power (Pw). For fertile frond biomass: (d) photosynthetically active radiation (PAR), (e) sea surface temperature (SST), (f) wave power (Pw). Each panel plots the values for a predictor variable (x-axis) against the partial residuals (y-axis), after removing the effects of the other predictors. The dashed lines show the estimated 95% confidence limits. The y-axis label indicates the estimated degrees of freedom for the smoothed spline term.

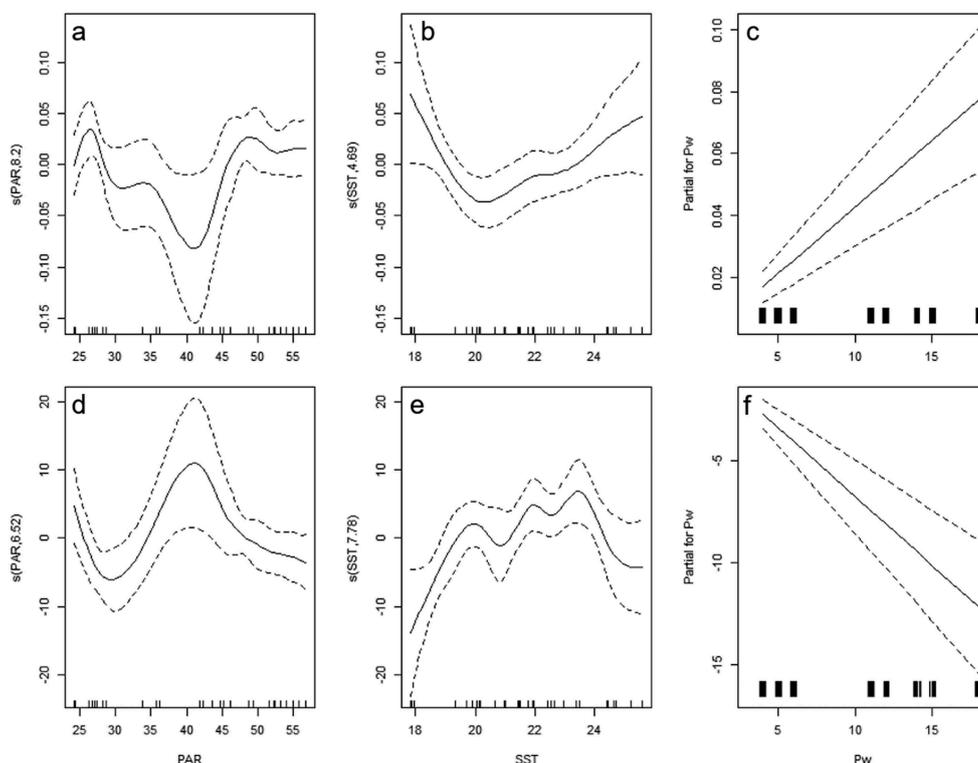


Fig. 12. Partial residual plots for the GAMs terms explaining variation in the length of non-fertile and fertile *Cystoseira abies-marina*. For non-fertile frond length: (a) photosynthetically active radiation (PAR), (b) sea surface temperature (SST), (c) wave power (Pw). For fertile frond length: (d) photosynthetically active radiation (PAR), (e) sea surface temperature (SST), (f) wave power (Pw). Each panel plots the values for a predictor variable (x-axis) against the partial residuals (y-axis), after removing the effects of the other predictors. The dashed lines show the estimated 95% confidence limits. The y-axis label indicates the estimated degrees of freedom for the smoothed spline term.

(Table 1). The residual plot of PAR showed a bimodal pattern with the higher length at low ($< 25\text{--}27 \mu\text{mol m}^{-2} \text{d}^{-1}$) and high ($35\text{--}50 \mu\text{mol m}^{-2} \text{d}^{-1}$) levels of radiation (Fig. 12d). For SST, we observed a bimodal pattern, with positive residuals between $21\text{--}24^\circ\text{C}$ (Fig. 12e). A clear pattern of negative residuals (i.e. low length) was observed under increased wave power (Fig. 12f).

Annual frond production

The mean annual frond production of *C. abies-marina* in Gran Canaria was $5380 \text{ g dwt m}^{-2}$ ($1829.52 \text{ g C m}^{-2}$) (Supplementary table 6). Frond production showed two peaks, in spring and autumn, and null values in summer and late autumn–early winter (Fig. 13). The daily turnover ratio was highest in spring for all sites, although CON and SAL also showed high rates in autumn (Supplementary table 6).

Discussion

Despite the important role that the genus *Cystoseira* plays as a habitat-former on Atlantic coasts, we have a limited knowledge of the population dynamics of most species; this is especially true for less conspicuous species such as *C. abies-marina*. To our knowledge, ours is the first study to address the seasonal dynamics of macroscopic fronds of this species, providing insight into the frond size-structure and possible intraspecific relationships of *C. abies-marina*. We provide a more precise phenology than the descriptive studies carried out previously (González & Afonso-Carrillo, 1990; Medina, 1997). In particular, we linked quantitative data on canopy structure with seasonality of environmental drivers. However, results should be interpreted with caution, as our

study is limited to four sites on one island for one year.

We found a temporal shift in the frond size structure of *C. abies-marina* on the island of Gran Canaria, mainly related to the prevalence of the fertile stage, which showed the largest variability in relation to environmental predictors. The models that best fit included three environmental factors (Pw, PAR and SST) and explained a moderate variation in the seasonality of the fertile stage. Two predictors (PAR and SST) did not differ much between sites, but wave power showed considerable spatial and temporal variation. In general, the density, biomass and length of the fertile stage decreased with increased wave power. The lower, seasonally constant, wave power observed at the eastern sites (SAL and CLA) seems to be connected with the highest temporal consistency of their canopy descriptors. At these sites, in particular, we found fertile fronds throughout the entire year. In winter, under decreased SST and PAR, the density and biomass of fertile fronds also decreased. At PLC and CON, sites located on the more exposed northern coast, canopy descriptors followed a more seasonal pattern, with the highest density and biomass of fertile fronds in the months of lower wave energy, and minimum density and biomass in the winter months, when the wave energy, mostly induced by NW swells, is maximum, while SST and PAR are low.

Previous work on *C. abies-marina* from the Canarian Archipelago (González & Afonso-Carrillo, 1990; Medina, 1997) and some *Cystoseira* species from the Mediterranean (Ballesteros, 1988, 1990a, 1990b; Delgado *et al.*, 1994; Sales & Ballesteros, 2012) showed a simple seasonal pattern, with maximum biomass in late spring and early summer, and minimum in autumn and winter. However, in our study, at CON, SAL and

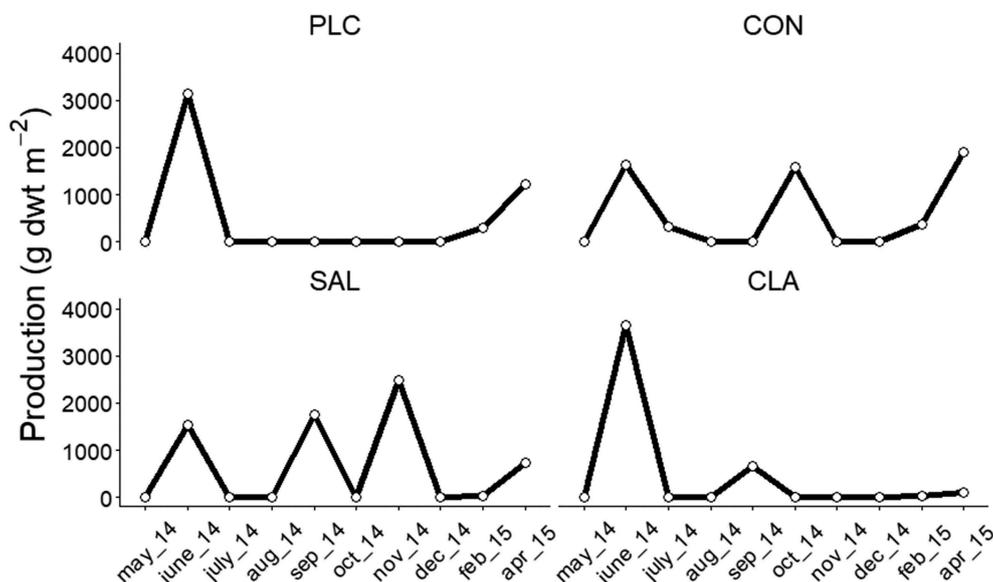


Fig. 13. Annual *Cystoseira abies-marina* frond production for each site on Gran Canaria Island: Playa Canaria (PLC), El Confital (CON), Salinetas (SAL) and Clavellinas (CLA).

CLA, the algal biomass cycle showed a rather bimodal pattern, with production peaking in spring and a less accentuated peak in late summer–early autumn. This pattern is similar to that found for *Cystoseira nodicaulis* on the north coast of Spain (Arenas *et al.*, 1995) and *Cystoseira brachycarpa* on the north-western coast of France (Hoffmann *et al.*, 1992). The contrasting seasonality, relative to Mediterranean and northern Atlantic species of *Cystoseira*, may result from the narrower annual environmental variation around the Canarian Archipelago, in comparison with Mediterranean and Atlantic shores (Arenas *et al.*, 1995; Tuya *et al.*, 2006). For example, the seagrass *Cymodocea nodosa*, in the Canary Islands, shows a smoothed seasonal production pattern compared with the Mediterranean (Tuya *et al.*, 2006). There may be other mechanisms which help to explain the second period of production, particularly that the modular construction of *C. abies-marina* allows the plant to regrow following losses suffered in its senescent phase, and the highly efficient nutrient uptake mechanisms (Delgado *et al.*, 1994; Rico & Fernández, 1997).

As previously indicated, the population structure of *C. abies-marina* was spatially and temporally variable, associated with wave power, demonstrating the importance of exposure to waves in determining algal canopy density, biomass and morphology (Hurd, 2000; Engelen *et al.*, 2005). For many macroalgae, specimens subjected to heavy waves are typically smaller, thicker and have stronger holdfasts than those growing in calmer waters (Hurd, 2000; Thomsen & Wernberg, 2005). This morphological plasticity modulated by wave energy also reduces hydrodynamic drag forces to minimize dislodgement (de Bettignies *et al.*, 2015). Previous, spatially non-replicated, work on *C. abies-marina* (Medina, 1997) showed that canopies from an exposed location were larger, more branched and had greater biomass than canopies from a less exposed location. Our results were not congruent with Medina (1997), since we found a clear decrease in all canopy descriptors under increased wave exposure scenarios, both spatially (i.e. inter-site differences) and temporally (i.e. in winter for each site).

In this study, we have reported a temporally stable situation in terms of frond size-structure; small fronds (0–6 cm, class 1 and 2) predominate throughout the entire year. This finding suggests the prevalence of positive interactions in the closed canopies of *C. abies-marina*. High-density canopies favour high humidity at low tide, maintaining a low temperature and reducing the water velocity, decreasing the amount of drag experienced by small fronds; this is in accordance with other clonal seaweeds (Collado-Vides, 2002; Scrosati, 2005; Rivera & Scrosati, 2008). In *C. abies-marina* stands, algal biomass is concentrated in the largest fronds, which are highly branched, so they can induce shading and/or whiplash on the understorey of smaller fronds below.

However, this effect does not seem to affect their success. In turn, strategies to adapt to the stressful conditions of the low intertidal and upper subtidal, where crowded conditions seem to drive facilitative relationships, may improve population persistence, as demonstrated for other canopy-forming algal populations (Santelices, 2004; Bennett & Wernberg, 2014). In any case, experimental work, at local scales, would be necessary to unravel the direction of interactions between small and large-sized fronds.

The annual production of *C. abies-marina* in Gran Canaria (5380.9 g dwt m⁻² year⁻¹) was higher than that previously estimated in the Canary Islands (1293.2 g dwt m⁻² year⁻¹; Medina, 1997) and other Mediterranean *Cystoseira*-dominated assemblages (Ballesteros, 1988, 1990a, 1990b; Sales & Ballesteros, 2012a). The primary annual production of *C. abies-marina* was as large as that observed for kelps and other furoids around the world (Chung *et al.*, 2011; Krumhansl & Scheibling, 2012). The dramatic decline of *C. abies-marina* forests in recent decades, ~9.2 km² in Gran Canaria (Valdazo *et al.*, 2017), means the loss of high primary production (16 831.6 Mg C year⁻¹). Although more research is key to understanding the carbon flows from macroalgal forests, a considerable proportion of the carbon provided by *C. abies-marina* forests could end up sequestered by means of detrital export into the deep sea, or adjacent marine sediments (Krause-Jensen & Duarte, 2016).

Currently, *C. abies-marina* is nationally and regionally protected within the framework of the Spanish and Canarian Catalogues of Protected Species, as over the last few decades, there has been a massive decline across the entire Canarian archipelago (Medina & Haroun, 1994; Valdazo *et al.*, 2017). Population dynamics are poorly understood for most of the *Cystoseira* species from Macaronesia, so better knowledge of *C. abies-marina* makes an important contribution. More efforts are necessary to better understand key ecological processes shaping these dynamics. For conservation and restoration purposes, it is necessary to know if there are demographic constraints (e.g. Allee effects), whereby population persistence displays positive density-dependence (Berec *et al.*, 2007). In addition, *C. abies-marina* should be considered within blue carbon conservation and restoration strategies to mitigate climate change in response to carbon neutral strategies. These future studies will improve conservation actions for this habitat-forming organism.

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Supplementary Information

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at <https://doi.org/10.1080/09670262.2019.1696989>

Supplementary table 1. Environmental and anthropogenic characteristics of the study sites.

Supplementary table 2. Results of the two-sample Kolmogorov–Smirnov test (D) checking for differences in size-structure between sites and months.

Supplementary table 3. Optimal GAM models explaining annual variation in the frond density of *C. abies-marina*.

Supplementary table 4. Optimal GAM models explaining annual variation in the frond biomass of *C. abies-marina*.

Supplementary table 5. Optimal GAM models explaining annual variation in the length of *C. abies-marina*.

Supplementary table 6. Annual production of *C. abies-marina* fronds.

Supplementary fig. 1. Temporal changes in environmental predictors. (A) photosynthetically active radiation (PAR, Einstein s⁻¹ cm⁻²); (B) sea surface temperature (SST, °C); (C) wave power (Pw, Kw m⁻¹); (D) Chlorophyll a (Chla, mg m⁻³).

Supplementary fig. 2. Temporal variations in the frond length of *Cystoseira abies-marina* for each site.

Author contributions

J. Valdazo: original concept, sample collection, laboratory work, data analysis, writing of manuscript; M.A. Viera-Rodríguez: original concept, editing of manuscript; F. Tuya: original concept, data analysis, editing of manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

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