



Temporal and spatial variability in population traits of an intertidal fucoid reveals local-scale climatic refugia

Raquel Sánchez de Pedro^{a,*}, Andrea N. Fernández^a, Ignacio José Melero-Jiménez^{a,b},
María Jesús García-Sánchez^a, Antonio Flores-Moya^a, Elena Bañares-España^a

^a Universidad de Málaga, Andalucía Tech, Departamento de Botánica y Fisiología Vegetal, Campus de Teatinos, 29010, Málaga, Spain

^b Department of Plant Pathology and Microbiology, Institute of Environmental Sciences, The Hebrew University of Jerusalem, Rehovot, Israel

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ABSTRACT

Global change is imposing significant losses in the functional traits of marine organisms. Although areas of climatic refugia ameliorate local conditions and help them to persist, the extent to which mesoscale effects contribute for intraregional variability on population traits and conservation is uncertain. Here we assess patterns of conservation status of *Fucus guiryi*, the main intertidal habitat-forming seaweed in the Strait of Gibraltar (southern Spain and northern Morocco). We investigated the demography, reproductive phenology, and morphology at northern and southern side populations. Population traits were compared seasonally within populations from each side, and at spatial scale in early summer 2019. In the last decade three populations became extinct; two marginal populations had dispersed individuals with a narrower fertility season and miniaturized individuals below 3 cm; and five populations showed variable density and cover with more than 20% of reproductive individuals over the seasons. Highest density, cover, morphology, and reproductive potential was detected at one population from each side, suggesting local-scale climatic refugia in upwelling areas located inside marine protected areas. Southern recruits were more warm-tolerant but grew less at colder conditions than northern ones, revealing a mesoscale heterogeneity in thermal affinities. This study evidenced functional losses and distinct reproductive strategies experienced by *F. guiryi* at peripheral locations and urges to prioritize its conservation and restoration at contemporary climatic refugia.

1. Introduction

From deep-water marine forests to the seaweeds almost inhabiting the boundary of the terrestrial realm, canopy-forming macroalgae play essential roles by providing multiple ecosystem services as “blue forests” (Coombes et al., 2013; Saha et al., 2020; Wahl et al., 2015; Wernberg and Filbee-Dexter, 2019). These foundational species act as ecosystem engineers (*sensu* Jones et al., 1994), and are exposed to numerous climatic and anthropogenic pressures that are leading to significant and widespread changes in their distribution and functional traits (Assis et al., 2017; Casado-Amezúa et al., 2019; Harley et al., 2006; Pessarrodona et al., 2019; Piñeiro-Corbeira et al., 2018). In this context, assessing their conservation status is crucial to preserve their ecological value (Barrientos et al., 2020; Helmuth et al., 2006; Straub et al., 2019).

In cold- and warm-temperate intertidal rocky habitats, brown seaweeds from the order Fucales (commonly known as “fucoids”) are the main foundational species structuring these ecosystems. Several fucoids

have experienced shifts in their distributional ranges towards colder areas in the past decades (Casado-Amezúa et al., 2019; Duarte and Viejo, 2018; Monteiro et al., 2017; Nicastro et al., 2013), significant losses in cover and density (Lourenço et al., 2016), and even long-term decreases in size and reproductive potential have been detected for some species (Riera et al., 2015). Despite fucoids can cope with natural broad fluctuations in abiotic conditions, due to their adaptation to inhabit intertidal areas (Helmuth et al., 2006), several populations are becoming extinct due to the accelerated pace of human-induced global warming and their indirect effects (storms, marine heatwaves, increased herbivory) among other anthropogenic pressures (i.e. coastal eutrophication, trampling, marine invasions) (Dethier et al., 2005; Martins et al., 2019; Rita et al., 2012; Wahl et al., 2015). As a consequence, the positive structuring and functional role that play these organisms on the associated assemblages of marine flora and fauna, are being altered or even eliminated leading to habitat shifts (Coombes et al., 2013; Pessarrodona et al., 2019, 2021; Straub et al., 2019; Watt and Scrosati, 2013).

Yet, climatic refugia are a shining a light into the darkness for

* Corresponding author.

E-mail address: rsdpc@uma.es (R. Sánchez de Pedro).

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Abbreviations

ESAL	Strait of Gibraltar-Alboran Sea demarcation
F_v/F_m	Optimum quantum yield
GBIF	Global Biodiversity Information Facility
GDM	Guadalmesí
IB	Individual bushiness
IL	Individual length
LF	Length to first dichotomy
MPA	Marine protected area
PDG	Piedras Gordas
RGR	Relative growth rate
RH	Receptacle height
RL	Receptacle length
RW	Receptacle width
SAM	San Amaro
SoG	Strait of Gibraltar
SST	Sea surface temperature
STC	Santa Catalina
TRF	Tarifa
WF	Width of frond

biodiversity (Duarte and Viejo, 2018; Hu and Guillemín, 2016; Keppel et al., 2012). They are defined as areas where local and mesoscale effects ameliorate local thermal regimes and create more benign conditions (Ashcroft, 2010; Assis et al., 2016; Lourenço et al., 2016). Several studies have pointed out the positive role of local-scale climatic refugia on the persistence of fucoid populations by allowing them to acclimate and adapt within and across generations to ongoing ocean warming and climatic extreme events (Álvarez-Canali et al., 2019; Lourenço et al., 2016; Verdura et al., 2021). These areas promote higher local abundances of standing biomass and denser canopies (Álvarez-Losada et al., 2020), which enhance the positive cascading effects within their associated communities (Alestra and Schiel, 2015; Ladah et al., 2003; Monteiro et al., 2017; Watt and Scrosati, 2013). Denser canopies do not always provide benefits on their understorey recruits. On the one hand, they can ameliorate abiotic stress and can provide more suitable microclimatic conditions for the development and survival of the most sensitive microscopic stages (Coelho et al., 2000; de Caralt et al., 2020). On the other hand, adult canopy forests might affect negatively recruits' survival via light competition or dislodgment by whiplash (Tamburello et al., 2019).

Climatic refugia for fucoids are directly linked to upwelling areas, since they alleviate thermal extremes and provide nutrient inputs making them highly productive areas (Lourenço et al., 2016, 2020). Nutrients can also increase thermal tolerance in some seaweeds, helping them to endure acute warming events such as marine heatwaves (Colvard and Helmuth, 2017; Gouvêa et al., 2017). In addition, local climatic conditions can be modified by mesoscale effects, such as wave exposure, currents and tidal range (Micheli et al., 2016; Taylor and Schiel, 2003).

The Strait of Gibraltar (SoG) is located between the Iberian Peninsula (Southern Europe) and Northern Africa. In the case of Southern Europe, the SoG shores are one of the five Spanish marine demarcations described in the Spanish Marine Strategy (MITECO, 2018) developed under the Marine Strategy Framework Directive (MSDF; Directive, 2008/56/ES) as "Strait of Gibraltar and Alboran Sea" (ESAL). The ESAL demarcation is recognized as climatic refugia for both terrestrial and marine species, where elements from three marine biogeographical provinces (Lusitanian, Mauritanian, Mediterranean) and the Atlantic-Mediterranean subregion blend conforming a unique biodiversity hotspot (Coll et al., 2010; Flores-Moya et al., 2021; García Gómez et al., 2003; Guerra-García et al., 2009; Rodríguez-Sánchez et al., 2008). However, this area is being threatened by anthropogenic pressures

derived from intensive human activities (Gómez, 2003), for example the increment in coastal artificial substrata (Sedano et al., 2021) and the massive expansion of the invasive macroalgae *Rugulopteryx okamurae* (E. Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (García-Gómez et al., 2020, 2021a).

Fucus guiryi Zardi, Nicastro, E.S. Serrão and G.A. Pearson is a key intertidal fucoid in the ESAL demarcation. This species belongs to an east-Atlantic *Fucus* spp. complex (lineage 2) with a shared evolutionary history (Billard et al., 2010; Prinz, 2021) and distributes from the Canary Islands and Atlantic coast of Morocco to Ireland (Norris and Conway, 1974). Populations of *F. guiryi* from northern shores of the SoG (Tarifa; Fig. 1) correspond to the species *Fucus limitaneus* (Montagne) Montagne (Almeida et al., 2022), which extends from Macaronesia and West Sahara to central Portugal and peripheral populations in the ESAL region (González-García and Conde, 1993; Melero-Jiménez et al., 2017). Within this complex, smaller-size individuals and less dense populations occur towards their peripheral and southern locations (Zardi et al., 2015) but that functional variability actually corresponded to different species based on molecular evidences (Almeida et al., 2022). Nonetheless, at its southernmost distribution limit, *F. guiryi* has experienced significant regressions and decreases in individual size and reproductive capacities, leading to local extinctions except at some climatic refugia (Álvarez-Canali et al., 2019; Ferreira et al., 2014; Riera et al., 2015).

In the SoG, populations of *F. guiryi* harbour a distinct pool of genetic diversity (Almeida et al., 2022), due to its ecological isolation at this relatively small peripheral location. This species is present at both sides of the SoG, at the northern side in Andalusian coasts (Flores-Moya et al., 1995; Guerra-García et al., 2011; Melero-Jiménez et al., 2017), and at the southern side in Ceuta (Spain) and Northern coast of Morocco (Bañares-España et al., 2017; Benhissoune et al., 2002; González-García and Conde, 1993; Ruiz-Tabares et al., 2003; Zardi et al., 2011). However, its presence is restricted to natural rocky substrates (Sedano et al., 2021), which contributes to a low ecological connectivity among populations as occurs for other foundational species (Bermejo et al., 2018; Buonomo et al., 2018). Since geographical and local-site variations have been highlighted as pivotal determinants of the persistence of *F. guiryi* at its southernmost distribution (Álvarez-Canali et al., 2019), local-scale heterogeneity in population, morphological and reproductive ecology traits might also take place among peripheral populations at the SoG, as it occurred at its southernmost limit of distribution (Ruiz-Medina et al., 2023).

In this study we aim to assess the temporal and spatial functional variability of populations of *F. guiryi* at both sides of the SoG to assess its conservation status in this peripheral area within its distribution. Although SoG is close to an upwelling centre and constitutes a potential climatic refugia for this species, we hypothesized that local-scale effects are likely to contribute for intraregional variability on population traits and conservation. To ascertain this, we explored how the presence of this species, and its population traits vary across temporal and spatial scales and how they can be modulated by several environmental variables (i.e., temperature, wave exposure, nutrients). We expected that populations with higher density, reproductive potential and individual size would point out to local-scale climatic refugia within the SoG, which should be prioritized for conservation efforts. Finally, we hypothesize that recruits from south-side populations possess higher thermal tolerance than northern ones, due to their closeness to their upper thermal limits towards the Mediterranean peripheral populations.

2. Material and methods

2.1. Selection and description of survey locations

Sampling points were selected from locations where the presence of *F. guiryi* on SoG was reported in previous studies (Bañares-España et al., 2017; Melero-Jiménez et al., 2017; Ruiz-Tabares et al., 2003) and GBIF occurrences (Fig. 1). Then, we classified the ten surveyed locations into

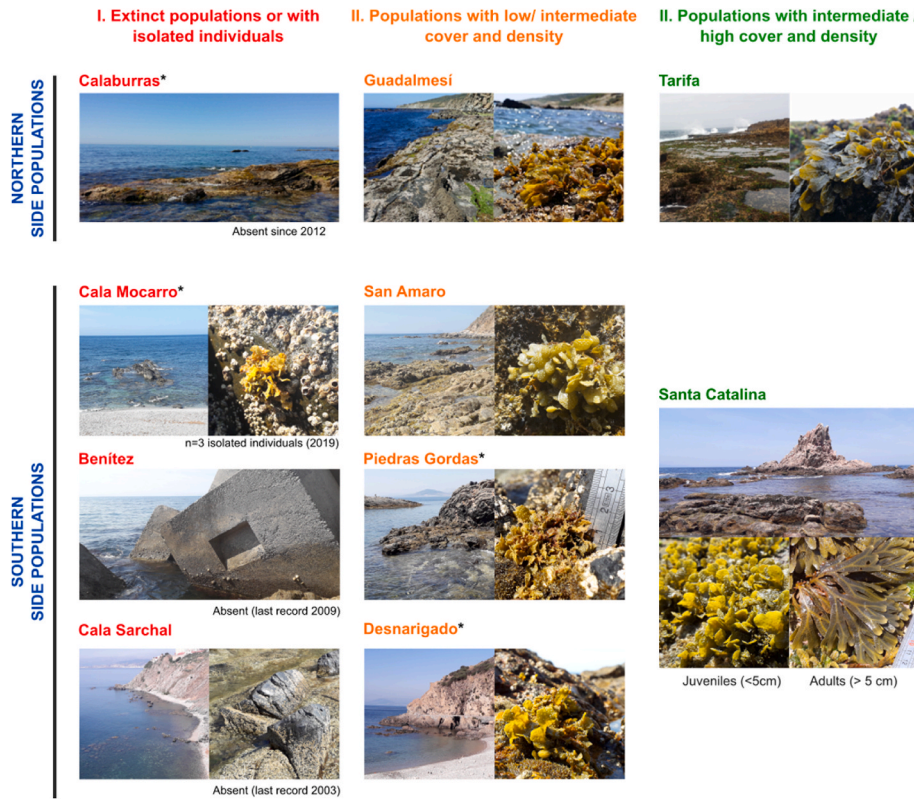


Fig. 1. Surveyed populations of *Fucus guiryi* in the Strait of Gibraltar-Alboran Sea region during 2018–2021 following a preliminary classification based on presence/absence and population cover and density. Pictures show general site landscapes and details on *F. guiryi* habitus when present. For Santa Catalina (Ceuta, southern side) population, areas of high/low density are depicted, as well as juvenile and adult individuals in the area of high density close to the Isle of Santa Catalina.

three conservation status groups, based on the presence/absence of *F. guiryi* and visual assignments population density (continuous belts vs. scattered individuals). The conservation state I was assigned to extinct populations or populations with isolated individuals of reduced size; the conservation state II corresponded to extant populations with low-intermediate density and cover; the conservation state III was attributed to extant populations with intermediate-high density and cover (Figs. 1 and 2). Specifically, we selected a total of five populations from groups II and III: Tarifa (TRF) and Guadalmesí (GDM) in the northern side of SoG, and Santa Catalina (STC), San Amaro (SAM) and Piedras Gordas (PDG) in the southern side of SoG (Fig. 2). All the populations except SAM and PDG, both in the southern side of SoG (Fig. 2), are included in a Marine Protected Area (MPA). This classification let us to evaluate and compare the spatial and temporal change of phenotypic characteristics of *F. guiryi* populations. Additional habitat characteristics for the selected sites are described in detail in Table A1.

2.2. Temporal and spatial variability in functional traits of *F. guiryi*

We compared the demography, morphology, reproductive phenology within each side of the study area (Appendix B, Field survey protocol). Monitoring of population traits (cover, density, size distribution), individual morphology (individual length, IL; length to first dichotomy, LF; width of frond, WF; and individual bushiness, IB) and reproductive phenology (minimum length of a reproductive individual and receptacle length, RL; width RW, and height, RH) was followed during two concatenated time periods in two northern (2018–2019) and three southern (2019–2021) populations of *F. guiryi* in the SoG (Figs. 1 and 2, Table 1). In the southern side, in the population of Santa Catalina two sub-areas were distinguished and sampled accordingly based on population distribution, cover and morphology (Fig. A.1).

To detect spatial patterns of variability in population conservation,

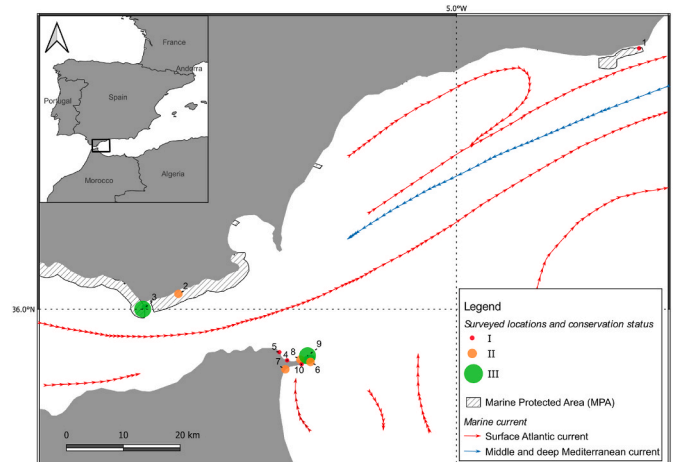


Fig. 2. Map of locations surveyed in the preliminary assignment of the conservation status of populations of *Fucus guiryi* in the Strait of Gibraltar (SoG). Populations are represented with coloured dots corresponding to different conservation status: I (red) extinct populations or populations with isolated individuals of reduced size; II (orange) extant populations with low-intermediate density and cover; III (green) extant populations with intermediate-high density and cover. Dot size was proportional to algal biomass and cover. Hatched filled areas represent marine protected areas (MPAs). Principal marine currents are depicted as blue and red lines (middle and deep Mediterranean and surface Atlantic currents, respectively). Numbers depict populations in the northern side of the SoG [(1) Calaburras (Málaga, Spain); (2) Guadalmesí (Cádiz, Spain); (3) Tarifa (Cádiz, Spain)] and southern side of SoG (Ceuta, Spain) [(4) Benítez; (5) Cala Mocarro; (6) Desnarigado; (7) Piedras Gordas; (8) San Amaro; (9) Santa Catalina; (10) Sarchal].

Table 1

Variables measured during the field surveys at selected locations, indicating frequency of sampling and sample size (quadrats, transects or individuals).

	Variable	Definition	Sampling frequency	Sample size
Population traits	Cover	Percentage of a transect covered by <i>F. guiryi</i>	6 months (spring, fall)	n = 3–4 transects along 20 m of coast fringe
	Individual density	Number of individuals per square meter standardized by cover	6 months (spring, fall)	n = 3–4 quadrats
Individual morphology	Individual length (IL)	Distance from holdfast to the tip of the thallus	3 months	All individuals from 3 to 4 quadrats (variable) in spring/fall samplings and n = 20 in summer/winter samplings
	Individual Bushiness (IB)	Ratio between individual length and maximum circumference	3 months	n = 10 individuals
	Length to first dichotomy (LF)	Distance from the holdfast to the first dichotomy	3 months	n = 10 individuals
	Wide of frond (WF)	Frond width at intermediate distance between first dichotomy and the thallus tip	3 months	n = 10 individuals
Reproductive phenology	Percentage of reproductive individuals	Individuals with receptacles per square meter.	3 months	All individuals from 3 to 4 quadrats (variable) in spring/fall samplings and n = 20 in summer/winter samplings
	Receptacle metrics	Receptacle length (RL), width (RW) and height (RH)	3 months	n = 10 individuals
	Receptacle developmental stage	Stage of development of receptacles: Vegetative thalli – stage I (ST1) Thalli with developing receptacles – stage II (ST2) Thalli with mature receptacles – stage III (ST3)	3 months	All individuals from 3 to 4 quadrats (variable)

the same demographic and morphological variables were compared across populations in early summer 2019, when the timespan of both sampling intervals overlapped. By that time of the year, fucoids maximize their growth and fertility, and their recruits can be more sensitive to warming (Sánchez de Pedro et al., 2022, 2023).

2.3. Contribution of environmental variables on climatic refugia

To detect the relative contribution of local environmental variables on detected local climatic refugia we analysed the influence of sea surface temperature (SST), wave exposure (as wave height) and nutrients (nitrate, phosphate, ammonium) on i) IL and IB and ii) population density from early summer 2019. Monthly mean data for these environmental variables were retrieved for the different sampling points between June 2018 and June 2019 from public open repositories following the methodology described in Appendix C. These oceanographic variables were chosen based on the variables that were more likely to predict the population traits of *F. guiryi* in other warm-temperate locations within its distribution (Álvarez-Canali et al., 2019; Riera et al., 2015; Zardi et al., 2015).

2.4. Thermal physiology of recruits

Recruits of *F. guiryi* were *ex situ* isolated from early summer parental thalli from STC in early summer 2019, following the sampling and laboratory methods detailed by Sánchez de Pedro et al. (2022, 2023). Embryos of *F. guiryi* were exposed to control (15 °C) and warming conditions (25 °C) under laboratory-controlled conditions. Survival, growth, and optimum quantum yield (F_v/F_m) responses were compared 1 day after fertilization by the methods described in Sánchez de Pedro et al. (2022, 2023) for northern recruits from Tarifa in early summer 2018.

2.5. Statistical analysis

Seasonal and spatial variability in functional trait responses of *F. guiryi* were analysed within each side of SoG (northern, southern) and among populations (in early summer 2019) by means of non-parametric Kruskal-Wallis ANOVA, followed by pairwise comparisons when significant results were obtained. This analysis was applied to IL, IB, WF, LF and receptacle metrics (RH, RW, RL), due to unbalanced design and lack of data homoscedasticity.

Reproductive phenology data were analysed by means of permutational multivariate analysis of variance (PERMANOVA), to detect differences in the percentage of receptacles with season and population as factors. To back up interpretations, homogeneity of data was checked by permutational multivariate analysis of dispersion (PERMDISP; Anderson, 2004).

To test the relationship between functional traits of *F. guiryi* and monthly environmental data recorded from June 2018 to June 2019, we applied stepwise conditional linear regression.

To test the differences in physiological performance of recruits we applied *t*-test and factorial ANOVAs with side (northern–TRF, southern–STC) and temperature (15, 25 °C) as fixed factors. Proportional data (survival and relative growth rates) were arcsine-square-root transformed to meet normality assumption. *Post-hoc* Tukey honest significant differences (HSD) analysis were applied when significant ANOVA results were obtained. Data homoscedasticity (factorial ANOVA) or sphericity (repeated measures ANOVA) were tested by Levene or Mauchly tests, respectively.

Non-parametric analyses were performed in IBM SPSS Statistics (version 25) (IBM Corp., Armonk, NY). PERMANOVA and PERMDISP test were performed in R 4.2.0 version using the package *vegan* 2.4–2 (R Core Team, 2017). Time series analyses of oceanographic and biogeochemical variables were made using the function *ts* from package *stats* in R. All graphs and univariate regression analysis were performed in GraphPad Prism 8.0.1. (GraphPad Software, San Diego, California, USA). Stepwise multiple linear regressions were performed and plotted in Python 3.11.2 using *pandas* (McKinney, 2010; Reback et al., 2020), *NumPy* (Harris et al., 2020), *Matplotlib* (Hunter, 2007) and *scikit-learn* (Pedregosa et al., 2011) Python modules.

3. Results

3.1. Population traits

3.1.1. Density and cover

Three distinct groups of populations were identified based on population cover and density comparisons (Table 2): (1) a low cover and density group with GDM and PDG (average cover $4 \pm 3\%$ and density of 15 ± 6 ind. m^{-2}); (2) an intermediate cover and density group with TRF and SAM (average cover $17 \pm 7\%$ and density of 15 ± 6 ind. m^{-2}); and (3) an intermediate cover with high-density group only represented by STC-HD population, which had a population density 2.5 to 9 times

Table 2

Mean ± SD of cover percentage and density of individuals of *Fucus guiryi* from populations of the Strait of Gibraltar (Cádiz, Spain), obtained from n = 4 quadrats and transects. Different superscript letter(s) and asterisks indicate homogeneous groups of data derived from pairwise comparisons for each variable (lowercase, seasonal within northern side; uppercase letters, seasonal within southern side; asterisks, spatial comparisons across all populations in early summer 2019).

Side	Cover (%)						Density (ind. m ⁻²)					
	Northern			Southern			Northern			Southern		
	Population	TRF	GDM	STC-LD	STC-HD	SAM	PDG	TRF	GDM	STC-LD	STC-HD	SAM
SP18	14 ± 8 ^{abc}	7 ± 3 ^{abc}	–	–	–	–	77 ± 23 ^a	35 ± 15 ^{ab}	–	–	–	–
F18	16 ± 5 ^c	7 ± 2 ^{ab}	–	–	–	–	49 ± 24 ^{ab}	28 ± 13 ^{ab}	–	–	–	–
ES19 ^a	15 ± 7 ^{bc*}	6 ± 4 ^{a**}	n.d.	21 ± 8 ^{A*}	16 ± 7 ^{A*}	2-9 (!)	39 ± 16 ^{ab*}	15 ± 11 ^{b**}	n.d.	137 ± 23 ^{A*}	76 ± 31 ^{C***}	40 ^{**}
F19	–	–	11 ± 3	20 ± 6 ^A	14 ± 8 ^A	–	–	–	51 ± 19	67 ± 30 ^B	42 ± 10 ^D	–
SP21	–	–	9 ± 2	n.d.	Disperse	Disperse	–	–	79 ± 22	n.d.	Disperse	Disperse

Abbreviations: TRF–Tarifa, GDM–Guadalmesí; STC-HD–Santa Catalina high density, STC-LD–Santa Catalina low density, SAM–San Amaro, PDG–Piedras Gordas; SP–Spring, ES–Early summer, F–Fall. (!) Data from Bañares-España et al. (2017). No data (n.d.)

^a Kruskal-Wallis ANOVA, Cover: $X^2_{(17,4)} = 14, P = 0.007$; Density: $X^2_{(14,3)} = 8.1, P = 0.04$.

greater than the other populations from the SoG in early summer 2019, confirming the *a priori* visual classification (Fig. 1).

Population density in the northern side ranged from 15 to 77 ind. m⁻² (Table 2). Differences in cover between northern populations arose after fall 2018, due to a significant decrease in cover in GDM (Table 2). Within each population, no significant effect of seasonality was detected. In the southern side, density of *F. guiryi* at STC was ca. 1.7-times higher than at SAM (two-way ANOVA, $F_{1,8} = 8.91, P = 0.02$). Both populations reached their maximum growth by the end of the summer (two-way ANOVA, $F_{1,8} = 13.1, P < 0.01$). Algal cover did not differ across populations or samplings, ranging from 9 to 21% (Table 2). An exception was detected at PDG population, which presented lower cover with disperse individuals in a patchy distribution. In fact, during the sampling of fall 2019 it was not possible to apply the quadrat method due to the drastic reduction in cover and density at PDG, and the same occurred at SAM in spring 2021 (Table 2). The STC-HD area was not possible to sample in spring 2021 due to high-speed tidal currents in the area that did not allow to cross to the Isote Ileo (Fig. A.1).

3.1.2. Population structure

Northern populations differed in their size hierarchy distribution at all seasons (Fig. D.1). At TRF, 70% of individuals were within the 2–6 cm size class, and a few specimens reached the highest one (12–14 cm). For

size classes 6–12 cm, there was a significantly higher percentage of individuals at the Tarifa population, while at GDM, there was a predominance of the individuals below 4 cm. Both populations showed parallel changes in individual size distribution between populations, denoting a similar seasonal trend (Fig. D.1).

Population size structure in the southern side was only possible to assess in STC and SAM. At STC-HD, a clear shift in population structure was observed from early summer to fall 2019, indicating a growth of the individuals. Juvenile size range (0–2 cm) was not detected in spring 2021, while some individuals reached up to sizes of 14 cm. At STC-LD, most individuals had sizes between 4 and 10 cm, while at STC-HD most of them were above 8 cm (Fig. D1). In spring 2021, STC-LD showed a higher percentage of individuals between 2 and 4 cm, and less than 10% of them reached size classes above 8 cm. Population structure at SAM did not show a clear normal distribution as that found at STC. Between early summer and fall 2019, only a small fraction of individuals reached the 10–12 size class, while the percentage of juveniles kept constant. In spring 2021, data were inferred from single individual measurements instead of quadrat samplings, but size distributions were like the previous ones (Fig. D.1).

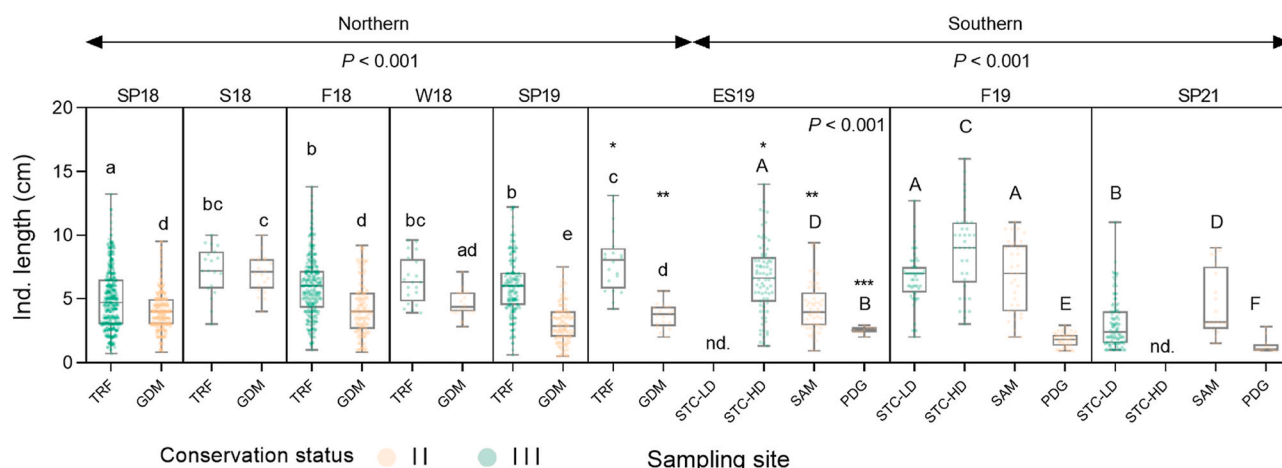


Fig. 3. Individual length of *Fucus guiryi* thalli from populations at the Strait of Gibraltar. In boxplots, boxes indicate the lower and upper 1.5 IQR (interquartile range) and whiskers represent min to max values. Data exceeding these limits are considered as outliers. Different letter(s) and asterisks indicate homogeneous groups among seasons and populations derived from pairwise comparisons (lowercase–northern populations; uppercase–southern populations; asterisks–comparisons across all populations in ES19). P-values from ANOVA analyses within side (N, S) and between sides (N vs. S in ES) are shown. Abbreviations and sample sizes in spring and fall samplings (N): TRF–Tarifa (N = 169–353). GDM–Guadalmesí (N = 161–353); STC-HD–Santa Catalina high density (N = 37–77), STC-LD–Santa Catalina low density (N = 54–99), SAM–San Amaro (N = 35–54), PDG–Piedras Gordas (N = 10–45); SP–Spring, ES–Early summer, S–Summer, F–Fall, W–Winter. n. d.–no data. S and W samplings had a sample size of N = 20. Conservation status represents extant populations with low-intermediate density and cover (II, light orange dots) and extant populations with intermediate-high density and cover (III, light green dots).

3.2. Individual morphology

Fucus guiryi from the SoG presented wide variations on its morphology among populations (Figs. 3 and 4). Thalli from TRF and STC showed the longest individuals, but at STC thalli had also wider fronds (Figs. 3 and 4). Individuals from these two populations were 2-times longer than those from GDM or SAM (Fig. 3), while individual bushiness (ratio length: maximum circumference) followed the opposite trend (Fig. 4). Length to the first dichotomy (LF) was greater at the northern than at the southern side, with maximum LF at GDM (Fig. 4). Minimum values for all morphological variables except IB were all detected at the most meridional population of PDG (Figs. 3 and 4). Individuals of *F. guiryi* from TRF had higher length than at GDM within the study period (Kruskal-Wallis ANOVA, $H_{1598,11} = 359$; $P < 0.0001$), except in summer 2018 (Fig. 3). Individual length increased from spring to summer in 2018 (growing period) and decreased from summer to fall in 2018 (decay of receptacles). Individual length ranged from 1.9 to 12.7 cm at TRF and from 0.9 to 9.1 cm at GDM (Fig. 3). Despite minimum IL were similar between populations, specimens from TRF had significantly higher median, mean and maximum IL (Fig. 3).

Individual length also differed among southern populations (Kruskal-Wallis ANOVA, $H_{445,9} = 232$, $P < 0.001$), with maximum IL at STC-HD at both 2019 samplings (Fig. 3). In fall 19 thalli from this area were significantly longer than in the low-density area or in the nearest population of San Amaro (Fig. 3). Individuals from STC-LD and SAM showed similar lengths in 2019 but they were smaller in STC-LD in spring 2021. Individual length from *F. guiryi* at the most Mediterranean-influenced population (PDG) was ca. 60% lower than in the other populations and it experienced a significant decrease over the period of study (Fig. 4). Individuals with lengths below 3 cm were observed at different microhabitats: continuous patches on horizontal rocky substrates, rock crevices (Fig. A.2) or shaded vertical rocks. In a complementary analysis we compared the morphology of PDG individuals from these three microhabitats in fall 2019, when they became fertile (Appendix E). Herein, we detected that thalli of *F. guiryi* from continuous patches growing on horizontal surfaces were longer than those growing on rock crevices or horizontal rocky platforms (Table E1). Given such microscale variability, only metrics from individuals from continuous patches were included in the population comparison.

Individual bushiness (IB) was higher for individuals from Tarifa in spring (TRF: 1.5 ± 0.4 cm; GDM: 0.8 ± 0.2 cm) (K-W ANOVA, $H_{97,4} = 48.7$, $P < 0.001$). In fall, 25–52% of individuals from GDM experienced severe breakage of apical fronds, after a period of intense wave action and extreme air summer temperatures between 41 and 45 °C, which constrained the measure of all the morphological variables (Fig. A.2). No seasonal or population differences were detected in the distance to the first dichotomy (LF, mean pooled value 1.34 ± 0.52 cm) and the width of the apical frond (WF, mean pooled value 1.07 ± 0.15 cm) (Fig. D.2).

In southern populations, seasonality and site had a significant effect on the length and width of fronds but not in IB (Fig. D.2). Maximum LF values were found at SAM and STC-LD in spring 2021, followed by STC-HD in fall 2019 (Fig. D.2). Width of the apical frond was similar among populations, except for its maximum in STC-HD (early summer 2019) and minimum at PDG (fall 2019). Among the microhabitats identified at PDG (Appendix E), individuals from continuous patches had wider fronds but lower individual bushiness. Given their reduced size it was not possible to measure these variables at PDG in spring 2021.

3.3. Reproductive phenology

3.3.1. Percentage of reproductive population

The period of reproductive peak (highest percentage of population individuals with mature receptacles) differed among populations, with a first group of “summer bloomers” including the northern populations and SAM and a second group of “fall bloomers” comprising the rest of southern populations (Fig. 5). Individuals from TRF reached the

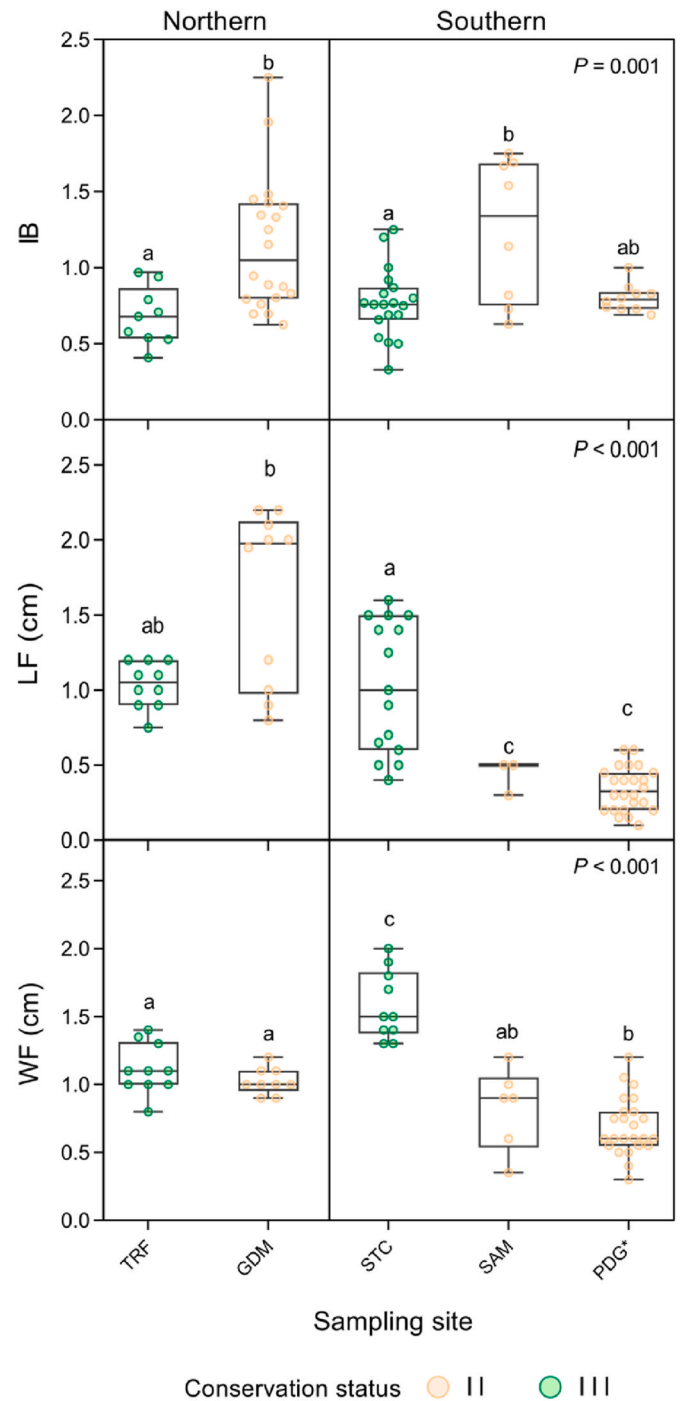


Fig. 4. Thallus morphology of *Fucus guiryi* from five populations at the Strait of Gibraltar. In boxplots, boxes indicate the lower and upper 1.5 IQR (interquartile range) and whiskers represent min to max values. Individual bushiness (IB), length of the frond between the holdfast and the first dichotomy (LF), width of apical frond (WF). P -values from ANOVA analyses are shown. Different letter(s) indicate homogeneous groups among populations derived from pairwise comparisons. Abbreviations and sample size (N): TRF–Tarifa (N = 10), GDM–Guadalmés (N = 9–20), STC–Santa Catalina (10–19), SAM–San Amaro (N = 3–8), PDG–Piedras Gordas (N = 10–24). Asterisks indicate that data of PDG were from F19 due to the reduced size found in ES19. Conservation status represents extant populations with low-intermediate density and cover (II, light orange dots) and extant populations with intermediate-high density and cover (III, light green dots).

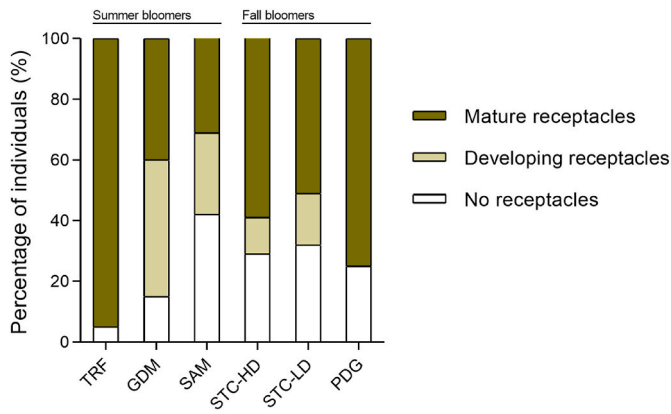


Fig. 5. Percentage of individuals of *Fucus guiryi* from five populations of the Strait of Gibraltar reaching each stage of receptacle development. Populations have been grouped by the season in which the maximum percentage of fertile individuals was detected (ES19 or F19). Abbreviations: TRF–Tarifa, GDM–Guadalmesí, STC-HD–Santa Catalina (high density), STC-LD–Santa Catalina (low density), SAM–San Amaro, PDG–Piedras Gordas.

maximum percentage of individuals with mature receptacles among all populations (Fig. 5). Within each group of populations, no significant differences were detected in the development of receptacles. Populations of *F. guiryi* were iteroparous, except for GDM with only summer mature receptacles and PDG whose individuals only showed visible and highly reduced receptacles in fall 2019 (Fig. A.2).

Percentage of individuals reaching each reproductive stage followed a similar trend at both northern populations, with developing receptacles throughout the year, with a reproductive peak in summer and a high percentage of developing receptacles in winter (Fig. D.3). However, TRF had a significantly higher percentage of individuals with mature receptacles than GDM in early summer 2019 (Fig. D.3). In the southern side, the greatest percentage of mature individuals was found at STC. For the rest of populations, a higher percentage became more fertile in fall than in summer, indicating a reproductive peak shift from summer to fall. This trend was also observed in the significant increase of the proportion of mature apices from summer to fall 2019 at STC-HD (see section 3.3.2). However, heavy marks of apical grazing by that time of the year suggested that these data might be underestimated (Fig. A.2).

3.3.2. Receptacle developmental stage

The proportion of apices reaching maturity was compared among populations during their respective periods of maximum fertility (Fig. D.4). Populations of TRF and STD-LD were the ones with a significantly higher proportion of apices bearing mature receptacles (Stage III, ST3) (Fig. D.4).

At seasonal scale, we found that less than 40% of apices from TRF reached maturity (ST3) regardless of season (Fig. D.5). During the fertility peak of early summer 2018, we did not find differences in the proportion of mature apices between northern populations, but a higher proportion of developing receptacles was detected at TRF. In contrast, a marked difference was noted between both populations in early summer 2019: specimens from TRF had almost 4 times greater proportion of mature apices (Figure D5). At southern populations, both areas of STC (HD and LD) reached similar proportion of individuals reaching ST3 with also similar proportion of apices with mature receptacles (Fig. D.3, Fig. D.4). Nonetheless, at STC-HD less individuals bared multiple mature receptacles, probably linked to the grazing of apices by herbivores (Figs. D.6, A.2). In SAM population a distinct reproductive phenology was detected in 2019 from early summer to fall, where the percentage of individuals with mature receptacles decreased from 25% to c. 10% but an increase in developing receptacles occurred (Fig. D.3). By contrast, the proportion of apices at each stage was maintained between samplings (Fig. D.6). In spring 2021, 20% of individuals had receptacles

(developing or mature) but these presented a highly variable proportion of fertile apices as denoted by the scattered data (Fig. D.6). Individuals from PDG only presented receptacles in fall 2019, when 70% of individuals had fertile receptacles (Fig. 5).

3.3.3. Receptacle metrics

The receptacle size varied among populations of *F. guiryi* and

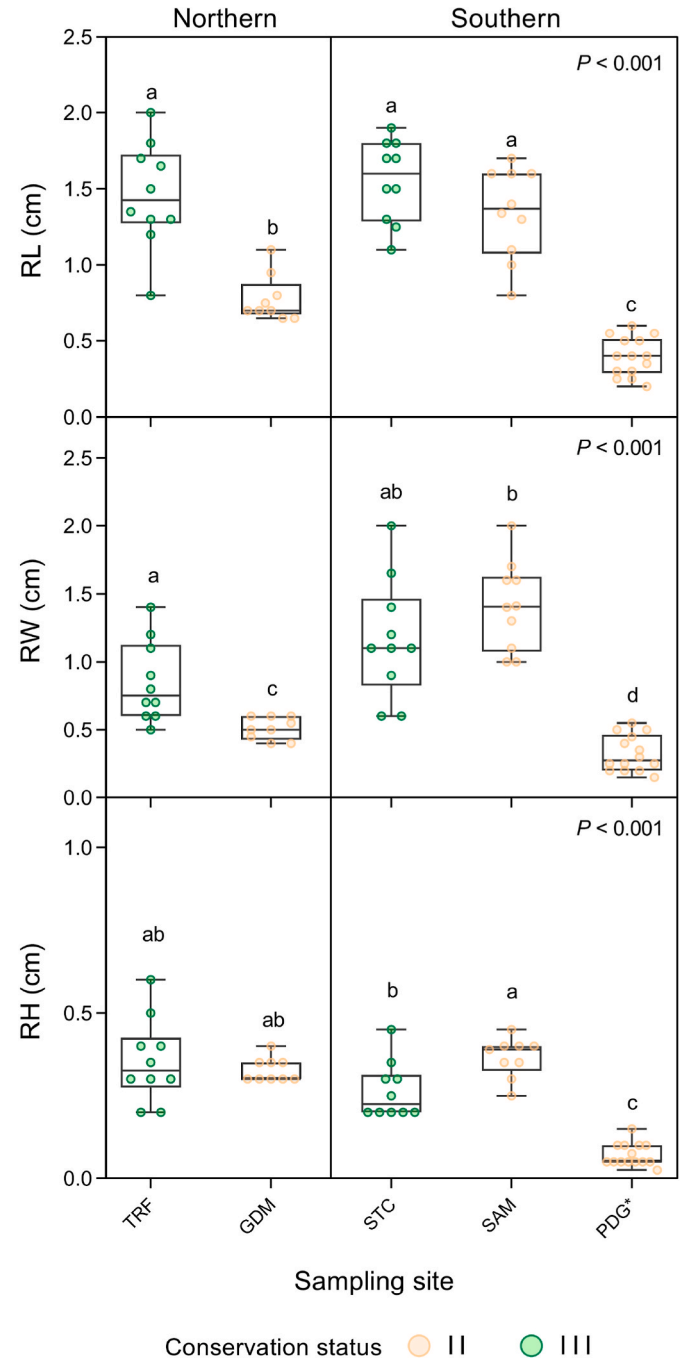


Fig. 6. Receptacle length (RL), width (RW) and height (RH) of *Fucus guiryi* from northern and southern populations at the Strait of Gibraltar. P-values from ANOVA analyses are shown. Letters indicate homogeneous groups among data within each receptacle metric. Abbreviations: TRF–Tarifa, GDM–Guadalmesí, STC–Santa Catalina, SAM–San Amaro, PDG*–Piedras Gordas. Asterisk indicates that individuals from PDG were only fertile in fall 2019. Conservation status represents extant populations with low-intermediate density and cover (II, light orange dots) and extant populations with intermediate-high density and cover (III, light green dots).

followed similar trends than thallus morphology (Fig. 6). Individuals from TRF and STC showed similar receptacle size, followed by a second group with SAM and GDM and the extremely reduced receptacles from PDG (Fig. 6). Among the three examined microhabitats in PDG, individuals from continuous patches on horizontal rocks had bigger (RL, RW) but less thick (RH) receptacles (Table E1). In northern populations, receptacles from GDM experienced a 50% decline in length and width during the study period, while those from TRF did not vary (Fig. D.7). On the contrary, receptacle metrics at southern populations did not follow a clear site or seasonal pattern (Fig. D.7). Receptacles from STC-HD had maximum length and width but similar height than in the other populations, and they decreased by 25 and 50% from early summer to fall 2019, denoting receptacle decay (Fig. D.7). At STC-LD, an increase in receptacle size was detected between fall 2019 and spring 2021 (Fig. D.7). Since SAM population was surveyed at all seasons, both changes in receptacle size were detected (Fig. D.7). PDG showed receptacles below 0.5 cm length and width and 0.1 cm in height (Fig. 6).

3.4. Multiple linear regression with environmental variables

The individual length of *F. guiryi* at the SoG was weakly but significantly explained by the maximum SST of July of the previous year and the mean wave height in October (Table D1). The individual bushiness was weakly but significantly affected by the maximum SST of the coldest month (Table 3, Figure D.8). Populations exposed to higher winter temperatures promoted IB (Table 3, Figure D.8). The coefficient of multiple determination indicated that population density was negatively affected by higher values of mean SST of February and maximum SST in July, which explained 77% of variance of the data (Table 3, Figure D.8). It should be noted that nutrient concentrations (ammonium, nitrate, phosphate) did not explain any spatial variations detected in any of the three variables examined (Supplementary Data 1).

3.5. Thermal tolerance of recruits (northern vs. southern)

Recruits from the southern population of STC presented similar zygote size than those from TRF in early summer 2018 but showed 1.4-times higher optimum quantum yield (Table 4). Warming conditions significantly promoted embryo elongation after 14 days by 10% in southern recruits, while yielded negative effects on the elongation of northern recruits (Table 4). As a result, under control conditions (15 °C) northern recruits outperformed southern ones with almost twice the relative growth rates (RGR). On the contrary, under warming conditions (25 °C), southern recruits had 2.3 times higher relative growth rates than northern ones, and these rates did not differ from the obtained at 15 °C. Differences in survival between populations were similar than for RGR at 15 °C after two weeks of culture. While 100% of northern recruits were able to survive under cold conditions, only nearly half of southern recruits could survive. Although survival decreased by 43 and 18% in northern and southern recruits from 15 to 25 °C (Table 4), no differences were detected between populations at 25 °C (Table 4).

Table 3

Stepwise Multiple Linear Regression analysis of population traits of *Fucus guiryi* and environmental conditions (mean, minimum and maximum SST and wave height) during the previous 12 months.

Variable	Predictor	Coefficient \pm SE	β \pm SE	Relative importance	R ²	F	t	P
Individual length	Intercept	203 \pm 54.7			0.20	22.34	3.71	<0.0001
	SST _{max} hottest month (Jul)	-9.3 \pm 2.5	-1.01 \pm 0.27	70%			-3.70	0.0003
	Wave height _{mean} (Oct)	-12.2 \pm 5.5	-0.60 \pm 0.27	25%			-2.22	0.028
Individual bushiness	Intercept	-4.4 \pm 1.43			0.17	18.07		<0.0001
	SST _{max} coldest month (Jan)	0.32 \pm 0.09	0.42 \pm 0.11	-			3.10	0.004
Population density (Log-transformed)	Intercept	51.25 \pm 7.86			0.77	23.58	6.52	<0.0001
	SST _{mean} coldest month (Feb)	-2.26 \pm 0.34	-1.64 \pm 0.24	64%			-6.71	<0.0001
	SST _{max} hottest month (Jul)	-0.71 \pm 0.14	-1.21 \pm 0.25	35%			-4.96	<0.0001

β , total effect of the predictor variables; R², coefficient of multiple determination.

4. Discussion

Our study revealed a wide heterogeneity in the conservation status of *F. guiryi* among the populations at the SoG, based on different spatial and seasonal patterns in population traits and reproductive phenology. Northern vs. southern differences were not detected among these traits, but they were found in the distinct thermal physiology of recruits, with a warmer affinity towards south-eastern. Local-scale processes are pivotal for the persistence of this species at its peripheral distribution, positively influenced by lower temperatures during the hottest month and lower wave height in fall. According to our initial hypothesis, only the populations of TRF and STC would represent present and long-term climatic refugia, with individuals from STC showing the highest thermal tolerance. The conservation status and detected climatic refugia from our study provide a solid basis for the consideration of *F. guiryi* as an endangered species and will help to prioritize areas for its preservation at its south-eastern peripheral distributional range.

Regarding the complexity of the sampling design and limitations in the data acquisition, we opted for a classical frequentist approach (random data, fixed parameters) for the analysis of data by applying non-parametric analyses. The main limitation derived from them is that this approach might have not captured all the variation in the data, and the unbalanced design might have impaired the analyses. Alternatively, in this multi-trait framework we might have also adopted a Linear Mixed Model (LMM) or a Mixed Model for Repeated Measures (when season was included as a factor) (Zuur et al., 2007). That approach with fixed data and random parameters helps to deal with unbalanced and incomplete data sets. This would be of particular interest since there was some sort of clustering among the studied locations, that supported the classification made from *in situ* direct observations (Fig. 1) and will be considered in future designs.

4.1. Spatial and seasonal patterns in populations traits and reproductive phenology

Fucus guiryi has experienced a marked regression in its distribution in the last 20 years, as reported for other areas, including local extinctions, attributed to climatic and anthropogenic pressures (Lourenço et al., 2016; Martins et al., 2019; Riera et al., 2015). In the actual distributional limit at the northern side, Punta de Calaburras (Mijas, Málaga), the presence of *F. guiryi* was modulated by meteorological changes driven by the North Atlantic Oscillation (Melero-Jiménez et al., 2017), but it disappeared since 2012 being its current distribution limited to Punta Carnero (Tarifa, Cádiz, pers. obs.). In the southern coast of ESAL, its presence was reported at multiple locations in the early '00s (Benhis-soune et al., 2002; Riadi et al., 2000), and more recently (2012–2014) at Al-Hoceima National Park (Morocco), together with the data provided by our study. In addition, we confirmed that *F. guiryi* became extinct or drastically reduced at several previously reported populations in Ceuta (Fig. 1) (Ruiz-Tabares et al., 2003).

The individual sizes measured in our study were consistent with

Table 4

Physiological and morphological traits of zygotes and 2-week-old embryos of *Fucus guiryi* at control (15 °C) and warming (25 °C) conditions, harvested from northern (Tarifa, Sánchez de Pedro et al., 2022; 2023) and southern (Santa Catalina, Ceuta, this study) populations at the Strait of Gibraltar, during the period of maximum fertility (northern – June 2018, southern – June 2019). Asterisks indicated significant differences for each variable (Student *t*-test for F_v/F_m and zygote size and ANOVA analyses for the rest of variables analysed, $P < 0.05$).

	Zygote F_v/F_m	Zygote size (diameter, μm)	2-week embryo length (μm)		RGR (% d^{-1})		Percentage of survival (%)	
Temperature (°C)	Initial	Initial	15*	25*	15*	25*	15*	25
Northern ^a	0.32 ± 0.1	71.1 ± 3.8	170 ± 5	90 ± 1.3	6.1 ± 0.20	1.6 ± 0.2	100 ± 0	57 ± 34
Southern	0.44 ± 0.1	72.7 ± 10.2	111 ± 12	122 ± 14	3.3 ± 0.9	3.7 ± 0.9	45 ± 24	27 ± 18

Optimum quantum yield (F_v/F_m). Relative growth rate (RGR).

^a Data calculated from supplementary data of Sánchez de Pedro et al., 2023; Sánchez de Pedro et al. (2022).

those reported by Zardi et al. (2015) and also specimens from the Canary Islands (Álvarez-Canali et al., 2019; Niell et al., 1987; Riera et al., 2015). The population density and the minimum length of reproductive individuals from all SoG populations were around the mean values detected for *F. guiryi* in the Portuguese coasts, as well as the density of the reproductive population. Only for IB, individuals from the northern side (TRF, GDM) reached higher values than for southern east Atlantic *F. guiryi*. These comparisons indicate a consistent mean morphology and similarities in population traits across its distributional range except at peripheral and less conserved populations that show drastic local declines (Riera et al., 2015; Álvarez-Losada et al., 2020; This study). Also, they suggest the existence of local-scale climatic refugia at TRF and especially at STC-HD, since population densities and individual sizes were higher than it could be expected at its latitudinal range. Local conditions might explain largely such ecomorphological differentiation, including the distinct warming-affinity of their recruits, given the wide phenotypic plasticity that *Fucus* species exhibit (Cairrão et al., 2009; Niell et al., 1987; Wahl et al., 2011).

We observed that most of the populations examined followed the expected seasonal trends in population dynamics for temperate macroalgae (Hurd et al., 2014; Lüning, 1990). Growing season was detected from winter through summer followed by a decay of receptacles towards fall, based on the lower percentage of mature individuals, percentage of apices with mature receptacles and receptacles size.

The reproductive phenology of *Fucus* greatly varies among latitudes and species (Graiff et al., 2017; Hatchett et al., 2022; Viejo et al., 2011). As reviewed by Hatchett et al. (2022), lineage 2 of *Fucus* (which includes *F. guiryi*) has its reproductive peak in spring-summer. Atlantic populations from the southern side of SoG (northern Ceuta Bay, Fig. 2), as well as populations from the northern side agreed with that pattern, as they were iteroparous (presented mature oogonia over the year), as it was confirmed by successful fertilization at TRF and STC over that period (Sánchez de Pedro et al., 2023; Sánchez de Pedro et al., 2022). In contrast, the two most peripheral populations towards the Mediterranean (PDG, DNG, southern Ceuta Bay, see Fig. 1) had a distinct pattern in the reproductive phenology, since they were semelparous and shifted their reproductive peak from summer to fall. Peripheral populations of *Fucus* species experience changes on their reproductive phenology, commonly shifting from sexual to asexual populations (Hatchett et al., 2022; Tatarenkov et al., 2005). For marginal populations of *F. guiryi*, we hypothesize that such reduction in the time window of reproductive season might be a previous step towards an asexual population, as it reduces energy investment and resources allocation for reproduction. Following the line of reasoning of Hatchett et al. (2022), the selection of warm-resistant phenotypes might be advantageous for the maintenance of the population in the long term, considering the functional losses already experienced by them, and it provides a pivotal information to design cost-effective restoration strategies.

Reproductive peaks in *F. guiryi* in the SoG coincided with the period of higher thermal stress. At evolutionary scale, this might represent an ecological strategy of “bet-hedging” (sensu Furness et al., 2015), where the risk of mortality is compensated by an increase in the number of recruits. This mechanism might increase the biological efficacy of

recruitment by increasing the abundance of genotypes that might by chance survive harsher abiotic conditions, which has been reported in other Fucales (Al-Janabi et al., 2016). The detected shift of the reproductive peak towards fall would imply that gametogenesis occurred during summer. This is congruent with our previous studies (Sánchez de Pedro et al., 2022) where we observed that late summer recruits acquired thermal-tolerance via “warm-hardiness” during gametogenesis. In this line of reasoning, we conjecture that the detected shift might represent an adaptive advantage to persist towards its climatic extremes at peripheral locations. This would be of particular relevance in populations where canopy might not significantly reduce understorey abiotic conditions due to their low densities (i.e., PDG, SAM), contrary to what occurs in areas where dense canopies ameliorate such conditions for *F. guiryi* recruits (Monteiro et al., 2017; Sánchez de Pedro et al., 2019). On the other hand, energetic investment in reproductive effort over the less favorable period would probably be at expense of parental growth (Roleda et al., 2007). We hypothesize that if this process is sustained over time it might lead to a negative feedback between reproduction and morphology that may explain the rise of smaller morphotypes and miniaturization of *F. guiryi* in peripheral populations within its distribution (Ruiz-Medina et al., 2023). For other warm-temperate seaweeds, these concomitant losses in morphological and reproductive traits have indeed been linked to climate change (Alfonso et al., 2022).

4.2. Effect of environmental and local-scale variables on population traits

The SST and wave height were the variables which primarily drove the populations traits of *F. guiryi*, being in accordance with those detected at other areas (Álvarez-Canali et al., 2019; Martins et al., 2019; Riera et al., 2015; Zardi et al., 2015). Although favorable conditions for the persistence of *F. guiryi* occur around stable or intermittent centres of upwelling (Lourenço et al., 2016), smaller scale variations in population traits seem to be dominated by local-scale variations in wind direction, topography, currents, biotic factors (Álvarez-Canali et al., 2019; Martins et al., 2019; Ruiz-Medina et al., 2023). These factors can ameliorate extreme emersion stress conditions by maintaining thalli moistened for longer periods at low tide, apart from the positive role of nutrient supply on their thermal tolerance (Colvard and Helmuth, 2017; Sánchez de Pedro et al., 2023).

Our study demonstrated that temperature and wave height had differential effects depending on the trait. Populations with shorter individuals and lower population densities occurred at sites with higher SST during the hottest month and higher wave height in autumn. Northern populations, despite being c. a. 8 km apart, show marked differences in their microclimatic conditions that might explain the detected heterogeneity in their population traits. In July 2018 *F. guiryi* from the northern side experienced thermal extremes c. a. 10 °C above the upper thermal limits reported for furoids (Bennett et al., 2018) (*in situ* air summer temperature in July 2018: 45.6 °C at GDM-data not shown; 40.6 ± 4.1 °C at TRF, Sánchez de Pedro et al., 2023, Sup. Info). Such variations might be attributed to the differences in community assemblages between them (Table A1). The Tarifa site harbours a richer

and more diverse benthic assemblage (Guerra-García et al., 2011), while at GDM, the substrate had a much higher proportion of bare rock (Fig. 1, Table A1). These thermal extremes are likely to have damaged apical fronds at GDM, which followed by fall wave action would explain the severe losses in individual length and reproductive structures at this population (Fig. A.2), similar to the damage observed for *F. serratus* from coastal open stretches in the north of Spain (Duarte and Viejo, 2018). Although intertidal seaweeds commonly confront strong hydrodynamism (D'Amours and Scheibling, 2007; Hurd, 2000), its climate-drive intensification might impose a threat to their conservation (Grilo et al., 2011; Micheli et al., 2016).

The inverse effect of maximum winter temperature on IB and population density might be explained by self-thinning effects (Karez, 2003). Individual bushiness was positively influenced by warmer winters, but this increase in IB might prevent small juveniles to reach higher size classes and thus, decrease population density. This fact would be supported by our population structure data from northern populations, since the percentage of individuals from the lower-class size did not largely vary over our study. Also, in a previous work (Sánchez de Pedro et al., 2023), we suggested the physiological benefit of warmer winter temperatures on the growth of recruits of *F. guiryi*, which would be in accordance with its warm-temperate biogeographical distribution (Almeida et al., 2022).

The better status of conservation of *F. guiryi* at TRF and STC might be also related to their location inside MPAs (Table A1). Human trampling negatively affects density and cover of seaweeds acting synergistically with wave action (Bertocci et al., 2012; Micheli et al., 2016). Trampling is common due to recreational activities in accessible intertidal areas, and in some furoid it has caused long-term changes in population structure (Keough and Quinn, 1998; Rita et al., 2012; Schiel and Taylor, 1999). The contrasting conservation status between close populations in our study might be to a certain extent due to their different accessibility. Despite northern populations are both inside an MPA (Fig. 2, Table A1), TRF is placed on a military facility at Isla de las Palomas with restricted access (Guerra García et al., 2000). In the southern side, STC is located inside a Natura 2000 Site of Community Importance and a few kilometres away from the city of Ceuta, while SAM is outside that MPA and more exposed to anthropogenic impacts (Fig. 1, Table A1). Santa Catalina was classified within the coast of Ceuta as an area of intermediate ecological vulnerability based on species composition 20 years ago (Ruiz-Tabares et al., 2003), while nowadays it represents one of the more pristine areas.

Our study detected microhabitat variability between areas from the same population (STC-HD and STC-LD, Fig. A.1) distanced 60 m apart and even at smaller scales among different microhabitats (PDG, Appendix E). Individuals around the “Islote Ileo” (STC-HD) represented a microrefugia with the most suitable conditions for the persistence of *F. guiryi* within the SoG, based on the maximum values of population density, and individual morphometry. This area is less accessible and thus less impacted by human trampling, but also, it has a unique and complex local hydrodynamism and local topography that creates strong tidal currents around the Islote Ileo. The presence of a steep vertical wall of 60 m depth in front of this zone facilitates a strong upwelling of the deep Mediterranean current (Ocaña et al., 2009). Future studies should measure microhabitat conditions in this area to ascertain the relative influence of natural and anthropogenic stressors on population traits.

4.3. Warm vs. cold affinities between southern and northern recruits from the SoG

Our study evidenced a warm-affinity increase in recruits of *F. guiryi* towards the southern-eastern of Strait of Gibraltar, indicating a meso-scale pattern in thermal tolerance. Their similar survival at warming conditions but higher growth capacity and lower physiological stress in southern recruits might explain the better conservation status of STC. Nevertheless, this upper thermal niche filling occurred at the expense of

a cold-performance loss. Intraspecific differences in thermal tolerances have been reported in furoids at larger latitudinal ranges (García et al., 2021; Jueterbock et al., 2014; Pearson et al., 2009). However, based on the low distance between our populations, we suggest that the enhanced thermal-tolerance might be due to the influence of local factors such as nutrients (Colvard and Helmuth, 2017), microclimatic conditions (Monteiro et al., 2017), or even the existence of distinct genotypes due to their ecological isolation (Al-Janabi et al., 2016). Furthermore, the higher canopy at the southern population might contribute to ameliorate the microscale conditions at low tides for their recruits (Monteiro et al., 2017). We previously suggested that seasonal environmental parental history might influence thermal tolerance of *F. guiryi* recruits (Sánchez de Pedro et al., 2023), a hypothesis that would be reinforced by the results from this study at spatial scale: recruits from parents exposed to less disrupting stressors can become more thermotolerant.

4.4. Opportunities and challenges to the conservation of *F. guiryi*

Microclimatic conditions ameliorate or exacerbate global climatic warming leading to “climate refugia” or “climate hotspots” (Nadeau et al., 2022). Here we identified two local-scale climatic refugia (TRF, STC) and three climate change hotspots (PDG, GDM, SAM). Since extreme climatic events are increasing because of climate change, particularly towards the Mediterranean (Garrabou et al., 2022), populations dynamics of *F. guiryi* might be drastically reduced at populations with lesser conservation status. The reported functional losses detected during our study denoted an ongoing process of regression at extant populations. At these “climatic hotspots” there would be the urgent necessity to assess, monitor and ameliorate local and climatic impacts and characterize and preserve their distinct genetic structure given their high risk of extinction. Nevertheless, the long-term persistence of microscopic life stages in apparently extinct populations might be possible, according to the reappearance of *F. guiryi* at populations from southern Portugal after 20 years (Prinz, 2021), as well as its intermittent presence in northern Alboran Sea (Melero-Jiménez et al., 2017).

Indirect effects of climate change and anthropogenic stressors also have a prominent impact on the widespread losses of marine forests (Coombes et al., 2013; Faria et al., 2022; Oliveira et al., 2015; Rijstenbil et al., 2000). For instance, herbivory pressure has been identified as the main threat to *F. guiryi* towards its range edge (Martins et al., 2019; Verlaque, 1990). This factor might have contributed to the wide heterogeneity in population traits in our study, via losses in reproductive structures and canopy cover (Martins et al., 2019). This might explain the reduced percentage of mature receptacles at STC observed at the after the reproductive peak in fall 2019 (see Fig. A.2).

Another knowledge gap exists in assessing the potentially harmful effects of the invasive species *R. okamurai* over *F. guiryi*, considering the devastating effects observed on native marine forests, leading to ecosystem homogenization and loss of native species (García-Gómez et al., 2021b). In fact, some of the sites where *F. guiryi* became extinct or drastically reduced were areas heavily impacted by accumulation of tons of beach-casted *R. okamurai* (*pers. obs.*) (i.e. Cala Mocarro, Figs. 1 and 2), which was classified as one with the highest ecological value two decades ago (Ruiz-Tabares et al., 2003).

5. Recommendations

The local-scale variability among the conservation status of *F. guiryi* at the Strait of Gibraltar detected in our study provides pivotal information to prioritize the populations and MPAs that should be primarily protected (Tarifa and Santa Catalina), since they offered the more suitable environmental conditions to ensure their long-term preservation. Conservation efforts on MPAs are generally more effective than outside areas (Barrimentos et al., 2022; Medrano et al., 2020; Spalding et al., 2016). On the other hand, restoring *F. guiryi* would present a key opportunity and challenge for its conservation within the UN Decade on

Ecosystem Restoration 2021–2030. However, it would require developing species and site-specific protocols as done for other temperate fucooids (Falace et al., 2018; Savonitto et al., 2020) as well as prioritization frameworks (McGowan et al., 2020). Finally, based on the conservation status of *F. guiryi* in the area, we would recommend its inclusion in the List of Wild Species in Regime of Special Protection and the Spanish Catalogue of Endangered Species (Royal Decree 139/2011), as well as international Red Lists.

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CRediT authorship contribution statement

Raquel Sánchez de Pedro: Conceptualization, Methodology, Formal Analysis, Investigation, Writing – original draft, review & editing, Validation, Visualization. **Andrea N. Fernández:** Investigation, Writing – review & editing. **Ignacio J. Melero-Jiménez:** Investigation, Writing – review & editing, Visualization. **María Jesús García-Sánchez:** Conceptualization, Supervision, Writing – review & editing. **Antonio Flores-Moya:** Conceptualization, Supervision, Funding acquisition, Project administration, Resources, Writing – review & editing. **Elena Bañares-España:** Conceptualization, Supervision, Funding acquisition, Methodology, Investigation, Project administration, 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.

Data availability

Data associated with this manuscript will be archived in the open repository of the University of Málaga should the manuscript be accepted.

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Appendix A. Supplementary data

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