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PII: S0141-1136(20)30534-1

DOI: <https://doi.org/10.1016/j.marenvres.2020.105159>

Reference: MERE 105159

To appear in: *Marine Environmental Research*

Received Date: 9 June 2020

Revised Date: 24 August 2020

Accepted Date: 21 September 2020

Please cite this article as: Máñez-Crespo, J., Tuya, F., Fernández-Torquemada, Y., Royo, L., Pilar-Ruso, Y.d., Espino, F., Manent, P., Antich, L., Castejón, Iné., Curbelo, L., de la Ossa, José.A., Hernan, G., Mateo-Ramírez, Á., Pereda-Briones, L., Jiménez-Ramos, Rocí., Egea, L.G., Procaccini, G., Terrados, J., Tomas, F., Seagrass *Cymodocea nodosa* across biogeographical regions and times: Differences in abundance, meadow structure and sexual reproduction, *Marine Environmental Research* (2020), doi: <https://doi.org/10.1016/j.marenvres.2020.105159>.

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Seagrass *Cymodocea nodosa* across biogeographical regions and times: differences in abundance, meadow structure and sexual reproduction

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1. ABSTRACT

Seagrasses are key habitat-forming species of coastal areas. While previous research has demonstrated considerable small-scale variation in seagrass abundance and structure, studies teasing apart local from large-scale variation are scarce. We determined how different biogeographic scenarios, under varying environmental and genetic variation, explained variation in the abundance and structure (morphology and biomass allocation), epiphytes and sexual reproduction intensity of the seagrass *Cymodocea nodosa*. Regional and local-scale variation, including their temporal variability, contributed to differentially explain variation in seagrass attributes. Structural, in particular morphological, attributes of the seagrass leaf canopy, most evidenced regional seasonal variation. Allocation to belowground tissues was, however, mainly driven by local-scale variation. High seed densities were observed in meadows of large genetic diversity, indicative of sexual success, which likely resulted from the different evolutionary histories undergone by the seagrass at each region. Our results highlight that phenotypic plasticity to local and regional environments need to be considered to better manage and preserve seagrass meadows.

Keywords: angiosperms, phenotypic plasticity, environmental variability, demographic compensation hypothesis, Mediterranean, Canary Islands, Seagrass distribution range, meadow genetic diversity, Seed bank, Shoot density

2. INTRODUCTION

Identifying factors driving patterns of abundance, size and reproduction of species throughout their distribution ranges has always been one of the main objectives in ecology and conservation (Hardie & Hutchings, 2010; Thomas et al., 2004). While different hypotheses have been put forward to explain these patterns, few of them have been supported with empirical data (Villellas et al., 2015). For example, one of the most cited hypotheses in macroecology is the “Abundant-Centre Hypothesis” (ACH; Brown, 1984), which states that the largest abundances of a species are found in the middle zones throughout its distribution range while, on the other hand, lowest abundances occur at the range limits. However, several empirical studies (Angert, 2006; Jongejans et al., 2010; Sagarin & Gaines, 2002; Villellas et al., 2015), mainly with plants, reject this hypothesis as a general norm. In fact, it has been observed that local population dynamics play a crucial role in determining population abundances. For instance, the “Demographic Compensation Hypothesis” (DCH) has been proposed, in this sense, to explain the stochasticity of species’ abundances across their ranges (Kilkenny & Galloway, 2008; Villellas et al., 2015). This hypothesis considers the relevance of processes influencing the vital rates of species, which allow them to persist, despite being at their distribution range limits (Villellas et al., 2015). The DCH considers a spatio-temporal framework, incorporating local environmental variability, while also taking into account genetic flow, population size, and variations in life history traits of populations at localities across the distribution range of a target species (Jongejans et al., 2010; Zanne et al., 2018).

Variation in the abundance and structure (e.g. size, morphology) of plants can arise from large-scale variation in the evolutionary histories of species across their ranges of distribution, which is often reflected in genetic variation (Masucci et al., 2012), but also

from varying environmental scenarios throughout varying scales of spatial and temporal variability (Reynolds & D'Antonio, 1996). There is a general consensus that plant populations at their limit ranges exhibit less genetic variability and are more divergent than populations from the center of their distribution ranges (Hardie & Hutchings, 2010). For clonal plants, which are capable of both sexual and asexual reproduction, this is typically associated with a reduction in the intensity of sexual reproduction at their range limits (Billingham et al., 2003; Eckert, 2001; Paulo et al., 2019a). In these areas, the environment often imposes harsh conditions for the normal development of plant populations and, consequently, established populations tend to favor asexual over sexual reproduction, as it allows a faster expansion or persistence of plants via clone formation, eliminating the need of the high energy investment that sexual reproduction requires (Alberto et al., 2006; Eckert, 2001).

Importantly, the phenotypic plasticity of plant species to acclimate to a fluctuating environment, for example in terms of demographic or morphological responses, varies along environmental gradients and according to the intrinsic biological peculiarities of the species (Kilminster et al., 2015; O'Brien et al., 2017; Villellas et al., 2015). For instance, differences in demography and population dynamics between central and marginal populations of two species of monkeyflowers (*Mimulus*) differed strikingly between both species; whereas *M. lewisii* exhibited higher survivorship and fecundity in central populations, population growth and investment on sexual reproduction was, in contrast, dominant in marginal populations of *M. cardinalis*. Critically, a reduction in sexual reproduction at the limits of the distribution range could be associated with more threatened populations under a changing environment, because of associated lower genetic diversity (Wernberg et al., 2018), which would decrease the capacity of individuals to adapt and survive to new conditions (Eckert, 2001).

While identification of sources of spatial and temporal variability of species across their distribution ranges is a pivotal goal in ecology and conservation, it becomes particularly important for habitat-forming species (Araújo et al., 2014; Casas-Güell et al., 2015; Del Vecchio et al., 2018), given that they directly and indirectly supply resources that the rest of organisms from the same ecosystem require (Jones et al., 1997).

Seagrasses are a group of angiosperms that have adapted to a fully submerged life in marine environments (Hemminga & Duarte, 2000), having successfully colonized both temperate and tropical coastal areas around the world where they create coastal ecosystems of great ecological, socio-cultural and economic importance (Lilley & Unsworth, 2014; Sherwood et al., 2017). These seagrass species are “habitat formers”, providing habitat and food for many organisms, creating the base of many coastal food webs (Coll et al., 2011), and acting as important carbon sinks (Fourqurean et al., 2012). Due to the high occupation of coastal areas by humans, and the negative impact of associated anthropogenic activities, seagrass meadows are receding throughout the world (Papathanasiou & Orfanidis, 2018; Waycott et al., 2009). Therefore, unravelling the sources of variability related to the structure and functioning of these meadows throughout their distribution range is key for decision-making to ensure their conservation. The abundance (e.g. shoot density) and structure (e.g. biomass allocation and plant size) of seagrasses may vary across their distribution ranges (Larkum et al., 2006; Short & Coles, 2001). While a large body of research has demonstrated considerable small-scale (local) variation in seagrass abundance and structure, studies teasing apart small (local) from large-scale variation are scarce (Mascaró et al., 2009; Xu et al., 2018).

Ecological studies partitioning the relevance of scales of spatial and temporal variation of biota, particularly from the marine realm, have been typically framed using nested ANOVA models (Anderson et al., 2000; Burnham et al., 2011; Mundry, 2011). However, in the last decade, the suite of statistical tools available to ecologists, as well as the complexity of biological data analyses, have grown concurrently (Gutiérrez-Cánovas & Escribano-Ávila, 2019; Zuur et al., 2010). Model selection strategies, in particular, allows for the inclusion of a wide range of predictor variables, operating at varying scales, to explain ecological patterns from local to biogeographic scales and through seasons to years (Diniz-filho et al., 2008; Melis et al., 2006). In this sense, such approach has not been used before, to best of our knowledge, to study variation in seagrass structure through varying scales of spatial and temporal variability.

In this study, our goal was to determine how different biogeographic scenarios, which are here typified by varying scenarios of environmental and genetic variation, contribute to explain variation in seagrass abundance (shoot density), structure (morphology and biomass allocation), associated epiphytes, and intensity of sexual reproduction. We used *Cymodocea nodosa* as our model species, given that this seagrass is distributed throughout the whole Mediterranean Sea, as well as through the adjacent Atlantic coast, from Southern Portugal to the Northern African coasts, encompassing different environmental and ecological conditions, as well as evolutionary scenarios (Alberto et al., 2006; Tuya et al., 2019).

3. MATERIALS AND METHODS

3.1. Study species

Cymodocea nodosa (Ucria) Ascherson is a marine dioicous angiosperm, which reproduces mainly vegetatively (forming ramets), but also sexually through seeds. This

species is found in subtidal and intertidal zones, from subtropical to temperate regions, along the NW coast of Africa, Madeira and the Canary Islands, the south Atlantic coast of the Iberian Peninsula and the entire Mediterranean Sea (Pavón-Salas et al., 2000; Mascaró et al., 2009; Tuya et al., 2014), forming meadows that provide habitat for different fish and invertebrates species (Espino et al., 2011). These seagrass meadows are found in sandy-muddy bottoms, reaching up to 30-40 meters deep, but also inhabiting coastal lagoons at very low depth. This is a fast-growing species (*sensu* Orth et al., 2006) with an annual reproduction pattern, typically producing two seeds per plant (Caye & Meinesz, 1985).

3.2. Study area and sampling design

To assess the spatial variability in meadows of the seagrass *Cymodocea nodosa* across nearshore Atlantic and Mediterranean waters, we selected three regions, from west to east: Gran Canaria Island (eastern Atlantic Ocean), Alicante (south-western Mediterranean) and Mallorca Island (Balearic Sea) (Figure 1).

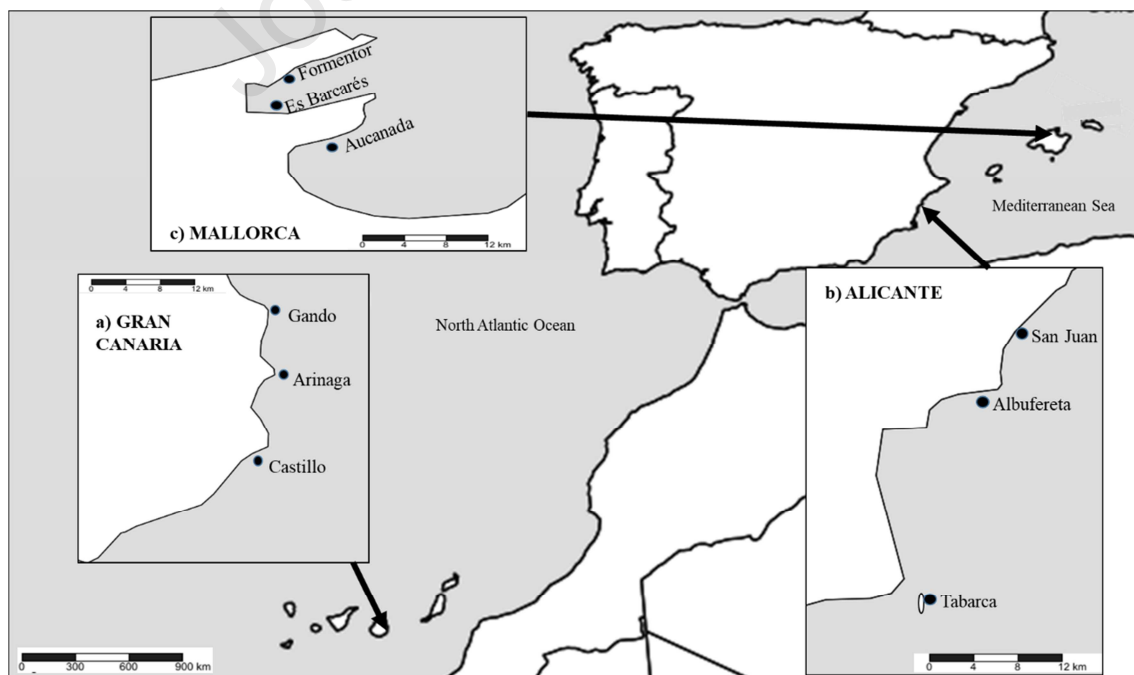


Figure 1. Location of the *Cymodocea nodosa* meadows studied in each region: Gran Canaria (North Atlantic Ocean), Alicante (Mediterranean Sea) and Mallorca (Balearic Sea).

At each region, we selected three seagrass meadows, which were seasonally monitored throughout two successive years. To encompass intra-regional (local) variation in seagrass genetic diversity, we selected the meadows within a gradient of intra-regional genetic diversity (Tuya et al., 2019). This approach accounts for the different evolutionary histories of each region, but also incorporates levels of local (small-scale) variation (Table 1). In particular, seagrass populations on Gran Canaria Island suffered a “founder effect” in their colonization of the archipelago (Alberto et al., 2006). This has resulted in large differences in seagrass allelic richness and heterozygosity between Gran Canaria and Mediterranean regions (Alberto et al., 2006; see Table 1 in Tuya et al., 2019). At each of the nine meadows, a range of seagrass attributes (e.g. leaf morphology, plant biomass, abundance; see details below) were seasonally collected, from November 2016 to November 2018, for a total of 9 sampling times (except for Autumn 2017 in Mallorca due to bad weather) via SCUBA.

		Na		Ne		Ho		He		R
		mean	SD	mean	SD	mean	SD	mean	SD	mean
Gran Canaria	Castillo	1.800	0.200	1.431	0.171	0.237	0.103	0.242	0.083	0.625
	Gando	2.900	0.348	1.598	0.196	0.278	0.085	0.308	0.071	0.647
	Arinaga	2.600	0.340	1.378	0.164	0.191	0.071	0.212	0.066	0.545
Alicante	San Juan	1.900	0.547	1.411	0.394	0.377	0.137	0.313	0.100	0.636
	Tabarca	2.000	0.577	1.385	0.398	0.244	0.086	0.339	0.102	0.952
	Albufereta	2.700	0.300	2.041	0.268	0.510	0.098	0.463	0.076	0.929
Mallorca	Formentor	4.000	0.632	2.772	0.262	0.675	0.076	0.620	0.041	0.914
	Aucanada	3.500	0.792	2.276	0.434	0.558	0.096	0.477	0.088	0.778
	Es Barcarés	3.500	0.582	2.099	0.298	0.479	0.084	0.500	0.065	0.971

Table 1. Summary of the genetic descriptors at the nine studied meadows (mean \pm SD). Na: allele number; Ne: effective allele number; Ho: observed heterozygosity; He: expected heterozygosity, R: clonal richness. Results of this table are also presented in Tuya et al. (2019).

3.3. Environmental data

We extracted local (i.e. at the meadow-scale) monthly means of Sea Surface Temperature (SST), surface Photosynthetically Active Radiation (PAR) intensity, and Chlorophyll-a, through the entire study period (2016-2019), from the Moderate Resolution Imaging Spectroradiometer facility (MODIS-Aqua), available at the NASA Giovanni system facility (<https://giovanni.gsfc.nasa.gov/giovanni/>). All data correspond to a spatial resolution of a 4 x 4 km grid.

3.4. Seagrass attributes and epiphytes

Leaf morphology and epiphytic load

A total of 20 seagrass shoots were randomly collected by hand at each meadow and sampling time. In the laboratory, we quantified the number of leaves per shoot, as well as the length and width (mm) of all leaves. Macroscopic epiphytes were removed using a razor blade and epiphytes and leaves were subsequently oven-dried to estimate epiphytic load (i.e. dry weight, DW, of epiphytes per DW of leaf biomass). Total leaf area was calculated as the sum of all individual leaf areas per shoot, and the Leaf Area Index (LAI) was subsequently calculated, at each meadow and time, by multiplying the mean leaf area per shoot by the mean shoot density (see below).

Plant biomass allocation and abundance

Seagrass tissues were collected, at each meadow and time, using corers (20 cm of inner diameter, $n=10$). In the laboratory, seagrass samples were subsequently cleaned of sediment, fractioned into leaves, rhizomes and roots and dried (60°C , ca. 48 h) to obtain the biomass of each compartment (i.e. above and belowground compartments). We further estimated the Root Weight Ratio (RWR, Reynolds & D'Antonio, 1996; modified by Mascaró et al., 2009), i.e. the relative allocation of biomass to the above (leaves) against the belowground (rhizome and roots) compartments.

Shoot density, i.e. a measure of seagrass abundance, was obtained by randomly deploying a 20 x 20 cm quadrat ($n=10$) and counting seagrass shoots within each quadrat. The density of shoots was expressed per m^2 .

Intensity of sexual reproduction

As an indicator of sexual reproduction, seeds were counted from corers (10 cm of inner diameter, $n = 50$), haphazardly placed in each meadow in October 2016, 2017 and 2018, i.e. six months after the main flowering season of the species in the Mediterranean (Terrados, 1993) and the Canary Islands (Reyes et al., 1995). We estimated seed production as the product of seed density (seeds per m^2) per shoot density (shoots per m^2).

3.5. Data analysis

We firstly visualized and tested for correlations (Pearson correlations) between each pair of explanatory variables (environmental data and genetic attributes; Fig. A.1) through the 'corrplot' R library (Wei & Simko, 2017). This was necessary to limit the inclusion of over-correlated predictor variables ($R^2 > 0.7$, (Harrison et al., 2018)) in the

subsequent modelization. When two predictive variables were correlated, we selected that one with, *a priori*, larger biological significance (Bolker, 2008). For example, in the case of genetic descriptors operating at the meadow-scale (Table 1), we only included the observed heterozygosity (H_o). Genetic diversity (H_o) was correlated with meadow genotypic diversity (clonal richness, R , Table 1), a correlation which has also been observed for other seagrass species (e.g. *Posidonia oceanica*; Jahnke et al., 2015), so both mechanisms covary and cannot be disentangled.

To partition the relative effects of environmental (mean monthly SST and mean monthly surface PAR at each meadow during the study) and genetic attributes (H_o) on seagrass responses, Generalized Linear Models (GLMs) were implemented in the R statistical environment (R Core Team 2019). For each seagrass response variable, we selected a particular family error structure and link function (see results, Table 2) to reach the assumptions of linearity and homogeneity of variances, which were checked through visual inspection of residuals and Q-Q plots (Harrison et al., 2018). In the particular case of the RWR, we used the 'betareg' R (Cribari-Neto & Zeileis, 2010) package to fit a beta family error distribution, which is ideal for proportional data. To validate our model selection, we used the 'MuMIn' R library (Bartoń, 2019), a flexible package for conducting model selection and model averaging with a variety of candidate GLMs. Model averaging is a way to incorporate model selection uncertainty; the parameter estimates for each candidate model are weighted using their corresponding model weights and summed. This is a way to obtain models containing the most parsimonious predictor variables for each response variable. Models were ultimately ranked by their AICc (Akaike Information Criterion corrected for small sizes), and importance weights (w_i) for individual predictor variables were then provided. The sum of all the importance weights of the models adds up to a value of 1.

This model-selection strategy was implemented for all seagrass responses, except for seed densities, for which the model only included one predictor, H_0 , given that collection of seeds was carried out once each year.

While seagrass structure traits might considerably vary across small-scales, environmental data (here, SST and PAR) typically vary at larger spatial scales, mostly to reflect regional and/or seasonal variation. While environmental drivers may explain both temporal (i.e. seasons and years) and spatial (i.e. sites and regions) variation in seagrass responses, genetic attributes (H_0) exclusively denote spatial variation in seagrass structure at local and, majorly, regional scales (Table 1).

4. RESULTS

4.1. Environmental descriptors

Environmental descriptors varied through time with a clear seasonal pattern at each region (Figure 2). While PAR peaked in spring and summer in all regions, temperatures reached their maximum values in summer in the Mediterranean, whereas highest temperatures were observed in autumn in Gran Canaria Island. In general, both mean monthly SST and mean monthly surface PAR availability were less variable in Gran Canaria than in the other two regions (Figures 2a and 2b, respectively). For instance, while temperatures ranged between ca. 19°C and 23°C in Gran Canaria, they exhibited a wider range (i.e. from ca. 14°C to 27°C) in the Mediterranean meadows.

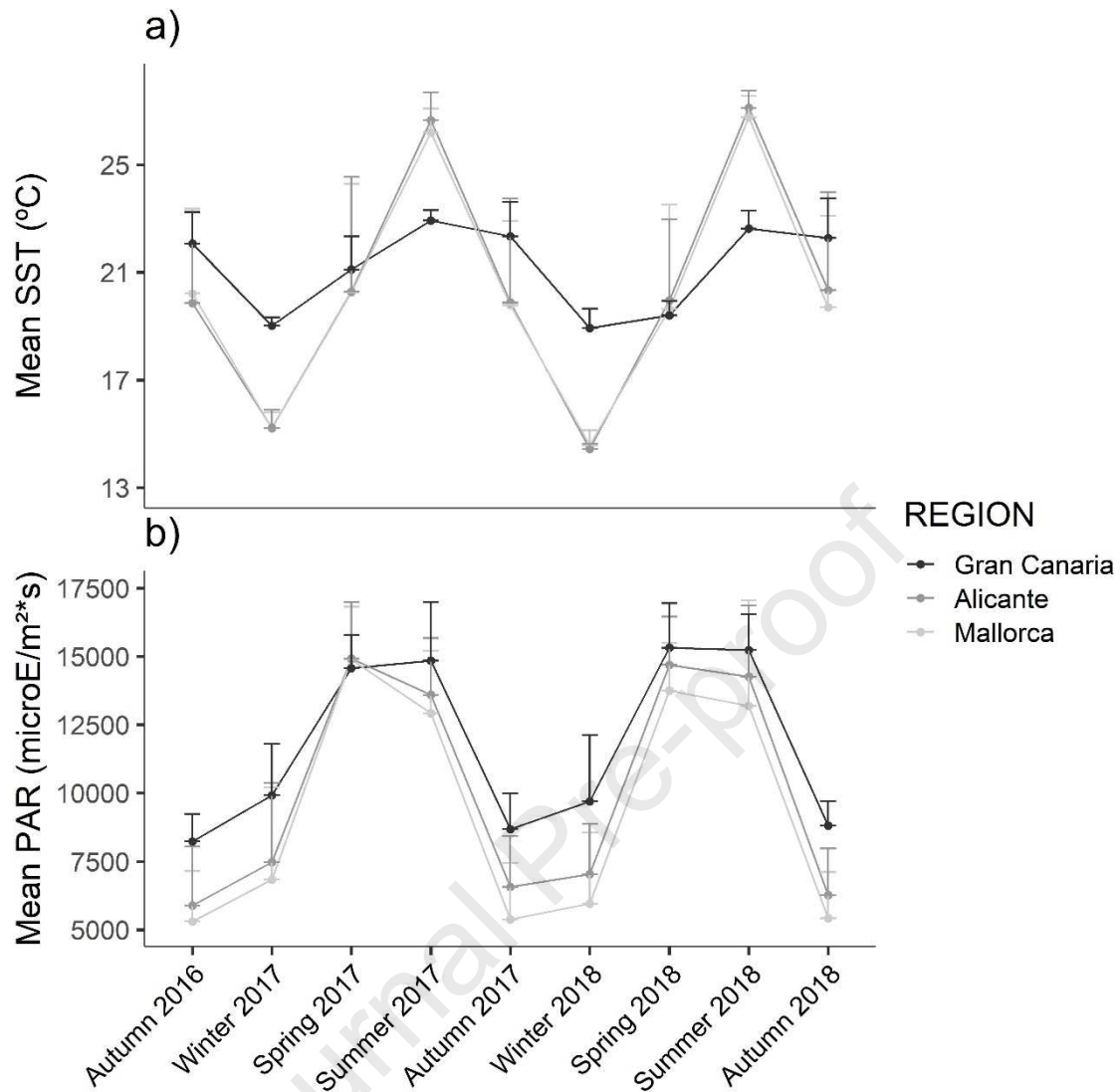


Figure 2. Mean (+ SD) in a) monthly SST and b) monthly surface PAR intensity throughout the study period at each region.

4.2. Seagrass attributes

Leaf morphology and epiphytic load

Overall, leaf width varied between ca. 0.15 and 0.23 cm at Gran Canaria and Alicante and ca. 0.13 to 0.27 cm at Mallorca (Figure 3a, Figure S2). Leaf area varied between ca. 1.38 and 10.1 cm² per shoot across all regions throughout the study (Figure 3b, Fig. A.3) and LAI ranged between ca. 0.2 and 0.9 in Gran Canaria, between ca. 0.16 and

0.58 in Alicante, and between ca. 0.07 and 0.35 in Mallorca (Figure 3c, Fig. A.4). Most variation in seagrass leaf morphological descriptors (Figure 3) was accounted by variation in PAR ($p < 0.001$, Table 2, Table A.1). Coefficients derived from the GLMs (Table 2) revealed that leaf width, leaf area and LAI increased with PAR.

Leaf width family=Gamma (link=log)					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	-2.119	0.149	14.564	<0.001	-
PAR	0.0001	0.00001	5.062	<0.001	1
SST	0.010	0.009	1.122	0.262	0.32
Ho	0.100	0.179	0.558	0.58	0.19
Leaf area family=Gamma (link=log)					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	0.459	0.387	1.186	0.235	-
PAR	0.0001	0.00001	5.901	<0.001	1
Ho	-1.021	0.457	2.23	0.025	0.72
SST	0.026	0.023	1.15	0.249	0.24
Leaf area index family=Gamma (link=log)					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	-2.406	0.434	5.54	<0.001	-
PAR	0.0001	0.00001	5.65	<0.001	1
Ho	-0.753	0.605	1.24	0.213	0.31
SST	0.019	0.031	0.625	0.531	0.19
Epiphytic loads family=Inverse gaussian (link=inverse)					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	1.885	3.557	0.530	0.596	-
Ho	-6.295	3.018	2.085	0.037	0.53
SST	0.213	0.134	1.582	0.114	0.39
PAR	0.0001	0.00001	1.401	0.161	0.35
Aboveground biomass family=Gamma (link=inverse)					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	1.420	0.227	6.276	<0.001	-
PAR	-0.019	0.004	5.156	<0.001	1.00
Ho	0.337	0.257	1.311	0.190	0.35
SST	-0.009	0.013	0.639	0.523	0.19
Belowground family=Gaussian (link=identity)					

biomass					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	2.450	2.462	0.995	0.320	-
Ho	9.614	2.425	3.964	<0.001	1.00
PAR	-0.0002	0.0001	1.919	0.055	0.79
SST	0.213	0.12	1.78	0.07	0.50
RWR family=Beta					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	2.45	2.46	0.995	0.319	-
PAR	-0.0002	0.0001	1.198	0.055	1.00
Ho	9.61	2.425	3.963	<0.001	1.00
SST	0.0213	0.119	1.783	0.07	-
Shoot density family=Gaussian (link=log)					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Intercept	6.260	0.166	37.613	<0.001	-
PAR	0.00004	0.00001	3.803	<0.001	1.00
Ho	0.264	0.236	1.117	0.264	0.32
SST	-0.002	0.001	0.138	0.890	0.17
Seed production family=Negative binomial					
Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Null	-	28	217.07	-	-
Ho	186.05	21	31.02	<0.001	1.00

Table 2. Results of the model selection of the relative importance of predictor variables affecting seagrass abundance and structure, epiphytic load and intensity of sexual reproduction. The family error structure and their link functions are included for each response variable. Values of model estimates and associated SE are also included; p-values of significant predictors are also shown and highlighted in bold when significant (<0.05).

In addition, variation in leaf area was also partially accounted by spatial variation associated with Ho ($p < 0.025$; Table 2, Table A.1); leaf area decreased with increasing

309 Ho. Epiphytic load was only explained by spatial variation associated with Ho ($p < 0.05$,
310 Table 2, Figure. 3d).

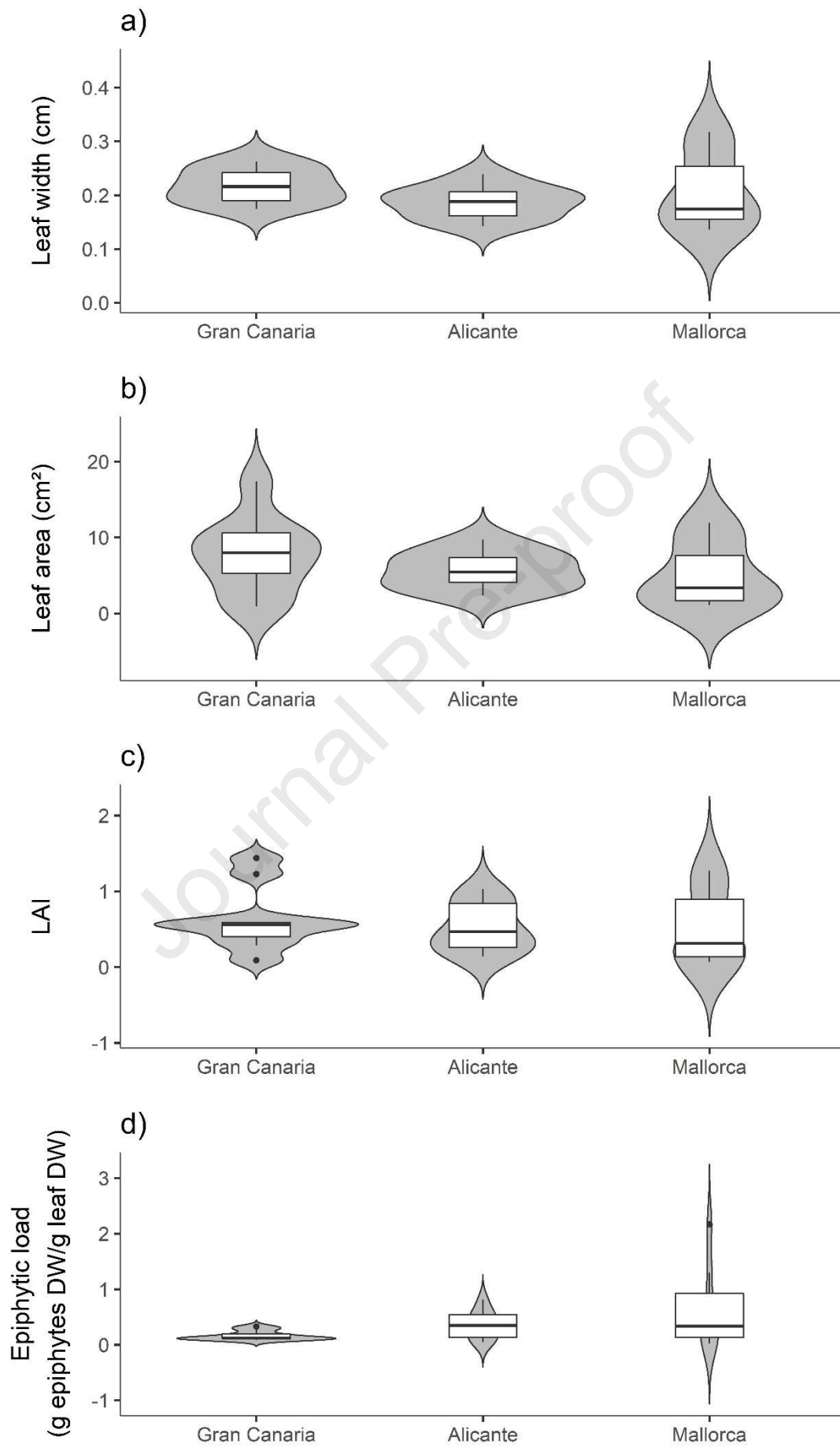


Figure 3. Violin plots for seagrass leaf morphological descriptors, at each of the three regions, including: a) Leaf width, b) Leaf area, c) Leaf area index and d) Epiphytic load. Boxplots denote the minimum and maximum values, as the lower and upper part of the whiskers. Each box represents the second quartile, and the median is represented as a black horizontal line. Outliers are represented as dot points.

Plant biomass allocation and abundance

Aboveground biomass varied between ca. 24.80 and 158.30 g DW m⁻² in Gran Canaria, between 3.90 and 424.40 g DW m⁻² in Alicante, and between ca. 15.30 and 78.80 g DW m⁻² in Mallorca (Figure 4a, Fig.A.5). Most variation in aboveground biomass was accounted by variation associated with PAR ($p < 0.0001$, Table 2), with aboveground biomass increasing with increasing PAR (Table 2, Table A.1).

Belowground biomass ranged between ca. 10.00 and 539.20 g DW m⁻² in Gran Canaria, between 16.30 and 322.80 g DW m⁻² in Alicante, and between 36.30 and 242.20 g DW m⁻² in Mallorca (Figure 4b, Fig. A.6). Both Ho and PAR significantly contributed to explain variation in belowground seagrass biomass (Table 2, Table A.1). Belowground biomass decreased with increasing PAR, while increased with increasing Ho (Table 2).

The RWR varied between ca. 0.21 and 0.66 in Gran Canaria and between ca. 0.53 and 0.99 in Alicante and Mallorca (Figure 4c, Fig. A.7). Both PAR and Ho contributed to explain variation in RWR (Table 2, Table A.1), following similar patterns to those of belowground biomass (Table 2).

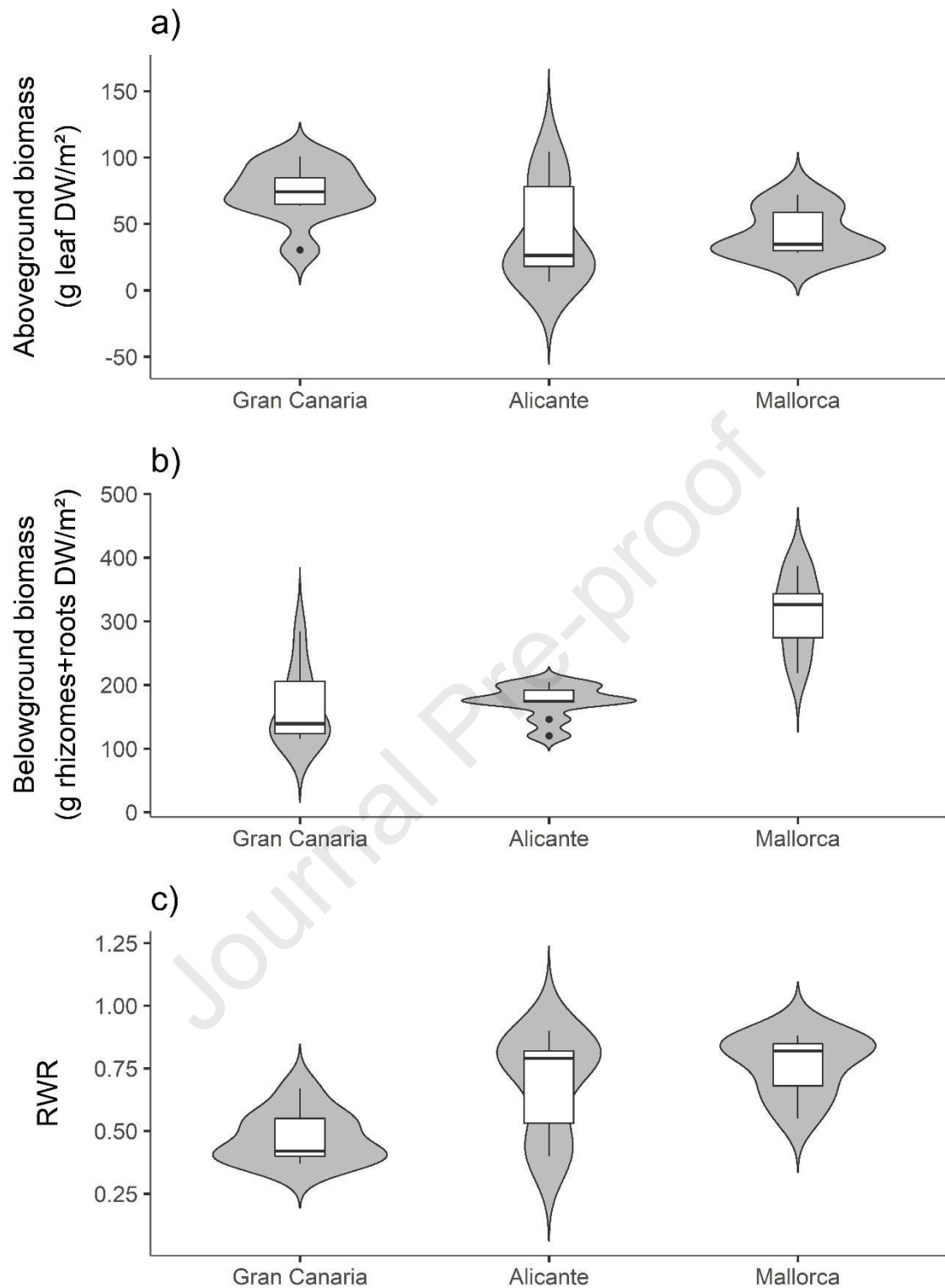


Figure 4. Violin plots for seagrass biomass allocation at each of the three regions, including: a) Aboveground biomass, b) Belowground biomass and c) Root to Weight Ratio (RWR).

Seagrass shoot density ranged between ca. 597 and 1140 shoots m^{-2} at the three regions (Figure 5, Fig. A.8). Variation in shoot density was explained by variation in PAR ($p < 0.0001$, Table 2, Table A.1), with shoot density increasing with increasing PAR (Table 2).

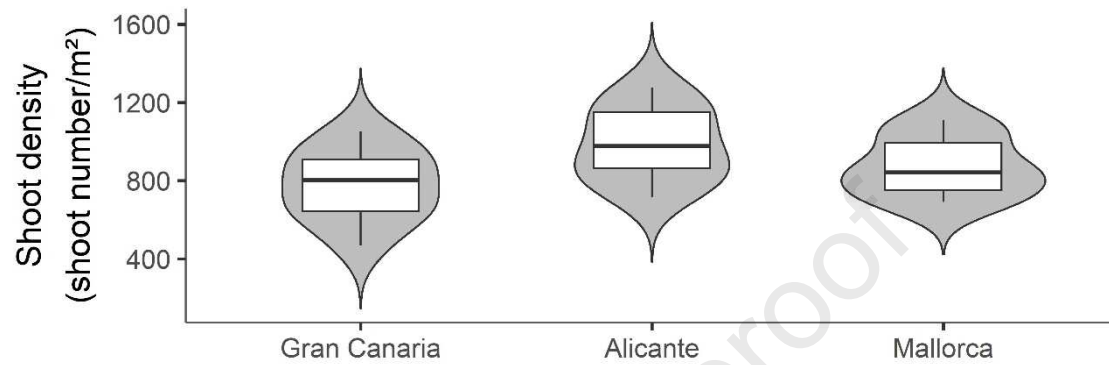


Figure 5. Violin plots for seagrass shoot density at each of the three regions.

4.3 Intensity of sexual reproduction

We observed large differences in seed production between Gran Canaria (ca. 0.0003-0.018 seeds per shoot) and the Mediterranean regions (0.013-0.84 seeds per shoot, Figure 6). These differences were denoted by a significant effect of Ho ($p < 0.0001$, Table 2); the larger the Ho of the meadow, the higher the production of seeds (Table 2).

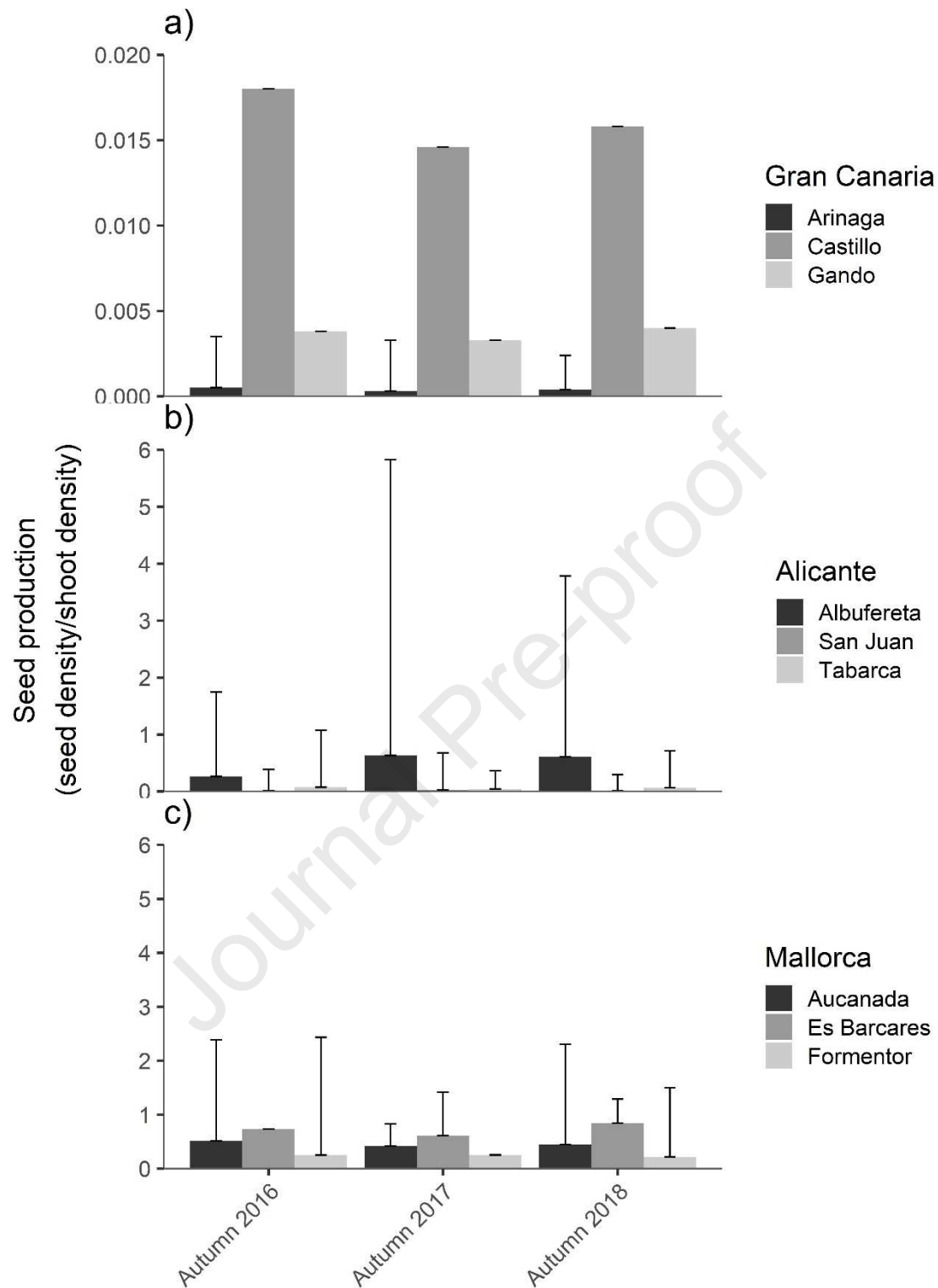


Figure 6. Seagrass production at each meadow from a) Gran Canaria, b) Alicante and c) Mallorca. Error bars are + SD of means (n=50). Note the difference in scale for the Y axis in panel a.

354

355 **5. DISCUSSION**

356 In this study we initially aimed at describing variation in the abundance and structure
357 (i.e. morphology and biomass allocation) of a seagrass (*Cymodocea nodosa*) across
358 regions under different environmental conditions and evolutionary contexts. Our results
359 indicate that both regional and local-scale variation, as well as temporal variation,
360 differentially contribute to explaining variation in seagrass attributes across populations,
361 thus supporting the Demographic-Compensation Hypothesis (Villellas et al., 2015).

362 Phenotypic plasticity is the capacity of organisms to adjust to environmental
363 heterogeneity through alteration of physiological, morphological and/or demographic
364 responses (Pigliucci, 2001). In our study, morphological (leaf width, leaf surface and
365 LAI), structural (above-ground biomass) and abundance (shoot density) attributes of the
366 seagrass leaf canopy exhibited a significant and positive relation with PAR, most likely
367 reflecting regional seasonal variation, as it has been previously described for this
368 species (Enríquez et al., 2004; Guidetti et al., 2002; Tuya et al., 2006). Typically, *C.*
369 *nodosa* has a peak in leaf canopy development in spring and summer (seasons of high
370 PAR), while decreasing (senescence) in autumn and winter (Cancemi et al., 2002;
371 Reyes et al., 1995), and such patterns were stronger in Gran Canaria, which exhibits
372 lower annual PAR variability but a higher annual mean PAR.

373 Beyond PAR regional patterns driving seagrass attributes, we also detected that leaf
374 morphology exhibited strong local differences across meadows, and this variation was
375 also significantly accounted by local genetic diversity. The same occurred among
376 regions with respect to variation in epiphytic loads. We observed that meadows from
377 the Atlantic waters had less variability than those from the Mediterranean Sea. Large

variability through local scales in epiphytic loads of Mediterranean meadows has been reported in the past (e.g. Castejón-Silvo & Terrados, 2012). At present, however, we lack conclusive reasons behind such biogeographical differences.

Leaf area was larger at meadows from Alicante and Gran Canaria, which are deeper than meadows from Mallorca (ca. 5 - 12 vs. 1.5 – 4 m, respectively), and shoot densities were also higher in the former two regions. Interestingly, this is the opposite pattern that is typically observed whereby an inverse relationship between these two variables exists, with shoot densities being lower in deeper meadows, as a way to decrease self-shading. For example, a 40 to 60% reduction in shoot density (e.g. from 305 shoots/m² to 128 shoots/m²; Aoki et al. 2020, and from 76.1 shoots/m² to 34 shoots/m²; Becarero et al. 2019) has been observed for *Z. marina* when colonizing deeper waters. Most likely, however, in our study meadows, shoot densities are not high enough to promote self-shading. Indeed, our study encompassed the upper bathymetric distribution ranges of the species, where light limitation and thus self-shading are unlikely to be an issue.

Investment in belowground compartments (i.e. roots and rhizomes) has been previously related with several abiotic processes, such as wave exposure (De Los Santos et al., 2009; Peralta et al., 2006), light availability (Olesen et al., 2002) and sediment nutrients (Jiang et al., 2019). In our study, we observed that belowground biomass was (positively) predicted by meadow genetic diversity, suggesting that allocation of resources to belowground tissues was mainly driven by differences not related to light or temperature. In this sense, meadows with the highest belowground biomasses (i.e. those from Mallorca), are not only those with the highest genetic diversity, but are also probably more exposed to wave action, as they occupy (relatively) shallow waters. Such investment in belowground tissues, therefore, could be explained by potentially stronger

hydrodynamic conditions at these shallow-water sites, which require enhanced anchorage of plants (Beca-Carretero et al., 2019; Peralta et al., 2006). Seagrasses at very low depth, moreover, do not have to invest a large amount of resources in aboveground tissues to absorb light, as our data has indicated. Hence, these seagrasses can invest their resources in a larger production of belowground organs, which can promote their capacity to uptake nutrients. With regard to the RWR, low values are often connected with eutrophic conditions, as less root tissue is required to incorporate nutrients (Oliva et al., 2012). In this study, we observed very low values at Arinaga (Gran Canaria), which has undergone several eutrophication events associated with human activities and, in particular, impacts derived from the development of an industrial port (Manent et al., 2020).

High seed production was observed in meadows exhibiting high genetic diversity (i.e. observed heterozygosity), which is usually indicative of sexual reproduction success (Jahnke et al., 2015; Paulo et al., 2019b; Ruiz et al., 2018). Differences in meadow heterozygosity amongst regions may be a result of the different evolutionary histories experienced by the meadows from each region and by the level of genetic connectivity among extant meadows. In this sense, meadows from Gran Canaria suffered a “founder effect”, whereby all meadows derived from a few common genotypes, and such bottleneck limited the allelic richness and heterozygosity of these meadows (Alberto et al., 2006; Blanch et al., 2006; Tuya et al. 2019).

In addition, sexual reproduction (and thus heterozygosity) may also be driven by environmental conditions. For instance, plant populations at their range edges, or under low environmental variation, tend to decrease the intensity of sexual reproduction relative to vegetative (asexual) propagation, because it diminishes the energetic costs needed to guarantee population persistence (Eckert, 2001). Thus, in Gran Canaria

meadows, an evolutionary “founder effect” coupled with a less variable environment may have driven populations to favor asexual propagation relative to sexual reproduction (Alberto et al., 2006; Manet et al. 2020). In contrast, sexual reproduction is often enhanced under short-term stressful conditions particularly after undergoing disturbances (Cabaço & Santos, 2012; Jahnke et al., 2015; T. Liu et al., 2013; Qin et al., 2014; Ruiz et al., 2018; Salo & Gustafsson, 2016a), and the production of seeds has been associated with rapid recovery after disturbances (Larkum et al., 2006; Paulo et al., 2019b). Indeed, meadows with high heterozygosity would favor the conditions for initial acclimation and adaptation to disturbances (Evans et al., 2017; Procaccini et al., 2007; Salo & Gustafsson, 2016b). As a result of these different evolutionary and environmental constraints, leading to low genetic diversity and sexual reproduction, meadows of *C. nodosa* from Gran Canaria are likely to be more vulnerable to disturbances than meadows from other regions (e.g. Fabbri et al., 2015; Tuya et al., 2014; Tuya et al. 2019; Manent et al. 2020). In the case of Mallorca meadows, i.e. those with the highest genetic diversity and seed densities, their location in shallow waters, where winter swells may directly disrupt plants (Infantes et al., 2012; Paulo et al., 2019b; Pereda-Briones et al., 2018), may be an ecological driver promoting sexual reproduction.

Cymodocea nodosa is considered an “opportunistic” seagrass (*sensu* Kilminster et al., 2015), i.e. a species that has the ability to rapidly colonize soft bottoms, producing large amounts of seeds and seedlings, particularly to recover from disturbances. Given the results we have obtained, this species appears to display a more “persistent” seagrass pattern (i.e. a seagrass species for which the investment on sexual reproduction could compromise asexual reproduction) in Gran Canaria Island. In contrast, a more “colonizer” pattern (i.e. a seagrass species that invest in sexual reproduction without

compromising their ability to also reproduce asexually) is observed in Mallorca meadows. This observation somehow follows Jahnke et al. (2019), which concluded that inter-population ecological divergence of a seagrass (*P. oceanica*) is explained through adaptations to local environmental conditions.

Overall, our results highlight that phenotypic plasticity to local and regional environments need to be considered to better manage and preserve seagrass meadows. In brief, not only do we need to differentiate among species, but also among potential ecotypes within seagrass species (King et al., 2018; Vivanco Bercovich et al., 2019).

ACKNOWLEDGEMENTS

This research was supported by a Doctoral fellowship from Universidad de Los Lagos (Chile) to Julia Máñez-Crespo and the work was funded by a project (RESIGRASS, CGL2014-58829) supported by the Secretaría de Estado de Investigación, Desarrollo e Innovación (MINECO, Government of Spain) to F. Tomas and F. Tuya. We acknowledge Tony Sánchez, F. Otero-Ferrer, N. Bosch, Luis M. Ferrero Vicente, Andrea García Hierro, Paula Anglada Vink, Donna Van der Lenn, Tiny Westra and José L. Sánchez-Lizaso for their help during fieldwork and different aspects of this study. We acknowledge Marina Alicante for providing nautical support for subtidal works at Alicante. This study followed the national rules of Spain and permits were obtained when necessary to carry out subtidal experimentation.

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HIGHLIGHTS

- Seagrasses are key habitat-forming species worldwide
- Different biogeographic scenarios explain variation in seagrass structure
- Attributes of seagrass leaf canopy evidenced regional seasonal variation
- Belowground allocation was driven by local-scale variation
- High seed densities occurred in meadows of high genetic diversity

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Julia Máñez-Crespo: Conceptualization, Formal Analysis, Investigation, Writing-Original Draft, Data Curation **Fernando Tuya:** Conceptualization, Writing-Review and Editing, Investigation, Supervision, Data Curation, Project Administration and Funding acquisition and Supervision, **Yolanda Fernández-Torquemada:** Investigation, **Laura Royo:** Investigation, **Yoana del Pilar-Ruso:** Investigation, **Fernando Espino:** Investigation, **Pablo Manent:** Investigation, **Laura Antich:** Investigation, **Inés Castejón:** Investigation, **L. Curbelo:** Investigation, **José A. de la Ossa:** Investigation, **Gema Hernan:** Investigation, **Ángel Mateo-Ramírez:** Investigation, **Laura Pereda-Briones:** Investigation, **Rocío Jiménez-Ramos:** Investigation, **Luis G. Egea:** Investigation, **Gabriele Procaccini:** Conceptualization and Investigation, **Jorge Terrados:** Conceptualization and Investigation, **Fiona Tomas:** Conceptualization, Writing-Review and Editing, Investigation, Supervision, Data Curation, Project Administration and Funding acquisition and Supervision

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: