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REPORT

Environmental drivers of distribution and reef development of the Mediterranean coral *Cladocora caespitosa*

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Abstract *Cladocora caespitosa* is the only Mediterranean scleractinian similar to tropical reef-building corals. While this species is part of the recent fossil history of the Mediterranean Sea, it is currently considered endangered due to its decline during the last decades. Environmental factors affecting the distribution and persistence of extensive bank reefs of this endemic species across its whole geographic range are poorly understood. In this study, we examined the environmental response of *C. caespitosa* and its main types of assemblages using ecological niche modeling and ordination analysis. We also predicted other suitable areas for the occurrence of the species and assessed the conservation effectiveness of Mediterranean marine protected areas (MPAs) for this coral. We found that phosphate concentration and wave height were factors affecting both the occurrence of this versatile species and the distribution of its extensive bioconstructions in the Mediterranean Sea. A set of factors (diffuse attenuation coefficient, calcite and nitrate concentrations, mean wave height, sea surface temperature, and shape of the coast) likely act as environmental barriers preventing the species from expansion to the Atlantic Ocean and the Black Sea. Uncertainties in our large-scale statistical results and departures from previous physiological and ecological studies are also discussed under an integrative perspective. This study reveals that Mediterranean MPAs encompass eight of the ten banks and 16 of the 21 beds of *C. caespitosa*. Preservation of water clarity by avoiding phosphate discharges may improve the protection of this emblematic species.

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Introduction

The Mediterranean Sea is considered a hot spot of biodiversity shaped by geological events, climatic changes, and its narrow connection with the Atlantic Ocean (Boudouresque 2004; Templado 2014). The Mediterranean basin supports an assortment of temperate and subtropical elements as well as a high number of endemics (Coll et al. 2010). Extensive coral reef systems developed in the Mediterranean during warm geological periods (Dabrio et al. 1981; Pomar 1991), but at the end of the Miocene, the Mediterranean coral fauna underwent a drastic modification that led to the disappearance of almost all zooxanthellate corals and the well-established shallow-water coral reefs (Vertino et al. 2014). Present Mediterranean shallow-water rocky bottoms are dominated by frondose algae, while long-lived, filter-feeding organisms proliferate within sciaphilous benthic communities (Zabala and Ballesteros 1989). The colonial zooxanthellate

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scleractinian *Cladocora caespitosa* is the only coral that can be considered as a remnant of the ancient Mediterranean reefs. *Cladocora caespitosa* is physiologically and morphologically similar to typical tropical reef-building corals in being zooxanthellate, colonial, and able to form extensive bioherms that may fuse in reef-like structures (Schuhmacher and Zibrowius 1985; Kružić et al. 2008a). Nevertheless, as these formations do not reach the water surface, Schuhmacher and Zibrowius (1985) classified *C. caespitosa* as constructional and formally ahermatypic. The oldest fossil banks of *C. caespitosa* were described in Aguirre and Jiménez (1998) from the Upper Pliocene shallow marine deposit of the Almería-Nijar basin (SE Spain). This coral species became very common in some Quaternary peri-Mediterranean basins and diverse Holocene and Pleistocene fossil banks have been described in different areas (e.g., Cuerda et al. 1986; Bernasconi et al. 1997). Furthermore, Laborel (1987) mentioned the existence of extensive dead banks of *C. caespitosa* (dated from around 2500–3000 yr ago) on the coasts of Tunisia and Corsica. Nowadays, when abundant, the colonies form beds of globose to hemispherical colonies, or a large framework of colonies (banks) (Peirano et al. 1998; Kružić and Požar-Domac 2003). The putative relict *C. caespitosa* banks may derive from beds as a consequence of the fusion of adjacent colonies under undisturbed conditions (Bianchi 2009). Apart from these assemblages, separate colonies in medium or low densities are irregularly distributed along the Mediterranean coast.

The decline of *C. caespitosa* compared to its fossil distribution prompted Augier (1982) to include the coral in a list of marine endangered species. The regression of its populations is still in progress, mainly driven by mortality events in recent decades possibly due to the effects of global climate change (Rodolfo-Metalpa et al. 2000, 2005; Garrabou et al. 2009; Kersting et al. 2013a). Although climate change appears to be a major threat to the species and a major contributor to its continuing decline (Morri et al. 2001), other threats to its survival are noted, such as the spread of invasive algae (Kružić 2007; Kersting et al. 2014b, 2015), eutrophication due to anthropogenic activities such as sewage discharge or fish farming (Kružić and Požar-Domac 2007), trawling, and high sedimentation rates caused by dredging (Casado-Amezúa et al. 2015), among others. Moreover, bioconstructions formed by *C. caespitosa* harbor a high diversity of micro- and macrofauna (Koukouras et al. 1998; Pitacco et al. 2014), and thus the species is considered a keystone species where it occurs. Consequently, *C. caespitosa* has been included as endangered in the IUCN Red List, and continuous monitoring of populations has been recommended (Casado-Amezúa et al. 2015).

Cladocora caespitosa is found in a wide variety of environments, from shallow waters to about 35 m depth. It lives on hard and soft bottoms, both exposed to strong currents and in sheltered places (Bellan-Santini et al. 2002). The species has not been found in dark enclaves, but indirect and diffuse light is sufficient to ensure the existence of the zooxanthellae in this coral (Hoogenboom et al. 2010). The factors that govern the distribution of this emblematic species in the Mediterranean are not well understood, nor is why this coral only exists as remnant bank reefs in a few localities. Increased mortality at higher temperatures apparently contradicts paleontological and retrospective growth indications that this coral is favored by warmer conditions, and clearly requires further investigation (Peirano et al. 2004). Though many studies have explored the ecology and physiology of *C. caespitosa* at local scales, an analysis encompassing its distributional range is of interest to obtain a more comprehensive understanding of its environmental requirements. Here, we use ecological niche modeling (ENM) and ordination analysis to provide insight into the environmental response of the coral estimated through its occurrence and degree of accretion. ENM has been widely used in terrestrial studies to predict species distributions by combining environmental data under different climatic conditions (past, present and future) with occurrence records. These correlative models can provide corroborative evidence for biogeographical hypotheses and input for conservation decision-making, among other contexts (e.g., Peterson et al. 2011). Likewise, ENM provides insight into species responses to the environment and predicts their potential distribution in previously unsampled waters (Wiley et al. 2003). In addition, we use ordination analyses to identify factors conditioning the different bioconstructions of *C. caespitosa*, under the assumption that the optimal ecological conditions for the species are those found where most-developed assemblages occur. Finally, given its endangered status, an assessment of the representation of this emblematic coral within MPAs is also produced.

In brief, the objectives of this study were (1) to explore the relationship between environmental parameters and both occurrence of *C. caespitosa* and the distribution of the different types of assemblages (banks and beds) in the Mediterranean basin and sub-basins, (2) to predict potentially suitable habitats where new populations could be found, and (3) to assess the current MPA system effectiveness for conservation of *C. caespitosa*. In addition, by contrasting our large-scale statistical results with existing physiological and local environmental studies, we aimed to identify uncertainties in our study and offer an integrative perspective.

Materials and methods

Species data and study area

We compiled occurrence data for *C. caespitosa* from published studies, personal observations, and the Global Biodiversity Information Facility (http://www.gbif.org/). We removed duplicates and checked for records with georeferencing errors. After that process, one observation remained per cell (156 presence cells) using a $0.083° × 0.083°$ (~ 9.2 km) resolution. The study area comprised the species' known geographic range, the Mediterranean basin, and adjacent areas (the nearby coasts of the Atlantic Ocean and the Black Sea). We delimited appropriate habitats according to the bathymetric distribution of the species (in the depth range 0–35 m) from the 30 arc-s general bathymetric chart of the oceans (GEBCO; http://www.gebco.net/).

Selection of predictors and environmental niche modeling

We selected an initial set of predictors based on our a priori assumptions about the species' environmental requirements (light availability, nutrients, temperature, etc.). We statistically tested each predictor's ability to explain the presence of the species to select those most relevant for inclusion in the models. Satellite-derived data for nitrate (1928–2008), phosphate (1922–1986), pH (1910–2007), photosynthetically available radiation (PAR; 1997–2009), and calcite (2002–2009) were obtained from the Bio-ORACLE dataset (Tyberghein et al. 2012; http://www.oracle.ugent.be/). Seafloor morphology (bottom aspect and bottom slope) was computed from GEBCO data using the package "raster" in R (Hijmans 2016). Summer and winter maximum, minimum, and mean values of significant wave height were derived from near-real-time merged data for 2009–2015 from Aviso (http://www.aviso.altimetry.fr/). The same measures (2003–2007) for SST, and for the diffuse attenuation coefficient for downward irradiance at 490 nm (K_d; Huot et al. 2005), were derived from the OSTIA system (http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html; Stark et al. 2007). K_d is calculated from satellite images and provides an excellent estimate of the traditional Secchi disk depth (SDD), as there is an inverse correlation between K_d and SSD (Chen et al. 2007). Smaller K_d values ($\sim$ larger SDD) are found in waters with less attenuation of light as a function of depth, thus in waters with higher clarity.

In addition, six landscape metrics computed at the class level in FRAGSTATS (McGarigal et al. 2012) were considered as indicators of the shape of the coast: (1) a measure of the edge contrast along the coastline (ECON_MN); (2) fractal dimension index (FRAC_AM), a metric for shape complexity; (3) the mean perimeter-to-area ratio (PARA_MN) of the patch; (4) percentage of each landscape (sea or land) along the coast (PLAND); (5) the index of shape complexity in relation to a square (SHAPE_MN); and (6) the index of the total edge contrast (TECI) (see Electronic supplementary material, ESM, Table S1). These landscape metrics are good indicators of coastal features such as long beaches, gulfs, and capes (Chefaoui 2014; they also enhanced predictive performance when integrated as predictors of a subtidal seagrass (Chefaoui et al. 2016).

All variables were initially checked for Pearson correlations to discard among derived metrics ($r \geq |0.80|$, $p < 0.001$). Then the relevance of each predictor to define the niche of the species was assessed using ecological niche factor analysis (ENFA; Hirzel et al. 2002). ENFA relies on presence data to compute a factor analysis that identifies marginality and specialization factors. Marginality is the ecological distance between the mean conditions found in the habitat and the species optimum (the mean of the species). Specialization computes the ratio of the variance of the global distribution to that of the species distribution in the multidimensional space (Hirzel et al. 2002). We removed predictors that had marginality or specialization scores below 0.2 using a preliminary ENFA. A further ENFA was done with the remaining variables to obtain their contribution to relating the presence of *C. caespitosa* with environmental factors.

Due to the lack of reliable absence data for this coral, we selected a presence-only algorithm (Mahalanobis distance, MD) as the main method to estimate the potential distribution of *C. caespitosa*. MD generates an elliptical envelope (Clark et al. 1993), which has superior performance over rectilineal envelopes as it uses all the observations to calculate the optimum for the species (Farber and Kadmon 2003). Variables were scaled to equal their variance before computing the suitability map. ENFA and MD were fit using "adehabitat" in R (Calenge 2006).

We also produced a presence–absence model for comparison using generalized linear models (GLMs) and generalized additive models (GAMs) to fit our data with logit link function and binomial error distribution. To reduce the uncertainty of the absences, pseudo-absences were randomly selected from environmentally distant habitats previously defined by MD (habitat suitability = 0), using a similar procedure to Chefaoui and Lobo (2008). Stepwise model selection using the Akaike information criterion (AIC) was performed in both directions, and the proposed model was compared to the null model to estimate the percentage of deviance explained (D^2). To validate the

model, we randomly divided the data into a training set (70%) and an evaluation set (30%). The area under the receiver operating characteristic curve (AUC) and the sensitivity (true positive rate) was calculated. Models were fitted in R using the "gam" and "MASS" packages.

Ordination analysis of *C. caespitosa* assemblages

We compiled available information describing abundance and morphology of colonies from the literature and expert observations, and classified the assemblages according to Peirano et al. (1998) into two categories: "banks" formed by colonies connected in a framework and reaching several decimeters in height and several square meters in surface area; or "beds" consisting of a great number of subspherical colonies close to each other, concentrated in a small area but with a low coverage (Fig. 1). As intermediate stages may be found, we considered as beds any stage not reaching a true bank. In this way, 31 populations were classified as banks (10 localities) or beds (21 localities) (Fig. 2; ESM Table S2).

To explore the influence of environmental factors on the types of assemblages of *C. caespitosa*, we used non-metric multidimensional scaling (NMDS), a robust unconstrained ordination technique commonly used in community ecology (Minchin 1987). By means of a two-dimensional NMDS, we compared the environmental variables defining the locality (cell) of each assemblage to identify clusters based on the two types of colonies. We also used NMDS to compare environmental differences among the eight Mediterranean subregions (Notarbartolo di Sciari and Agardy 2010) where the assemblages were found (ESM Table S2). We computed a two-dimensional NMDS based on a distance matrix derived from the Bray–Curtis dissimilarity index. We extracted the correlation coefficient scores and assessed the significance of each environmental vector fitted onto the NMDS axes. Permutation tests ($n = 999$) were used to determine the significance of vector fits with ordination axes. Then we performed a smooth surface fitting of variables within ordinations estimated by a GAM. NMDS analyses were conducted using metaMDS, envfit and ordisurf functions in the "vegan" package in R (Oksanen et al. 2013).

Marine protected area gap analysis

We obtained GIS data on Mediterranean MPAs from the world database on protected areas (https://www.protectedplanet.net/) and the updated database of Natura 2000 sites designated under the EU Habitats Directive (http://www.eea.europa.eu/). From these sites, we excluded those with no effect on coral protection such as Special Protection Areas for wetlands (Ramsar sites), for birds (Birds Directive), and marine mammal sanctuaries. We overlaid *C. caespitosa* occurrences and the locations of the two types of assemblages on MPAs to assess the coverage of protection. A buffer of 1 km around each point was created to avoid underrepresentation due to possible georeferencing errors. In addition, we calculated statistics for habitat suitability (HS) values predicted for the coral inside the regions covered by the different systems of MPAs.
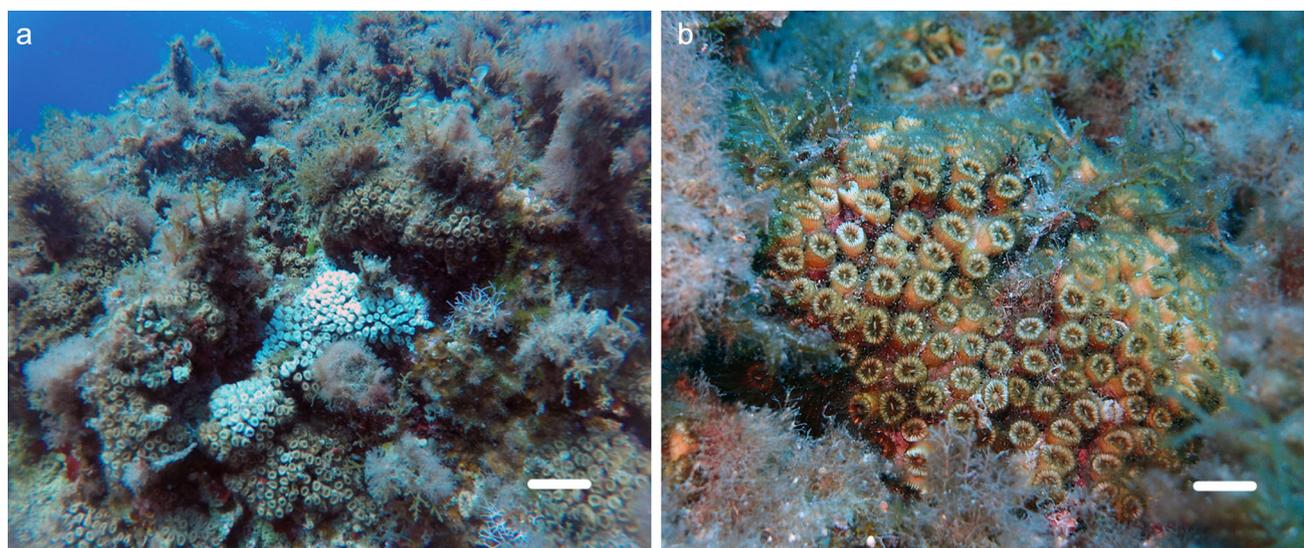

Fig. 1 Bed of *Cladocora caespitosa* among algae near Espardell Island (Formentera, Spain). a Irregular colonies comprising the bed, some partially dead (*scale bar* 10 cm). b Detail of a living colony (*scale bar* 1.5 cm). Photographs by Mar Soler and Paula Rodríguez-Flores (October 2016)
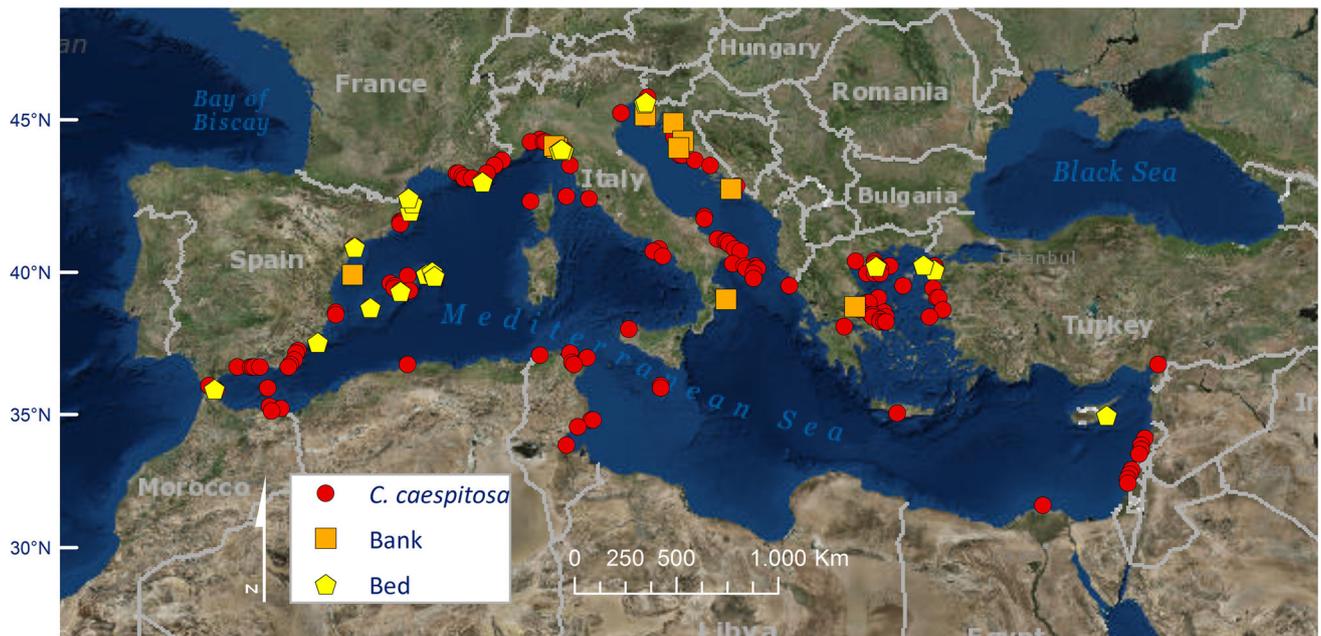
Fig. 2 Occurrence of *Cladocora caespitosa* (*red circles*) and the two types of assemblages analyzed: banks (*orange squares*) and beds (*yellow pentagons*)

Results

Ecological niche modeling and predicted distribution

A total of 17 variables remained after correlation analysis and were examined using the preliminary ENFA (ESM Table S3), which resulted in a final set of 11 variables used in the rest of the analyses (Table 1). Final ENFA results

concluded that all variables from this final set were relevant for marginality and/or specialization factors, thus contributing to explaining the presence of *C. caespitosa* across the whole Mediterranean basin (Table 1). According to the ENFA, the presence of *C. caespitosa* is related to waters with lower concentrations of calcite and phosphate than the mean conditions of the study area (Table 2; Fig. 3). Higher SST in summer and winter than mean conditions also seems to determine the presence of *C. caespitosa*. The

Table 1 Marginality and specialization factor scores of ecological niche factor analysis (ENFA) for each environmental predictor used to model the niche of *Cladocora caespitosa*, and fitted vector scores and results of permutation tests used to determine the significance of correlation of the variables with non-metric multidimensional scaling (NMDS) axes

Variables (units)	ENFA		Vector scores		Correlation			
	Marginality	Specialization	NMDS1	NMDS2	NMDS1	NMDS2	r^2	P
Bottom slope (°)	0.26	0.01	0.42	0.48	0.66	0.75	0.41	0.003
Calcite (mol m^{-3})	−0.38	−0.03	0.78	−0.43	0.87	−0.49	0.80	0.001
FRAC_AM (unitless)	0.00	−0.83	0.33	0.28	0.77	0.64	0.19	0.063
Mean winter K_d (m^{-1})	−0.36	0.17	0.74	−0.32	0.92	−0.40	0.65	0.001
Nitrate (μmol N L^{-1})	−0.28	−0.23	0.05	0.52	0.10	1.00	0.27	0.007
PAR max. (mol quanta m^{-2} d^{-1})	0.24	0.04	−0.41	0.64	−0.54	0.84	0.58	0.001
Phosphate (μmol P L^{-1})	−0.44	0.17	0.46	0.8	0.49	0.87	0.85	0.001
Mean summer SST (°C)	0.28	−0.11	−0.34	−0.15	0.00	0.40	0.14	0.111
Mean winter SST (°C)	0.32	0.09	−0.2	0.54	−0.35	0.94	0.33	0.007
Mean winter wave height (m)	−0.27	−0.39	0.09	0.61	0.14	0.99	0.38	0.001
SHAPE_MN (unitless)	−0.28	0.17	0.03	0.58	0.06	1.00	0.34	0.003

r^2 squared correlation coefficient, *SST* sea surface temperature, *PAR* photosynthetically available radiation; K_d diffuse attenuation coefficient, *FRAC_AM* area-weighted mean fractal dimension index, *SHAPE_MN* mean shape index

Table 2 Summary statistics of variables used in environmental niche modeling and non-metric multidimensional scaling for *Cladocora caespitosa* for the whole study area, for cells with presence records, and for the different coral assemblages (banks and beds)

Variables (units)	Study area		Presence		Banks		Beds	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Bottom slope (°)	1.75	0–18.65	2.45	0.034–9.88	2.46	0.68–6.58	2.15	0.36–4.92
Calcite (mol m^{-3})	0.004	0–0.056	0.0015	0–0.038	0.001	0.0002–0.004	0.002	0–0.009
FRAC_AM (unitless)	1.097	0–1.14	1.102	1.03–1.14	1.09	1.084–1.106	1.09	1.04–1.14
Mean winter K_d (m^{-1})	0.22	0.02–4.03	0.101	0.03–0.44	0.09	0.06–0.18	0.11	0.03–0.31
Nitrate (µmol N L^{-1})	1.26	0.003–12.5	0.78	0.25–1.087	0.66	0.48–1.01	1.06	0.29–1.99
PAR max. (mol quanta m^{-2} d^{-1})	57.35	36.16–64.61	58.55	53.39–63.28	56.55	54.78–58.33	57.45	53.44–60.98
Phosphate (µmol P L^{-1})	0.18	0.024–0.83	0.12	0.034–0.21	0.09	0.03–0.18	0.15	0.058–0.22
Mean summer SST (°C)	20.34	13.57–25.08	21.22	18.57–24.75	20.82	19.66–21.63	20.79	18.57–23.79
Mean winter SST (°C)	14.72	6.5–22.85	16.14	12.41–20.46	15.13	13.27–16.33	15.53	12.66–19.32
Mean winter wave height (m)	1.33	0.18–3.51	1.19	0.89–1.62	1.1	0.91–1.4	1.27	0.94–1.57
SHAPE_MN (unitless)	2.6	0–5.16	2.38	1.27–5.05	1.94	1.42–2.89	2.39	1.31–4.81

FRAC_AM area-weighted mean fractal dimension index, *PAR max.* maximum photosynthetically available radiation, *SST* sea surface temperature, *SHAPE_MN* mean shape index
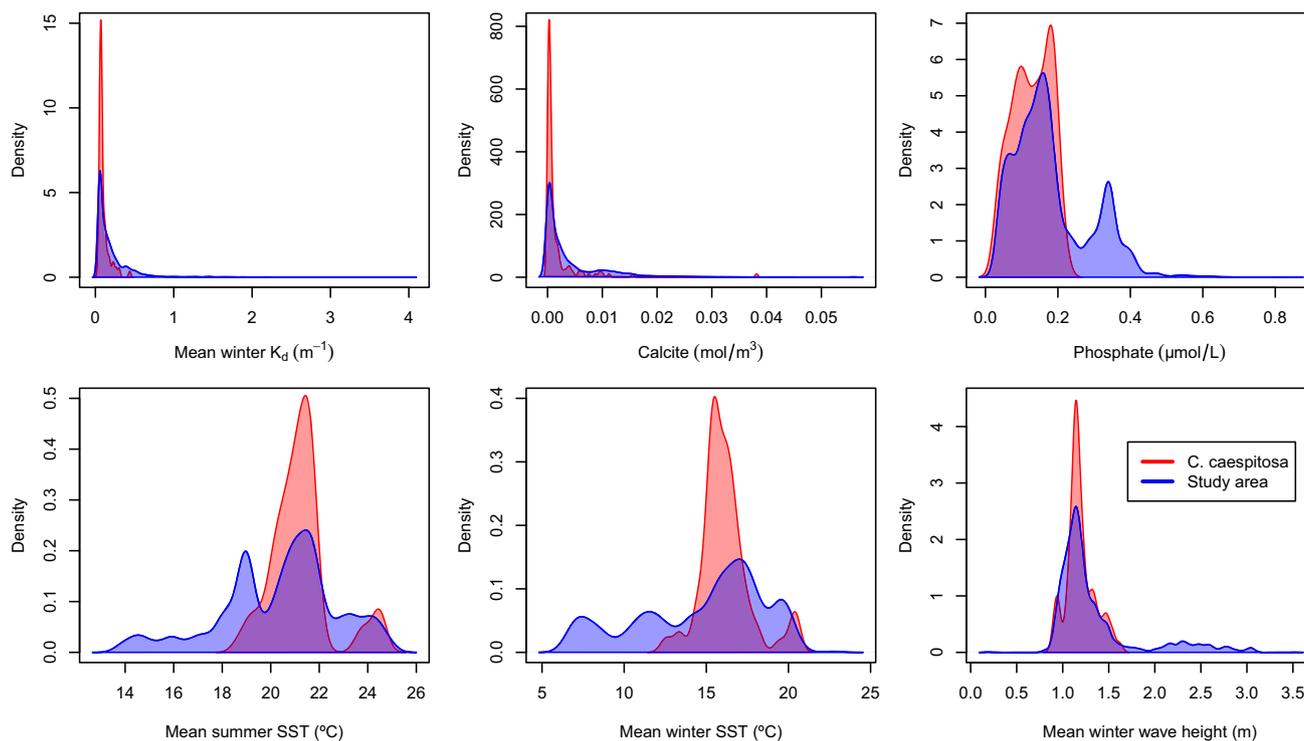
Fig. 3 Kernel density plots of the distribution of occurrences of *Cladocora caespitosa* (*red*) against habitat variables in the study area (*blue*)

coral occurs in waters with lower values of K_d (<0.44 m^{-1}) and higher maximum PAR, evidencing its preference for clear waters. In addition, coasts with lower mean wave height than the whole area are more suitable for the species. Finally, we found that lower mean shape index (SHAPE_MN) was also relevant for the species, indicating

that the species mainly occurs on coastlines with complex shapes.

GLM had lower AIC (AIC = 16) and fitted our data better ($D^2 = 100\%$) than quadratic and cubic smoothing splines used by GAM (AIC = 68). Six variables were identified as significant by the GLM (ESM Table S4). GLM validation achieved an AUC = 0.99 and

sensitivity = 0.94 (ESM Fig. S1). The GLM prediction discriminated between the known range of distribution of the species and the rest of the study area, but was not able to ascertain the appropriateness for the species in the Mediterranean Sea (ESM Fig. S2).

The MD analysis showed suitable habitat for the occurrence of *C. caespitosa* only within the Mediterranean Sea basin, excluding the Black Sea and Atlantic Ocean (Fig. 4).

Discrimination of factors influencing the types of assemblages

The NMDS ordination plot (stress value = 0.15) showed that the two types of assemblages (banks and beds) shared environmental space, with the exception of the banks located in the Adriatic Sea (Fig. 5a, b). The second axis of the ordination (NMDS2) described the multivariable gradient better, with the largest variance among clusters, and the major direction of the gradient was indicated by the phosphate concentration and wave height, which showed highly significant correlations ($p < 0.001$) with the NMDS2 axis (Table 1). *Cladocora caespitosa* banks were mostly found in waters with lower values of phosphate and wave height than beds (Fig. 5c, d).

We found only two subregions that separated from the others—the Adriatic and Tyrrhenian Sea (Fig. 5b). Adriatic waters, where the biggest banks are now found, had significantly lower phosphate concentrations and wave height (Fig. 5b). In contrast, the Tyrrhenian Sea assemblages are found in waters with higher calcite concentrations and lower water clarity.

MPA gap analysis

We found that eight of the ten banks and 16 of the 21 beds were represented in MPAs (ESM Table S5). Of the 156 occurrences analyzed, 61 (39.1%) were included in protected areas (ESM Table S6). The Natura 2000 network provides higher coverage than other national and international areas recognized by governments or under regional and international conventions. Moreover, there is overlap between the Natura 2000 network and other protected areas; rarely was a location protected exclusively by a non-Natura 2000 site. Regions covered by Natura 2000 network sites showed HS scores slightly higher (mean = 0.35) than those obtained for non-Natura 2000 sites (mean = 0.29). The median HS value inside the Natura 2000 network was also superior (Fig. 6).

Discussion

Environmental response of *C. caespitosa* and its assemblages

This is the first study disentangling the environmental factors that determine the distribution and development of the main assemblages of the endemic reef-former *C. caespitosa* across the Mediterranean Sea. We found that the most extensive populations (banks) shared similar conditions to most of the beds (Fig. 5). Phosphate concentration and wave height seem to be convergent factors influencing the presence of this emblematic species and the distribution of its extensive bioconstructions. Gradients of these
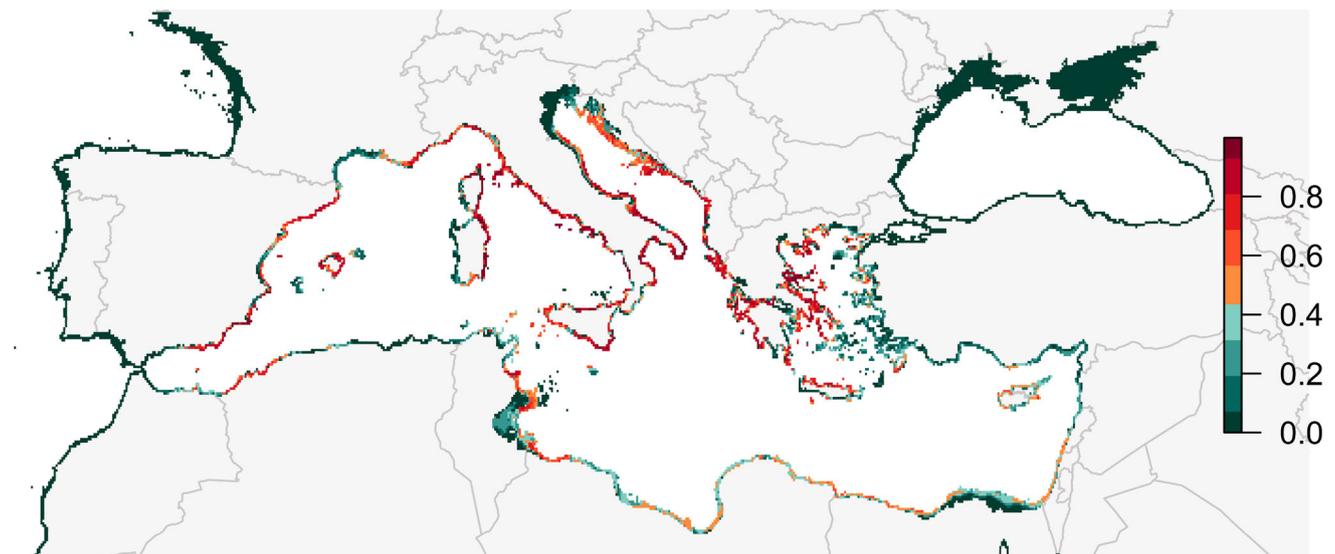

Fig. 4 Potential distribution of *Cladocora caespitosa* predicted by the Mahalanobis distribution algorithm. Habitat suitability ranges from 0 (less suitable) to 1
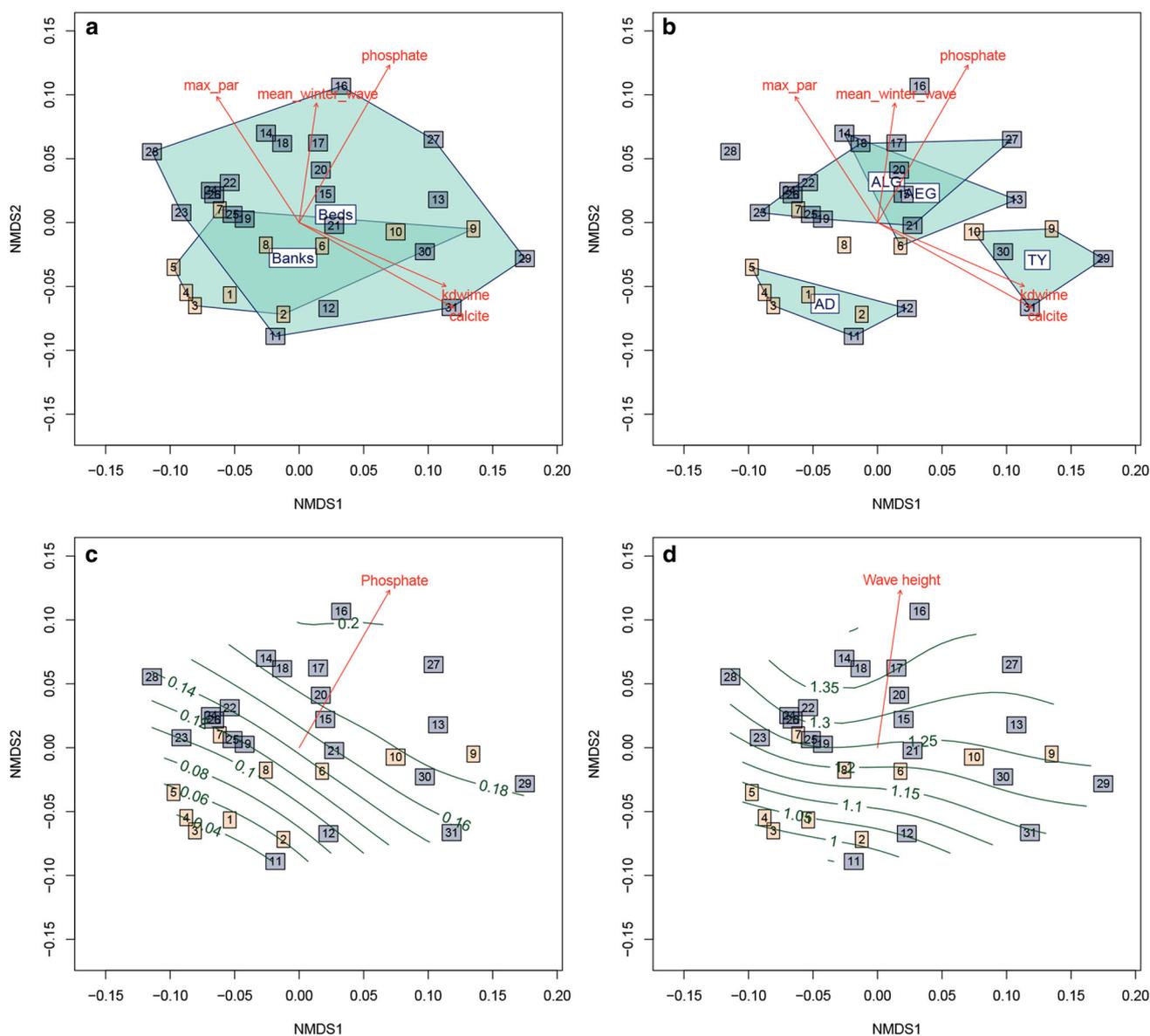
Fig. 5 Non-metric multidimensional scaling (NMDS) ordination of 31 populations of *Cladocora caespitosa* based on their environmental dissimilarity and Mediterranean subregions proposed by Notarbartolo di Sciara and Agardy ([2010](#)): Alborán Sea, Algero-Provencal Basin (ALG), Tyrrhenian Sea (TY), Adriatic Sea (AD), Tunisian Plateau/Gulf of Sidra, Ionian Sea, Aegean Sea (AEG), and Levantine Sea. **a** Extensive populations (banks; in *orange*) show separate conditions

with respect to most of the beds (in *blue*). Vectors of environmental variables which significantly ($p < 0.001$) contributed to NMDS axes are plotted in *red*. **b** Adriatic and Tyrrhenian subregions are separate from the other subregions. Smooth surfaces of relevant variables found in the previous NMDS fitted using a generalized additive model using the R function "ordisurf" for **c** phosphate, and **d** wave height

variables were significantly related to the degree of development of the assemblages, as banks were found in locations with lower wave height and phosphate concentration. In addition, ENFA inferred that *C. caespitosa*, regardless of its type of assemblage, is favored by waters with (1) lower concentrations of calcite and phosphate than the mean conditions of the study area, (2) higher mean SST in summer and winter, (3) lower values of K_d and higher PAR max., evidencing its preference for clear waters, (4)

lower mean wave height, and (5) lower mean shape index (SHAPE_MN), indicating that the species mainly occurs on complex coastlines.

Our model inferred a preference of *C. caespitosa* for water clarity, and also that larger bioconstructions (banks) occur in clearer waters on average. This agrees with other studies that relate high-light conditions with maximal symbiont (zooxanthellae) density (Hoogenboom et al. [2010](#); Ferrier-Pagès et al. [2011](#)), and maximal autotrophic

Fig. 6 Comparison among habitat suitability (HS) values predicted by Mahalanobis distance for *Cladocora caespitosa* in the entire study area and the regions covered by marine protected areas (MPAs) in the Natura 2000 network or not. *Notches* at medians allow comparison among different sample sizes and show that median HS scores predicted within the Natura 2000 network are superior than those for other MPAs
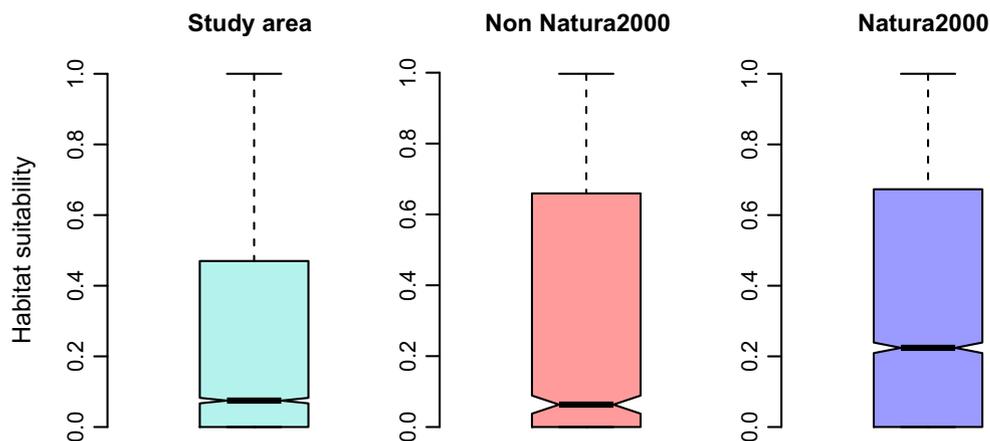
carbon acquisition (Fonvielle et al. 2015), similar to tropical symbiotic corals (Ferrier-Pagès et al. 2013). Nevertheless, unlike in tropical latitudes, the strong seasonal changes in irradiance in the Mediterranean Sea might drive the coral host and its symbionts to continuous metabolic acclimatization. In fact, metabolic optimization for acquisition of inorganic or organic nutrients via autotrophy or heterotrophy depending on light intensity has been shown in several studies of *C. caespitosa* (Hoogenboom et al. 2010; Tremblay et al. 2012; Ferrier-Pagès et al. 2013). Zooxanthellae autotrophy is especially important during summer (Hoogenboom et al. 2010; Ferrier-Pagès et al. 2011), when the coral has a higher growth rate (Montagna et al. 2007). In winter, when light conditions and temperature are not optimal, heterotrophy plays an important role maintaining metabolism and calcification (Ferrier-Pagès et al. 2011). While we found a positive correlation between occurrence and water clarity, this species' ability to regulate autotrophic and heterotrophic metabolism probably provides the versatility required under the Mediterranean's changing light conditions. Metabolic versatility may allow *C. caespitosa* to live in contrasting light conditions, including turbid waters (especially those derived from organic matter) and deeper waters with strong currents (Laborel 1961; Peirano et al. 1998; Kružić and Benković 2008; Rodolfo-Metalpa 2008a), by shifting to heterotrophy in response to light limitation, as high food supply by currents in turbid waters has also been found to enhance skeletal growth (Ferrier-Pagès et al. 2013). However, the Marmara Sea (excluding the Dardanelles) and a large expanse of the Black Sea are out of the observed tolerance range for water clarity (Table 2).

The Mediterranean coasts, unlike those of the Black Sea, are characterized by nutrient-poor water and widespread phosphate deficit. The size of reef formations follows a gradient in which extensive bioherms (banks) grow at the lowest concentrations of phosphate (ranging from 0.03 to

0.18 μmol P L^{-1}) (Fig. 5). We found the same tendency in relation to the general distribution of the coral as it occupies seawater with lower concentrations of phosphate than the mean found in the study area (Fig. 3). One explanation for these results could be the negative effect of phosphate on calcification of marine exoskeletons (Simkiss 1964; Fabricius 2005), as found at Mljet bank where coral calcification decreased or even completely stopped when exposed to eutrophication (Kružić et al. 2012). Recently, El Kateb et al. (2016) found that the extinction of some populations of *C. caespitosa* in Gabes was probably caused by discharge from the phosphate industry among other factors. Moreover, Fabricius (2005) found that long-term exposure to high levels of nutrients caused more changes to coral communities than short-term exposure. Although the phosphate discharges reported by some of these studies also represented a complete degradation of the environmental system, and should be interpreted with caution, the long-term averaged data used in our study (from 1922 to 1986) might be evidencing a large-scale response of *C. caespitosa* to phosphate concentrations. In addition, excess phosphate probably limits *C. caespitosa* growth, in particular the development of banks, by enhancing macroalgal competition for space and the proliferation of mucilage that can cover the coral colonies (Kružić and Požar-Domac 2007). However, in some oligotrophic waters, such as in Columbretes and Formentera islands, *C. caespitosa* shows some ability to compete with algae, forming mixed assemblages and developing some of the most extensive populations known to date (Kersting and Linares 2012; Kersting et al. 2017). Thus, further research is required to test the sensitivity of *C. caespitosa* to phosphate concentration.

We found that *C. caespitosa* does not occur where the average winter wave height is higher than 1.6 m, which could prevent the occurrence of this coral in the Atlantic Ocean, where, in addition, the mean irradiance is about 20% lower at similar latitudes than in the Mediterranean

(Templado 2014). The moderate relevance in ENFA of the landscape metric (SHAPE_MN) might also indicate that complex coastlines provide habitats sheltered from high waves at shallow depths. In addition, NMDS results highlight that wave height where banks occur is significantly lower than in bed locations. Schiller (1993) also noted that colony size is limited by storm disturbance and boring organisms in shallow habitats. The borers erode the lower dead part of the colonies, weakening them and making them more vulnerable to wave action. Colonies also occur in places subject to strong or moderate currents (Laborel 1961; Kružić et al. 2008a), which allow water exchange and can provide abundant suspended particulate food. Further, a complex coastline could be associated with irregular bottom topography and microscale habitat heterogeneity. This combination allows the coral to occupy sheltered habitats uniting wave protection and elevated water exchange with the open sea, common features in the location of two of the main buildups, in Mljet National Park (Kružić and Benković 2008) and Columbretes Island (Kersting and Linares 2012). Previously, Kersting and Linares (2012) suggested that hydrodynamic conditions, bottom morphology and the reproductive strategy of the species converge for the development of large bioconstructions.

All occurrences of *C. caespitosa* were in waters with mean winter SST above 12 °C, suggesting that low SST limits overall distribution of the species. We also found that this coral prefers higher SST in summer and winter than the mean conditions. Our results are consistent with those obtained by Montagna et al. (2007) who point to SST as an important factor for calcification in *C. caespitosa*, with growth ceasing below 14–16 °C. Such low mean SST can only occur during winter in some regions of our study area, mainly the Black Sea, the northern Adriatic and Atlantic, and the Gulf of Lyon. Similarly, SST is significantly correlated with corallite growth rate and calcification (Kružić et al. 2012); the optimum temperature for these processes is often coincident with that for photosynthesis of zooxanthellae.

It has been hypothesized that the largest fossil banks of *C. caespitosa* grew in a warmer past Mediterranean Sea (Peirano et al. 2004). However, this is somehow contradictory to the recent mortality events attributed to global warming (Cerrano et al. 2000; Rodolfo-Metalpa et al. 2000, 2005; Garrabou et al. 2009; Kersting et al. 2013a; Kružić et al. 2016). In aquarium experiments on thermal tolerance of *C. caespitosa* collected in the Ligurian Sea, Rodolfo-Metalpa et al. (2005) found that a long-term increase in SST at 24 °C or above could produce gradual necrosis of tissues and kill the coral. Nevertheless, Kersting et al. (2013a) pointed out that *C. caespitosa* was exposed to temperatures greater than 24 °C for more than 60 d in

Columbretes Islands without significant necrosis. These differences in mortality in aquaria (Ligurian Sea) and in situ (Columbretes Islands) could be related to thermal acclimatization (as the colonies are naturally subjected to different thermal regimes), or to other factors acting together with temperature such as pathogens or food shortage (Kersting et al. 2013a). The different reproductive period observed between Adriatic and western Mediterranean populations (early summer vs early autumn, respectively; Kersting et al. 2013b) may suggest that thermal acclimatization may occur in different areas. On the other hand, Kersting et al. (2015) investigated the potential local adaptation to thermal stress in two populations in the western Mediterranean subjected to contrasting thermal and necrosis histories and found no significant differences between populations. The fact is that recurrent mortality events were coincident with registered positive thermal anomalies during summer (Cerrano et al. 2000; Garrabou et al. 2009; Kersting et al. 2013a; Jiménez et al. 2014).

Bottom slope and calcite were not useful environmental variables. Almost the entire study area is inside the coral's suitable range of slope. Calcite concentration has not been shown to be a limiting factor for this coral; on the contrary, *C. caespitosa* and its extensive accretions are found in waters with lower calcite concentrations than the mean of the study area. Aragonite is the primary constituent of the external skeleton of this coral (Sondi et al. 2011) and its saturation in water is proportional to calcite concentration. Though calcification is a complex process, probably affected by environmental stresses such as ocean acidification and climate change (e.g., Hoegh-Guldberg et al. 2007), precipitation of aragonite in corals is mainly controlled by the intra-skeletal organic matrix rather than surface ocean pH or calcium carbonate in seawater (Falini et al. 2015).

Assemblages found in the Adriatic and the Tyrrhenian Sea (Ligurian Sea) differed environmentally from elsewhere (Fig. 5b). This provides evidence for coral adaptation to the particular conditions found in each Mediterranean subregion regarding phosphate and calcite concentrations, water clarity, and the hydrodynamics and currents associated with different wave height. Another indication of the species' ability to adapt to the conditions of the different Mediterranean subregions is the unusual plasticity of its reproductive traits (i.e., gonochoric vs hermaphroditic, oocyte size, spawning period) that differs in the western Mediterranean populations from those of the Adriatic (Kersting et al. 2013b).

Potential distribution and uncertainties of the analyses

Our model did not find suitable habitats outside the Mediterranean Sea, even though MD can estimate the potential niche, wider than the realized niche (Farber and Kadmon 2003). This result suggests a strong environmental barrier preventing the species from expanding to the Atlantic and the Black Sea. Water clarity, winter SST, calcite, nitrate, and wave height seem to be important in preventing the presence of the species outside the Mediterranean Sea according both to ENFA and GLM. In addition, suitable habitats were detected by the MD model on Algerian coasts, and by GLM in the Gulf of Cadiz beyond the Strait of Gibraltar, corresponding with regions that require additional sampling. However, common uncertainties associated with global models may affect the ENM. Although we tried to use the most relevant variables for the species, there are other factors such as large-scale historical constraints, sampling bias, dispersal limitation and biotic interactions that are known to affect species distributions (e.g., Svenning and Skov 2004; Beale and Lennon 2012; Chefaoui and Serrão 2017) and are difficult to take into account. The MD algorithm renders the distance between the environmental conditions optimal for the species and a given point (Calenge et al. 2008). Thus, suboptimal locations may show low habitat suitability despite being able to host populations. Given the lack of reliable absences, we had to select pseudo-absences from pre-defined unsuitable habitats for the GLM. Due to the environmental distance between the Mediterranean and the adjacent seas, GLM could discriminate between the known distributional range and the rest of the study area, but it was not able to ascertain the appropriateness for the species in the Mediterranean Sea.

There is also uncertainty regarding the lower suitability of the majority of the North African coast as it might be related to sampling bias also observed for other species such as the seagrass *Cymodocea nodosa* (Chefaoui et al. 2016) which may produce inaccurate estimations of the niche and derived distributions (e.g., Kadmon et al. 2004; Hortal et al. 2008). In addition, some of the dissimilarities between the general trends identified here, and research studies on local conditions might be explained by the effect of scale. The spatial resolution available for oceanic variables, coupled with the large extent of our study, do not allow discrimination of microhabitats or factors determining local complexity (e.g., high-resolution bottom morphology) that may affect the presence of the coral. Local studies have demonstrated the high ecological plasticity of *C. caespitosa* (e.g., Hoogenboom et al. 2008; Kersting and Linares 2012; Kersting et al. 2017a). It can live in different light and SST conditions (Rodolfo-Metalpa et al. 2008b),

as well as in habitats ranging from photophilic communities to circalittoral coralligenous assemblages (Kersting and Linares 2012). While turbid waters with alluvial input and high concentrations of nutrients have been reported for banks and beds located in the eastern Ligurian Sea (Peirano et al. 1999) and in the Adriatic (Kružić and Benković 2008; Pitacco et al. 2014), the coral assemblages of Columbretes and Formentera islands are bathed by clear oligotrophic waters far from any alluvial input. Our study does not allow understanding of microconditions; instead, we describe global preferences that determine the distribution of this coral on a large scale, such as the contrasting conditions found for bioherms of similar degrees of development among Adriatic, Thyrrenian, and other Mediterranean subregions.

Dispersal capabilities and biotic factors may also influence the growth and distribution of colonies. *Cladocora caespitosa* polyps release eggs and sperm bundles covered in a mucus coating, and fertilization takes place in the surrounding water (Kružić et al. 2008a). This mechanism forces the eggs to remain near the parental colonies and probably causes the patchy distribution of the coral (Kersting and Linares 2012), which shows a tendency for a contagious dispersion, also favored by its asexual reproduction by fragmentation or polyp removal (Kružić et al. 2008a). The negative buoyancy of the eggs may also favor retention mechanisms (Kersting et al. 2014a). Therefore, the reproductive biology of this coral reduces dispersal and self-recruitment predominates, with sporadic long-distance dispersion and low recruitment rates (Casado-Amezúa et al. 2014; Kersting et al. 2014a). Thus, current banks and beds of *C. caespitosa* probably come from an initial stochastic factor, a successful sporadic settlement event of larvae supplied from an external source, and it is followed by subsequent self-recruitment. Under this mode of dispersal, it is possible that not all suitable habitats for the species have been colonized, and therefore, we may have underestimated potential areas.

There are also biotic interactions which may affect distribution. Peirano et al. (1998, 2004) hypothesized that, even if the species is competing successfully with frondose algae in particular places, its local abundance is primarily controlled by competition with those species. Non-calcareous erect algae displace other rocky-bottom organisms where light is not a limiting factor and when the availability of nutrients is abundant and fluctuating (Zabala and Ballesteros 1989). Conversely, photosynthetic suspension feeders such as *C. caespitosa* will be favored over frondose algae in intermediate situations of dim light and sufficient particulate organic matter due to their capacity to combine autotrophic and heterotrophic feeding modes. Therefore, although this coral has a preference for high irradiance, the dominance of photophilic algae and the impact of waves in

Mediterranean shallow waters probably limits the occurrence of *C. caespitosa* banks and beds to deeper waters or dim light environments at which the algal compensation point occurs (Morri et al. 1994; Peirano et al. 1999; Rodolfo-Metalpa et al. 1999). Despite that, mixed assemblages of autochthonous algae and colonies of *C. caespitosa* can be found in some places, such as Columbretes and Formentera islands (Kersting and Linares 2012; Kersting et al. 2017a, b). A negative effect of invasive algae on the coral has also been reported. The invasive alga *Caulerpa taxifolia* was identified as the cause of the death of a population on the French coast (Morri et al. 2001). Another invasive alga (*Caulerpa racemosa* var. *cylindracea*) smothered the coral causing retraction and tissue damage on the Mljet *C. caespitosa* bank (Kružić et al. 2008b).

MPA effectiveness

We found that Mediterranean MPAs protect eight of the ten banks, 16 out of the 21 beds, and 39.1% of presence locations of *C. caespitosa* not classified as an assemblage. Most of the banks (80%) are currently protected; Bonassola and Atalanta are the only banks not covered (although they are close to Fondali Ponta Levanto and Koilada Kai Ekvoles Spercheiou–Maliakos Kolpos Natura 2000 sites, respectively). Despite the efforts to date to protect the species, seven of the studied beds remain unprotected (ESM Table S5). In addition, less than half the occurrences of the species are within boundaries of any MPA system (ESM Table S6). We found that Mediterranean MPAs in the Natura 2000 network provide higher coverage of current locations of the coral and preserve regions with higher habitat suitability than other national and international MPA systems. Despite the fact that the main threat to the species seems to be climate change, protected sites may play an important role preserving *C. caespitosa* from other anthropogenic factors such as anchoring, dredging, fish farming or bottom trawling. *Cladocora caespitosa*, similar to other long-lived coral species, is characterized by a slow growth rate (Kersting and Linares 2012) and slow dynamics (Kersting et al. 2014a) which makes it more susceptible to threats. Given the importance of this endangered coral as the only forming extensive accretions in the Mediterranean basin, and its role in the maintenance of the structure of benthic communities, protection offered by current MPAs is crucial. Though we cannot appraise in this study whether current protection will be enough in the future, an increase in the coverage of MPAs and measures to preserve the clarity of the water and prevent phosphate discharges near banks and beds could help to preserve this emblematic species.

This study is of interest at a time of identifying trends and sites that could be targeted for monitoring actions.

Studies on the present environmental response of this coral, besides providing insight into its current status, may help identify reefs that become more marginal or suboptimal through changing environmental parameters (Kleypas et al. 1999). As Perry and Larcombe (2003) suggested, it is more appropriate that these kinds of marginal coral settings be considered not as restricted or disturbed reef systems, but as alternative states of coral assemblages. Much more research is needed to understand the dynamics of these so-called marginal reefs.

Although the great ecological plasticity of *C. caespitosa* is an advantage in a changing and diverse environment, some of the ongoing or future changes identified or expected in the Mediterranean (Templado 2014) may have an adverse impact on this species. The high frequency of mortality of this coral over the last decade probably exceeds its recovery potential, as shown by low recruitment rates (Kersting et al. 2014a). Important potential impacts include the high frequency of short-term extreme events such as heat waves and severe storms, the strengthening of stratification, slowing down of thermohaline circulation, increase in nutrient concentrations, decline in water transparency, and spread of mucilage and invasive algae (Kersting et al. 2014b, 2015; Casado-Amezúa et al. 2015). Considering that the projected progressive warming of seawater might lead to higher metabolism rates and lower prey availability due to longer stratification periods (Coma et al. 2009), the survival threshold of this coral could be exceeded sooner than expected under the influence of single stressors (Movilla et al. 2012). Mass mortality of other scleractinian corals and gorgonian species has already reached depths of 45 m in the Adriatic Sea (Kružić et al. 2016). Since colonies living at shallower depths are more exposed to thermal stress, they will probably suffer higher mortality than those in deeper waters, as has already been found in the Columbretes Islands (Kersting et al. 2013a). If this is so, it is expected that under a scenario of increasing frequency of positive thermal anomalies, deep colonies and populations may be important for the long-term persistence of the species. Further work is needed to determine the processes that affect the resilience of this species and how the different impacts interact synergistically on it, as well as the historical causes of the decline of its reefs. In addition, we recognize the urgent need to conserve this coral under the changing climatic conditions of the Mediterranean basin.

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