

1 **Modelling the spatial distribution of the seagrass *Posidonia oceanica* (L.)**  
2 **along the North African coast: implications for the assessment of Good**  
3 **Environmental Status.**

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6 Zucchetta M.<sup>1</sup>, Venier C.<sup>2</sup>, Taji M. A.<sup>3,4</sup>, Mangin A.<sup>5</sup>, Pastres R.<sup>1</sup>

7 <sup>1</sup> Department of Environmental Sciences, Informatics and Statistics. CEMAS – Centre for Estuarine and coastal Marine  
8 Sciences. University Ca' Foscari Venice, Italy

9 <sup>2</sup> National Research Council - Institute of Marine Science Venice, Italy

10 <sup>3</sup> University Hassan II-Casablanca, Faculty of sciences Ain Chock

11 <sup>4</sup> ACRI-EC, Casablanca, Morocco

12 <sup>5</sup> ACRI-ST, Sophia-Antipolis, France

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15 Corresponding Author: Matteo Zucchetta. Department of Environmental Sciences, Informatics and Statistics. CEMAS –  
16 Centre for Estuarine and coastal Marine Sciences. University Ca' Foscari Venice, Castello 2737/b 30122, Venice, Italy.

17 email: matzuc@unive.it; phone: +39 39 041 234 7732

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19 **Keywords**

20 *Posidonia oceanica*; Species Distribution Model; MERIS; remote sensing; Ecosystem Approach

21 **Highlights**

- 22
- We used satellite data to characterise environmental conditions in five large areas of the Mediterranean Sea

- 23 • Species Distribution Model for *Posidonia oceanica* has been developed to describe suitable habitats along the  
24 North African coast
- 25 • The ratio between the observed and modelled potential *P. oceanica* distribution has been computed to  
26 contribute to the assessment of the Good Environmental Status

## 27 **Abstract**

28 *Posidonia oceanica* (L.) Delile, 1813 is a seagrass species endemic to the Mediterranean Sea, which is considered as an  
29 indicator of environment quality in coastal areas. This species forms large meadows, which are sensitive to several  
30 anthropogenic pressures and the decrease in their extension is considered a priority issue for the Mediterranean Sea. The  
31 aim of this study was to develop a Species Distribution Model for *P. oceanica*, to be applied to the Mediterranean North  
32 African coast, in order to obtain an estimation of the potential distribution of this species in the region. The Species  
33 Distribution Model was calibrated using high resolution data from 4 Mediterranean sites, located in Italy and Spain, as  
34 the study area is a data-poor zone with regard to seagrass distribution (i.e. only for some areas detailed distribution  
35 maps are available). The model was then validated using available data concerning the North African coast. The  
36 probability of presence of the species in a given area was modelled using a binomial generalized linear model as a  
37 function of the bathymetry and water transparency, dissolved organic matter, sea surface temperature and salinity,  
38 mainly obtained from satellite data. Model selection procedure suggests that water transparency plays a major role, but  
39 also other variables, such as salinity and sea surface temperature, are important at larger spatial scales in explaining  
40 meadows distribution. The availability of high resolution time-series of input data allowed us to apply the validated  
41 model to the whole North African coast. Suitable areas are strongly related to the coastal realm, and cover a large  
42 portion of North African coasts, with Tunisian and Lybian ones being the most relevant zones for this species. In  
43 particular, the shelf of the Gulf of Gabes includes large areas with environmental conditions suitable for the species.  
44 Based on model prediction, we developed a robust indicator of potential habitat suitability, which could be used for the  
45 assessment of Good Environmental Status, as requested by the Ecosystem Based Approach, to be implemented at the  
46 scale of the whole Mediterranean basin in the framework of the Barcelona Convention.

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## 48 **1. Introduction**

49 Many human activities are regularly carried out in marine environments, to take advantage of the several benefits  
50 provided by these ecosystems (Halpern et al., 2008). In some areas, cumulative anthropogenic pressures may translate  
51 in a combination of impacts on different components of the ecosystems (Halpern et al., 2008; Halpern and Fujita, 2013).  
52 Consequently the management of marine resources should be achieved within a comprehensive governance. The  
53 recognition of these needs led to the adoption of an Ecosystem Based Approach as a policy principle, both within the  
54 European Union (EU), i.e. Marine Strategy Framework Directive (MSFD; 2008/56/EC), or within the framework of  
55 regional conventions, like the Helsinki and the Barcelona conventions (on the Protection of the Marine Environment of  
56 the Baltic Sea Area, and on the Protection of the Marine Environment and the Coastal Region of the Mediterranean). In  
57 particular, the Contracting Parties of the Barcelona Convention decided to progressively apply the Ecosystem Approach  
58 (EcAp) and define a roadmap for its implementation (UNEP MAP, 2008). Even if a full harmonization has not yet been  
59 achieved (Cinnirella et al., 2014) the UNEP MAP (Mediterranean Action Plan of the United Nations Environment  
60 Programme) EcAp shares many objectives and tools with the EU regulation, on the basis of the assessment of Good  
61 Environmental Status (GES; or Healty Enviroment) of an ecosystem. There is a large overlap between the MSFD  
62 descriptors and UNEP MAP EcAp ecological objectives (EO) (Cinnirella et al., 2014). However, there are some  
63 discrepancies in the number of indicators, hence hereafter we will refer to the UNEP EcAp objectives and indicators, if  
64 not explicitly stated. The role and application of ecological indicators is of paramount importance, as the UNEP MAP  
65 EcAp considers 64 indicators to assess 11 ecological objectives (UNEP MAP, 2013). Not all the indicators are already  
66 operational, and their definition and implementation can be quite troublesome, even for the components of the  
67 ecosystem that are well known or considered particularly important. Some tools that can be used to perform the  
68 assessment in a cost-effective manner are: remote sensing techniques and ecological models. The former can be used as  
69 a source of input data for the application of indicators in data poor areas (Garmendia et al., 2015). The latter are  
70 typically used for the extrapolation of reference conditions (Borja et al., 2012). Species Distribution Models (SDMs; i.e.  
71 tools that allow spatial predictions of environmental suitability for species; Peterson et al., 2011; Guisan et al., 2013), in  
72 particular, could be useful to improve the definition and application of ecological indicators dealing with the  
73 distribution of species or habitats.

74 Many of the indicators used within the implementation of the EcAp are based on the characteristics of biological  
75 elements, such as the ones related to the UNEP MAP EO 1 - Biodiversity (*Biological diversity is maintained*)  
76 (corresponding to Descriptors 1 of MSFD), EO 2 - Non-indigenous species (*Non-indigenous species do not adversely*  
77 *alter the ecosystem*) (Descriptors 2 of MSFD), EO 3 Harvest of commercially exploited resources (*Commercially*

78 *exploited fish and shellfish are within biological limits*) (Descriptors 3 of MSFD), and EO 4 - Marine food webs  
79 (*Alterations of marine webs do not have long term adverse effects*) (UNEP MAP, 2014) (Descriptors 4 of MSFD). To  
80 this regard, seagrasses are among the biological elements that could represent an important source of information for the  
81 fulfillment of the GES. In particular, *Posidonia oceanica* (L.) Delile, 1813 is the most abundant species (Ruiz et al.,  
82 2009), in the Mediterranean Sea, and it is commonly considered a good bio-indicator of the ecological status (e.g. see  
83 Marbà et al., 2006; Montefalcone, 2009). Indeed, indicators concerning *P. oceanica* have been already used in the  
84 implementation of the WFD directive (e.g. Gobert et al., 2009; Lopez y Royo et al., 2010). As regards the UNEP-MAP  
85 EcAP its distribution should be considered in the framework of the EO 1 - Biodiversity, in relation to the operational  
86 objectives 1.4 (*Key coastal and marine habitats are not being lost*) with the indicators 1.4.1 and 1.4.2 (*Potential*  
87 */observed distributional range of certain coastal and marine habitats listed under SPA – Special Protected Areas -*  
88 *protocol and Distributional pattern of certain coastal and marine habitats listed under SPA protocol*).

89 The development/application of numerical operational indicators presents two typical problems, such as: i) the lack of  
90 data in every area that should be evaluated; ii) the difficulties of defining reference conditions (UNEP MAP, 2013). For  
91 these reasons, the definition of indicators to assess the distribution characteristics of *P. oceanica* meadows could benefit  
92 of the use of remote sensed information and of modelling techniques, aimed at relating the distribution of the species to  
93 other environmental variables (SDMs).

94 In this work, particular attention is paid to the Southern Mediterranean coasts, as it was carried out within an EU FP7  
95 project (Marine Ecosystem Dynamics and Indicators for North Africa - MEDINA, [www.medinaproject.eu](http://www.medinaproject.eu)), aimed at  
96 assessing the coastal ecosystem status in North African countries, and at evaluating and enhancing the monitoring  
97 capacity for those regions. Indeed, in this area the availability and accessibility of field data is an issue, which constrain  
98 the definition and application of indicators (Garmendia et al., 2015).

99 The aim of this work is to show how remote sensing data can provide reliable input data for SDMs, supporting the  
100 definition and application of ecological indicators for the evaluation of environment status, with a particular attention  
101 for data-poor areas. The specific objectives are:

- 102 - to develop a distribution model for *P. oceanica*, to be applied to the coasts of North Africa, taking advantage of the  
103 Medium Resolution Imaging Spectrometer (MERIS) imagery;
- 104 - to show how SDMs can contribute to the evaluation of the status of North African coastal ecosystems;

105 - to give some recommendations on the choice of the most suitable scale of application, taking into account the  
106 resolution of remote sensed ocean colour products, GES evaluation scale, *P. oceanica* spatial heterogeneity and data  
107 availability.

## 108 **2. Materials and methods**

### 109 **2.1. Species and study area**

110 *P. oceanica* represents the most widespread seagrass species in the Mediterranean Sea (Ruiz et al., 2009). It forms  
111 continuous meadows from the surface to a maximum depth of about 40-45 meters (Procaccini et al., 2003; Ruiz et al.,  
112 2009). This species can occupy several types of substrate (Di Maida et al., 2013), such as rocky and sandy bottom, but  
113 is not present in areas influenced by estuaries, where the inputs of freshwater and fine sediments are too high  
114 (Procaccini et al., 2003). Several environmental drivers influence the presence of *P. oceanica*, such as: water  
115 temperature, salinity, currents, waves, sedimentation rate and, above all, water transparency (Zupo et al., 2006, Ruiz et  
116 al., 2009; Vacchi et al., 2014), even if the physiological role of light limitation is not completely known (Ruiz et al.,  
117 2009). The increasing human pressures on coastal zones, such as coastal development, pollution, trawling, and mooring,  
118 is leading to a regression of this species in the Mediterranean Sea, due to both direct and indirect impacts (Duarte, 2002;  
119 Ruiz and Romero, 2003; Montefalcone et al., 2007; Boudouresque et al., 2009; Marbà et al., 2012; Bonaccorsi et al.,  
120 2013). *P. oceanica* meadows are protected by the Habitat Directive 92/43/EU (Annex I, code 1120) and are included in  
121 the list of priority habitats of the SPA/BIO Protocol of Barcelona Convention (Relini and Giaccone, 2009).

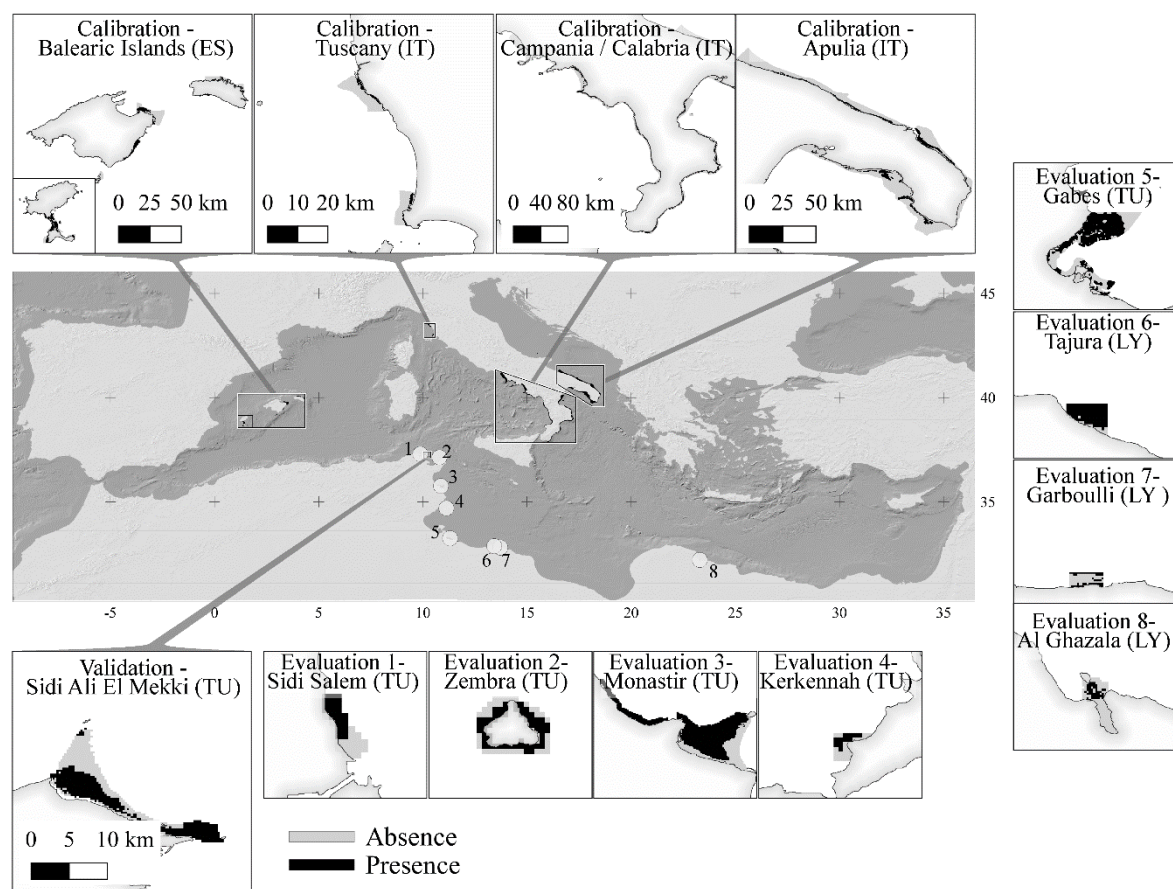
### 122 **2.2. Input data**

#### 123 **2.2.1. Response variable: *Posidonia oceanica* data**

124 Many studies describing the distribution of this seagrass species are available in the literature, but often these studies are  
125 carried out at different spatial scales and using different techniques (e.g. Zupo et al., 2006; Montefalcone, 2009; Innangi  
126 et al., 2015). For this study we selected the datasets for calibrating the distribution model on the basis of the following  
127 criteria: a) areas larger than 25 km along their major axis, in order to contain a sufficient number of records (i.e. raster  
128 cells of predictor variables); b) resolution high enough to take advantage of the 300m resolution of the MERIS imagery;  
129 c) data collected from 2003 to 2011 (to be coupled with MERIS); d) data include a description of the lower depth limit  
130 of distribution of *P. oceanica*; e) considering the limitations of ocean colour products in coastal waters, data should not  
131 be confined in an areas too close to the coast (lower limit at least at 1km from the coastline).

132 According to (Giakoumi et al., 2013), *P. oceanica* is unevenly distributed along all the North African coasts but datasets  
 133 fulfilling the above criteria were available only for the one site, namely (Sidi Ali El Mekki - Tunisia, Ben Cheikh Almi,  
 134 2007) (Fig. 1; see Table S.M. 1 for the main characteristics of the areas), which was used for validating the model. The  
 135 latter was calibrated using data collected in 4 large areas in Spain (Balearic Islands; 250 x 50km, in 2002;  
 136 <http://lifeposidonia.caib.es>) and in Italy, in the Apulia region (250 x 75km, data collected in 2006; CRISMA, 2006), in  
 137 the Campania and Calabria regions, (410 x 270km, data collected in 2002/2004; <http://www.sidimar.tutelamare.it/>), and  
 138 in the Tuscany region (68 x 25km, data collected in 2009; Mancusi et al., 2011) (Fig. 1; Table S.M. 1).

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141 Figure 1. Study area, with highlighted the indication of presence and absence of *P. oceanica* in the calibration,  
 142 validation and evaluation areas.

### 143 2.2.2. Independent variables: environmental data

144 The set of candidate independent variables (predictors) of the SDM model is summarized in Table 1. We used the  
 145 Medium Resolution Imaging Spectrometer (MERIS) sensor imagery of the Envisat mission, as the main source of input

146 data, due to its spectral and spatial resolution. MERIS data have been processed at their full resolution (ca. 300m).  
 147 Environmental variables that could not be derived from MERIS imagery were obtained from field sampling-, model- or  
 148 remote sensing- based data, available in public repositories. Seabed characteristics have been considered fixed in time,  
 149 while we used yearly average values of the other variables, in order to relate seagrass distribution data to the  
 150 environmental conditions at the time of seagrass data collection. Environmental variables are available for the whole  
 151 Mediterranean Sea, but for the aim of this work, MERIS data were reprocessed at full resolution only for the calibration  
 152 and validation areas and for the whole North African coastal area.

153

154 Table 1. Environmental variables considered in this study.

Label	Indicator	Units	resolution	Source	Availability	Reference
depth	Water depth	m	30 arc seconds	GEBCO	Fixed	Becker et al., 200
slope	Sea bottom slope	%	30 arc seconds	Bathymetry derived	Fixed	-
ave_kd	Coefficients of downwelling irradiance (kd490) - yearly mean	m <sup>-1</sup>	~300 m	SATELLITE - MERIS	2002-2011	This study
ave_adg	Absorption due to gelbstoff and detritus at 443nm - yearly mean	m <sup>-1</sup>	~300 m	SATELLITE - MERIS	2002-2011	This study
ave_zeu	Euphotic depth	m	~300 m	SATELLITE - MERIS	2002-2011	This study
ave_bbp	Particle backscatter at 443nm (bbp_443_gsm) - yearly mean		~300 m	SATELLITE - MERIS	2002-2011	This study
zeurel	Ratio zeu/depth	%	~300 m	SATELLITE - MERIS	2002-2011	This study
ave_sal	Salinity - yearly mean	PSU	~7 km	MODEL - MyOcean2	1987-2013	<a href="http://www.myocea">http://www.myocea</a>
ave_sst	Sea Surface Temperature - yearly mean	°C	2 km	SATELLITE - Aqua MODIS	2002-ongoing	<a href="http://emis.jrc.ec.euro">http://emis.jrc.ec.euro</a> Hoepffner et al., 20
ave_par	Photosynthetically Available Radiation - yearly mean	Einstein m <sup>-2</sup> year <sup>-1</sup>	2 km	SATELLITE - Aqua MODIS	2002-ongoing	<a href="http://emis.jrc.ec.euro">http://emis.jrc.ec.euro</a> Hoepffner et al., 20
rei	Relative Exposure Index (derived from fetch, wind frequency and wind speed) (Fonseca & Bell, 1998)		0.25 degrees (wind) & 30 arc seconds (fetch)	Wind data: SATELLITE - Cross-Calibrated Multi-Platform (CCMP)	1987-ongoing	Atlas et al., 2011; Fonseca & Bell, 1998

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### 157 2.2.3. MERIS data

158 All images available for the years in which seagrass distribution data were collected were considered and averaged by  
 159 years. For the whole North Africa coast all variables were extracted for the period 2003-2011. From MERIS data, we

160 estimated five input variables, namely: 1) the diffuse light attenuation coefficient, 2) coloured dissolved organic matter  
161 (i.e. the light absorption due to gelbstoff and detritus); 3) Particle backscatter at 443nm; 4) Euphotic depth, estimated  
162 considering the coefficient of extinction of light; 5) Euphotic depth/ depth ratio, combining the estimation of euphotic  
163 depth with the bathymetry.

#### 164 **2.2.4. Other variables**

165 Water depth was extracted from GEBCO bathymetry (Becker et al., 2009) and resampled at the same resolution of  
166 MERIS imagery. Bottom slope have been obtained from the resampled bathymetry data. Sea surface temperature and  
167 photosynthetically available radiation were obtained from Moderate Resolution Imaging Spectroradiometer (MODIS)  
168 data, extracted from the JRC EMIS portal (<http://emis.jrc.ec.europa.eu>; Hoepffner et al., 2010). Water salinity has been  
169 extracted from modelled reprocessed data (<http://www.myocean.eu>). In order to estimate wind induced disturbance of  
170 waves, a Relative Exposure Index (Fonseca and Bell, 1998) has been computed using satellite collected wind data  
171 (Atlas et al., 2011) and fetch maps (300 m resolution) estimated following the Shore Protection Manual (Rohweder et  
172 al., 2008).

173 All data have been interpolated at the resolution of MERIS data.

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### 175 **2.3. Numerical analysis**

176 Species Distribution Models are statistical tools relating species distribution to environmental conditions. In order to  
177 develop the distribution model for *P. oceanica*, a set of presence and absence data are needed, possibly recorded in  
178 areas covering the different range of environmental conditions of the study area. Data concerning *P. oceanica*  
179 distribution are typically summarised by presence/absence maps, discriminating occupied zones from those not  
180 occupied by meadows in a given area. To link distribution with environmental data, the presence/absence maps were  
181 converted in rasters of the same extent, resolution and alignment of the ones representing physical-chemical variables.  
182 Biological and environmental data were overlaid to build a matrix in which each row represents one raster cell and each  
183 column a variable (*P. oceanica* presence/absence and environmental variables).

#### 184 **2.3.1. Calibration and validation dataset**

185 The available data were split in three dataset: 1) calibration; 2) inner validation; 3) validation. Data from the calibration  
186 areas were extracted by a random sampling stratified per area: 2000 observations were extracted for each site and putted  
187 together in the calibration dataset (8000 observation). The remaining observations (about 64000) were grouped in the  
188 inner validation dataset and used for a first test of the model. The validation dataset is composed by 1046 observations.



189 Available data of *P. oceanica* distribution for North African coasts not satisfying all the criteria to be included in the  
190 calibration dataset, see Fig. 1, were used to further evaluate model prediction capabilities. Most datasets came from  
191 small sized areas of Lybia (Pergent et al., 2006; PNUE-PAM-CAR/ASP, 2009) and Tunisia (El Asmi et al., 2003;  
192 Orueta & Limana, 2003; Vela et al., 2005; Ben Cheikh Almi, 2007; PNUE-PAM-CAR/ASP, 2009) apart from data  
193 concerning the large area of the Gulf of Gabes (Tunisia, Hattour and Ben Mustapha, 2013) (Figure 1; Table SM. 1).

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### 195 **2.3.2. Development of *Posidonia oceanica* Distribution model (PoDM)**

196 Binomial Generalized Linear Models (GLMs) have been fitted to link presence and absence of *P. oceanica* to the  
197 predictors considered in this study. As regarding model selection, in this study 15 alternatives model structures (i.e.  
198 combination of different predictors) were considered, belonging to 5 different groups of models (Table 2) according to  
199 the following alternative hypotheses concerning the dependence of the probability of presence on *P. oceanica*  
200 distribution on the subset of environmental variables : 1) depth and the diffuse attenuation coefficient; 2) depth in  
201 combination with water transparency-related variables; 3) depth, water transparency and bottom morphology; 4) bottom  
202 depth and morphology, water transparency and other chemical-physical variables (salinity and shelter from wind  
203 induced waves); 5) all the previously considered factors and water temperature. For each group of models, alternative  
204 formulations have been considered, in order to assess, in particular, interactions of depth and the diffuse attenuation  
205 coefficient of light versus their additive effect (Table 2).

206 The selection of the best model was based on the Akaike Information Criterion, corrected for small samples ( $AIC_C$ ;  
207 Grueber et al., 2011). In case of a lack of support for one single 'best' model ( $\Delta AIC$  smaller than 4 for the two models  
208 with the lower  $AIC_C$  values), predictions of different models were combined computing the weighted average  
209 predictions, using  $AIC_C$  weights ( $W_{AIC}$ ) (Burnham and Anderson 2002) for the set of models whose cumulative weight  
210 ( $W_{AIC}$ ) represents 95% of the total ensemble. Calculations were carried out using the 'MuMIn' (Barton, 2014) packages,  
211 within the R statistical environment (v. 3.1.1; R Core Team 2014).

212

213 Table 2. Candidate formulations considered in the model selection procedure.

Category	Mod	Formulation
depth and light attenuation	1. M1	depth+ave_kd
	2. M1a	depth*ave_kd
depth and variables related to water transparency	3. M2a	depth*ave_kd+ave_par+ave_radg+ave_bbp
	4. M2b	depth+ave_kd+ave_par+ave_radg+ave_bbp
	5. M2c	depth+ave_kd+ave_par+ave_radg+ave_bbp+zeurel
	6. M2d	depth*ave_kd+ave_par+ave_radg+ave_bbp+zeurel
depth, variables related to water transparency and sea bottom morphology	7. M3a	depth*ave_kd+ave_par+ave_radg+zeurel+slope
	8. M3c	depth*ave_kd+ave_par+zeurel+slope
depth, variables related to water transparency, sea bottom morphology and other chemico-physical variables	9. M4a	depth*ave_kd+ave_par+ave_radg+zeurel+slope+log(rei+1)+ave_sal
	10. M4b	depth*ave_kd+ave_par+zeurel+slope+log(rei+1)+ave_sal
	11. M4c	depth*ave_kd+ave_par+ave_radg+zeurel+slope+log(rei+1)
	12. M4d	depth*ave_kd+ave_par+zeurel+slope+ave_sal
depth, variables related to water transparency, sea bottom morphology, other chemico-physical variables and temperature	13. M5a	depth*ave_kd+ave_par+ave_radg+zeurel+slope+log(rei+1)+ave_sal+ave_sst
	14. M5b	depth*ave_kd+ave_par+zeurel+slope+ave_sal+ave_sst
	15. M5c	depth*ave_kd+ave_par+ave_radg+zeurel+slope+log(rei+1)+ave_sst

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### 2.3.3. Validation of the PoDM

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We used several statistics to infer model predictive capabilities: sensitivity (conditional probability that a presence is correctly classified); specificity (conditional probability that an absence is correctly classified); percent of correctly classified observations (PCC); Cohen's kappa (Kappa); and the area under the receiver operator curve (AUC) (Fielding and Bell, 1997). The threshold used to translate continuous model predictions (probability of presence) in a

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221 classification of sites as presence or absence was defined as the value that minimises the difference between sensitivity  
222 and specificity. This criterion has been applied to the inner validation dataset to find the classification threshold.

### 223 **2.3.4. Model predictions**

224 Once the model has been validated, it was applied using raster layers of environmental data for the areas of interest as  
225 input. In particular, for the calibration, validation and evaluation areas only the data relative to the years in which the *P.*  
226 *oceanica* distribution were recorded have been considered. For the whole North African coasts, the yearly prediction  
227 and the overall average for the period 2003-2011 have been estimated. The outputs of the model describe the probability  
228 of presence of *P. oceanica* meadows given the environmental conditions. The suitable areas for *P. oceanica* are  
229 identified transforming the average probability of presence in a presence/absence classification.

### 230 **2.3.5. Potential Distribution Indicator**

231 In order to evaluate the use of SDMs predictions for the assessment of GES within the framework of the Biodiversity  
232 ecological objective, we developed an indicator concerning the Operational Objectives 1.4.1 of UNEP MAP EcAp,  
233 with reference to *P. oceanica* habitat. In particular, we propose to take the ratio between the observed (*in situ* recorded)  
234 and potential (model predicted) distribution as the Potential Distribution Indicator (PDI), which could be linked with the  
235 indicators 1.4.1 and 1.4.2 (Potential / observed distributional range and distributional pattern of certain coastal and  
236 marine habitats listed under SPA protocol). PDI is computed as follow: 1) the area is divided in regular squares,  
237 defining an evaluation grid 2) in each square of the grid the surface of the observed ( $S_{obs}$ ) and predicted ( $S_{pred}$ ) meadows  
238 is estimated 3) if  $S_{obs} = 1$  and  $S_{pred} = 0$ , then  $PDI = 1$ ; 4) if  $S_{obs} = 0$  and  $S_{pred} = 0$ , then  $PDI = null$  (cannot be assessed);  
239 5) otherwise  $PDI = S_{obs} / S_{pred}$ .

#### 240 **2.3.5.1. Sensitivity analysis of the Potential Distribution Indicator**

241 Uncertainty analyses of the P.D.I. indicator were carried out to understand its sensitivity to changes in environmental  
242 conditions and to the spatial scale of application.

243 As the predicted distribution for the period 2003-2011 is not necessarily representative of a pristine situation, we use  
244 model predictions to explore the sensitivity of the indicator to different reference conditions. In particular, we  
245 hypothesised differences in water transparency (Kd coefficient), by considering as potential distribution (denominator  
246 in the PDI formula): a) suitable areas (see previous paragraph), estimated as areas potentially occupied by *P. oceanica*  
247 in each year of the period 2003-2011 (local conditions); b) suitable areas estimated as areas potentially occupied by *P.*  
248 *oceanica* considering the predictions of the model after that water transparency (Kd) has been modified to represent not  
249 the average situation but an optimal one, reflecting the highest level of transparency recorded for each area. This water

250 transparency was estimated as the 5<sup>th</sup> percentile of  $K_d$  for the period 2003-2011 (local  $K_d^{05}$ - conditions); c) the suitable  
251 areas estimated as areas potentially occupied by *P. oceanica* considering the predictions of the model setting water  
252 transparency to the 5<sup>th</sup> percentile of  $K_d$  of the whole Mediterranean Sea (Mediterranean  $K_d^{05}$  - conditions). In order to  
253 build the changed transparency scenarios, monthly MERIS-derived  $K_d$  values at 2 km resolution for the whole  
254 Mediterranean between 2003 and 2011 were considered (Hoepffner et al., 2010), and the 5<sup>th</sup> percentile was computed  
255 for each cell of the raster grid and for the whole basin.

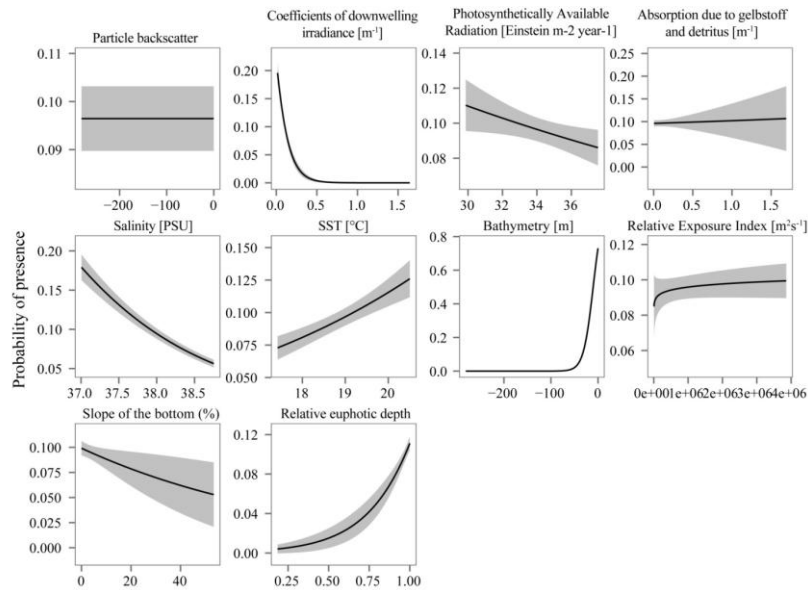
256 The spatial resolution of PDI could potentially affect the results, i.e. the application of the indicator could be sensitive to  
257 the scale of application. A sensitivity analysis has been carried out to estimate the impact of the change in the size of the  
258 squares to the estimation of the potential habitat occupancy. For each area used in the calibration and validation process,  
259 a set of 8 grids with different cells size - with a side length of 0.6 (2 raster cells), 1.2, 2.4, 3.6, 4.8, 6.0, 9.0 and 15.0 km  
260 (50 raster cells) - were created. These grids have been used to compute PDI and to compare for each area the robustness  
261 of the mean PDI value, in order to understand the sensitivity to the grid size in the evaluation of the PDI for a given  
262 area.

## 263 **3. Results**

### 264 **3.1. *Posidonia oceanica* Distribution Model development**

265 According to the criteria set in section 2.2.1, we could identify a set of two models, namely M5a and M5b in Table S.M  
266 2, in which on the basis of the  $W_{AIC}$  the 95% confidence set. These models belongs to the most complex group  
267 considered, including all types of variables, and the structure of model M5b is nested in the one of model M5a, i.e. all  
268 predictors of the simplest model are present also in the other one, even if the shared variables are weighted differently in  
269 the fitted models. The most influential variables were found to be the bathymetry and the diffuse attenuation coefficient,  
270 followed by euphotic depth, salinity and sea surface temperature, while the other variables play a negligible or null role.  
271 In general, the probability of presence of *P. oceanica* is higher in shallow, clear water (Fig. 2). The average probability  
272 of presence decreases for higher salinities and for steeper slopes of the bottoms (Fig. 2). A higher level of uncertainty  
273 seems related to the responses to Relative Exposure Index, the absorption due to gelbstoff and photosynthetically  
274 available radiation (Fig. 2). Parameter estimates for all models are reported in supplementary materials (Table S.M. 2).

275



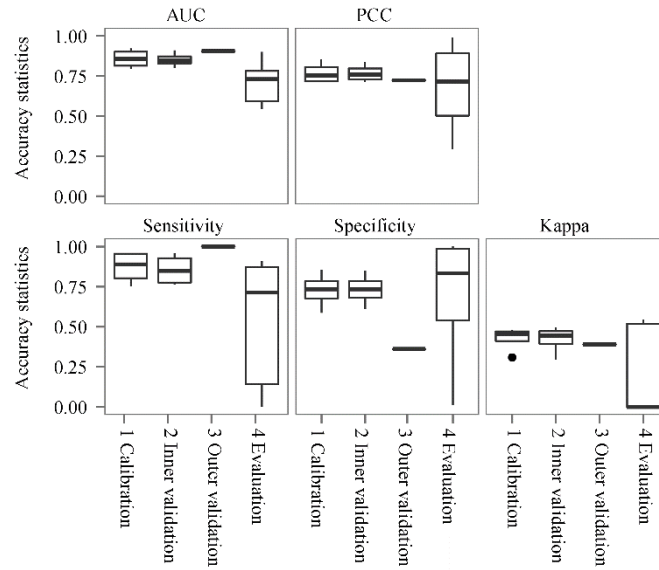
276

277 Figure 2. Average response curves of the fitted *P. oceanica* Distribution Model.

278

### 279 3.2. PoDM validation

280 As the model predicts the probability of presence of *P. oceanica*, it is necessary to define a threshold, in order to  
 281 compare its output with presence/absence data. Such threshold was defined as the value that minimises the difference  
 282 between sensitivity and specificity (of the inner validation dataset) and was set to 0.22. The statistics computed for the  
 283 calibration and inner validation dataset show similar levels of accuracy (Fig. 3), indicating a good capability of  
 284 estimating a higher probability of presence for an occupied site than for an unoccupied one (AUC), classifying correctly  
 285 about 77-78% of the observation (PCC). Furthermore, the probability of correctly classifying presence (sensitivity) is  
 286 slightly higher than that of absence (specificity). No degradation of the overall performances was recorded applying the  
 287 model to the outer validation (Sidi Ali El Mekki) dataset (Fig. 3), apart from a strong imbalance between sensitivity and  
 288 specificity, suggesting that the transfer of the model to the validation area leads to an overestimation of presences. A  
 289 much higher variability is associated to the evaluation dataset, where, in general, a worsening of the performances of the  
 290 model can be registered.



291

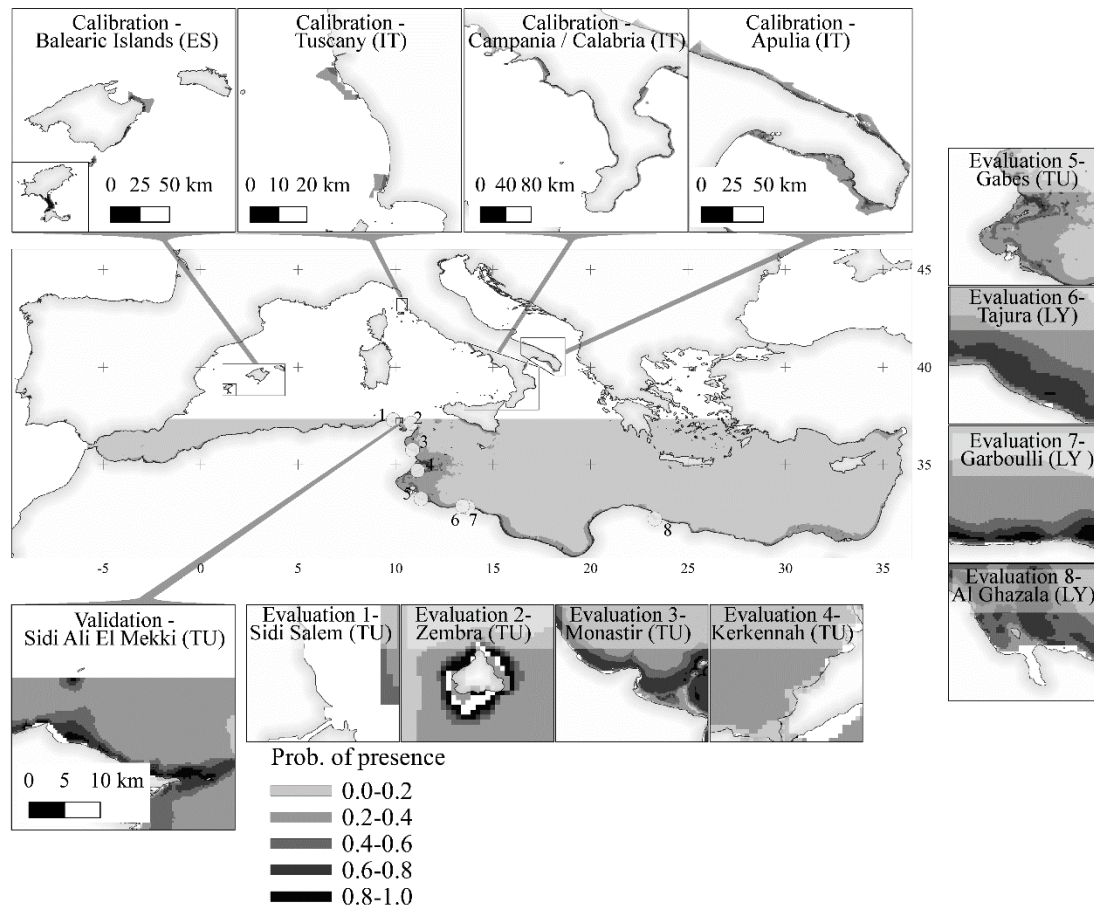
292 Figure 3. Accuracy statistics for the of *P. oceanica* Distribution Model predictions. AUC: Area Under the (Receiver  
 293 Operator) Curve; PCC: percentage of correctly classified observations; Kappa: Cohen's Kappa.

294

### 295 3.3.PoDM application

296 The results of the application of the model are summarized in Fig. 4, which shows the probability of presence of *P.*  
 297 *oceanica* along the whole North African coasts. Suitable areas for *P. oceanica* are strongly related to the coastal realm,  
 298 and cover a large portion of the coast, with different level of probability. The model indicates that the probability is  
 299 higher along the Tunisian and Libyan coasts, with the large shelf of the Gulf of Gabes zone representing a very  
 300 important area, including a relative high fraction where environmental conditions are suitable for the species.

301 As regards the evaluation sites, the comparison between the observations (Fig. 1) and the predicted probability of  
 302 presence (Fig. 4) shows a good level of agreement for Tajura, Monastir, Gulf of Gabes, while model predictions are not  
 303 very accurate in Garboulli and the areas are too close to the coasts such as Sidi Salem, because of the presence of null  
 304 values in remote sensing input data.



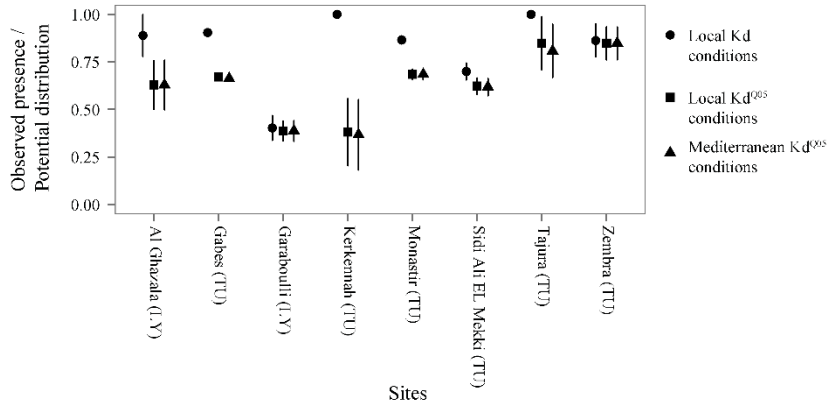
305

306 Fig. 4. Estimated probability of presence of *P. oceanica* in North African coast with highlighted the details of  
 307 calibration, validation and evaluation areas.

### 308 3.4. Potential Distribution Index

309 Considering the environmental conditions and the water transparency observed in the period 2003-2011 (local Kd  
 310 conditions) most of the areas showed relative high estimation of the Potential Distribution Index (Fig. 5), with only  
 311 Garaboulli in Lybia and Sidi Ali El Mekki in Tunisia showing relative low values. The output of the Observed /  
 312 Potential distribution can change taking clearer waters as reference conditions, using predictions with the simulated (5<sup>th</sup>  
 313 percentile) values of the coefficient of light attenuation recorded in each area (i.e. each cell of the raster grid; local  
 314 KdQ<sup>05</sup>- conditions) and in the whole Mediterranean Sea (Mediterranean KdQ<sup>05</sup> - conditions) in the period 2011–2013.  
 315 Indeed, the predictions obtained with the optimal Kd conditions (both local and Mediterranean) are similar, but the  
 316 differences between the values of the Observed / Potential distribution indicator computed with observed environmental  
 317 conditions and the clearer water scenarios can be large, with the exception of some sites (Fig. 5). It is interesting to note  
 318 that the Observed / Potential Indicator can be similar for the three scenarios for sites with high (Zembra), intermediate  
 319 (Sidi Ali El Mekki) and low values of the indicator (Garaboulli; Fig. 5).

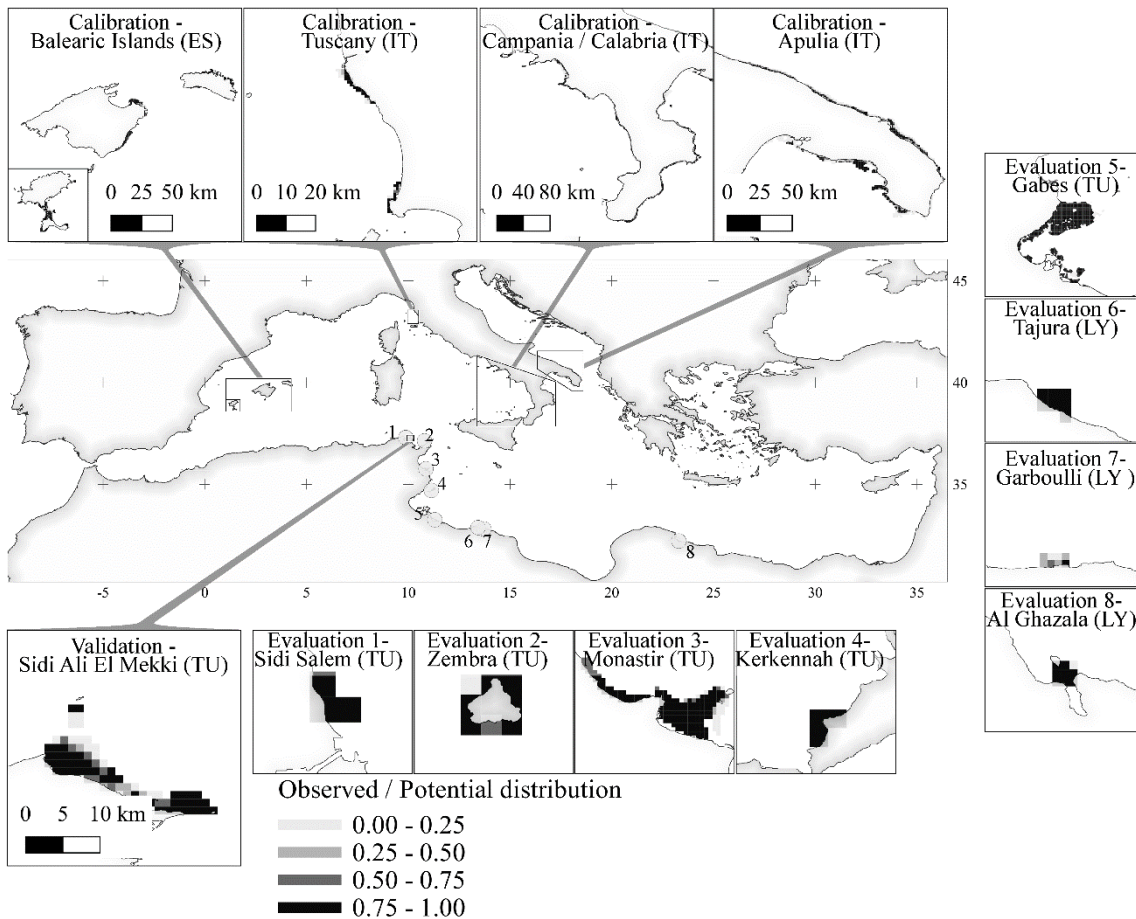
320 At the chosen evaluation grid size (1.2 km), most of the cells characterised by relative low values of PDI are associated  
 321 with meadows margins (Fig. 6), while the inner part of the meadows tends to have an observed area/potential area ratio  
 322 relatively high. However the average estimation for some areas (e.g. Al Ghazala and Zembra) shows a relative large  
 323 standard error, while all the others are characterized by a low spatial variability, and this pattern does not seem to be  
 324 related to the size of the areas or to the mean PDI value (Fig. 6).



325  
 326 Figure 5. Means and standard error (bar) of the Potential Distribution Index of *P. oceanica* estimated with the 1.2 km  
 327 grid for the North African areas (Validation and Evaluation areas) using local environmental conditions of the period  
 328 2003-2011 (circles), the local Kd conditions (squares), and the Mediterranean Kd conditions (triangles).

329





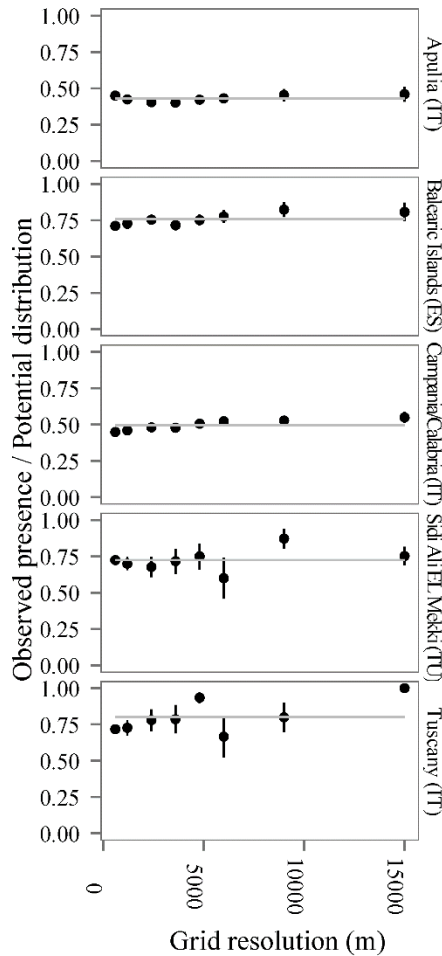
330

331 Fig. 6. Potential Distribution Index of *P. oceanica* in the North African coast evaluated for a grid with a resolution of 1.2  
 332 km, with highlighted the details of calibration, validation and evaluation areas.

333

334 ***Effect of scale***

335 The use of different sizes for the squares of the evaluation grid has a negligible impact on the estimation of PDI for the  
 336 calibration and validation areas (Fig. 7). However, increasing the size of the squares leads to a slight increase in PDI,  
 337 but this pattern - as evaluated with a linear regression- is significant only for Balearic Island ( $F = 5.23$ ,  $p = 0.02$ ) and for  
 338 the Campania/Calabria areas ( $F = 17.45$ ,  $p < 0.001$ ). Even in these cases, the slope of such a relationship is small: the  
 339 coefficients of the regressions are  $6.85 \cdot 10^{-6}$  for Campania/Calabria and  $7.33 \cdot 10^{-6}$  for Balearic Islands, implying an  
 340 increase of PDI of 0.068 and 0.073 in relation to an increase of the size of the squares of the evaluation grid of 10 km.  
 341 The evaluation carried out for the validation area Sidi Ali EL Mekki and for the calibration area Tuscany suggests that  
 342 the smaller areas are associated with a higher uncertainty (standard error), as if the spatial variability of PDI had a  
 343 stronger influence on the evaluation of smaller areas.



344

345 Figure 7. Impact of the resolution of the grid on the Potential Distribution Index of *P. oceanica* for the calibration and  
 346 validation areas (mean and standard error). The grey lines represent the mean values of PDI for each area, computed  
 347 across the grids of different resolution.

348

#### 349 4. Discussion

350 The development of the *Posidonia oceanica* SDM shows how remotely sensed data can facilitate the development of  
 351 such models, and their application at high spatial resolution over large areas, like the North African coasts. The  
 352 combination of the distribution predicted by the model with the (*in situ*) recorded occupancy data, allowed us to build a  
 353 simple indicator that summarises information on the occupation of potential sites and on the distribution pattern in given  
 354 areas that could be used in the assessment of Good Environmental Status. This information is quite robust in terms of  
 355 spatial resolution of the application, simplifying the hypothetical workflow toward GES evaluation, by minimizing the  
 356 risk of taking wrong decision when defining and applying this indicator.

#### 357 **4.1. *Posidonia oceanica* Distribution model**

358 *P. oceanica*, being the most abundant seagrass species in the Mediterranean is also the most studied (Boudouresque et  
359 al., 2009; Ruiz et al., 2009). One of the characteristics largely studied is the effects of environmental factors on the  
360 conditions of the plant, in terms of growth, survival at individual or population/meadows scale (e.g. Kendrick et al.,  
361 2005; Díaz-Almela et al., 2009; Gacia et al., 2012; Sghaier et al., 2013). Nevertheless some basic physiological  
362 information are still lacking, mainly due to difficulties of keeping plants in controlled environments (Ruiz et al., 2009).  
363 Most of the studies are observational in nature and based on correlation inferences for establishing the effects of  
364 abiotic/environmental variables on *P. oceanica*. Due to the sensitivity to anthropogenic pressures, the conditions of *P.*  
365 *oceanica* at different levels are often used as indicators of environment state (Montefalcone, 2009). For instance,  
366 seagrass-based indicators can be developed at individual level (e.g. evaluating the growth rate of the plant), at  
367 population level (e.g. meadows extension and characteristics) or at community level (state of the associated flora and  
368 fauna) (Marbà et al., 2006; Montefalcone, 2009; Ruiz et al., 2009; Personnic et al., 2014).

369 In some cases, the association between environmental conditions and seagrasses characteristics allowed the  
370 development of quantitative numerical models, which could be used to estimate the plant response to changes in  
371 environmental conditions (e.g. Valle et al., 2013; 2014; Vacchi et al., 2014). These models, when used to estimate the  
372 spatial distribution of the species, can be classified within the broad family of SDM. As for SDM in general, also the  
373 characteristics of the models developed for *P. oceanica* are strongly influenced by the purposes for which they were  
374 fitted. Here we proposed a statistical model fitted using 300m resolution grids, which could be considered very high  
375 taking into account the scale of the application and the resolution of other large scale marine SDMs (Ready et al., 2010;  
376 Martin et al., 2014; Valle et al., 2014). The high resolution application and the model transfer was possible taking  
377 advantage of MERIS imagery data from the Envisat mission, and will be an available option in the future exploiting the  
378 Ocean and Land Colour Instrument within the forthcoming Sentinel-3 mission of ESA. This approach influenced the set  
379 of environmental variables candidate to be included in the model. Indeed, we considered the most important variables  
380 for *P. oceanica* (Boudouresque et al., 2009; Ruiz et al., 2009), paying a particular attention to the ones that can be  
381 estimated remotely, while others had to be left out because they are not available at the Mediterranean scale (eg. bottom  
382 typology, available only for the western part of the basin; <http://www.emodnet.eu/seabed-habitats>) or it would not be  
383 feasible to derive them at this large scale (eg. model derived waves energy estimation). In general, some of the variables  
384 are expected to have an impact on a small scale (e.g. hydrodynamics and bottom topography), while others act at  
385 moderate (water quality) or very large (climate) scale, and it is common to consider different input variables in different  
386 scale SDM (e.g. for a seagrass species see Valle et al., 2014). In general our model stresses the importance of light

387 availability, confirming the general knowledge for seagrasses and for *P. oceanica* in particular (Boudouresque et al.,  
388 2009; Ruiz et al., 2009), while other variables, particular important at higher resolution, such as wave energy (Vacchi et  
389 al., 2014) seem less influential in our model. This could be a problem related to the oversimplification of the fetch-  
390 based approach, but it is also likely to be influenced by a scale factor. Wave energy, for example, seems particularly  
391 relevant for the influence of the upper distribution limit at local scale (Infantes et al., 2009; Vacchi et al., 2012) of *P.*  
392 *oceanica*, while other authors report water temperature as an important variable influencing phenology or flowering, or  
393 other meadows characteristics at larger scales (Diaz-Almeida et al., 2009). Many of these environmental variables show  
394 changes over space or over time following natural dynamics or being related to human induced disturbance (*sensu*  
395 Boudouresque et al., 2009), but within these variables, the limitation of light is often strongly connected with water  
396 quality and strongly depends on anthropogenic pressures. Within the framework of using the potential distribution of *P.*  
397 *oceanica* meadows as an indicator of Good Environmental Status, we think that a distribution model strongly based on  
398 light availability at the bottom could represent a useful tool.

## 399 **4.2. Observed/potential distribution ratio and implication for GES**

### 400 **estimation**

401 In this work we used the PoDM predictions to develop a simple indicator representing the portion of suitable *P.*  
402 *oceanica* habitat actually occupied by this plant. Such an indicator could be used to assess the environmental status  
403 comparing the observed distributional range of *P. oceanica* with the potentially occupied sites (i.e. suitable areas)  
404 (Operational Objective 1.4, indicator 1.4.1 "*Potential /observed distributional range of certain coastal and marine*  
405 *habitats listed under SPA protocol*") or as a measure of the pattern of distribution of the meadows in a given area  
406 (Operational Objective 1.4, indicator 1.4.2 "*Distributional pattern of certain coastal and marine habitats listed under*  
407 *SPA protocol*"), according to the scale of the application. We referred to the UNEP MAP Ecological Objectives and  
408 indicators, but the proposed tools could be useful also in the context of the MSFD implementation, regarding the  
409 Descriptor 1 (Biodiversity) and in particular the criteria 1.4 (Habitat distribution) and 1.5 (Habitat extent). The  
410 contribution of SDMs in implementing and applying indicators for environmental assessment is focused on some  
411 specific tasks of the stepwise procedure of indicator development: the predictions of the statistical distribution model  
412 are used for the numerical evaluation (i.e. metric definition and computation) and for the definition of reference  
413 conditions. In the present work the predicted distributions represent a reference condition against which the observed  
414 distribution is compared, allowing us to express the indicator as a quality ratio given the recorded environmental  
415 conditions. Of course this standardized value does not represent exactly the reference conditions *sensu* the European

416 WFD (i.e. the conditions of the indicator in absence of human pressure or pristine areas), but, rather, a way of  
417 identifying areas which should be occupied by *P. oceanica* meadows, based on recent environmental conditions  
418 (evaluated on a 9 years period). Modelling techniques are commonly used to derive implicit or explicit reference  
419 conditions to standardise indicators (Clarke, 2013) and for setting the threshold needed to assess GES (Borja et al.,  
420 2013). The water transparency scenarios exercise, used to build the optimal Kd reference conditions, can be considered  
421 an example of a model-based exploration of reference conditions. The application of one indicator alone is not  
422 sufficient to assess the environmental status of a given area under the context of an Ecosystem Approach but *P.*  
423 *oceanica* meadows are listed among the priority habitat to be considered (UNEP MAP, 2013), and, although several  
424 attempts of integrated assessment have already been carried out, most of the Countries are still focusing on the  
425 development of individual indicators (Borja et al., 2013). Moreover it is worth noting that the implementation of the  
426 indicator 1.4.1 is considered problematic by UNEP MAP, in general for the assessment of the marine habitats under the  
427 SPA protocol, and in particular for the meadows of *P. oceanica* for the lack of distribution models to assess the  
428 potential distribution (UNEP MAP, 2013). Therefore PoDM and the PDI indicator represent a potential contribution to  
429 support the assessment. Furthermore our example could be easily extended to other habitats, in particular if large scale  
430 distribution models are already available, like the one for *Coralligenous and maerl habitats* (Martin et al., 2014), or  
431 extended to other operational objectives within the Biodiversity ecological objective.

432 The assessment of Good Environmental Status should be carried out for the whole Mediterranean Sea, or at least at  
433 subregional scale (UNEP MAP, 2013). This poses the problem to understand how to integrate information used for the  
434 computation of the indicator on a global assessment: it is necessary to aggregate the data putting together different cells  
435 of the prediction/observation rasters to estimate the proportion of the area occupied. Surprisingly, the upscaling  
436 procedure seems to have a minor impact on the evaluation carried out by PDI. On the other side, the uncertainty (i.e. the  
437 standard deviation associated to the mean value of PDI for each area) shows a slight increase when aggregating data  
438 with coarser evaluation grids. As a result the application of the method is quite robust to the resolution of the  
439 evaluation, and this could lead to some general suggestion in applying similar indicators: it is better to have fine scale  
440 prediction, and aggregate them on an intermediate scale. What probably would be much more relevant is the effect of a  
441 change in resolution if the threshold between GES and not GES is kept fixed: given the increasing trend with cell size of  
442 PDI (see Fig. 7), it is important that the thresholds are defined exactly at the same scale at which the final evaluation is  
443 carried out.

### 4.3. Assumptions and future perspective

One strong assumption behind the application of the PDI indicator is that the suitable habitat identified by the PoDM represents the potential distribution of *P. oceanica* in a given area. The prediction of SDMs calibrated using presence/absence data does not represent its fundamental niche (Soberon, 2007; Peterson et al., 2011). However we recommend to develop models using true presence/absence data, as it leads to models with strongest discriminating capabilities (Valle et al., 2014). Hence with the application of PDI we compare the actual presence with the likelihood of presence given the observed environmental conditions. This condition represents the reference baseline against which the occupancy is evaluated. Considering a relative large time period, we ensure a quite robust estimation, but the estimated condition does not represent 'pristine condition'. This could have a severe influence on the estimation, because the present conditions can be heavily influenced by the impacts of human activities. The coefficient of light attenuation ( $K_d$ ) simulation exercise, gives some useful insight on reference conditions definitions. In some cases, enhancing the environmental conditions used to obtain the reference conditions – in our example changing water transparency, a parameter strongly related to water quality – can have a strong impact on the estimation of the reference conditions and hence on the computation of the indicator. This could be interpreted as if the observed environmental conditions are far from a pristine situation. In this case, a model based exploration, extended to all the environmental variables, could help in defining robust reference conditions. On the other side, for some areas changes in water transparency did not alter significantly the predictions of the model, suggesting that the observed water transparency could be close to the ideal one for *P. oceanica*. An exploration of the effects of changes of other environmental variables could help in deciding if these conditions represent acceptable reference systems.

If the water transparency is not suitable for the presence of *P. oceanica* meadows this could be either because the characteristics of water quality is altered by human activity or because the area is characterized by a natural high turbidity level. But if the model suggests the presence of the species, its actual absence (*in situ* observed), could be related with some other environmental pressures on the ecosystems, like anchoring, dredging, trawling or other activities that mechanically damage plants. This point is particularly relevant, as the physical damage of meadows is considered the most severe cause of *P. oceanica* regression in many countries (Boudouresque et al., 2009). On the other side, a meadow could also occupy a fraction of the suitable areas, because of past disturbance or extreme events. In fact the species is characterized by a very low recovery time, and may take several years to recover after a regression phase (Boudouresque et al., 2009; Montefalcone, 2009; Vacchi et al., 2014).

The typical strategy for indicator definition are based on (Hering et al., 2010): the availability of historical data to hindcast the conditions to a time when pressure did not significantly affect the ecosystem -and this is not possible for *P.*

474 *oceanica*, as a pre-modern baseline is not available (Boudouresque et al., 2009; Bonaccorsi et al., 2013)-; on the  
475 possibility of identifying a pristine area (a control area); or on the extrapolation the expected indicator response in  
476 theoretical pristine conditions. This could also be achieved by modelling the relationship between the indicator and  
477 human stressors, and projecting expected values in undisturbed areas (Hering et al., 2010; Borja et al., 2013). For  
478 instance, the application of PoDM in an undisturbed area for which the impacts of human activities are known to be  
479 minor and for which a detailed distribution map of seagrasses is available, like the case of a well-established protected  
480 area (e.g. Port-Cros National Park; Boudouresque et al., 2009) could allow one to estimate the ratio of suitable areas  
481 normally occupied by the species. Replicating such an exercise over a number of different areas in different sites of the  
482 Mediterranean Sea (sites with different environmental characteristics) would allow one to estimate the reference  
483 conditions for undisturbed areas. Another possible approach would be to use data on anthropogenic pressures to be  
484 included as predictors in the SDM (e.g. in Crimmins et al., 2013), in order to project in a given area the expected  
485 distribution in the absence of human disturbance (e.g. setting the level of anthropogenic to zero). The definition of a  
486 threshold for the definition of GES falls outside the scope of this work and needs further analysis, however it is worth to  
487 note that a model-based exploration of the effects of changes in environmental conditions could be adopted also in the  
488 definition of such a threshold. As an example, ‘what if’ scenarios could be built to link the effects of human activities  
489 and regulations on environmental variables and hence on the expected *P. oceanica* distribution. If an Ecosystem  
490 Services (ESS) evaluation approach is applied to the different scenarios, it would be possible to define the *P. oceanica*  
491 potential distribution (and hence the environmental conditions) related to an ecosystem status not in pristine conditions,  
492 but still providing an adequate levels of ESS to be considered as being in a good environmental conditions.

## 493 **5. Conclusions**

494 Species Distribution Models are very popular tools in many applied studies, in particular to deal with many aspects  
495 related to the conservation of species or to project their distribution in relation to new or changed environmental  
496 conditions (Elith and Leathwick, 2009; Elith et al., 2010; Guisan et al., 2013). Their development and application is less  
497 frequent in marine environments than in the terrestrial one, mostly due to data limitation (Franklin, 2010; Robinson et  
498 al., 2011), but taking advantage of some recent progress -like the building of public available global database  
499 (Tyberghein et al., 2011) - their use within the study of aquatic systems is increasing (Dambach and Rödder, 2011;  
500 Robinson et al., 2011). Satellite derived Earth Observations can ease the development of SDMs (He et al., in press),  
501 providing high temporal frequency predictors over large areas or entire regions, tackling the fact that environmental  
502 conditions often resulted more temporally dynamic than in terrestrial environment (Franklin, 2010). Taking advantage  
503 of the case study of the seagrass *P. oceanica* in the Southern Mediterranean Sea we showed how remotely sensed data

504 of environmental variables and *in situ* seagrass information can be integrated in SDMs. These tools can contribute to the  
505 assessment of environmental status required within the framework of the Ecosystem Approach adopted by the Country  
506 facing the Mediterranean Seas (UNEP, 2012). The proposed approach to the development of indicators related to the  
507 evaluation of the distribution of key marine habitats still lacks the definition of the threshold necessary to classify the  
508 evaluation as an attainment or a failure to reach a Healthy Environment (or Good Environmental Status), but already  
509 proved to have some highly desired characteristics, such as a certain degree of robustness with regards to the resolution  
510 of its application. We want to stress how the application of SDM combined with EOs can ease the estimation of  
511 Environmental Status assessment, but without underplaying the role of *in situ* monitoring, that represents a crucial  
512 phase to enhance the modelling tools that can be built, to infer reference conditions and to carry out the environmental  
513 status assessment itself.

## 514 **6. Acknowledgments**

515 This work is part of the EU FP7 Collaborative Project MEDINA (Marine Ecosystem Dynamics and Indicators for North  
516 Africa, Grant agreement no: 282977; [www.medinaproject.eu](http://www.medinaproject.eu), <http://www.medinageoportal.eu/>). We would like to thank  
517 Alain Jeudi de Grissac who helped in gathering information on *P. oceanica* distribution in North African Coast. We  
518 also thank two anonymous reviewers for providing helpful comments on an earlier version of the manuscript.

519



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## 8 Supplementary material

Table SM1. Calibration, validation and evaluation areas.

Site	Country	Type	Extent (km)	Year	Reference
Apulia	Italy	Calibration	250 x 75	2006	CRISMA, 2006
Campania/Calabria	Italy	Calibration	410 x 270	2002/2004	<a href="http://www.sidimar.tutelamare.it">www.sidimar.tutelamare.it</a>
Balearic Island	Spain	Calibration	250 x 50	2002	<a href="http://lifeaposidonia.caib.es/">http://lifeaposidonia.caib.es/</a>
Tuscany	Italy	Calibration	68 x 25	2009	Mancusi et al., 2011
Sidi Ali el Mekki	Tunisia	Validation	25 x 11	2007	Ben Cheikh Almi, 2007
Garaboulli	Lybia	Evaluation	5 x 3	2009	PNUE-PAM-CAR/ASP, 2009
Al-Ghazala	Lybia	Evaluation	9 x 3.5	2009	PNUE-PAM-CAR/ASP, 2009
Tajura	Lybia	Evaluation	3.7 x 3.7	2009	PNUE-PAM-CAR/ASP, 2009
Gulf of Gabes	Tunisia	Evaluation	230 x 250	2010	Hattour and Ben Mustapha, 2013
Kerkennah	Tunisia	Evaluation	2.2 x 1.8	2007/2008	PNUE-PAM-CAR/ASP, 2009
Monastir	Tunisia	Evaluation	49 x 16	2008	PNUE-PAM-CAR/ASP, 2009
Sidi Rais	Tunisia	Evaluation		2003	El Asmi et al., 2003
Sidi Salem	Tunisia	Evaluation	3.3 x 0.7	2007	Ben Cheikh Almi I., 2007
Zembra	Tunisia	Evaluation	4 x 3.8	2003	Orueta & Limana, 2003

1

2 Table SM.2. Parameter estimates for the candidate models and for the average model.

<b>Model</b>	<b>Intercept</b>	<b>ave_kd</b>	<b>depth</b>	<b>ave_kd:depth</b>	<b>ave_bbp</b>	<b>ave_par</b>	<b>ave_radg</b>	<b>zeurel</b>	<b>slope</b>	<b>ave_sal</b>	<b>log(rei + 1)</b>	<b>ave_sst</b>	<b>df</b>	<b>logLik</b>	<b>AICc</b>	<b>delta AICc</b>	<b>weight</b>
M5b	22.93	-8.00	0.09	0.03	-	-0.03	-	4.19	-0.01	-0.73	-	0.19	9	-3122.19	6262.39	-	0.65
M5a	23.47	-8.13	0.10	0.01	-	-0.05	0.19	4.18	-0.01	-0.77	0.08	0.22	11	-3120.84	6263.72	1.33	0.33
M4d	22.59	-7.99	0.09	0.01	-	0.02	-	4.89	0.00	-0.68	-	-	8	-3127.23	6270.48	8.09	0.01
M4b	22.84	-7.97	0.09	0.00	-	0.01	-	4.93	0.00	-0.70	0.05	-	9	-3126.78	6271.57	9.18	0.01
M4a	22.83	-7.96	0.09	0.00	-	0.01	-	4.93	0.00	-0.70	0.05	-	10	-3126.78	6273.58	11.19	0.00
M2d	-6.17	-7.19	0.09	0.12	8.06	0.10	-	4.84	-	-	-	-	8	-3177.08	6370.19	107.79	0.00
M2c	-6.87	-8.46	0.09	-	7.52	0.11	-	5.33	-	-	-	-	7	-3180.02	6374.04	111.65	0.00
M4c	-4.87	-7.47	0.09	0.13	-	0.10	-	4.78	0.00	-	-0.10	-	9	-3179.10	6376.23	113.84	0.00
M3c	-5.91	-7.84	0.09	0.11	-	0.09	-	4.89	0.00	-	-	-	7	-3181.54	6377.09	114.70	0.00
M5c	-5.29	-7.50	0.09	0.13	-	0.09	-	4.61	-0.01	-	-0.09	0.05	10	-3178.79	6377.61	115.22	0.00
M3a	-5.88	-7.40	0.09	0.11	-	0.09	-	4.86	0.00	-	-	-	8	-3181.20	6378.42	116.03	0.00
M2b	-1.33	-6.85	0.08	0.18	8.17	0.10	-	-	-	-	-	-	7	-3188.53	6391.07	128.68	0.00
M2a	-1.66	-8.76	0.10	-	7.32	0.11	-	-	-	-	-	-	6	-3195.36	6402.74	140.34	0.00
M1a	2.16	-7.76	0.08	0.21	-	-	-	-	-	-	-	-	4	-3201.59	6411.18	148.79	0.00
M1	2.33	-9.87	0.10	-	-	-	-	-	-	-	-	-	3	-3210.56	6427.12	164.73	0.00
Average model estimates	23.11	-8.05	0.09	0.02	-	-0.04	0.19	4.19	-0.01	-0.74	0.08	0.20					
Adjusted SE	3.23	0.75	0.00	0.05	-	0.03	0.65	1.37	0.01	0.07	0.06	0.05					

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4