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Mediterranean seascape suitability for *Lophelia pertusa*: living on the edge

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Abstract

Ecological niche modelling is used in deep-sea research to investigate the environmental preferences and potential distribution of data-poor species. We present a mesoscale assessment of Mediterranean seascape suitability for the cold-water coral *Lophelia pertusa* (= *Desmophyllum pertusum*, Linnaeus, 1758*)*. We estimated seascape suitability and uncertainty maps using an ensemble approach of three machine-learning algorithms (Generalized Boosting Model, Random Forest, Maximum Entropy) based on environmental predictors. Bathymetry, bathymetric slope and pH were the most important predictors for the models. Overall the models reached good to excellent performance, with a very reliable prediction of the most suitable areas. In the Mediterranean Sea, *L. pertusa* encounters environmental settings close to its physiological limits but, despite the highly variable quality of the Mediterranean seascape, we identified high suitability areas mostly along the upper slope and at submarine canyons of the Western and Central margins. The existing MPAs do not overlap with high suitability areas, and therefore *L. pertusa* is only protected at the deepest fringe of its potential distribution by the implementation of the bottom trawling exclusion beyond 1000 m depth. This seascape suitability assessment may assist future research, including high-resolution modelling targeting high-suitability areas, investigation on the resilience of *L. pertusa* populations and development of conservation actions.

Keywords: Cold-water corals; potential distribution; climate change; conservation; ensemble model

1 Introduction

The geographical distributions of species in the deep sea remain largely unknown. This knowledge deficit has hindered the development of effective management measures framed by recent policy initiatives (e.g., European Habitats and Marine Strategy Framework Directives) that aim to preserve the biodiversity and functioning of ecosystems. Conservation options heavily rely

on spatial explicit information (Reiss et al., 2015; Savini et al., 2014) and depend on modelling approaches at broad spatial scales (Burgman et al., 2005). This methodology allows capturing the multiple interactions between the organisms and their habitats and the spatio-temporal dynamics of the landscape (Turner et al., 1995). The mapping of areas with suitable conditions for the settlement of habitat forming species such as some cold-water corals (CWC) is an important aspect of conservation and management of deep-sea biodiversity.

Cold-water corals are among the most emblematic deep-sea organisms and play an important role in the structure and functioning of marine ecosystems. CWC increase the complexity of the habitat, provide spawning, nursery and feeding areas and support attendant assemblages with significantly enhanced biodiversity and biomass when compared to the surrounding environment (Buhl-Mortensen et al., 2010; Capezzuto et al., 2018; Corbera et al., 2019; Linley et al., 2017). CWC are also involved in the provision of other important ecosystem functions and services (Giovanni Chimienti and D'Onghia, 2019) including nutrient cycling and carbon sequestration (Soetaert et al., 2016). Due to their low tolerance to disturbance (low resistance), slow growth rates (low recovery rates), and consequently poor resiliency, these organisms can be highly impacted by anthropogenic activities (D'Onghia et al., 2017; Fabri et al., 2017; 2014; Giusti et al., 2019; Taviani et al., 2019a) and climate change (Georgian et al., 2016; Movilla et al., 2014).

Among the reef-building CWC species, *Lophelia pertusa* is one of the most studied. Classified as deep-sea cosmopolitan along the western and eastern margins of the North Atlantic Ocean (Roberts et al., 2016), it is also widely reported from the Gulf of Mexico and the Caribbean Sea and in many mid-ocean islands (Rogers, 1999). In the Mediterranean Sea, there are many records of dead or subfossil remains, mostly dated from the late Pleistocene, 30000-15000 years B.P. (Delibrias and Taviani, 1985). Climate change that marked the end of the last glacial period, and its influence on patterns of productivity and deep-sea water circulation are hypothesized as the causes for a major decline of the once thriving Mediterranean populations (Delibrias and Taviani, 1985; Fink et al., 2015; Taviani et al., 2019b). Reports of presently living colonies in the Mediterranean Sea are few and restricted to the western-central Mediterranean basin (Chimienti et al., 2018; 2019). However, taking into account that few surveys targeting *L. pertusa* were conducted in the Mediterranean Sea and, nonetheless, several recent studies reported new occurrences of living colonies (e.g., Angeletti et al., 2014; Corbera et al., 2019; Taviani et al., 2019a), the present Mediterranean distribution of *L. pertusa* is probably underestimated (Zibrowius, 2003).

Recent studies have successfully used ecological niche models (ENMs) to estimate the potential distribution and the environmental suitability of various deep-sea species (e.g., Basher et al., 2014; Davies and Guinotte, 2011; González-Irusta et al., 2015; Lo-Iacono et al., 2018). The panoply of ENMs available encompasses different approaches, modelling techniques, occurrence data inputs, and ecological concepts (Peterson et al., 2015; Valverde et al., 2008).

Correlative ENM forecasts based on presence-only data rely on a set of ecologically relevant predictors and provide meaningful results even for poor-data species. The modelling process consists in determining statistically the species environmental profile based on the values of predictors for the known occurrence locations and then project this profile over the model's geographical space (Guillera-Arroita et al., 2015; Miller, 2010). The output is a continuous representation of the species potential distribution. Model predictions depend not only on the adopted modelling technique and settings defined by practitioners but are also subject to different types of uncertainties related to data quality and quantity (e.g., sample size, sampling bias, spatial resolution issues (Burgman et al., 2005; Zhang et al., 2015)). These issues and their implications on the model performance have prompted the use of ensemble forecasting frameworks that combine the output of multiple models into a single estimation. This methodology produces frequently more accurate predictions than single model methods (Turner et al. 2018) and allows highlighting consensual forecasts by mapping model uncertainty based on the agreement/disagreement of individual models (Araújo and New, 2007).

The main objective of this work is to predict and map the Mediterranean seascape environmental suitability for *L. pertusa* using a multiple model ensemble forecasting approach that can provide support for management decisions and conservation actions. We provide here a succinct and easily readable potential distribution map, assess the performance of the model and derive the prediction uncertainty maps for the modelled geographical area. We also hypothesize that *L. pertusa* in the Mediterranean Sea is subjected to conditions near its physiological tolerance and that its persistence in this region is being challenged by climate change. To our best knowledge, this study is the first focusing on assessing the seascape suitability for *L. pertusa* in the Mediterranean Sea, encompassing the whole basin and using a multi-algorithm approach that provides both the prediction of seascape suitability and a measure of uncertainty of the forecast.

2 Material and methods

2.1 Modelling area and occurrence data

We modelled the seascape suitability of the Mediterranean Sea for *L. pertusa* using present-day living occurrences reported for the study area. We extracted the occurrence records in the Mediterranean Sea from the Global Distribution of Cold-water Corals Database (version 3.0, Freiwald et al., 2017), further updated with records for the Mediterranean Sea obtained from the literature (Supplementary Table S1). We excluded colony records referring to transects covering a distance greater than 230 m to reduce the geographic uncertainty of the occurrence data. For shorter transects (8 out of 48), we considered the centroid of the transect as the location of the colony. Considering the modelling resolution (1/8 arc minute, ca. 230×230 m), this lack of accuracy was assumed as negligible. To remove duplicates and spatially auto-correlated occurrences, we proceeded with the spatial thinning of species occurrences (Aiello-Lammens et al., 2015), that reduced multiple occurrences within 230 m radius to a single record. This procedure minimizes the sampling bias and prevents the over-fitting of predictions without losing an excessive amount of information.

2.2 Environmental predictors

We based the selection of environmental predictors (Table 1) on the species ecology and previous modelling studies for *L. pertusa*. The bathymetry (meters) was extracted from the EMODnet Digital Bathymetry dataset and used to derive the bathymetric slope (degrees). Seven predictors related to ocean conditions were extracted from data assimilative ocean models available through the Copernicus Marine Environment Monitoring Service (CMEMS): salinity (psu), temperature (ºC), dissolved oxygen (mmol m^{-3}), phosphate concentration (mmol m^{-3}), phytoplankton carbon biomass (mmol m^{-3}), pH and current velocity (m s^{-1}). We used a continuous representation of near seafloor conditions for these variables following the methodology described by Davies and Guinotte (2011) but using kriging instead of inverse distance weighting as the interpolation method. This option was based on studies showing higher performance for the first method (Assis et al., 2018; Hofstra et al., 2008). The fitting of the universal kriging model was based on the 12 nearest values of each focal cell. The assessment of the up-scaling process of the environmental data was conducted using the data provided by the World Ocean Atlas 2013 (WOA 2013,version 2, E. H. Garcia et al., 2013; H. E. Garcia et al., 2013; Locarnini et al., 2013; Zweng et al., 2013). Only the values of the WOA 2013 deeper than 50 m were retained for the assessment of the quality of the interpolation process and compared with the interpolated data layers with the closest depth. Relationships were statistically analyzed using the Pearson's correlation coefficient. The predictors' covariance was also assessed; the bathymetry and pH were highly correlated (r = 0.86 , Supplementary Fig. S1) however, we opted to retain both predictors since: 1) the bathymetry is frequently identified as one of the most

relevant predictors to estimate the environmental suitability for CWC in regional studies (e.g., Barbosa et al., 2019; Georgian et al., 2014); 2) the pH level is particularly relevant under the current state of ocean acidification (Hennige et al., 2014).

Table 1 – Details of the environmental predictors used in the model fitting and respective sources.

Variable (units)	Native Resolution	Derived from	Source	Reference
Bathymetry (m)	0.002º		EMODnet Digital Bathymetry (DTM 2016)	EMODnet Bathymetry Consortium, 2016
Bathymetric slope (°)		Bathymetry		
Phytoplankton carbon biomass - PCB (mmol m^{-3})	0.063º		Mediterranean Sea Biogeochemistry Reanalysis - CMEMS	Teruzzi et al., 2019
Phosphate (mmol m^{-3})				
pH				
Dissolved O_2 (mmol m^{-3})				
Salinity (psu)	0.063º		Mediterranean Sea Physics Reanalysis - CMEMS	Simoncelli et al., 2019
Temperature (°C)				
Current velocity (m s^{-1})				

The modelling process was conducted using R (R Core Team, 2016) and the "Biomod2" package (Thuiller et al., 2009) – version 3.3-15) which supports different modelling techniques. The ensemble model output resulted from the consensus of three machine-learning algorithms: Generalized Boosting Model (GBM, also known as Boosted Regression Trees), Random Forest (RF), and Maximum Entropy (MaxEnt). The machine-learning class algorithms are among the most appropriate for mapping and discriminating areas with different suitability degrees while keeping a high predictive performance (Carvalho et al., 2017; Mi et al., 2017; Reiss et al., 2015; Scales et al., 2016). Moreover, the predictions of these algorithms are considered more robust to predictors' correlations (Anderson et al., 2016) and to issues related to sample size (Hernandez et al., 2006; Mi et al., 2017; Wisz et al., 2008). They are also adequate for handling complex interactions between species response and predictor variables (Wisz et al., 2008).

The selected algorithms require pseudo-absence or background information for building the models. We generated ten datasets with 100 randomly sampled pseudo-absences each for GBM and RF algorithms, following the recommendations by Barbet-Massin *et al*. (2012). A minimum distance of 10 km from any presence point was imposed using the geographical constraint strategy offered in "Biomod2" to avoid pseudo-replicates. Considering the nature of MaxEnt (Philips and Miroslav, 2008), the procedure applied to the models using this algorithm differed slightly from the previous – 10000 random background points were selected to reach the optimal performance of the algorithm, and no geographic constraints were applied. Although a sampling

bias correction in the selection of the background data for MaxEnt models is recommended (Philips and Miroslav, 2008), this procedure was hindered by the paucity of publicly available data for the Mediterranean Sea that affects the current knowledge regarding *L. pertusa* distribution. The adjustment of the model complexity is also recommended by Merow (2013) but we maintained the default settings supplied by "Biomod2" because of the lack of truly independent evaluation data for model tuning. The tuning process is fundamental for models aiming high transferability (i.e., to be projected to other areas or periods) but it is less important in studies aiming to project the prediction of the model to the same area used for its calibration (Anderson and Gonzalez, 2011). We weighted equally each observation (either presence or pseudo-absence/background point) during the calibration process.

2.2.1 Evaluation of models' performances

A total of 300 single models were generated resulting from ten runs of the three algorithms for the ten datasets using either pseudo-absences (GBM and RF) or background points (MaxEnt). The evaluation of the models was performed by splitting the original datasets randomly into two subsamples: 75% of the data were selected for the calibration of the models, and the remaining 25% were used to test their predictions. This procedure was repeated 10 times using the method implemented in "Biomod2", similar to a cross-validation procedure. This method results in a quite robust test of the model performance in the absence of independent data (Thuiller et al., 2009).

There is no consensus on the most appropriate metrics to assess the accuracy of a model and, instead, a multi-metric approach is encouraged. We chose three of the most commonly used metrics: the area under the curve of the Receiver Operator Characteristic (ROC), the True Skill Statistic (TSS), and the Boyce Index. The ROC is a threshold independent metric, neutral to species prevalence, which measures the discrimination capacity regarding relative proportions of correctly and incorrectly classified predictions (Pearce and Ferrier, 2000). The ROC values range from 0 to 1, with 1 corresponding to a perfect classification. The TSS is also independent of the species prevalence and compares the number of correct predictions subtracted by those assigned by chance in a perfect theoretical forecast (Omri et al., 2006); this statistic ranges from -1 to 1, with values near 1 indicating a good agreement between predictions and observations. The Boyce Index (Boyce et al., 2002; Hirzel et al., 2006), calculated separately using the "ecospat" package (Di Cola et al., 2017) for R, is a threshold independent evaluator ranging also from -1 to 1. Values close to 1 indicate a good agreement between the model predictions and the presences distribution in the evaluation dataset, i.e., areas with a high number of occurrences are scored with high suitability values (Hirzel et al., 2006). Conversely, values close to -1 indicate that areas with a high number of occurrences are scored with low suitability values, and thus the model performed poorly. Values close to zero indicate that the model is not different from a random forecast. For each algorithm, we calculated the mean of each metrics.

The contributions of the variables to the models can differ between algorithms and between runs. We estimated the importance of each predictor using a randomization procedure. We used the built-in method in "Biomod2" that uses Pearson correlation between the standard predictions and the predictions where the variable of interest has been randomly permuted. If the correlation value between the two predictions is high, the variable permutated is considered not important for the model prediction. This method is independent of the modelling techniques and thus allows direct comparisons between models (Thuiller et al., 2009). This procedure was repeated ten times for each predictor during the modelling process.

2.2.2 Ensemble modelling

Ensemble forecasting was performed by combining a subset of the single models. Only models with a TSS equal or greater than 0.8 were retained to build the consensus maps. As for the evaluation of models, there is no consensus on the most appropriate metric to select the single models used to build the ensemble model (Scales et al., 2016). However, the TSS and the ROC are among the metrics most frequently used. We opted to use the TSS over the ROC because the reliability of the latter has been heavily criticized (Lobo et al., 2008).

We combined the habitat suitability values of each grid cell using three consensus algorithms (Thuiller et al., 2009): 1) the mean of the probabilities over the selected models; 2) the binary models' committee averaging; and 3) the coefficient of variation of probabilities. The first algorithm provides the prediction of seascape suitability while the other two provide a measure of uncertainty of the predictions.

The ensemble model based on the mean of probabilities of the selected models (TSS ≥ 0.8) is a continuous representation of the habitat suitability index (HSI) ranging from 0 to 1000, with values close to 1000 representing the most suitable areas. The committee averaging returns the average of binary prediction (transformation of the models' output to presence/absence estimations) based on a threshold that maximises the values of TSS; it gives both a prediction and a measure of uncertainty. Values close to 1 or 0, mean that all models agree to predict presence and absence, respectively, while values around 0.5 correspond to the highest uncertainty in the predictions. The coefficient of variance (i.e., standard deviation/mean of probabilities) can also be used as a measure of the model uncertainty: lower scores correspond to better predictions and higher scores to higher levels of uncertainty.

To rank the seascape features in the Mediterranean Sea by suitability, we intersected the output of the mean ensemble model with the seafloor geomorphological classification produced by Harris *et al*. (2014), the authors used the nomenclature defined, primarily, by the International Hydrographic Organization for the seafloor feature types. According to the terminology used by Harris *et al* (2014), and references therein) we identified the following features in the Mediterranean Sea:

- Shelf valleys - features incising the continental shelves or intersecting the shelf breaks no longer than 10 km in length.
- Terraces on the continental slope - “isolated or group of relatively flat horizontal or gently inclined surfaces, sometimes long and narrow, which are bounded by a steeper ascending slope on one side and by a steeper descending slope on the opposite side”.
- Continental rise - identifiable by the occurrence of a smooth sloping seabed adjacent to the base of the continental slope, in general, with a sediment layer > 300 m thick.
- Sills - “seafloor barriers of relatively shallow depth restricting water movement between basins”.
- Seamounts - “discrete or group of large isolated elevations, greater than 1000 m in relief above the sea floor, characteristically of conical form”.
- Guyots or tablemounts - “isolated or group of seamounts having a comparatively smooth flat top”.
- Submarine canyons - “steep-walled, sinuous valleys with V-shaped cross sections, axes sloping outwards as continuously as river-cut land canyons and relief comparable to even the largest of land canyons”.
- Ridges - “isolated or group of elongated narrow elevations of varying complexity having steep sides, often separating basin features”.
- Troughs: “long depressions of the sea floor characteristically flat-bottomed and steep sided and normally shallower than a trench”.
- Trenches: “long narrow, characteristically very deep and asymmetrical depressions of the sea floor, with relatively steep sides”.
- Bridges - blocks of material that partially infill trenches and troughs.
- Fans - “relatively smooth, fan-like, depositional features normally sloping away from the outer termination of a canyon or canyon system”.

Additionally, we used the MPAtlas database of the Marine Conservation Institute (www.mpatlas.org) to analyze the overlap between areas of suitability and the existing marine protected areas (MPAs) in the Mediterranean Sea.

3 Results

We estimated the environmental suitability of the seascapes for *L. pertusa* in the Mediterranean Sea. A total of 30 occurrences of living colonies sparsely distributed across the western and central Mediterranean basins were used in our model (Fig. 1). No records of living colonies of *L. pertusa* were reported in the literature for the eastern Mediterranean Sea.

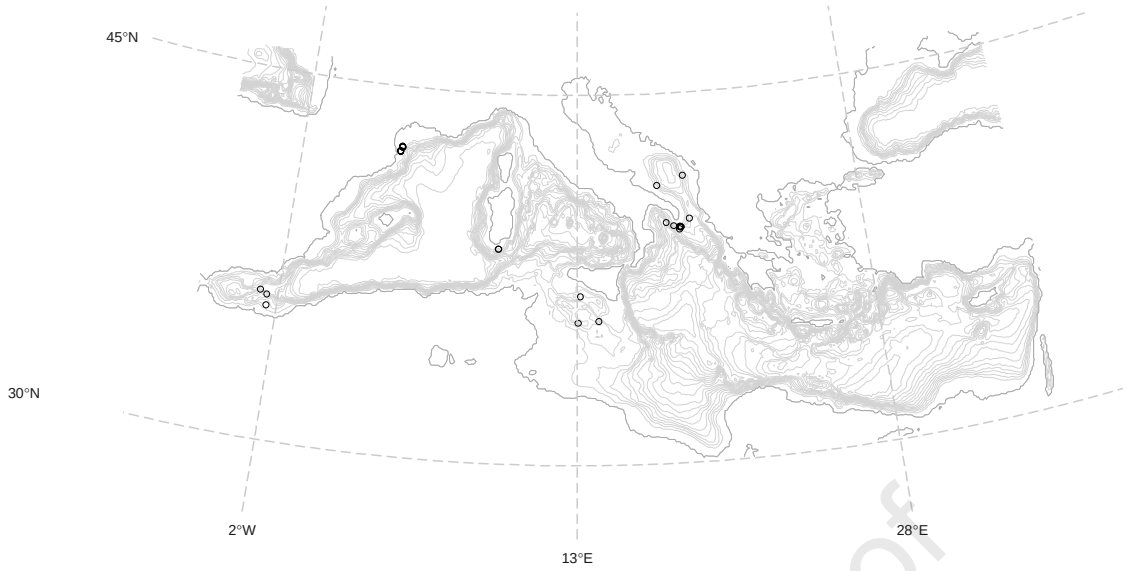
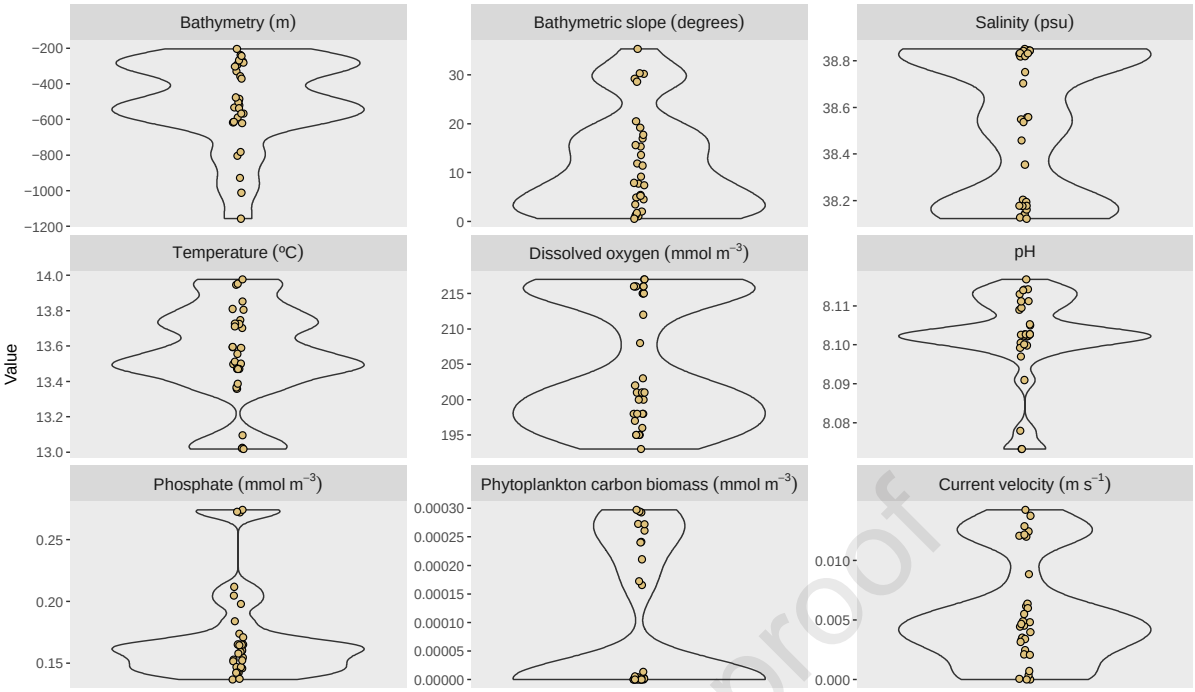


Fig. 1 - The distribution of the living colonies of *L. pertusa* in the Mediterranean Sea used in the ecological niche model.

3.1 Environmental profiling

The intersection of the record of presences with the values of the environmental predictors (Fig. 2) illustrates how the species distribution is related to these variables. On the other hand, the response curves (Fig. 3) describe the suitability variation along the observed range of values for the different predictors. The MaxEnt models returned the most complex behavior but possibly the best representation of the species response to the extremes of environmental gradients (with predicted responses close to zero, Fig. 3). The GBM and RF models showed smoother response curves and similar trends, but lower sensitivity to the environmental gradient variation. The response curves of the ensemble model combine the responses of the selected single models. The colonies of *L. pertusa* were mainly concentrated at depths between 200 and 620 m and in gentle slope areas. According to our model (Fig. 3), suitability is high between 180 and 950 m and peaks at depths close to 300 m; it also rises progressively with increasing slope and maintains high values at slopes >8°.



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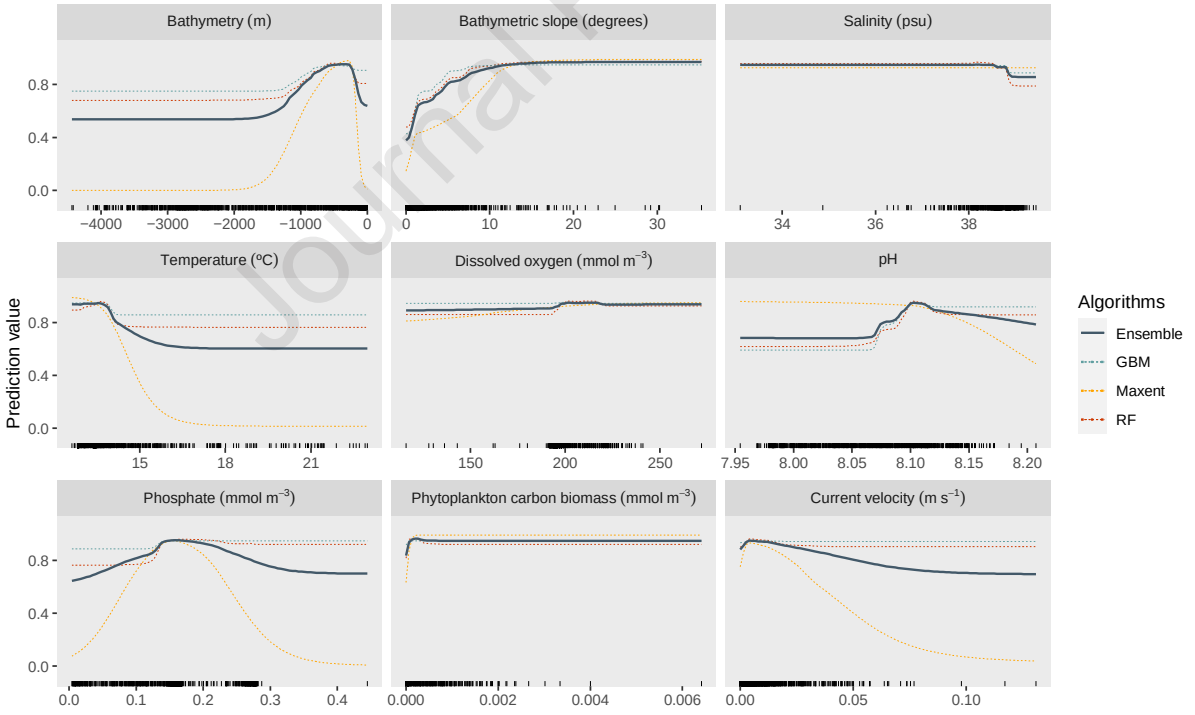
277 Fig. 2 - Violin plots showing the distribution of the species occurrences (white area illustrates the relative
278 frequency of occurrence) intersected with the environmental predictors.

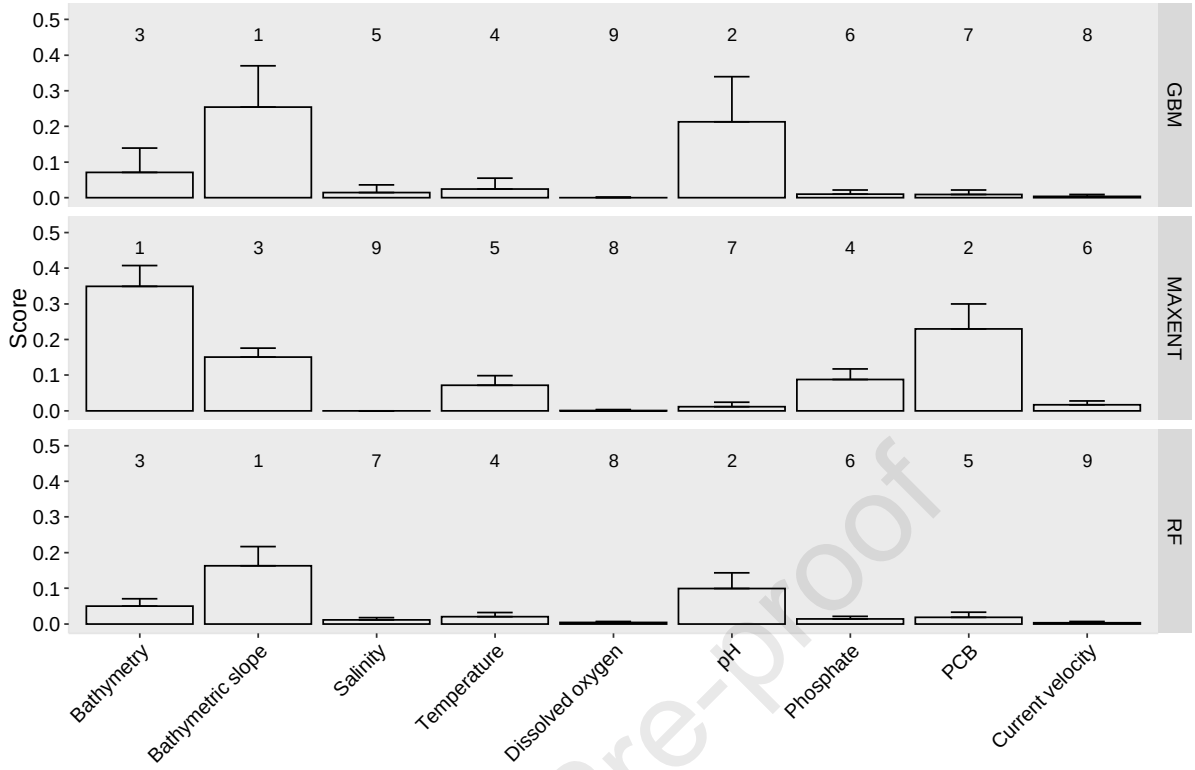


279

280 Fig. 3 - Univariate response curves for each environmental predictor according to the mean ensemble model
281 (solid line) and the average response of single models (dashed lines) according each algorithm. The variables
282 environmental gradients are represented in the x-axis and the suitability prediction values in the y-axis. The
283 shaded areas correspond to the range of values observed for the single models according to each algorithm. The
284 rug lines (x-axis) correspond to the data points of the *L. pertusa* occurrences and pseudoabsences used in the
285 models' fitting.

The occurrences of *L. pertusa* in the Mediterranean Sea were concentrated at temperatures between 13-14 ºC and salinity values ranging from 38.1 to 38.8 (Fig. 2). Values beyond these intervals result, according to the ensemble model, in a decrease in the environmental suitability for the occurrence of *L. pertusa* colonies in the modelling area (Fig. 3). The colonies were detected at concentrations between 193-217 mmol m^{-3} of dissolved oxygen (DO), with values greater than 197 mmol m^{-3} offering more suitable conditions for the species occurrence (Fig. 3). All colonies were subject to pH levels ranging from 8.07 to 8.12 and phosphate concentrations of 0.14-0.27 mmol m^{-3} (Fig. 2). Values out of these ranges result in the decrease of the environmental suitability for the species occurrence in the Mediterranean Sea (Fig. 3). The live colonies of *L. pertusa* were subjected to very low concentration of the phytoplankton carbon biomass and to current velocities lower than 0.014 m s^{-1} (Fig. 2). The increase of the current velocity results in a progressive reduction in the environmental suitability of the species occurrence (Fig. 3).

The contributions of the variables to the predictions differ between algorithms (Fig. 4). The bathymetric slope, pH and bathymetry showed, in this order, the highest contributions in GBM and RF estimates, while bathymetry, phytoplankton carbon biomass and bathymetric slope were the most relevant contributors for MaxEnt estimates. On the other hand, DO, current velocity, and salinity were amongst the least important contributors to models' estimates. The variables' contributions to the ensemble model are not presented because this model is composed of a combination of the results from different algorithms and therefore such contributions cannot be interpreted in a meaningful way (Aguirre-Gutiérrez et al., 2013).



307

308 Fig. 4 - Predictors contributions scored as the relative importance to models considering all pseudo-absence
309 datasets and evaluation runs by algorithm (ranging between 0 and 1). The higher the value, the more important
310 the variable is to the model, while the value zero means no influence at all. The interaction between predictors
311 was not considered.

312 ### 3.2 Performance of the models

313 The performance of the models was assessed using ROC, TSS and Boyce index (Fig. 5). ROC
314 values greater than 0.95 and TSS scores equal or greater than 0.8, were considered highly
315 accurate. According to the different metrics, the GBM and RF models reached good to excellent
316 average predictive scores, while the MaxEnt models performed worst. According to the Boyce
317 index individual performance, the RF models attained high levels of agreement between the
318 presence dataset and grid cells with high HSI.

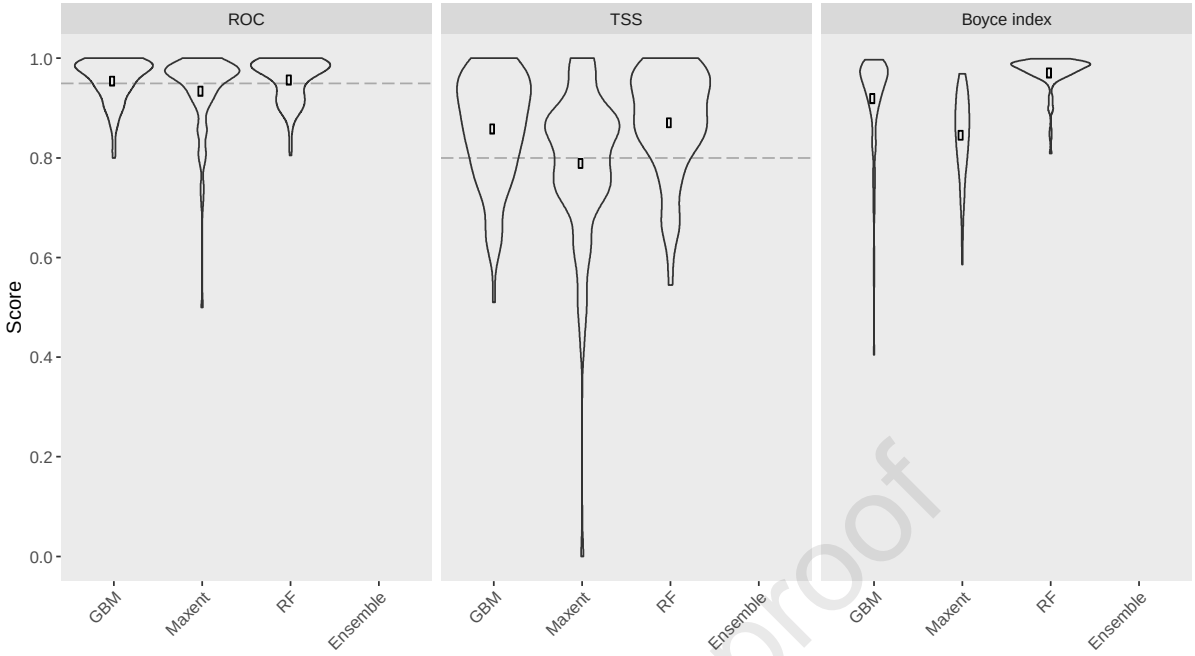


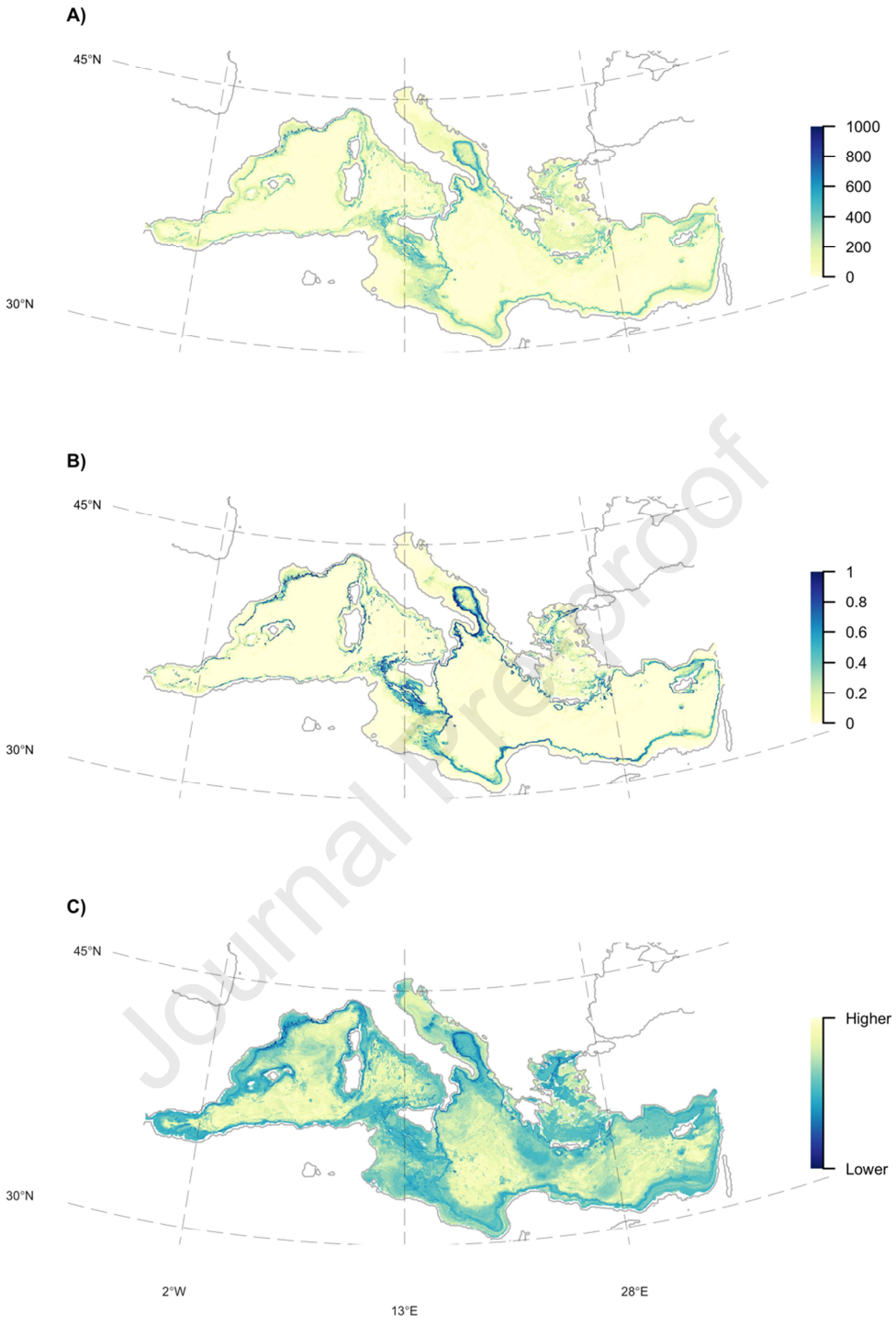
Fig. 5 - Performances of the models grouped by modelling algorithms (presence/pseudo-absence datasets and repetitions pooled) according to ROC, TSS and Boyce evaluation scores. The models' scores above the threshold indicated by the dashed lines are considered highly accurate. The average scores of single models are indicated by the white dots (n = 100). Black dots are the scores for the ensemble model.

The ensemble model forecast was built from the consensus of 198 out of the 300 simulated models, selected according to the defined TSS threshold (0.8). For the three metrics, the scores of the ensemble model were higher than the average scores of the single models indicating that it out-performed the estimation from the single algorithms.

3.3 Seascape suitability

The highest HSI values were found mainly along the upper slope of the Mediterranean margins, in the Western region (e.g., canyons in the Gulf of Lion), in the Central region of the Mediterranean Sea off the Island of Malta, and in the North of the Ionian Sea (deep-water coral provinces of Santa Maria di Leuca) and in the South Adriatic Sea (Fig. 6A). The HSI reached values close to zero in shallower (e.g., North Adriatic, and Tunisian and Libyan continental shelves) and abyssal depths.

The result of the committee averaging model (Fig. 6B) indicates high reliability (agreement between the presence/absence binary transformation of the single models' prediction) of the ensemble forecast for the most suitable and most unsuitable areas and low reliability (values around 0.5) overall for the upper slope of the Central and Southeastern Mediterranean regions. The coefficient of variance (Fig. 6C) returned overall a low uncertainty of the ensemble forecast along the upper slope of the Mediterranean margins and higher uncertainty for the abyssal areas and parts of the Northern Adriatic Sea.

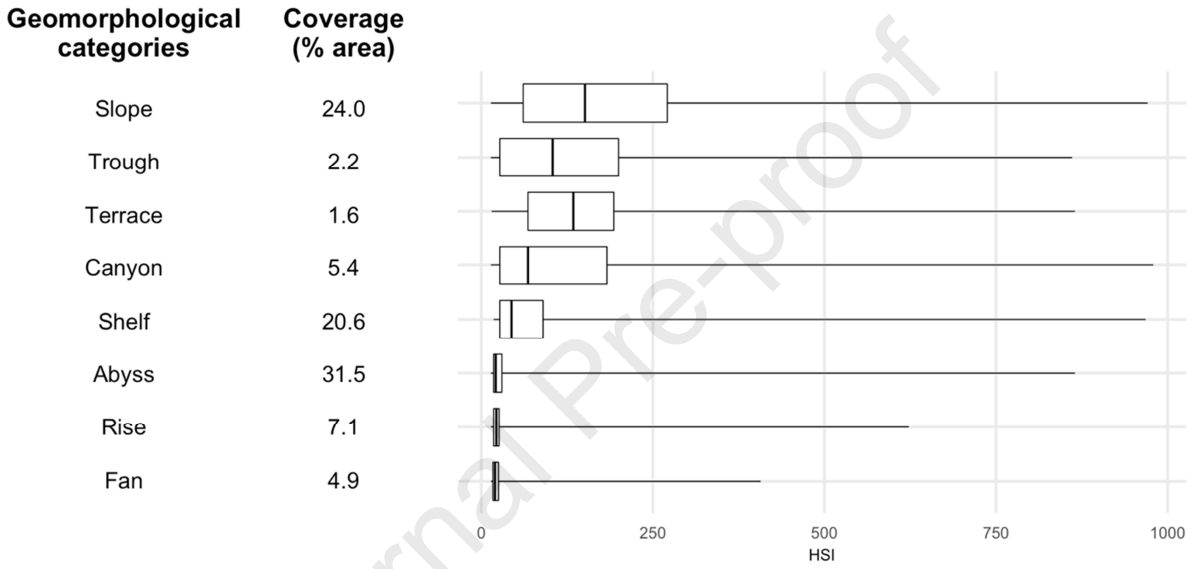


342

343 Fig. 6 - (A) Ensemble model based on the mean probabilities of the selected models and expressed as HSI
344 (ranging from 0 to 1000, representing the least and the most suitable areas, respectively). (B) Map of the
345 committee averaging score; this map offers a measure of reliability of the ensemble model (values close to 1 or 0
346 indicate a good agreement among the single models' predictions regarding the potential presence or absence,
347 respectively; values around 0.5 mean that the estimates of the models are evenly distributed by 0 and 1 values).
348 (C) The coefficient of variance (i.e., standard deviation/mean) of the probabilities estimated for the selected
349 models is also a measure of uncertainty: dark colours correspond to better predictions, while lighter colours mean
350 that prediction uncertainty is higher.

351 Among the 15 geomorphologic features identified by Harris *et al*. (2014) in the Mediterranean
352 Sea, ridges, shelf valleys, trenches, seamounts, guyots, bridges and sills represent individually

353 less than 1% of the seascape area (0.9, 0.9, 0.4, 0.3, 0.1, 0.01, <0.01%, respectively). The
354 continental slopes and submarine canyons are, regarding the area covered, the two most
355 relevant features with high HSI values estimated by our model (Fig. 7); together with troughs and
356 terraces, they cover 33.2% of the Mediterranean seascape. The variation of the HSI estimates
357 within each category was large, indicating a highly heterogeneous environment, and the limits of
358 the third quartile remained below 287 for all categories. The geomorphologic categories showing
359 the highest proportions of low suitability habitats (in all cases the third quartile showed HSI
360 scores lower than 90) were the abyssal areas, continental shelves and rise, and submarine fans,
361 in total accounting for 64.1% of the Mediterranean seascape.



362

363 Fig. 7 - Classification of seascape suitability of the geomorphologic feature categories (Harris et al., 2014)
364 present along the Mediterranean Sea by decreasing order of the 3rd quartile. The lines indicate the HSI value
365 ranges and the boxplots show the 1st quartile, the median and the 3rd quartile. The coverage percentages were
366 given by the area of the shape of the polygons that defined the individual features in Harris et al. (2014).
367 Features with an area lower than 1% were omitted.

368 A total of 898 MPAs, mostly encompassing coastal and shelf depths, confer some legal
369 protection within the modelling region. From these MPAs, a clear majority allows multiple uses,
370 and only 6.46%, covering a total area of 9863 km^2 ca. of 0.4% of the Mediterranean Sea area,
371 have restriction to some type of fisheries or are no-take zones (Supplementary Fig. S2). Note
372 that these values exclude the vast bottom trawl closure area, the largest non-fishing area in the
373 Mediterranean Sea, covering depths greater than 1000 m, as well as the Shark and Cetacean
374 Habitat Protected Areas and the Marine Mammal Sanctuary where the allowed fishing activities
375 do not have relevant impacts on the seabed. The analysis of the overlap between the seascape
376 suitability and Mediterranean MPAs showed that the vast majority of the areas with highest HSI
377 values were not covered by any MPA (Supplementary Fig. S2). The few exceptions were the
378 deepest areas located in the South of Italy, the Central Mediterranean region off the Island of
379 Malta and the area around the Island of Crete which was covered by the bottom trawl closure.

4 Discussion

The output of a presence-only model is an estimation of the species environmental preferences (Guillera-Arroita et al., 2015) and can be interpreted as a measure of habitat suitability for the species occurrence. Species respond differently to a large variety of processes and environmental constraints at local, regional and global scales. Hence, the analysis of the organisms' distribution should take into consideration different levels of the environment spatial hierarchy (Mackey and Lindenmayer, 2001). Our aim was not to provide a fine-scale assessment of the Mediterranean seascape suitability for *L. pertusa*, for which the spatial resolution of the ensemble model is not adequate. Instead, we present a continuous assessment of the environmental conditions, compare the model results with the empirical knowledge on the Mediterranean distribution of *L. pertusa* and provide relevant information to identify focal areas for future efforts using higher resolution models currently only applicable at local scales. To our best knowledge, this work is the first mesoscale (seascape level) estimation of the habitat suitability for *L. pertusa* that encompasses the whole Mediterranean Sea using an ensemble ENM with a multi-algorithm approach, providing both the prediction of seascape suitability and a measure of uncertainty of the forecast.

4.1 A challenging ecological niche

The concept of ecological niche is central for the ENM approach, and the quality of the forecast can be partly inferred from the response curves and their ecological plausibility. Despite some variations between algorithms the bathymetry, bathymetric slope and pH showed the highest contributions to the forecasts. Bathymetry and bathymetric slope are frequently selected as relevant predictors to estimate the seascape suitability for *L. pertusa* (e.g., Barbosa et al., 2019; Rengstorf et al., 2013; Ross and Howell, 2013). Similarly, for the pH, predictors related to ocean acidification and the calcification of the corals' skeleton (e.g., aragonite saturation state – Ω_{ARAG}) are also among the variables with higher contribution in ENM studies focusing in *L. pertusa* (e.g., Davies and Guinotte, 2011; Morato et al., 2020). The limited availability of modern-day observation data for the Mediterranean Sea regarding the carbonate chemistry hampers the development of accurate chemistry models for the region. For this reason, we opted for not including the Ω_{ARAG} in our ENM study. Notwithstanding, *in situ* data indicates that the Mediterranean seawater is likely to remain supersaturated in the future (Fajar et al., 2015); therefore, the Ω_{ARAG} may not be a major limiting factor for the *L. pertusa* distribution in the Mediterranean Sea as it might be for other regions owing to the shallowing of the aragonite saturation horizon (Lunden et al., 2013). In fact, the optimal bathymetric range estimated by our model (Fig. 3) and the currently known distribution of the species in the region coincide with depths considerably shallower than 2500 m (Fig. 2) for which seawater remains supersaturated (Fajar et al., 2015; Schneider et al., 2007). Our results also agree with Davies and Guinotte (2011) that the species distribution coincide mostly with areas with low concentrations of

nutrients and limited organic inputs. A strong link between CWC occurrence and the hydrodynamic regime has often been reported (e.g., Rengstorf et al., 2014) but our results indicate current velocity as one of the predictors contributing less to the model predictions. This result can be partially explained by the relatively coarse resolution of our model that is insufficient to represent the fine-scale local hydrodynamics and its complex interaction with topography, probably underestimating the actual influence of this predictor on the species fine-scale spatial distribution (Davies and Guinotte, 2011; Rengstorf et al., 2014). Salinity and dissolved oxygen concentration were classified as relevant environmental predictors in previous ENM studies with *L. pertusa* (e.g., Barbosa et al., 2019; Davies and Guinotte, 2011). In our study, these two variables were however among the ones with lower contribution for the models' prediction. This result may be related to the low spatial variability close to the seabed of these predictors in the Mediterranean Sea (Supplementary Fig. S3). Surrogates of terrain variables derived from bathymetry such as rugosity are also widely recognised as important proxies for habitat suitability for CWC in local high-resolution models (e.g., Lo Iacono et al (2018)). However, we intentionally excluded these variables because terrain attributes are highly scale-dependent and their computation at coarse resolutions results in significant differences between the derived data and the local characteristics (Rengstorf et al., 2012).

The distribution of living CWC in the Mediterranean Sea has been historically considered as restricted, partly owing to the near homoeothermic conditions (12.7-14.5 ºC, Delibrias and Taviani, 1985). Our results show that in the Mediterranean Sea, *L. pertusa* lives at temperature and salinity values (T: 13-14 ºC; S: 38.1-38.8) that may be close to the upper limit of the species tolerance. In fact, these values are considerably higher than the ones found in areas of the northeast Atlantic Ocean with thriving *L. pertusa* reefs (T<10 ºC, S< 35.6, Dullo et al., 2008). Studies on the physiological response of *L. pertusa* to temperature variations revealed that significant effects are observed on the calcification rate, despite the species capacity for thermal adaptation (Naumann et al., 2014). Although *L. pertusa* shows some biogeographic physiological plasticity to face environmental changes (Georgian et al., 2016), the populations in the Mediterranean Sea may be already subjected to the limits of their physiological tolerance, as already assumed by other authors (Freiwald et al., 2009; Maier et al., 2009).

The species distribution is also determined by the seawater chemistry that constraints the calcification of the carbonate skeleton (Maier et al., 2009). Our model suggests a considerable decrease of the seascape suitability for *L. pertusa* with pH reduction. Lowering pH values by 0.15-0.3 units in laboratory comparing to present North Atlantic Ocean conditions resulted in a reduction of the calcification rate of 30-56% (Maier et al., 2009). The Mediterranean Sea shows a westward trend of decreasing pH (Álvarez et al., 2014) and, despite the high buffering capacity of the Mediterranean Sea (Schneider et al., 2007) this trend may be accentuated by further accumulation of carbon from anthropogenic origin in the intermediate and deep waters (Fajar et al., 2015). Therefore, the synergies of multiple stressors, especially in the current scenario of

455 global change, is expected to accentuate the already challenging environmental setting for the
456 species occurrence in the Mediterranean Sea.

457 4.2 Performance, predictive capacity and limitation of the ENM models

458 The good performance scores of the single models were surpassed by the ensemble model
459 scores in all metrics, strengthening our confidence in its predictive capacity. The estimates of the
460 committee averaging and coefficient of variance, indicating overall low uncertainty levels for the
461 forecast of the ensemble model further support the advantages of using this modelling approach.
462 The projection of the ensemble model over the Mediterranean Sea (Fig. 6A) encompasses areas
463 of medium to high HSI scores located along the upper slope along the Gulf of Lion and Central
464 Mediterranean region (i.e., around Corsica and Sardinia, off Malta and south of the Adriatic Sea).
465 The lowest HSI values cover vast areas including the continental shelves (<100 m depth) and the
466 deepest regions (>1500 m).

467 ENMs are scale-dependent, and predictions are overestimated for larger grid cells (Seo et al.,
468 2009); hence ground-truthing surveys are always required. Moreover, regardless of their
469 performance, ENMs commonly overestimate the species potential distributions since they
470 assume that their occurrence is largely influenced by the ecological niche, ignoring other
471 important drivers for species prevalence (Georgian et al., 2014). A species may be absent in
472 areas with suitable conditions owing to biotic interactions, oceanographic barriers (e.g., water
473 column stratification, prevailing currents) and other complex ecological mechanisms preventing
474 dispersal and/or colonization (Rogers, 2003). Moreover, ENM predictions are always coupled
475 with a certain level of uncertainty associated to the data characteristics (i.e., quality and quantity)
476 and to the methodological decisions made during the modelling process. Nevertheless, the
477 influence of various limitations on the models' forecasts are difficult to quantify. Among the main
478 sources of uncertainty affecting deep-sea ENM are the limitations in the occurrence datasets
479 which, in the case of *L. pertusa*, derive, at least partly, from an insufficient coverage by surveys
480 targeting CWC in the Mediterranean Sea. In the Mediterranean Sea, field observations indicate
481 that *L. pertusa* is less common than in other oceans and has a more patchy distribution, often
482 occurring as isolated colonies (Howell et al., 2011; Orejas et al., 2009). The increasing number of
483 biological surveys in the Mediterranean Sea and the growing tendency to use remote sensing
484 and underwater technologies in oceanographic cruises, is likely to increase the number of coral
485 areas detected in this region (Taviani et al., 2017). Recent efforts to catalogue coral occurrences
486 in the Mediterranean Sea (Chimienti et al., 2019; Taviani et al., 2019a) highlighted the existence
487 of an “almost uninterrupted, albeit patchy, belt of CWC sites” along the south-western Adriatic
488 margin (Angeletti et al., 2014) and a coral reef of considerable size was observed in the Lacaze-
489 Duthiers submarine canyon (Gori et al., 2013). These and other well-known CWC areas were
490 scored with high HSI by our model: the Santa Maria di Leuca coral province (e.g., Tursi *et al*.
491 (2004)), the South Adriatic (e.g., Freiwald *et al.* (2009), Angeletti *et al*. (2014), South of the Island

of Malta (e.g., Maier *et al*. (2012), the Melilla CWC Province (Lo-Iacono et al., 2014), and several submarine canyons (e.g., the Cap de Creus (Orejas et al., 2011) and Lacaze-Duthiers (Fabri et al., 2014) in the Gulf of Lion, Nora (Taviani et al., 2017) in the South of the Island of Sardinia, Bari (Freiwald et al., 2009) in the South Adriatic Sea). The number of occurrences used in our models probably influenced the ENM forecasts. Hence, to improve the predictive capacity of our model, we selected algorithms that show good performances with a small number of presences (Hernandez et al., 2006; Mi et al., 2017; Wisz et al., 2008). The more reliable predictions of the models coincided with known living CWC provinces and surrounding areas. On the other hand, in the eastern Mediterranean Sea, where many fossil CWC occurrences are reported but no living colonies of *L. pertusa*, an almost continuous belt along the continental slope was classified with intermediate HSI values. Hence, future modelling efforts updated with more species records may improve the seascape suitability forecast for the region. Uncertainties in the models' predictions may also derive from the spatiotemporal variability of the environmental predictors. We applied an up-scaling process to improve the spatial resolution of the environmental data extracted from the CMEMS ocean models. The interpolated variables were positive and significantly correlated ($p<0.001$, Supplementary Fig. S4-7) with the *in situ* collected data, generally reflecting the patterns observed in the WOA data, both along the depth, longitude and latitude gradients. These results attest to the accuracy of the interpolated layers and therefore minimize the uncertainty on the models' predictions that can be derived from environmental data.

4.3 Mediterranean seascape suitability

Previous studies using predictive modelling at global and regional scales identified the continental slopes (Davies and Guinotte, 2011) and geomorphologic features such as canyons (Rengstorf et al., 2013) as offering the most suitable conditions for *L. pertusa* occurrence. The ranking of submarine canyons with some of the highest HSI scores in our ensemble model confirms previous indications that, as a consequence of their complex topography and influence on hydrodynamics, these geomorphologic features may be considered CWC hotspots (Orejas et al., 2009; Van den Beld et al., 2017). The high-energy environments and roughed topography commonly associated with canyons can result in low sediment coverage and higher availability of hard substrates for reef development (Sánchez et al., 2014). Such conditions may also be frequently found in escarpments and rocky outcrops on continental slopes. Seamounts (and guyots) are also recognized as preferential areas for CWC development (Roberts et al., 2009). Despite the relatively coarse resolution of our model (230 x 230 m) and the low percentage coverage occupied by seamounts in the Mediterranean Sea (Harris et al., 2014), some areas classified with higher HSI in regions such as the Alboran Sea (Fig. 6A), coincide with the location of these features (Rovere and Würtz, 2015).

Apart from the ecological reasons mentioned above, species distributions can be constrained by the type, intensity and frequency of anthropogenic disturbance. Human activities can lead to

local extinctions of vulnerable species from otherwise environmental suitable locations (Clark et al., 2016). Many studies exposed severe impacts on CWC populations (Fabri et al., 2014; Taviani et al., 2019a) that result from fishing activities, litter accumulation and waste disposal. Conservation measures to mitigate some of these detrimental activities are implemented in areas classified as Sensitive Habitats by the European Commission and/or marine Sites of Community Importance (p-SCI) included in the Natura 2000 network (Madurell et al., 2013). However, these examples correspond mainly to MPAs covering coastal and shelf regions and therefore not effectively protecting *L. pertusa*. The bottom trawl closure area is a clear exception, but despite its great importance and extent, the exclusion of fishing activities below the 1000 m may only provide partial protection to *L. pertusa* since it barely overlaps with the deepest fringe of the most suitable areas. Besides, locations classified with high HSI coincide with areas with medium to high cumulative human impacts in Mediterranean ecosystems (Micheli et al., 2013). Considering these issues, the conservation of *L. pertusa* habitat and the persistence of its Mediterranean populations could be at risk with serious consequences for the biodiversity and functioning of deep-sea ecosystems (particularly at the continental slopes). In this context, canyons may have a supplementary conservation value acting as natural refuges for CWC against some of the anthropogenic impacts (e.g., bottom trawling (Van den Beld et al., 2017), particularly because the Mediterranean Sea is one of the world's regions where canyons are more densely and closely spaced (Harris and Whiteway, 2011) occupying naturally delimited and therefore potentially more manageable areas for conservation purposes.

4.4 Conclusion

Regardless of their limitations, ENMs are important to compile and interpret information on the species ecology, provide insights on their potential distributions and are particularly relevant for research on data-poor species (Morato et al., 2020; Vierod et al., 2014). Our seascape suitability assessment broadens the perception of the Mediterranean potential distribution of *L. pertusa*, and its ecological constraints, previously based on fragmented information from punctual biological surveys and local modelling efforts. The results show that *L. pertusa* in the Mediterranean Sea seems to be subjected to physiological stress due to the current environmental conditions observed in the area. Despite eventual biogeographic plasticity in the physiological response of *L. pertusa*, the resilience of the Mediterranean reefs may be compromised by a further intensification of stressful conditions. This scenario is likely to occur under the current climate change trend, increasing anthropogenic pressure and lack of adequate protection of CWC habitats in the Mediterranean Sea. The mapping of the seascape environmental suitability of *L. pertusa* may assist future research efforts, including further modelling studies with higher resolution data on the areas identified as most suitable, the development of action plans for their conservation and the investigation of the mechanisms governing the persistence of *L. pertusa* reefs in the Mediterranean Sea.

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Author Contributions

FM, JC and MC conceived the study; FM and MC analysed the results; FM, JC and MC wrote the manuscript. All authors reviewed the manuscript.

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Highlights

- We mapped the potential distribution of *Lophelia pertusa* in the Mediterranean Sea
- We provide uncertainty estimates for the model predictions
- Mediterranean colonies are subjected to challenging environmental conditions
- The most suitable areas occur in the continental slope of the west and central basins
- The overlap of the Mediterranean MPAs with the most suitable areas is limited

Declaration of interests

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

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