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Integrating functional traits into correlative species distribution models to investigate the vulnerability of marine human activities to climate change

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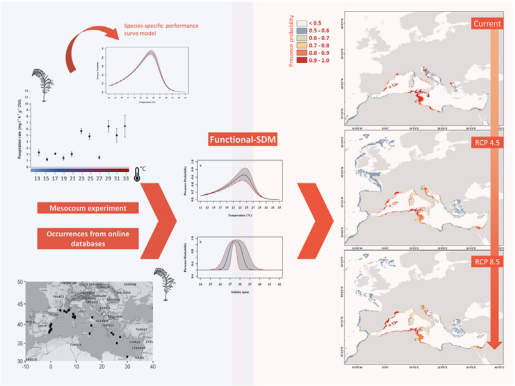
HIGHLIGHTS

- Climate change and local stressors may facilitate the spread of NIS and native outbreak forming species.
- Temperature influences species thermal tolerance limits, phenology and distribution patterns.
- F-SDM produces more ecologically informed predictions.
- F-SDM is a useful tool in early warning ecological systems and management.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change and particularly warming are significantly impacting marine ecosystems and the services they provided. Temperature, as the main factor driving all biological processes, may influence ectotherms metabolism, thermal tolerance limits and distribution species patterns. The joining action of climate change and local stressors (including the increasing human marine use) may facilitate the spread of non-indigenous and native outbreak forming species, leading to associated economic consequences for marine coastal economies. Marine aquaculture is one among the most economic anthropogenic activities threatened by multiple stressors and in turn, by increasing hard artificial substrates at sea would facilitate the expansion of these problematic organisms and face negative consequences regarding facilities management and farmed organisms' welfare. Species Distribution Models (SDMs) are considered powerful tools for forecasting the future occurrences and distributions of problematic species used to preventively aware stakeholders. In the current study, we propose the use of combined correlative SDMs and mechanistic models, based on individual thermal performance curve models calculated through non-linear least squares regression and Bayesian statistics (functional-SDM), as an ecological relevant tool to increase our ability to investigate the potential indirect effect of climate change on the distributions of harmful species for human activities at sea, taking aquaculture as a food productive example and the benthic cnidarian *Pennaria disticha* (one of the most pernicious fouling species in aquaculture) as model species. Our combined approach was able to improve the prediction ability of both mechanistic and correlative models to get more ecologically informed "whole" niche of the studied species. Incorporating the mechanistic links between the

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organisms' functional traits and their environments into SDMs through the use of a Bayesian functional-SDM approach would be a useful and reliable tool in early warning ecological systems, risk assessment and management actions focused on important economic activities and natural ecosystems conservation.

1. Introduction

Climate change (CC) is driving rapid and significant changes at global scales with conspicuous consequences for ecosystems and the human well-being (Rockström et al., 2009; Hoegh-Guldberg and Bruno, 2010). Sea level rise and more frequent extreme weather events (e.g., storms and heat waves) are among the main CC effects impacting on all ecological organization levels, from organismal traits (influencing individual performance/fitness) to population dynamics and ecosystem structure and functioning (Kearney and Porter, 2009; Kearney et al., 2010; Saito et al., 2021). Particularly, temperature (through environmental warming) may play a key role in this context of change as all biological rates are temperature dependent (Brown et al., 2004; Kooijman, 2010; Yvon-Durocher et al., 2012). Temperature influences ectotherms' biochemical reactions and metabolic rates, therefore determining species thermal tolerance limits, phenology and distribution patterns (Walther et al., 2002; Helmuth et al., 2006; Somero, 2010; Sunday et al., 2012). The cascading effect of CC impacts would ultimately be reflected on ecosystems functioning and the services they provided, in turn influencing economically important ecosystem-dependent marine human activities, such as fisheries and aquaculture (Barange et al., 2018; Bosch-Belmar et al., 2019, 2020; FAO, 2020). Changing temperature would directly affect aquaculture farmed organisms' performance by influencing their growth and reproduction rates (Sarà et al., 2018a) and has impacts on local fishery catch by provoking spatial distribution shifts of important commercial species (Barange et al., 2018). In addition, the joining action of CC and local human stressors may facilitate the spread and recruitment of non-indigenous species (Sarà et al., 2018b) and the proliferation and expansion of native outbreak forming species (Groeneveld et al., 2018), both bringing about economic consequences for coastal economies all over the world.

Marine aquaculture, through biofouling accumulation is one among the most important anthropogenic source to facilitate the spread of these (often deleterious) organisms by increasing hard artificial substrates, which provide new and additional suitable habitats for species benthic stages (Guenther et al., 2010; Fitridge et al., 2012; Mangano et al., 2019). While aquaculture biofouling may represent a benefit for local water quality due to the water filtering activity of biofoulers (Floerl et al., 2016), it is generally perceived as the most important barrier to efficient and sustainable production in marine aquaculture (Claereboudt et al., 1994; Fitridge et al., 2012). Several fouling organisms have been reported in the literature by their negative impact on facilities and farmed organisms' welfare (Leblanc et al., 2003; Fitridge et al., 2012; Fitridge and Keough, 2013; Bosch-Belmar et al., 2017). Cnidarians and particularly their benthic stages or colonial species (e.g., hydroids) are among the most notorious problematic organisms for aquaculture biofouling management, since recurring contact with their stinging cells may result in severe skin and gill injuries, complicating operators handling and endangering cultured organisms' health (Fosså et al., 2003; Baxter et al., 2011; Tezcan and Sarp, 2013; Bosch-Belmar et al., 2016a, 2016b). This is a sensitive issue from both management and biodiversity conservation, thereby managers and practitioners would benefit from tools increasing their ability to visualize the "ecologically relevant spatial scale" of the issue in order to provide "temporally adjusted" mitigation and conservation measures. Species Distribution Models (SDMs) are considered among the most powerful and practical tools for forecasting the future occurrences and distributions of problematic species being able to impair the current asset of the local biodiversity to preventively aware stakeholders and apply efficient early warning systems and mitigation measures. Traditionally, SDMs used the correlation between the current distribution of a given species and the local environmental variability to stochastically infer on the changes of habitat suitability and to predict the future expansion of species in space and time (Morin and Lechowicz, 2008; Fitzpatrick and Hargrove, 2009; Woodin et al., 2013; Sarà et al., 2018b). However, they do not explore mechanisms underlying species biological processes (Martínez et al., 2015), and they are not able to provide useful ecological information about the potential local persistence over time. Functional trait-based mechanistic models, instead, include information regarding the relationships between environmental conditions and the organism performance estimated independently of current distributions (Buckley et al., 2011; Cooke et al., 2013) and they may assist in increasing the predictive performance of modelling effort. Nevertheless, while pure correlative-stochastic models are often not highly precise in depicting the distribution of a species in time and space, and pure functional-trait based models (Marn et al., 2020; Tan and Zhang, 2020) are still considered too much time consuming and data-hungry to be applicable at large scale (Buckley et al., 2011), the combination of both approaches may result in hybrid models that incorporate the output of a mechanistic model as a predictor into a correlative model (Kearney and Porter, 2009). And this could be a proper data-analysis strategy to grasp most of the pros of both approaches. Bayesian techniques possess the sufficient power and reliability to integrate species physiological data into correlative-stochastic SDMs (Talluto et al., 2016; Gamliel et al., 2020), enhancing the realism of modelling the biology and ecology of species (sensu Elith and Leathwick, 2009, Orr et al., 2020).

Here, we propose the use of combined correlative SDMs and mechanistic models, based on individual functional traits (functional-SDM, hereafter acronymed as F-SDM) as a tool used to proof whether is possible to increase our ability to investigate the potential indirect effect of CC on the distributions of pernicious species on human activities at sea, taking aquaculture (as a key food production sector) as an example. We choose the aquaculture in that it is recognized as one of the fastest growing sources of protein globally (FAO, 2020) and within most productive activities both terrestrial and at sea it is threaten by multiple stressors (Sarà et al., 2021). Our target species in this F-SDM exercise was one among the most harmful benthic cnidarian fouling species (*Pennaria disticha*) in European waters (Tezcan and Sarp, 2013; Bosch-Belmar et al., 2017). F-SDM was used to predict the current and future distributions of *P. disticha* under a context of environmental climate IPPC change (RCP4.5 and RCP 8.5; IPCC, 2014) to provide a practical functional-based management and an ecological relevant tool to guide the spatial planning at sea to managers, policymakers, technical staff and marine farmers.

2. Material and methods

Similar to the approaches proposed by Talluto et al. (2016) and Gamliel et al. (2020), some of the most recent studies focused on the integration of physiological data on correlative-SDM, we divided the analytical flow of the present work into two main blocks: 1) the parameter estimation through Bayesian techniques of a physiological model which relates the temperature and the functional response of *Pennaria disticha*. This step allows building prior distributions from a laboratory experiment. 2) Parameter estimation of the F-SDM with informative priors used to improve the posterior estimates, to predict the potential present and future distributions of the species.

2.1. Thermal physiological model

The first step to obtain the posterior values used in the SDM model was the implementation of a physiological temperature response model. Model parameters were obtained from specific ad-hoc mesocosm experiments, as in the present case study. We used individual respiration rate as a proxy of organism metabolism (Sarà et al., 2013).

2.1.1. Sampling and respirometry measurements

In September 2020, around 200 specimens of *Pennaria disticha* were collected along the coast of Palermo (Italy) (38°11′12.786″N; 13°21′ 41.1336″E). In the study site, *P. disticha* colonies were patchy distributed between 1 and 2 m depth, hydroids were gently collected cutting off the hydrorhiza in order to preserve the hydrocaulus. Samples were brought back to the Laboratory of Ecology - University of Palermo within 1h and prepared for the experiments. Individuals, ranging between 8 and 12 cm (hydrocaulus length), were immediately inspected with a stereomicroscope (ZEISS Axio Zoom V16), and all epibiotic organisms were manually removed by forceps. Thus, to mimic the animal's sessile condition and minimize any physiological disturbance caused by floating at the surface of the water, colonies were tied to a weight through a cotton thread and stored in tanks filled with filter seawater and aerated by water pumps. Hydroids were starved and acclimated for 24h at the temperature recorded during sampling (23 °C) before the experiment.

To perform oxygen consumption measurements, nine specimens were randomly collected from the tanks and placed individually in a respirometric chamber (130 ml) containing filtered (Whatman GF/C 0.45 μm) air-saturated, 38 psu seawater. Three respirometric chambers were filled only with filtered seawater and used as controls. To ensure the constant mixing of the water, each chamber was stirred with a magnet bar and an individual stirring device (Bosch-Belmar et al., 2016a). Respirometric chambers were further randomly divided into three temperature-controlled water baths and the concentration of dissolved oxygen was measured simultaneously by means of three optical oxygen meters (Pyro Science Firesting O2) each equipped with four optodes (12 optodes in total). Measurements were performed in continuum for 1h. Temperatures were kept stable through a circulated thermal bath (Grant Optima TX150) and monitored throughout the recording period HOBO Pendant® loggers (mod. MX2201, ±0.5 °C accuracy). To investigate the thermal tolerance of *P. disticha*, respiration rate (RR, mg O_2 l^{-1} h^{-1} DW-g^{-1}) was measured at 11 different temperature levels (13 °C, 15 °C, 17 °C, 19 °C, 21 °C, 23 °C, 25 °C, 27 °C, 29 °C, 31 °C and 33 °C). Starting from the water acclimation temperature, the temperature in each group was increased/decreased to the next level at a rate of 1 °C per hour (e.g., Prusina et al., 2014; Montalto et al., 2017). Respiration rate was calculated according to Sarà et al. (2013):

$$\mathrm{RR} = (\mathrm{C_{t0}} - \mathrm{C_{t1}})\ \mathrm{Vol_r}\ 60\ (\mathrm{t_1} - \mathrm{t_0})^{-1}$$

where “Ct_0” is oxygen concentration at the beginning of the measurement, “Ct_1” is the oxygen concentration at the end of the measurement, and “Vol_r” is the volume of water in the respirometric chamber. After the measurement, each replicate was dried at 105 °C for 24 h and weighed to determine the Dry Weight (DW, g).

2.1.2. Regression physiological model

Let Y be the response variable indicating the performance variable (RR), firstly, we categorized it to make the experimental laboratory data and the presence/pseudo-absence data comparable. We followed the protocol described by Talluto et al. (2016) by fixing a threshold value above which Y indicates the species' presence. The cutoff value was chosen based on published data about *Pennaria disticha* main hydrocaulus growth at different environmental temperatures (Bosch-Belmar et al., 2019). As many seasonal hydroids, *P. disticha* life cycle includes an active and growing colonial stage during favorable environmental conditions, resulting in a polyp shedding in response to adverse circumstances, remaining a resting stage that would regenerate the colony when favorable situation would be present again. The species showed positive growth values when temperature reached 17 °C, corresponding with a respirometric rate of 2 mg O_2 l^{-1} h^{-1} DW-g^{-1}; such a value was then used as our putative threshold value. Once the threshold value was fixed, the respiration rate was converted into species presence probability (PP) by assuming that at each specific temperature, respiration rate follows a normal distribution (described by a mean and a standard deviation), then calculating the probability of the metabolic rate to be positive at each temperature (see Talluto et al., 2016 for more details). To identify the best thermal tolerance curve fitting on present study data, the “rTPC” R package was used (Padfield and O'Sullivan, 2020). Accordingly, a total of 24 different non-linear least-squares thermal performance models were launched and compared, and this allowed us to identify the Sharpe-Schoolfield (Schoolfield et al., 1981) as the “best” fitting model (i.e. presenting the lowest AICc score). The Sharpe-Schoolfield is a non-linear regression model, and it well describes the thermal performance curves of organisms when they are characterized by enzymatic deactivation at high temperatures. The probability of presence was modelled as:

$$\mathrm{PP} = \frac{r_{tref} * exp\ \frac{-e}{k}\left(\frac{1}{temp+273.15} - \frac{1}{t_{ref}+273.15}\right)}{1 + \ exp\ \frac{e_h}{k}\left(\frac{1}{t_h} - \frac{1}{temp+273.15}\right)}$$

where “k” is the Boltzmann's constant with a value of 8.62e^{-05}; “r_{tref}” is the rate at the standardised temperature; “e” is the activation energy (eV); “e_h” is the high temperature de-activation energy (eV); “t_h” is the temperature (°C) at which enzyme is 1/2 active and 1/2 suppressed due to high temperatures; “t_{ref}” is the standardization temperature in degrees Celsius (temperature at which rates are not inactivated by high temperatures, 17 °C in the present study); “temp” was the temperature in degrees Celsius.

The above-mentioned model was based on four parameters: r_{tref}, e, e_h and t_h, estimated in a Bayesian framework in JAGS (Plummer, 2003) using the package “rjags” (Plummer, 2011) and will constitute part of our prior information. We used 4000 Markov Chain Monte Carlo (MCMC) samples for burn-in and estimated the four parameters' posterior distributions using 9000 additional samples. We visually examined convergence of model parameters and found that the model adequately converged.

2.2. Model formulation process

In the following subsections, we combined the prior information obtained from the regression physiological model with a Bayesian SDM for the presence/pseudo-absence data.

2.2.1. Species georeferenced records

Geographic recordings of *Pennaria disticha* were obtained from the Global Biodiversity Information Facility (https://www.gbif.org/) and the Ocean Biogeographic Information System (www.iobis.org/). Duplicated records and those within the same pixel were eliminated to avoid spatial data autocorrelation. Non-georeferenced data were removed from the analysis as they were not used in the model. We found no records that warranted deletion from dubious localities.

Pennaria disticha is considered a widely distributed species native to the Atlantic Ocean (Cohen and Carlton, 1995). Therefore, different authors consider it as cryptogenic (Mead et al., 2011; Calder et al., 2019) and recent molecular studies showed the coexistence of different *Pennaria* clades (within not defined species) (Miglietta et al., 2015; Vaga et al., 2020). Due to the current complex taxonomic situation of the species, we decided to perform the modelling using georeferenced data belonging to the Mediterranean Sea and Eastern Atlantic Ocean records (named as Clade 2 by Miglietta et al. (2015) and Vaga et al. (2020)), narrowing the predicting habitat suitability model to these areas instead of launching it at global scale.

2.2.2. Environmental variables

Four environmental variables were used as predictors of *Pennaria disticha* habitat suitability, based on global surface estimates (Copernicus Marine Service Information, https://resources.marine.copernicus.eu). Depth, temperature, salinity and primary production were reported as important variables in previous modelling studies of the species (AquaMap, 2019). Sea surface salinity and primary production were used as additional vague predictors into the F-SDM, while depth was used as a masking layer with a threshold of 100 m as a cutoff, based on information of consulted biodiversity database. To predict future distribution, we used future daily sea surface temperature, salinity and primary production for the year 2050 (Assis et al., 2018). In this study, we used modelling projections forced by Representative Concentration Pathways RCP4.5 and 8.5 (IPCC, 2014), which represented a likely range of future global greenhouse gas and aerosol emissions at the time of the study. All environmental predictors were upscaled to a resolution of 20 arcmin for analyses due to the occurrence records' location uncertainty.

2.2.3. Presence/pseudo-absence data

Since occurrence data available in GBIF and OBIS was mainly based on presence only, we first created pseudo-absence data for the species. The selection of pseudo-absence data may have substantial implications for model performance (Barbet-Massin et al., 2012). To overcome this limitation, we employed a three-step method (Senay et al., 2013; Iturbide et al., 2015; Gamliel et al., 2020). Environmentally unsuitable areas were identified using a presence-only support vector machine algorithm implemented by Senay et al., 2013. Then we created different pseudo-absences datasets using different sized buffers around known presence locations integrated with the unsuitability background zones previously defined. Following, we performed single SDM models for each created dataset, and finally we selected the optimum buffer extent from the generated models. Pseudo-absences were selected outside the realized niche by considering the environmental variables, but in accessible geographic areas that potentially could be reached by dispersal. This provided a balance between using the spatial and environmental space to select pseudo-absence points and has been shown to outperform other methods (see Iturbide et al. (2015) for details). In temperate zones, the active colonial phase of *P. disticha* is present only from late spring to early autumn, specifically from May to November in the northern hemisphere. To consider the species seasonality, a raster of average values for each of the considered environmental variables was constructed using the R packages "raster" (Hijmans, 2020) and "ncdf" (Pierce, 2019), just including the months in which the species was reported. Subsequently, a value for each variable considered was associated with each point of presence or pseudo-absence, thus finalizing the construction of the dataset to be used in the F-SDM.

2.2.4. Bayesian functional-SDM

The equation used to model the presence probability of *Pennaria disticha* and the three environmental variables was:

$$\mathrm{PP} = \frac{r_{tref} * exp\ \frac{-e}{k}\left(\frac{1}{temp+273.15} - \frac{1}{t_{ref}+273.15}\right)}{1 + exp\ \frac{e_h}{k}\left(\frac{1}{t_h} - \frac{1}{temp+273.15}\right)} +$$

$$s_{max} * \exp\left(-0.5\left(\frac{|sal - sal_{opt}|}{a}\right)^2\right) +$$

$$p_{max} * \exp\left(-0.5\left(\frac{|prod - prod_{opt}|}{b}\right)^2\right)$$

where "r_{tref}", "e", "e_h" and "t_h" are the Sharpe-Schoolfield model coefficients equal to the posterior of the physiological sub-model; "s_{max}", "sal_{opt}" and "a" are the coefficients describing a gaussian relation between PP and salinity (used as non-informative prior); and "p_{max}", "$prod_{opt}$" and "b" are the coefficients describing a gaussian relation between PP and primary production (used as non-informative prior). Model setting was estimated as described above for the regression physiological model. As described by Gamliel et al. (2020), we estimated cross-validation model performance from the training data (70% of total dataset) to the testing data using the Boyce index (Hirzel et al., 2006). The Boyce index ranges from −1 to 1, where 0 means the model did not differ from random and 1 indicates a perfect fit to the data (Hirzel et al., 2006).

2.2.5. Model prediction

The final parameters of the F-SDM were used to predict the probability of presence of *Pennaria disticha* in the current climatic conditions and in the two 2050 future scenarios (RCP4.5 and 8.5). Specifically, PP was calculated at pixel level by using the environmental values reported in the current, 2050 RCP 4.5 and 2050 RCP 8.5 rasters. The obtained value was converted into probability through the inverse logit function. Prediction maps of *Pennaria* PP were visualized in ArcGIS.

3. Results

Across the range of the experimental temperature tested in the present study (13 °C- 33 °C), the amount of consumed oxygen changed from 1.22 ± 0.68 mg l^{-1} h^{-1} g^{-1} DW (estimated at 15 °C) to 5.70 ± 1.30 mg l^{-1} h^{-1} g^{-1} DW (estimated at 23 °C). At the warmest temperatures an abrupt increase in the hydroid respiration rate was observed from 27 °C (1.54 ± 0.30 mg l^{-1} h^{-1} g^{-1} DW) to 29 °C (6.46 ± 0.95 mg l^{-1} h^{-1} g^{-1} DW) and was maintained through 31 °C and 33 °C (5.02 ± 1.07 mg l^{-1} h^{-1} g^{-1} DW and 6.49 ± 5.15 mg l^{-1} h^{-1} g^{-1} DW respectively). This response would be related with the transition from the optimal to the *pejus* temperature range (Sokolova et al., 2012). Consequently 29 °C, 31 °C and 33 °C temperatures were considered as not informative for the statistic model and for this reason they were excluded from the subsequent analysis. We tested 24 different models to shape the species thermal performance curve. The selected physiological model (*Sharpe Schoolfield* model) for *P. disticha* showed unimodal response to temperature. Optimum temperature was identified at 24.14 °C and the critical temperature (temperature at which enzyme is ½ active and ½ suppressed due to high temperatures) was 27.31 °C. Bayesian-physiological model showed the optimum value similar to that reported by the *Sharpe-Schoolfield* model, resulting in an optimum temperature of 24.31 ± 0.3 °C (Fig. 1). Posterior results of F-SDM suggested a non-significant effect exerted by primary production. As a main consequence, we ran a second combined model without that variable. In doing so, we highlighted the importance of temperature and salinity in addressing the spatial distribution of *P. disticha*, as confirmed by the

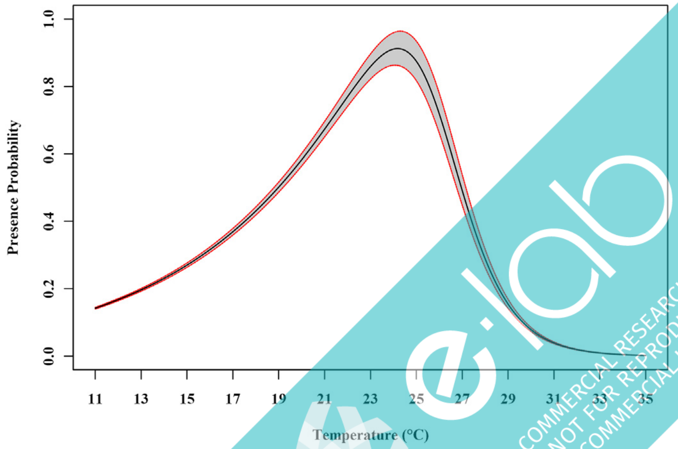

Fig. 1. *Pennaria disticha* presence probability based on its thermal performance curve. Grey shaded areas corresponded with the confidence intervals.

Boyce index (0.5 ± 0.18) and ROC value (0.979) and the significance of all considered posterior parameters. The Fig. 2a showed the link between the functional information as expressed by the optimum temperature and the putative highest presence probability of *P. disticha*. The temperature of 24.11 °C overlapped with that obtained in the laboratory when measuring the species thermal performance curve (Fig. 1). Salinity was also an important variable for the distribution of this species as showed in Fig. 2b, which highlights that the salinity optimum was at around 37.6 psu. However, the Gaussian curve's narrow base was indicative of the restricted salinity tolerance of *Pennaria*. Our modelling effort showed a wide distribution of this species in the Mediterranean Sea under the current seawater temperature. The highest presence probability was found in the central Mediterranean basin (Fig. 3), specifically in the southern part including almost all Tunisian and southern Sicilian coasts. While the western and eastern coasts showed overall low PP values (0.59 ± 0.12 and 0.55 ± 0.08 respectively, Fig. 4), and the most suitable habitats within these sectors were detected around the Spanish Balearic sector and the northern part of the Aegean Sea (Fig. 3a).

PP predictions based on RCP4.5 and RCP8.5 future scenarios are reported in Fig. 3b and c. Predictive modelling effort showed a general increment of *P. disticha* PP across the Mediterranean Sea, especially in the Spanish Mediterranean and northern African coasts (Algeria and Morocco) where the species PP increased up to 0.8-1.0 range. The eastern Mediterranean region presented an enlargement of the species habitat suitability forward the southern part of the Aegean Sea (PP between 0.5 and 0.6). The central basin seems will be a more suitable habitat for *Pennaria* colonies with respect to the current conditions (expanding through all Italian coasts), even if the mean probability for the region could remain almost unvaried (Fig. 4). In addition, prediction maps from both RCPs showed new habitat colonization probabilities for the colonial cnidarian going through the Strait of Gibraltar to the Atlantic Ocean. Represented by a PP between 0.5 and 0.6, the suitable habitat for *P. disticha* is expected to extend towards the Spanish and Portuguese Atlantic coasts and the western French, Irish and English waters.

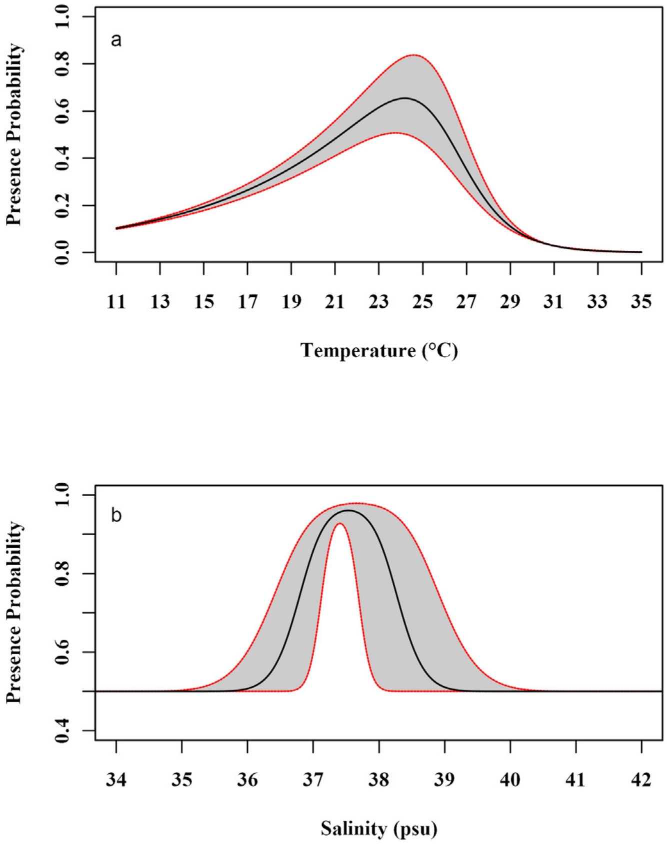

Fig. 2. Presence probability of *Pennaria disticha* according to temperature (a) and salinity (b) variables. Grey shaded areas corresponded with the confidence intervals.

4. Discussion

Present study benefited from the integration of functional traits into the stochastic correlative models. Thermal tolerance-based modelling showed that current potential distribution of *P. disticha* will latitudinally and longitudinally shift under IPCC climate change scenarios. *Pennaria disticha* distribution will be wider into the western waters of the Mediterranean Sea and there will be a “trans-shipping” risk to move through the Gibraltar Strait towards the European Atlantic coasts. Temperature and salinity were identified as significant variables in the combined F-SDM in accordance with previous literature, highlighting the key role of both factors influencing the metabolism and ecological responses of cnidarians to changing environments (Boero et al., 2016; Eder et al., 2018; Danko et al., 2020). Variable salinity may significantly impact some benthic cnidarians survival, growth and asexual reproduction rates (Gili and Hughes, 1995; Folino-Rorem and Renken, 2018; Danko et al., 2020), but temperature would be the main regulating factor in their life cycle, playing an important role in determining the seasonal occurrence and the persistence over time (Boero, 1984; Boero and Fresi, 1986; Gili and Hughes, 1995) and triggering reproductive and species-specific propagation events (Boero, 1984). In the Mediterranean Sea, where *P. disticha* presence probability is expected to increase, more frequent optimal conditions across time and space could result in increasing the likelihood of the active colonial stage presence in the environment (as reported by Puce et al. (2009) for the Ligurian Sea hydroids populations). As a main consequence, this could increase the risk for marine aquaculture facilities. *Pennaria disticha* is considered a warm-water affinity species, with fast growth rates (Bosch-Belmar et al., 2019) and an aggressive behaviour to compete for the natural and artificial substrates (Mead et al., 2011). Since it is usually found in the fouling artificial substrates and algae, we hypothesize that this species should disperse by using different human-mediated dispersal strategies (Vaga et al., 2020). Such features may make *P. disticha* as the perfect candidate to colonise the fouling community of most marine farms and hard substrates around the European waters due to functional traits conferring it a non-neglected invasiveness potential (Knapp et al., 2011; Mead et al., 2011; Miglietta et al., 2015).

Organism response to climate change is a function of its ecological, physiological and genetic traits, combined with that organism's exposure to environmental stressors (Barrows et al., 2020). Being environmental temperature the most important abiotic driver of metabolism (at all biological organization levels), above all in ectotherms (Pörtner, 2010) climate warming (here tested through the RCP 4.5 and RPC 8.5 scenarios) can be considered as an umbrella under which all other stressors play out (Jackson et al., 2021). Moreover, being able to predict the future expansion of species both for the recipient communities (e.g., fouling) and for associated economic activities is crucial to design management measures. The potential impairment of the fouling community due to the reinforced presence caused by climate change of species such as *Pennaria* may alter the ecosystem functioning (sensu Cardinale et al., 2006, Sarà et al., 2018b) and by cascade this may affect the provision of supporting and regulating ecosystem services (Jax, 2010; Baltar et al., 2019).

Due to *P. disticha* potential impact on aquaculture, changes in the realized and/or fundamental niche breadth could directly influence the effectiveness of aquaculture management measures. With respect to previous studies, the improvement of this study was the integration of specific laboratory experiments to explore the species thermal tolerance range with strong statistical (Bayesian-based) approaches to project the thermal performance, a trait of the fundamental niche, across the space and along the temporal axis. Moreover, since organisms' thermal responses not always follow a pure gaussian distribution, we used a

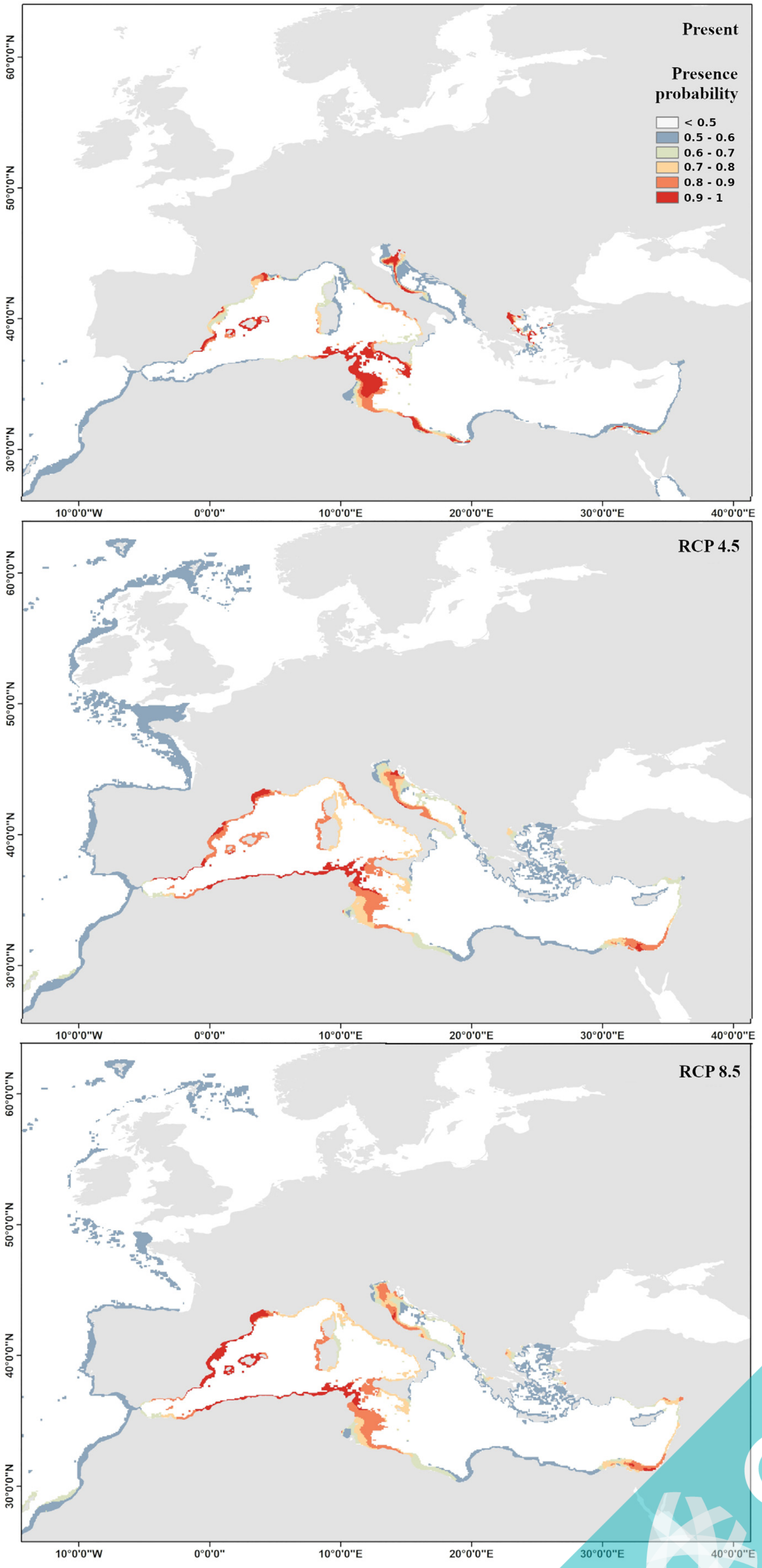

Fig. 3. Forecasted distribution maps for *Pennaria disticha* according to current environmental conditions (a), and future 2050 predicted scenarios: RCP4.5 (b) and RCP8.5 (c).

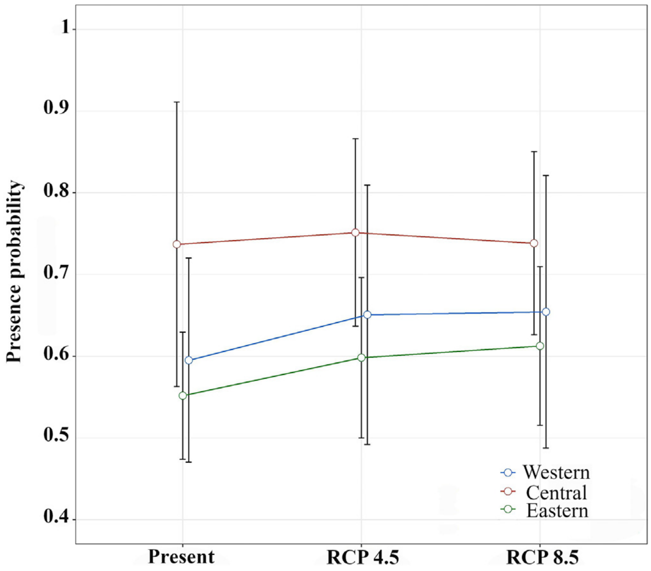

Fig. 4. *Pennaria disticha* mean presence probability in the western, central and eastern Mediterranean basin forecasted by the present and future 2050 scenarios (RCP4.5 and RCP8.5).

non-linear least-squares method to fit the best thermal performance curve model to our data and the Bayesian statistics to improve the model parameters precision. In doing so, our F-SDM improved the ability to predict both mechanistic and correlative models to get a more ecologically informed "whole" niche of *P. disticha*. Thus, considering the effect of environmental variables on the organism performance and metabolic rates, being the physiological limitations the main constraints on a species distribution and proliferation (Kearney and Porter, 2009), it becomes essential to increase our ability to generate an effective adaptive ecosystem management (Mangano et al., 2020). While a potential limitation to the development of functional trait-based SDMs is certainly the scant information available dealing with the species-specific physiological tolerance (Williams et al., 2008), what is likely more consuming deals with our ability to link functional trait data (sensu Schoener, 1986; morphological, behavioral and physiological traits of organisms) with georeferenced databases (Kearney and Porter, 2009). The collection of large databases of functional traits and their successive adaptation at relevant spatio-temporal scale to avoid scale-mismatch (Bellwood et al., 2019; Bütikofer et al., 2020) should be a priority in conservation science and a challenge for future conservationists and climate change ecologists. This is an essential step as individual functional traits and habitat features interact to drive the distribution of species in the environment. Increase our understanding on how they fit across the space and time is a cornerstone to measure the consistency of populations across different scales (Gotelli, 2008) and to successively infer on how environmental change affects biodiversity and ecosystem functioning (McGill et al., 2015).

Accordingly, to incorporate the mechanistic links between the organisms' functional traits and their environments into SDMs through the use of a Bayesian F-SDM approach is useful and reliable to risk assessment studies and for the early warn ecological systems. This will increase the adaptation of food sectors to anthropogenic-mediated change and will reduce the mismatch between the human perception towards climate effects and what ecologists will propose in terms of management and conservation when suggesting how to cope with climate change.

5. Conclusions

The joining action of changing climatic conditions and the human intervention on marine ecosystems may facilitate the spread of some species, including those harmful for marine economic activities. Developed functional traits-based modelling showed that the current distribution of *P. disticha* will shift under forecasted climate change scenarios, posing a risk for European marine aquaculture facilities. Bayesian F-SDM approach improved the ability to predict both mechanistic and correlative models to get a more ecologically informed species niche, proving to be a useful and reliable management tool to human-managed ecosystems and economic sectors.

CRediT authorship contribution statement

MBB conceived the study and with GM, CG and GS designed it through the different steps. GM and MBB developed the F-SDM and with AA fine-tuned the Bayesian methodology. MBB drafted the early version of this manuscript and with all other authors drafted the present version.

Declaration of competing interest

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

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