frontiers | Frontiers in Marine Science

ORIGINAL RESEARCH
published: 04 April 2022
doi: 10.3389/fmars.2022.810555

Predictive Metabolic Suitability Maps for the Thermophilic Invasive Hydroid *Pennaria disticha* Under Future Warming Mediterranean Sea Scenarios

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Temperature is a fundamental variable for all biological processes. It influences the metabolism and tolerance limits of all living organisms, affecting species phenology and distribution patterns. It also facilitates the spread of non-indigenous species and the proliferation and expansion of native outbreak-forming species. *Pennaria disticha* is a colonial benthic cnidarian reported to be invasive in different Indian and Pacific coastal areas, as well as a harmful member of fouling communities found in Mediterranean marine aquaculture farms. Using the most basal functional trait (i.e., thermal tolerance), we explored the potential of *P. disticha* to colonize different habitats across the Mediterranean Sea in future warming scenarios. Respiration rate was measured as a proxy of *P. disticha* metabolism under 12 different experimental temperatures. The obtained thermal tolerance dataset was used to create a thermal performance curve (TPC). We then scaled modeled curve to occurrence probability to map species potential metabolic habitat suitability and phenological shifts within the Mediterranean Sea when subjected to different warming scenarios. Prediction maps for future climatic conditions showed a potential temporal and spatial expansion of *P. disticha* in the Western and Central Mediterranean. The present data increases our understanding of the ecological performance and potential distribution of an invasive and outbreak-forming species. This information will contribute to the development of early warning systems and to the design and implementation of risk assessment and management plans.

Keywords: harmful species, thermal tolerance, metabolic-based maps, early warning system, thermal habitat suitability

OPEN ACCESS

Edited by:
Stelios Katsanevakis, University of the Aegean, Greece

Reviewed by:
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Conor McManus, Division of Marine Fisheries, Rhode Island Department of Environmental Management, United States

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Specialty section:
This article was submitted to Marine Ecosystem Ecology, a section of the journal Frontiers in Marine Science

Received: *07 November 2021*
Accepted: *24 February 2022*
Published: *04 April 2022*

Citation:
Bosch-Belmar M, Piraino S and Sarà G (2022) Predictive Metabolic Suitability Maps for the Thermophilic Invasive Hydroid Pennaria disticha Under Future Warming Mediterranean Sea Scenarios. Front. Mar. Sci. 9:810555. doi: 10.3389/fmars.2022.810555

INTRODUCTION

The combination of climate change and local anthropogenic stressors can facilitate the spread and recruitment of non-indigenous species (Sarà et al., 2018; Geraldi et al., 2020) and the proliferation and expansion of native outbreak-forming species, such as jellyfish (Purcell et al., 2007), exacerbating their overall ecological impacts and economic consequences worldwide.

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Indeed, as documented by ongoing species range shifts and changes in phenology (Parmesan, 2006; Elith and Leathwick, 2009; Hoegh-Guldberg and Bruno, 2010; Sunday et al., 2015), climate change and ocean warming are expected to increasingly affect the structure and function of marine ecosystems, whose species need to adapt or to shift their geographical or vertical distribution to preserve their climatic niche (Coll et al., 2012; Garcia Molinos et al., 2016). For instance, global warming—combined with other anthropogenic impacts (Purcell et al., 2007; Boero et al., 2008; Richardson et al., 2009)—may amplify the spread of several jellyfish species by increasing their reproduction rate, reproductive period and/or their range of distribution toward higher latitudes (Purcell, 2005; Lucas et al., 2014a,b; Milisenda et al., 2018). Temperature, however, remains a key factor influencing the metabolism and phenology of cnidarians, despite the paradigmatic potential for life cycle adjustments and physiological plasticity bestowed upon this group (Boero et al., 2016; Foo and Byrne, 2016).

The increasing likelihood of negative interactions between marine gelatinous organisms and humans has also been reported in recent years (Purcell et al., 2007; Brotz and Pauly, 2012; Lucas et al., 2014b; Bosch-Belmar et al., 2020), driven by the coinciding rise of human activities at sea and cnidarians proliferative potential (Gibbons and Richardson, 2013). Marine aquaculture sprawl is known to facilitate the spread of jellyfish and other cnidarians as it provides additional suitable habitats such as artificial benthic substrates (Sarà et al., 2007) for the asexual proliferation of sessile life stages, i.e., the polyps (Boero et al., 2008; Richardson et al., 2009; Duarte et al., 2013). Specifically, hydroids (i.e., the sessile polyp colonies of the class Hydrozoa) represent a significant component within marine fouling communities on natural and artificial substrates. Common underwater net and submerge structures cleaning activities in aquaculture facilities, as well as seasonal hydroids reproductive events, may release thousands of free-living stinging propagules (such as tiny jellyfish, larvae, or fragmented tentacles) into the water column that may directly and repeatedly contact with fish skin and gills (Baxter et al., 2011; Bosch-Belmar et al., 2017). The toxic compounds delivered by their stinging cells threaten the health of farmed organisms, negatively affecting the effectiveness and productivity of aquaculture operations and related revenues (Baxter et al., 2012; Fitridge and Keough, 2013; Sievers et al., 2013; Bosch-Belmar et al., 2020).

Among the most common and injuring components of the fouling community, the conspicuous colonial hydroid *Pennaria disticha* is not only able to affect farmed organisms but also to produce painful stings and severe dermatitis to field aquaculture operators and bathers (Tezcan and Sarp, 2013; Bosch-Belmar et al., 2017). It may pose a significant threat since some of its main traits (e.g., warm-water affinity, high growth rate, iteroparous reproduction, and the persistence of a resting stage when environmental conditions are not optimal) conferred the species a significant invasiveness potential (Schuchert, 2006; Knapp et al., 2011; Bosch-Belmar et al., 2019; Vaga et al., 2020).

Despite its potential impact on marine ecosystems and relevant economic activities, there is a lack of knowledge on the ecological performance of harmful species (such as stinging cnidarians, like *P. disticha*) and the potential influence of future temperature conditions on their metabolism, phenology, and distribution. Ecologists and biologists may count on functional traits to assist stakeholders in predicting the potential distribution of harmful species driven by environmental (including climatic) change. These traits usually include important aspects such as tolerance and sensitivity to environmental conditions, driving the ability of each species to adapt its own metabolic machinery and biological performance in space and time (Sarà et al., 2013). Here, we used the "simplest" and the most basal functional trait, thermal tolerance, to explore if and how *P. disticha* is expected to colonize different habitats across the Mediterranean Sea in different future warming scenarios. Individual respiration rate was used as a metabolic proxy (Angilletta et al., 2002; Sokolova et al., 2012; Gould et al., 2021) to study the effects of temperature on the organismal performance of *P. disticha* and link the species potential habitat suitability based on this functional trait with the IPCC temperature projections under different climatic scenarios (Butenschön et al., 2016). We generated metabolic-based maps that can be considered as an informative baseline and used to implement adaptive measures for management and conservation of biodiversity and natural resources. They provide a useful predictive tool for stakeholders and entrepreneurs of the Blue Economy, who are faced with increased ecosystem vulnerability due to constantly changing environmental conditions.

MATERIALS AND METHODS

Laboratory Experiments

A total of 90 colony specimens of *Pennaria disticha* was sampled along the coast of Palermo (Sicily, Central Mediterranean Sea) (38°11′12.786″N; 13°21′41.1336″E). Hydroid colonies were collected by gently removing the creeping stolons (*hydrorhiza*) from the substrate to preserve the integrity of the erect colonial stem (*hydrocaulus*) and its lateral branches (*hydrocladia*). Samples were immediately brought back to the wet enclosure of the Laboratory of Ecology at the University of Palermo and prepared for the experiments. *Hydrocauli* ranging between 8 and 12 cm in length were carefully inspected with a stereomicroscope, and all epibiotic organisms were manually removed using forceps. Prior to the experiments the hydroids were starved and acclimated for 24 h at the temperature recorded during sampling (23°C).

To measure oxygen consumption at each investigated temperature, nine different colonies were randomly collected from the tanks and placed individually in a respirometric chamber (130 ml) containing filtered (Whatman GF/C 0.45 μm) saturated-air, 38 psu seawater. Three respirometric chambers were filled with filtered seawater only and they were used as controls. To ensure the constant mixing of water, each chamber was stirred with a bar magnet and an individual stirring device (Bosch-Belmar et al., 2016). Respirometric chambers (12 in total: 3 controls and 9 containing *P. disticha* specimens) were randomly divided into three temperature-controlled water baths and the concentration of dissolved oxygen was measured simultaneously by means of 3 optical oxygen meters (Pyro Science Firesting

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O_2), each equipped with four optodes. Measurements were performed in continuum for 1 h. Temperatures were kept stable by means of a circulated thermal bath (Grant Optima TX150). To investigate the thermal tolerance of *P. disticha*, respiration rate (RR, mg O_2 h^{-1} DW-g^{-1}) was measured at 11 different temperatures as follows: 13, 15, 17, 19, 21, 23, 25, 27, 29, 31, and 33°C. Temperature range was based on the areal extremes of the *Pennaria disticha* spatial distribution. In other words, minimum and maximum temperatures were obtained from the species' occurrence reported in the GBIF online database[1] for the Mediterranean Sea. Starting from the water acclimation temperature, the temperature in each group was increased or decreased to the next level at a rate of 1°C per hour (e.g., Schröer et al., 2011; Prusina et al., 2014; Montalto et al., 2017). Respiration rate was calculated according to Sarà et al. (2013):

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

where Ct_0 was the oxygen concentration at the beginning of the measurement, Ct_1 was the oxygen concentration at the end of the measurement and Vol_r was the volume of water in the respirometric chamber. At the end of the measurement session, the organisms from each replicate were dried at 105°C for 24 h and then weighed to determine the Dry Weight (DW, g).

Thermal Performance Model

By using the "rTPC" R package (Padfield et al., 2021), a total of 23 thermal performance models were performed and compared, allowing us to identify the *Sharpe-Schoolfield* model as the best fit with our respiration rate (RR) data (i.e., presenting the lowest AICc score; see **Supplementary Table 1** and **Supplementary Figure 1**). The *Sharpe-Schoolfield* is a non-linear regression model describing the thermal performance curves (TPC) of an organism based on enzymatic deactivation at high temperatures (Schoolfield et al., 1981). This model estimated four distinct parameters used in the prediction of the monthly presence of the species based on its RR values (**Supplementary Figure 2**). The model equation is:

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

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; "r_{tref}" is the standardization temperature in degrees Celsius (temperature at which rates are not inactivated by high temperatures); "temp" was the temperature in degrees Celsius.

Bootstrapping was used to calculate 95% prediction limits for the selected TPC model and confidence intervals around its temperature optimum.

Environmental Data

Sea surface temperature (SST) was selected to perform the model since *P. disticha* is a species usually habiting shallow waters where light and temperatures drive its reproduction (Schuchert, 2006). Mediterranean monthly mean SST raster files were created based on current daily SST data downloaded from the Copernicus Marine Service Information.[2] To predict future distribution, we used forecasted daily SST for the year 2050 (Assis et al., 2018) within modeling 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. RCP4.5 scenario represents moderate emissions while RCP8.5 forecasts more extreme effects of climate change. All SST raster layers were upscaled to a resolution of 0.08 × 0.08 decimal degrees.

Metabolic Suitability Prediction Maps

The final parameters of the TPC model (**Supplementary Figure 2**) were used to predict the potential occurrence of the active colonial stage of *Pennaria disticha* in the present-day climatic conditions and in two 2050 future scenarios of greenhouse gas (GHG) emissions (RCP4.5 and RCP8.5). In the Mediterranean and other temperate seas, *P. disticha* has an iteroparous, multiannual life cycle, with a sharply seasonal phenology (Brinckmann-Voss, 1970); the active colonial stage (i.e., the erect polyp colony) arise and sexually reproduce in the warmest months of the year. After reproduction, the polyps shrink, shedding all feeding and reproductive hydranths, to rest throughout the coldest period in a quiescent form, i.e., the creeping stage (the *hydrorhiza*). This remains anchored to the substrate until suitable environmental conditions return that trigger the re-growth of the erect polyp colony (Gili and Hughes, 1995). This is the life stage that represents a major multiannual source of impact on Mediterranean marine fish farms. At the same time, the hydroid colony plays a role as a seasonal habitat former in shallow rocky bottom communities.

To create thermal habitat suitability maps based on the species metabolism, data on experimentally measured respiration rate was converted into probability of occurrence at different temperatures. We scaled the different oxygen consumption values to the RR value at the temperature optimum predicted by the model, using the following formula:

$$OP = \frac{RR_t}{RR_{Opt}}$$

where OP was the occurrence probability, RR_t was the respiration rate value at temperature *t*, and RR_{Opt} was the value of respiration rate at the optimum temperature predicted by the *Sharpe-Schoolfield* model.

Spatial occurrence probability based on RR values was calculated at pixel level using the environmental values reported

[1] https://www.gbif.org/

[2] https://resources.marine.copernicus.eu

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in the (a) current, (b) 2050 RCP 4.5, and (c) 2050 RCP 8.5 raster layers using the following formula:

$$SOP_{im} = \frac{PRR_{im}}{RR_{Opt}}$$

where SOP_{im} was the spatial occurrence probability in the spatial pixel "*i*" for the month "*m*," PRR_{im} was the predicted respirartion rate in the spatial pixel "*i*" and the month "*m*," and RR_{Opt} was the value of respiration rate at the optimum temperature predicted by the model.

To signal the temporal and spatial difference between the present and the future predictions for the species habitat suitability, subtractions between future and present raster files were carried out for each month and RCP scenario. In this way, new raster layers were created, where increasing or decreasing spatial occurrence probability of the species at pixel level was represented.

RESULTS

Thermal Performance Curve

Across the temperature range tested (from 13 to 33°C), the amount of consumed oxygen changed from 1.22 ± 0.68 mg h^{-1} g^{-1} DW (estimated at 15°C) to 5.70 ± 1.30 mg h^{-1} g^{-1} DW (estimated at 23°C). At the warmest temperatures, a sharp increase in the hydroid respiration rate was measured from 27°C (1.54 ± 0.30 mg h^{-1} g^{-1} DW) to 29°C (6.46 ± 0.95 mg h^{-1} g^{-1} DW) and maintained up to 31 and 33°C (5.02 ± 1.07 and 6.49 ± 5.15 mg h^{-1} g^{-1} DW, respectively). Particularly, at 27 and 29°C, a regression of hydranths (polyp tentacles contraction) was observed, and at 31 and 33°C autotomy of hydrants was repeatedly recorded in all experimental individuals. This response may be related to the transition from the optimal to the *pejus* temperature range (Sokolova et al., 2012), or even to a direct switch to the *pessimum* range, as has been observed for some marine organisms at high temperatures (Jost et al., 2012). Consequently, data from 29, 31, and 33°C were considered uninformative for the TPC model and associated with an increasing likelihood of reproductive failure and/or ongoing mortality of the colonies. Respiration rate data were then fitted using the *Sharpe-Schoolfield* model, and the obtained TPC predicts a temperature optimum for the species at 24.1°C (**Figure 1**). Furthermore, the fitted model identifies a maximum (27.6°C) thermal limit for the species, in accordance with the temperature value corresponding to the morphological changes observed during the experiments (**Figure 2**). The model estimated four distinct parameters used in the prediction of the monthly presence of the species based on its RR values (**Supplementary Figure 2**).

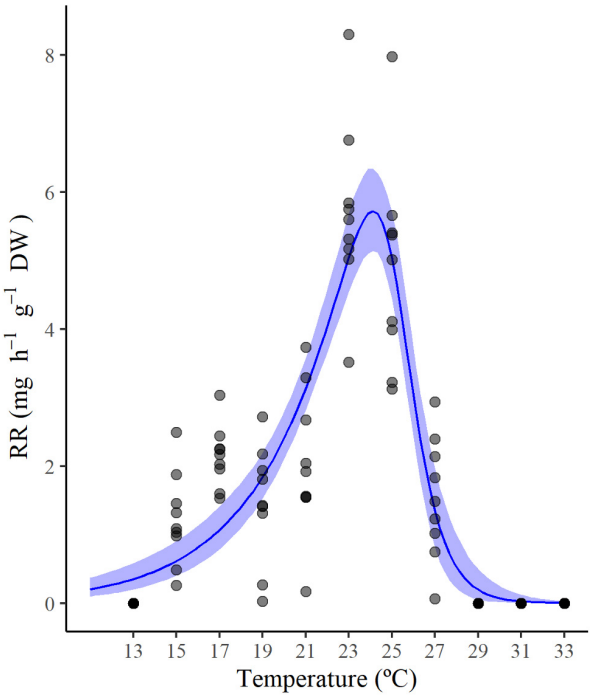


FIGURE 1 | Thermal performance curve of *Pennaria disticha* according to the selected model (Sharpe-Schoolfield). Shaded area corresponds to the confidence intervals. Darker dots represent overlapped individual respiration rate values.

Metabolic Suitability Prediction Maps

To create prediction maps, measured respiration rates were converted into probability of occurrence. This allows to graphically identify the different ranges of habitat suitability probability on the TPC (**Figure 3**). Thus, low probability values (from 0 to 0.2) would correspond to low RR placed in the final part of the modeled curve tails, representing the low performance of the species at those temperatures (ideally closer to the lower and higher lethal limits). Based on metabolic rates (i.e., the optimum thermal conditions for the species), our modeling effort suggested that the whole Mediterranean basin may have suitable conditions for the growth and reproduction of *Pennaria disticha* hydroid colonies. Prediction metabolic maps showed that the potential seasonal occurrence of active polyp colonies of *P. disticha* in the Mediterranean Sea may vary among different basin sections. In the Adriatic Sea and in the Western and central sub-regions, the highest habitat suitability (>0.6) for the hydroid is restricted between June to October, while in the Eastern basin it may span from May to December (**Figure 4**). Prediction maps illustrating the distributions under the RCP 4.5 and 8.5 (2050) scenarios showed a potential temporal and spatial expansion of *P. disticha* in the Central and Western Mediterranean. The habitat suitability of the species is increased by 2 months, potentially from May to November in the western and central parts of the basin (**Figures 5**, **6**). Specifically, the species occurrence would increase in May (up to 0.6) in southern Tunisia and the Greek coasts, and slightly (up to 0.4) in the northern Spanish and Sardinian areas. Also, a potential marked enlargement of the metabolic-based habitat suitability for *P. disticha* is predicted in November for the whole basin, increasing latitudinally from 0.6 to 0.8 and 1 in the southern Mediterranean coasts to 0.6 and 0.8 in the Spanish coasts,

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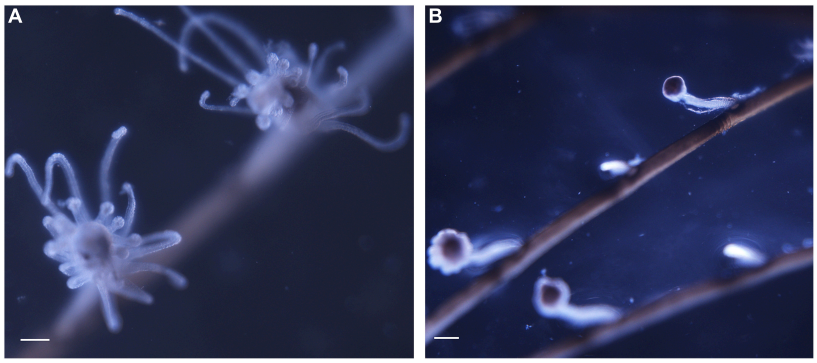


FIGURE 2 | Morphological features of experimental colonies at different tested temperatures: **(A)** healthy and performant polyp at 23°C and **(B)** damage hydrants at 29°C. Scale bar = 500 μm.

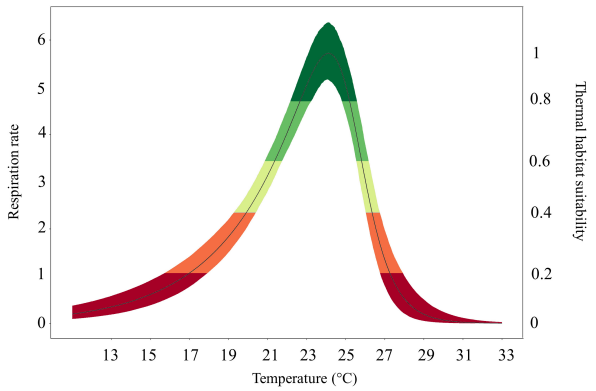


FIGURE 3 | Thermal habitat suitability scale within the thermal performance curve of the species ranging from low (0) to high (1) species occurrence probability. Different colors (representing the species thermal habitat suitability) would correspond to: *optimum* temperature range (dark green colored), lower and upper *pejus* ranges (light green and yellow colored), *pessimum* (orange colored), and *lethal* ranges (red colored) according to Sokolova et al. (2012).

the North Tyrrhenian and the Adriatic seas. No remarkable expansion can be detected between present-day and future predictions of spatial distribution and/or monthly occurrence of *P. disticha* in the Eastern Basin. Even if future climatic conditions may facilitate the spread of *P. disticha* and may increase its occurrence probability within the Mediterranean, a decrease in the potential thermal suitability of the species is predicted in the warmer months (July, August, and September), under both RCP 4.5 and 8.5 across the Adriatic and the Aegean Seas, as well as in the eastern Tunisian coast (**Figures 7**, **8**).

DISCUSSION

Temperature is the main factor regulating biological processes across all levels of ecological organization (Brown et al., 2004; Kooijman, 2010; Yvon-Durocher et al., 2012). Even small increases of SST may significantly influence individual metabolic rates and population growth. In turn, metabolic shifts may lead to changes in species ontogeny, phenology, geographical distribution, and biotic interactions (Levy et al., 2016). Species distribution, coexistence, and degree of resilience to stressful or changing environmental conditions, critically depend on species-specific reproductive traits and outputs (Angilletta, 2009). Seasonal hydroids, such as *P. disticha*, enter their active phenotype (the polyp colony) when conditions are optimal for energy capture (feeding) and for the initiation of sexual reproduction. *Pennaria* colonies also exhibit a prolonged resting dormancy period preceded by regression of hydranths, loss of the erect stem and branches, and the accumulation of stem cells in creeping stolons; making this thermophilic species resistant to prolonged periods (months) of adverse conditions, i.e., able to overwinter at low water temperatures (Gili and Hughes, 1995). Temperature, as the main regulator of *Pennaria's* complex life cycle, is the trigger for the activation and termination of each of those stages.

Pennaria disticha was originally described in the Mediterranean Sea (Goldfuss, 1820) but it is now commonly recorded worldwide in temperate and tropical waters, encountered on rocky coasts at shallow depths (Brinckmann-Voss, 1970; Schuchert, 2006). Coinciding with the rise of water temperature in the Ligurian Sea over the last 40 years, *P. disticha* has been increasingly recorded in the Northern Tyrrhenian Sea (Bianchi and Morri, 1994; Puce et al., 2009; Parravicini et al., 2015). The species has also been recorded in the Southern and Central Adriatic, and recently, for the first time, within the fouling community of mussel farms near Cattolica (Emilia Romagna region) in the southern part of the Northern Adriatic (Di Camillo et al., 2018). The current prediction maps (**Figure 4**) faithfully described the annual period of the colonial stage occurrence reported by scientific literature (Schuchert, 2006; Bosch-Belmar et al., 2019), and showed a large thermal suitability area for the species within the entire Mediterranean Sea, even in areas where the species has only been rarely recorded or not yet recorded (i.e., the upper part of the northern Adriatic Sea). The forecasted rise in water temperature will boost the ecological success of *Pennaria disticha* in the Mediterranean basin, through enlargement of its geographical distribution and phenological shifts. According to the metabolic predictions, the species

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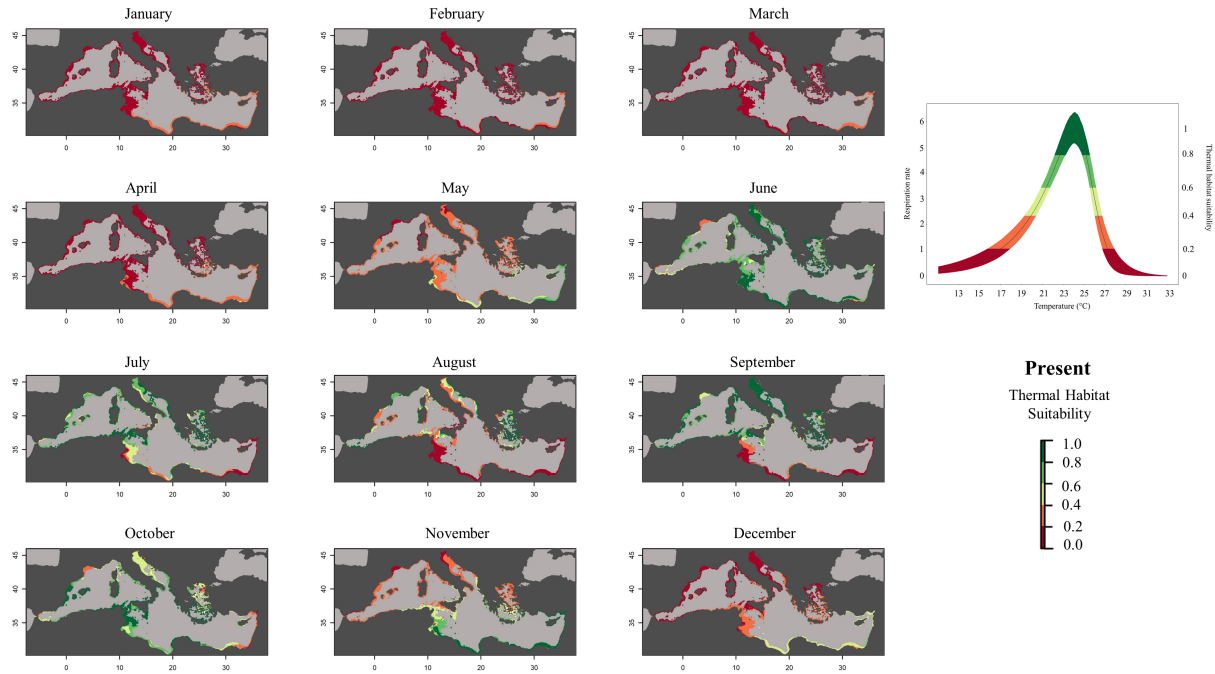


FIGURE 4 | Current predicted habitat suitability probability of *Pennaria disticha* based on respiration rate values (mg h^{-1} g^{-1} DW).

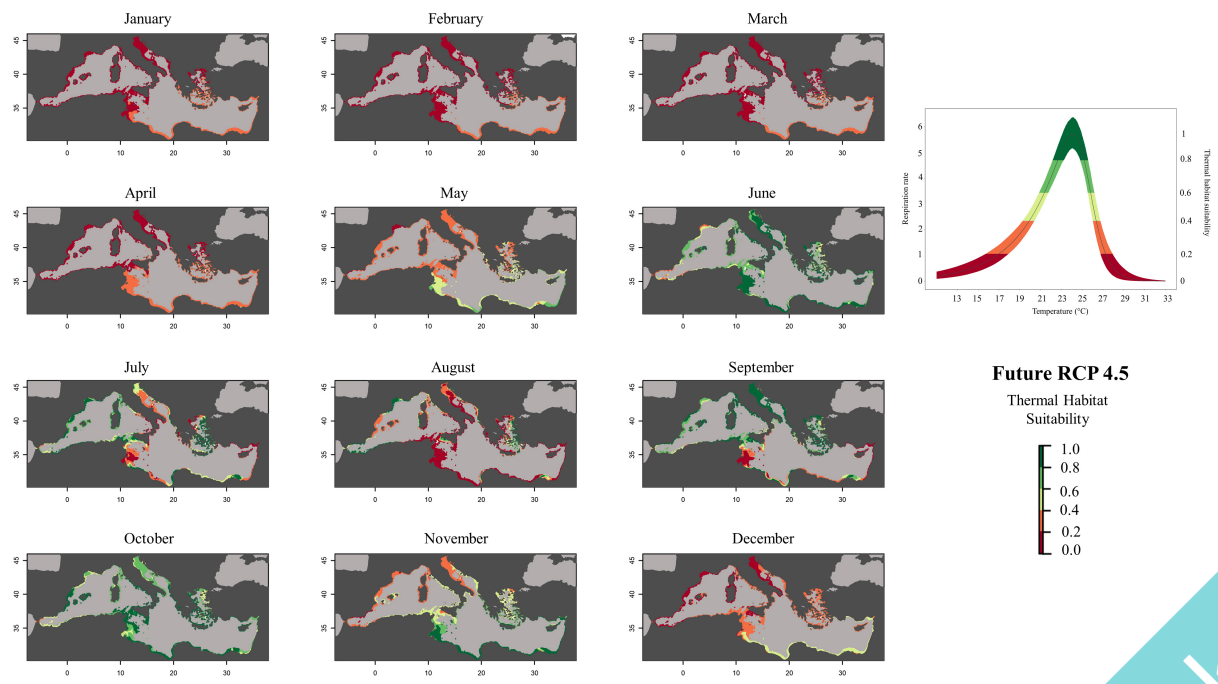


FIGURE 5 | Future (RCP 4.5, 2050) predicted habitat suitability probability of *Pennaria disticha* based on respiration rate values (mg h^{-1} g^{-1} DW).

should shift its active stage (the polyp colony) into a prolonged period (reflected by the increasing occurrence probability), from spring to late autumn.

Our integrated experimental and modeling effort showed that *P. disticha* should reach "maximum performance" at 24.1°C, with a left skew curve characterized by lower performance at lower temperatures. This trait is usually representative of a "high-temperature" specialist (Angilletta, 2009). This means that above the species-specific optimum value of T, any further increase may lead to energy reallocation,

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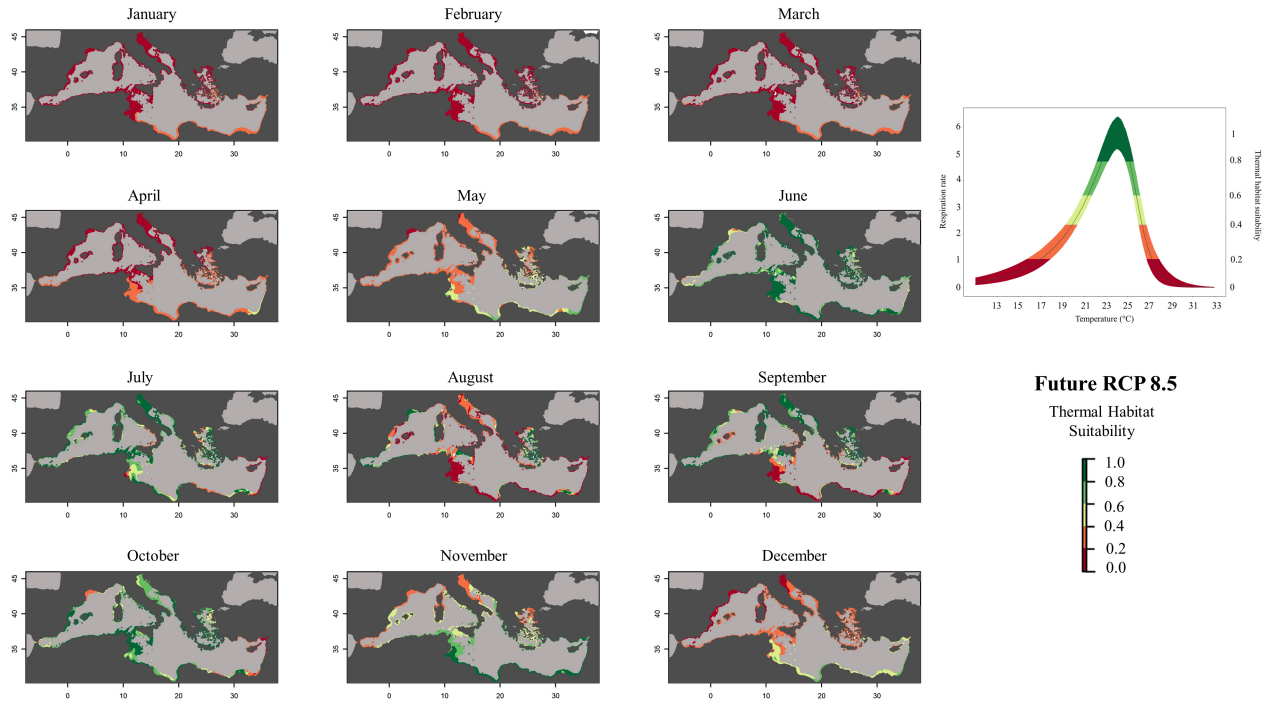


FIGURE 6 | Future (RCP 8.5, 2050) predicted habitat suitability probability of *Pennaria disticha* based on respiration rate values (mg h^{-1} g^{-1} DW).

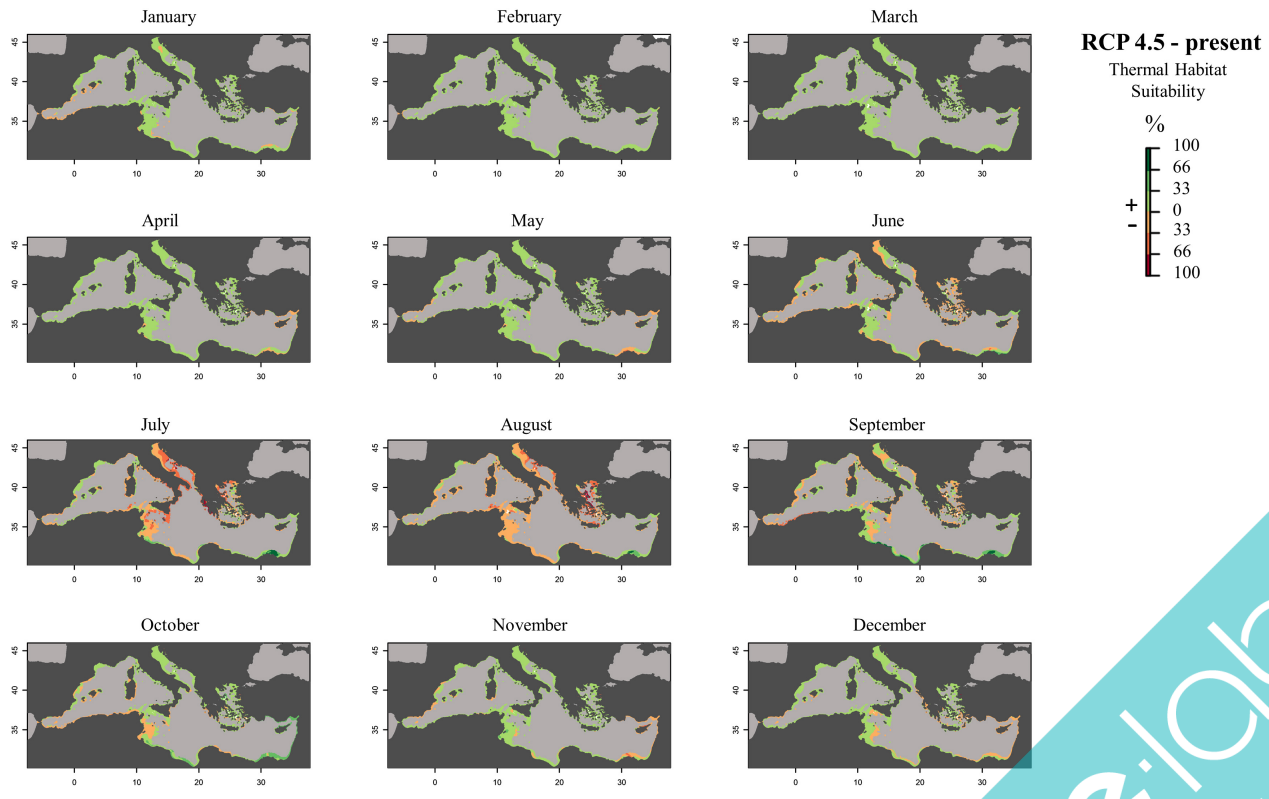


FIGURE 7 | Monthly prediction maps representing the subtraction between future (RCP 4.5) and present habitat suitability raster files: positive percentage values represent an increase in the suitability of the habitat in the future scenario, while negative percentage values represent a decrease in the occurrence probability of the species in that area.

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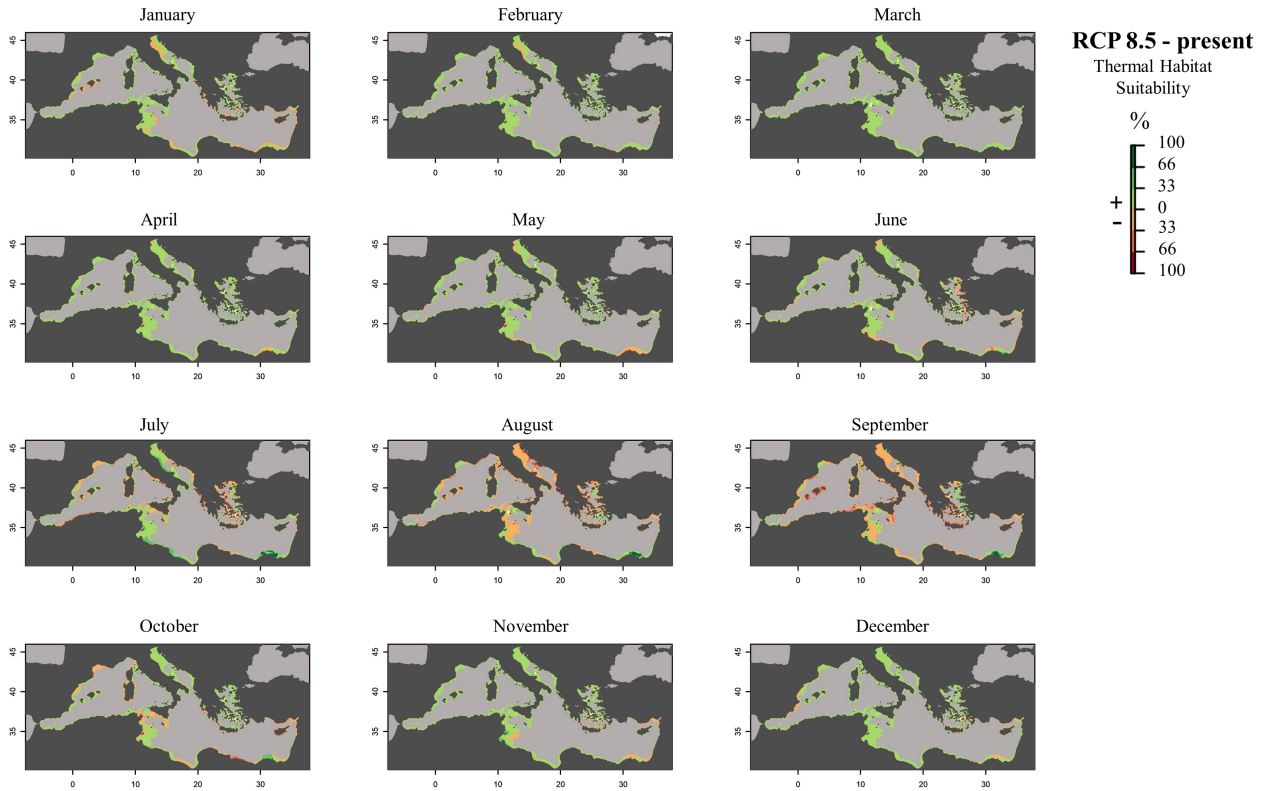


FIGURE 8 | Monthly prediction maps representing the subtraction between future (RCP 8.5) and present raster files: positive percentage values represent an increase in the suitability of the habitat in the future scenario, while negative percentage values represent a decrease in the occurrence probability of the species in that area.

rapid reduction in growth rate, reproductive failure, and even mortality (Matzelle et al., 2015). Accordingly, our laboratory experiments highlighted a typical sequence of temperature-dependent morphological changes. At T = 28–29°C, the polyps displayed tentacle contraction. At T ≥ 30°C, autotomy of polyps (i.e., detachment of the upper part of the polyp including mouth and tentacles) was commonly observed in all experimental colonies. Autotomized polyps were unable to regenerate the colonial stem and eventually died. This suggests increased likelihood—in scenarios with high GHG level—of reproductive failure and mortality, with direct negative consequences at population level. This detrimental morphological change, recorded under mesocosm conditions, is mirrored by the metabolic-based model maps, which predicted a future "unlikely" thermal suitability for the species during the warmest months in the Southern and Eastern Mediterranean areas (**Figures 5**, **6**), where mean monthly temperatures are expected to exceed the maximum thermal tolerance limits of the species. Thus, in warmer months, *P. disticha* colonies would be subjected to "thermal stressful status" with significant effects on reproduction and species dispersal. Similar to other hydroids (e.g., *Ectopleura* spp.) that may respond to increasing temperature through autotomy and dispersal of polyps bearing germ cells (Boero, 1984), *P. disticha* might also cope with and acclimate to warming seas by bringing forward the development and maturation of the free-living, planktonic sexual stage (short-living eumedusoids). Nevertheless, further research is needed to investigate the potential of *P. disticha* to adapt to the cumulation of multiple human-driven impacts.

The present results indicate, that in the future, we can expect an increasing detrimental role of *P. disticha* in Mediterranean waters given the predicted changing conditions in thermal profiles. As this species is a structural, deciduous habitat-former able to modify the microhabitats where it attaches affecting substrate morphology and water circulation, the potential effect on local biodiversity of natural rocky and artificial hard substrates such as those of aquaculture facilities will be amplified. The species' invasive potential, facilitated by rising temperature, will increasingly negatively impact the fish aquaculture sector. As a result, aquaculture management plans will need to be implemented with increased awareness of all potential threats, including the seasonal occurrence of invasive and outbreak-forming species. Temperature thresholds in performance of *P. disticha* can be associated with the vulnerable temperature range for Mediterranean fish marine aquaculture and used to inform fish farm operators of the periods when the active (and potentially harmful) colonial stage may be present, and of the temperature range when production of the free-living, medusoid sexual stages can be foreseen (around 25°C, Bosch-Belmar et al., 2019). Increased information on problematic species biology and potential distribution would contribute to the development of early warning systems, informed risk assessments, and

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more effective management plans. These actions are considered essential for conservation policymakers and marine economic sector managers who are faced with dynamic environmental change and increased ecosystem vulnerability.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

MB-B and GS conceived the study and designed it through the different steps. MB-B performed the experiments and developed the metabolic suitability prediction maps. MB-B drafted the early version of this manuscript and with GS and SP prepared the present version. All authors contributed to the article and approved the submitted version.

FUNDING

This study was funded by the Italian University and Research Minister (MIUR) through the PRIN MAHRES (cod. 2017MHHWBN) project.

ACKNOWLEDGMENTS

We are grateful to G. Milisenda for valuable statistics and modeling advice and C. Giommi and M. Tantillo for their kind assistance during the laboratory experiments.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.810555/full#supplementary-material

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