

Characterization of *Haplosporidium pinnae*'s biogeographical distribution by means of Ecological Niche Modelling techniques and consequences of climate change upon its range

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1. Abstract

This study provides a biogeographical characterization of protozoan endoparasite *Haplosporidium pinnae* distribution following the associated Mass Mortality Event of endangered bivalve *Pinna nobilis* in 2016. The epizootic has reached mortality rates between 80% - 100% and was first reported in the south-western Mediterranean Sea. It has since spread to north-western waters, followed by the Tyrrhenian and Ionian seas of the central Mediterranean, and has most recently reached the Aegean sea and the Çanakkale Strait in Turkey, most likely due to oceanic currents or intermediate host transmissions. In this study, we use presence-only Ecological Niche Modelling (ENM) techniques with the Maximum Entropy (*MaxEnt*) software, in order to accurately predict habitat suitability as a proxy of distribution range of *H. pinnae* in relation to biotic and abiotic conditions, such as definitive host presence, surface current velocity, water temperature and salinity by collecting occurrence data from published articles and websites like the Global Biodiversity Information Facility (GBIF), as well as gathering environmental information from the Bio-ORACLE database. By comparing ENM projections under present and future scenarios, taking anthropogenic interferences, such as climate change, exploitation and global warming into account, we can analyse the consequences of these variables upon *H. pinnae* and other Haplosporidian parasite populations, as these species are highly sensitive to environmental conditions and are often extremely host-specific.

2. Introduction

Haplosporidium pinnae is a protozoan parasite pertaining to phylum Haplosporidia, which constitutes a group of endoparasites known to be mainly pathogenic for marine and freshwater invertebrates, such as molluscs, crustaceans, annelids, trematodes and turbellarians (Perkins et al., 2000; Arzul & Carnegie, 2015). Despite being historically

troublesome to catalogue (Burrenson & Ford, 2004), molecular analysis and taxonomical debate currently describe Haplosporidia as containing four genera: *Haplosporidium*, *Minchinia*, *Bonamia* and *Urosporidium* (Arzul & Carnegie, 2015; Azevedo & Hine, 2017). Haplosporidian parasites are recognized as the main agents for multiple Mass Mortality Events (MMEs) worldwide due to their pathogenic nature (Moro-Martínez et al., 2023). Notable examples are *Haplosporidium nelsoni* and *Bonamia ostreae*, responsible for causing multinucleated sphere unknown (MSX) disease in *Cassostrea virginica* (Ford & Tripp, 1996) and Bonamiosis ostreae disease in *Ostrea edulis* (Burrenson & Ford, 2004), respectively.

Following the endemic bivalve *Pinna nobilis*' MME in early 2016, which is recorded to have begun in the south-eastern coastal waters of the Iberian Peninsula and the Balearic Islands, and which reached 100% mortality rates within three months (Darriba, 2017; Vázquez-Luis et al., 2017), it was quickly proposed that a new Haplosporidian parasite was responsible for the event. Histological and molecular analysis led to *Haplosporidium pinnae* being recognized as the main causative agent (Catanese et al., 2018), although a study by Carella et al. (2019) indicates co-occurrence between *H. pinnae* and *Mycobacterium* sp., which can alter the progression and effects of disease pathogenesis in currently unknown ways due to the lack of research in this area because of the complexity of co-infection analysis (Bakaletz et al., 2004; Griffiths et al., 2011; Johnsons & Hoverman, 2012).

Since the MME, *Pinna nobilis* has been classified as Critically Endangered by the Spanish Sectoral Environmental Conference in July 2017, as well as Annex II of the Barcelona Convention, SPA/BD Protocol 1995 and Annex IV of the EU Habitats Directive 2007. It has been on the IUCN Red List for Critically Endangered species since 2019. Efforts have been made to protect and conserve *P. nobilis*, as it is the largest saltwater bivalve in the Mediterranean Sea, reaching up to 120 centimetres in length (Zavodnik et al., 1991) and reported to have a maximum lifespan of over 45 years (Rouanet et al., 2015). Prior to the MME, multiple conservation methods were being proposed to protect *P. nobilis* as its population had been in decline for some time due to a long list of stressors, such as human exploitation, loss of habitat, marine pollution, invasive species and climate change (Basso et al. 2015).

P. nobilis plays a major role in reducing water turbidity and retaining organic matter (Trigos et al., 2014), it also provides hard substrate colonised by epibionts in soft-bottom habitats (Addis et al., 2009; Rabaoui et al., 2009) and, when in large density populations, can create biogenic reefs (Katsanevakis et al., 2016). Because of this, *P. nobilis* has often been used as an indicator of ecosystem status in the Mediterranean (Cabanellas-Reboredo et al., 2019).

Since MME detection in early 2016, the parasite had spread to north-eastern Spain, France, Italy and Tunisia by 2017 and 2018. Infections were then detected in the Adriatic Sea in late 2018 and early 2019 (Catanese et al., 2018; Panarese et al., 2019; Katsanevakis et al., 2019; Labidi et al., 2023). *P. nobilis* mortalities were recorded in western Turkey and the Çanakkale Strait around 2019 and 2020 (Öndes et al., 2020; Özalp & Kersting, 2020). Most recently, a mass mortality event was recorded in the Sea of Marmara, home to one of the few remaining healthy *P. nobilis* populations up until late 2020 and early 2021 (Çinar et al., 2021). It is likely that the parasite will fully reach the Black Sea soon, if it has not already.

Despite the high mortality rates in *P. nobilis*, congeneric species *Pinna rudis*, which shares habitat and many physical characteristics with *P. nobilis* (Cabanellas-Reboredo et al., 2019; Gvozdenovic et al., 2019), is seemingly resistant to the pathogen, showing no abnormal mortality rates compared to before the MME (Nebot-Colomer et al., 2016; Kersting & García-March, 2017). Because of this apparent resistance, tests have been conducted on *P. nobilis* x *P. rudis* hybrids to further explore natural immunity as an option to conserve *Pinna nobilis*. These tests have been yielding promising results, though further research is necessary (Vázquez-Luis et al., 2021; Coupé et al., 2023).

While *H. pinnae*'s origin and specific method of propagation are currently unknown, it is likely that it first reached southern Spain by port or similar anthropic activity (Vázquez-Luis et al., 2017). As for dispersion, the possibility of an unknown intermediate host has not been discarded (Cabanellas-Reboredo et al., 2019), though oceanic surface currents are accepted as a probable transmission method for now (Arzul et al., 2009; Arzul & Carnegie, 2015), demonstrated by drift simulations run by Cabanellas Reboredo et al. (2019). Like other researched Haplosporidian endoparasites, *H. pinnae* seems highly sensitive to environmental conditions (Ford et al., 1982; Hofmann et al., 2001; Burreson & Ford, 2004) with studies of *H. nelsoni* and *B. exitiosa* disease prevalence showing seasonal patterns (Andrews et al., 1982; Ford et al., 1988; Hine et al., 2002; Audemard et al., 2014) wherein prevalence reaches a peak at high summer temperatures and higher salinity ranges while decreasing in lower salinities.

A clear example of Haplosporidian dependence on environmental conditions is *H. nelsoni*'s associated MME in 1957 in Delaware Bay, U.S.A. (Haskin et al., 1966). In this case the parasite spread up along an estuary following a drought in the mid-1960s (Andrews & Wood, 1967; Farley et al., 1975), which allowed for a rise in salinity and temperatures. This made the north-eastern coast reach habitable conditions for *H. nelsoni* (Burreson & Andrews, 1988; Smith & Jordan, 1993; Burreson & Ragone Calvo, 1996; Hofmann et al., 2001; Tarnowski et al., 2002). In the 1980s, *H. nelsoni*'s reported range was extended to cover the entire East Coast, from Florida to Maine (Haskin & Andrews., 1988; Hillman et al., 1988; Kern et al., 1988; Lewis et al., 1992), arguably as a consequence of changes in water conditions due to global warming. Changes in climate can affect disease outbreaks (Harvell et al., 1999; Harvell et al., 2002) so it is clear that, similar to *H. nelsoni*, alterations in environmental conditions caused by a variety of factors, namely anthropic activity, can benefit the expansion of *H. pinnae*'s suitable habitat, as well as that of other marine pathogenic agents.

In order to understand, describe and predict a species' full distribution range and its suitable habitat extension, we make use of Ecological Niche Models (ENMs), which are empirical or mathematical approximations to the ecological niche of a species (Barbosa et al., 2012). Due to the lack of common definitions and terminology regarding Ecological Niches (ENs) and ENMs (Sillero, 2011), for the purpose of this study we will describe the EN making use of Hutchinson's (1957) Fundamental Niche (FN) description. This describes the FN as the *n*-dimensional volume within an environment that has both biotic and abiotic conditions that favour the survival and reproduction of a given species.

3. Materials and Methods

3.1 Data Collection

Haplosporidium pinnae occurrence coordinates were collected from the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>; 2023), as well as from articles researching the parasite and *P. nobilis*' MME dating from 2017. Although not all articles included specific coordinates, these were extrapolated in accord with the procedural protocol suggested by Sillero et al. (2021). *Pinna nobilis*' coordinates were solely collected from GBIF (Table 3, see Appendix).

3.2 Data Calibration and Environmental Variables

Rstudio was used to plot and overlay both *H. pinnae*'s and *P. nobilis*' coordinates with packages "raster" (Hijmans, 2023), "sp" (Bivand, Pebesma & Gomez-Rubio, 2013), "ggplot2" (Wickham, 2016), "readxl" (Wickham & Bryan, 2023) and "rgbif" (Chamberlain et al, 2023) to correctly format and introduce data. *H. pinnae*'s coordinates were thinned using R package

“spThin” so as to avoid any possible data bias (Aiello-Lamens et al., 2015). We stacked and cropped *H. pinnae*’s calibration and projection maps on QGIS (<https://www.qgis.org/es/site/>; version 3.34.1, 2023) with environmental data collected from BioOracle (<https://www.bio-oracle.org/>; version 2.2, 2023). The calibration layer was cropped in accord with the “M” concept from the BAM framework of Soberón and Peterson (2005), where “M” is defined as the area available to the species in an ecological sense. Projection or “G” maps were cropped to cover the Mediterranean and near bodies of water, thus ranging from the Bay of Biscay to the Black Sea, using the World Geodetic System 1984 (WGS84) as a coordinate system.

As environmental variables, we selected mean surface temperature, mean surface water salinity and mean surface current velocity. We downloaded both present and future datasets, with future prediction intervals ranging from 2040 to 2050 and 2090 to 2100. Both future datasets were downloaded with a Representative Concentration Pathway (RCP) of 4.5, in order to obtain a moderate prediction of a future greenhouse gas concentration scenario for both 2050 and 2100. A 4.5 RCP scenario assumes that greenhouse gas concentrations peak in 2040 and then decline (van Vuuren et al., 2011). Variables were converted into .asc files, so that the ENM program *MaxEnt* (version 3.4.4) could read them properly (Phillips et al., 2004).

3.3 Ecological Niche Modelling

MaxEnt was then used to model *H. pinnae*’s probability of distribution by making use of presence-only predictions. To obtain the projection models for present, future (2040 - 2050) and future (2090 - 2100) layers, parameters were kept as default, while 100 bootstrap runs were conducted, with 10% of data being withheld and tested in each iteration. For every run, we took the point-wise mean and standard deviation of the 100 models applied to the environmental layers for each projection, thus obtaining results with a 95% confidence level. Models were evaluated using the Receiver Operating Characteristic (ROC) Area Under the Curve (AUC) method which is interpreted as the probability that a randomly chosen presence location is ranked higher than a randomly chosen background point. The closer the AUC value is to 1, the better our model is compared to a completely random one (Phillips et al., 2006).

4. Results

4.1 Present Occurrences

The following figure (Figure 1) shows the evolution of *Haplosporidium pinnae* occurrence detections, beginning in autumn of 2016 in southern Spain (blue dots) and progressing eastward up until 2020 (green dots for 2017, yellow dots for 2018 and red dots for 2020). It is worth noting that the figure does not represent when the parasite reached each region, but rather when surveys that detected it were conducted, hence the gap between 2018 and 2020. Individual dots do not represent individual parasite cases, instead indicating areas of detection, so we can confidently say that surrounding areas are also occupied by *H. pinnae*. This linear expansion supports the current theory that the parasite makes use of surface currents to disperse (Arzul et al., 2009; Arzul & Carnegie, 2015).

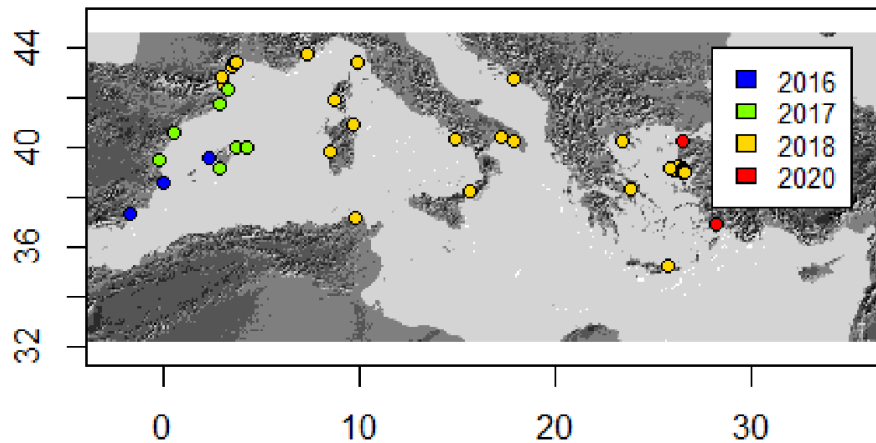


Figure 1. Plotted occurrence coordinates for *Haplosporidium pinnae*, colour coded according to the time frame during which occurrence detections were recorded, where blue is 2016, green 2017, yellow 2018 and red 2020. The map focuses on the Mediterranean basin. The X and Y axes represent longitude and latitude respectively using the WGS84 system as reference.

4.2 Ecological Niche Models

ENM projection models show the average distribution probabilities for each time frame. Present conditions for environmental variables (mean surface temperature, mean surface current velocity and mean surface salinity) resulted in Figure 2, which indicates probability of distribution with values ranging from 0 to 1, where redder areas indicate a higher probability.

Model data correlates with the occurrence data plotted in R (Figure 1). We see that the parasite favours shallow and coastal waters, with an intermediate distribution probability throughout the northern coast, while showing a particular affinity for the southern French coast, the northern Adriatic Sea and the Sea of Marmara. Despite not having been detected in either the Black Sea or the Bay of Biscay, both regions also show high presence probabilities. The entire south-eastern Mediterranean coast indicates an extremely low chance of containing *H. pinnae* occurrences.

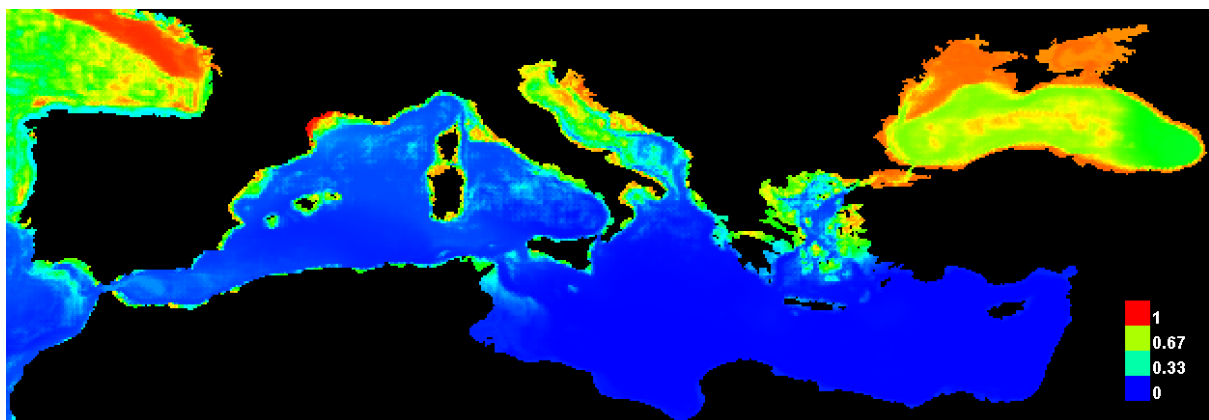


Figure 2. Present projection Ecological Niche Model for *Haplosporidium pinnae* ranging from the Bay of Biscay to the Black Sea. Presence probability is represented in colour gradient, with red indicating very high likelihood (1) and blue being very low (0).

The following figure (Figure 3) indicates the average results for *H. pinnae*'s future (2040 to 2050) ENM predictions. Overall, we see a far lower probability of occurrence in all areas other than the Bay of Biscay or the Black Sea. Regions that presented probability values between 0.33 and 0.67 have decreased notably, and many now indicate a very low chance of parasite presence. High latitudes and shallow waters are still likely regions, but to a lesser extent. We also see that both the northern Bay of Biscay coast and the Black Sea have a higher chance of containing the parasite. The inner Adriatic Sea and southern French coast maintain an intermediate probability.

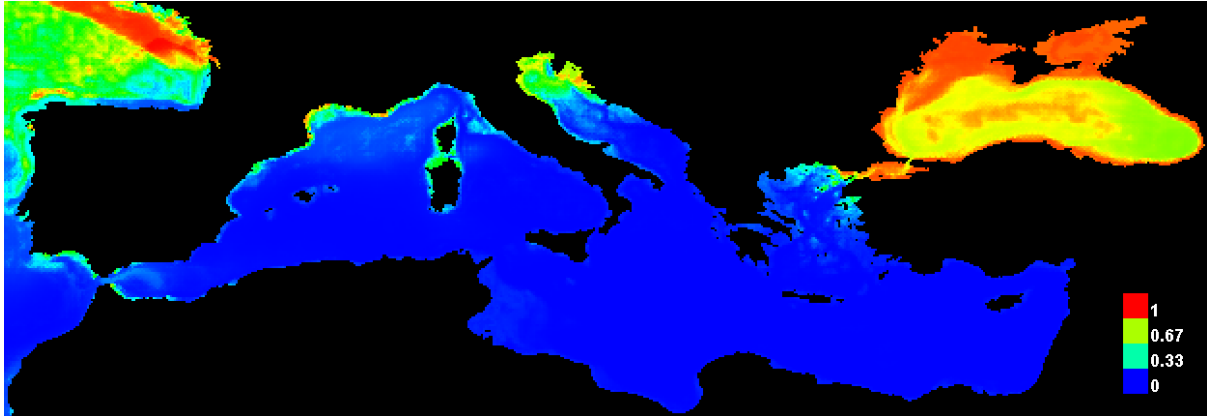


Figure 3. Future (2040 to 2050) projection Ecological Niche Model for *Haplosporidium pinnae* ranging from the Bay of Biscay to the Black Sea. Presence probability is represented in colour gradient, with red indicating very high likelihood (1) and blue being very low (0).

The third model (Figure 4) presents the average results for *H. pinnae*'s ENM based on future (2090 - 2100) environmental conditions. Figure 4 has minor differences in comparison to Figure 3. Notably, the Aegean Sea has become unlikely to contain the parasite, while the Sea of Marmara and most of the Black Sea have also decreased slightly, though still having an intermediate to high probability. In this model, the northern Bay of Biscay coast has the highest presence probability, with values nearing absolute certainty. In this scenario, large part of the Mediterranean is very unlikely to support *H. pinnae* occurrences, with few exceptions being yet again the Inner Adriatic and southern France, as well as having low to intermediate likelihood values in the western Spanish coast.

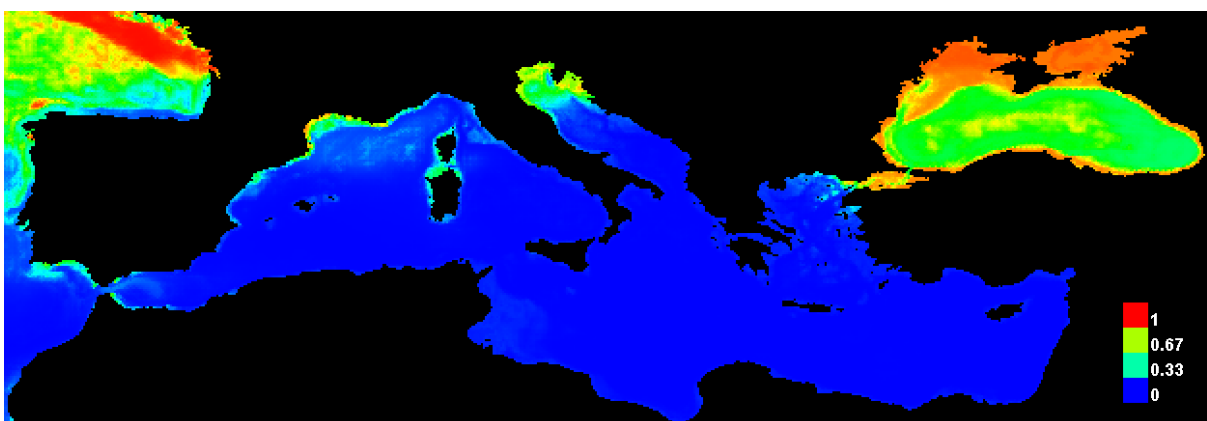


Figure 4. Future (2090 to 2100) projection Ecological Niche Model for *Haplosporidium pinnae* ranging from the Bay of Biscay to the Black Sea. Presence probability is represented in colour gradient, with red indicating very high likelihood (1) and blue being very low (0).

4.3 Model Evaluations and Variable Contributions

All models resulted in AUC values superior to 0.9 (Table 1) and low standard deviation (SD $\pm$) values, qualifying for excellent predictions in *MaxEnt*, though it is worth noting that the more specific a species' habitat is, the higher AUC value tends to be, as an artefact of the AUC statistic (Phillips, 2017). The second model (Future 2040 - 2050) had both the highest AUC value (0.929) and the lowest standard deviation (0.012 $\pm$) indicating a highly fit model projection result.

Projection Layers	AUC	SD $\pm$
Present	0.923	0.015
Future (2040 - 2050)	0.929	0.012
Future (2090 - 2100)	0.923	0.015

Table 2: Model evaluation results for each *H. pinnae* ENM projection. Values given are Area Under the Curve (AUC) and Standard Deviation (SD $\pm$). All AUC values are superior to 0.9 and all SD $\pm$ values are inferior to 0.02.

MaxEnt also provided estimated environmental variable contributions normalised to percentages, thus indicating which conditions affect the model the most (Table 3). In all three models, mean surface current velocity had a contribution percentage superior to 60%, indicating a high relevance when projecting *H. pinnae*'s EN. These results coincide with studies led by Arzul et al. (2009), Arzul and Carnegie (2015), and Cabanellas-Reboredo et al. (2019). Mean surface temperature also plays an important part, as it had a contribution percentage near 30% in all three projections. Mean surface salinity resulted in lower percentages than expected (inferior to 15% in all cases), considering the relevance of environmental conditions on Haplosporidian parasites (Harvell et al., 1999; Harvell et al., 2002). It is worth noting that the projection models did not account for seasonal fluctuations, but rather annual averages, so *Haplosporidium pinnae*'s possible summer prevalence peak is not taken into account. Based on results from studies conducted by Andrews et al. (1982), Ford et al. (1988), Hine et al. (2002) and Audemard et al. (2014), it is likely that *Haplosporidium pinnae*'s life cycle relies on peak temperatures and salinities pertaining to summer conditions, whilst current velocities affect the parasite's dispersal.

Projection Layers	Mean Surface Current Velocity	Mean Surface Temperature	Mean Surface Salinity
Present	63%	29.1%	7.9%
Future (2040 - 2050)	60.3%	30.1%	9.7%
Future (2090 - 2100)	61.3%	28.6%	10.1%

Table 3: Environmental variable percentage contribution for every ENM projection. Variables are mean surface current velocity, mean surface temperature and mean surface salinity. In all three models, current velocity has a contribution percentage superior to 60%, followed by surface temperature.

5. Discussion

Ecological niches are a product of biotic and abiotic conditions (Grinnell, 1917; Hutchinson, 1957). Factors such as climate change and global warming have an effect on said conditions, which lead species to alter their distribution accordingly in search of suitable habitats (Hutchinson, 1957). While ENM results show that the Bay of Biscay and the Black Sea would become likely to contain the parasite, there are no *Pinna nobilis* occurrences in either of those regions to date. The rapid development of *H. pinnae*'s multiple MMEs which have had mortality rates surpassing 90% has led to the death of most *Pinna nobilis* populations (Vázquez-Luis et al., 2017; Panarese et al., 2019; García-March et al., 2020), so the parasite will probably either die out or remain dormant due to the lack of host availability. The decline in *P. nobilis* populations also makes it hard to monitor the parasite's distribution and activity. While the possibility of reallocating *P. nobilis* individuals by means of artificial recruitment (such as larval collectors or breeding farms) has been considered (Vázquez-Luis et al., 2017; Kersting et al., 2020), ENM results show that it would be highly complicated to provide *P. nobilis* with a new habitat where it could not be reached by the parasite, especially considering current issues with conservation, as mortalities have been recorded in captive individuals due to both stress and *Vibrio mediterranei* infections (Prado et al., 2019).

Overall, *H. pinnae*'s ENM results indicate a high sensitivity to environmental conditions, with possible EN regions decreasing drastically in each time frame, to the point that for future (2090 - 2100) conditions, most of the Mediterranean becomes unsuitable for the parasite. It is already well known that protozoan endoparasites are very sensitive to factors such as temperature and salinity, and that these can alter the relationship between host and parasite in a number of significant ways, namely the time that passes between infection and symptoms or the lethality of infection (Krone, 2007). Because of this, it is possible that in the same way *H. pinnae*'s EN becomes limited by the effects of climate change, other parasites benefit and expand their own possible distributions, thus becoming a larger threat as a direct consequence of human activity. As seen in the International Panel on Climate Change's (IPCC) Sixth Assessment Report, we are at a point where it has become impossible to stop the main effects of human-caused climate change. Notably, the Mediterranean is predicted to have a decreased precipitation frequency and increased drought intensity (<https://www.ipcc.ch/report/ar6/syr/>; IPCC, 2023).

Considering the rapid spread and lethality of *H. pinnae* over the last seven years, we remark on the importance of establishing agile response protocols to quarantine marine regions or control the transmission of marine pathogens, as well as dedicating further research into conservation techniques to ensure the survival of threatened hosts as the only way to protect endemic species of not only the Mediterranean, but any region. While *P. nobilis* populations had already been in steady decline (Basso et al., 2015), we cannot rule out the possibility that a new parasite will suddenly reach a region that has developed suitable environmental conditions as a consequence of climate change, where it will cause an MME of similar calibre to those associated with *H. pinnae*, albeit on another, possibly more well-known and economically relevant, host species. For this reason we emphasise the threat that is presented by both anthropic environmentally detrimental activities and the lack of collective environmental awareness.

As a possible conservation alternative, studies by Vázquez-Luis et al. (2021) and Coupé et al. (2023) investigated the hybridization of *P. nobilis* and congenial species *P. rudis* as well as researching the immune genes and toll-like receptors (TLRs) which have led to *P. rudis*' natural immunity as well as some rare cases of *P. nobilis* immunity (Coupé et al., 2023). Though these studies have accrued positive results, further research is required. We add that hybridization should not be considered a definitive solution, as it is also possible that *H.*

pinnae or another Haplosporidian parasite develops the capacity to infect *P. rudis* individuals (Bowden, 2013).

During the past decades, ENM techniques have been developed to the point where we are able to harness large amounts of raw data and obtain reliable and insightful approximations to biogeographical distributions (Anderson, 2012). Ecological niche models, sometimes called species distribution models, offer the ability to not only monitor a species' current distribution but also the possible expansion of its range, or rather its EN, as a consequence of climate change. Due to the limited accessibility to both the software and the environmental or occurrence data, the full potential of ENMs in fields such as species conservation or pathogen dispersal has not been reached, though it is still a very useful tool. We emphasise the importance of facilitating public access to occurrence and environmental data so that ENMs may be used to their full capacity.

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8. Appendix

Table 3: GBIF datasets and articles used to collect *H. pinnae* and *P. nobilis* coordinates.

Species	Source
<i>Pinna nobilis</i>	iNaturalist (2023)
<i>Pinna nobilis</i>	de Vries et al. (2023)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2022)
<i>Pinna nobilis</i>	Carnegie Museums (2023)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2021)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2020)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2020)
<i>Pinna nobilis</i>	Chic et al. (2020)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2021)
<i>Pinna nobilis</i>	Generalitat Valenciana (2023)
<i>Pinna nobilis</i>	MNHN, Chagnoux S (2023)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)
<i>Pinna nobilis</i>	García et al. (2023)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel N (2022)
<i>Pinna nobilis</i>	Naturgucker (2014)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)
<i>Pinna nobilis</i>	Garrabou et al. (2018)
<i>Pinna nobilis</i>	Casassovici et al. (2022)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)

<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2017)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2022)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2018)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)
<i>Pinna nobilis</i>	Robert and Lepareur (2022)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2018)
<i>Pinna nobilis</i>	Generalitat de Catalunya (2022)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2021)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2018)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2016)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2016)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2018)
<i>Pinna nobilis</i>	Díaz and Martínez-Ortí (2022)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2020)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2016)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2018)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)
<i>Pinna nobilis</i>	Danis and Coupremagne (2018)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2018)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2023)
<i>Pinna nobilis</i>	Harvard University M, Morris P. J. (2023)

<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2017)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2020)
<i>Pinna nobilis</i>	Slieker et al. (2023)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2020)
<i>Pinna nobilis</i>	Inventaire National du Patrimoine Naturel (2016)
<i>Pinna nobilis</i>	Poursanidis & Koutsoubas
<i>Pinna nobilis</i>	Haus der Natur Salzburg (2023)
<i>Pinna nobilis</i>	Chaney et al. (2023)
<i>Pinna nobilis</i>	Senckenberg (2022)
<i>Pinna nobilis</i>	Natural History Museum of Utah (UMNH) (2023)
<i>Pinna nobilis</i>	Pauwels et al. (2021)
<i>Pinna nobilis</i>	Samyn et al. (2023)
<i>Pinna nobilis</i>	Goud et al. (2023)
<i>Pinna nobilis</i>	Finnish Biodiversity Information Facility (2023)
<i>Pinna nobilis</i>	Academy of Natural Sciences (2023)
<i>Pinna nobilis</i>	National Institute of Oceanography and Experimental Geophysics (2017)
<i>Pinna nobilis</i>	Ekström (2023)
<i>Pinna nobilis</i>	Mavraki et al. (2021)
<i>Pinna nobilis</i>	Natural History Museum (2023)
<i>Pinna nobilis</i>	Chavan et al. (2018)
<i>Pinna nobilis</i>	European Bioinformatics Institute (EMBL-EBI) (2023)
<i>Pinna nobilis</i>	Gratacós-Teixidor et al. (2019)

<i>Pinna nobilis</i>	Biologiezentrum Linz Oberösterreich (2021)
<i>H. pinnae</i>	Katsanevakis et al. (2019)
<i>H. pinnae</i>	European Bioinformatics Institute (EMBL-EBI) (2023)
<i>H. pinnae</i>	Catanese et al. (2018)
<i>H. pinnae</i>	Darriba, (2017)
<i>H. pinnae</i>	Labidi et al. (2023)
<i>H. pinnae</i>	Künili et al. (2021)
<i>H. pinnae</i>	Grau et al. (2022)
<i>H. pinnae</i>	Carella et al. (2020)