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Mapping the Azores Marine Park Vulnerability to Temperature Changes

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ABSTRACT

Aim: Identifying highly vulnerable regions to climate change is increasingly incorporated in marine management planning given the expected redistribution of species with latitude, longitude, and depth following temperature changes. Here, we developed a spatially explicit vulnerability framework incorporating sensitivity, exposure, and adaptive capacity of species living in one of the largest networks of Marine Protected Areas (MPAs) within the EU.

Location: Azores Marine Park, North Atlantic.

Methods: We quantified benthic, benthopelagic, and pelagic species sensitivity to temperature changes based on adult thermal affinity and georeferenced their distribution with quality-controlled records from various data compilers. To assess their exposure, we extracted historical (1995–2020) temperatures across latitudes, longitudes, and depths and calculated mean interannual change (i.e., increase or decrease) and variability. We estimated the adaptive capacity of species with traits related to relocation ability during adult and early life stages (i.e., “Motility” and “Developmental Mechanism”) using the FUN Azores trait database. To map the results, we pooled the species into 3D-regions of 0.25° × 0.25° resolution and 50 and 500 m depth bands at shallow and deep areas, respectively. We assigned a sensitivity, exposure, and adaptive capacity score to each region based on species scores and combined them into a final vulnerability class (i.e., “Highly Vulnerable” (HV), “Advisable Monitoring” (AM), “Expected Relocation” (ER), and “Least Concern” (LC)).

Results: HV and AM regions exist only in the benthic environment across various MPAs and depths. Increased mobility of species explains the absence of the most vulnerable categories in the benthopelagic and pelagic environments.

Main Conclusions: We advise strong conservation measures in HV areas and to maintain connectivity with climate refugia and monitoring of environmental variables and populations in areas classified as AM and ER, respectively. Our results suggest that the Azores deep-sea benthos is the most vulnerable environment to both warming and temperature variations.

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1 | Introduction

Temperature changes are transforming ocean ecosystems (Beaugrand et al. 2002; Sunday et al. 2011, 2012; Chaudhary et al. 2021; Thorne and Nye 2021) with impacts now being detected in the deep sea as well (e.g., warmings of 0.01°C–0.1°C per decade in certain areas; Purkey and Johnson 2010 and Sweetman et al. 2017). Adaptation to environmental temperature changes for ectotherms (i.e., species whose body temperatures match their surroundings) is achieved by physiological adjustment to the environment or by actively remaining in their thermal niche through adult migration and/or dispersal at early life history stages (Hastings et al. 2020). Species with higher thermal limits are expected to tolerate warming, and eurythermal species may be able to relocate to new habitats if some areas become unsuitable (Hastings et al. 2020). The speed and direction required for organisms to track temperature change is assessed as climate velocity (Loarie et al. 2009; Arafeh-Dalmau et al. 2021). Changes in community structure are, therefore, not only expected as a result of differential species survival rates but also of relocation rates.

A conservation challenge as oceans warm is to implement spatial planning across habitats increasingly impacted by multiple drivers (e.g., acidification, decreased primary productivity and resource extraction) in the three-dimensional space. Marine Protected Areas (MPAs) are typically implemented to restrict damaging human activities (e.g., fishing), thus protecting key ecosystem services and functions that would otherwise be threatened. While we can directly control the frequency and intensity of some delimited pressures (e.g., fishing), threats that cross MPA boundaries, such as climate-related temperature changes can have strong impacts on protected and/or recovered species and communities (Bruno et al. 2018; Bates et al. 2019; Smale et al. 2019). To promote ecosystem resistance and resilience (i.e., capacity of an ecosystem to recover key functions and services after perturbation) to climate change, we need to maintain habitat heterogeneity in space (i.e., including appropriate representation, replication, and spread of environmental conditions), while protecting connectivity pathways (Benedetti-Cecchi et al. 2024) and avoiding additional threats (McLeod et al. 2009; Kavousi and Keppel 2018). With these recommendations, climate refugia become more available for adults to produce source larvae that, in turn, will find a place to settle, grow, survive and reproduce when the conditions become inhospitable (Wilson et al. 2020; Arafeh-Dalmau et al. 2021).

A primary objective is to forecast which species and regions will be more or less vulnerable to environmental temperature changes. Vulnerability assessments, for example, estimate potential future adverse impacts within various socio-ecological contexts (Turner et al. 2003; Pörtner et al. 2023). These evaluations are crucial tools for identifying highly vulnerable species, communities and ecosystems whereby vulnerability arises from the interplay of sensitivity, exposure and adaptive capacity of a species, community or ecosystem (Dawson et al. 2011; Foden et al. 2013). Sensitivity indicates the direct impact of specific threats on a species' survival and reproductive success, or on a community or ecosystem's persistence and growth (Dawson et al. 2011; Foden et al. 2013). Exposure is defined by the spatial and temporal overlap of a particular threat. Adaptive capacity refers to the ability to recover following disturbances (Dawson et al. 2011; Foden et al. 2013). The combination

of the three provides crucial information on the impacts of threats to marine life.

The biological and ecological characteristics of a species or “traits” are useful tools to estimate the sensitivity and adaptive capacity to a disturbance. Thus, trait-based approaches are commonly used in conservation science to predict the impacts of climate change from the scale of populations to ecosystems (Dawson et al. 2011; Foden et al. 2013; Stanton et al. 2014; Wilson et al. 2020; Pörtner et al. 2023). Indeed, thermal affinity (e.g., warm versus cold adapted), dispersal capabilities (e.g., developmental mechanism), life history characteristics (e.g., longevity), and species distribution are among the most common traits that relate species sensitivity and adaptability to climate disturbances (Harvey et al. 2022).

The Azores Marine Park (AMP) comprises seamounts and ridges, which exhibit strong vertical temperature gradients contributing to sharp ecological zonation with distinct biological communities across depths. Predicted ocean warming by 2081–2100 will most likely alter species distributions and, therefore, those distinct biological communities (Bindoff et al. 2022). Furthermore, the resource-rich nature of seamounts has incentivised commercial fishing in deep waters, a threat that combines with the potential for mining in exploitation sites (Assembleia Legislativa da Região Autónoma dos Açores, Decreto Legislativo Regional no. 13/2016/A 2016). As a response to increasing pressures, during the 2000s there has been an investment in marine science (i.e., increased number of research projects), monitoring of MPAs, and the implementation of protective measures for certain habitats typified by foundation species (i.e., sponge aggregations, hydrothermal vent fields, and deep-sea coral gardens and reefs) and ecologically important species, which are fished (e.g., the long-lived and late-maturing orange roughy *Hoplostethus atlanticus*; Abecasis et al. 2015).

In MPAs, most climate change vulnerability assessments focus on warm water corals (Wilson et al. 2020). Here, we adapt a vulnerability framework across diverse ecosystems, from benthic, benthopelagic, and pelagic domains adopting a trait biogeography perspective by: (1) subdividing the AMP into three-dimensional spatial units (i.e., cubes with specific latitude, longitude, and depths); (2) scoring temperature sensitivity for each species and species pools at each 3D-region; (3) identifying historical temperature mean and variation at each 3D-region and potential climate refugia; (4) exploring the adaptive capacity of each species and pools of species using traits; (5) assigning a vulnerability class (i.e., “Highly Vulnerable”, “Advisable Monitoring”, “Expected Relocation”, and “Least Concern”) to each 3D-region for each temperature metric: mean interannual temperature change (i.e., temperature tendency) and temperature variability within the study timeframe; and (6) mapping the four different vulnerability classes in the AMP. We synthesise our findings and identify vulnerability hotspots based on the data available for a snapshot spatial analysis.

2 | Materials and Methods

2.1 | Area of Study

The Azores Marine Park (AMP) is one of the largest networks of Marine Protected Areas (MPAs) within the EU and is also unique in integrating Areas Beyond National Jurisdiction

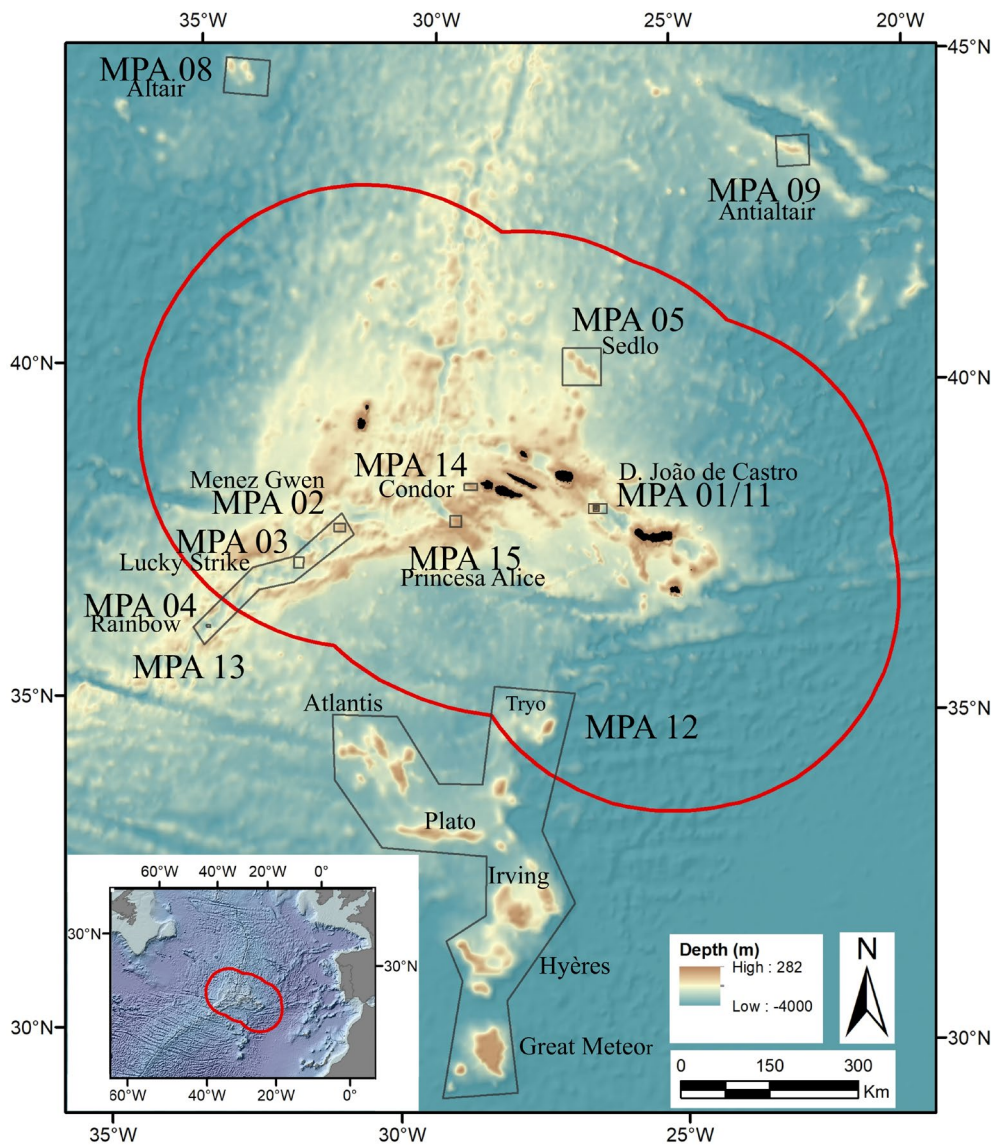


FIGURE 1 | The 12 Marine Protected Areas (MPAs) from the Azores Marine Park included in the FUN Azores trait database and this study. Red line delimits the Exclusive Economic Zone.

(Calado et al. 2011; Maestro et al. 2020). This network of 15 MPAs covers a total area of 111,393 km², encompassing 13 MPAs that include ridges, seamounts, and hydrothermal vent ecosystems. Here we focus on 12 explored MPAs (Figure 1; UNEP-WCMC 2022), noting that MPA 10—MARNA is largely unexplored.

2.2 | Spatio-Temporal Resolution

We created a three-dimensional grid with fixed coordinates (0.25° × 0.25°) and depths where species and environmental data were grouped together (Figure 2). We expected stronger vertical temperature gradients in the photic zone than in the deep aphotic zones, and therefore, created the depth bands accordingly. Above 200 m, every 50 m (i.e., 0–50 m, 50–100 m, 100–150 m, 150–200 m) and below 200 m every 500 m (i.e., 500–1000 m, 1000–1500 m, 1500–2000 m, 2000–2500 m, 2500–3000 m, 3000–3500 m) with a transition band at 200–500 m.

We obtained a community baseline by pooling together data from all recorded years (1905–2018) because data were scarce and unbalanced through time. Therefore, our results can only be interpreted at a broad spatial scale and include the full MPA Network rather than providing details on a specific seamount. By combining species into delimited regions of fixed latitude, longitude and depth, we increase precision; however, each region cannot be interpreted as closed ecosystems, communities or assemblages (Stroud et al. 2015) but a pool of species that coincide in space.

2.3 | Species Records

In September 2023, we extracted all species records from the 12 Marine Protected Areas of the AMP with data across all depth bins from databases that follow a series of quality control checks on the data provided by end-users (i.e., EMODnet—<http://emodn.ec.europa.eu/en>, OBIS—<https://obis.org/>, GBIF—<https://>

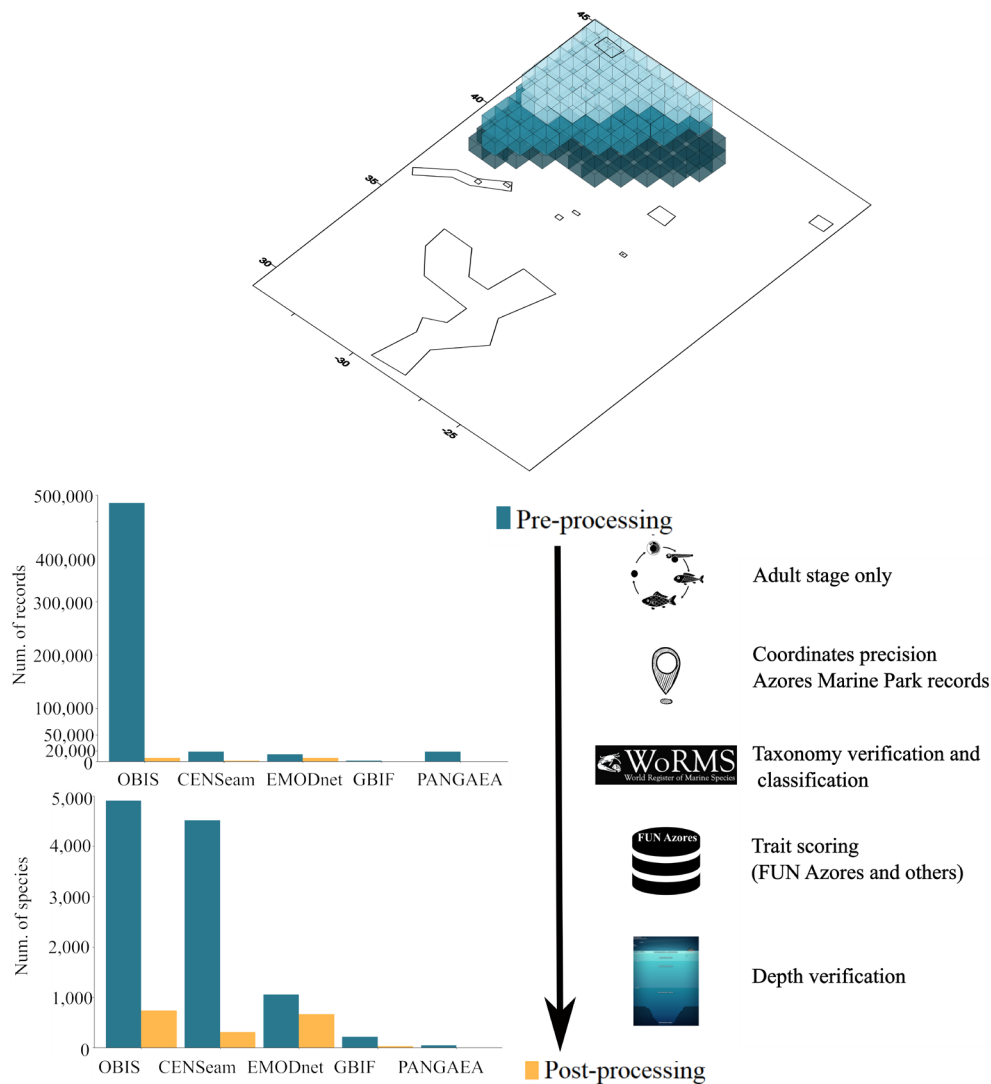


FIGURE 2 | Methodology for data acquisition. Top, creation of a 3D-mesh with a cell resolution of $0.25^\circ \times 0.25^\circ$. Bottom, steps involved in the processing and management of the raw data.

www.gbif.org/; Vandepitte et al. 2015) and specific databases (CenSeam—<http://www.coml.org/global-census-marine-life-seamounts-censeam/>, PANGAEA—<https://www.pangaea.de/>). We considered species present in the epibenthic and pelagic environments and the species that link the two compartments (i.e., benthopelagic). We filtered and cleaned the final dataset following a series of steps described below (Figure 2). The nature of the dataset prevented any abundance-based analysis.

Older species records may have different taxonomic names, and we, therefore, updated taxonomic nomenclature for each species record according to the WoRMS (<https://www.marinespecies.org/>) standards. Taxonomic resolution of our final data set is at the genus or species level, excluding coarser taxonomic resolution because of lack of precision in trait information at higher ranks. Genera from ecologically important species (Gomes-Pereira et al. 2014) - such as *Dentomuricea* sp., for which the only species described so far is *Dentomuricea meteor* (McFadden et al. 2023), and *Pheronema* sp., for which the only species observed in the area is *Pheronema carpenteri* (Howell et al. 2016; Carreiro-Silva et al. 2017; OBIS: Ocean Biodiversity Information System 2023) - were scored as such.

We pooled all species occurrence records by proximity to a resolution of 0.25 latitude \times 0.25 longitude degrees for the data analysis; therefore, to match precision, we only accepted records with a latitude and longitude with at least two decimal places. We only considered adult records of the species, excluding larvae and juveniles. Lack of current knowledge on early life stages' sensitivity to climate change for most species drove the exclusion of these records despite their sensitivity being independent from adults' sensitivity (Levin 2006). At present, we lack information on early life-history stages for most species.

We removed records with obvious depth errors (i.e., minimum depth for a species could not exceed maximum depth and none of them could fall lower than known bathymetric constraints) and classified the recorded depths into depth bands. We scored a depth of zero for Mammalia, Aves, and Reptilia (i.e., sea surface) as these records were reported from deck-based observers. When the depth record was missing on benthic records, we extracted its corresponding bathymetry if the coordinates were precise enough (i.e., at least four decimals). We narrowed down uncertainty using trait information from the "FUN Azores" trait database (Campanyà-Llovet et al. 2023a,

2023b). For example, all specimens reported from a specific pelagic trawl had the same reported depth of 0–1000 m, resulting from the lack of precision from the sampling methodology used. If a particular species has a global depth distribution of 500–1500 m according to the “FUN Azores” trait database, we modified the reported depth for that species in that pelagic trawl to the overlap between the different information sources (i.e., 500–1000 m).

The resulting dataset comprised 426 benthic, 58 benthopelagic, and 375 pelagic species. Most of the benthic species occurred at bathyal depths (i.e., 200–2000 m) and include 264 representatives of Actinopterygii, Anthozoa, Bryozoa, Chondrichthyes, Decapoda, Echinodermata, Foraminifera, Hydrozoa, Mollusca, Porifera, Annelida, and Nematoda. By contrast, 131 shallow (<200 m) species and 25 deep species (>2000 m) were present in our dataset. More species were found at shallower depths from the pelagic environment (i.e., 245 species of mostly Actinopterygii, Aves, Chondrichthyes, Decapoda, Foraminifera, Hydrozoa, Mollusca, Mammalia, Ostracoda and Reptilia) compared to 97 and 34 species at bathyal and deeper depths (>2000 m). The benthopelagic environment was richer in species at bathyal depths (i.e., 52 species of mostly Actinopterygii and Chondrichthyes), in contrast to 4 and 3 species in shallow and deeper areas, respectively.

2.4 | Vulnerability Index

We scored the following traits for the vulnerability assessment: temperature max. and range to assess sensitivity of the species, adult motility and developmental mechanism to evaluate their adaptive capacities at different life stages.

2.4.1 | Temperature Sensitivity Based on Traits

We used the species' realised thermal niche as a proxy for thermal sensitivity because marine species are body temperature conformers (i.e., temperature ranges of species can correspond to the range of organismal thermal tolerance; Sunday et al. 2012; Hastings et al. 2020). We lacked information on species thermal limits derived from experimental studies at such broad coverage and therefore, we focused on species realised niches instead, which reflect natural conditions as part of a complex ecosystem. We extracted temperature minimum and maximum values from the Encyclopedia of Life—TraitBank through the Cypher query form (https://eol.org/service/cypher_form) using Cypher query language (<https://neo4j.com/>). To assess temperature sensitivity of each species to warming and temperature variability, we considered the maximum temperature reported in the field for each species and the temperature range of each species (i.e., maximum temperature minus minimum temperature), respectively. The terms stenotherm and eurytherm are defined as species that can tolerate narrow or wide environmental temperature ranges in the absence of standardised thresholds across species (Logan and Buckley 2015). Our definition of stenotherm and eurytherm is calculated based on relative species values (as often used in the literature; Logan and Buckley 2015) across the full dataset. For each environmental zone (i.e., benthic,

benthopelagic, and pelagic), we calculated the 25th, 50th, and 75th percentiles in maximum temperature and in temperature ranges separately, which resulted in four categories of maximum temperature tolerance and four categories of temperature breadth (Table S1). To calculate the sensitivity score, we assigned an ordinal category to each species from 1 (less sensitive: above 75th percentile) to 4 (more sensitive: below 25th percentile). We then calculated the temperature sensitivity score for each 3D-region by averaging the sensitivity score of each species recorded from the region and categorised each spatial unit as sensitive or non-sensitive if it fell over or under the 50th percentile of the sensitivity scores of all regions.

2.4.2 | Temperature Exposure Based on Historical Data

We extracted historical temperature datapoints (i.e., 1995–2020) in the 4D domain (i.e., latitude, longitude, depth and time) from the Copernicus data portal (www.copernicus.eu/) using Python. The temporal range coincided with the best available dataset. We imported the net.cdf files into R using the package “ncdf4” (Pierce 2023). We assigned each datapoint into a cube of the original three-dimensional mesh according to its four dimensions and calculated the mean interannual temperature change per cube to inform the magnitude of change and its associated standard deviation to estimate temperature variation within each 3D-region across years. We classified each region into general increasing temperature if the mean interannual change per region was positive, and into high or low variability in relation to the 50th percentile of temperature variability across years.

Historical data highlights areas that have endured the greatest temperature anomalies, which we expect to be more exposed in the future. We corroborate this assumption with a predicted dataset in sea surface temperature extracted from NOAA data portal (<https://data.noaa.gov/>). Particularly, we looked at the climate anomaly between RCP8.5 (2050–2099) and the historical reference period (1995–2005, where more data was available) and change in variability (i.e., ratio for the de-trended variance in the future divided by the past), both in degrees Celsius (°C). We also imported the net.cdf files into R using the package “ncdf4” (Pierce 2023) and assigned each datapoint to a cell of a mesh of the highest resolution possible (i.e., 1° latitude × 1° longitude degree resolution). However, our vulnerability assessment is based on historical instead of forecasted data to work with the highest spatial resolution (0.25° × 0.25° instead of 1° × 1°).

2.4.3 | Adaptive Capacity of Species Based on Traits

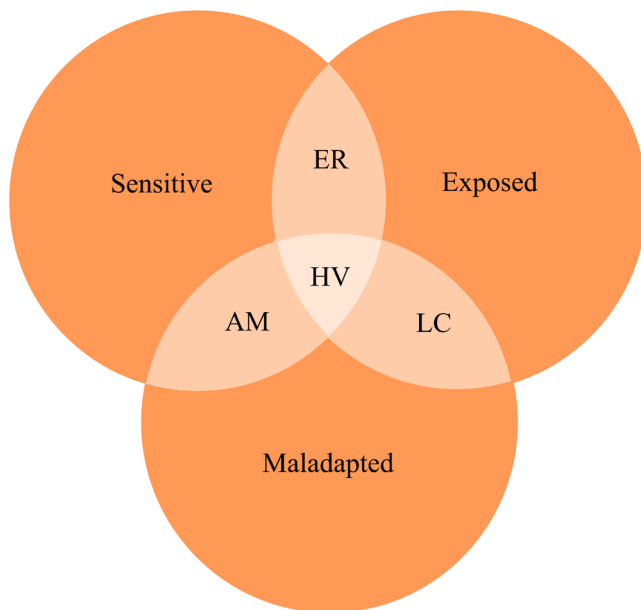
We considered two traits from “FUN Azores” trait-database (Campanyà-Llovet et al. 2023a, 2023b) to estimate the adaptive capacity of a species to negative impacts of temperature variability throughout years (Table S2): “Motility” describes the capacity of a species to find a new and more favourable environment in its adult stage; “Developmental Mechanism” describes the capacity of a species to colonise new and more suitable environments at early life stages (Costello et al. 2015). We assigned an adaptive capacity score per species according

to its trait modalities (Table S2), and we then calculated the adaptive capacity score for each 3D-region by averaging the score of each species recorded within that spatial unit. We finally categorised each spatial unit as adaptive or maladaptive if it fell over or under the mean adaptive capacity of all species included in this study.

2.4.4 | Final Vulnerability Score

Vulnerability of each 3D-region is determined by the region's exposure to temperature change and the sensitivity and adaptive capacity of its component species (Figure 3). A final vulnerability category for each 3D-region was based on the combination of the three elements. Therefore, exposed regions with a high sensitivity score and low adaptive capacity fall into the "Highly Vulnerable" category. If the same conditions apply but there is not exposure, the region falls into the "Advisable Monitoring" category. We classified "Expected Relocation", if the region is exposed and its sensitivity score is high but its species are also adaptable. Regions of "Least Concern" were reserved for cases where the sensitivity score is low. We applied the same procedure to assess vulnerability to temperature change (i.e., increasing tendency) and temperature variation, producing two scores for each 3D-region.

All data management and analyses were performed in R (R Core Team 2022).



HV: Highly vulnerable
 AM: Advisable monitoring (Latent vulnerability)
 ER: Expected relocation (Capacity to adapt)
 LC: Least concern (Not sensitive)

FIGURE 3 | Venn diagram representing the four vulnerability types.

2.4.5 | Correlations Between Temperature and Species Traits

To assess the relationship between species characteristics and species temperature tolerances (i.e., temperature maximum, minimum, and range) we ran spearman correlations with the function *cor* from the "stats" package in R programming software (R Core Team 2022), *rcorr* from the "Hmisc" (Harrell Jr 2025) package to calculate *p*-values (significant level = 0.05) and *corrplot* from the "corrplot" package (Wei and Simko 2024) to plot the results. We selected traits that define a species ecological niche from the "FUN Azores" trait database (i.e., "Maximum Body Size", "Motility", "Environmental Position", "Trophic Position"; Campanyà-Llovet et al. 2023a, 2023b) or new traits adapted from the "FUN Azores" trait database (i.e., "Number of Depth Ranges" and "Number of Substrate Types").

2.4.6 | Biogeography

We mapped the final derived vulnerability 3D-region classifications in R using the package "terra" (Hijmans 2023) and "ggplot2" (Wickham 2016). Geographic coordinate system used for all the mappings corresponds to WGS 84 (World Geodetic System 1984—EPSG 4326) and for map projections WGS 84/ UTM Zone 26N (EPSG: 32,626 code; <https://epsg.io/>). For each environment (i.e., benthic, benthopelagic, and pelagic), we mapped vulnerability scores to temperature increases and vulnerability scores to temperature variation, resulting in six vulnerability maps.

3 | Results

3.1 | Vulnerability

Vulnerability assessment based on two temperature metrics (i.e., mean interannual temperature difference and corresponding variability) led to similar patterns in the classification of each 3D-region. Thus, those spatial units with sensitive and maladapted species are often experiencing both warming and high temperature variability (e.g., the chondrichthyes *Hydrolagus affinis* and *Bathyraja richardson*, and the corals *Errina dabneyi*, *Placogorgia terceira*, and *Alcyonium profundum*).

3.1.1 | Highly Vulnerable and Advisable Monitoring Locations

We found twenty-four highly vulnerable regions throughout the different MPAs and depths in the benthic but not in the pelagic or benthopelagic compartments (Figures 4, 5, and S1–S4): 12 vulnerable to both temperature increase and variability and 12 vulnerable to increasing temperatures only. The 12 "Highly Vulnerable" (HV) regions to both temperature increase and variability (Figures 4 and 5) are found at northern latitudes in Sedlo seamount (MPA05) at 1000–1500 m and 2000–2500 m; at central latitudes within the Mid-Atlantic Ridge (MAR; MPA13) where venting activity is frequent, at

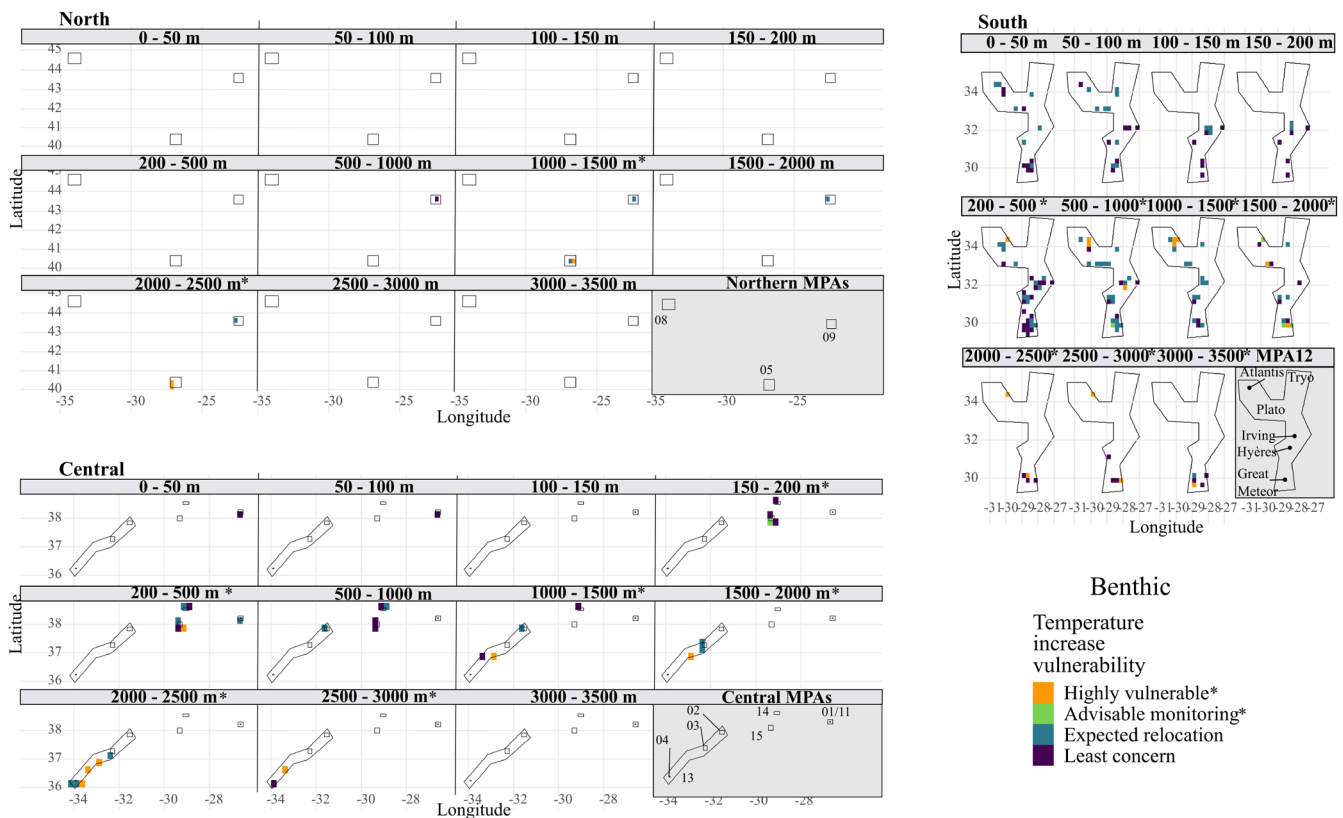


FIGURE 4 | Vulnerability to temperature increases biogeographic map for the benthic environment. We only classified areas where biological information was available for the vulnerability assessment. MPAs: 01/11—D. João Castro, 02—Menez Gwen, 03- Lucky Strike, 04—Rainbow, 05—Sedlo, 08—Altair, 09- Antialtair, 12—Great Meteor complex, 14—Condor, 15—Princesa Alice. See annex for the equivalent figures on the pelagic and benthopelagic compartments.

1000–3000 m depth; and at southern latitudes (MPA12) often surrounded by “Advisable Monitoring” 3D-regions: Atlantis seamount at 200–1500 m and 2000–3000 m, Plato seamount at 1500–2000 m, Irving at 500–1000 m, and Great Meteor at 1500–3000 m. Twelve additional regions are highly vulnerable to increases in temperature but not to variability (Figure 4): Princesa Alice (MPA15) 200–500 m, additional vent (MPA13) areas at 1500–2500 m, and MPA12 (i.e., Atlantis 200–2500 m, various depths at great Meteor below 2000 m, and Irving seamount at 500–1000 m). Overall, in the Azores Marine Park (AMP), “Advisable Monitoring” is far less common and found near “Highly Vulnerable” 3D-regions.

3.1.2 | Expected Relocation and Least Concern Regions

The difference between “Expected Relocation” and “Least Concern” 3D-spatial units is the sensitivity of the species pool to temperature changes. When the average score within a spatial unit falls below the 50th percentile of all spatial regions (i.e., least sensitive), their adaptive capacity and degree of exposure become irrelevant and are classified as “Least Concern” but when they are sensitive but adaptive, we expect them to relocate. In the AMP, both types of 3D-regions prevail at all depths and environments (Figures 4, 5, and S1–S4). All shallow water (i.e., 0–200 m) 3D-regions are classified in one of the two categories regardless of environment and temperature measure except for one benthic unit in Princesa Alice (MPA 15), where monitoring

is advisable (Figure 4). All pelagic and benthopelagic units are only classified into one of the two categories (Figures S1–S4) as well. In the pelagic environment, “Expected Relocation” is most prevalent below 200 m depth and “Least Concern” dominates the 0–50 m depth layer.

3.2 | Exposure

3.2.1 | Temperature Changes

Regions with various degrees of exposure to temperature increases and variability are found throughout all latitudes and depths within the AMP (Figures 6 and 7).

At all latitudes there are regions with increasing temperatures (i.e., mean interannual variability $> 0^{\circ}\text{C}$) accompanied by high temperature variability (i.e., mean interannual variability $> 0.56^{\circ}\text{C}$), suggesting volumes of high temperature instability: in the north below 1500 m (Altair, MPA08), at central latitudes in MPA 02/03/04/13 between 2000 and 3000 m, and in the south in MPA12 at 100 to 150 m and 2500 and 3000 m depths (Figures 6 and 7). However, in most of the 3D-regions from all MPAs at 150–200 m, temperature decreased and varied considerably (i.e., mean interannual variability $> 0.56^{\circ}\text{C}$).

Some regions experience high temperature variability (i.e., mean interannual variability $> 0.56^{\circ}\text{C}$) across all years, with a nearly

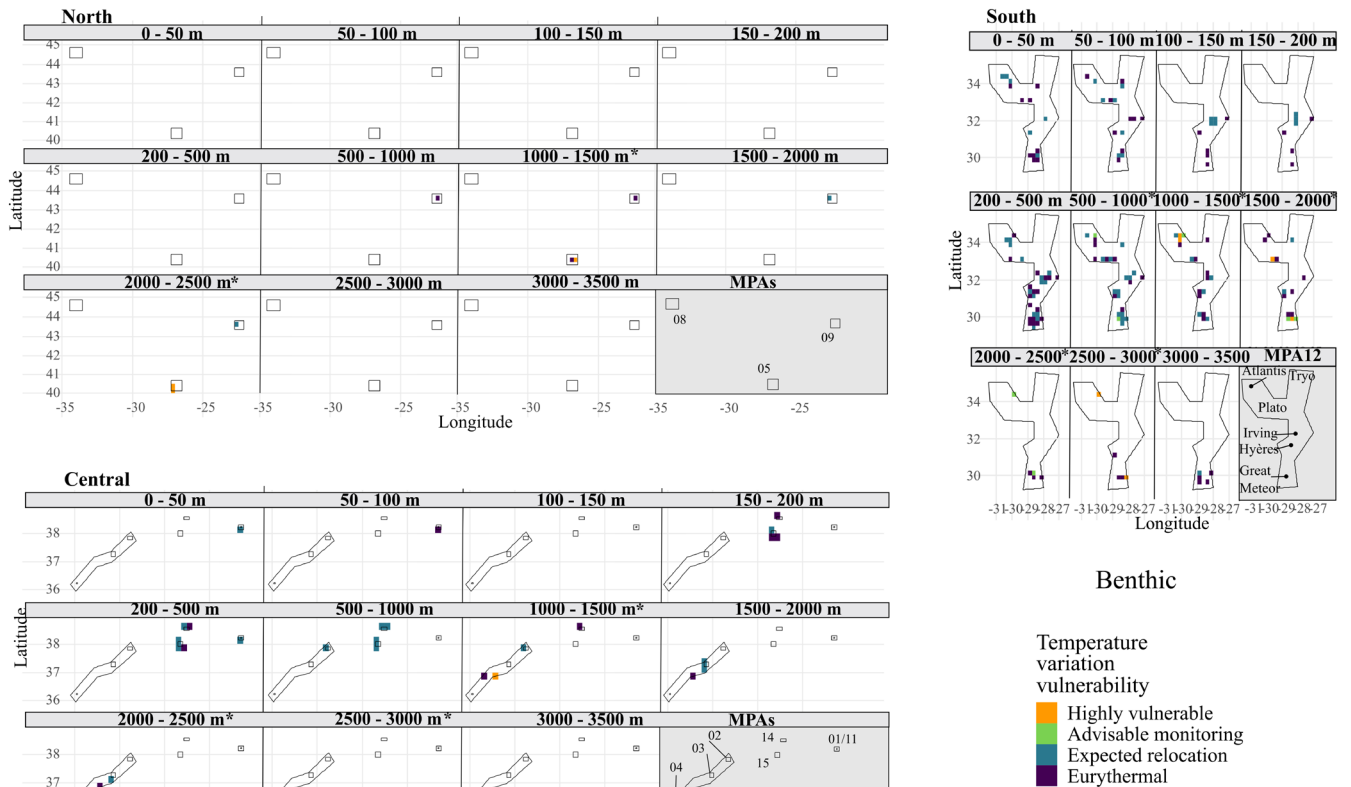


FIGURE 5 | Vulnerability to temperature variation biogeographic map for the benthic environment. We only classified areas where biological information was available for the vulnerability assessment. MPAs: 01/11—D. João Castro, 02—Menez Gwen, 03- Lucky Strike, 04—Rainbow, 05—Sedlo, 08—Altair, 09- Antialtair, 12—Great Meteor complex, 14—Condor, 15—Princesa Alice. See annex for the equivalent figures on the pelagic and benthopelagic compartments.

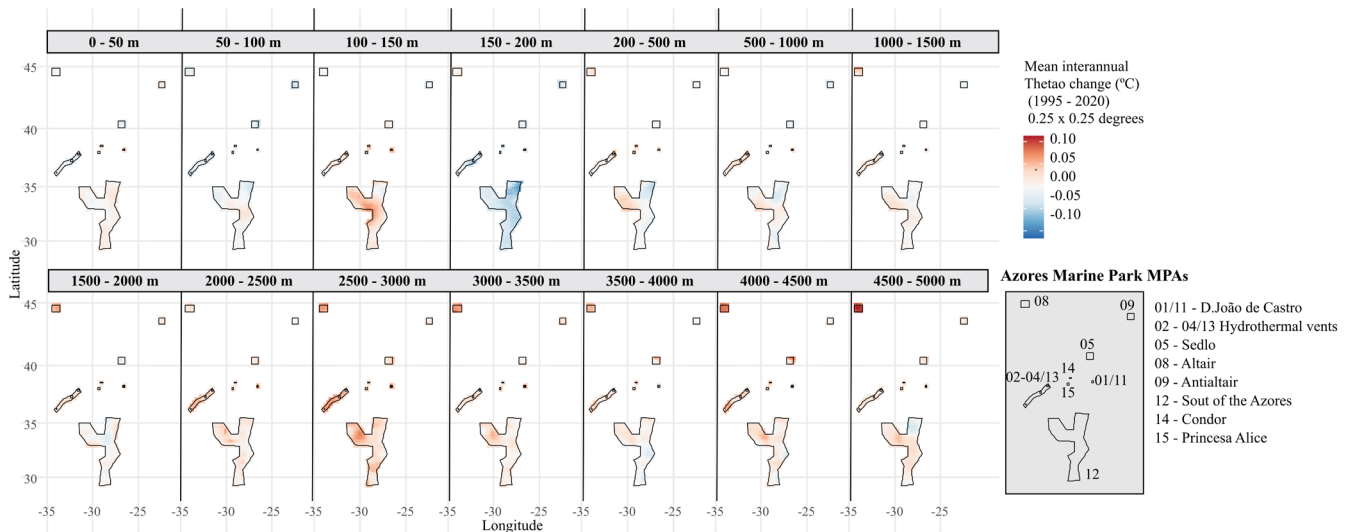


FIGURE 6 | Historic (1995–2020) mean interannual thetao (i.e., potential temperature) for the Azores Marine Park.

net zero mean final temperature: at mid latitudes Antialtair (MPA 09), Sedlo (MPA 05), and central MPAs (i.e., Condor—MPA14, Princesa Alice—MPA 15-, D. João de Castro—MPA 01/11, and the hydrothermal vents southwest from the Azores—MPA 02–04/13) at the lower shelf (i.e., 150–200m) and lower bathyal (i.e., 2000–2500m and 3500–4500m).

Substantial heterogeneity in temperature variability is found in MPA12, south of the Azores, probably because of its large spatial extension. The top part is highly variable at most depths, while temperatures have been rather constant at the southern part, leading to the co-occurrence of two extremes in one MPA at some depths (i.e., 100–150m, 1500–2000m, 3000–3500m, 4500–5000m).

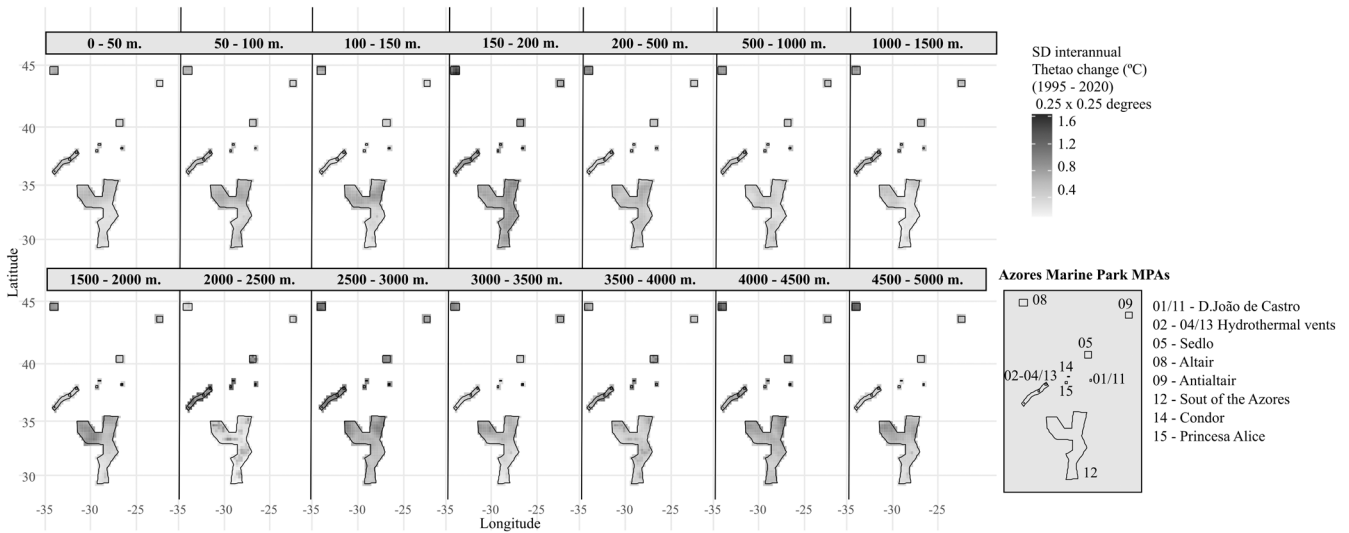


FIGURE 7 | Historic (1995–2020) standard deviation thetao (i.e., potential temperature) for the Azores Marine Park.

3.2.2 | Temperature Stability

We identified regions of low temperature variability (i.e., $< 0.3^{\circ}\text{C}$ or below the 1st percentile of the temperature variability data) that could be considered refugia for highly sensitive species if the other environmental and biological conditions apply (Figures 6 and 7) across all latitudes, longitudes, and depths.

Near-zero mean interannual temperature change is common at shallower depths (i.e., 0–100m) where near-zero variability is also common, suggesting historically stable environments (Figures 6 and 7). Other areas with low mean interannual temperatures are upper and lower bathyal (i.e., 500–2000m and 3000–4000m), except for Altair (MPA 08); although variability can be high in specific locations, suggesting an unstable environment without a clear trend or direction.

At 1500 and 2000 m depths, there are areas of low temperature variability and low mean interannual temperature changes, including Sedlo seamount (MPA05), MPA13, and the southern part of MPA12, which includes Great Meteor seamount. These areas fall between two depth bands with HV regions above and below those depths, where species could potentially relocate to avoid large temperature variations. In a similar manner but at different depths, at 2000 to 2500 m depth in the northern part of MPA12, including Atlantis and Plato, there is low temperature variability and a temperature increase with HV regions at the above and below depth bands.

3.2.3 | Temperature Projections

Temperature projections (RCP8.5) point to higher temperature increases at lower latitude locations, coinciding with the highly vulnerable 3D-regions identified using historical data in the southern area (Figure S5). Temperature variability projections highlight central cells of the study area covering MPA13 (hydrothermal vents southwest from the Azores), Banco Princesa Alice, Condor (MPA14), Sedlo seamount, and northern parts of MPA12 (Meteor complex south from the Azores) as the volumes

where temperature variability will be most acute, coinciding with most of the highly vulnerable spatial units identified using historical data (Figure S5).

3.2.4 | Correlation Between Temperature Sensitivity and Species Traits

The breadth of temperature and temperature limits of species significantly correlate with certain traits that define a species' ecological niche. For example, “Environmental Position” of the species, whereby benthopelagic and pelagic species have a broader temperature range with higher maximum and lower minimum temperatures (Figure S6). “Number of DRepth ranges”, “Number of Substrates” used, and “Trophic Position” are also correlated with “Environmental Position” and therefore, with most temperature metrics (i.e., maximum and minimum temperatures as well as full range). Benthopelagic and pelagic eurybathic species inhabiting the water column are more eurythermal and have higher temperature maxima and lower temperature minima.

4 | Discussion

Here, we applied a biogeographic trait-based approach to vulnerability assessments across depths in the Azores Marine Park (AMP) and found that deep benthic environments are similarly or more impacted than shallow-water areas. We corroborate previous reports identifying significant impacts of climate change in deep ocean habitats (Sweetman et al. 2017 and Brito-Morales et al. 2020). In fact, we find higher species sensitivities, greater exposure, and overall vulnerabilities within the bathyal domain. Our approach identifies locations with highly vulnerable species and relates their position to potential climate refugia. Around the globe, different areas are unequally vulnerable to climate and environmental change, which is why approaches like the ones presented in this study are valuable. For example, semi-enclosed areas such as the Baltic and Adriatic and shallow coastal areas are considered more exposed to warming

(Belkin 2009). The lack of “Highly Vulnerable” areas in shallow waters of the AMP is likely because shallow waters in the AMP are pelagic, where highly motile species have a greater capacity to relocate to new environments if the conditions become unfavourable (Birchenough et al. 2015). Most areas in the AMP are classified as “Expected Relocation” classification, which leads to substantial species turnover in most areas; therefore, community monitoring is advised.

4.1 | Vulnerability

4.1.1 | Highly Vulnerable 3D-Regions and 3D-Regions Where Monitoring Is Strongly Advised

Locations with the largest temperature variation in the AMP included cold-affinity (low thermal limits) and stenothermal species and therefore were scored as “Highly Vulnerable” (HV). All HV regions fell into the benthic compartment and none into their pelagic or benthopelagic counterparts. For these benthic species, temperature sensitivity combines with a low capacity to escape to other areas, through direct emigration as an adult or indirectly through the survival of early life stages elsewhere. Rates of change in distribution are slower in the benthic compared to the pelagic compartment because of various degrees of connectivity (Birchenough et al. 2015), which results in different adaptive capacities and therefore vulnerabilities to environmental change, as observed in the results from the AMP. While pelagic and benthopelagic species are also influenced by temperature changes (Brito-Morales et al. 2022) and large pelagic fish can be impacted by increasing metabolic demands with ocean warming and decreased food availability (Petrik et al. 2020), these species tend to have broader temperature ranges and higher temperature maxima than their benthic counterparts through occupying various ocean depths (Figure S6). Furthermore, the higher capacity of movement in species that use pelagic areas translates to higher scores for the “Expected Relocation” category, and thus lower vulnerability. The differences observed between both the benthic and pelagic compartments can have impacts on the whole marine food web and dependent fisheries following benthopelagic coupling (Birchenough et al. 2015; Kirby et al. 2007).

“Highly Vulnerable” benthic 3D-regions were found across all latitudes (northern, central, and southern latitudes) at bathyal depths. At northern latitudes, Sedlo seamount (MPA05), chondrichthyes *Hydrolagus affinis* and *Bathyraja richardsoni* drive the high vulnerability of the area at a 1000 and 2000m depth. These are species with relatively low maximum temperatures (i.e., <5°C), low thermal ranges (i.e., <5°C) and low dispersal capabilities. *Bathyraja richardsoni* has a strong niche specificity for egg-laying, choosing narrow thermal, salinity, and oxygen ranges associated with coral gardens (Henry et al. 2016; Maguire et al. 2023); in fact, Sedlo Seamount MPA is an important reproductive area (Calado et al. 2011).

At central latitudes, MPA13, which is embedded in the Mid-Atlantic Ridge (MAR) where volcanic activity is frequent, we find six highly vulnerable 3D-regions from 1000 to 3000m depths. Several species of corals reside in these regions and have small thermal ranges and are exclusive to cool temperatures

(i.e., *Errina dabneyi*—endemic to the Azores-, *Placogorgia terceira* and *Alcyonium profundum*). Even so, there is uncertainty on the scoring of early life-history traits (i.e., planktonic non-adult dispersal, without specification of feeding mode), which highlights the need for further research and sustained protection in this MPA.

The top of seamounts also emerged as being vulnerable. For instance, although historical temperature variation at the top of Condor Seamount (MPA14; 150–500 m) has not been as strong as in other 3D-regions, species reported from the seamount are either highly vulnerable or fall within a region that is advisable for monitoring. Cold coral gardens at the top of the seamount provide habitat for associated species and promote high local biodiversity (Tempera et al. 2012; Porteiro et al. 2013; Braga-Henriques 2014). Species in these vulnerable 3D-regions are sensitive to warming and temperature variability, with reduced motility. While most species are planktonic developers with uncertainty on their feeding mode, lecithotrophic larvae (i.e., non-feeding larvae) occur in the area, which increases their vulnerability status.

“Highly Vulnerable” benthic regions in Atlantis and Plato seamounts (MPA12) are characterised by species sensitive to temperature (either increases or variation), such as *Spondylus gussonii*, a small sessile bivalve (i.e., <10 cm) that is often found attached to cold-water corals such as *Desmophyllum* sp. and *Madrepora* sp. (Schembri et al. 2007). We also have species in that area with planktonic or lecithotrophic larvae, and therefore, uncertain or low dispersal capabilities, which reduced the adaptive capacity score of the species and the region. Knowledge of developmental mechanisms is usually scarce (Campanyà-Llovet et al. 2023a) because of the difficulties associated with studying such small-sized organisms in a vast ocean, which are also difficult to manipulate (Levin 2006). Following the precautionary principle, we resolve uncertainty as less capacity to adapt. At the same time, lecithotrophic larvae support dispersal to close and similar environments, which is advantageous when environmental specificity is higher for the species but disadvantageous when environmental conditions change, reducing the adaptive capacity potential of the species (Ávila et al. 2007). Other contributors to the “Highly Vulnerable” status of a specific region in MPA12 are the sessile stenothermal adults with lecithotrophic larvae, such as the corals *Acanella arbuscula* and *Deltocyathus moseleyi* and the sponge *Atlantisella incognita*. Motile stenothermal adults with lecithotrophic or uncertain planktonic development, such as the sea urchin *Hygrosoma petersii* and the bivalve *Rhinochlamys teres*, also increase vulnerability, showing how motile species can also contribute to the sensitivity status of a region. In fact, despite their high motility, 22 species of Chordata, including *Hydrolagus affinis* and *Bathyraja richardsoni*, showed low temperature ranges (<2.6°C) and maxima (<10.7°C) compared to other benthic species, showing how motility does not necessarily imply eurythermia.

Abrupt topographies in the marine environment influence ocean circulation and biological productivity (Genin 2004). The anticyclonic vortex circulation above Great Meteor (within MPA12) favours the aggregation of zooplankton communities and small fishes that in turn attract larger predators (Fock et al. 2002). The “Highly Vulnerable” or “Advisable

Monitoring” regions surrounding Great Meteor seamount host stenothermal species with lecithotrophic (or probable lecithotrophic larvae), including the corals *Parantipathes hiron-delle*, *Deltocyathus moseleyi*, and *Viminella flagellum* (Rakka et al. 2021). The limited distribution of these species suggests a relatively closed system; in fact, endemic species are common in some taxonomic groups (copepods and nematodes; George and Schminke 2002; Gad 2009).

4.1.2 | Expected Relocation

In most cases, we expect substantial turnover (i.e., change in species composition) where greater temperature change is expected. Losses will occur for highly sensitive species that migrate from unsuitable regions. These sites may also receive new species. Indeed, distributional shifts of species follow local climate velocities (Loarie et al. 2009; Arafeh-Dalmau et al. 2021). Even so, the environmental suitability of the surrounding regions, the ability of a species to migrate, prey distribution, location of spawning grounds, and diet all play important roles in determining species direction and speed of relocation (Thorne and Nye 2021). Drifters are classified as discretely motile to highlight the different capacities of these species to move. Their movement is restricted to the water masses, but they can relocate into the most convenient water mass through vertical migrations (Bandara et al. 2021). Significant distribution shifts of drifters such as zooplankton have been previously reported with time in response to climate variation (Beaugrand et al. 2002). Non-adult dispersal is crucial to connect MPA networks such as the AMP. The distance travelled and settlement efficiency depend on many factors, including the feeding mode of the larvae (planktotrophic or lecithotrophic). Planktotrophic larvae will travel further and facilitate exploration of new environments that provide different survival, growth, and reproductive conditions, which makes them more adaptable when environmental conditions change (Ávila et al. 2007). The combination of these relocation capabilities and the impacts of environmental change on adults and early life history stages (Andreollo et al. 2015) determines the resulting biogeographic redistributions in latitude and depth.

Potential climate refugia adjacent to “Highly Vulnerable” regions will serve as corridors or suitable new habitats that are already protected against other anthropogenic threats (i.e., potential mineral extraction and fishing) and thus are crucial for population survival. For example, Sedlo at 1500–2000 m has low temperature variation and falls between “Highly Vulnerable” regions in that MPA at 1000–1500 m and 2000–2500 m depth bands. Other regions with low temperature variation include Plato at 1000–1500 m, right above “Highly Vulnerable” regions on that seamount.

We expect that with increasing temperatures, new species will begin to populate the AMP in the benthic, benthopelagic, and pelagic compartments (Hastings et al. 2020; Chaudhary et al. 2021), influencing the vulnerability status of each location within the park. If “Highly Vulnerable”, “Advisable Monitoring”, and “Expected Relocation” 3D-regions are not monitored, sensitive species could be replaced by species that are sensitive at lower latitudes seeking more favourable

environmental conditions in the AMP. Monitoring will thus identify new opportunities, such as allowing exploitation of any new species that cause harm or identifying where retreating species in other habitats may need protection to compensate for population declines elsewhere.

4.2 | Recommendations

Following the need of most species to relocate, we need to maintain large MPA sizes or MPA networks to ensure habitat representation, replication, and spread (McLeod et al. 2009; Kavousi and Keppel 2018). Adults will require suitable relocation habitats, while larvae need suitable conditions to both settle and survive. A diverse thermal seascape, which includes habitat heterogeneity, will ultimately provide climate refugia (i.e., regions that have remained relatively constant throughout the years while the neighbouring regions have been impacted by temperature oscillations) and incorporate existing connectivity networks for relocation (Wilson et al. 2020; Arafeh-Dalmau et al. 2021). Climate refugia, in some cases, also promote biodiversity persistence (Kavousi and Keppel 2018). The identification of climate refugia and regions where climate conditions are changing rapidly is therefore important to consider in the design and management of protected areas (Brito-Morales et al. 2018). However, refugia may be variable in time, taxon-specific, and need to be refugia for all the climatic threats (Kavousi and Keppel 2018), and thus, close monitoring of the environmental conditions in these areas is required. The lack of cooccurrence of thermally stable areas with water masses known to influence the area (i.e., Mediterranean outflow water, Azores current and counter-current, and Antarctic; Puerta et al. 2020; Frazão et al. 2022) hampers predictions of refugia and reinforces the need for monitoring.

Impacts of climate variation on marine ecosystems are emerging, and implemented socio-economic adaptations to climate-driven changes are unable to offset climate-change impacts under low-emission scenarios on systems and services they provide (Bindoff et al. 2022). Although at lower spatial resolution, the overlap between projected temperature increases and increased variability (i.e., $1^\circ \times 1^\circ$ and one depth) with highly vulnerable regions or regions with monitoring is advisable, found in this study (i.e., $0.25^\circ \times 0.25^\circ$ and 11 depth bands) reinforces their vulnerability status. Therefore, solutions are required with urgency at the appropriate scales. Based on the results of this study, we recommend:

- Implementing conservation strategies that incorporate expected climate change impacts in highly vulnerable sites to minimise impacts from local human-related threats.
- Monitoring environmental conditions of sites where species are vulnerable but not historically exposed to thermal variations (i.e., “Advisable Monitoring”).
- Monitoring potential thermal refugia to determine if these regions are fulfilling a refugia role and conferring protection from additional threats.
- Monitoring populations that are expected to track climate velocities.

- Monitoring community structure in sites where high turnover is anticipated due to species relocation.
- Increasing the knowledge of key traits used to assess the vulnerability of species, such as distinguishing between planktotrophic and lecithotrophic planktonic larvae.
- Protecting and enhancing research efforts in areas with limited knowledge to avoid irreversible damage before knowledge is gained.

Given that climate variations cross any MPA (Bruno et al. 2018; Bates et al. 2019; Smale et al. 2019), we believe this approach can be applicable to any area with sufficient knowledge of benthic, benthopelagic, and pelagic species. Future studies should also focus on the cumulative effects of all climate change variables to assess vulnerabilities in the area to increase protection effectiveness across networks.

Author Contributions

Neus Campaña-Llovet conducted the conceptualisation, data curation and validation, formal analysis, visualization, methodology and wrote the original manuscript. Amanda Bates and Ana Colaço contributed to the conceptualisation of the study and reviewed and edited the original draft. Ana Colaço was responsible for the funding acquisition and project administration. All authors contributed to the article and approved the submitted version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The primary codes and data used to analyse the datasets can be found in Dryad <https://doi.org/10.5061/dryad.w3r22811m>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Vulnerability to temperature increases biogeographic map for the benthopelagic environment. We only classified areas where biological information was available for the vulnerability assessment. MPAs: 01/11—D. João Castro, 02—Menez Gwen, 03- Lucky Strike, 04—Rainbow, 05—Sedlo, 08—Altair, 09- Antialtair, 12—Great Meteor complex, 14—Condor, 15—Princesa Alice. **Figure S2:** Vulnerability to temperature variation biogeographic map for the benthopelagic environment. We only classified areas where biological information was available for the vulnerability assessment. MPAs: 01/11—D. João Castro, 02—Menez Gwen, 03- Lucky Strike, 04—Rainbow, 05—Sedlo, 08—Altair, 09- Antialtair, 12—Great Meteor complex, 14—Condor, 15—Princesa Alice. **Figure S3:** Vulnerability to temperature increases biogeographic map for the pelagic environment. We only classified areas where biological information was available for the vulnerability assessment. Unclassified regions are shown in grey. MPAs: 01/11—D. João Castro, 02—Menez Gwen, 03- Lucky Strike, 04—Rainbow, 05—Sedlo, 08—Altair, 09- Antialtair, 12—Great Meteor complex, 14—Condor, 15—Princesa Alice. **Figure S4:** Vulnerability to temperature variation biogeographic map for the pelagic environment. We only classified areas where biological information was available for the vulnerability assessment. Unclassified regions are shown in grey. MPAs: 01/11—D. João Castro, 02—Menez Gwen, 03- Lucky Strike, 04—Rainbow, 05—Sedlo, 08—Altair, 09- Antialtair, 12—Great Meteor complex, 14—Condor, 15—Princesa Alice. **Figure S5:** Projected temperature anomaly (top) standard deviation (bottom) for the Azores Marine Park under RCP 8.5 scenario. **Figure S6:** Trait correlations between temperature measures (i.e., range, maximum, and minimum) and relevant FUN Azores database traits. Significant levels at 0.05. **Table S1:** Temperature thresholds used for each environmental position and temperature metric based on the boxplot distribution of all the species contained. **Table S2:** Conceptual framework to assess the degree of adaptive capacity to change for each species based on their trait modalities.