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Present and future distribution of the deep-sea habitat-forming sponge - *Pheronema carpenteri* (Thomson, 1869) in a changing ocean

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ABSTRACT

Sponges play vital roles in the ecosystem function of the deep sea. Some species, such as the birds' nest sponge *Pheronema carpenteri*, can form highly structured and dense habitats (i.e., aggregations), which contribute to the increase of nearby biodiversity. Climate change is expected to have a pronounced impact on the deep sea, particularly on Vulnerable Marine Ecosystems such as those formed by the glass sponge *Pheronema carpenteri*. These ecosystems are especially vulnerable to climate change and other anthropogenic activities since they are formed by sensitive species with slow growth rates and limited dispersal capability, which can hinder their adaptive capability and recovery after disturbance. The impact that climate change will have on *Pheronema carpenteri* remains unclear, although it is expected to influence the species' available suitable habitat and distribution range. The aim of this study was to predict the distribution of the glass sponge *Pheronema carpenteri* both for present day and under several future climate scenarios in the North Atlantic. An ensemble modelling approach was employed, combining Maximum Entropy, Generalized Additive Models and Random Forest techniques. Changes in available suitable habitat were projected to present day and to three future climatic scenarios (RCP 2.6, RCP 4.5 and RCP 8.5). Depth, temperature and dissolved oxygen were identified as the key predictor variables of habitat suitability, which patterns suggest a strong influence of the Mediterranean Outflow Water in shaping the present day distribution of the species, particularly in the eastern North Atlantic. Our results indicate a potential expansion of available suitable habitat in the northernmost region of the study area, with a contraction at lower latitudes, more prominent in the Portuguese archipelago of the Azores. Under the worst-case scenario (RCP 8.5), the area of suitable habitat will likely double compared to present, occupying approximately 6% of the total study area. The management and conservation of areas where *Pheronema* aggregations can occur should be articulated between different countries, particularly in the Northeast Atlantic since, cumulatively, most of *Pheronema's* climate refugia occurs within their EEZs. Nonetheless, a significant proportion of the species' climate refugia is located in areas within the High Seas (i.e., Rockall plateau).

1. Introduction

Although it is the vastest biome on Earth, the deep sea is still mostly unexplored. It hosts high and unique biodiversity, including vulnerable marine species and structural habitats, which will likely be greatly impacted by changes in global climate. Ocean warming and consequent thermal stratification will result in ocean deoxygenation, since O_2 is less soluble in warmer waters, and the reduced vertical mixing will lead to a decrease in organic matter and nutrients flux between deeper and shallower waters (Doney et al., 2012). Changes in ocean chemistry will alter carbonate cycles and lead to areas of the ocean becoming unsuited for calcifying organisms (Guinotte et al., 2006; Orr et al., 2005). These stressors will strongly influence deep-sea organisms as they can translate into changes in metabolic demands, body size, species distributions and food web composition, potentially leading to overall decrease in local biodiversity and alteration of ecosystem functions (Levin and Le Bris, 2015; Sweetman et al., 2017). However, given the exceptional conditions in the deep sea, much is unknown as to how different deep-sea

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organisms will respond to such changes.

One key component of deep-sea ecosystems are diverse and structurally complex habitats, such as coral gardens, coral reefs and sponge aggregations - that are classified as Vulnerable Marine Ecosystems (VMEs) (United Nations General Assembly, 2006). These habitats are widely acknowledged as biodiversity hotspots, but their contribution also extends to enhanced biogeochemical cycling and food supplies, and the provision of shelter and nursery grounds for other deep-sea organisms (Buhl-Mortensen et al., 2019; Ramirez-Llodra et al., 2010; Xavier et al., 2023). Given their heterogeneous, complex and often fragile structures, these habitats are particularly vulnerable to climate change and other anthropogenic stressors. Such impacts may be further exacerbated by complex interactions between climate and other stressors such as fishing and deep-sea mining (Brito-Morales et al., 2020). The species that characterise these can have limited environmental thresholds and low dispersal capability, which limits their adaptive potential to climate change, and their slow growth rates and long lifespans may hinder their capability to recover after disturbances (FAO, 2018).

Bird's nest sponge (*Pheronema carpenteri*) aggregations are among the habitats listed as VMEs (ICES, 2020). Despite little being known about the species' life-history and reproductive patterns, the aggregations it forms are structurally complex and functionally relevant to the deep-sea ecosystem. *Pheronema carpenteri* is fragile and particularly vulnerable to anthropogenic activities and climate change and, although there is no information on growth rates for the species, it is likely to have long lifespans and slow-growth rates (Hogg et al., 2010). This deep-sea glass sponge (Class Hexactinellida) is often encountered in very high densities, forming monospecific aggregations of up to 475 individuals per km^2 which can be found in regions such as the North Atlantic Ocean (Maldonado et al., 2016; Rice et al., 1990). *Pheronema carpenteri* is also known to occur across all Northeastern Atlantic from the southern Icelandic coast (Klitgaard and Tendal, 2004), across the Azores (Topsent, 1928), north of Spain and Portuguese coast, to the Moroccan coast (Barthel et al., 1996), at depths between 300 m and 3500 m (de Voogd et al., 2023). Dense aggregations of *P. carpenteri* are crucial for local ecosystem function, adding structural complexity and habitat for other species and the associated spicule mats further enhance structural complexity and shape macrobenthic and infaunal communities (Bett and Rice, 1992; Maldonado et al., 2016). It is also likely that these aggregations influence benthopelagic coupling and the marine biogeochemical cycling, serving as substantial silicon sinks as shown for other similar species (Maldonado et al., 2005).

Considering the importance and crucial role VMEs such as *P. carpenteri* aggregations play in the deep-sea, it is important to determine how they will respond in an ocean under climate change (Malhi et al., 2020). Understanding the impacts of climate change on these ecosystems will help inform better management and conservation measures. However, given the complex nature and inaccessibility of the deep sea, sampling is especially challenging and expensive, and at present remains practically impossible to derive a full understanding of deep-sea VME and benthic species distribution. Occurrence records are often incomplete and biased towards extensively explored areas, such as the Mid Atlantic Ridge and the continental shelves surrounding developed countries (Davies and Guinotte, 2011; Yesson et al., 2012). To address this, modelling methods have emerged as a useful tool to use, given their capability to predict species' distributions and suitable habitat, even from incomplete and discontinuous information. They have been widely used to predict distributions and areas of suitable habitat of several deep-sea VME species, at different scales (e.g., global habitat suitability for Scleractinians (Davies and Guinotte, 2011), octocorals (Yesson et al., 2012) and Antipatharians (Yesson et al., 2017); regional distribution of deep-sea sponges (including *P. carpenteri*) in the North Atlantic (Howell et al., 2016, 2022) and the Barents Sea (Gonzalez-Mirelis et al., 2021)). Additionally, the use of modelling approaches is especially useful since they currently represent the most feasible method to predict how some deep-sea species will respond to different climate scenarios, and forecast potential shifts in their suitable habitat and hence their distribution (Anderson et al., 2022; Beazley et al., 2021; Gasbarro et al., 2022; Morato et al., 2020).

For instance, Morato et al. (2020) predicted a reduction of more than 50% of suitable habitat for key framework-forming scleractinian corals (*Desmophyllum pertusum* - formerly *Lophelia pertusa* - and *Madrepora oculata*) and the potential disappearance of three octocoral species (*Acanella arbuscula*, *Acanthogorgia armata* and *Paragorgia arborea*) in the North Atlantic region by 2100 (under the worst-case climate change scenario, RCP 8.5). More recently, Anderson et al. (2022) predicted range shifts and decreases in suitable habitat of cold-water corals in New Zealand, and Gasbarro et al. (2022) predicted considerable reductions in *Desmophyllum pertusum* suitable habitat on the continental shelf of the southeast United States, particularly in shallower areas, leading to a deepening of the species' distribution as a response to climate change. In contrast to corals, deep-sea sponges have been emerging as potential "climate change winners''. Under two climate change scenarios (RCP 4.5 and 8.5), Beazley et al. (2021) predicted a 4-fold increase in the suitable habitat of the glass sponge *Vazella pourtalesii* in the northwest Atlantic region, with a shift to deeper waters and higher latitudes, as a response to the warming of its current habitat. Both corals and sponges play an important role in deep-sea ecosystems as habitat forming species and if current projections are true, with potential reductions of coral presence due to climate change, sponges are likely to become the main providers of habitat complexity and sustain ecosystem processes in the future (Bell et al., 2013, 2018). However, not all sponge species may be generalized as climate change winners since climatic resilience may be species specific. While some sponge species show high tolerance to ocean deoxygenation (Micaroni et al., 2022), ocean warming and acidification can negatively affect pumping capacity and skeletal formation in others (Stevenson et al., 2020). Therefore, it is important to explore how different sponge species may cope with a changing climate and ocean.

In this study, we focused on the habitat-forming glass sponge *Pheronema carpenteri* in the North Atlantic region. Using an ensemble approach that integrates Maxent, GAM and random forest models, we calculated the present day distribution of this species, and assessed which abiotic factors explain its distribution. We used a curated species occurrence dataset and a set of both static (depth, bathymetric position index, slope) and dynamic (particulate organic carbon flux to seafloor, bottom water dissolved oxygen, temperature and pH) environmental variables. We further projected how its suitable habitat may change under three climate change scenarios (RCP 2.6; RCP 4.5; RCP 8.5) across two different timeframes, near future (2041–2060) and far future (2081–2100). We identified areas of climate refugia and our findings are discussed considering the governance of marine resources within each country's Exclusive Economic Zone, to assess management strategies and potential conservation efforts for *P. carpenteri* in the face of responses to climate change.

2. Materials and methods

2.1. Study area, occurrence and pseudo-absence data

Observation records of *Pheronema carpenteri* in the North Atlantic were collected from diverse sources including taxonomic and ecological literature, information available from scientific expeditions of authors' collaborators, as well as online databases such as the ICES Vulnerable Marine Ecosystems data portal (ICES, 2022) and the Ocean Biodiversity Information System (OBIS, 2022). Searches were constrained to the species name *Pheronema carpenteri* and included *Pheronema grayi* as it has been shown to constitute a junior synonym of the same species (Reiswig and Champagne, 1995). Additionally, search was constrained to the geographical extent used in this study (North Atlantic, see Fig. 1). Each dataset was carefully inspected for duplicated records (i.e., same geographical position reported), which were considered as only one

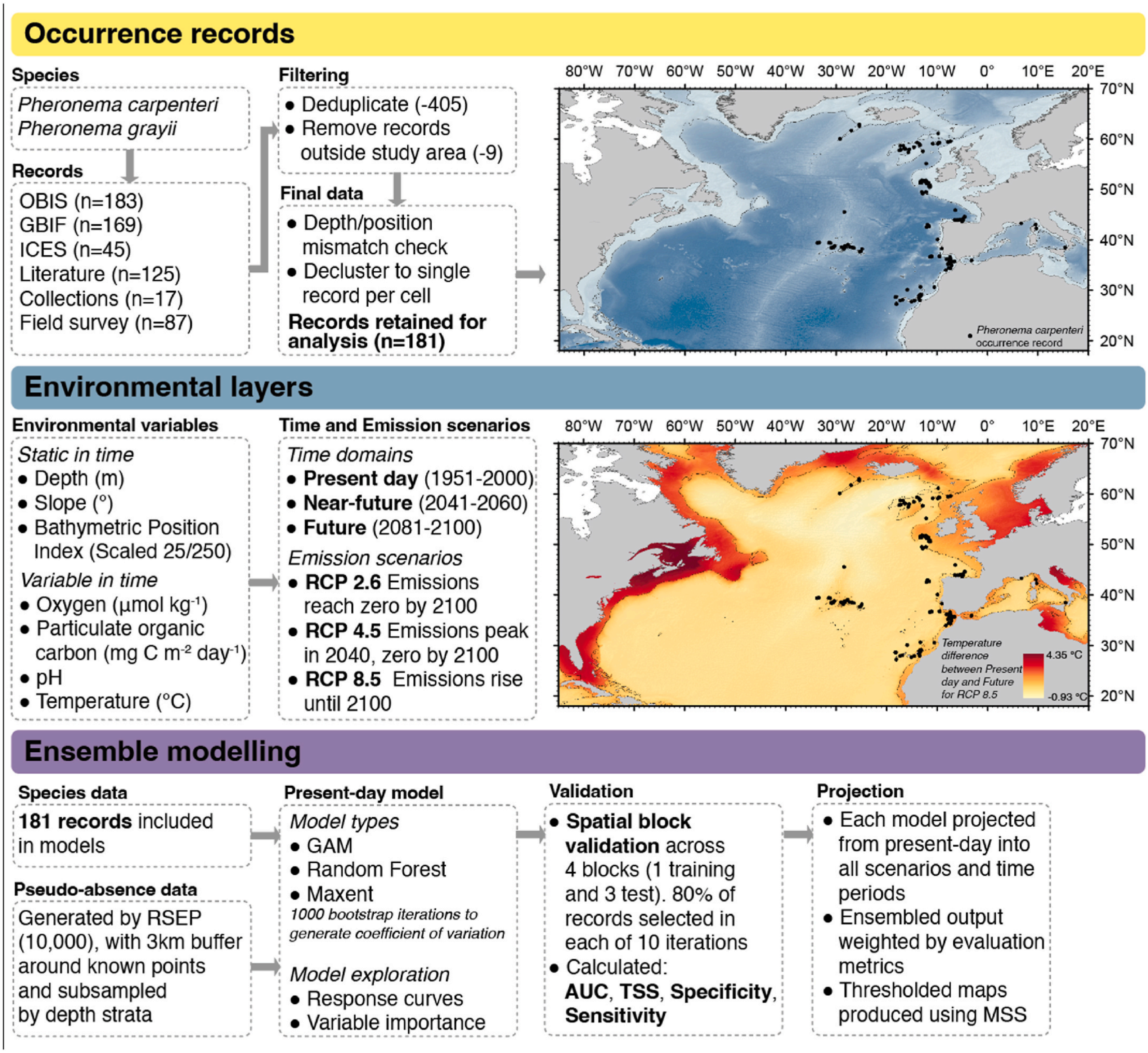


Fig. 1. Diagram of occurrence data selection, environmental layers and ensemble modelling approach, study area and final occurrence points included in models.

record in this study. From a total of 626 records, the final dataset totalled 212 deduplicated occurrence records (Fig. 1, Table S2, Supp. Material). To prevent potential mismatches of the occurrence records' spatial position, when available, depth values reported for the occurrence points were compared with the ones extracted from the depth raster layer used in this study. Occurrence points for which the depth values differed by more than 30% (sampled depth vs. depth layer) were excluded from the occurrence dataset. Additionally, occurrence points were reduced to one occurrence per 9 km^2 grid cell (declustering) to reduce the influence of sampling intensity on resulting models. The final dataset totalled 181 occurrence points (Fig. 1).

Many modelling approaches require information on presence-absence data, where presence and absence are the confirmed points of occurrence or non-occurrence of a species, respectively. With deep-sea species it is not common to have true absence points since exhaustive sampling throughout a study area would be needed to confirm true absence. In addition, the vast majority of deep-sea studies are focused on specific species of interest, rather than providing objective sampling of a given geographical region. Therefore, instead of considering a presence-absence matrix for modelling, we utilized a presence-(pseudo)absence approach, where pseudo-absence points are simulated and extracted from the study area or 'background' (Barbet-Massin et al., 2012). The method used to generate pseudo-absences can strongly influence model outputs, with some considering environmental profiles (e.g., RSEP - *Random Sampling with Environmental Restriction* or TS - *Three-step selection*) or not (e.g., RS - *Random Sampling*). RSEP has been shown to obtain higher model performance (i.e., higher AUC) and more reliable suitability maps (Iturbide et al., 2015, 2018; Morato et al., 2020). In this study pseudo-absence points were generated using the *mopa* R package, applying the RSEP method for pseudo-absence generation (Iturbide et al., 2015, 2018). First, the OCSVMprofiling function was used to profile the environmental range of the background based on the presence data and define the geographic region from which to sample pseudo-absence points. A total of 10,000 pseudo-absence points were then randomly generated in the region previously defined, considering an exclusion buffer of 3 km around the occurrence points. Finally, the pseudo-absence points were randomly subsampled by depth strata based on the proportion of all public records of Porifera from the OBIS database to further constrain the pseudo-absence points into regions where sampling and detection of sponge species was conducted.

2.2. Environmental data

Environmental predictors consisted of two types of predictor variables - terrain and environmental - that are static and variable through time, respectively (Morato et al., 2020; Sweetman et al., 2017) (Fig. 1). All predictor variables were rescaled to a 3 × 3 km resolution and projected with an Albers equal-area conical projection centred in the middle of the study region. Static variables included depth, which was extracted from a bathymetric grid built from a bilinear interpolation from the 2014 GEBCO grid and 2018 EMODnet Digital Bathymetry. The Bathymetric Position Index (BPI) was computed using the Benthic Terrain Model 3.0 tool in ArcGIS with an inner radius of 3 and an outer radius of 25 grid cells (Walbridge et al., 2018; Morato et al., 2020) and to avoid extreme values, this variable was then standardised using the scale function in R *Raster* package (Hijmans, 2021). An additional terrain variable (slope) was created in the same R package using the function terrain. Yearly average values from four environmental variables were obtained from models developed during the Coupled Model Intercomparison Project Phase 5 (CMIP5) (GFDL-ESM-2G; (Dunne et al., 2012), IPSL-CM5A-MR; (Dufresne et al., 2013), MPI-ESM-MR; (Giorgetta et al., 2013). These included particulate organic carbon (POC) flux to seafloor (mg C m^{-2} day^{-1}), bottom water dissolved oxygen (μmol kg^{-1}), temperature (°C), and pH. POC flux was extracted and converted to export POC flux at the seafloor using the Martin curve (Martin et al., 1987), as reported in Morato et al. (2020). Each variable was selected based on their biological relevance for *P. carpenteri* as well as being available from the CMIP5 models.

All environmental variables were considered for three different emission scenarios, corresponding to the Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5 to cover a range of different potential climate responses (Stocker et al., 2013). RCP 2.6 is the most restrictive emission scenario, representing considerable efforts to reduce emissions to zero by 2100, with projections of global temperature increasing by ~1 °C and sea level rise ~0.4 m. In the intermediate scenario (RCP 4.5), emissions peak in 2040, then decline until 2100. In this scenario, global temperature and sea level are expected to rise by ~1.8 °C and ~0.47 m, respectively. The third scenario (RCP 8.5) is considered the worst-case scenario, where no mitigation efforts are made, and emissions continue to rise until 2100. This represents an increase in global temperature by ~3.7 °C and in sea level of ~0.63 m. Three different timeframes were considered for each RCP namely, present day (1951–2000), near future (2041–2060) and far future (2081–2100). Collinearity between predictor variables was assessed through Spearman correlation coefficient and Variance Inflation Factor (VIF). Variables were considered correlated if Spearman correlation coefficient >0.85 or VIF >10 (see Table S3, Supp. Material). All variables were kept for further analysis since none were correlated.

2.3. Ensemble modelling, evaluation and projections

An ensemble modelling approach was adopted for this study following its use in previous studies to predict species distributions and habitat suitability in the deep sea (Beazley et al., 2021; Georgian et al., 2019; Matos et al., 2021; Morato et al., 2020). Moreover, ensemble approaches have been shown to improve accuracy and predictive power since single models can have high variance and be highly dependent on the input data, possibly compromising predictive capability when used for climate change projections (Araújo and New, 2007). Three different modelling methods were used: maximum entropy (*Maxent* (Phillips et al., 2017, 2004););); Generalized Additive Models (*GAM* (Hastie and Tibshirani, 1986);); and random forest (*rf* (Breiman, 2001);) following the approaches described by (Morato et al., 2020). Both Maxent and random forest are machine-learning methods based on maximum entropy and bagging approaches, respectively, while GAM is a commonly used generalized linear modelling approach (see Guisan et al., 2017 for more details on each method).

In brief, MaxEnt models were created using the function maxent in the R package *dismo* (Hijmans et al., 2017). Experimental testing of model settings, including the regularization parameter (β) did not improve the performance of preliminary models, so default settings were used and have been shown to perform well in previous studies (convergent threshold $= 10^{-5}$, $\beta = 1$, all feature types allowed) (Phillips and Dudík, 2008). Prevalence was set as the proportion of occurrences over pseudo-absences, as per Morato et al. (2020). Random Forest regression models were computed using the *randomForest* R package and function of the same name (Liaw and Wiener, 2002) with default parameters and 500 trees. Various parameters were investigated in preliminary models, with a value of 4 selected for the parameter 'mtry' as it improved model performance, whereas no improvement was detected when modifying the number or depth of trees. No variable selection was undertaken for Maxent or RandomForest, with all variables retained. GAMs were constructed using the gam function in the R package *mgcv* (Wood, 2011), with a smoothing degree of 4 ($k = 4$) selected after experimental testing of preliminary models for all variables. The final GAM model was selected based on the Akaike Information Criterion (AIC) using the function dredge from the R package *MuMIn* (Bartoń, 2023), and included the variables BPI, depth, POC flux to seafloor, dissolved oxygen, slope and temperature. The contribution of each environmental variable to the predictions was assessed using a randomization procedure adapted by Morato et al. (2020) from Thuiller et al. (2009), which computes the Pearson correlation between the original predictions and predictions where the variable under evaluation was randomly permutated. The operation was repeated 10 times for each combination of model, variable and species. This procedure allowed for direct comparison between models since it estimated the importance of each variable independently of the model used. In order to provide intuitive values of variable importance, where higher values indicate higher importance, results are reported as 1-Pearson correlation.

As described by Elith et al. (2006), response curves were generated to assess the relationship between predicted habitat suitability and each predictor variable, both terrain and environmental (see Fig. S1, Supp. Material). Performance of present day models was evaluated using a cross-validation method based on a random "block" selection of training and testing data, which was implemented using the get. block function of the *EnMEVAL* package in R (Guinotte and Davies, 2014; Muscarella et al., 2014). The study area was divided in four subareas, each with a similar number of occurrence points. Three of the subareas were used as training datasets and one as test dataset, with a random selection of 80% of data in each iteration to avoid selecting the same data in different block iterations (Morato et al., 2020). This process was repeated across 10 validation iterations, with four different statistical metrics used to assess model performance: area under the curve (AUC) of the receiving operating characteristic, specificity, sensitivity and true skill statistic (TSS). In brief, the AUC refers to the ability of the model to identify between occupied and unoccupied sites, with values close to 1 indicating strong predictive capacity and values < 0.5 indicating a performance worse than random. Specificity and sensitivity refer to the model's ability to predict absences (true negative rate) and presences (true positive rate), respectively. TSS combines sensitivity and specificity to provide an overall assessment of model performance with values ranging from −1 to 1, with 1 indicating perfect prediction and values $<$ 0 indicating the model performed worse than random. For a more detailed description of these statistical metrics, see Fielding and Bell (1997), Allouche et al. (2006) and Guisan et al. (2017).

Each model was then used to project a relative index of habitat suitability (HSI) across the study area for present day (1951–2000) and for each of the climatic scenarios (RCP 2.6, RCP 4.5, RCP 8.5) in the near future (2041–2060) and far future (2081–2100). Uncertainty of each model was computed by bootstrapping with 1000 iterations and the coefficient of variation (CV) of the bootstrap output calculated for each modelling approach and projection (see Fig. S4, Supp. Material). Ensemble HSI and uncertainty were computed for all periods and climatic scenarios by calculating the average of all indexes by grid cell after weighting the outputs of the three models with the evaluation metrics AUC and TSS (Rowden et al., 2017). Ensemble model performance validation used the same methods as the individual models. To generate binary outputs, the maximum sensitivity and specificity (MSS) threshold was applied to HSI values as per Morato et al. (2020) and Tong et al. (2023), defining suitable habitat areas (above threshold) and unsuitable habitat areas (below threshold) for all scenarios. Finally, the degree of extrapolation from the present day environmental conditions that *P. carpenteri* occupies was assessed using the extrapolation detection tool, compute_extrapolation, from the *dsmextra* R package (see Fig. S5, Supp. Material) (Bouchet et al., 2020).

2.4. *Governance and management tools*

For each grid cell within the study area, the latitude and depth of each grid cell, along with the value for the ensemble habitat suitability index for each time period and scenario was extracted to explore how habitat suitability may change through space. Additionally, information on which Exclusive Economic Zone (EEZ) each grid cell occupied was extracted from available EEZ data (Flanders Marine Institute, 2023). Grid cells that fell outside Exclusive Economic Zones were defined as “High Seas”, and only cells corresponding to potentially suitable habitat were considered. The proportion (%) of suitable habitat within each EEZ for each scenario was calculated considering the total predicted habitat for present day and relative to that of each of the scenarios. Climate refugia was considered as suitable habitat areas that were common to the present day and all six scenarios. To simplify interpretation of results, countries with less than 1% suitable habitat within their EEZ’s for present day or at least one of the projected scenarios were pooled and the proportion of suitable habitat considered collectively (under “Other”).

3. Results

3.1. *Model performance and variable importance*

Overall, the three modelling approaches and the final ensemble model performed well (AUC, 0.89–0.94; TSS, 0.69–0.87) and capably predicted presences (i.e., sensitivity) and pseudo-absences (i.e., specificity) (Table 1). Relative variable importance for each model and the ensemble model predictions was calculated as 1-Pearson correlation. Depth was the environmental variable that contributed the most for all models, as well as within the ensemble approach (0.68). Temperature was also one of the top three variables contributing the most to all models (temperature importance between 0.42 and 0.45), and dissolved oxygen was one of the three variables contributing the most to GAM (0.52), rf (0.40) and the ensemble approach (0.43). Particulate organic carbon was among the top three environmental variables only for Maxent (0.41). The three remaining predictor variables (BPI, slope, pH) all contributed less than 0.07 to all models, and pH did not contribute to the GAM model (0.00) (see Table S4, Supp. Material).

Table 1
Summary of individual and ensemble model performance statistics. Statistical metrics considered were area under the curve (AUC) of the receiver operating characteristic; true skill statistic (TSS); sensitivity and specificity. Statistics were calculated using the maximum sensitivity and specificity (MSS) prediction threshold. Each metric is presented as the mean of 10 iterations and associated standard deviation (mean ± SD).

	AUC	TSS	Sensitivity	Specificity
Maxent	0.93 ± 0.04	0.78 ± 0.09	0.88 ± 0.05	0.90 ± 0.06
GAM	0.93 ± 0.02	0.77 ± 0.06	0.86 ± 0.05	0.91 ± 0.08
rf	0.89 ± 0.03	0.69 ± 0.11	0.79 ± 0.11	0.56 ± 0.19
Ensemble	0.94 ± 0.03	0.87 ± 0.06	0.87 ± 0.05	0.74 ± 0.08

3.2. *Predictions and projections*

Relative likelihood of occurrence and habitat suitability areas were projected for present day and for all the scenarios and time periods across the study area. *P. carpenteri* was predicted to likely occur in the present day mainly within the East Atlantic Area, from Morocco, along the European continental margin and some offshore seamounts (i.e., Rockall and Hatton Bank), as well as on the Azores archipelago. Most areas predicted as suitable for present day show suitability indices between 0.4 and 0.8, while the area with the highest suitability index (HSI >0.8, in red) was on the Porcupine Seabight, off the west coast of Ireland. And although no occurrences have been recorded for the area, suitable habitat was also predicted to exist in the West Atlantic area, off the east coast of the United States and Canada (Fig. 2).

Based on the ensemble model output, in all three climate change scenarios (RCP 2.6, 4.5 and 8.5) both in the near future (2041–2060) and far future (2081–2100), it was projected that areas in the northernmost region of the study area might represent suitable habitat for *Pheronema carpenteri*, namely on the Rockall Plateau area, along the Reykjanes Ridge (south of Iceland), and also at higher latitudes of the West Atlantic area, particularly on the Grand Banks and Flemish Cap off the coast of Canada, extending northwards along the Labrador Basin. However, suitability indices were lower (~0.2–0.6) when compared to present day, particularly in the Rockall Plateau area and on the southern coast of Ireland, where highly suitable (HSI >0.6) habitat was projected for present day. Considering the “worst-case” scenario (RCP 8.5) projections in the far future, *P. carpenteri* is likely to occur across higher latitudes of the study area (e.g., Iceland basin). Under this same scenario, a substantial reduction, of more than 75%, of suitable habitat is likely to occur on the Azores archipelago, with only small areas of suitable habitat remaining on offshore seamounts (HSI <0.4) (Fig. 2).

Similar patterns are more evident in the generated binary maps, for which a threshold of 0.16 (MSS) was considered. Projections above this threshold were considered as suitable habitat and below were considered as unsuitable habitat for *Pheronema carpenteri* (Fig. 3). Present day projections of suitable habitat represented 634,833 km^2 (equivalent to 3.11%) of the total study area (20,435,733 km^2) and projections for the different scenarios showed an estimated increase of suitable habitat between 0.75% (RCP 2.6, near future) and 1.41% (RCP 8.5, near future) (see Table S5, Supp. Material). Projections for the “worst-case” scenario of climate change (RCP 8.5) in the far future corresponded to 6.08% of the total study area considered as suitable habitat for *P. carpenteri*. This represents a potential 2-fold increase of suitable habitat in far future projections (Fig. 3).

Present day showed a latitudinal distribution of suitable habitat with two peaks, at approximately 37 and 57° N, resembling a bimodal distribution (Fig. 4A). For near future (2041–2060) and far future (2081–2100) scenarios, less available suitable habitat was projected at lower latitudes, in comparison to present day and a shift towards higher latitudes was noticeable. This was particularly evident in the “worst-case” scenario (RCP 8.5) for the far future (Fig. 4A). The projected suitable habitat across the depth gradient resembled a normal distribution for present day with mean value of 1480 m depth (Fig. 4B) (see also Table S6, Supp. Material). Projections for the near future and far future reveal a greater spreading of suitable habitat available across the depth range, with minimal shallowing of the mean depth (1335–1396 m). As in the latitudinal distribution, this pattern is more prominent in

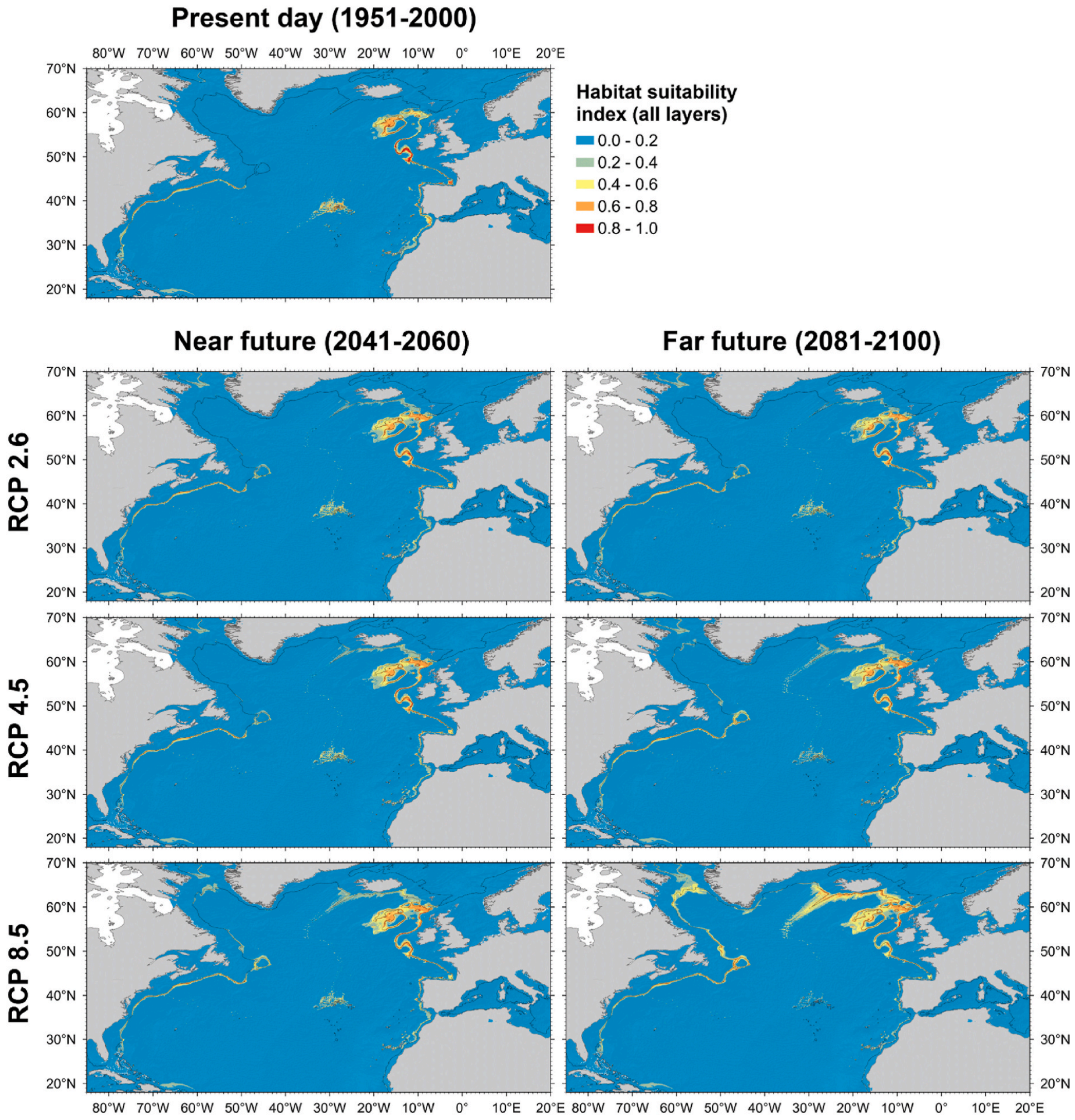


Fig. 2. Relative likelihood of occurrence, resulting from the ensemble model, of *Pheronema carpenteri* under present day and representative concentration pathways RCP 2.6, RCP 4.5, RCP 8.5 under near future (2041–2060) and far future (2081–2100) climatic conditions.

the “worst-case” scenario of climate change (RCP 8.5) in the far future (Fig. 4B).

3.3. Management and conservation

Climate refugia was considered as the areas for which suitable habitat was projected in present day, near future and far future for all the different scenarios (Fig. 5). A total of 44 autonomous territories/countries are likely to contain suitable habitat for *P. carpenteri* (see Table S8, Supp. Material). Of those, 13 autonomous territories/countries had more than 1% of the species’ suitable habitat for at least one of the scenarios – Portugal, Ireland, United Kingdom, United States of America, Spain, Canada, Morocco, Faroe Islands, France, Bahamas, Iceland, Greenland, Norway. The remaining 31 autonomous territories/countries were categorized as “Other” and represented only between 2% and 3.6% of the total potential suitable habitat for *Pheronema carpenteri* across all scenarios. Suitable habitat areas that did not fall into any EEZ were considered as High Seas which, depending on the scenario, represented between 22.2% and 24.2% of the species’ total potential suitable habitat. For present day, most of the suitable habitat within EEZs fell within the Portuguese EEZ (15.6%), followed by Ireland (11.3%), United Kingdom (10.4%), United States of America (10.1%), Spain (6.9%), Canada (6.5%) and Morocco (5.0%). All the other autonomous territories/countries considered had less than 3% of suitable habitat falling within their EEZ for present day. Under the different scenarios of climate change, suitable habitat is projected to decrease in EEZs at lower latitudes (e.g., Morocco, Portugal, Spain) and increase in EEZs at higher latitudes (e.g., Greenland, Faroe Islands, Iceland). Once again, these differences were more prominent in projections into the far future (2081–2100) of the RCP 8.5, where potential suitable habitat could decrease up to 3.8% (Portugal) and increases could be up to 14.7% (Iceland) in comparison to present day. Climate refugia for *P. carpenteri* is likely to occur mainly (47.8%) within northeastern Atlantic EEZs (Morocco, Portugal, Spain, France, Ireland and United Kingdom), although 25.4% is likely contained within the High Seas (Fig. 5).

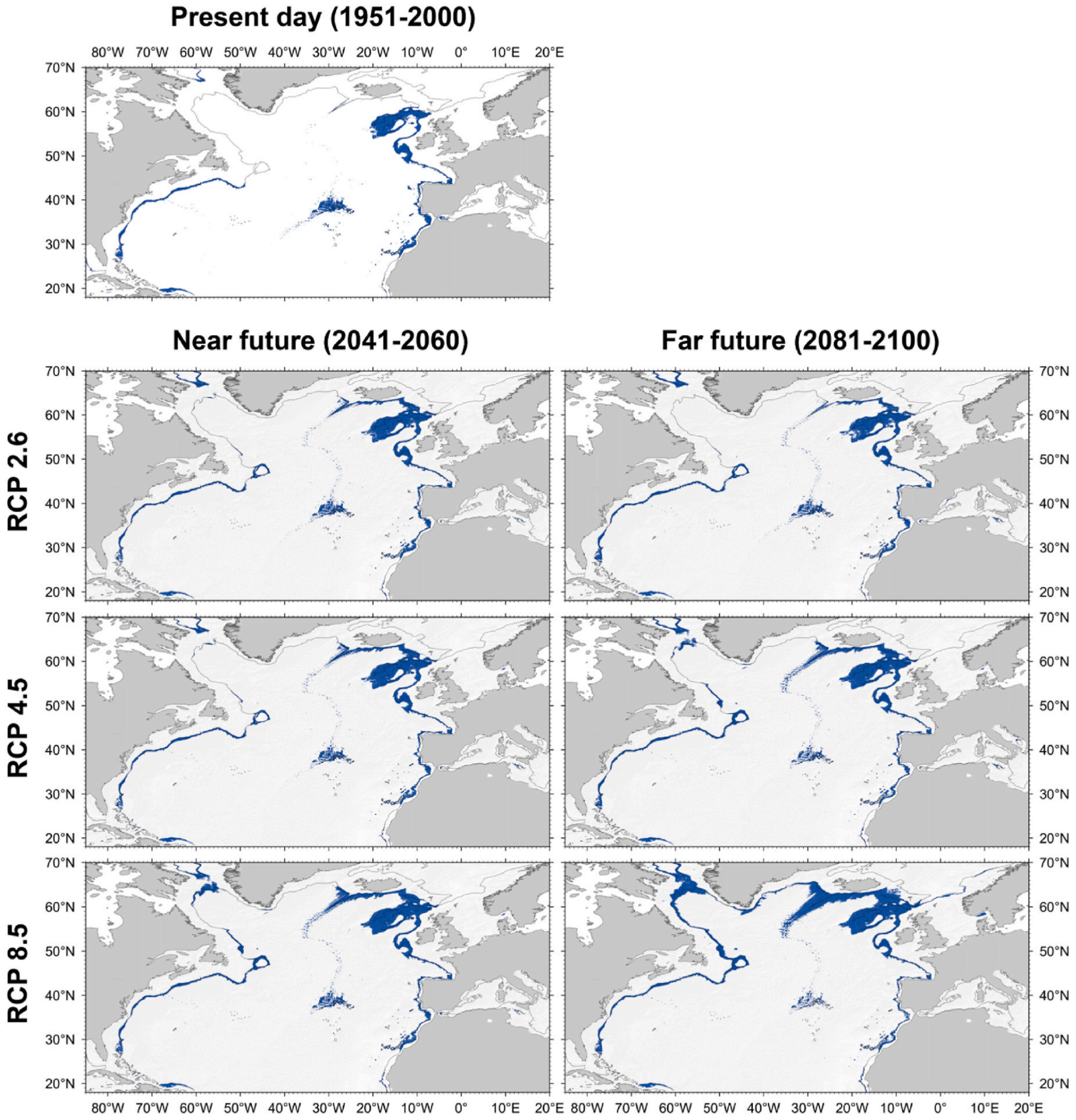


Fig. 3. *Pheronema carpenteri* suitable habitat (in blue) predicted for present day and projected for three representative concentration pathways (RCP 2.6, 4.5 and 8.5) in near future (2041–2060) and far future (2081–2100) climatic conditions. Suitability converted to binary maps using maximum sensitivity and specificity (MSS) threshold of 0.16.

4. Discussion

Under several IPCC climate scenarios that projected ocean conditions to the near future (2041–2060) and far future (2081–2100), ensemble habitat suitability models suggest an increase in the extent of potential suitable habitat for a key habitat-forming glass sponge, *Pheronema carpenteri*, in the North Atlantic Ocean relative to models for the present day. Our projections for present day habitat suitability show that approximately 3% of the study area, i.e., ~634,833 km^2, may be able to support the occurrence of *P. carpenteri*. Simulations under all scenarios of climate change both in the near and far future, indicate an increase in area of suitable habitat nearly doubling to approximately 6%, i.e., 1,243,350 km^2, with the "worst-case" scenario (RCP 8.5, far future). These increases are expected to occur largely in the northern North Atlantic, with a range contraction at lower latitudes, particularly in the Portuguese archipelago of the Azores. Similar patterns of poleward expansion in response to climate change has been hypothesized for several other deep-sea species including glass sponges (Beazley et al., 2021) and some fish species (Morato et al., 2020) in the North Atlantic, following climatic changes predicted for the deep-sea environment (Sweetman et al., 2017).

4.1. Environmental drivers of Pheronema carpenteri distribution

Present day distribution of *Pheronema carpenteri* was found to be largely driven by depth and temperature, which is consistent with previous studies for this species in the Northeast Atlantic (Graves et al., 2022; Howell et al., 2016, 2022). Dissolved oxygen and POC flux were also important explanatory variables for the ensemble model and present day distribution of the species. Our present day projections span over a bathymetric range with a mean of 1480 m, which is approximately 300 m deeper to what was found previously (mean = 1191 m, Howell et al., 2016). Information on individual sponge species thermal tolerances is extremely scarce and does not exist for *P. carpenteri*. In this

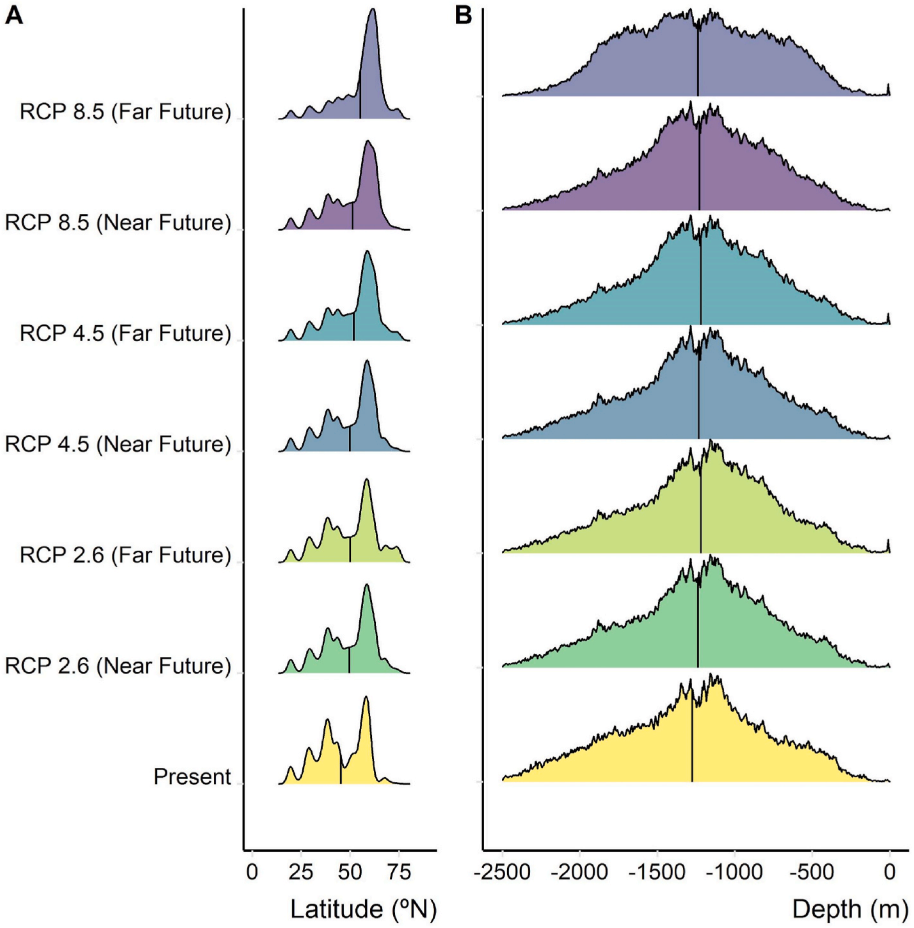
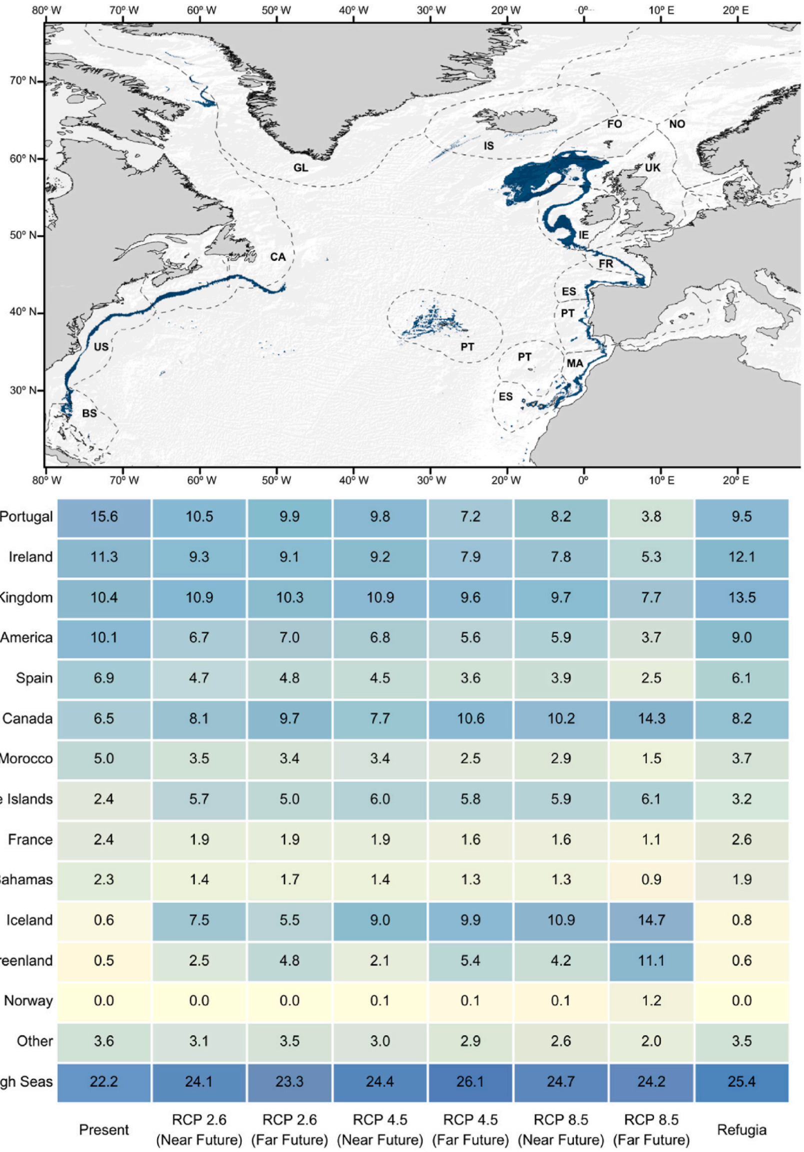


Fig. 4. Latitude and depth variation across the different scenarios. Lines represent mean values of latitude and depth.

study, the species was found over a temperature range between 1.85 and 13.95 °C (mean = 6.65 °C), which is narrower and with a slightly higher mean than found in the study by Howell et al. (2016) (2.73–20.9 °C, mean = 5.17 °C). Particulate organic carbon, i.e., microbial cells, detritus and other aggregated material, is an important source of nutrition for sponges in general. In our study, *Pheronema* was present over a wide POC range from 0.19 to 60.4 mg C m^{-2} day^{-1} (mean = 8.71 mg C m^{-2} day^{-1}), rather similar to those observed in the water masses present in the North Atlantic between 1000 and 2000 m depth (between 0.8 and 33; mean = 7.6 mg C m^{-2} day^{-1}, Puerta et al., 2020). While we lack information regarding the trophic ecology of *Pheronema*, recent *in-* and *ex-situ* experiments performed on other deep-sea habitat-forming hexactinellids (*Aphrocallistes vastus* and *Rhabdocalyptus dawsoni*) have shown that these exhibit high grazing rates, consuming vast amounts of POC from both terrestrial and oceanic sources as well as tidally-resuspended sediment (Kahn et al., 2015, 2018; Yahel et al., 2007). Dissolved oxygen was also revealed as an important environmental driver for the present day distribution of *Pheronema* which was found to occur across a rather low dissolved oxygen range of 0.13–0.29 μmol kg^{-1} (mean 0.25 μmol kg^{-1}). Leys and Kahn (2018) have shown that compared to demosponges, glass sponges exhibit rather low oxygen needs, and can even tolerate hypoxia by reducing feeding activity through halting of water filtering.

Considering that several of the environmental drivers contributing the most to the ensemble model are also those that characterise water masses (e.g., temperature, dissolved oxygen), we hypothesize that the Mediterranean Outflow Water (MOW), a saline and warm water mass, is likely to contribute to the shaping of *P. carpenteri* distribution patterns in the North Atlantic. The distribution of *P. carpenteri* along the slope of the European and Northwest African margins coincides with the occurrence of this water mass, which exits the Mediterranean basin through the Strait of Gibraltar and spreads into the North Atlantic both northwards along the Western European slope (towards the Porcupine Bank and Rockall Trough), southwards along the African slope (at least as South as the Canary islands), and westwards towards the Azores plateau (Bashmachnikov et al., 2015; Liu and Tanhua, 2021; Pascual-Collar et al., 2019). This water mass has more influence at depths between 700 and 1500 m (Bashmachnikov et al., 2015), which coincides with the known bathymetric range of *P. carpenteri*. The influence of water masses in *P. carpenteri* distribution has been hypothesized in other studies, which attributed a restricted bathymetric distribution to the spatial distribution of water masses on the continental slope (Barthel et al., 1996). Moreover, the MOW was previously related to the occurrence of *P. carpenteri* in different locations in the Northeast Atlantic, further supporting this hypothesis (Puerta et al., 2022; Sitjà et al., 2019; Somoza et al., 2021).

Although no statistical correlation was found between the variables used in our model, it is important to acknowledge that depth can serve as a proxy for several environmental variables (e.g., temperature, food supply, dissolved nutrients). It is likely that there are other environmental variables possibly relevant for the species that were not considered in this study due to lack of high-resolution data, such as substrate type. *P. carpenteri* occurs mainly in soft muddy sediments (Barthel et al., 1996; Sitjà et al., 2019), although it can also occur associated with rocky substrate in the Azores (Creemers et al., 2019). As *P. carpenteri* is a glass sponge, with a siliceous skeleton, it would be expected that silicate would also be an important predictor of the species' distribution. However, incorporation of silicate into the present day



	Present	RCP 2.6 (Near Future)	RCP 2.6 (Far Future)	RCP 4.5 (Near Future)	RCP 4.5 (Far Future)	RCP 8.5 (Near Future)	RCP 8.5 (Far Future)	Refugia
Portugal	15.6	10.5	9.9	9.8	7.2	8.2	3.8	9.5
Ireland	11.3	9.3	9.1	9.2	7.9	7.8	5.3	12.1
United Kingdom	10.4	10.9	10.3	10.9	9.6	9.7	7.7	13.5
United States of America	10.1	6.7	7.0	6.8	5.6	5.9	3.7	9.0
Spain	6.9	4.7	4.8	4.5	3.6	3.9	2.5	6.1
Canada	6.5	8.1	9.7	7.7	10.6	10.2	14.3	8.2
Morocco	5.0	3.5	3.4	3.4	2.5	2.9	1.5	3.7
Faroe Islands	2.4	5.7	5.0	6.0	5.8	5.9	6.1	3.2
France	2.4	1.9	1.9	1.9	1.6	1.6	1.1	2.6
Bahamas	2.3	1.4	1.7	1.4	1.3	1.3	0.9	1.9
Iceland	0.6	7.5	5.5	9.0	9.9	10.9	14.7	0.8
Greenland	0.5	2.5	4.8	2.1	5.4	4.2	11.1	0.6
Norway	0.0	0.0	0.0	0.1	0.1	0.1	1.2	0.0
Other	3.6	3.1	3.5	3.0	2.9	2.6	2.0	3.5
High Seas	22.2	24.1	23.3	24.4	26.1	24.7	24.2	25.4

Fig. 5. *Pheronema carpenteri* climate refugia areas, considering present and future habitat suitability, expressed as percentage of suitable habitat within each EEZ, for autonomous regions/countries with more than 1% of suitable habitat for at least one of the scenarios, and the High Seas. Dashed lines represent the EEZs (200 nm), and country codes follow the ISO international standard.

model found that its importance was relatively low compared to the other environmental variables considered, corroborating the findings in previous distribution models developed for this species (Howell et al., 2016, 2022). In fact, a recent study has shown that the physiological processes involved in the biosilicification of different classes of sponges is different, highlighting just how complex and not fully understood this process is (Shimizu et al., 2024).

4.2. Potential future distribution of Pheronema carpenteri in a changing ocean

Our projections indicate an overall increase in area of suitable habitat under all scenarios of climate change both in the near and far future. Under the "worst-case" scenario (RCP 8.5, far future), suitable habitat available in the study area may double to approximately 6%, i.e., 1,243,350 km^2 in comparison to present day. These increases are expected to occur largely in the northern North Atlantic. However, under climate change there might be a range contraction at lower latitudes, particularly in the Portuguese archipelago of the Azores, which is more evident under the "worst-case" scenario.

Although the prospect of suitable habitat expansion under climate change seems optimistic, interpreting the ability of *P. carpenteri* to occupy the areas that are likely to represent suitable habitat under near and far future conditions can be challenging since there are significant knowledge gaps about the life history, growth rate and ecology of *P. carpenteri*. Little is known about the reproductive ecology of glass sponges, but the few studies available suggest that these may be hermaphroditic and viviparous, producing lecithotrophic larvae able to disperse for a relatively short period of time, between a few hours and 1–2 weeks, before settlement (Leys et al., 2007; Riesgo et al., 2013). These characteristics make it unlikely that *Pheronema* larvae would disperse over large distances, suggesting that recruitment is likely to occur at relatively small spatial scales. In fact, dispersal simulations along the Irish and UK coast, which corresponds to the northern range of the current known *P. carpenteri* distribution, suggest that the species is potentially divided in several different metapopulations that are unable to support each other due to a lack of physical connection (Ross et al., 2019). Such a disconnect between different regions would likely hinder the capability of this species to disperse into potentially newly suitable areas, unless there are climate-related changes in oceanic currents and conditions at the seafloor, for instance around Iceland, that may transition to suitable habitat by 2041–2060 under all tested climate scenarios.

Considering the study region, our model suggests that there are areas of suitable habitat on the Atlantic coasts of the USA and Canada, both in the present day and projected for all climate scenarios and timeframes. However, no currently known occurrences have been confirmed for that area. This may indicate the presence of biophysical barriers such as water masses that have shaped the predominantly eastern Atlantic longitudinal distribution of the species (Puerta et al., 2020). Many of the areas that may become suitable for *P. carpenteri* in the future are currently occupied by other sponge species, such as those that form multi-specific aggregations (i.e., *Geodia*/ostur aggregations) (Howell et al., 2016). It is possible that the expansion of *P. carpenteri* into newly suitable areas may be restricted by established communities due to competition for space by other species, but conversely, changing conditions may also alter the distribution of competing species. However, there is a significant lack of information on the competitive dynamics of deep-sea species, particularly for sponges, that make further interpretation speculative. To further explore this, the development of additional models under similar scenarios for multiple habitat-forming sponge species would help determine whether areas of future suitable habitat for *P. carpenteri* would remain suitable for potential competitors.

Similar to previous studies, temperature was one of the most important environmental variables in our models for *P. carpenteri* (Graves et al., 2022; Howell et al., 2016), and projected latitudinal shifts are likely due to warming waters. Sweetman et al. (2017) suggested that the areas where multi-specific aggregations occur at present, particularly in the northern latitudes of the Atlantic Ocean, are expected to experience the greatest changes in environmental conditions at the seafloor (i.e., in temperature, pH and dissolved oxygen) by 2100. Temperature has been identified has one of the most important environmental variables shaping ostur and *Geodia* species distribution in the NE Atlantic (Howell et al., 2016) and projected changes under climate change can be beyond the tolerance of *Geodia* and other ostur species, possibly leading to a contraction of their suitable habitat, which may translate into available niche for *Pheronema* to colonize. However, this potential shift in species composition at higher latitudes would possibly result in a loss of sponge and associated species biodiversity in these areas, given the mono- vs multi-specific nature of the aggregations formed by *P. carpenteri* and those found in the boreo-Arctic, respectively.

Projections to near and far future also show that suitable habitat may expand across the bathymetric range of this species, although mean and median depth values of suitable habitat were somewhat similar over the different projected scenarios (~1400 m for projected scenarios vs ~1480 m for the present day). It is likely that more suitable habitat will become available both in deeper and shallower waters, which is particularly evident in the “worst-case” scenario (RCP 8.5). Nevertheless, and although projected maximum depths can go down to more than 4000 m depth (RCP 8.5, far future), it has been previously observed that *P. carpenteri* occurs in restricted bathymetric ranges (Barthel et al., 1996; Rice et al., 1990), and it is likely that this will be the case for the different projected scenarios, with half of projected suitable habitat comprised between 900 m and 1600 m depth. Compared to present day, it appears that a slight shallowing of this bathymetric range is likely to occur (i.e., 50% predicted suitable habitat for present is between 960 m and 1676 m depth while 50% of projected suitable habitat for the worst-case scenario in the far future lies between 881 m and 1616 m depth). The projected slight shallowing of the range could be explained by the effect of environmental factors such as internal tidal waves and water masses. Barthel et al. (1996) observed a successional phenomenon where small specimens, which were thought to be population recruits, were found upper slope from dead and larger/older individuals on the continental slope off Morocco. The authors attributed this phenomenon to internal tidal waves in the area, which influences the resuspension of organic matter and food supply, causing this upslope movement to areas with better food supply. Additionally, and assuming the hypothesis that *Pheronema*’s distribution could be shaped by the MOW water mass, it would be expected that any changes in temperature or velocity of this water mass could also directly impact *Pheronema*’s distribution in the future (García-Lafuente et al., 2021).

4.3. Potential and limitations of distribution modelling

Species distribution models represent a valuable tool to predict deep-sea species distributions and assess potential vulnerability or resilience to climatic pressures. For species with such a knowledge gap, that little is known about their life-history and reproduction, interpretation of model outputs can be challenging and should be considered carefully. The choice of an ensemble approach was based on improved accuracy and predictive power, since the use of single modelling approaches can compromise predictive capability when used for climate change projections (Araújo and New, 2007). This approach has been successfully used previously for deep-sea organisms (Georgian et al., 2019; Matos et al., 2021; Morato et al., 2020). The choice of environmental drivers considered in the ensemble model were based on availability and biological relevance for the species. However, it is likely that there are other environmental variables such as substrate type, current speed, or dissolved organic matter (DOM), possibly relevant for *P. carpenteri* that were not considered in this study.

Other sources of uncertainty that can affect model outputs are the number occurrence records, which for deep-sea sponges is relatively small compared to other invertebrate (e.g., corals) and vertebrate (e.g., fish) taxa. More occurrence records would make the ensemble model more robust and likely improve its predictive capability. Nevertheless, and considering the challenges of sampling in the deep-sea, the dataset used in our study represents the most complete dataset for *Pheronema carpenteri* in the North Atlantic. Also, global IPCC climate models have associated uncertainties which are propagated to species distribution models that use them. As global models, they might not represent climate change effects at more local or regional scales. These models are being constantly updated and, although a new IPCC assessment report was published recently with climate scenarios represented by Shared Socioeconomic Pathways (SSPs) (IPCC, 2021) and not Representative Concentration Pathways (RCPs), in our study were still considered the RCPs (IPCC, 2013). This was done to allow a more direct comparison with previous studies undertaken for other deep-sea benthic organisms in the North Atlantic (Beazley et al., 2021; Morato et al., 2020). Moreover, the resolution of the model (3 × 3km), while suitable for prediction of regional scale (i.e. North Atlantic) changes in the distribution of *Pheronema carpenteri*, may be insufficient to inform finer-scale marine spatial planning. Particularly at national levels, where MPAs and other conservation measures can cover less than 10 km^2 (e.g. Foster et al., 2017), the resolution of environmental variables at a finer scale would improve inferences for marine spatial planning.

4.4. Implications for governance and management

Our results indicate that a high proportion (65,8 %) of suitable habitat for *P. carpenteri* for the present day is located within seven EEZs (Portugal, Ireland, United Kingdom, USA, Spain, Canada and Morocco). However, considering that no occurrences have been observed in the West Atlantic, predictions of suitable habitat in the USA (10.1%) and Canada (6.5%) should be interpreted with caution. Our results are supportive of earlier predictions of *P. carpenteri* distribution made by Howell et al. (2016). In that study, 67.38% of *Pheronema* suitable habitat was predicted to fall within seven EEZs (Iceland, Italy, Spain, United Kingdom, Azores-Portugal, France, Greenland). However, some differences are observed, with a considerably higher proportion attributed to the Mediterranean area (within Spain, Italy and France EEZs), which was not observed in our predictions, where only a small area within the Alboran Sea is predicted as suitable habitat. Indeed, *Pheronema* has been seldomly reported for this enclosed Sea (Boury-Esnault et al., 2015) and is not known to form aggregations in the area. Such differences may be related to the modelling approach, as well as the environmental data used, as shown by Piechaud et al. (2014) for other species. Since single models can have higher variance, the use of an ensemble approach may improve model accuracy and predictive power (Araújo and New, 2007).

Our projections indicate that the amount of suitable habitat will decrease within EEZs at lower latitudes and increase in EEZs at higher latitudes. However, the proportion of climate refugia within each country will remain, to a large extent, approximately the same. The main exception is the Portuguese EEZ that includes 15.6% of the suitable habitat at present but may ultimately enclose only 3.8% of suitable habitat by 2100 (RCP 8.5) and correspond to a proportion of total climate refugia of 9.5% largely located on the mainland shelf. This points to a higher vulnerability of these already geographically isolated populations for which greater conservation efforts may be necessary, for example in terms of avoiding cumulative impacts. Conversely, Iceland may see an increase from 0.6% to 14.7% of suitable habitat within its EEZ.

Climate refugia areas have also been identified within Northwest Atlantic EEZs (Bahamas, USA and Canada). However, this should be interpreted with caution, as with the other climate refugia areas identified in this study, additional processes such as oceanographic connectivity, biotic constraints on suitability and variables that were not incorporated into our models should be explored if considering these areas for management and conservation actions. By definition, climate change refugia areas enable the persistence of a resource, which in this case is the occurrence of *Pheronema* (Morelli et al., 2016). Since there are no confirmed records of *Pheronema* in the NWA, at present, areas with confirmed occurrences at present and that have suitable habitat into the future should be considered when implementing management and conservation actions in the short to medium term.

Both in present and under the different climate change scenarios, the High Seas also represent a significant portion of the total suitable habitat available for *Pheronema carpenteri* (between 22.2% and 24.2%), as also found in the study by Howell and collaborators (21.3%). The majority of climate refugia in the High Seas lies on, or on the vicinity of the Rockall plateau, where several bottom fisheries closures have been established by the Northeast Atlantic Fisheries Commission (NEAFC) to protect VMEs such as coral gardens/reefs, and sponge aggregations, including those formed by *Pheronema* (NEAFC Rec. 19: 2014, Rec. 10: 2018). These measures, which are in force until the end of 2027, currently prohibit all bottom fishing activities likely to contact the seafloor (e.g., trawling, gillnets and longlines), the former of which have been shown to considerably degrade *Pheronema* populations in nearby areas (Vieira et al., 2020). Our findings further emphasise the relevance of these closures that may in the long run protect an important proportion of *Pheronema*'s climate refugia.

Considering the increasing need to develop climate-resilient management and conservation measures, our study provides an important contribution to the identification of climate refugia areas of a key habitat-forming deep-sea sponge. From that perspective, focussing on these refugia areas may prove the most efficient strategy to ensure long-term sustainability and climatic resilience of *Pheronema* and the ecosystem functions it sustains. However, more research on the life-history and dispersal capabilities of *Pheronema carpenteri* would be needed to confirm the plausibility of these climate refuge areas. Such a framework would require the articulation of efforts between the various countries as well as regional and global agencies and agreements (e.g., OSPAR, NEAFC, BBNJ) as a mean to establish a coherent, interconnected and climate-smart network of area-based management tools (e.g., MPAs) and other effective conservation measures (e.g., fisheries closures) both within national jurisdictions and on the High Seas.

CRediT authorship contribution statement

Inês Gregório: Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Joana R. Xavier:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Andrew J. Davies:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Data curation.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2024.104390.

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