ICES Journal of Marine Science, 2026, Vol. 83, Issue 7, fsag123
https://doi.org/10.1093/icesjms/fsag123
Original article

Habitat suitability and future refugia for vulnerable marine ecosystems sea pens across European seas

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Abstract

Sea pen fields play a key role in providing three-dimensional habitats on muddy and sandy seabeds, altering local currents, increasing food availability for juvenile fish, and offering shelter in otherwise low-complexity environments. These important habitats face increasing pressures from bottom trawl fisheries and climate change, the latter of which remains poorly understood in terms of species response. As a result, sea pen fields are classified as Vulnerable Marine Ecosystems (VMEs) and therefore protected by international legislation including United Nations resolutions and the Deep-sea Access Regulation of the European Commission, highlighting the need for targeted management plans. To assess the current distribution and potential impact of climate change on three VME sea pen indicator species (Pennatula phosphorea, Pennatula rubra, and Pteroeides griseum) at pan-European scale, we applied an ensemble of species distribution models to predict their habitat suitability. Presence–absence data collected from trawl surveys, databases, and literature were used for model development. Probability of presence was estimated as a function of several environmental predictors, including temperature, current velocity, oxygen concentration, bathymetry, and substrate type. Our results show that the response at the species level is similar for substrate type and current preference, but differs in the range of maximum summer temperature, which has a structuring effect on the distribution of these three species. Predicted habitat shifts for the 2091–2100 timeframe are driven by rising summer temperatures as well as changing dissolved oxygen content. This study provides the first large-scale assessment of the current distribution of these three sea pens in European waters and identifies climate refugia from the Mediterranean Sea to the northeast Atlantic with high confidence levels, delivering new information of relevance for the conservation of VMEs.

Keywords climate refugia, species distribution modelling, vulnerable marine ecosystems, bottom trawling, pennatulids

Received: 22 January 2026. **Revised:** 11 June 2026. **Accepted:** 12 June 2026

Introduction

In benthic ecosystems, Marine Animal Forests (MAFs) occur when sessile habitat-forming species are present in dense aggregations, playing a fundamental ecological role (Orejas et al. 2022). They increase physical complexity, provide biogenic substrata for benthic associated species, as well as micro-areas of food and shelter for juvenile organisms. Soft bottoms, composed primarily of sand and mud, cover about 88% of the western European ocean floor (Millot and Vaz 2024), and soft-bottom animal forests are highly important in providing structural complexity to otherwise flat ecosystems (Georges et al. 2024).

Pennatuloidea, commonly known as sea pens, are a highly specialized superfamily of octocorals primarily adapted to life on soft sediments (Kushida and Reimer 2019, García-Cárdenas and López-González 2023). The colony morphology consists of a primary polyp (oozooid) forming an axis (rachis) bearing secondary polyps that perform feeding, reproductive, and circulatory functions (Williams 2011, Williams et al. 2012). A basal muscular peduncle enables anchoring into soft sediment, occasional detachment and re-anchoring), and partial withdrawal into the sediment to avoid perturbation (Fabricius and Alderslade 2001, Chimienti et al. 2018a).

When found in dense aggregations, sea pens can form extensive sea pen fields that increase local habitat complexity and alter current flow (Williams 2011), providing several important ecological functions (Porporato et al. 2014, Miatta and Snelgrove 2022). These habitats face multiple threats, including fishing pressure and climate change. The soft bottoms of the continental shelf are intensively exploited by fisheries using mobile bottom-contacting gears such as trawls, dredges, and Danish seines, particularly in European waters (Eigaard et al. 2017), where sea pens are a common bycatch (Carpentieri et al. 2021). The impact of fishing pressure on sea pen fields occurs through direct removal of colonies and sediment disturbance. The unknown resilience of sea pen fields to anthropogenic pressure combined with their ecological importance has prompted their classification as Vulnerable Marine Ecosystems (VMEs) (FAO 2009), including fields dominated by *Pennatula* spp., *Pteroeides* spp., and *Funiculina quadrangularis*. This VME designation highlights the need for integrating Fishery Restricted Areas (FRAs) and other protection measures into fisheries management plans.

Research on the impact of climate change on habitat-forming cnidarians was first focused on reef-forming warm-water corals, examining bleaching events and calcification changes associated with temperature increases and ocean acidification (Anthony et al. 2008, Chimienti et al. 2021). Little is known, however, about the response of non-symbiotic octocorals, such as sea pens, to rising temperatures. Despite lacking a hard skeleton, sea pens possess a calcified central axis and carbonate sclerites (Williams 2011), raising questions about their potential resilience to both thermal stress and ocean acidification. Rising temperatures and changing current regimes have been reported to cause mass mortality events of *Pteroeides griseum* in the Northern Aegean Sea (Özalp 2021) and of other octocorals in the Mediterranean (Garrabou et al. 2022). The large-scale effect of climate change on the habitats of these species should be taken into consideration in VME management plans, which requires a deeper understanding of their habitat selection.

Species distribution models (SDMs) offer a powerful tool for addressing these challenges and are widely used in spatial ecology (Elith and Leathwick 2009, Guisan et al. 2013). The environmental requirements of a species are estimated using a regression and/or classification algorithm to predict distribution and habitat suitability in unsampled locations. With climate change projections, it is possible to estimate the potential shift in the geographical range of species' habitat suitability, provided that the model adequately describes the environmental requirements of the species (Araújo and New 2007, Araújo et al. 2019). SDMs have been applied to sea pens within various frameworks, from taxon-level global assessments (Yesson et al. 2012) to species-level habitat mapping (Bastari et al. 2018, Downie et al. 2021), and more generally to inform VME conservation. However, to our knowledge, there are no applications of large-scale SDMs to sea pens at the species level from a climate perspective, even though species-specific tolerance and acclimatization capacity should be the primary factors determining how these VMEs will respond to changing climate conditions. In this work, SDMs were applied to the three most represented VME indicator sea pens in fishing trawl surveys: the phosphorescent sea pen *Pennatula phosphorea*, the red sea pen *Pennatula rubra*, and the spiny sea pen *Pteroeides griseum*. *Pennatula phosphorea* is cosmopolitan, widely distributed from the Mediterranean Sea to the northeast Atlantic and the Norwegian fjords (Ross et al. 2021); *P. rubra* is widespread in the Mediterranean Sea (Chimienti et al. 2018a, 2018b) where it is endemic; *P. griseum* is reported from the Mediterranean Sea and the northeast Atlantic up to the Bay of Biscay (Porporato et al. 2014). They are continental shelf species, with a general depth range from 30 m down to about 300–500 m. Their distribution has been studied using SDMs in regional seas (Bastari et al. 2018, Ross et al. 2021, Lozano et al. 2024), but not yet at large scale and from a climate change perspective.

The aims of this study are threefold: (1) understand the ecological niche of three sea pen species at a pan-European scale, (2) evaluate the effect of climate change on their habitat selection under the most pessimistic emission scenario, and (3) identify potential climate refugia to inform conservation strategies for sea pen fields.

Material and methods

Study area

The study area covers European waters from the North and Celtic Seas to the Mediterranean Sea. The area used for prediction is cropped according to the species' known range and upper latitudinal limits, and the sampling depth limit of scientific trawl surveys used (1000 m) (Fig. 1).

Presence/absence data

The occurrence datasets, comprising a total of 40 247 data points before filtering, were sourced from databases and fisheries independent demersal trawl surveys (Giraldo 1988, Giraldo 1988, Travers-Trolet and Verin 2014, Travers-Trolet and Verin 2014, Scarcella et al. 2019, Scarcella et al. 2019, Spedicato et al. 2020, Spedicato et al. 2020, Joint Nature Conservation Committee (JNCC) 2021, JNCC 2021, GBIF 2024, ICES 2024, OBIS 2024) (GBIF 2024, ICES 2024, OBIS 2024). The trawl surveys constitute the bulk of the dataset and provide extensive coverage and a scientific sampling strategy, including species absences, which are essential to

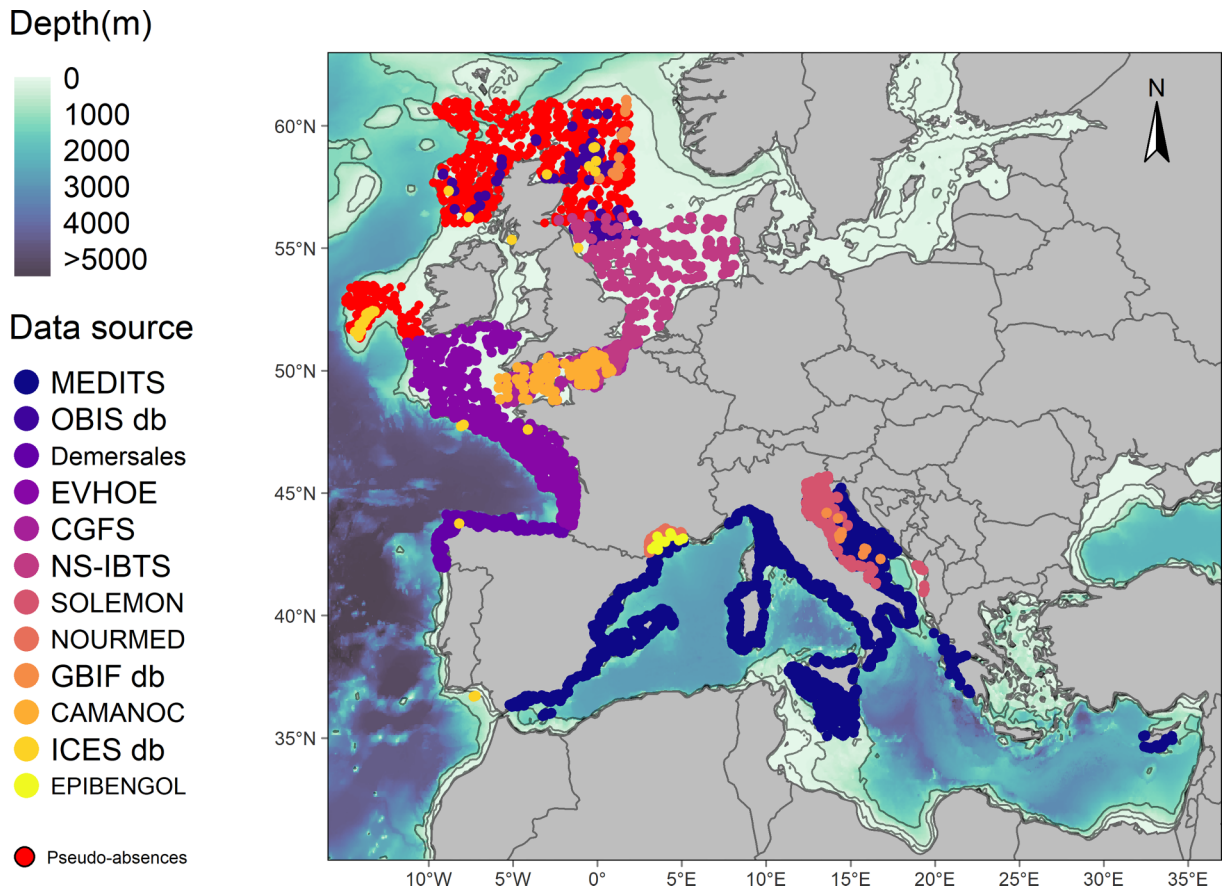

Figure 1 Map of the study area with source and location of data points used to compile the occurrence dataset for the three sea pen species. See Table S1 for the explanation of the acronyms.

obtain good-quality SDM outputs. Database records were quality-checked and filtered according to the level of definition of metadata, information on the sampling method and geographical precision, in order to avoid potential taxonomic misidentification. While studying abundance instead of only occurrence would be preferable, the detection issue posed by the fact that scientific trawling may be suboptimal to sample these organisms makes abundance measurements potentially unreliable (Chimienti et al. 2018b), especially when different surveys with varying gears and protocols are merged.

In the case of *P. phosphorea*, OBIS database records provided a substantial number of presences in the Celtic and North Seas, for which absence data from trawl surveys were missing. To include these records into a presence–absence modelling framework, pseudo-absences were randomly generated within the same geographic extent as these presence records. The target presence–absence ratio (∼1:9) was chosen to match the empirical ratio typically observed in trawl survey data (5%–15% presences depending on species and area), thereby ensuring consistency with the remainder of the dataset. The resulting dataset for *P. phosphorea* therefore combines true survey absences (from trawl surveys in the Mediterranean and northeast Atlantic) with geographically constrained pseudo-absences (in the Celtic and North Sea sub-regions lacking survey absence data).

When extracting data from open databases, we retained records for which coordinate precision was below 4 km and with information on the sampling gear used. To account for geolocation error due to trawl length, we standardized our predictor grids to a resolution of 0.05 decimal degrees per cell (about 4 km at the study area's mean latitude). The data used for modelling were aggregated to retain only one point per grid cell, prioritising presences. This approach standardizes sampling effort and mitigates false absences due to poor detection rate, as most trawl surveys consist of repeated observations of the same stations over time. Details of the data sources are mapped in Fig. 1, while presence–absence locations are shown in Fig. 2, and the surveys used are documented in the Supplementary Material (Table S1).

Environmental predictors

A wide range of environmental parameters was investigated according to their ecological relevance (Fourcade et al. 2018) and availability. Seabed properties including bathymetry (EMODnet Bathymetry Consortium 2020) and substrate mean grain size (Millot and Vaz 2024) were included. Oceanographic variables: bottom temperature, salinity, dissolved oxygen, and current speed—were extracted from Bio-ORACLE Version 3.0 (Assis et al. 2024), which provides decadal climatologies and Shared-Socioeconomic Pathway (SSP) climate projections (Riahi et al. 2017). Environmental

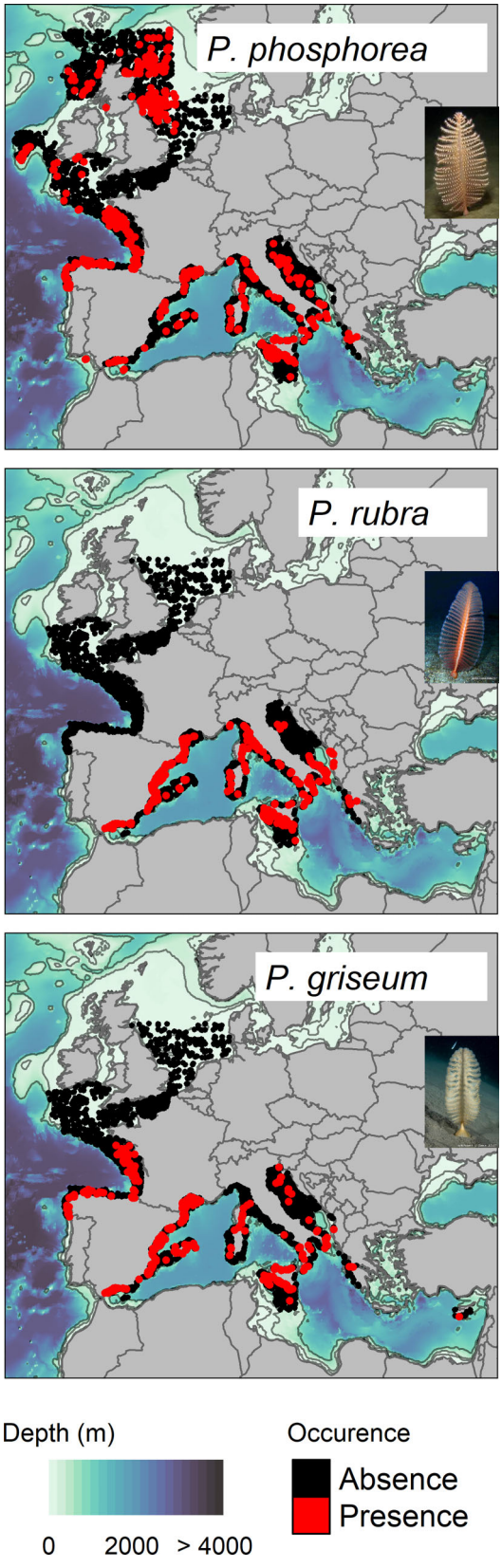

Figure 2 Data points used in modelling the three sea pen species after the application of filtering criteria, including real and pseudo absences for *P. phosphorea*.

variables for the 2001–2010 timeframe were selected as the baseline reference period.

The SSP585 scenario for the 2091–2100 period was selected as the sole projection target, as it provides the most contrasted signal relative to the reference period and yields the most ecologically interpretable signal for long-term VME conservation planning. Projections for intermediate timeframes (2041–2050) and the SSP245 scenario were also produced and showed qualitatively similar distributional shifts, albeit of substantially lower magnitude, reflecting the smaller environmental anomalies projected under intermediate forcing, particularly at the 2041–2050 timeframe. These intermediate projections therefore add limited insights within the scope of the present study compared to the most pessimistic scenario. The anomalies between the reference period and 2100 conditions are provided in the supplementary material (Figure S16–24). All data analysis, model fits and figures were produced in R version 4.3 (R Core Team 2023).

Environmental predictor selection was based on Generalized Additive Models (GAMs), as they are the most interpretable algorithm used, allowing assessment of a priori fitting to ecological assumptions. Specifically, GAMs enable verification that response curves align with niche theory, typically exhibiting a bell-shaped relationship (Guisan et al. 2013, ICES 2021). For each species and algorithm, we fitted the whole occurrence datasets to a set of candidate variables: log-transformed average substrate grain size, bathymetry, long-term minimum of dissolved oxygen, long-term maximum and range of current velocity, and long-term maximum temperature. These candidate variables were chosen based on their ecological relevance to the species investigated and non-collinearity amongst themselves (Spearman's correlation coefficient < 0.7). Substrate grain size is a key factor for the anchoring of sea pens and for all benthic fauna (Snelgrove 1998). Bathymetry influences the distribution of sea pen species (Williams 2011) as well as productivity and several other ecological aspects. Long-term maximum temperature serves as a proxy for thermal tolerance, representing the warmest month of the year, which can be linked to survival during acute heat stress events (Özalp 2021, Garrabou et al. 2022). Oxygen content is essential for respiration, which is metabolically linked with temperature (Previati et al. 2010). Current velocity and its properties are key factors for suspension feeders, determining food availability, oxygenation, and larval dispersal (Orejas et al. 2016). Selected predictors are mapped in Fig. 3, and Correlation analyses are provided in the supplementary material (Figures S2 and S3).

The dredge function of the MuMIn R package (Bartoń 2023) was used to compute the Bayesian Information Criterion (BIC) for all possible predictor combinations in GAM models fitted to the whole aggregated dataset. We retained the model with the lowest BIC, as it penalizes models with too many covariates (Stoica and Selen 2004), helping to avoid overfitting. The species-specific variable selection was then applied to all three algorithms.

Modelling procedure

Three model algorithms were chosen to study habitat suitability based on their different fitting strategies: GAM, Random Forest (RF), and Maxent. GAM uses spline regression to fit nonlinear species-environment relationships, conceptually close to niche theory (Hastie and Tibshirani 1986). RF is a machine-learning al-

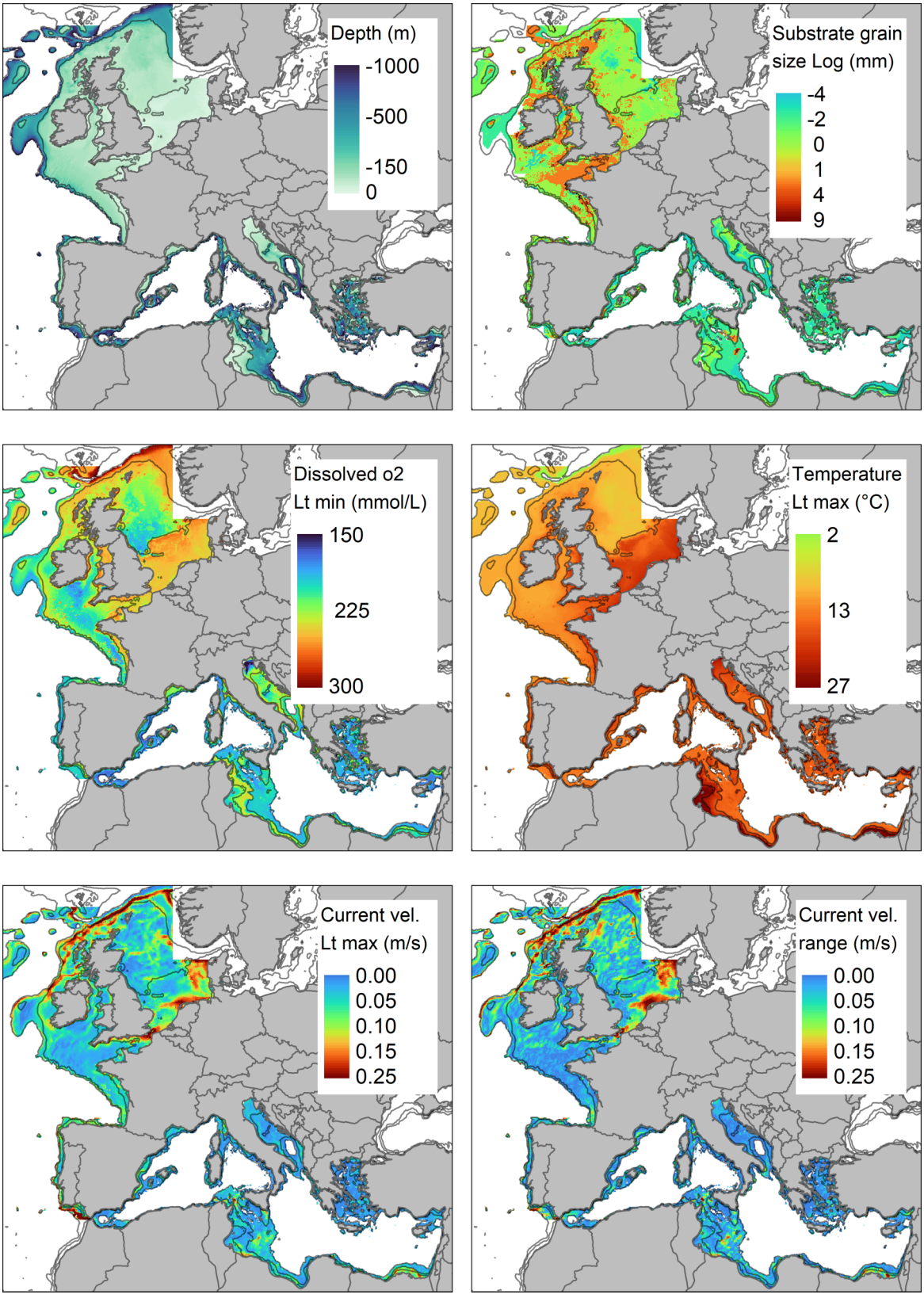

Figure 3 Maps of the retained environmental predictors used in the models (2001–2010 conditions). Lt: Long-Term.

gorithm based on regression trees, known for its predictive performance (Breiman 2001). Maxent was chosen as an entropy-based technique that has become a standard in species distribution modelling (Phillips et al. 2006). Maxent conventionally operates using background points randomly sampled from the study area rather than true absences; its application here with presence–absence data is a non-standard approach (Guillera-Arroita et al. 2014) that we retain because the output was ecologically coherent and cross-validation performance was satisfactory. Using different algorithms is particularly advantageous in ensemble forecasting, as convergence across algorithms increases confidence in results that are difficult to validate independently, such as climate change projections (Araújo and New 2007).

The modelling procedure was based on that of (Georges et al. 2024), following a repeated spatial block cross-validation approach. Specifically, the dataset was partitioned into five spatially independent subsets using 25-km wide blocks (blockCV package; Valavi et al. 2019), and this partitioning was repeated ten times with different random block assignments, yielding 50 training/testing splits per algorithm. For each split, 4/5 of the data were used to fit the models and 1/5 for evaluation. This yields a total of $5 \times 10 \times 3 = 150$ models per species, providing robust estimation of model variability and uncertainty (Georgian et al. 2019, ICES 2021). Block sizes and model tuning parameters were set after diagnosis of response curves, model parameters and semi-variograms of residuals on full-dataset models for each algorithm (Figure S4, S5). GAMs were fitted on a binomial error distribution with a fixed maximum degree of freedom of 4, preventing overfitting while allowing bell-shaped relationships. RFs were constructed with regression trees (Breiman 2001) with 500 trees, two variables per tree and a minimum of five terminal nodes. Maxent models were fitted with default regularisation of the maxnet function (Phillips 2021), with complementary log-log outputs used as probability of presence.

Evaluation metrics included the True Skill Statistic (TSS), Area Under the receiver-operator Curve (AUC), sensitivity, and specificity. Variable importance (VI) was calculated using permutation following Fisher et al. (2019). Response curves were also calculated for each model to evaluate the fitted species-environment relationship.

Ensemble model projections

Once all models were fitted, the mean AUC across all 150 models was calculated and used as a relative threshold, retaining only models with AUC values above this mean for ensemble projection. Because all species achieved mean ensemble AUC values ≥ 0.80, the retained models necessarily exceeded the commonly accepted absolute minimum threshold of AUC > 0.70 (Araújo et al. 2019), providing a baseline guarantee of good model performance. The ensemble Habitat Suitability (HS) is the mean HS of the retained individual models, and is then binarized into presence (1) and absence (0) using a threshold maximizing the True Skill Statistic, corresponding to the value that maximizes the sum of sensitivity and specificity, employing the optimal threshold function of the Presence–Absence R package (Freeman and Moisen 2008). This binarization is applied to both current and future conditions. Climate scenarios are classified as habitat loss (present but not future), habitat gain (absent at present but suitable in the future), and refugia (suitable under both current and future conditions).

Uncertainty and confidence level

Uncertainty is quantified in three separate ways: (1) Cross-Validation Uncertainty (CVU), calculated as the standard deviation of the retained HS predictions across model replicates, identifying areas where models diverge according to training dataset differences, an established approach in ensemble SDMs (Araújo and New 2007, Georgian et al. 2019, Georges et al. 2024); (2) Algorithm Uncertainty (AU), where algorithm-specific predictions are compared to quantify differences in species-environment relationships across algorithms and their consequences for present and future scenarios as a measure of model consensus (Araújo and New 2007, Georgian et al. 2019); and (3) Extrapolation Uncertainty (EU), using the dsmExtra R package(Mesgaran et al. 2014), to identify areas where predictions extend beyond the range of predictor values observed in the training data.

For the sake of synthesis, these three uncertainty metrics were combined into a composite confidence classification applied to refugia areas, a novel contribution building on the framework developed in (Georges et al. 2024). Confidence is classified as: "Uncertain" when CVU > 0.7, AU $= 1$ (only one of three algorithms identifies refugia), or EU indicates extrapolated conditions; "Good" when CVU is between 0.4 and 0.7, AU $= 2$ (two of three algorithms agree), and EU does not indicate extrapolation; "High" when CVU < 0.4, AU $= 3$ (all algorithms agree) and EU does not indicate extrapolation. All individual uncertainty maps are supplied in the supplementary material.

Results

Modelling performance

On average, models reached a mean AUC of 0.80, which is considered indicative of good performance (ICES 2021). The best fit was achieved for *P. rubra* (mean ensemble AUC of 0.84). Sensitivity and specificity values were broadly comparable across species and algorithms (Table 1), with no strong systematic difference; where a marginal tendency towards higher sensitivity was observed, this indicates slightly better prediction of presences than absences. Notably, specificity was marginally higher than sensitivity for Maxent and RF predictions of *P. griseum*. Among the algorithms, RF consistently outperformed the other methods across all species, followed by Maxent and GAMs RF models accounted for approximately half of all retained models in ensemble projections (Table 1).

Extrapolation analysis showed that the vast majority of the study area is within the range of the data observed in the reference datasets, except for the deep Gulf of Cadiz (due to extreme current velocity) and the northernmost Arctic continental slope (due to very low temperatures and very high oxygen content) (Figure S14).

Pennatula phosphorea

The results of the habitat suitability modelling of *P. phosphorea* showed a high contribution of depth and temperature to its distribution (Fig. 4). Long-term maximum temperature showed an inflection point between 10°C and 15°C, after which suitability gradually decreases, consistently across all three algorithms. For depth, GAMs and Maxent identified an optimum around 50–150 m,

Table 1. Summary of performance metrics for all 150 fitted models (mean ± standard deviation), grouped by algorithm. Presence–absence threshold used and number of models retained in the ensemble and for each algorithm type. AUC = Area Under the receiver-operator Curve, TSS = True Skill Statistic.

Species	Algorithm	AUC	TSS	Sensitivity	Specificity	PA Threshold	Retained n (%)
P. rubra	Ensemble	0.84 ± 0.035	0.55 ± 0.065	0.81 ± 0.079	0.75 ± 0.082	0.2082	82 (55%)
	GAM	0.81 ± 0.030	0.50 ± 0.056	0.79 ± 0.091	0.71 ± 0.095		8 (16%)
	Maxent	0.84 ± 0.026	0.56 ± 0.047	0.81 ± 0.071	0.75 ± 0.063		28 (56%)
	RF	0.87 ± 0.022	0.60 ± 0.048	0.82 ± 0.071	0.78 ± 0.068		46 (92%)
P. phosphorea	Ensemble	0.80 ± 0.033	0.48 ± 0.060	0.75 ± 0.074	0.72 ± 0.071	0.2486	77 (51%)
	GAM	0.78 ± 0.026	0.44 ± 0.046	0.74 ± 0.081	0.69 ± 0.071		11 (22%)
	Maxent	0.80 ± 0.028	0.47 ± 0.052	0.75 ± 0.081	0.71 ± 0.077		24 (48%)
	RF	0.83 ± 0.026	0.52 ± 0.051	0.77 ± 0.056	0.75 ± 0.051		42 (84%)
P. griseum	Ensemble	0.80 ± 0.031	0.49 ± 0.057	0.75 ± 0.085	0.75 ± 0.082	0.243	75 (50%)
	GAM	0.79 ± 0.030	0.46 ± 0.050	0.75 ± 0.091	0.71 ± 0.088		13 (26%)
	Maxent	0.81 ± 0.029	0.51 ± 0.054	0.74 ± 0.087	0.76 ± 0.078		33 (66%)
	RF	0.81 ± 0.029	0.51 ± 0.053	0.74 ± 0.080	0.77 ± 0.063		29 (58%)

while RF showed broadly similar habitat suitability across deeper depths (>500 m), reflecting lower depth discrimination by this algorithm. Oxygen and substrate were important secondary contributors, though algorithms disagreed on their precise response: a possible affinity for approximately 200 μmol l^{-1} of dissolved oxygen and the finest grain size substrates was apparent in GAMs and Maxent response curves, but less clearly structured in RF. Current velocity contributed little to predictions in GAMs and Maxent; RF identified a threshold near 0.1 m s^{-1} below which suitability was low, but showed little discrimination above this value (Fig. 4).

The most suitable habitats for *P. phosphorea* were found in the North Sea and, to a lesser extent, on the continental platforms of the whole study area. Climate scenarios show habitat shifts with some habitat loss in the northernmost area, driven primarily by declining dissolved oxygen content, and habitat gain in deeper waters throughout the study area, likely driven by increasing temperatures in shallow zones. A hotspot of very high confidence refugia was found in the North Sea, while refugia were found across the whole study area, though with higher uncertainty levels in the Bay of Biscay and the Mediterranean Sea.

Pteroeides griseum

P. griseum habitat suitability is primarily driven by temperature, depth, and oxygen (Fig. 5). Temperature affinities varied by algorithm: GAMs and Maxent showed a well-defined bell-shaped response with an optimum between 11°C and 20–25°C, while RF did not identify a clear temperature maximum, suggesting that the thermal constraint is better captured by the regression-based algorithms. A depth optimum between 50 and 200 m was apparent in all algorithms, with a broader range extending to 400 m (GAMs) or 500 m (Maxent). All algorithms identified an optimum near 200 μmol l^{-1} of dissolved oxygen minimum, though they disagreed on the minimum oxygen threshold: ∼100 μmol l^{-1} for Maxent, 150 for GAMs, and no clear minimum for RF. For current velocity, GAMs and Maxent identified a preference for low to moderate current speeds (near 0.1 m s^{-1}), while RF showed little discrimination above this threshold. Grain size was not retained as a predictor for *P. griseum* following BIC-based variable selection, suggesting that substrate type was less structuring for this species than for the other two.

Suitable habitats for this species are found on the continental platforms of the study area, particularly in the Bay of Biscay and the Mediterranean Sea. The climate projection shows habitat loss off the Portuguese coast, in the Bay of Biscay, and in the northernmost parts of the Adriatic, while habitat gains are predicted northward in the English Channel and in deeper/southern parts of the Adriatic Sea. Good confidence refugia were found across the study area, matching the areas identified as currently suitable.

Pennatula rubra

For *P. rubra* (Fig. 6), temperature was the main contributor to habitat suitability prediction, followed by depth and, to a lesser extent, by oxygen, substrate and current velocity. While all models agreed on a temperature minimum of ∼13°C, only GAMs identified a clear optimum at 16°C–17°C; the other algorithms did not identify a clear temperature maximum, suggesting the upper thermal limit is less constrained in the data for this species. Depth showed limited influence in GAMs, while RF and Maxent identified an optimum between 50 and 100 m. For oxygen, a pattern similar to that observed for *P. griseum* was found: an optimum near 180–200 μmol l^{-1} in GAMs and Maxent, with disagreement among algorithms regarding minimum oxygen conditions for habitat suitability.

The climate projection showed habitat gain across the Mediterranean basin, particularly in the Adriatic Sea, and localised habitat loss in the eastern basin attributable to rising temperatures in the shallowest parts of the species' distribution. Climate refugia were predicted with good or high confidence levels across the entire Mediterranean basin, with some habitat suitability predicted beyond the Strait of Gibraltar on the southern coast of Portugal.

Shared patterns across species

The model outputs highlight a preference for finer substrate classes, ranging from sandy muds (0.09 mm) to muddy sands (0.38 mm), for *P. phosphorea* and *P. rubra*, consistently across algorithms. Grain size was not retained as a predictor for *P. griseum* following BIC-based variable selection, indicating that sub-

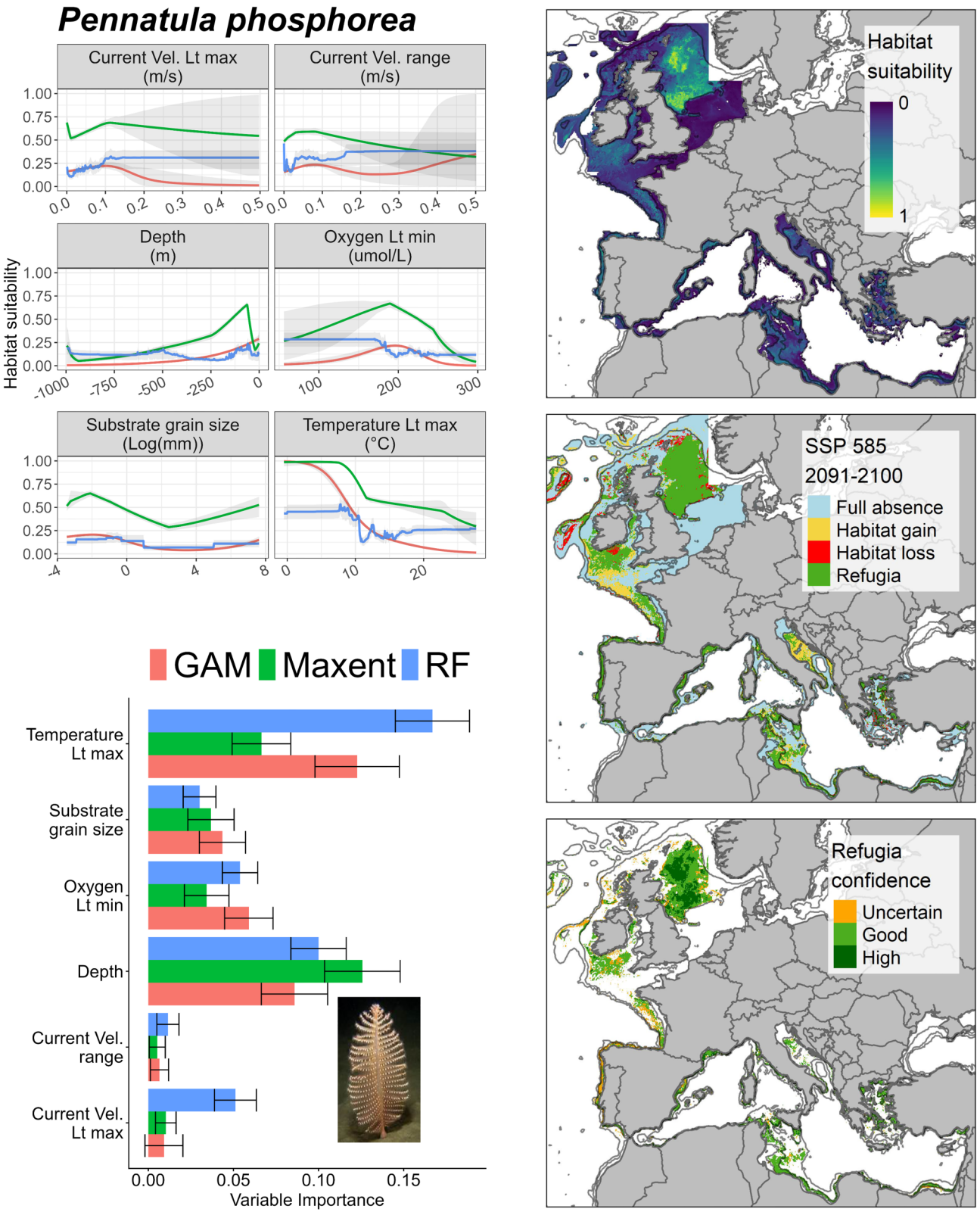

Figure 4 Modelling results summary for *Pennatula phosphorea* : Top left : Algorithm-wise response curves, Bottom left : Variable importance, Top right: Present-day habitat suitability, Middle right: Climate scenario for 2091–2100 (SSP585) and Bottom right : Confidence level on refugia areas.

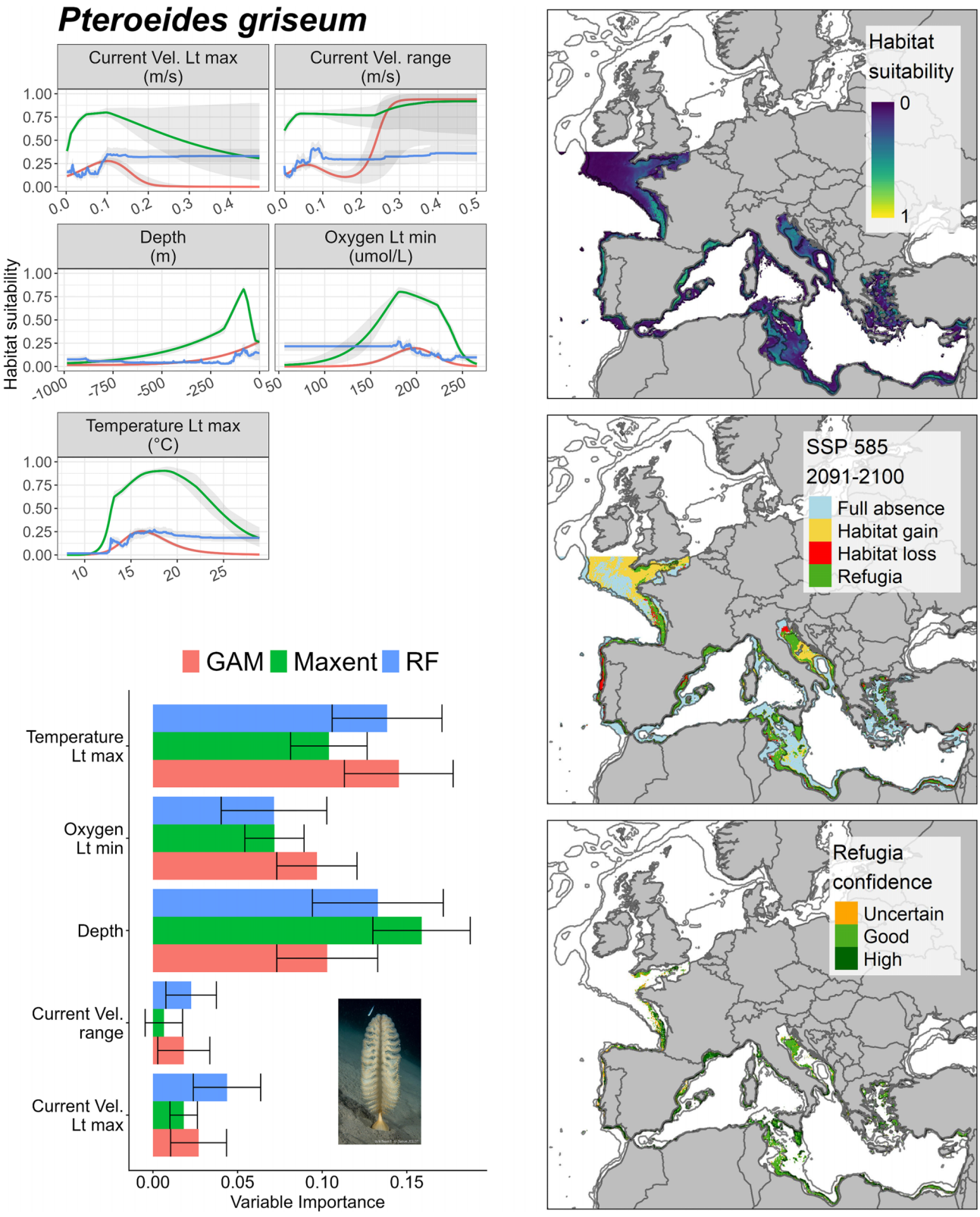

Figure 5 Modelling results summary for *Pteroeides griseum* Top left : Algorithm-wise response curves, Bottop left : Variable importance, Top right: Present-day habitat suitability, Middle right: Climate scenario for 2091–2100 (SSP585) and Bottom right : Confidence level on refugia areas.

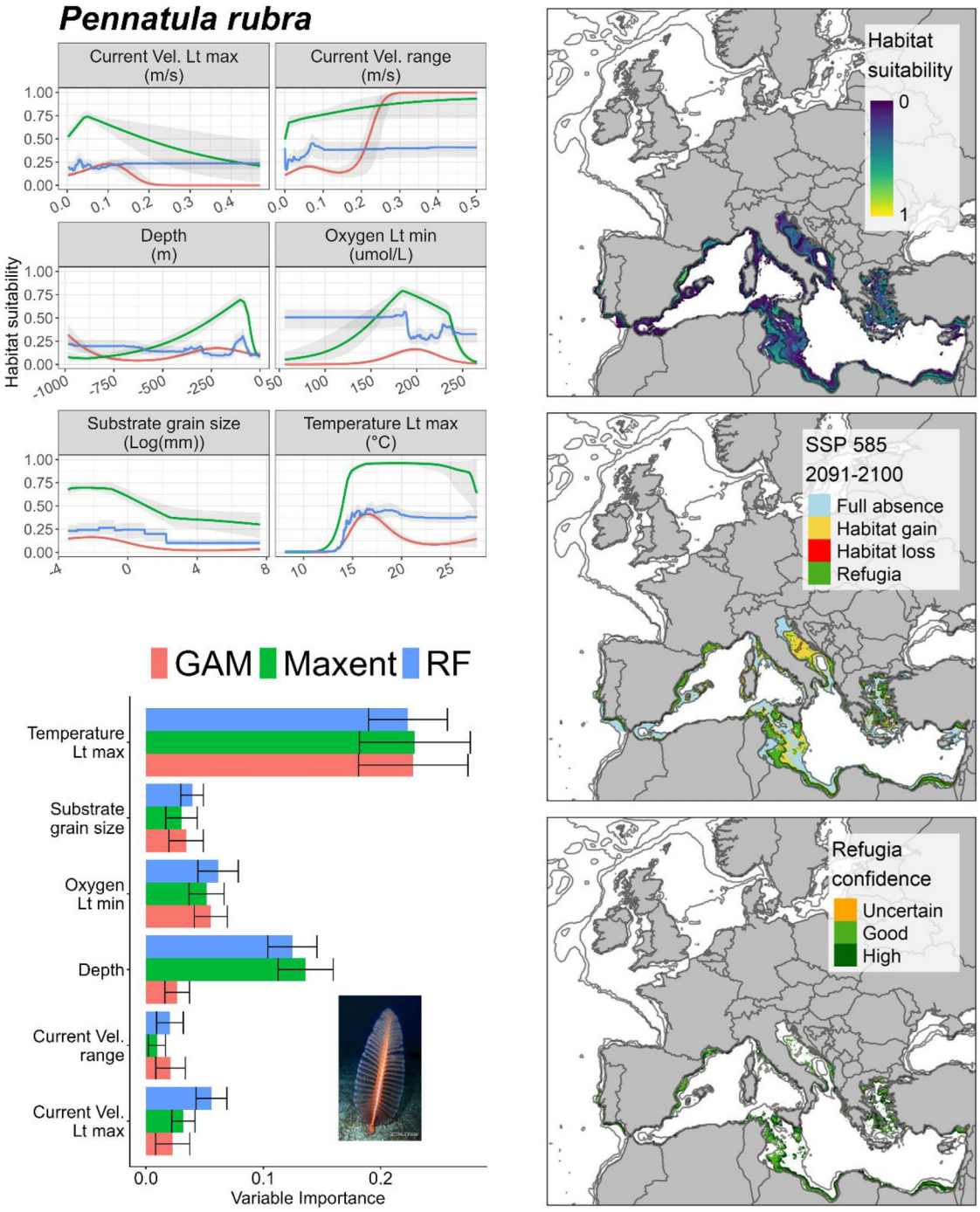

Figure 6 Modelling results summary for *Pennatula rubra* : Top left : Algorithm-wise response curves, Bottom left : Variable importance, Top right: Present-day habitat suitability, Middle right: Climate scenario for 2091–2100 (SSP585) and Bottom right : Confidence level on refugia areas.

strate composition was less structuring for this species within the range of conditions sampled. Regarding current velocity, all algorithms showed low habitat suitability below 0.1 m s^{-1}, but differed above this threshold: GAMs and Maxent suggested an optimum near 0.1 m s^{-1}, while RF showed little discrimination for higher values, reflecting the generally low predictive importance of this variable. All three species showed a response curve optimum near 200 μmol l^{-1} of dissolved oxygen long-term minimum in GAMs and Maxent predictions; RF showed less pronounced discrimination around this threshold, particularly for *P. rubra* and *P. phosphorea*. Temperature was the most discriminating predictor among species: *P. phosphorea* showed the strongest affinity for cold waters, *P. griseum* exhibited a narrower temperature range (better defined in GAMs and Maxent than in RF), and *P. rubra* appeared to tolerate higher temperatures. Habitat suitability was mostly predicted between 50 and 200 m across all continental platforms. Habitat loss generally occurred at the shallower or deeper limits of suitable habitats, while potential habitat gains were located in deeper or more poleward directions, with regional exceptions described per species above.

Discussion

In this study, the distribution and projected shifts in habitat suitability of three VME indicator species were modelled and mapped at a pan-European scale. Under the pessimistic SSP585 emission scenario for 2091–2100, the distribution of these species is expected to shift generally towards higher latitudes and/or deeper waters, though regional patterns differ. Our study suggests that habitat loss may occur due to rising summer temperatures and changing oxygen minima. Nevertheless, the wide current distribution of these species suggests a possible resilience to climate change, reflecting their capacity to colonise both the Atlantic and the Mediterranean across depths ranging from 50 to 500 m.

Environmental preference and current distribution

The models highlight similar habitat requirements for all three species for current regimes and oxygen minimum, and similar substrate affinity for the two species for which grain size was retained as a significant predictor (*Pennatula rubra* and *Pennatula phosphorea*). Differences occur in temperature tolerance and, to a lesser extent, depth. Temperature emerges as the most discriminating predictor among species. *Pennatula phosphorea* shows a marked decline in suitability above 15°C for long-term maximum temperature, consistent with its distribution spanning from the Arctic Circle to the Mediterranean (Ross et al. 2021a). For *Pteroeides griseum*, temperature affinity ranged from 10°C to 20°C, although uncertainty remains regarding the true maximum thermal tolerance, particularly because RF did not identify a clear upper limit. This is spatially reflected by its distribution, which does not extend into the North Sea, where *P. phosphorea* is common (Downie et al. 2021). Finally, *Pennatula rubra* displays an affinity for higher temperatures, coherent with its restriction to the Mediterranean Sea.

The physiological responses to high temperatures of the species investigated here remain largely unstudied. *P. phosphorea* thermal tolerance has been inferred from distributional data and SDMs (Downie et al. 2021, Ross et al. 2021a), but direct experimental evidence is lacking for all three species. Temperature has been identified as an important SDM predictor for sea pens in other European settings, including Scottish waters (Downie et al. 2021) and the Gulf of Cadiz (Lozano et al. 2024). At a higher taxonomic level, Yesson et al. (2012) noted that temperature is the most important predictor for the sub-order Subselliflorae (Now accepted as pennatuloidae) globally. More experimental studies on the species in question are needed to complement SDM results and to understand the effects of warming conditions at the physiological level.

A dissolved oxygen optimum near 200 $\mu mol\,l^{-1}$ was apparent in GAM and Maxent predictions for all three species, though RF showed less pronounced discrimination around this threshold. Studies on macrobenthos within and around Oxygen Minimum Zones (OMZs) have shown that sea pens are frequently abundant at the deeper edges of OMZs but not in their core (Hunter et al. 2011). In our study area, truly hypoxic conditions are rare, which may explain the occasional discrepancies between algorithms under low oxygen conditions. The role of oxygen in structuring sea pen distributions may be partly indirect: at the physiological level, increased temperatures have been shown to decrease polyp activity and reduce oxygen consumption in octocorals (Previati et al. 2010), and oxygen is less soluble in warmer, deeper and less ventilated waters. The depth optimum observed across species (50–300 m) also overlaps with the mesophotic zone characterised by high zooplankton biomass and seasonal mixed layer dynamics (Houpert et al. 2015), suggesting that the depth-oxygen-temperature interaction collectively shapes sea pen habitat suitability.

Pennatula phosphorea and *P. rubra* both show a preference for finer substrate classes, consistent with the anchoring requirements of the muscular peduncle. Grain size was not retained as a predictor for *P. griseum* during BIC-based variable selection, suggesting that within the environmental conditions sampled, substrate texture did not contribute sufficient discriminatory power for this species, possibly because *P. griseum* occupies a narrower and more homogeneous bathymetric range in which sediment variability is limited. The substrate preference for *P. phosphorea* and *P. rubra* aligns with (Greathead et al. 2015), who found a preference for high-mud, low-gravel substrates for sea pens in Scottish waters, and with(Georgian et al. 2019) in the South Pacific. For current velocity, all algorithms showed low suitability below 0.1 $m\,s^{-1}$, suggesting a potential minimum threshold requirement for food delivery and larval dispersal. Above this threshold, the response varied among algorithms: GAM and Maxent identified a moderate optimum near 0.1 $m\,s^{-1}$, while RF showed little discrimination for higher velocities. The generally low contribution of current variables to predictive power may reflect limitations in the representation of this predictor at the large spatial scale investigated, likely because current layers represent depth-integrated estimates that may not accurately reflect near-bottom velocities experienced by sea pens, where boundary layer effects can cause substantial differences from mid-water estimates (Orejas et al. 2016). The English Channel and southern North Sea appear to act as an environmental gap for the species considered in this study. The presence of coarse substrate, high current velocity and shallow waters ($<$50 m) in these regions may create adverse conditions for sea pens, rendering both *P. phosphorea* and *P. griseum* largely absent from the English Channel and southern North Sea.

Species distribution shifts under climate change

Projections for 2091–2100 under SSP585 predict a wide range of shifts in habitat suitability. Habitat losses are primarily observed in shallow waters, where summer temperatures are projected to exceed the thermal thresholds of these species (between 20°C and 25°C depending on the species), and in deeper regions where declining oxygen concentrations fall below the species' preferred range. Habitat gains are projected in deeper waters across the study area, and poleward in terms of latitudinal range, although the extent varies by species and region. Specifically, in the Adriatic Sea, projected changes point towards deeper and more southerly distributions rather than a simple poleward shift, highlighting the importance of regional bathymetric context. These patterns are consistent with the general responses described for cold-water species under climate change (Morato et al. 2020, Chaikin et al. 2022, Millot et al. 2024).

For *P. phosphorea*, the habitat loss observed in the northernmost parts of the study area is associated with depletion of dissolved oxygen minimum, predicted to decrease to 80 μmol l^{-1} in some areas, falling outside the observed preferred range. A similar situation is observed in the Aegean Sea, related to rising temperatures expected in the eastern Mediterranean (Pastor et al. 2020). For *P. griseum*, habitat loss is predicted in Portuguese waters and the deeper parts of the Bay of Biscay (declining oxygen minimum) and in shallow Mediterranean areas, including the Catalan Sea, north Adriatic, and eastern Mediterranean (rising temperatures). Finally, *P. rubra* shows a relatively stable distribution, with gains in deeper Mediterranean waters and localised losses in the eastern basin. Predictions for *P. rubra* should be interpreted cautiously given the unknown dispersal capacities of this endemic Mediterranean species and the potential for changes in inter-specific competition in newly available areas.

Uncertainty on ocean acidification

Ocean acidification constitutes an additional source of uncertainty that could not be directly assessed in the present study. Sea pens possess calcified internal axes and carbonate sclerites whose vulnerability to declining pH remains unknown, though ocean acidification is known to impact calcification in scleractinian corals (Anthony et al. 2008). During preliminary analyses, pH long-term minimum was evaluated as a potential predictor but was ultimately excluded because the low frequency of observations under strongly acidic conditions ($<$ 7.8 pH) produced unstable, algorithm-dependent outputs with no ecologically interpretable species-environment relationship. This highlights the data limitations for assessing acidification effects within occurrence-based SDMs and underscores the need for experimental studies on the sensitivity of pennatuloidan carbonate structures to declining pH.

Modelling performance

Model performance was satisfactory: values for AUC of $\sim$0.80 and TSS of $\sim$0.50 are considered good but not excellent performance, consistent with expectations for a wide-ranging continental shelf species with broad environmental tolerance (Georgian et al. 2019). This outcome is considered realistic given the spatial partitioning employed for evaluation (Valavi et al. 2019), which more accurately reflects the ability to project to unsampled areas than non-spatial cross-validation. The lower performance of GAMs relative to RF and Maxent reflects the inherent trade-off between interpretability and predictive power, which justified their central role in variable selection despite their lower individual AUC scores.

Uncertainty metrics

Our study carefully considered uncertainties in the fitted models using calibrated datasets. CVU highlighted areas at the limits of the environmental range where training dataset composition influenced predictions most strongly. AU was low in clearly suitable habitats and increased in transitional zones, particularly in the Mediterranean Sea under projected SSP585 conditions where temperature increases exceed the thermal range of some species. GAM and RF predictions diverged most strongly regarding the tolerance of *P. phosphorea* to high temperatures ($>$24°C), which is reflected in the low proportion of high-confidence refugia in the Mediterranean for this species. Extrapolation uncertainty was low overall, with the exception of the northernmost continental slopes (very high oxygen minimum and current speeds) and eastern Mediterranean shallow waters under 2100 SSP585 conditions (very high temperatures).

Study limitations

The reliability of species distribution modelling depends on the quality of calibration data and the realism of derived response curves (Guisan et al. 2013). As most observations come from trawl surveys, there is inherent uncertainty in occurrence data due to the requirement for reliable species identification, taxonomic expertise is not always available in surveys focused on commercial species. The aggregation procedure, which prioritizes presences across repeated annual observations at the same stations, helps counteract occasional false absences but does not guarantee full taxonomic accuracy.

The resolution of the environmental layers ($\sim$4 km) limits the capacity to resolve microscale processes and habitat requirements (Yesson et al. 2012), which are essential for accurately predicting fine-scale species distributions. The substantial size of the study area and the diversity of habitats covered nonetheless provide reasonable confidence in large-scale environmental requirements. Finally, our modelling framework assumes static species niches and does not account for potential physiological acclimatization, evolutionary adaptation, biotic interactions, or larval dispersal constraints, factors that could modulate the realized habitat shifts under climate change.

Conclusion

This study provides the first large-scale habitat suitability assessment of three VME indicator sea pen species across European waters, combining ensemble modelling with a composite uncertainty framework to identify climate refugia. Climate scenarios showed species-specific responses: habitat loss is likely in specific shallow Mediterranean areas due to rising maximum temperatures, and in specific deep Atlantic locations due to declining oxygen minima. High-confidence refugia were identified with consistent algorithm agreement across the study area, from the North Sea to the Mediterranean. These findings underscore the necessity for careful consideration of climate scenarios in management strategies aimed at safeguarding VMEs from bottom-fishing impacts. A precautionary approach to conservation should prioritize limiting fishing pressure on VME refugia areas to preserve the long-term effectiveness of Fisheries Restricted Areas. Reducing uncertainty associated with species and ecosystem responses to climate change requires further research, particularly experimental studies on the physiological responses of sea pens to thermal stress, oxygen depletion and ocean acidification.

Acknowledgements

The authors thank all survey officers and crews of the scientific surveys used within the datasets, especially the MEDITS, SoleMon, and International Bottom Trawl surveys, as well as the curators of the databases used. The authors thank as well the anonymous

peer reviewers whose comments greatly improved the quality of the work.

Author contributions

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Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflicts of interest

None declared.

Funding

This work was funded through the Fish-Med PhD program " Tecnologie innovative e uso sostenibile della pesca e delle risorse biologiche del mar Mediterraneo" (CNR-IRBIM/University of Bologna) and the REDRESS project (https://redress-project.eu/, Restoration of deep-sea habitats to rebuild European Seas, N°101135492).

Data availability

Due to the restricted nature of some databases and survey records, the authors do not have permission to publish the full occurrence dataset. We encourage interested parties to contact the corresponding author for guidance on accessing specific data chunks. The scripts used to create the models, as well as the output layers, will be made accessible upon publication in a public repository.

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Handling editor: Howard Browman

Received: 22 January 2026. **Revised:** 11 June 2026. **Accepted:** 12 June 2026