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Licence to predict – Investigating approaches to modelling low-occurrence deep-sea Irish Antipatharia with a new evaluation metric

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Abstract

Species distribution modelling has proven effective in locating cold-water coral hotspots in the deep sea. Maximum entropy (MaxEnt) and gradient boosting (GBM) are equally good at modelling rare species, but previous efforts to predict the distribution of deep-sea Antipatharia have mostly employed MaxEnt. This study investigates how algorithm choice (MaxEnt or GBM) and the application of backward stepwise variable pre-selection influence model performance and generalisation. Thirty-six models (four frameworks for nine black coral morphospecies) were built and evaluated using AUC, TSS, and the average TSS index (ATI), a novel metric that calculates TSS drops between training and test data to measure generalisation capability.ATI identified concerns in model generalisation that were not captured by AUC and TSS, making it a valuable tool for evaluating predictive model quality in conservation applications. MaxEnt outperformed GBM in predicting black coral distribution, and the pre-selection of variables did not improve performance. Satisfactory results were only obtained for the two MaxEnt models of *Stichopathes gravieri*, providing insights into the implications of using small datasets in conservation efforts.

The inconsistencies in our findings do not lead us to recommend the use of a single model type in future studies; rather, we stress the importance of careful evaluation of model metrics with ecological knowledge of the species distribution when applying a dataset to conservation purposes.

Keywords: species distribution modelling; MaxEnt; Gradient boosting; Evaluation metrics; Antipatharia.

Introduction

Black corals (Anthozoa: Antipatharia), named for their skeletal colour, are widespread, long-lived, and slow-growing organisms that are commonly found at depths greater than 50 m (Roberts *et al.*, 2009; Wagner *et al.*, 2012). Black corals are known to create habitats – named gardens, or forests – inhabited and used as a spawning ground by a great variety of organisms, including endangered and commercially valuable species, and species that are adapted to live exclusively on black corals (Wagner *et al.*, 2012; Chimienti *et al.*, 2020). Black corals are severely impacted by the shift of fishing effort towards deeper waters (Buhl-Mortensen & Mortensen, 2004; Danovaro *et al.*, 2021) and increases in extraction activities (Bradshaw *et al.*, 2012; Wagner *et al.*, 2012; White *et al.*, 2012; Roberts & Cairns, 2014); impacts are exacerbated by their slow recovery rates. Because of these characteristics, antipatharians have been nominated as vulnerable marine ecosystem (VME) indicators, and black coral gardens are listed as VMEs – ecosystems whose components are at risk from the effects of human impacts – in the Northeast Atlantic Ocean (FAO, 2009). Therefore, it is crucial to understand the distribution of black corals to inform conservation management and promote their protection.

The role of species distribution models (SDMs) as tools to inform conservation management has been increasingly significant in recent years (Kenchington *et al.*, 2019). By analysing the correlation between species occurrence and environmental conditions within their distribution range, the models can generate mapped predictions of the likelihood of species presence, thereby aiding in conservation planning (Elith & Franklin, 2013). In deep-sea ecology, SDMs have been successfully used to infer the distribution of taxa and habitats, including several VMEs such as Scleractinia reefs, coral gardens, and sponge grounds (e.g., Howell *et al.*, 2011; Ross & Howell, 2013; Ross *et al.*, 2015b; Howell *et al.*, 2016; Lo Iacono *et al.*, 2018; Chu *et al.*, 2019; Bollinger *et al.*, 2022; Howell *et al.*, 2022; Palummo *et al.*, 2023). The deep sea is a remote habitat difficult to investigate because of its vast extent and the economic and technical challenges related to its exploration (Bell *et al.*, 2022). Therefore, few, single observations are the most common type of data that can be collected in these environments (Winship *et al.*, 2020; ICES, 2021).

Modelling algorithms such as maximum entropy (MaxEnt) (Phillips *et al.*, 2006), and gradient boosting (Ridgeway, 2007; Elith *et al.*, 2008) have repeatedly been selected as the best performing to model datasets with a low number of occurrences (Elith *et al.*, 2006; Elith & Graham, 2009; Reiss *et al.*, 2011; Merow *et al.*, 2014; Shabani *et al.*, 2016; Valavi *et al.*, 2022), although caution was expressed with both algorithms when the sample size was very low (Wisz *et al.*, 2008). Previous studies on the distribution of black corals employed MaxEnt (Yesson *et al.*, 2017; Etnoyer *et al.*, 2018; Lauria *et al.*, 2021; Lavorato *et al.*, 2021), or combined the predictions of MaxEnt and gradient boosting with other small models using an ensemble approach (Lo Iacono *et al*., 2018). However, no previous study has explicitly investigated the performance and transferability capabilities of gradient boosting machines in modelling Antipatharia habitat suitability.

MaxEnt is a machine learning modelling method that predicts the distribution of a species by finding the most uniform distribution possible while satisfying the relationship between the species occurrence and environmental parameters (Phillips *et al.*, 2006). MaxEnt predicts the probability of species occurrence in a landscape of interest by fitting combinations of functions (also known as feature classes, being linear, product, quadratic, hinge, threshold, and categorical) to a set of environmental covariates (Elith *et al.*, 2011; Phillips *et al.*, 2006). The ability of MaxEnt to fit complex models can lead to predictions that are too specific to the training dataset; thus, MaxEnt allows the selection of a regularization parameter that smooths the distribution to prevent model overfitting and underfitting (Phillips *et al.*, 2006; Phillips & Dudík, 2008; Elith *et al.*, 2011). To increase the model performance, optimal feature classes and regularization parameters can be selected with the help of evaluation metrics such as the Akaike information criterion (Burnham & Anderson, 1998).

Gradient boosting machines (GBM) are algorithms that perform an iterative process on presence-absence data to improve boosted regression tree accuracy by sequentially fitting decision trees in order to reduce error introduced with each model (Friedman, 2002; Elith *et al.*, 2008). To ensure a good fit on the dataset, the tuning of the following hyper-parameters is usually recommended: the fraction of the training set observations randomly selected to propose the next tree in the expansion (bag fraction); the learning rate, a shrinkage parameter that determines the contribution of each tree to the model; and the tree complexity that controls the depth of the interactions. Together, learning rate and tree complexity control how many trees are needed to build an optimal model (Elith *et al.*, 2008).

The performance of SDMs can be evaluated through several evaluation metrics. The area under the receiver operating characteristic (ROC) curve, AUC, is a frequently used method to measure and compare model performance in presence-absence models (Lobo *et al.*, 2008). Being threshold-independent, it provides a measure for the overall ability of the model to discriminate between presences and absences (Shabani *et al.*, 2018). The true skill statistic (TSS) is a threshold-dependent metric that is measured as ‘sensitivity + specificity – 1’, and ranges from 1 (the model correctly predicts all the presences and absences), to -1 (none of the true occurrences are correctly predicted). TSS is useful in the context of species distribution models as it accounts for chance agreement and provides a consistent measure of accuracy that is evaluated based on the model threshold (Cohen, 1960; Allouche *et al.*, 2006; Shabani *et al.*, 2018). When calculated on training data, TSS indicates how well the model is able to correctly classify the presences and absences within a dataset. When calculated on test data, it indicates how well the model generalizes on unexplored locations.

The performance of a model does not depend only on the occurrence data, but also on the environmental variables selected as model predictors, which should represent the ecological niche in which the modelled species live (Elith & Franklin, 2013). However, the challenges of worldwide deep-sea exploration such as funding, inefficiency, and limited access to existing tools and resources make it difficult to obtain comprehensive occurrence and predictor datasets (Bell *et al.*, 2022). Locations that are easier to reach or more topographically interesting can be sampled more than others, and these data are then used to model the environmental conditions across a larger spatial extent. Predictor layers are often available at different spatial scales, which do not always match the scale of the ecological processes that we want to represent with predictive modelling (Winship *et al.*, 2020). In the deep oceans, environmental predictors are often correlated, which again can lead to biased results (Segurado *et al.*, 2006; De Marco & Nóbrega, 2018). To account for variable collinearity, Elith & Leathwick (2009) recommend pre-selection of predictors with a further modelling step to reduce the number of correlated variables used in the model and increase its accuracy. Variable pre-selection should, however be evaluated for each individual study as, while being supported by several studies (Ross & Howell, 2013; Anderson *et al.*, 2016), other papers argue that a strict pre-selection may not benefit the model (Elith *et al.*, 2011; Piechaud *et al.*, 2014).

The biases introduced by scarce occurrence and prediction datasets highlight the need for new technologies and methodologies to approach conservation management in the deep sea. Reliable models that predict the distribution of deep-sea taxa are invaluable for developing policies to conserve these ecosystems and protect vulnerable species (Kenchington *et al.*, 2019). This study aims to address the challenges posed by deep-sea data scarcity by proposing a methodological approach capable of estimating the reliability of predictions in challenging environments. Specifically, this study aims to (i) analyse the predictive capability, model performance, and generalization of MaxEnt and gradient boosting models when a small dataset of black corals is used to inform predictive mapping for conservation management, and (ii) evaluate the benefits of variable pre-selection through backward stepwise selection prior to modelling, and assess its impact on model scores.

Methods

This research was conducted in the deep waters of the Atlantic Ocean off the west coast of Ireland. The study area corresponds to the area of prediction (Fig. 1) and overlaps with most of the Irish exclusive economic zone (EEZ). It extends as far north as the Rosemary Bank, a seamount situated at the top of the Rockall Trough. The Irish continental slope, the Whittard Canyon, and Edoras Bank respectively define the eastern, southern, and western boundaries of the study area.

Environmental data

The predictors selected for this study are: (1) bathymetry; broad- and fine-scale bathymetric position indices (BBPI and FBPI); overall, planform and profile curvature; terrain rugosity; slope; salinity; bottom temperature; and water mass velocity (horizontal and vertical components) (Table 1). This array of predictors contains both geomorphological and environmental variables that were chosen for their ecological importance in determining the presence of cold-water corals. Terrain variables refer to physical characteristics of seabed features that can influence coral distribution. Terrain variables such as BBPI and FBPI are used to identify geological features such as canyons or gullies (Howell *et al.*, 2022). Rugosity and slope are used to identify areas of particular substrates and energy level, and are known to influence the distribution of cold water corals (Wagner *et al.*, 2012; Anderson *et al.*, 2016; Bargain *et al.*, 2018). Although sometimes correlated with terrain variables, environmental predictors such as salinity and bottom temperature are site-specific, and are used to identify different water masses, which influence coral zonation (Arantes *et al.*, 2009; Roberts *et al.*, 2009; Williams *et al.*, 2010). Current velocity influences parameters such as transport of food particles and sediment, and larval dispersal (Thiem *et al.*, 2006; Taviani *et al.*, 2011; Wagner *et al.*, 2012, Anderson *et al.*, 2016).

Raster grids for the first ten predictors were available from (Howell *et al.*, 2022) (Table S1). The bathymetric layer was created from high-resolution multibeam bathymetry data and resampled at a resolution of 200 m (Howell *et al.*, 2022) to cover the selected portion of the Northeast Atlantic (Fig. 1a). The ArcGIS Benthic Terrain Modeler add-in (Walbridge *et al.*, 2018) was subsequently employed to derive bathymetric position indexes, curvatures, and terrain features (rugosity and slope) from the bathymetry data (Guinan *et al.*, 2009; Ross & Howell, 2013; Howell *et al.*, 2022). Inner and outer radii of BBPI were set by Howell *et al.* (2022) to 5 and 50 raster cells to facilitate the identification of canyons and hills; they were set at 1 and 5 raster cells for FBPI to facilitate the identification of features at <1 km scale. Layers for bottom salinity and bottom temperature, matching the extent of the bathymetry layer, were constructed using generalized additive models with information derived from CTD data (Howell *et al.*, 2022). The horizontal and vertical bottom velocity layers were extracted from the Marine Institute Regional Ocean Modelling System (ROMS) averaged over the year 2020 at a resolution of 1.9 km

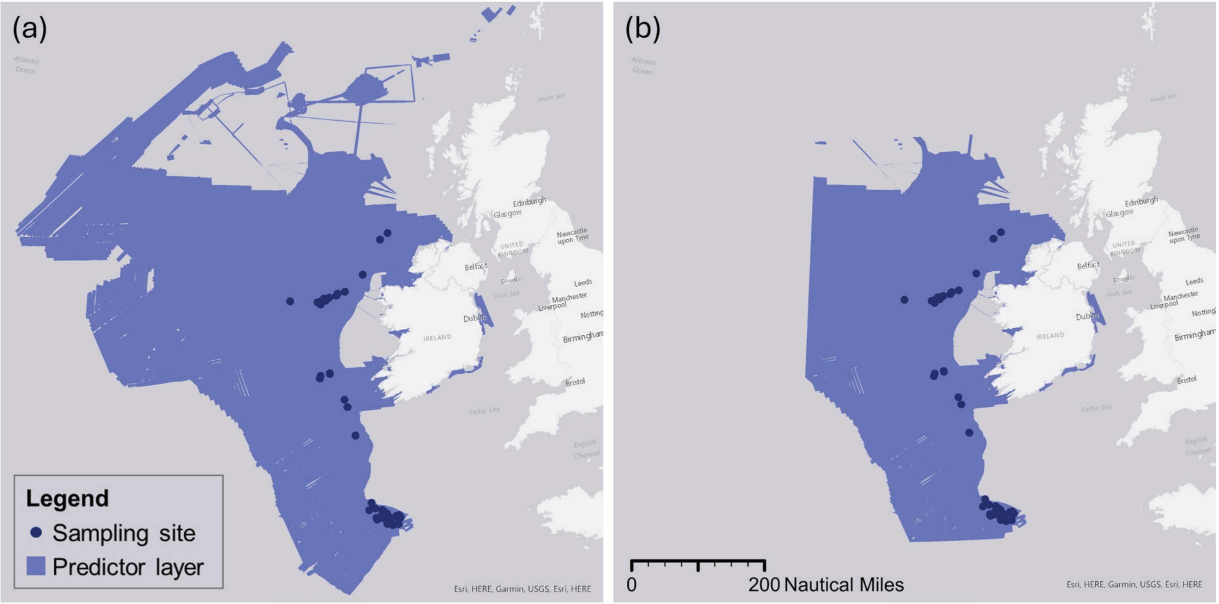

Fig. 1: Study area and sampling sites. (a) Extent of bathymetry layer; (b) Extent of velocity layer..

Table 1. Range of environmental predictors for the explored cells.

Variable name and description	Unit	Minimum	Maximum	Source
Bathy – Bathymetry	m (meters)	365.27	2768.33	Howell *et al.*, 2022
BBPI – Broad-scale bathymetric position index	–	-779	618	
Curv – Overall curvature	m^{-1} (1/meters)	-0.31	0.35	
FBPI – Fine-scale bathymetric position index	–	-120	129	
PlanC – Planform curvature	m^{-1} (1/meters)	-0.19	0.19	
ProfC – Profile curvature	m^{-1} (1/meters)	-0.19	0.20	
Rug – Rugosity	–	0.00003	0.02003	
Sal – Bottom salinity	PSU (Practical Salinity Unit)	34.94	35.95	
Slo – Slope	° (angle)	0.85	37.13	
Temp – Bottom temperature	°C (Celsius degrees)	3.21	10.79	
VelX – Current velocity (horizontal component)	m/s (meters per second)	-0.32	0.19	Nagy *et al.*, 2020
VelY – Current velocity (vertical component)	m/s (meters per second)	-0.61	0.19	

(Nagy *et al.*, 2020). To align with the cell size of the other layers, velocity data were resampled to 200 m using the nearest neighbour method (implemented with the ArcGIS Subdivide Polygon tool) (Table S1). The velocity layers have a smaller extension when compared with the other predictors, failing to cover the full predicted area (Fig. 1b). Hence, when velocity was used as a variable in the model, the extent of predictions is delineated from a north-south line that excludes the Rockall Plateau and the Feni Ridge.

Occurrence data

Occurrence data were generated from the analysis of high-definition videos recorded using a Kongsberg OE 14-366 colour zoom camera mounted on ROV Holland I, deployed from RV Celtic Explorer. The video data were collected during five expeditions conducted from 2013 to 2018 (Table S2), comprising a total of 98 ROV dives, typically 4-12 hours in duration, across the North Porcupine Bank (CE13008, CE18012), the Whittard Canyon (CE13008, CE14009, CE16006, CE17008), the Gollum Channel, and Belgica and Hovland mounds (CE17008). The dives covered a depth range from 605 m to 2710 m.

The presence of black corals was annotated using the Video Annotation and Reference System (VARS) software (Schlining & Stout, 2006). When possible, the corals were identified to the lowest taxonomic level based on an in-house identification guide, compiled from local knowledge, DNA sequencing of samples collected during video transects, and external taxonomic expertise. The colonies were grouped into morphospecies based on their morphological characteristics. The complete dataset comprises 11,363 black coral records, with 37 morphospecies annotated. The entries were linked to spatial information, and their longitude and latitude were defined.

The occurrence data for all observed morphospecies were aligned with the 200 m predictor raster grid and consolidated into one observation positioned in the middle of each grid cell (Downie *et al.*, 2021; Howell *et al.*, 2022), and the occurrence dataset was reduced to 393 cells. Grid cells containing at least one observation of the morphospecies were considered presence points. Cells explored by video transect but with no species presence detected were treated as pseudoabsences for that species, as it is impossible to confirm the absence of a morphospecies from a whole 200 m x 200 m cell (Howell *et al*., 2022). To ensure model accuracy and performance and to mitigate the effects of a poor dataset (Stockwell & Peterson, 2002; Wisz *et al.*, 2008), only morphospecies present in at least five per cent of the total explored cells were included in the modelling process. Hence, nine morphospecies were modelled in this study*: Antipathes dichotoma, Bathypathes* m2*, Leiopathes* m1*, Parantipathes hirondelle, Cladopathes plumosa, Stauropathes arctica, Stichopathes gravieri, Stichopathes* m1, and *Stichopathes* m3 (details for each morphospecies are in Table S3).

Following Ross & Howell (2013), occurrence data and environmental predictors for each morphospecies were integrated by linking occurrence points with corresponding environmental variable values.

Modelling

Each morphospecies was modelled with four different algorithm combinations: (1) MAV (MaxEnt All Variables), a maximum entropy model without variable pre-selection; (2) MSV (MaxEnt Selected Variables), a maximum entropy model with variable pre-selection; (3) GAV (GBM All Variables), a gradient boosting model without variable pre-selection; and (4) GSV (GBM Selected Variables), a gradient boosting model with variable pre-selection.

A principal component analysis and a correlation analysis were conducted to identify groups of collinear variables (|r| > 0.7); (Dormann *et al.*, 2013). The principal component analysis (Fig. 2) of the environmental predictors used in this study revealed three main clusters of variables: (1) depth, salinity, and temperature, negatively correlated with slope, rugosity, and vertical and horizontal velocity; (2) Overall curvature, planform curvature and FBPI, negatively correlated with profile curvature; (3) BBPI, negatively correlated with rugosity. Furthermore, the correlation analysis (Fig. S1) identified the following pairs of highly correlated variables: (1) depth – temperature (r = 0.856); (2) overall curvature – FBPI (r = 0.769); (3) overall curvature – planform curvature (r = 0.835); (4) overall curvature – profile curvature (r = 0.901); (5) FBPI – profile curvature (r = 0.701); and (6) salinity – temperature (r = 0.816). To investigate the information brought by all predictors, and to retain one variable for each correlated pair, initial "starting combinations" were created (Table S4). As species zonation is primarily influenced by temperature rather than depth (e.g., Järnegren & Kutti, 2014; Ross *et al.*, 2015a), only the variable combinations involving temperature were kept: (1) TC: BBPI, overall curvature , rugosity, slope, temperature, vertical velocity, horizontal velocity; (2) TFP: BBPI, FBPI, planform curvature, rugosity, slope, temperature, vertical velocity, horizontal velocity; and (3) TPP: BBPI, planform curvature, profile curvature, rugosity, slope, temperature, vertical velocity, horizontal velocity.

In the MAV and MSV algorithm combinations, the distribution of each morphotype was modelled using MaxEnt v. 3.4.4. MaxEnt was used following a sampling-with-data (SWD) approach, that entails using absence or pseudo-absence data when these are available, rather than using randomly generated background points (Phillips *et al.*, 2006, Phillips & Dudík, 2008; Howell *et al.*, 2022). This helps correct for the sample bias introduced by having presence and background (absence) data from the same sampling campaign (Phillips & Dudík, 2008).

A default MaxEnt model (auto features on, no threshold; regularization = 1) was built for each initial variable combination. Corrected Akaike information criterion (AICc) was calculated for all three models (Burnham & Anderson, 1998), and the predictor array of the model with the lowest AICc was used as a starting array for variable selection. The contribution of each variable was estimated through a jackknife test of variable importance, and the variables that least contributed to the model gain were progressively eliminated following the parsimony approach outlined in Howell *et al.* (2022). The variable combination scoring the lowest absolute AICc was considered optimal. All the possible arrays of probability functions (automatic, hinge, and threshold features) were tested, and the one yielding the model with the lowest AICc was kept. More MaxEnt models were built using a standard array of regularisation parameters (R = 0.001, 0.01, 0.1, 1, 3, 5, 7, 10), and AICc was calculated for each one. Middle regularisation values were iteratively tested until the model with the lowest AICc was found, and the R of that model was used to build the optimal model (Table S6, S7).

In the GAV and GSV algorithm combinations, the

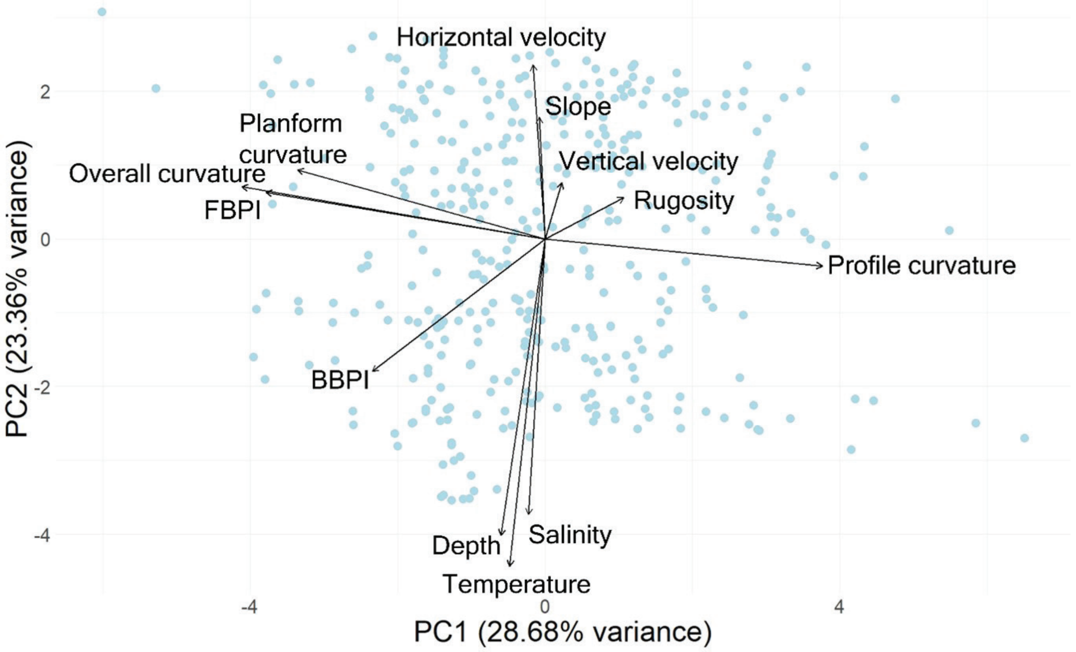

Fig. 2: Principal component analysis showing the degree of correlation between the environmental predictors used in this study

morphospecies were modelled using R v. 4.1.2 (R Core Team) with the 'gbm' package v. 2.1.8.1 (Ridgeway, 2007). The optimal bagging fraction was selected using the gbm.bfcheck() function from the 'gbm.auto' package v. 1.5.0 (Dedman *et al.*, 2017). Because of the small occurrence dataset, a tree complexity of two (Elith *et al.*, 2008) was applied to all models. A model (optimal bag fraction, tree complexity = 2, learning rate = 0.01) was built for each of the three starting variable combinations, and AICc was calculated for each one. The variable combination that produced the model with the lowest AICc was used as a starting array for variable selection. The contribution of each variable was estimated with the summary() function of 'gbm'. The optimal number of trees and learning rate combination were determined through an iterative process minimizing the AICc value to identify the optimal model for predictions (Table S8).

Model evaluation

For each morphospecies, for each modelling approach, data were randomly sampled from the occurrence dataset and divided into ten 70% training and 30% testing subsets used to generate ten additional models. This train-test-split approach was selected as it can be more informative than a usual k-fold validation because it generates multiple estimates of model parameters and evaluation metrics from multiple data splits, reducing the variance of the estimates (Guisan *et al.*, 2017). To prevent spatial autocorrelation, each subset was manually assembled to ensure that test and training points were not sampled from the same sites (Peterson & Soberón, 2012). Only the subsets which had a prevalence ratio within a range of ±0.01 from the original dataset were kept (Howell *et al.*, 2022).

Each model produced probability values indicating the likelihood of presence of the morphospecies in a cell. These values were translated into binary presence-absence using optimality thresholds calculated with the R-package 'Presence-Absence' v. 1.1.9 (Freeman & Moisen, 2008a; Ross & Howell, 2013). Three thresholding techniques were selected: (1) maximization of kappa statistics 'MaxKappa', promising when only presence data are available (Freeman & Moisen, 2008b; Liu *et al.*, 2013); (2) maximization of sensitivity-specificity sum 'MaxSens+Spec', and (3) predicted-observed prevalence equality 'predprev=obs', the latter both suggested for their implications in conservation as they provide unbiased estimates of species prevalence (Freeman & Moisen, 2008b). Five model performance indices (Percent Correctly Classified – PCC, specificity, sensitivity, kappa, and AUC) were calculated and averaged to evaluate the performance of each thresholding method in the training, test, and full datasets (Fielding & Bell, 1997). The threshold returned by the method that maximized performance and minimized the standard deviation of the model, while ensuring a true skill statistics (TSS) value different from zero, was selected (and will be referred as the 'best threshold'). When in doubt between two methods, the one yielding the most restrictive (higher) threshold was chosen. This optimal threshold was applied to the predictive values returned by the optimal models for both model evaluation and mapping.

The performance of each optimal model was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC) and the true skill statistic (Fielding & Bell, 1997; Allouche *et al.*, 2006; Velasco & González-Salazar, 2019), for which probability values were transformed into binary predictions using the best threshold for each model.

Drops in model performance between training and test data were calculated for each algorithm-variable combination and used to evaluate the level of model generalization capability. For each morphospecies, TSS values were computed for the ten trained (TSS_{train}) and ten tested (TSS_{test}) models. The ratio of TSS_{test} to TSS_{train} was then determined to evaluate model performance on the test data. It is expected that model fits will decrease when comparing performance on the training data to that on the unseen test data, and a portion of this performance drop will reflect the inability of the model to generalize to the test data (overfitting). The ratios of TSS_{test} to TSS_{train} were averaged to derive a single score, referred to as the average TSS index (ATI), which summarizes the extent of model overfitting.

$$ATI = \frac{\sum \frac{TSS_{test}}{TSS_{train}}}{10}$$

By dividing the TSS of the test set by the TSS of the training set, ATI provides insight into the generalisation ability and performance of a model. An ATI score equal or close to 1 represents the ideal scenario and suggests that the model fits the training data well and generalises well on unseen data. An ATI score lower than 1 suggests a drop in performance between the training and test data, and is likely an indicator of model overfitting; the smaller ATI is, the worse the model generalises on new data. An ATI score greater than one is an unlikely scenario, in which the model cannot capture the environmental-occurrence relationships in the training dataset, while inflating generalisation because of predictable, imbalanced test data (e.g., far more pseudoabsences than presences).

Mapping

The environmental similarity between the sampling sites and the predictive extent was assessed using Multivariate Environmental Similarity Surfaces (MESS) analysis. This analysis was conducted using the MaxEnt software for MaxEnt models, and the MESS() function of the 'modEvA' package (Barbosa *et al.*, 2013) for GBM models. For each approach and for each morphospecies, a mask was created to retain only the cells that were environmentally similar to the sampled cells (MESS values > 0).

Probability values generated by the optimal MaxEnt (cloglog output) and GBM models were imported into ArcGIS Pro 3.0.3. The data were thresholded to create a probability layer that treated all the values below the optimal threshold as constant absences. The probability values output by the ten train-test models were used to calculate a standard deviation layer with the Cell Statistic Spatial Analyst.

The overlay proportion for each raster and the differences between the likelihood of presence predicted by different frameworks were calculated using the R package 'raster' v. 3.6-26.

Results

Variables contributing to each of the 36 models (nine species using four modelling strategies) built are provided in Table 2. Metrics (AUC, TSS, ATI) evaluating model quality for the four modelling strategies employed for each species are provided in Table 3.

ATI as a metric of model quality

AUC alone does not adequately discriminate against models. Using the thresholds proposed in Coetzee *et al.* (2009), all 36 models presented either useful (0.7<AUC<0.9; 13 models: 4 MAV, 8 MSV, 1 GAV) or excellent (AUC>0.9; 23 models: 5 MAV, 1 MSV, 9GAV, 8GSV). Where the four models appear excellent based on AUC for any given species, we could expect that those four models would predict similar distributions. The four models of *Stauropathes arctica* meet this AUC criterion of AUC > 0.9, but the predicted distributions generated by these models are widely different (Fig. 3). TSS values of these models also indicate that that the models should be useful, as all four models had TSS values >0.6 (Coetzee *et al.,* 2009), hence TSS and AUC combined do not discriminate model quality.

Several models built in this study scored well in both AUC and TSS, but model generalisation dropped when the model was tested on new locations, yielding low ATI scores and producing unreliable distribution maps. Examples of this are the models for *Stauropathes arctica*, with low ATI ranging from 0.086 to 0.404 across all the modelling approaches (Fig. 3). Similarly, the MAV, GAV, and GSV, models of *Stichopathes* m1 and *Cladopathes plumosa* returned ATI scores between 0.187 and 0.478, and 0.263 and 0.299 respectively. The models also resulted in predictive maps suggesting an erroneous distribution of the species, in the form of extended predictions outside the ecologically expected area of distribution of the species, or very conservative, likely overfitted predictions limited to a small number of cells (Fig. 4). .

Only for one species (*Stichopathes gravieri*) was more than one model obtained that had high AUC, TSS and ATI values. In this scenario, we would expect the predicted distributions of both models to be very similar. Both models of *Stichopathes gravieri* created in MaxEnt met these three criteria, with ATI values among the best observed in this study (Table 3). Both models predicted the presence of the corals in similar locations, which diversify from the canyons and slopes where occurrence data were collected (e.g., the coral is also predicted to occur on seamounts and coral mounds). The predicted distribution of the model built using all variables is slightly broader than that produced with a preselected variable array (Fig. 5). However there is agreement in the response curves returned by the two models (Fig. S4.1 and S4.2), which show BBPI and temperature as the sole drivers of the coral distribution (although more importance is given to depth in the MAV model, because of its collinearity with temperature). The map makes ecological sense, predicting *Stichopathes gravieri* on the continental slope and coral mounds/seamounts.

GBM or MaxENT for small datasets?

ATI suggested that all models produced in GBM were overfitted and did not reach acceptable thresholds of transferability. When the probability of distribution was examined over each predictor used in this study (Fig. S6), the models often failed to predict across the full variable range occupied by presence points, with GBM predictions often condensed within a narrow interval of the variable's range. On average, models built using the GBM approach obtained higher AUC and TSS values than MaxEnt models, but the low ATI values (Table 3) reveal a general trend of overfitting. In fact, low ATI values were evident across all modelling approaches, but there was a complete absence of high ATI values observed in GBM models (min 0.086, mean 0.252, max 0.478; Table 3). Moreover, signs of overfitting are detectable in all GBM models for most predictors (Fig. S4.3 and S4.4), with response curve that did not seem to agree on which the main drivers of the morphospecies distribution.

To pre-select or to not pre-select variables

Variable pre-selection in MaxEnt tends to lead to a decrease in TSS. Using the thresholds proposed in Coetzee *et al.* (2009), TSS values indicated six of the nine MaxEnt models without variable pre-selection were useful (0.6<TSS<0.8; five models) or good to excellent (TSS>0.9; one model). When variables were pre-selected, five models were below the useful threshold, four were above it, and no models were good to excellent. When the nine species are considered individually, preselecting variables in MaxEnt led to negligible change (<0.02) in TSS for two species, a small increase (<0.15) for two species, and decreases in TSS for five species, some of which were substantial (0.098, 0.221, 0.245, 0.399, 0.552). The effects of preselection were slightly more variable in GBM models, but since GBM appears less suitable for modelling low data black coral datasets, we do not consider that further here. Response curves of both MAV and MSV models agree in suggesting BBPI and depth/temperature as general drivers of the distribution of most corals. However, information brought by some predictors was lost when using the MSV approach (Fig.

Table 2. Summary of bathymetry (Bathy), BBPI, curvature (Curv), FBPI, planform curvature (PlanC), profile curvature (ProfC), rugosity (Rug), salinity (Sal), slope (Slo), temperature (Temp), horizontal velocity (VelX), and vertical velocity (VelY) permutation importance (i.e. the drop in model score when the values of that variable are randomly permuted) for each modelling framework rounded to one decimal point. The most contributing variable is indicated with a *. The symbol - indicates the variables excluded from the starting variable array, while ✕ indicates the variables excluded as a result of backward stepwise selection.

Morphospecies	Model	Bathy	BBPI	Curv	FBPI	PlanC	ProfC	Rug	Sal	Slo	Temp	VelX	VelY
Antipathes dichotoma	MAV	94.7*	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MSV	-	7.4	-	-	0.0	0.0	0.0	-	0.0	92.6*	0.0	0.0
	GAV	26.4*	3.1	5.1	0.8	1.1	1.3	3.9	15.1	0.7	13.7	9.9	18.9
	GSV	-	6.0	-	-	3.6	3.8	6.3	-	2.6	37.7*	13.9	26.1
Bathypathes m2	MAV	25.6	12.3	0.0	0.0	5.0	0.0	0.0	0.0	13.7	31.2*	1.4	10.9
	MSV	-	43.1*	-	2.6	25	-	✕	-	29.4	✕		✕
	GAV	6.3	4.0	8.8	9.5	10.5	4.4	1.9	12.7	10.9	7.4	2.5	21.1*
	GSV	-	10.3	-	-	16.8	12.9	5.4	-	11.3	17.9	6.5	18.8*
Leiopathes m1	MAV	35.0*	1.6	0.0	0.0	32.3	0.0	0.0	29.8	0.0	0.0	1.3	0.0
	MSV	-	41.7	15.8	-	-	-	✕	-	✕	42.4*	✕	✕
	GAV	10.0	12.7*	9.9	3.9	10.1	8.5	4.2	15.5	4.2	3.3	5.4	12.3
	GSV	-	19.0*	-	10.7	16.2	-	9.0	-	5.0	10.8	12.3	17.0
Parantipathes hirondelle	MAV	21.2	2.2	0.1	12.8	0.3	7.3	21.7*	6.2	8.6	0.0	2.9	16.6
	MSV	-	1.5	-	13.3	5.6	-	9.2	-	29.1	41.3*	0.0	✕
	GAV	3.5	0.7	11.1	9.5	9.0	6.0	2.5	19.9	32.8*	2.7	0.5	2.0
Cladopathes plumosa	MAV	3.7	30.9*	0.0	2.2	9.9	0.0	2.0	24.8	0.4	0.5	5.1	20.5
	MSV	-	34.8*	10.7	-	-	-	16.6	-	2.1	6.3	3.9	25.6
	GAV	0.0	26.6*	0.4	1.1	0.0	11.4	0.0	25.2	0.0	10.2	0.5	24.6
	GSV	-	21.1	3.1	-	-	-	5.3	-	-	34.0*	30.6	5.9
Stauropathes arctica	MAV	3.4	12.0	0.0	0.0	1.5	0.0	7.6	0.3	12.7	35.8*	3.6	22.9
	MSV	-	18.5	-	0.0	✕	-	22.4	-	6.3	26.1*	7.9	18.7
	GAV	3.5	11.0	5.3	5.2	3.0	10.1	14.0	10.0	2.9	24.0*	2.7	8.3
	GSV	-	-	21.4	-	-	-	30.2*	-	-	48.4	-	-
Stichopathes gravieri	MAV	66.8*	28.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	0.0	0.0
	MSV	-	41.9	0.0	-	-	-	0.0	-	0.0	58.1*	0.0	0.0
	GAV	26.0*	6.8	2.4	3.2	2.6	3.5	2.5	8.9	3.7	23.2	7.6	9.5
	GSV	-	12.7	4.8	-	-	-	5.5	-	5.1	48.9*	10.4	12.7
Stichopathes m1	MAV	18.7	2.1	0.1	0.0	4.5	0.0	1.5	0.2	10.0	58.0*	0.2	4.9
	MSV	-	9.6	-	3.3	13.9	-	0.0	-	0.0	73.2*	0.0	0.0
	GAV	10.3	2.3	13.2	8.5	4.3	5.6	4.9	5.4	2.6	12.2	14.6	16.0*
	GSV	-	-	5.0	12.8	10.9	-	8.4	-	-	19.7	22.0*	21.2
Stichopathes m3	MAV	17.8	0.0	2.7	7.5	0.0	0.0	0.4	6.7	0.0	64.9*	0.0	0.0
	MSV	-	0.1	-	-	0.0	18.3	0.9	-	0.0	76.8*	3.8	0.0
	GAV	2.0	1.4	6.9	11.6	4.6	5.6	3.9	49.1*	3.9	3.3	6.2	1.4
	GSV	-	4.8	-	-	9.9	19.7	12.3	-	4.8	29.8*	11.3	7.4

Table 3. For each morphospecies, number of cells treated as presence points (cell count) and summary of the evaluation metrics averaged for the modelling approach: area under the receiver operating characteristic curve (AUC), true skill statistics (TSS) values, and average TSS index (ATI).

Morphospecies	**Cell count**	**Maximum entropy**						**Gradient boosting**					
		Without variable preselection			With variable preselection			Without variable preselection			With variable preselection		
		AUC	TSS	ATI	AUC	TSS	ATI	AUC	TSS	ATI	AUC	TSS	ATI
Antipathes dichotoma	37	0.853	0.510	0.854	0.838	0.650	0.894	0.954	0.817	0.383	0.949	0.765	0.260
Bathypathes m2	42	0.867	0.521	0.292	0.756	0.300	0.663	0.957	0.422	0.250	0.946	0.756	0.222
Leiopathes m1	58	0.791	0.453	0.901	0.828	0.584	0.517	0.917	0.592	0.247	0.913	0.559	0.098
Parantipathes hirondelle	35	0.958	0.837	0.419	0.768	0.438	0.485	0.908	0.685	0.234	0.922	0.575	0.206
Cladopathes plumosa	21	0.912	0.608	0.263	0.882	0.363	0.182	0.904	0.719	0.272	0.895	0.702	0.299
Stauropathes arctica	27	0.928	0.758	0.221	0.906	0.756	0.282	0.955	0.616	0.086	0.935	0.753	0.404
Stichopathes gravieri	64	0.849	0.650	0.960	0.850	0.666	1.070	0.948	0.648	0.153	0.959	0.729	0.138
Stichopathes m1	28	0.942	0.794	0.275	0.743	0.242	0.806	0.990	0.885	0.187	0.958	0.703	0.478
Stichopathes m3	45	0.918	0.755	0.684	0.882	0.657	0.864	0.978	0.761	0.415	0.978	0.434	0.205
Average		0.891	0.654	0.541	0.828	0.517	0.640	0.946	0.683	0.247	0.939	0.664	0.257

S4). Velocity seemed to influence the distribution of morphospecies with more complex morphologies (fans and bushy: *Bathypathes* and *Stauropathes, and Leiopathes*), but these variables were excluded from the MSV models of *Bathypathes* m2 and *Leiopathes* m1, suggesting that pre-selection of variables does not necessarily enhance MaxEnt models.

Ecological distribution of the morphospecies

Ridgeline plots of variable distribution revealed that presences and pseudoabsences of most morphospecies overlapped, indicating unclear niche differentiation. *Bathypathes* m2, *Parantipathes hirondelle*, and *Stichopathes* m1 seem to occur more frequently within a depth range of 1000-2000 m. Similarly, *Parantipathes hirondelle*, *Cladopathes plumosa* and *Stichopathes* m3 do not seem to occur at salinities between 35.2 and 35.8 PSU. Models suggested current velocity as a driver of the distribution of corals with more complex colony shapes, but a niche was not identified through occurrence data.

It was possible to identify an environmental niche for *Stichopathes gravieri*. The models returned BBPI, depth and temperature as drivers of its distribution. This coral seems to mostly occur in habitats between 500 and 1500 m, from flats to depressions, and temperatures >8°C. Although it was observed on inclined terrains, “slope” was not a terrain variable relevant for the coral distribution (Fig. 6).

Discussion

ATI as a metric of model quality

The Average TSS Index (ATI) is good at describing the ability of a model to generalise to new locations. ATI allowed us to identify inaccurate models that otherwise would have been considered ‘good’ when evaluated through standard metrics. The use of one single evaluation metric is discouraged (Araújo *et al.*, 2019); for instance, AIC and AUC are often incorrectly used as the sole criteria by which models with the best prediction capacity are selected (Lobo *et al.*, 2008; Velasco & González-Salazar, 2019). Drops in model performance between calibration and evaluation data (AUC_{diff}) have previously been used to evaluate the degree of model overfitting (Warren & Seifert, 2011; Boria *et al.*, 2014). However, being a threshold-independent metric, AUC cannot measure the accuracy of prediction of SDMs, as these require a unique threshold to be selected to transform the probability of species presence into presence-absence predictions (Shabani *et al.*, 2018). Biases can therefore be introduced by using erroneous thresholds, but can also be counteracted by selecting relevant thresholds tailored to the probability values returned by the models. Nonetheless, neither TSS alone, nor the combined use of TSS and AUC, was sufficient to discriminate model quality in this study.

Where models with low ATI values produced in-

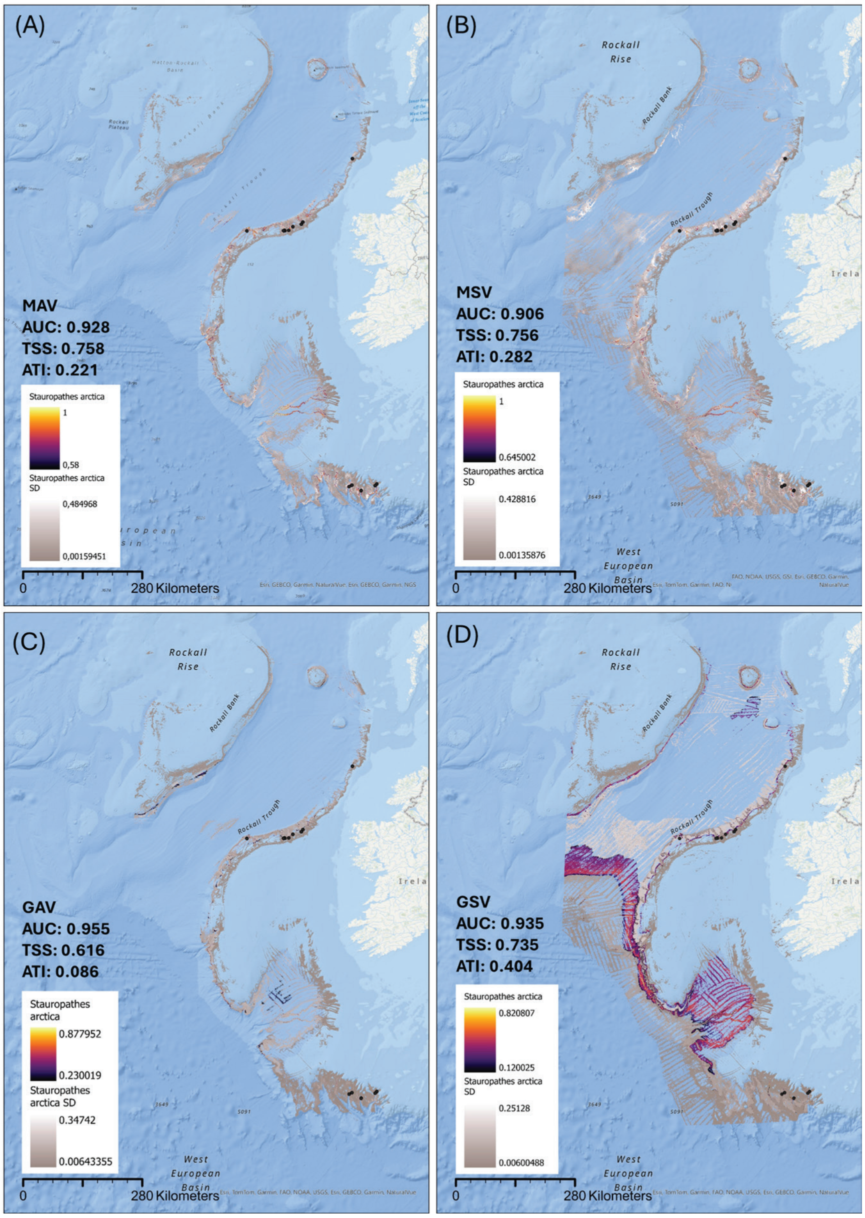

Fig. 3: Predicted distribution of *Stauropathes arctica* when using (a) MaxEnt with all variables, (b) MaxEnt with variable pre-selection, (c) GBM with all variables, and (d) GBM with variable pre-selection. Black dots refer to the cells treated as presences for the morphospecies.

consistent predicted distribution (e.g., *Sta. arctica, C. plumosa, Sti.* m1; Fig. 3 and 4), we cannot assume that any particular modelling framework is better. The models built for *Stauropathes arctica* predict a considerable occurrence of this coral in the Gollum Channel, but such a prevalence has not been documented in previous surveys (Tudhope & Scoffin, 1995). Models built for *Stichopathes* m1 (GAV, GSV) and *C. plumosa* (GSV) predict presence in the Rockall Basin, a region mainly characterized by fine-grain mud and sand sediment (Masson *et al.*, 2002). Although some antipatharians are able to live on soft substrates, the holdfast of these genera is adapted for hard surfaces (Wagner *et al.*, 2012) making the distributions predicted herein unlikely. These inconsistent predictions of a morphospecies' distribution are likely indicative of a paucity of information provided to the model, potentially through using too small occurrence datasets, a too broad cell-size, or because the resolution of environmental parameters is too low to capture the relationship between the environment and the coral observations throughout the whole spatial extent (ICES, 2021).

As per AUC and TSS, ATI scores should also not be used as a sole indicator, but should be evaluated with other indicators, maps, and response curves to obtain a full picture of the model goodness of fit and generalisation. For instance, good ATI scores were observed for the MSV models of *Stichopathes* m1 and m3, which displayed unrealistic predictive maps and an oversimplification of the model response, with most of the distribution explained by too few predictors. Inflated ATI scores were obtained as a consequence of dividing a low TSS_{test} by a low TSS_{train}. Therefore, ATI should also be paired with in-depth evaluation of model sensitivity and specificity to ensure that good ATI values reflect good model generalisation, and are not artifacts resulting from low TSS values in the training and test dataset. As ATI, like TSS,

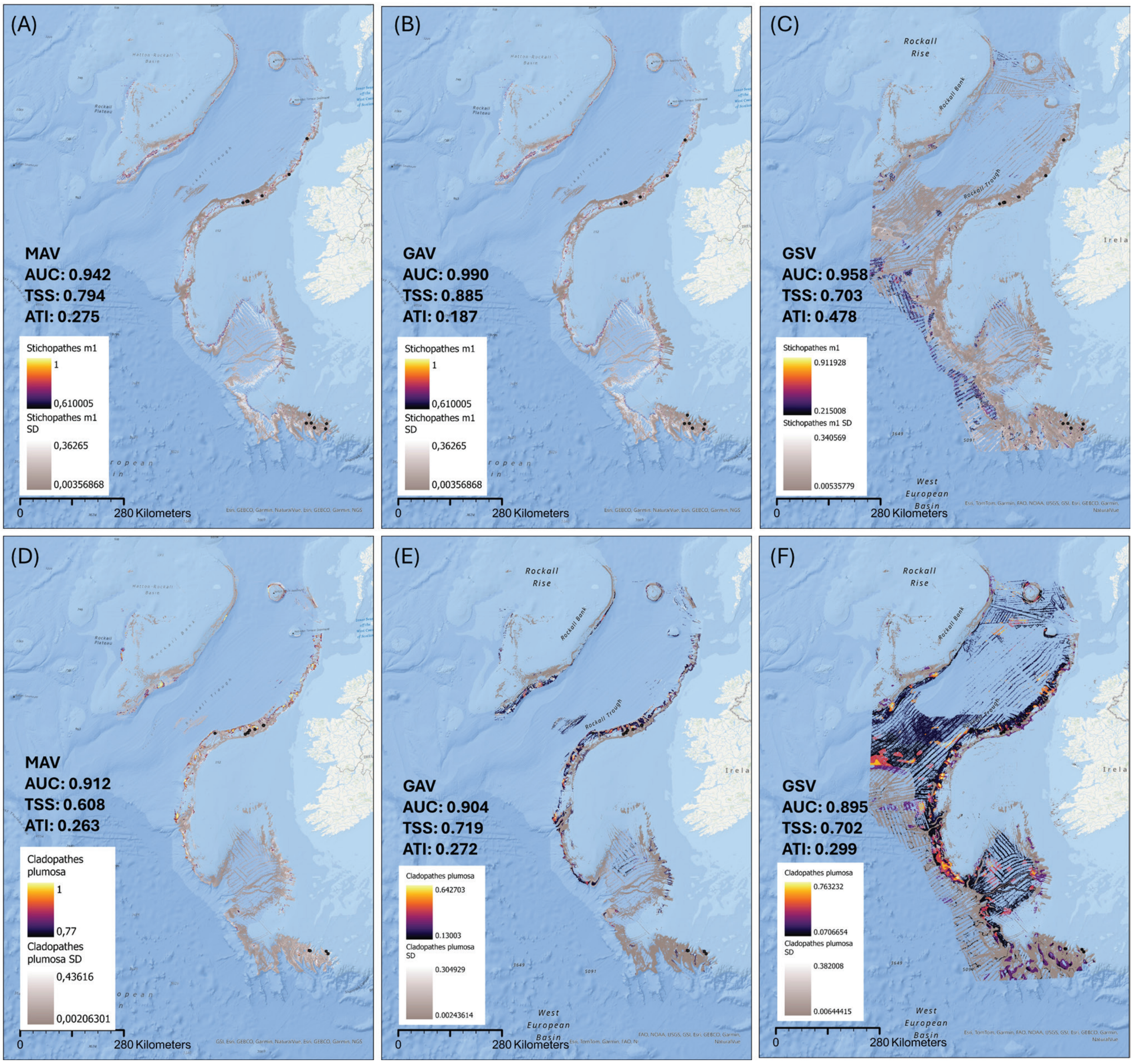

Fig. 4: Wide variations in the predicted distribution of *Stichopathes* m1 when using (a) MaxEnt with all variables, (b) GBM with all variables, and (c) GBM with variable pre-selection, and the predicted distribution of *Cladopathes plumosa* when using (d) MaxEnt with all variables, (e) GBM with all variables, and (f) GBM with variable pre-selection.Black dots refer to the cells treated as presences for the morphospecies.

is a threshold-dependent method, the threshold should be carefully selected for the model applied. This becomes particularly relevant when working with small datasets, where threshold selection can be inflated to boost model accuracy (Bean *et al*., 2012). Thus, the application of ATI in future studies should be supported by thoughtful selection of model threshold, and is not recommended for models that apply a standard threshold to all predictions without careful consideration of its implications on threshold-dependent metrics. Model ground-truthing or independent validation is encouraged before submitting predictive maps for conservation management. Given the challenging nature of collecting independent data in the deep-sea (Bell *et al*., 2022), a tool like ATI, capable of recognising early-stage issues with model generalization, could be used as an exploratory tool for species distribution models where independent data for ground-truthing is not available. In the absence of ground-truthing data, which is a common in deep-sea science, model agreement and plausibility of predictions could be useful tools to assess model generalisation.

When multiple models of a certain species are present, the literature advocates for using ensemble models (Breiner *et al*., 2015), which have already been used to successfully predict the distribution of cold water corals (e.g., Georgian *et al*., 2019; Bargain *et al*., 2018; Lo Iacono *et al*., 2018; Innangi *et al*., 2024; Vinha *et al*., 2024). By combining possible model outputs into a single set of predictions, ensemble modelling takes advantage of the relative strengths of individual algorithms and can reduce uncertainty in habitat prediction (Shabani *et al*., 2016; Araújo & New, 2007; Colin *et al*., 2017; Valavi *et al*., 2022). ATI might be a useful metric to discriminate models before building an ensemble, as it could give

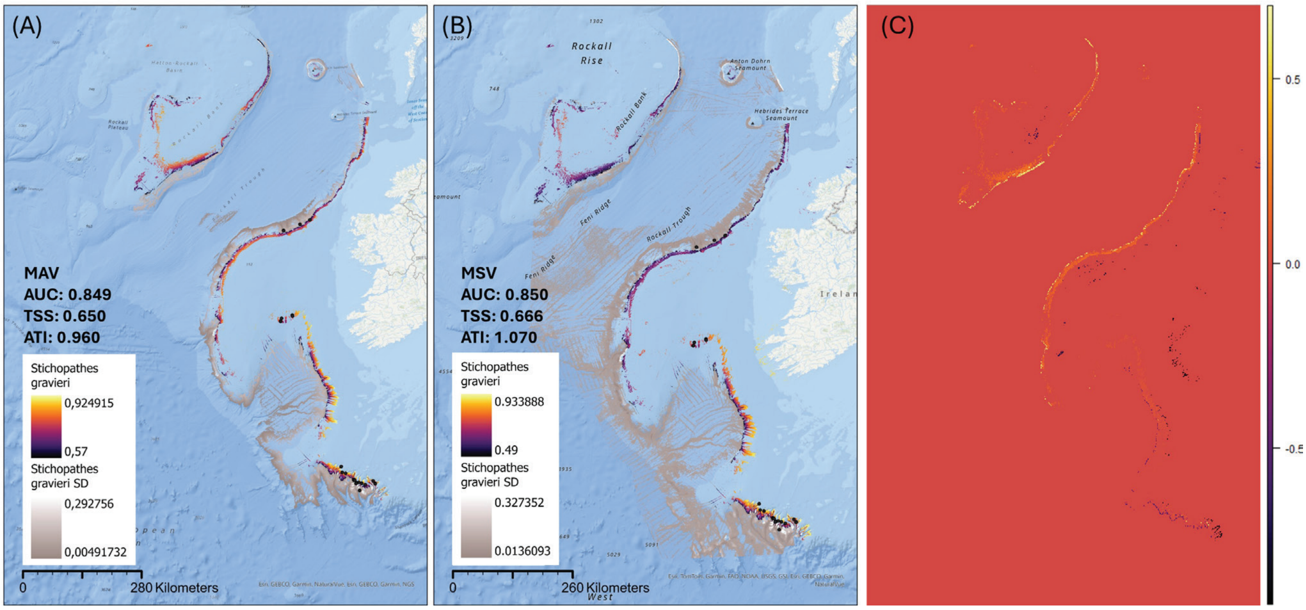

Fig. 5: Threshold-defined predicted distribution of *Stichopathes gravieri* when using Maxent without (a) and with (b) variable selection before modelling. (c) Difference between the threshold-defined likelihood of presence generated by the two frameworks. Brighter cells indicate areas where the species presence is predicted by MAV and not MSV; darker cells indicates areas where the species presence is predicted by MSV and not MAV. Black dots refer to the cells treated as presences for the morphospecies.

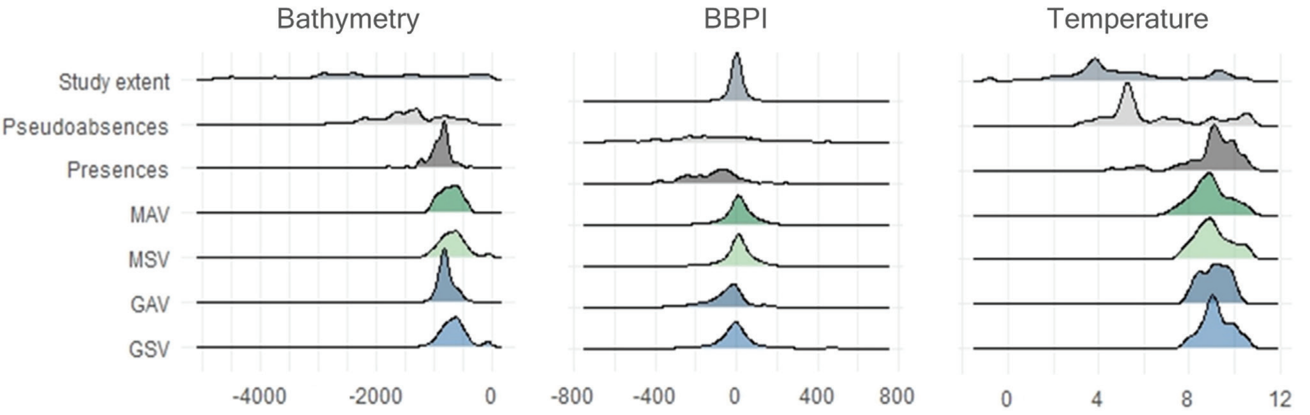

Fig. 6: Ridgeline plots showing the distribution of presences, pseudoabsences and predicted likelihood of presence of *Stichopathes gravieri* across the bathymetry, BBPI and temperature range of the study extent

more information on the generalisation and transferability of the models to be included in the ensemble (e.g., as a check for overfitting). In this study, for instance, ensembling MaxEnt and GBM models for *Stichopathes gravieri* could have introduced an error brought by the overfitted gradient-boosting models. ATI could also be used as a reference metric for weighted averaging of species distribution modelling, giving more importance to predictions of models that are good at generalising to new locations.

GBM or MaxEnt for small datasets?

In this study, MaxEnt appears to be better at predicting the distribution of black corals when small occurrence datasets are available. Through MaxEnt, it was possible to obtain a model of *Stichopathes gravieri* (for which we had the most comprehensive occurrence dataset) that balanced model performance and generalisation. This allowed for the environmental and spatial niche of the species to be defined; *Stichopathes gravieri* seems to be a generalist in terms of seabed features, but requires defined depth (500-1500m) and temperature (8-11°C) ranges.

GBM is known to perform worse than MaxEnt when the models are built using very small occurrence datasets (n = 10) (Wisz *et al.*, 2008). In this study, the occurrence data were likely not comprehensive enough of the whole range of environmental conditions that drive the distribution of our morphospecies. MaxEnt, which can build highly complex and nonlinear response curves (Merow *et al.*, 2014) between species occurrence and environmental predictors, produced models more favourable of generalisation. Gradient boosting builds sequential models that correct the error of previous ones. When the model is built with an insufficient dataset, as apparently in this study, GBM struggles to discriminate between the real occurrence-environment patterns and the noise present in the training data (Elith *et al.* 2008). Hence, a GBM model built with insufficient information will maximise performance at the expense of generalisation, leading to overfitting.

It is important to provide the model with the right amount of data to accurately describe the environmental range in which a species is likely to be found (Wisz *et al.*, 2008). Likely, the sample size for *S. gravieri* was large enough to comprehensively capture the environmental variation associated with the coral distribution, which resulted in a satisfactory MaxEnt model. In contrast, this variation was not fully represented in the smaller dataset of other morphospecies. The minimum recommended size suggested by Wisz *et al*. (2008) for MaxEnt models is too limited to produce reliable models across the vast spatial extent of the Irish margin, where complex interactions between geomorphological and environmental variables drive species occurrence. Biases introduced by small datasets could be overcome by using taxonomically broader groups, but with caution, as using data at low taxonomic levels can result in questionable maps, as species characterised by distinct life histories and environmental needs could potentially be mixed (Winship *et al.*, 2020).

When comparing the frequency distributions of predicted occurrence probabilities among the modelling frameworks, it is evident that GBM values were more skewed, and the median and mean were lower in all cases (Fig. S5). MaxEnt has been previously reported to overestimate the probability of occurrence in unsampled localities and to underestimate it in sampling sites (Fitzpatrick *et al.*, 2013; García-Roselló *et al.*, 2015), a bias that seems to be linked to the smoothing capabilities of the regularization feature integrated in the software (Fourcade *et al.*, 2014). The skewed distributions obtained for the GBM models seem more realistic, both in terms of predicted prevalence and in terms of reflecting the real distribution of probabilities. Although this may not be relevant in terms of mapping the species distribution since the application of an optimal threshold would maintain the best values for predictions, it is important to take this bias into consideration when estimating predictions for conservation purposes.

Despite MaxEnt appearing to perform better, these results do not suggest the exclusive use of a single model type in future studies, as the predictive ability of the models will change with the input data. Using multiple modelling strategies will ensure that issues related to unreliable predictions are dealt with. Methodological challenges such as the scarcity of presence data, sampling bias, and spatial autocorrelation are known to affect the balance between model complexity and goodness of fit of both MaxEnt and GBM models (ICES, 2021). Since maintaining this balance is crucial, it is important to adopt an evaluation framework that assesses both these aspects (Warren & Seifert, 2011; Araújo *et al.*, 2019) perhaps by including TSS and ATI as indicators of model generalisation, while knowing that these metrics cannot replace the benefit of ground-truthing studies.

To pre-select or to not pre-select variables.

The tendency for TSS to decrease with variable pre-selection suggests that pre-selection does not lead to improved models. Full automation of variable selection has been discouraged by previous work, as ecologically important variables could be excluded from the study (Davies & Guinotte, 2011; Yesson *et al.*, 2017; Tong *et al.*, 2023). In this study, including more ecologically relevant predictors when modelling with small datasets helped to compensate for the lack of data from unsampled areas, as proxy variables could detect unseen patterns. Important variables such as velocity were sometimes excluded from MaxEnt models, over-simplifying them and causing erroneous predictions.

While temperature, depth and other bathymetry-derived variables are all known key drivers of coral species distribution in deep-sea environments (Roberts *et al.*, 2009; Yesson *et al.*, 2017; Chu *et al.*, 2019; Auscavitch *et al.*, 2020; Lavorato *et al.*, 2021; Tong *et al.*, 2023), temperature is thought to be the primary driver of cold-water coral distribution across vast regions (e.g., Ross *et al.*, 2015a). When both variables were used in model building, bathymetry tended to explain black coral distribution more than temperature. This apparent contradiction is mainly due to the correlation between the two variables, as shown by the moderate effect of temperature observed in the response curves of MAV models. Moreover, MaxEnt is good at weighing the importance of each variable (Phillips *et al.*, 2006), as demonstrated by the many flat response curves of predictors that did not explain the distribution of the morphospecies. Therefore, including more ecologically relevant predictors when modelling with small datasets could help compensate for the lack of data from unsampled areas, as proxy variables could detect unseen patterns of coral distributions.

The loss of information caused by fitting fewer variables seemed to lead to more issues than the potential overfitting caused by the use of correlated variables. The use of correlated variable pairs has been consistently highlighted as a concern in predictive distribution modelling (Dormann *et al.*, 2013; Araújo *et al.*, 2019; Winship *et al.*, 2020; Zurell *et al.*, 2020) and is discouraged in modelling frameworks aimed at informing decision-making processes (ICES, 2021). However, correlated variables have previously been included in models because of their ecological significance (e.g., Davies & Guinotte, 2011) and our results suggest there are benefits of doing so. MaxEnt models consistently showed a balance in the response curves of correlated variables; for instance, when one variable was identified as a key driver, the response curve of its correlated predictors would be returned flat to moderate. Using too few predictors can lead to over-simplified models, which cannot properly infer the likelihood of species presence (Warren & Seifert, 2011). In this study, variable pre-selection caused the drop of relevant predictors such as velocity for *Bathypathes* and *Leiopathes* morphospecies.

Even though the same number of predictors was always available to MaxEnt and GBM, MaxEnt tended to build simpler models with fewer variables. This can be attributed to the ability of GBM models to capture complex interactions among predictors (Elith *et al.* 2008), which is particularly relevant in ecological modelling where environmental factors often interact in intricate ways (ICES, 2021).

Other limitations

A final consideration is the implications of modelling with an intrinsically biased dataset. Because of the technical challenges common to deep-sea research (Bell *et al.*, 2022), the occurrence points used in this study were mainly collected from canyons, slopes and escarpments. These habitats are characterised by a restricted range of terrains and variables that do not fully cover those found in the whole study area, highlighting a significant sampling bias in the data (Fig. S6). For most morphospecies, presences and pseudoabsences were spread across the full range of predictors, instead of occupying restricted niches. This likely 'confused' the models, that were not able to correctly classify which predictors were most relevant. Sampling bias can sometimes be overcome through spatial filtering (Boria *et al.*, 2014; Araújo *et al.*, 2019), but this would have overly thinned the already small datasets used in the study. Successful ecological modelling should use datasets that are representative of the real species distribution (Araújo *et al.*, 2019), but as different areas were not explored, our datasets may not be representative of the whole extent of the coral niche. Therefore, future expeditions and data collection should target unexplored ranges of the predictors to increase knowledge about the true extent of coral occurrence.

Although the small size of the occurrence dataset likely had the largest influence on model performance, there are other pertinent factors. Occurrence datasets retrieved from image data, as was the case here, can suffer from issues with taxon identification. While OTUs are useful and easily accessible taxonomic units for image-based datasets, organisms with slightly different niches can be grouped in the same morphospecies, introducing a bias (Winship *et al.*, 2020). In addition, cell size (200 m), leads to uncertainty since cells are never fully explored, and the downscaling of predictors (i.e. velocity) could also have introduced bias. Downscaling is a known cause of uncertainty in predictive modelling, as the values in the cells derive from a smooth mathematical function, instead of mirroring reality (ICES, 2021).

It is also important to consider the ecological implications of model resolution when comparing the predictions to the spatial scale of the study, as mismatches between the two may lead to certain species-environment relationships (Davies & Guinotte, 2011; Winship *et al.*, 2020) being overlooked. The resolution used herein (200 x 200 m) was shown to produce models of *Desmophyllum pertusum* reef and *Pheronema carpenteri* aggregations in our focal area that perform better than lower resolution (750 m x 750 m) models (Howell *et al.*, 2022). Nonetheless, if higher resolution terrain and environmental variables were available, then likely more subtle drivers of species distribution could be detected.

Conclusions

In this study, thirty-six models (four different modelling frameworks for nine black coral morphospecies) were explored. In all the models but one species, the models were deemed as unsatisfactory, likely because of the paucity of occurrence datasets. Nonetheless, most of the datasets were not below the minimum sample size recommended for MaxEnt models (>30) (Wisz *et al.*, 2008) and resulted from very extensive ship time (98 dives in five different locations of the North-east Atlantic) that encompassed several environmental conditions suitable for coral presence.

The Average TSS Index (ATI, an index reflecting the change in TSS from training and test datasets) highlights problems with models that are not recognised by considering AUC and TSS alone. This metric should be considered an exploratory tool to be used together with traditional evaluation methods, but which does not replace ecological knowledge of species distribution. Thus, this research presents a framework for evaluating future deep-sea coral models that could avoid erroneous predictions being used for conservation purposes. We additionally provide two realistic and highly similar models for the black coral *Stichopathes gravieri* across the entire Irish EEZ, along with a description of its environmental niche.

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Supplementary Material

The following supplementary material is available for this article:

Section A
Data for species distribution modelling
Variable selection
Model tuning
Model results and evaluation
Optimal models used in the study
Choosing the optimal thresholding methods
Ridgeline plots
Analysis of raster overlay
Analysis with exchange of variables

Section B
Modelling using ‘gbm’ package
Manual assemblage of train and test data
MESS analysis in R
Computing optimal thresholds