# Performance of deep-sea habitat suitability models assessed using independent data, and implications for use in area-based management

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ABSTRACT: Marine spatial management requires accurate data on species and habitat distributions. For the deep sea, these data are lacking. Habitat suitability modelling offers a robust defensible means to fill data gaps, provided models are sufficiently reliable. We tested the performance of published models of 2 deep-sea habitat-forming taxa at low and high resolutions (~1 km and 200 m grid-cell size), across the extended exclusive economic zones of the UK and Ireland. We constructed new data-rich models and compared new and old estimates of the area of habitat protected, noting changes in the protected area network since 2015. Results of independent validation suggest that all published models perform worse than expected considering original cross-validation results, but model performance is still good or fair for *Desmophyllum pertusum* reef, with poorer performance for *Pheronema carpenteri* sponge models. High-resolution models using multibeam data out-perform low-resolution GEBCO-based models. Newly constructed models are good to excellent according to cross validation. New model spatial predictions reflect published models, but with a significant reduction in predicted extent. The current marine protected area network and the European Union ban on bottom trawling below 800 m protect 40 and 60% of *D. pertusum* reef-suitable habitat, respectively, and 11 and 100% of *P. carpenteri*-suitable habitat, respectively, within the model domain. We conclude that high-resolution models of *D. pertusum* reef distribution are a useful tool in spatial management. The poorer performing *P. carpenteri* model indicates areas for more detailed study. While low-resolution models can provide conservative estimates of percentage area-based conservation targets following the precautionary principle, high-resolution sea-floor mapping supports the development of better-performing models.

KEY WORDS:  Deep sea · Habitat suitability modelling · Species distribution modelling · Marine conservation · Marine spatial planning · *Pheronema carpenteri* · *Desmophyllum pertusum*

## 1.  INTRODUCTION

As we begin the UN Decade of Ocean Science for Sustainable Development, the call for more holistic management of the marine environment is clear.

Marine spatial planning (MSP) is an important tool supporting implementation of the 'ecosystem approach' to environmental management, as outlined in the Convention on Biological Diversity (CBD), and enshrined in the UN Sustainable Development Goals

(UN General Assembly 2015). Maps lie at the heart of spatial management, including maps of human uses, socio-economics, political and legal arrangements and, critically, biophysical conditions and assemblages or communities of marine organisms, such as kelp forests and coral reefs. There is a pressing need to develop reliable and accurate maps of the spatial distribution of marine ecosystems to support conservation initiatives.

Efforts to map benthic marine communities have largely focussed on shallow-water environments (Andrefouët et al. 2006, Traganos et al. 2018). Mapping deep-water communities is much more difficult because there is no direct equivalent to optical remote sensing which provides wide coverage of high-resolution data with direct observation of terrestrial and shallow (<10 m) coastal habitats. The majority of deep-water benthic biological mapping has been achieved using modelling approaches. Species distribution modelling, also called habitat suitability modelling, uses data on the presence, absence, abundance or biomass of a species, assemblage or community, and relevant environmental data, to produce a statistical model of the relationship between species and their environmental drivers. The model can be used to make predictions of the distribution of the target species/community based on environmental data alone (Bryan & Metaxas 2007, Rengstorf et al. 2014, Howell et al. 2016). This type of mapping lends itself well to use in the marine environment, as the physical environment is often cheaper and simpler to measure than the biological components. There is a wealth of local, regional and global physical spatial models of the marine environment including oceanographic, bathymetric and productivity models. Benthic biological data are generally available for coastal marine areas and, together with physical environmental data, they offer great potential to produce relatively data-rich modelled maps. However, availability of benthic biological data decreases with increased distance away from the coast and into the deep sea (Webb et al. 2010), and this can present challenges in the development of reliable models.

The deep sea is increasingly subject to human use, and there is an urgent need to implement more effective, integrated management of deep-sea ecosystems through the use of area-based management tools and MSP. The last 15 yr have seen a growing trend in the use of predictive mapping techniques to generate models of the distribution of key species and assemblages in the deep sea (e.g. Bryan & Metaxas 2007, Guinan et al. 2009, Howell et al. 2011, 2016, Rengstorf et al. 2014, Robert et al. 2016, Pearman et al. 2020).

These efforts have focussed particularly on those species and assemblages that appear in key marine conservation legislation, and have produced modelled maps from a wide range of regions, of different extents and spatial resolutions. Models that provide large spatial coverage of a scale useful to national and regional MSP efforts tend to use low-resolution (>1 km$^2$) modelled global environmental data sets in their production (Howell et al. 2016). Higher-resolution environmental data sets, such as multibeam bathymetry, and regional or site-specific oceanographic models tend to only be employed in the construction of models with a more limited spatial extent (Pearman et al. 2020), rendering them less useful for national- and regional-scale MSP, but still informative.

While the potential applications of modelled maps in MSP have been demonstrated (Ross & Howell 2013, Howell et al. 2016, Stirling et al. 2016, Rowden et al. 2017), models are not yet widely used despite their obvious potential (Marshall et al. 2014, Reiss et al. 2015). This contrasts with many other fields, for example fisheries and climate science, where models are routinely used to forecast future scenarios, and the results are used to make management and policy decisions (Hilborn 2012, IPCC 2014). The reasons for this are not clear. In their review of common objections to the use of models in environmental decision making, Addison et al. (2013) identified 9 key objections that are symptoms of 3 fundamental issues: (1) misconceptions about the role of models in decision making, (2) poor modelling practice and (3) a lack of effective communication and/or trust between modellers and decision makers. Objections around modelling practice and outputs include issues with model accuracy and uncertainty. Model performance is usually tested using random subsampling from the full model build data set, so-called cross validation. However, the lack of true independence between testing and training data sets, as well as spatial sorting bias, is known to artificially inflate model performances (Veloz 2009, Hijmans 2012) leading to a phenomenon where many models appear to perform well yet provide very different spatial predictions (Piechaud et al. 2014, Howell et al. 2016). This may serve to compound concerns around model accuracy and uncertainty, and highlight the need for independent validation of model performance to help allay these concerns and encourage wider use of model output.

In the NE Atlantic, habitat suitability models (HSMs) for scleractinian cold-water coral reefs and the aggregation-forming deep-sea sponge *Pheronema carpenteri* have been developed for the continental shelf

claim areas of the UK and Ireland (Ross & Howell 2013, Ross et al. 2015).

Reefs of the scleractinian coral *Desmophyllum pertusum* are widely recognised as distinct biological communities or 'biotopes', and occur as thickets, discrete reefs and giant carbonate mounds up to 300 m high and several km in diameter. Within this region, reefs have been observed on Hatton, George Bligh and Rockall Banks, the Wyville-Thomson Ridge and in Explorer and Dangaard Canyons (Howell 2010, Howell et al. 2010), the Porcupine Seabight (Foubert et al. 2005, Huvenne et al. 2005), Porcupine Bank (Kenyon et al. 1998), southern Rockall Bank (Mienis et al. 2006, Wienberg et al. 2008) and the Outer Hebrides (Roberts et al. 2005), as well as farther north and south (Wheeler et al. 2007). Observations occur over depths from ~120 to ~1000 m, with most reported from 600 to 800 m. Reef structures are highly biodiverse (Roberts et al. 2006), and have an important role as essential fish habitat (Husebø et al. 2002, Auster 2005).

*P. carpenteri* is a small spherical glass sponge that occurs singularly or in dense aggregations, predominantly (but not exclusively) on fine sandy mud and mud substrata. Within UK and Irish waters, aggregations are a recognised biotope, and communities composed of this species have been described from 1250 m in the Porcupine Seabight (Rice et al. 1990), 1100 m in the Hatton-Rockall Basin (Hughes & Gage 2004, Howell et al. 2014) and from 1450 m on Goban Spur (Lavaleye et al. 2002), with historical records of additional aggregations from Ireland to Spain in 1000–2000 m water (Le Danois 1948) and in the Northern Rockall Trough (Wyville-Thomson 1874). Aggregations are associated with an increase in abundance and richness of macrofauna observed within spicule mats and sponge bodies (Rice et al. 1990, Bett & Rice 1992). Recent studies have suggested that known aggregations may be poorly connected (potentially isolated) (Ross et al. 2019) and experience a substantive impact from bottom trawl fishing (Vieira et al. 2020).

From a policy perspective, both *D. pertusum* reef and *P. carpenteri* aggregations are considered 'Vulnerable Marine Ecosystems' (VMEs) under United Nations General Assembly (UNGA) Resolution 61/105, and as 'threatened and/or declining species and habitats' under the OSPAR Convention for the Protection of the Marine Environment of the North-east Atlantic 1992. Understanding their distribution is therefore an important component to the development of area-based management of the region.

The models of Ross & Howell (2013) were constructed using global-scale environmental data layers including the General Bathymetric Chart of the Oceans (GEBCO) and are at a resolution of ~1 km². The models of Ross et al. (2015) were constructed using high-resolution multibeam data sets and are at a resolution of 200 × 200 m grid cell size. Both models were produced using the same underlying presence/absence biological data set for each response variable, *D. pertusum* reef habitat and *P. carpenteri* species. All 4 models performed well when tested using cross-validation methods, and in general, high-resolution models performed better than low-resolution models according to threshold-dependent evaluation. However, the spatial predictions and resulting maps derived from models of different resolution were notably different. The aim of this study was to undertake independent validation of these published models of VME distribution in the UK and Irish extended continental shelf claim areas, in order to assess model performance and inform future use in MSP and conservation. Specifically, we (1) independently validated model performance using newly collected independent data, (2) constructed new relatively data-rich models using the same modelling method as the prior publications and (3) quantified changes in predicted distributions and assessments of percentage protection targets for each VME (VME indicator taxa in the case of *P. carpenteri*) as a result of new models.

## 2. MATERIALS AND METHODS

### 2.1. Site and model description

The study considers the full extent of the Irish, and a partial extent of the UK, extended continental shelf claim area in the NE Atlantic (Fig. 1). A network comprising 3 different types of marine protected area (MPA) exists in this area for the protection of deep-sea habitats (Fig. 1): Special Areas for Conservation, OSPAR MPAs and North East Atlantic Fisheries Commission (NEAFC) closures to bottom trawling for the protection of VMEs. While the sites do not constitute a coherently designed MPA network, they enable illustration of the potential use of habitat maps in area-based management. In addition, there is a ban on bottom trawling below 800 m in European and UK waters.

Scleractinian reef models of Ross & Howell (2013) and Ross et al. (2015) were predominantly constructed using *Desmophyllum pertusum* reef presence/absence data. However, a small number of presence points for *Solenosmilia variabilis* reef were also included in the models. In our experience, *S. variabilis* appears to occupy the same topographic niche as *D.*

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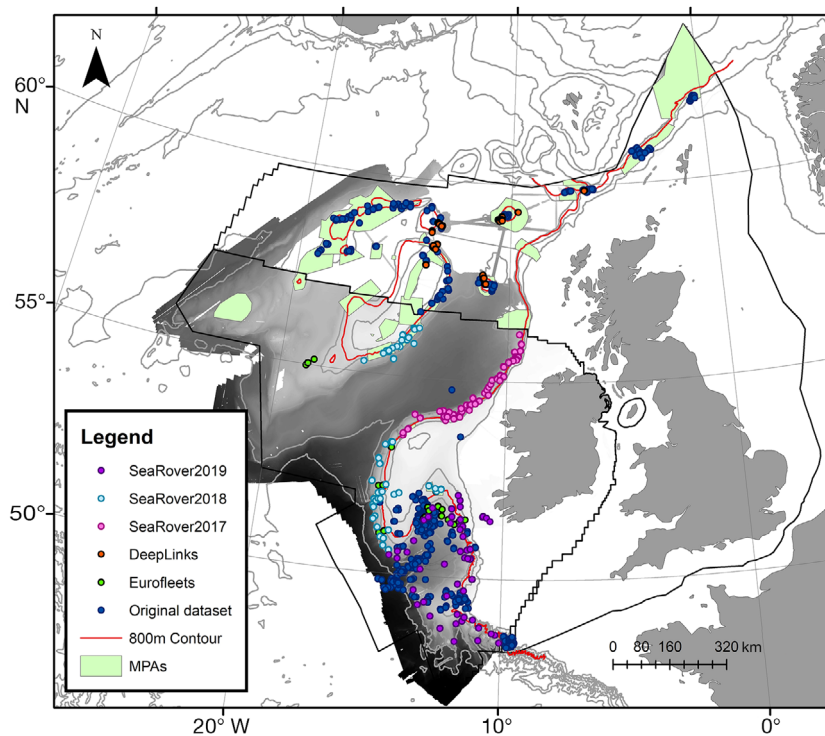
## 2.2. Biological data



Fig. 1. UK and Ireland Continental Shelf limits (black line) showing the original data sets from Ross & Howell (2013) and Ross et al. (2015) together with the new data set (compiled from 5 different surveys over 5 years) used to independently validate the models and subsequently build new models. The current network of deep-sea marine protected areas (MPAs) is shown, together with the 800 m isobath, below which bottom trawling is prohibited. Bathymetry shown is the 200 × 200 m gridded multibeam data set (see Section 2.1 paragraph 2 for detail) shaded for depth with contours of 200, 500 and 1000 m and intervals of 1000 m thereafter shown in grey. Map projected in British National Grid for aesthetic reasons

New data for both *P. carpenteri* and *D. pertusum* reef were compiled from 5 research cruises to the NE Atlantic: (1) Eurofleets2-funded DeepMap cruise CE15011 (2015), with remotely operated vehicle (ROV) 'Holland I'; (2) NERC-funded Deep Links JC136 (2016), with ROV 'ISIS'; (3–5) Sea Rovers RH17001 (2017), RH18002 (2018) and CE19015 (2019), jointly funded by the Irish Government and EU, with ROV 'Holland I'. These research cruises were not conducted for the sole purpose of model validation, but this was a consideration in transect line planning for all cruises. Transect lines ranged from approximately 100 m to 3.1 km, with an average length of 1.3 km. Collectively, these research cruises provide a data set consisting of 195 high-definition ROV video transects spread over the study area (Fig. 1). This collective data set is referred to throughout as the 'new' data set.

For the original data sets, presence of target habitat was determined from both quantitative and qualitative analysis of still image data taken at 1 min intervals along transects as described by Howell et al. (2010). *P. carpenteri* presence was determined from species lists from analysed sample data. *D. pertusum* reef habitat description follows that provided by Howell (2010), and subsequently adopted for use in the UK Deep Sea Habitat Classification (Parry et al. 2015). For the new independent data set, presence of the target habitat/species was determined by expert evaluation of image-based data alone. Habitat identification was undertaken by 2 annotators and designated when the habitat extent satisfied the OSPAR minimum biotope area threshold (25 m²). For quality assurance, 5% of transects were independently analysed by K. Howell following interobserver agreement standards used in published evidence (MacLeod et al. 2010).

## 2.3. Original model validation

For each of the 4 published models, the new biological data set was plotted in ArcGIS on raster grids of published model output, in their respective

*pertusum* but occurs in deeper water. Records included in the models were at the shallow end of their distribution only. The resulting models largely predicted the niche of *D. pertusum* reef but with a slightly deeper reach. This study evaluates and builds upon the original models using new *D. pertusum* reef data alone with *S. variabilis* reef data omitted. The models of Ross & Howell (2013) have a resolution 750 × 750 m grid cell size determined by the resolution of GEBCO at the latitude of the study site, and cover the full extent of both the Irish and UK continental shelf limit. The models of Ross et al. (2015) have a resolution of 200 × 200 m grid cell size and cover the full extent of the Irish, and the partial extent of the UK, continental shelf limit in the NE Atlantic. Both studies used their models to assess progress towards percent protection conservation targets, and reported that between 20 and 29% of scleractinian reef-suitable habitat and between 1.9 and 2.9% of *Pheronema carpenteri*-suitable habitat lies within the MPA network.

output projections, and ROV point-based position data were reduced to 1 point per cell to avoid over-/under-weighting the importance of specific environmental conditions. Where cells contained any ROV position points interpreted as presence points, the 1 point per cell was denoted as a presence, all other points were denoted as absence. As the original models were masked for novel climates, new data points that did not sit on old model predictions were removed from the data set as they were considered out of the original model domain. The final independent validation data sets for the 200 × 200 m model included 2018 data points for *D. pertusum* reef and 1937 data points for *P. carpenteri* aggregations; for the 750 × 750 m model, the independent validation data sets included 646 data points for *D. pertusum* reef and 597 data points for *P. carpenteri* aggregations (Table 1). To assess the potential effect of spatial autocorrelation in inflating model performance, independent validation was also undertaken by reducing the data sets to one point per ROV transect. For each response variable, a single presence point was randomly selected within each transect, and a single absence point from absence transects. This provided 173 and 163 validation points for the *D. pertusum* and *P. carpenteri* 200 × 200 m models, respectively, and 186 and 182 validation points for the *D. pertusum* and *P. carpenteri* 750 × 750 m models, respectively.

The probability values from published model layers (coglog MaxEnt output) were extracted for each data point. Threshold independent metrics of model performance (area under the receiver operating characteristic [ROC] curve, AUC) for each model were calculated and compared to the original published models. Threshold-dependent metrics of model performance (specificity, sensitivity and percent correctly classified [PCC]) were also calculated by converting extracted probability values to binary presence–absence using (1) the thresholds defined in the original publications, and (2) new thresholds that maximized model performance against the new data set.

## 2.4. Construction of new models

Newly collected high-resolution multibeam bathymetry data (see Supplementary Material 1 at www. int-res.com/articles/suppl/m695p033_supp.pdf) were added to the data described by Ross et al. (2015) and used to create grids with a cell size of 200 × 200 m that were re-projected from their original projection (WGS84) into Goode Homolosine Ocean (GHO) equal-area projection in order to allow for correct calculation of derived topographic layers and area.

### 2.4.1. Variable selection

Seven topographic variables were derived from the bathymetric data using the ArcGIS Benthic Terrain Modeler add-in (Walbridge et al. 2018): terrain ruggedness, curvature, plan curvature, profile curvature, slope, broad-scale bathymetric positions index (BBPI) and fine-scale bathymetric position index (FBPI). Information on the calculation and use of each of these variables can be found in the existing literature (Guinan et al. 2009, Ross & Howell 2013). The inner and outer radii for BBPI were 5 and 50 raster cells, respectively, facilitating identification of topographic features at the 10 km scale, such as canyons and hills. For FBPI, the inner and outer radiuses were 1 and 5 raster cells, respectively, allowing for the identification of features within the <1 km scale, such as gullies. Generalised additive models (GAMs) were used to build bottom temperature and salinity layers using *in situ* CTD data from ROV and drop camera transects, as well as archived CTD casts from the British Oceanographic Data Centre (BODC) database. GAMs were implemented in R (R Core Team 2020) using the 'mcgv' package (Wood 2011) with depth, latitude and longitude used as explanatory variables. A detailed description is given in Supplementary Material 2. New and original biological data sets for each of *D. pertusum* reef and *P. carpenteri* presence/absence were combined, reprojected into GHO and plotted in ArcGIS on raster grids of envi-

Table 1. Breakdown of biological data sets, showing total (presence/absence) data points, used to build habitat suitability models and independently validate the models of Ross & Howell (2013) and Ross et al. (2015). GEBCO: General Bathymetric Chart of the Oceans

| | Ross & Howell (2013) (GEBCO) | Ross et al. (2015) (200 × 200 m grid) | New model | Ross & Howell (2013) (GEBCO) validation | Ross et al. (2015) (200 m) validation |
|---|---|---|---|---|---|
| *Desmophyllum pertusum* | 864 (75/789) | 1284 (116/1168) | 3291 (227/3064) | 646 (64/582) | 2018 (122/1896) |
| *Pheronema carpenteri* | 864 (53/811) | 1284 (74/1210) | 3196 (139/3057) | 597 (32/565) | 1937 (66/1871) |

ronmental data. ROV/drop camera point-based position data were reduced to 1 point per cell, where cells containing any presence observations were denoted as a presence, all other points were denoted as absence. Environmental data were extracted for each data point.

Maximum entropy (MaxEnt) modelling (Phillips et al. 2006, Elith et al. 2011) is a presence-background modelling technique that has a successful performance record (Elith et al. 2006), particularly in studies with low prevalence (low number of presence records). Although MaxEnt was designed to account for covariation in data sets and can perform well with correlated variables (Feng et al. 2019), previous studies have found that pre-selection of variables leads to better-performing models (Ross & Howell 2013). Environmental variables were therefore first assessed for covariance using correlation matrices and variance inflation factors (VIFs) in R. Strong correlations and VIFs between variables (≥±0.7 and ≥3, respectively) were addressed by removing 1 variable from each correlated pair based on the jackknife procedure. Jackknifing calculates the individual contribution of variables to a model and produces model performance statistics (termed 'gain' in MaxEnt) for each. Once correlates were removed, a model with all remaining variables was built. Following principles of model parsimony, final sets of variables were selected by systematically removing the variable contributing the least to the model (based on model gain with and without that variable) until the drop in overall performance was deemed unacceptable. This process is described in detail in Supplementary Materials 3 and 4.

### 2.4.2. Modelling

If used with presence-only data, MaxEnt randomly selects a specified number of 'background' points that are considered to represent locations with an equal likelihood of having been sampled that act as the absence points to inform the model (Elith et al. 2011). Whilst 'absence' points are presented in this study for each target taxa/habitat, it is not possible to be certain that they are not present somewhere within a 200 m grid cell due to the limited field-of-view of camera equipment compared to the size of grid cells, and therefore the data within this study represent 'pseudo-absences'. Having pseudo-absence data allowed for the MaxEnt samples-with-data (SWD) approach to be used, whereby environmental values are provided in a spreadsheet for both the

presence and pseudo-absence points, instead of allowing MaxEnt to randomly select background points to act as absences. The benefit of the SWD approach is that as both the presence and pseudo-absence points come from the same sampling campaigns, it allows for the control of some bias in sampling locations and experimental design that can facilitate improved predictive performance (Phillips & Dudík 2008).

Preliminary models with different parameters were systematically trialled, including the changing of feature classes (linear, quadratic, product, hinge and threshold) and the regularisation parameter (0.1, 0.5, 1, 3, 5, 10) to avoid over-fitting/-smoothing (Phillips & Dudík 2008). The final feature classes selected for both target habitat models were linear, quadratic and product features. Through trialling, hinge and threshold features were removed due to lack of ecological applicability in this study; with these features turned on, the response curves produced did not make biological sense. The *D. pertusum reef* model used a regularisation parameter of 1, whilst the *P. carpenteri* model used 0.5. These parameters were chosen because they struck a balance between the model overfitting and over-generalising; this was apparent from the shape of the response curves and AUC scores. The final MaxEnt models were projected onto the study area in a raster format and constrained to sampled conditions using the MaxEnt novel climates output (i.e. areas where environmental values fall within those on which the model was trained). Environmental data layers used in the final models are plotted in Supplementary Material 5 and final model details are provided in Supplementary Material 6.

### 2.5. Evaluation of new models

Both presence and pseudo-absence records were used to evaluate the performance of the MaxEnt models by partitioning the data using a 70/30 split 10 times to create 10 sets of training and test data. These data sets were compiled manually rather than using the automated MaxEnt splitting tool to reduce spatial autocorrelation in the data. To achieve this, data sets were split such that whole transects fell into either a training or testing data set. This avoided a scenario where a single transect would be split into training and testing points, leading to a within-transect testing point validating the same transect (Howell et al. 2011). The prevalence within each test and training data set was compared

to the prevalence of the full data set, and any data sets identified as having >±1% change in the amount of presence data were discarded and another random partition made until all test and training data sets satisfied the criteria. Using the partitioned data, 10 new models were built for each habitat and evaluated using the 'PresenceAbsence' package (Freeman & Moisen 2008) in R, employing both threshold-independent (AUC) and threshold-dependent metrics.

Three thresholding techniques were used to assess model performance, as suggested by Liu et al. (2005) and recognising that different thresholding methods are chosen to achieve different ends. Thresholds used were sensitivity-specificity equality (Sens=Spec), sensitivity-specificity sum maximization (MaxSens+Spec) and minimum distance to the top left corner in the ROC curve plot (MinROCdist). Using the 'presence.absence.accuracy()' function, the thresholding techniques and resulting model performances were assessed with 3 widely used indices: sensitivity, specificity and PCC. True skill statistic (TSS) can be calculated from sensitivity and specificity and is used in place of Cohen's kappa as it corrects the overall accuracy of the model predictions using the accuracy expected to occur by chance (Allouche et al. 2006). For both AUC and threshold-dependent metrics, the mean and SD for each metric were calculated for the 10 partitioned data sets and for the full model.

## 2.6. Quantification of habitat distribution and MPA analysis

The thresholding technique that gave the highest average performance across the 3 chosen indices was selected for use in the final models. A binary raster of predicted presence and absence was produced as well as a raster of probability of predicted presence. Model fit was visualized by plotting the match–mismatch of binary predictions (Supplementary Material 7) In addition, the relative probability maps from all 10 partitioned test/training models were used to produce standard deviation rasters to convey spatial uncertainty in the model predictions (Supplementary Material 8). The number of predicted presence raster cells within different MPA polygons and below 800 m were calculated and then expressed as percentages of total presences in the whole study area, in UK waters and in Irish waters. Values derived from published and new models were compared.

## 3. RESULTS

### 3.1. Original model validation

Results of the independent validation suggest that all published models perform worse than expected based on cross-validation results for both threshold-dependent and -independent metrics (Tables 2 & 3). Model performance is still considered good (0.8–0.9) or fair (0.7–0.8) for scleractinian cold-water coral reef habitat models, with poorer performance for the *Pheronema carpenteri* models, particularly at low resolution. Independent validation using the thinned data set of 1 point per ROV transect (removing effects of spatial autocorrelation) gave similar results. The extremely low prevalence of the *P. carpenteri* data set (Table 1) means that model performance as measured by PCC is very much influenced by correct prediction of absences (specificity); it also means that threshold selection will be strongly influenced by specificity and might explain why the new thresholds are all very low. High-resolution models out-performed low-resolution models for both taxa.

### 3.2. New model development and evaluation

Results of variable correlation analysis and step-by-step documentation of the variable pre-selection procedure are provided in Supplementary Materials 3 and 4. Consideration of common performance indices (Table 4) allowed for selection of final thresholding methods. For both models, Sens=Spec was selected as the chosen thresholding method, providing thresholds for *Desmophyllum pertusum* reef and *P. carpenteri* aggregations of 0.44 and 0.37, respectively. For *D. pertusum* reef, the AUC value for the full internally validated model and all cross-validation models was deemed excellent (0.9+). The 0.44 threshold determined by Sens=Spec generated good (0.8+) results for PCC, sensitivity and specificity for all models.

For *P. carpenteri*, the AUC value for the full and all cross-validation models was deemed excellent. When thresholded at 0.26, all threshold-dependent metrics (PCC, sensitivity and specificity) for the full and training *P. carpenteri* models were classified as excellent (0.9+ full model and training sensitivity) or good (0.8–0.9 for training PCC and specificity) when internally validated. All cross-validation models were classified as good (0.8–0.9).

Table 2. Performance statistics for the published models of Ross & Howell (2013) according to original cross validation and new independent validation. Values given are means where followed by standard deviation given in brackets. Threshold values are predicted probabilities of presence. PCC: percent correctly classified; TSS: true skill statistic; AUC: area under the receiver operating characteristic (ROC) curve; MinROCdist: minimum distance to the top left corner in the ROC curve plot; Sens=Spec: sensitivity-specificity equality; MaxSens+Spec: sensitivity-specificity sum maximization. Method is left blank where no re-thresholding took place and threshold method used is that of the original model

| | Method | PCC | Sensitivity | Specificity | TSS (Sens+ Spec-1) | AUC | Threshold values |
|---|---|---|---|---|---|---|---|
| ***Desmophyllum pertusum* reef** | | | | | | | |
| Original cross validation with original threshold (Ross & Howell 2013) | MinROCdist | 0.82 | 0.75 | 0.82 | 0.57 | 0.86 | 0.48 |
| Independent validation with original threshold | | 0.68 (0.02) | 0.78 (0.05) | 0.67 (0.02) | 0.45 | 0.74 (0.02) | 0.48 |
| Independent validation but tuned to maximize model performance (new threshold selected) | Sens=Spec | 0.70 (0.02) | 0.70 (0.06) | 0.70 (0.02) | 0.40 | 0.74 | 0.50 |
| Independent validation with original threshold and thinned data set | MinROCdist | 0.77 (0.03) | 0.71 (0.08) | 0.78 (0.03) | 0.49 | 0.79 (0.04) | 0.48 |
| Independent validation but tuned to maximize model performance (new threshold selected) using thinned data set | Sens=Spec | 0.73 (0.03) | 0.74 (0.07) | 0.73 (0.04) | 0.47 | 0.79 (0.04) | 0.44 |
| ***Pheronema carpenteri*** | | | | | | | |
| Original cross validation with original threshold (Ross & Howell 2013) | MinROCdist | 0.95 | 0.96 | 0.95 | 0.91 | 0.99 | 0.19 |
| Independent validation with original threshold | | 0.91 (0.01) | 0.34 (0.09) | 0.95 (0.01) | 0.29 | 0.65 (0.05) | 0.19 |
| Independent validation but tuned to maximize model performance (new threshold selected) | MaxSens+ Spec | 0.92 (0.01) | 0.34 (0.09) | 0.95 (0.01) | 0.30 | 0.66 (0.05) | 0.45 |
| Independent validation with original threshold and thinned data set | MinROCdist | 0.89 (0.02) | 0.31 (0.12) | 0.95 (0.02) | 0.26 | 0.71 (0.07) | 0.19 |
| Independent validation but tuned to maximize model performance (new threshold selected) using thinned data set | MaxSens+ Spec | 0.90 (0.02) | 0.31 (0.12) | 0.95 (0.02) | 0.26 | 0.71 (0.07) | 0.375 |

Table 3. Performance of the published models of Ross et al. (2015) according to original cross validation and new independent validation. Values given are means where followed by standard deviation given in brackets. Threshold values are predicted probabilities of presence. Abbreviations as in Table 2. Method is left blank where no re-thresholding took place and threshold method used is that of the original model

| | Method | PCC | Sensitivity | Specificity | TSS (Sens+ Spec-1) | AUC | Threshold values |
|---|---|---|---|---|---|---|---|
| ***Desmophyllum pertusum* reef** | | | | | | | |
| Original cross validation with original threshold (Ross et al. 2015) | MinROCdist | 0.85 | 0.85 | 0.85 | 0.70 | 0.91 | 0.43 |
| Independent validation with original threshold | | 0.72 (0.01) | 0.88 (0.03) | 0.70 (0.01) | 0.58 | 0.87 | 0.43 |
| Independent validation but tuned to maximize model performance (new threshold selected) | Sens=Spec | 0.77 (0.01) | 0.75 (0.04) | 0.77 (0.01) | 0.52 | 0.87 (0.01) | 0.48 |
| Independent validation with original threshold and thinned data set | | 0.82 (0.03) | 0.82 (0.07) | 0.82 (0.03) | 0.64 | 0.90 (0.03) | 0.43 |
| Independent validation but tuned to maximize model performance (new threshold selected) using thinned data set | Sens=Spec | 0.82 (0.03) | 0.82 (0.07) | 0.82 (0.03) | 0.64 | 0.90 (0.03) | 0.435 |
| ***Pheronema carpenteri*** | | | | | | | |
| Original cross validation with original threshold (Ross et al. 2015) | MinROCdist | 0.96 | 0.96 | 0.96 | 0.92 | 0.96 | 0.34 |
| Independent validation with original threshold | | 0.90 (0.01) | 0.47 (0.06) | 0.91 (0.01) | 0.29 | 0.69 (0.04) | 0.34 |
| Independent validation but tuned to maximize model performance (new threshold selected) | MaxSens+ Spec | 0.84 (0.01) | 0.67 (0.06) | 0.84 (0.01) | 0.51 | 0.74 (0.04) | 0.07 |
| Independent validation with original threshold and thinned data set | | 0.86 (0.03) | 0.47 (0.13) | 0.90 (0.02) | 0.37 | 0.75 (0.08) | 0.34 |
| Independent validation but tuned to maximize model performance (new threshold selected) using thinned data set | MaxSens+ Spec | 0.84 (0.03) | 0.6 (0.13) | 0.86 (0.03) | 0.46 | 0.75 (0.08) | 0.175 |

Table 4. Threshold-dependent evaluation indices for training, test and full models. Final thresholds and associated evaluation metrics are shaded. Values given are means where followed by standard deviation given in brackets. Abbreviations as in Table 2

| Thresholding approach | Average training — internal validation | | | Average test — cross validation | | | Full model — internal validation | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | PCC | Sensitivity | Specificity | PCC | Sensitivity | Specificity | PCC | Sensitivity | Specificity | Threshold |
| ***Desmophyllum pertusum* reef** | | | | | | | | | | |
| Sens=Spec | 0.83 (0.01) | 0.82 (0.03) | 0.83 (0.01) | 0.83 (0.01) | 0.83 (0.05) | 0.83 (0.01) | 0.83 (0.01) | 0.82 (0.03) | 0.83 (0.01) | 0.44 |
| MaxSens+ Spec | 0.81 (0.01) | 0.89 (0.02) | 0.80 (0.01) | 0.80 (0.01) | 0.90 (0.04) | 0.79 (0.01) | 0.78 (0.01) | 0.91 (0.02) | 0.77 (0.01) | 0.41 |
| MinROCdist | 0.82 (0.01) | 0.87 (0.03) | 0.81 (0.01) | 0.81 (0.01) | 0.88 (0.04) | 0.80 (0.01) | 0.81 (0.01) | 0.88 (0.02) | 0.81 (0.01) | 0.42 |
| ***Pheronema carpenteri*** | | | | | | | | | | |
| Sens=Spec | 0.88 (0.01) | 0.88 (0.03) | 0.88 (0.01) | 0.89 (0.01) | 0.89 (0.05) | 0.89 (0.01) | 0.88 (0.01) | 0.88 (0.03) | 0.88 (0.01) | 0.37 |
| MaxSens+ Spec | 0.85 (0.01) | 0.96 (0.02) | 0.85 (0.01) | 0.87 (0.01) | 0.97 (0.02) | 0.86 (0.01) | 0.84 (0.01) | 0.97 (0.01) | 0.84 (0.01) | 0.21 |
| MinROCdist | 0.87 (0.01) | 0.94 (0.02) | 0.86 (0.01) | 0.89 (0.01) | 0.93 (0.04) | 0.89 (0.01) | 0.87 (0.01) | 0.93 (0.02) | 0.86 (0.01) | 0.31 |

### 3.3.  New model variable importance

When variables were considered in isolation for *D. pertusum* reef, model gain was highest for temperature (70.5% contribution), followed by rugosity (23.3%) and FBPI (6.2%) as depicted in the jackknife plot (Supplementary Material 6.0). Temperature also decreased the model gain the most when removed as a variable, further illustrating its importance as the major variable on which predictions are reliant. For the *P. carpenteri* model, when variables were considered in isolation, model gain was highest for depth (41%) followed closely by temperature (35.9%), then BBPI (20.1%) and profile curvature (3%). When omitted from the complete model, the variable that decreased model gain the greatest was depth, closely followed by temperature.

### 3.4.  Old (data poor) vs. new (data rich) high-resolution models

Model performance determined by cross validation suggests that new models (Table 4) are comparable but of lower performance than old models (Table 3). New model spatial predictions in general follow those of the models of Ross et al. (2015), although there are some notable differences (Fig. 2). Cold-water coral reef is predicted to be present on all banks, seamounts and the continental slope in the region, but the distribution is more restricted than that predicted by Ross et al. (2015). As with the previous model, *P. carpenteri* is predicted to be present on the continental slope, Porcupine Seabight, Rosemary Bank Seamount, around the Hatton-Rockall Plateau and particularly in the Hatton-Rockall Basin. Presence is also predicted near the Wyville-Thomson Ridge where historical records refer to 'the *Holtenia* grounds' (Wyville Thomson 1874). The most noticeable difference is in the change in predicted distribution in the south-west section of the Hatton-Rockall Basin (circled in Fig. 2c,d). Presence is predicted for both taxa inside the existing MPA network but, following the overall trend, the predicted distribution for *D. pertusum* reef is a contracted version of the 2015 predictions (Fig. 3). Predictions for *P. carpenteri* presence inside MPAs has changed little from the 2015 model.
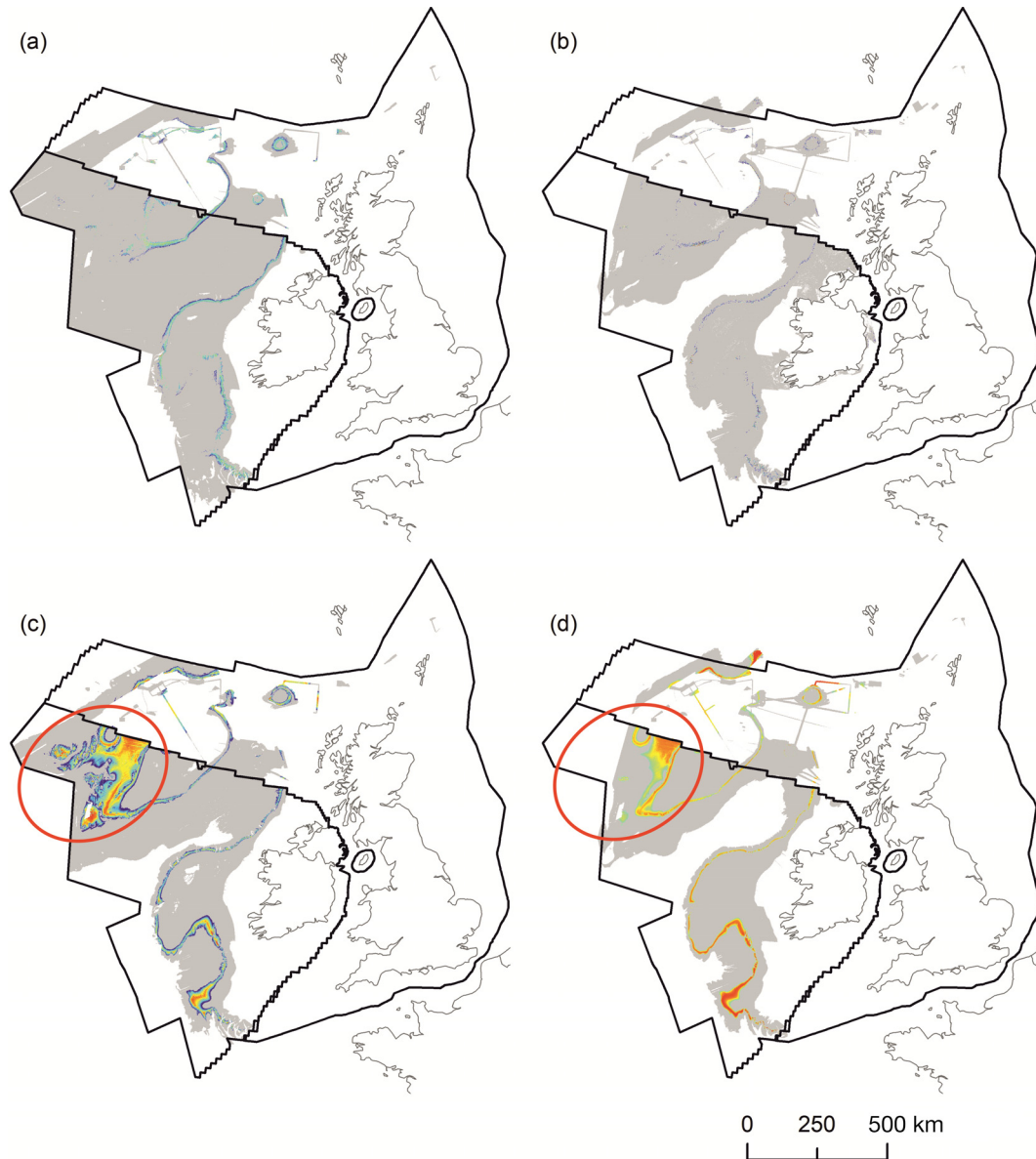
Fig. 2. Above threshold full model prediction maps for (a) scleractinian cold-water coral reef distribution from Ross et al. (2015), (b) *Desmophyllum pertusum* reef distribution with the new data set, (c) *Pheronema carpenteri* aggregation distribution from Ross et al. (2015 and d) *P. carpenteri* aggregation distribution with the new data set. Colour gradation from blue to red indicates low to high predicted habitat suitability. The Hatton-Rockall Basin is circled in red in panels c and d. Grey background indicates predicted absence. White background indicates the prediction has been masked for novel climates. Maps projected in British National Grid for aesthetic reasons

## 3.5. Comparison of percentage area protected by the 2015 MPA network

For both taxa, there is a significant reduction in predicted extent of suitable habitat in km² in the new models when compared to those of Ross & Howell (2013) and Ross et al. (2015) (Table 5). The difference is most striking for *D. pertusum* reef, where the low-resolution 2013 model predicts an extent 39 times larger, and the 2015 model 6 times larger, than the

new model for the whole study area. Some of this reduction will be due to the removal of all *Solenosmilia variabilis* data points from the model data, which will have led to a slight contraction in predicted depth range; however, it is clear from Fig. 3 that there is a general contraction in predicted distribution between new and old models. As *D. pertusum reefs* are only found shallower than 1200 m in this region, consideration of only those areas shallower than this depth reveal the same overall trend. How-
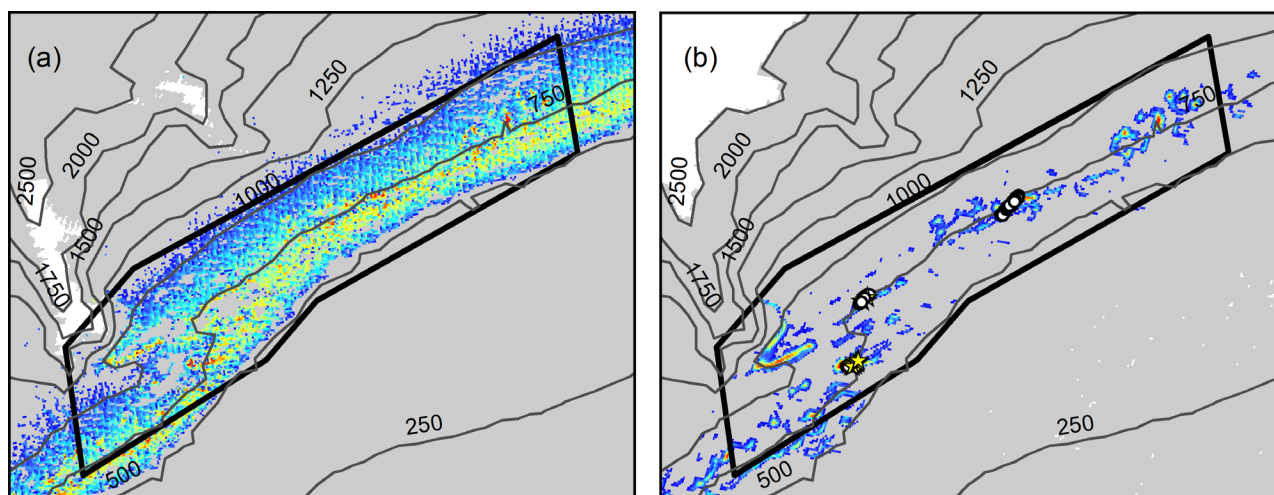
Fig. 3. Examples of changes to protected area model predictions. (a) Scleractinian cold-water coral reef distribution within the North-West Porcupine Bank marine protected area (MPA) from Ross et al. (2015); (b) *Desmophyllum pertusum* reef distribution within the North-West Porcupine Bank MPA with the new data set. Colour gradation from blue to red indicates low to high predicted habitat suitability. Remotely operated vehicle transects plotted showing presences as yellow stars and absence as white circles. Maps projected in British National Grid for aesthetic reasons

Table 5. Area of predicted suitable habitat broken down into entire model extent, and model extent in UK and Irish jurisdictions. Percentage of predicted suitable habitat protected by the marine protected area (MPA) and North East Atlantic Fisheries Commission (NEAFC) closure network used by Ross et al. (2015) for the purpose of comparison, also broken down by national MPAs and NEAFC closures

| | Desmophyllum pertusum reef | | | Pheronema carpenteri | | |
|---|---|---|---|---|---|---|
| | Ross & Howell (2013) GEBCO model | Ross et al. (2015) 200 × 200 m grid | New model | Ross & Howell (2013) GEBCO model | Ross et al. (2015) 200 × 200 m grid | New model |
| **Entire model extent** | | | | | | |
| Predicted suitable habitat (km²) | 185 240.25 | 30 106.10 | 4748.32 | 218 725.88 | 73 709.68 | 54 289.48 |
| Predicted suitable habitat within MPAs/NEAFC closures (%) | 12.81 | 20.00 | 31.61 | 1.29 | 2.64 | 6.62 |
| **Model extent within UK shelf claim** | | | | | | |
| Predicted suitable habitat (km²) | 57 425.06 | 8281.48 | 1244.00 | 87 516.00 | 9514.00 | 8886.76 |
| Predicted suitable habitat within MPAs/NEAFC closures (%) | 29.84 | 56.00 | 58.95 | 2.60 | 11.20 | 25.23 |
| **Model extent within Irish shelf claim** | | | | | | |
| Predicted suitable habitat (km²) | 48 139.31 | 21 665.48 | 3412.36 | 49 343.63 | 63 525.96 | 43 936.44 |
| Predicted suitable habitat within MPAs/NEAFC closures (%) | 13.67 | 12.60 | 21.65 | 1.10 | 1.39 | 2.86 |

ever, there is an increase in the estimates of the percentage of suitable habitat contained within the 2015 MPA network when calculated from the new model as compared to old models.

## 3.6. Assessment of percentage area protected by the MPA network present in 2020

Assessment of the proportion of suitable habitat included within the present day MPA network (Table 6) found that suitable environments for *D. pertusum*

reefs are the most well protected within the study area (~40% contained within MPAs), with protection at national levels varying from 84% in UK to 24% in Irish waters. This is a significant increase from the 12–32% protection under the 2015 network assessed using all models (Table 5). *P. carpenteri*-suitable habitat is the least well-protected of the 2 habitats assessed, with ~11% of predicted suitable environments included within a current MPA and protection at national levels varying from ~49% in UK to ~4% in Irish waters. However, this again is a significant increase over the 2015 MPA network, where the new

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Table 6. Area of predicted suitable habitat for *Desmophyllum pertusum* reef
and *Pheronema carpenteri* broken down into entire model extent, and model
extent in UK and Irish jurisdictions. Percentage of predicted suitable habitat
protected by the most up to data MPA/NEAFC Closure network and the
EU/UK 800 m trawl ban, also broken down by region

|                                          | *D. pertusum* reef | *P. carpenteri* |
|------------------------------------------|--------------------|-----------------|
| **Entire model extent**                  |                    |                 |
| Predicted suitable habitat (km$^2$)      | 4748.32            | 54 289.48       |
| 800 m trawl ban (%)                      | 60.11              | 100.00          |
| 2020 MPA/NEAFC network (%)               | 40.26              | 11.45           |
| **Model extent within UK shelf claim**   |                    |                 |
| Predicted suitable habitat (km$^2$)      | 1244.00            | 8886.76         |
| 800 m trawl ban (%)                      | 48.74              | 100.00          |
| 2020 MPA/NEAFC network (%)               | 83.64              | 49.30           |
| **Model extent within Ireland shelf claim** |                 |                 |
| Predicted suitable habitat (km$^2$)      | 3412.36            | 43 936.44       |
| 800 m trawl ban (%)                      | 64.25              | 100.00          |
| 2020 MPA/NEAFC network (%)               | 24.45              | 3.79            |

model suggested that only 7% of suitable habitat was protected by the 2015 MPA network. The addition of new MPAs in UK waters between 2015 and 2020 have taken the UK from around 59 to 84% protection for *D. pertusum* reef and from 25 to 49% protection for *P. carpenteri*. It should be noted, however, that the model of Ross et al. (2015) and the new model only cover a partial extent of the UK continental shelf limit, and data are biased to those areas that have been designated as MPAs. Thus, estimates of percentage protection are likely substantial overestimates. The EU ban on bottom trawling below 800 m is estimated to protect 100% of the habitat suitable for *P. carpenteri*, and 42% of *D. pertusum* reef-suitable habitat. Measured against IUCN targets, both habitats are within or above the recommended 20–30% protection level.

## 4. DISCUSSION

### 4.1. Original model validation

HSMs are potentially valuable tools in the field of marine environmental management, but there remain questions around the true accuracy and reliability of modelled maps that may serve as a barrier to growth in use. In this study, we tested the performance of 4 published models at 2 different resolutions, 750 × 750 m (Ross & Howell 2013) and 200 × 200 m (Ross et al. 2015): 2 for scleractinian cold-water coral reef habitat and 2 for the sponge *Pheronema carpenteri*. In the original published papers, all models performed well when tested using cross-validation meth-

ods, and performance was mixed when comparing low- and high-resolution models, according to threshold-dependent evaluation. While high-resolution *Desmophyllum pertusum* reef models outperformed low-resolution models, low-resolution models for *P. carpenteri* performed as well as high-resolution models according to threshold-dependent evaluation, and better than high-resolution models according to threshold-independent evaluation (AUC). Our study has shown that when tested using independent data, all models perform worse than expected based on published cross-validation results for both threshold-dependent and -independent metrics. Although models performed worse than under cross validation, model performance is still considered good (0.9–0.8) or fair (0.8–0.7) for scleractinian cold-water coral reef habitat models, with poorer performance for the *P. carpenteri* sponge models, particularly at low resolution and when measured by sensitivity. High-resolution models out-performed low-resolution models for both taxa when assessed using independent data.

Our findings are in broad agreement with the very small number of comparable studies that have independently validated deep-sea sponge and published coral HSMs, with some notable differences. Rooper et al. (2016, 2018) independently validated HSM for corals and sponges in the eastern Bering Sea slope, outer shelf in Alaska and Aleutian Islands. These models were developed based on data from bottom trawl surveys at a resolution of 100 × 100 m grid cell size and validated using camera-based surveys. These studies found that while model performance decreased when comparing cross validation to independent AUC scores, performance was still acceptable for coral models. This taken with our own findings suggests that high-resolution models (<200 × 200 m grid cell size) of deep-sea coral distributions can be accurate and can provide useful information for spatial management of these vulnerable taxa.

However, low-resolution models may not perform well. Bowden et al. (2021) recently evaluated 47 HSMs from 8 published studies, all focussed on the area around New Zealand, using independent data. All models were at 1 km (30 arc-seconds) grid cell size, and in all cases model performance was lower than in published cross-validation values. Anderson et al. (2016) found that their models of the distribution

of 4 scleractinian species (not *D. pertusum*) across the South Pacific Regional Fisheries Management Organisation area and adjoining exclusive economic zones were not successful in accurately predicting suitable habitat for reef-forming deep-sea corals when independently validated. These models were also constructed on a 30 arc-second grid (~1 km$^2$), and data resolution was given as a possible explanation for model failure in the face of independent testing. Specifically, Anderson et al. (2016) cited the limitations of the bathymetry data set used, which in turn affected the precision of each of the environmental predictor variables. Both studies reported on models of comparable resolution to the low-resolution model of Ross & Howell (2013) tested here.

Interestingly, the model of Ross & Howell (2013) appears to have performed better than those of Anderson et al. (2016) in the face of independent data. Anderson et al. (2016) cited missing critical predictor variables, particularly substrate type, lack of true absence data, spatial bias in distribution of presence records, and aspects of the topography in the study area, as possible reasons for the poor performance of their model. The model of Ross & Howell (2013) did make use of background data to account for spatial bias in the data set, which may have resulted in better performance when subjected to independent testing. However, a principal difference between the models of Anderson et al. (2016) and that of Ross & Howell (2013) is the focus of the models. Ross & Howell (2013) modelled scleractinian reef habitat, whereas Anderson et al. (2016) modelled scleractinian species presence. The difference is important, as the former occupies a restricted subset of the environmental niche of the latter (Howell et al. 2011), and a narrower niche width can result in a better performing model (Kadmon et al. 2003, Tsoar et al. 2007). This concept is used to explain the possible poor performance of the sponge models of Rooper et al. (2016, 2018). These authors suggested that the difference they observed in their high-resolution (100 × 100 m grid cell size) coral and sponge model performance may be a result of lumping species together into a large taxonomic group called 'sponges'. This essentially merged species with very different habitat preferences, ultimately giving the group a wide environmental niche. The coral group in their study was dominated by a single family (Primnoidae) and thus was less affected by this pooling action.

Niche width is unlikely to explain the poor performance of the *P. carpenteri* model. This hexactinellid (glass sponge) is found predominantly on fine sediments where it loosely anchors to the substrate using long spicules at the base of the organism. Aggregations in the NE Atlantic are found over a very narrow depth range from 1000 to 1300 m (Rice et al. 1990) and appear to occupy a very specific niche. Cross validation of HSMs created for this species suggested that model performance was excellent (Ross & Howell 2013, Ross et al. 2015). However, independent validation suggested that while the models have fair to good PCC and specificity, they have poor sensitivity, meaning that the resulting maps may be indicating an absence where there is in fact a presence. Examination of the spatial distribution of false negatives suggests that most (25 of 28 data points) are found on offshore seamounts and banks. These habitat types, and therefore this particular aspect of the environmental niche of *P. carpenteri*, was not represented in the data set used to build the published models and could help explain why the models partially failed. However, aspects of the ecology of *P. carpenteri* may also explain the poor model performance.

*P. carpenteri*, in common with other deep-sea sponge species that form aggregations, are thought to be associated with regions of enhanced bottom currents related to the interaction of internal waves with sloping boundaries (Rice et al. 1990, Klitgaard et al. 1997, Davison et al. 2019) and raised features like the Mid-Atlantic Ridge (van Haren et al. 2017). The causal link is suggested to be an increase in the supply of food as a result of the resuspension of organic matter (Rice et al. 1990). Oceanographic variables (and variability) may therefore be of critical importance in determining the distribution of *P. carpenteri*. The omission of such predictor variables from the models of Ross & Howell (2013) and Ross et al. (2015) may also explain why both models partially failed when tested with independent data. The inclusion of oceanographic variables in deep-sea marine species distribution modelling has been found to improve model performance when tested with cross validation (Rengstorf et al. 2014, Pearman et al. 2020), further supporting their inclusion in any future model development.

Our results suggest that for both scleractinian reef and *P. carpenteri* the high-resolution models outperform the low-resolution models when tested with independent data. This is an important finding, as it suggests that our ability to produce useful models of deep-sea benthic species and habitat distribution is dependent on the availability of high-resolution environmental data including bathymetry data. Current maps of the seafloor are derived using satellite altimetry, which gives an average achievable resolution on the order of 8 km (Mayer et al. 2018). The percentage of the seafloor that has been measured by

echo-sounders is considerably less than 18%, and only about 9% of the seafloor is covered by high-resolution multibeam sonar data (Mayer et al. 2018). Recently, an international effort has begun with the objective of facilitating the complete multibeam mapping of the world ocean by 2030. The Nippon Foundation General Bathymetric Chart of the Oceans (GEBCO) Seabed 2030 Project has the potential to significantly improve the quality of HSMs that can be produced for deep-sea taxa by providing high-resolution bathymetry data. However, access to high-resolution oceanographic model output, as well as unbiased data sets of the distribution of target species and assemblages, and a good understanding of the biology and ecology of those species and assemblages, are also necessary to improve the quality of models. Targeted efforts to collect these data over the next decade (Howell et al. 2020, 2021) will be important in the further development of this field.

The good performance of the high-resolution scleractinian reef habitat model suggests that it may be a useful tool in the spatial management of cold-water coral reefs in this region. Cold-water coral reef is considered a VME under UNGA Resolution 61/105, and, in the NE Atlantic is also classed as 'threatened and/or declining habitat' under the OSPAR Convention. Within European waters, it is also recognised as an Annex I habitat under the EU Habitats and Species Directive (92/43/EEC). Collectively, these policies require relevant management authorities to take actions to protect cold-water coral reef habitat. Specifically, A/RES/61/105 (p. 17; available at: https://documents-dds-ny.un.org/doc/UNDOC/GEN/N06/500/73/PDF/N0650073.pdf?OpenElement) states:

> 'In respect of areas where vulnerable marine ecosystems, including seamounts, hydrothermal vents and cold-water corals, are known to occur or are likely to occur based on the best available scientific information, to close such areas to bottom fishing and ensure that such activities do not proceed unless conservation and management measures have been established to prevent significant adverse impacts on vulnerable marine ecosystems'

Actions have so far been limited to those areas where cold-water coral reef has been observed either through visual or physical sampling means. However, the high-resolution model provides the best available scientific information on where cold-water coral reef is likely to occur in this region, and thus could be used to support decisions around further measures.

Similarly, the good performance of the high-resolution *P. carpenteri* model in terms of PCC and specificity, and fair AUC score, suggests that it may also be a useful tool in the spatial management of the

region. However, it must be noted that this is a presence/absence HSM, and therefore it only indicates likely presence/absence of suitable habitat for the species (a VME indicator taxon), not the aggregation (a VME). This, together with the notable deficiencies in the model outlined above, suggests it is less useful than the scleractinian reef habitat model, but may still have value in indicating areas for further consideration given the precautionary principle.

## 4.2. New model performance and interpretation

The newly constructed high-resolution models for *Desmophyllum pertusum* reef and *P. carpenteri* have been developed using more than twice the input data used in the original models of Ross et al. (2015) (Table 1), and consideration of oceanographic predictor variables (temperature and salinity) as terms in the models. Cross validation suggests good performance for both models. In general, model performance increases with increasing sample size; however, the nature of this relationship is variable and can depend on modelling method, prevalence and species range size (Stockwell & Peterson 2002, Wisz et al. 2008, van Proosdij et al. 2016). The inclusion of oceanographic variables in deep-sea HSMs has also been found to improve model performance (Rengstorf et al. 2014, Pearman et al. 2020). This suggests that the new models should perform better than the original 2015 models, although this can only be assessed using new independent data.

In this study, we used a presence–background approach rather than a presence–absence approach since our model input data are drawn from multiple surveys using multiple gear types and spanning more than 30 yr. In our opinion, absences cannot be inferred from our data set with certainty, and so we opted to be cautious in our use of absence data. However, it should be noted that evidence suggests presence–absence models perform better than presence-only models, particularly where species/assemblages occupy all suitable habitat, making absence data reliable (Brotons et al. 2004), although MaxEnt has been found to perform equally as well as presence–absence models (González-Irusta et al. 2015). Future modelling efforts may wish to consider use of presence–absence approaches where authors feel absence data are reliable.

Temperature was a significant term in both new models and is a fundamental variable that controls species distributions. *D. pertusum* has been observed living under a wide range of temperatures (4–13°C) (Freiwald et al. 2004), with an upper thermal toler-

ance of 15°C (Brooke et al. 2013). Response curves for MaxEnt models for *D. pertusum* reef (Supplementary Material 6) suggest that the highest likelihood of occurrence of reef habitat in the study area is at temperatures of ~8°C, which is almost the centre of the species thermal niche. No data are available on the thermal niche of *P. carpenteri*. Howell et al. (2016) reported this species to occur over a temperature range of 2.73–20.9°C (mean ± SD: 5.17 ± 2.03°C) in the northern North Atlantic. Response curves for MaxEnt models for *P. carpenteri* (Supplementary Material 6) suggest that this species occupies a narrow thermal niche, with peak likelihood of occurrence between 6 and 8°C, falling sharply to no occurrences below approximately 3°C or above 10°C. The wide range reported by Howell et al. (2016) is likely a result of poor position data from the older records used in that model in order to provide whole North Atlantic data coverage.

New model spatial predictions in general follow those of the models of Ross et al. (2015). However, there are some notable differences, particularly in the spatial prediction for *P. carpenteri* in the southern region of the Hatton-Rockall Basin (Fig. 2c,d). In this region, available CTD data suggest that the temperature is cooler than that at equivalent depths in the Rockall Trough and on the European continental slope, making this region less suitable for *P. carpenteri* than predicted by the 2015 model, which did not include temperature. Interestingly, the model of Howell et al. (2016), which did include temperature, also predicted this area as suitable habitat; however, the thermal niche of *P. carpenteri* was likely incorrectly defined in that model as previously noted. The principal difference in the spatial predictions for the *D. pertusum* reef model is a general contraction of the 2015 predictions in the current model. This is well illustrated in Fig. 3, where current model predictions are much more focussed than those of the 2015 model.

## 4.3. Re-assessment of current area closures and percentage protection targets for these VMEs

For both taxa there is a significant reduction in predicted extent in the new models when compared to the models of Ross & Howell (2013) and Ross et al. (2015) (Table 5). The 2013 low-resolution models predicted 39 times and 4 times greater extent for *D. pertusum reef* and *P. carpenteri*, respectively. This difference has important implications for onward use of models in decision making. For example, calculations of ecosystem services such as carbon sequestra-

tion (Barnes et al. 2019, 2021) or nutrient cycling (Hoffmann et al. 2009) based on modelled extent may be grossly overestimated if based on low-resolution models. Similarly, the 2015 models predicted a greater extent of suitable habitat than the new model by 6 times and 1.4 times for *D. pertusum* reef and *P. carpenteri*, respectively, suggesting that estimates of extent based on model predictions should be used with caution and considered likely overestimates.

In contrast, estimates of percentages of predicted suitable environments protected by the regional MPA network increased when calculated using the new model compared to the 2013 and 2015 models. The CBD originally set out a target of 10% of marine areas to be protected by 2010 (UNEP/CBD/COP/DEC/VII/5), later moved to 2020 (UNEP/CBD/COP/10/27), and that is now being followed up with calls for 30% by 2030. While these percentage area targets are not habitat specific, Aichi Target 11 makes specific reference to 'ecologically representative and well-connected systems of protected areas' (UNEP/CBD/COP/10/27/Annex, p. 119; available at: https://www.cbd.int/doc/decisions/cop-10/full/cop-10-dec-en.pdf), which implies that different marine habitat types should be protected at that level. The independently validated 2015 models suggest that for the area modelled and the 2015 MPA network, both the UK and Ireland have surpassed the original 10% protection target for *D. pertusum* reef, while the UK also surpassed this for *P. carpenteri* suitable habitat. In addition, the UK surpassed the 30% target for *D. pertusum* reef habitat in the modelled area. The picture is the same for the new model. However, in both the 2015 and the new model, Ireland protects <10% of suitable habitat for *P. carpenteri*, implying that further MPAs may be required. Ireland has committed to protecting 30% of its habitat by 2030 (Marine Protected Area Advisory Group 2020), and data such as these can help guide that process.

The situation is broadly similar when considering the 2020 MPA network, although the estimates of percentage of habitat protected in UK waters are much higher. It must be noted, however, that the current MPA network is not 'strictly protected' in line with IUCN specifications, and in some cases management measures have yet to be drawn up. It is also important to remember that the modelled area in UK waters is much more limited than that modelled in Irish waters due to the limited availability of multibeam mapping in UK waters. The areas that have been mapped (and thus used in modelling) in UK waters tend to be associated with protected status, thus the UK figures are likely gross overestimates.

Estimates of percentage of suitable habitat made from the low-resolution 2013 model are lower than all other estimates, and, reiterating the findings of Ross et al. (2015), suggest that low-resolution models result in conservative estimates in this context, which is in line with the precautionary principle and suggests low-resolution models may have a use in this area.

An interesting finding is that the ban on bottom trawling below 800 m in EU waters (UK is currently following) protects >30% of both habitats estimated from the new model with 100% of *P. carpenteri* suitable habitat protected. While a significant achievement, it is important to again consider the issue of representativeness in Aichi Target 11. Cold-water coral reefs occurring at different depths support different assemblages of associated species in line with the well-documented turnover of species along the depth gradient (Rowe & Menzies 1969, Howell et al. 2002, Carney 2005). In order to be representative, protection for cold-water coral reef sites must span its known depth range (thermal niche) necessitating protection of sites shallower than 800 m. In addition, the twin threats of ocean acidification and global warming mean that shallower areas of predicted suitable habitat in this region may be key refuge sites for cold-water coral reef (Jackson et al. 2014). Ocean acidification is causing the aragonite saturation horizon to shoal, exposing deep-water coral reefs to waters that are corrosive to coral skeletons (Guinotte et al. 2006). In parallel, seawater temperatures are increasingly exposing reefs to novel conditions. While live *D. pertusum* can tolerate long-term exposure to combined end-of-the-century temperature and $pCO_2$ scenarios (Hennige et al. 2015, Büscher et al. 2017), the dead coral skeletons that make up the reef framework are weakened by acidified conditions and become more susceptible to bioerosion and mechanical damage (Hennige et al. 2015). This ultimately leads to crumbling, collapse and loss of complexity of the larger habitat, and its associated ecosystem services (Hennige et al. 2020). In this region, the East Mingulay Special Area of Conservation (SAC), Wyville Thomson Ridge SAC, and North West Rockall Bank SAC represent important strongholds for reef habitat (Jackson et al. 2014), and therefore the 800 m bottom-trawling ban alone will not meet the qualitative aims of Aichi Target 11.

## 5. CONCLUSIONS

Independent testing of 4 published models has shown that for the taxa considered, high-resolution models (<200 × 200 m grid cell size) can be accurate and can provide useful information for spatial management of these vulnerable taxa. With respect to UNGA Resolution 61/105, the high-resolution cold-water coral reef model provides the best available scientific information on where this VME is likely to occur in this region, and thus could be used to support decisions around further measures. Our ability to produce useful models of deep-sea benthic species and habitat distribution is highly dependent on the availability of high-resolution environmental data including bathymetry data. To improve model performance, significant research effort is needed to map the seafloor, oceanographic environment and distribution of species and assemblages (presence, absence, density) in order to provide more, better-quality, model input data. In addition, further research effort is needed to provide a more complete understanding of the importance of environmental variables to target taxa, and their interactions at a variety of scales. For well performing high-resolution models (200 × 200 m), estimates of extent based on model predictions should be used with caution and considered likely overestimates. Low-resolution models (750 × 750 m) may be useful in providing conservative estimates in progress towards percentage protection targets but are not recommended for use in estimates of extent. For *Desmophyllum pertusum* reef and *Pheronema carpenteri*, the UK and Ireland have made good progress towards the 10% CBD target for conserving habitats and species within MPAs. This, together with the EU ban on bottom trawling below 800 m, provides a level of protection for both; however, representativity needs to be considered in these assessments. Assessment of UK progress is limited by a lack of available multibeam data.

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