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

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

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15 Running page head: Performance of deep-sea habitat suitability models

16

17 **Abstract**

18 Marine spatial management requires accurate data on species and habitat distributions. In  
19 the deep sea, these data are lacking. Habitat suitability modelling offers a robust defensible  
20 means to fill data gaps, provided models are sufficiently reliable. We test the performance  
21 of published models of two deep-sea habitat-forming taxa at low and high resolutions (~1  
22 km and 200 m grid-cell size), across the extended EEZs of UK and Ireland. We construct new  
23 data-rich models and compare new and old estimates of the area of habitat protected,  
24 noting changes in the protected area network since 2015. Results of independent validation  
25 suggest all published models perform worse than expected considering original cross-  
26 validation results, but model performance is still good or fair for *Desmophyllum pertusum*  
27 reef, with poorer performance for *Pheronema carpenneri* sponge models. High-resolution  
28 models using multibeam data out-perform low-resolution GEBCO-based models. Newly  
29 constructed models are good to excellent according to cross-validation. New model spatial  
30 predictions reflect published models, but with a significant reduction in predicted extent.  
31 The current marine protected area network and the European Union ban on bottom  
32 trawling below 800m protect 40% and 60% of *D. pertusum* reef-suitable habitat  
33 respectively, and 11% and 100% of *P. carpenneri* suitable habitat respectively within the  
34 model domain. We conclude high-resolution models of *D. pertusum* reef distribution are a  
35 useful tool in spatial management. The poorer performing *P. carpenneri* model indicate  
36 areas for more detailed study. Whilst low-resolution models can provide conservative  
37 estimates of percentage area-based conservation targets following the precautionary  
38 principle, high-resolution sea-floor mapping supports the development of better-performing  
39 models.

40

41 Key words: Deep sea; habitat suitability modelling; species distribution modelling; marine  
42 conservation; marine spatial planning

43 **1. INTRODUCTION**

44 As we begin the UN Decade of Ocean Science for Sustainable Development, the call for more  
45 holistic management of the marine environment is clear. Marine spatial planning (MSP) is an  
46 important tool supporting implementation of the 'ecosystem approach' to environmental  
47 management. An approach outlined in the Convention on Biological Diversity (CBD), and  
48 enshrined in the UN Sustainable Development Goals (UN General Assembly 2015). Maps lie  
49 at the heart of spatial management including maps of human uses, socio-economics, political  
50 and legal arrangements, and critically biophysical conditions and assemblages or communities  
51 of marine organisms, such as kelp forests and coral reefs. There is a pressing need to develop  
52 reliable accurate maps of the spatial distribution of marine ecosystems to support  
53 conservation initiatives.

54 Efforts to map benthic marine communities have largely focused on shallow water  
55 environments (Andrefouet et al. 2006, Traganos et al. 2018). Mapping deep-water  
56 communities is much more difficult because there is no direct equivalent to optical remote  
57 sensing which provides wide coverage of high-resolution data with direct observation of  
58 terrestrial and shallow (<10m) coastal habitats. The majority of deep-water benthic biological  
59 mapping has been achieved using modelling approaches. Species distribution modelling, also  
60 called habitat suitability modelling, uses data on the presence, absence, abundance or  
61 biomass of a species, assemblage or community, and relevant environmental data, to produce  
62 a statistical model of the relationship between species and their environmental drivers. The  
63 model can be used to make predictions of the distribution of the target species/community  
64 based on environmental data alone (Bryan & Metaxas 2007, Rengstorf et al. 2014, Howell et  
65 al. 2016). This type of mapping lends itself well to use in the marine environment as the

66 physical environment is often cheaper and simpler to measure than the biological  
67 components. There are a wealth of local, regional and global physical spatial models of the  
68 marine environment including oceanographic, bathymetric and productivity models. Benthic  
69 biological data are generally available for coastal marine areas and together with physical  
70 environmental data, offer great potential to produce relatively data-rich modelled maps.  
71 However, availability of benthic biological data decreases as you move away from the coast  
72 and into the deep sea (Webb et al. 2010), and this can present challenges in the development  
73 of reliable models.

74 The deep sea is increasingly subject to human use and there is an urgent need to implement  
75 more effective, integrated management of deep-sea ecosystems, through use of area-based  
76 management tools and marine spatial planning. The last 15 years has seen a growing trend in  
77 the use of predictive mapping techniques to generate models of the distribution of key  
78 species and assemblages in the deep sea (e.g. Bryan & Metaxas 2007, Guinan et al. 2009,  
79 Howell et al. 2011, Rengstorf et al. 2014, Robert et al. 2016, Howell et al. 2016, Pearman et  
80 al. 2020). These efforts have focused particularly on those species and assemblages that  
81 appear in key marine conservation legislation, and have produced modelled maps from a wide  
82 range of regions, of different extents and spatial resolutions. Models that provide large spatial  
83 coverage of a scale useful to national and regional MSP efforts, tend to use low-resolution (>1  
84 km<sup>2</sup>) modelled global environmental datasets in their production (Howell et al. 2016). Higher-  
85 resolution environmental datasets, such as multibeam bathymetry, and regional or site-  
86 specific oceanographic models, tend to only be employed in the construction of models with  
87 a more limited spatial extent (Pearman et al. 2020), rendering them less useful for national  
88 and regional scale MSP, but still informative.

89 While the potential applications of modelled maps in MSP have been demonstrated (Ross &  
90 Howell 2013, Howell et al. 2016, Stirling et al. 2016, Rowden et al. 2017), models are not yet  
91 widely used despite their obvious potential (Marshall et al. 2014, Reiss et al. 2015). This  
92 contrasts with many other fields, for example fisheries and climate science, where models are  
93 routinely used to forecast future scenarios, and the results used to make management and  
94 policy decisions (Hilborn 2012, IPCC 2014). The reasons for this are not clear. Addison et al.  
95 (2013), in their review of common objections to the use of models in environmental decision-  
96 making, identify nine key objections that are symptoms of three fundamental issues: (1)  
97 misconceptions about the role of models in decision-making, (2) poor modelling practice and  
98 (3) a lack of effective communication and/or trust between modellers and decision-makers.  
99 Objections around modelling practice and outputs include issues with model accuracy and  
100 uncertainty. Model performance is usually tested using random subsampling from the full  
101 model build dataset, so called cross-validation. However, the lack of true independence  
102 between testing and training data sets, as well as spatial sorting bias is known to artificially  
103 inflate model performances (Veloz 2009, Hijmans 2012) leading to a phenomenon where  
104 many models appear to perform well yet provide very different spatial predictions (Piechaud  
105 et al 2015; Howell et al 2016). This may serve to compound concerns around model accuracy  
106 and uncertainty, and highlight the need for independent validation of model performance to  
107 help allay these concerns and encourage wider use of model output.

108 In the North East Atlantic habitat suitability models for scleractinian cold water coral reef and  
109 an aggregation forming deep-sea sponge *Pheronema carpenleri* have been developed for the  
110 continental shelf claim areas of the UK and Ireland (Ross & Howell 2013, Ross et al. 2015).  
111 *Desmophyllum pertusum* reef is widely recognised as a distinct biological community or  
112 'biotope', and occurs as thickets, discrete reefs, and giant carbonate mounds up to 300 m

113 high and several km in diameter. Within this region reefs have been observed on Hatton,  
114 George Bligh and Rockall Banks, the Wyville-Thomson Ridge, and in Explorer and Dangaard  
115 Canyons (Howell 2010, Howell et al. 2010), the Porcupine Seabight (Foubert et al. 2005,  
116 Huvenne et al. 2005), Porcupine Bank (Kenyon et al. 1998), southern Rockall Bank (Mienis et  
117 al. 2006, Wienberg et al. 2008) and Outer Hebrides (Roberts et al. 2005) as well as further  
118 north and south (Wheeler et al. 2007). Observations occur over depths from ~120 m to ~1000  
119 m, with most reported from 600-800 m. Reef structures are highly biodiverse (Roberts et al.  
120 2006), and have an important role as essential fish habitat (Husebø et al. 2002, Auster 2005).

121 *P. carpenteri* is a small spherical glass sponge that occurs singularly or in dense aggregations,  
122 predominantly (but not exclusively) on fine sandy mud and mud substrata. Within UK and  
123 Irish waters, aggregations are a recognised biotope, and communities composed of this  
124 species have been described from 1250 m in the Porcupine Seabight (Rice et al. 1990), 1100  
125 m in the Hatton-Rockall Basin (Hughes & Gage 2004, Howell et al. 2014), and from 1450 m on  
126 Goban Spur (Lavaleye et al. 2002), with historical records of additional aggregations from  
127 Ireland to Spain in 1000-2000 m water (Le Danois 1948) and in the Northern Rockall Trough  
128 (Wyville-Thomson 1874). Aggregations are associated with an increase in abundance and  
129 richness of macrofauna observed within spicule mats and sponge bodies (Rice et al. 1990,  
130 Bett & Rice 1992). Recent studies have suggested that known aggregations may be poorly  
131 connected (potentially isolated) (Ross et al. 2019) and experience a substantive impact from  
132 bottom trawl fishing (Vieira et al. 2020). From a policy perspective both *D. pertusum* reef and  
133 *P. carpenteri* aggregations are considered Vulnerable Marine Ecosystems (VME) under United  
134 Nations General Assembly Resolution 61/105, and as ‘threatened and/or declining species  
135 and habitats’ under the OSPAR Convention for the Protection of the Marine Environment of

136 the north-east Atlantic 1992. Understanding their distribution is therefore an important  
137 component to the development of area-based management of the region.

138 The Ross & Howell (2013) models were constructed using global scale environmental data  
139 layers and are at a resolution of ~1 km<sup>2</sup>. The Ross et al. (2015) models were constructed using  
140 high resolution multibeam datasets and are at a resolution of 200x200 m grid cell size. Both  
141 models were produced using the same underlying presence / absence biological dataset for  
142 each response variable , *D. pertusum* reef habitat and *P. carpenteri* species. All four models  
143 performed well when tested using cross-validation methods, and in general high-resolution  
144 models performed better than low resolution models according to threshold-dependent  
145 evaluation. However, the spatial predictions and resulting maps derived from models of  
146 different resolution were notably different. The aim of this study is to undertake independent  
147 validation of these published models of VME distribution in the UK and Irish ECS claim areas,  
148 in order to assess model performance and inform future use in MSP and conservation.  
149 Specifically, we will 1) independently validate model performance using newly collected  
150 independent data, 2) construct new relatively data-rich models using the same modelling  
151 method as the prior publications, 3) quantify changes in predicted distributions and  
152 assessments of percentage protection targets for each VME (VME indicator taxa in the case  
153 of *P. carpenteri*) as a result of new models.

154

## 155 **2. MATERIALS & METHODS**

### 156 2.1. Site and Model Description

157 The study considers the full extent of the Irish, and a partial extent of the UK's extended  
158 continental shelf claim area in the N E Atlantic (Fig 1). A network comprising three different  
159 types of Marine Protected Area (MPA) exists in this area for the protection of deep-sea  
160 habitats (Fig 1). These are Special Areas for Conservation, OSPAR MPAs and North East  
161 Atlantic Fisheries Commission (NEAFC) closures to bottom trawling for the protection of  
162 VMEs. While the sites do not constitute a coherently designed MPA network, they enable  
163 illustration of the potential use of habitat maps in area-based management. In addition, there  
164 is a ban on bottom trawling below 800 m in European and UK waters.

165 Ross & Howell (2013) and Ross et al. (2015) scleractinian reef models were predominantly  
166 constructed using *Desmophyllum pertusum* reef presence / absence data. However, a small  
167 number of presence points for *Solenosmilia variabilis* reef were also included in the models.  
168 In our experience *S. variabilis* appears to occupy the same topographic niche as *D. pertusum*  
169 but occurs in deeper water. Records included in the models were at the shallow end of their  
170 distribution only. The resulting models largely predicted the niche of *D. pertusum* reef but  
171 with a slightly deeper reach. This study evaluates and builds upon the original models using  
172 new *D. pertusum* reef data alone with *S. variabilis* reef data omitted. Ross & Howell's (2013)  
173 models are of resolution 750x750 m grid cell size, and cover the full extent of both Irish and  
174 UK continental shelf limit. Ross et al. (2015) models are of resolution 200x200 m grid cell size  
175 and cover the full extent of the Irish, and partial extent of the UK's continental shelf limit in  
176 the N E Atlantic. Both studies used their models to assess progress towards percent protection  
177 conservation targets, and reported between 20 – 29% of scleractinian reef suitable habitat  
178 and 1.9-2.9% of *P. carpentieri* suitable habitat is within the MPA network.

179



## 180 2.2. Biological Data

181 New data for both *P. carpenteri* and *D. pertusum* reef were compiled from five research  
182 cruises to the northeast Atlantic: i) Eurofleets2 funded DeepMap cruise CE15011 (2015), with  
183 ROV Holland I; ii) NERC funded Deep Links JC136 (2016), with ROV ISIS; iii, iv, v) Sea Rovers  
184 RH17001 (2017), RH18002 (2018) and CE19015 (2019), jointly funded by the Irish Government  
185 and EU, with ROV Holland I. These research cruises were not conducted for the sole purpose  
186 of model validation, but this was a consideration in transect line planning for all cruises.  
187 Transect lines ranged from approximately 100m to 3.1 km, with an average length of 1.3 km.  
188 Collectively these research cruises provide a dataset consisting of 195 high definition ROV  
189 video transects spread across the study area (Fig 1). This collective dataset is referred to  
190 throughout as the new dataset.

191 For the original datasets presence of target habitat was determined from both quantitative  
192 and qualitative analysis of stills image data taken at 1 minute intervals along transects as  
193 described in Howell et al. (2010). *P. carpenteri* presence was determined from species lists  
194 from analysed sample data. *D. pertusum* reef habitat description follows that provided in  
195 Howell (2010), and subsequently adopted for use in the UK Deep Sea Habitat Classification  
196 (Parry et al. 2015). For the new independent dataset presence of the target habitat / species  
197 was determined by expert evaluation of image-based data alone. Habitat identification was  
198 undertaken by two annotators and designated when the habitat extent satisfied the OSPAR  
199 minimum biotope area threshold (25 m<sup>2</sup>). For quality assurance, 5% of transects were  
200 independently analysed by Howell following inter-observer agreement standards used in  
201 published evidence (MacLeod et al., 2010).

202

### 203 2.3. Original Model Validation

204 For each of the four published models, the new biological dataset was plotted in ArcGIS on  
205 raster grids of published model output, in their respective output projections, and ROV point-  
206 based position data were reduced to one point per cell to avoid over-/under-weighting the  
207 importance of specific environmental conditions. Where cells contained any ROV position  
208 points interpreted as presence points, the one point per cell was denoted as a presence, all  
209 other points were denoted as absence. As the original models were masked for novel  
210 climates, new data points that did not sit on old model predictions were removed from the  
211 dataset as they were considered out of the original model domain. The final independent  
212 validation datasets for the 200 x 200m model included 2018 data points for *D. pertusum* reef  
213 and 1937 data points for *P. carpenteri* aggregations; for the 750 x 750 m model, the  
214 independent validation datasets included 646 data points for *D. pertusum* reef and 597 data  
215 points for *P. carpenteri* aggregations (Table 1). To assess the potential effect of spatial  
216 autocorrelation in inflating model performance, independent validation was also undertaken  
217 by reducing the datasets to one point per ROV transect. For each response variable a single  
218 presence point was randomly selected within each transect, and a single absence point from  
219 absence transects. This provided 173 and 163 validation points for the *D. pertusum* and *P.*  
220 *carpenteri* 200x200m models respectively and 186 and 182 validation points for the *D.*  
221 *pertusum* and *P. carpenteri* 750x750 models respectively.

222 The probability values from published model layers (coglog Maxent output) were extracted  
223 for each data point. Threshold independent metrics of model performance (Area Under the  
224 Receiver Operator Curve, AUC) for each model were calculated and compared to the original  
225 published models. Threshold dependent metrics of model performance (specificity,

226 sensitivity, and percent correctly classified) were also calculated by converting extracted  
227 probability values to binary presence-absence using 1) the thresholds defined in the original  
228 publications, and 2) new thresholds that maximised model performance against the new  
229 dataset.

230

## 231 2.4. Construction of new models

232 Newly collected high-resolution multibeam bathymetry data (Supplementary Material 1.0)  
233 were added to that described in Ross et al. (2015) and used to create grids of cell size 200x200  
234 m that were re-projected from their original projection (WGS84) into Goode Homolosine  
235 Ocean (GHO) equal-area projection in order to allow for correct calculation of derived  
236 topographic layers and area.

237

### 238 2.4.1 Variable selection

239 Seven topographic variables were derived from the bathymetric data using the ArcGIS Benthic  
240 Terrain Modeller add-in (Walbridge et al. 2018): terrain ruggedness, curvature, plan  
241 curvature, profile curvature, slope, broad-scale bathymetric positions index (BBPI) and fine-  
242 scale bathymetric position index (FBPI). Information on the calculation and use of each of  
243 these variables can be found in the existing literature (Guinan et al. 2009, Ross & Howell  
244 2013). The inner and outer radii for BBPI were 5 and 50 raster cells, respectively, facilitating  
245 identification of topographic features at 10 km scale such as canyons and hills. For FBPI, the  
246 inner and outer radiuses were 1 and 5 raster cells, respectively, allowing for the identification  
247 of features within the <1 km scale such as gullies. Generalised Additive Models (GAMs) were

248 used to build bottom temperature and salinity layers using *in-situ* CTD data from ROV and  
249 drop camera transects, as well as archived CTD casts from the British Oceanographic Data  
250 Centre (BODC) database. GAMs were implemented in R (R Core Team 2020) using the ‘mcgv’  
251 package (Wood 2011) with depth, latitude and longitude used as explanatory variables. A  
252 detailed description is given in Supplementary Material 2.0. New and original biological  
253 datasets for each of *D. pertusum* reef and *P. carpenteri* presence / absence were combined,  
254 reprojected into GHO and plotted in ArcGIS on raster grids of environmental data. ROV/drop  
255 camera point-based position data were reduced to one point per cell, where cells containing  
256 any presence observations were denoted as a presence, all other points were denoted as  
257 absence. Environmental data were extracted for each data point.

258 Maximum Entropy (MaxEnt) modelling (Phillips et al. 2006, Elith et al. 2011) is a presence-  
259 background modelling technique that has a successful performance record (Elith et al. 2006),  
260 particularly in studies with low prevalence (low number of presence records). Although  
261 MaxEnt was designed to account for covariation in datasets and can perform well with  
262 correlated variables (Feng et al., 2019), previous studies have found that pre-selection of  
263 variables leads to better-performing models (Ross and Howell, 2013). Environmental  
264 variables were therefore first assessed for covariance using correlation matrices and Variance  
265 Inflation Factors in R. Strong correlations and VIFs between variables ( $\geq \pm 0.7$  and  $\geq 3$ ,  
266 respectively) were addressed by removing one variable from each correlated pair based on  
267 the jackknife procedure. Jackknifing calculates the individual contribution of variables to a  
268 model and produces model performance statistics (termed ‘gain’ in MaxEnt) for each. Once  
269 correlates were removed, a model with all remaining variables was built. Following principles  
270 of model parsimony, final sets of variables were selected by systematically removing the  
271 variable contributing the least to the model (based on model gain with and without that

272 variable) until the drop in overall performance was deemed unacceptable. This process is  
273 described in detail in Supplementary Material 3.0 and 4.0.

274

#### 275 2.4.2 Modelling

276 If used with presence-only data, MaxEnt randomly selects a specified number of ‘background’  
277 points that are considered to represent locations with an equal likelihood of having been  
278 sampled that act as the absence points to inform the model (Elith et al. 2011). Whilst  
279 ‘absence’ points are presented in this study for each target taxa/habitat, it is not possible to  
280 be certain that they are not present somewhere within a 200 m grid cell due to the limited  
281 field-of-view of camera equipment compared to the size of grid cells, and therefore the data  
282 within this study represent ‘pseudo-absences’. Having pseudo-absence data allowed for the  
283 MaxEnt samples-with-data (SWD) approach to be used whereby environmental values are  
284 provided in a spreadsheet for both the presence and pseudo-absence points, instead of  
285 allowing MaxEnt to randomly select background points to act as absences. The benefit of the  
286 SWD approach is that as both the presence and pseudo-absence points come from the same  
287 sampling campaigns, it allows for the control of some bias in sampling locations and  
288 experimental design that can facilitate improved predictive performance (Phillips & Dudík  
289 2008).

290 Preliminary models with different parameters were systematically trialed, including the  
291 changing of feature classes (linear, quadratic, product, hinge and threshold) and the  
292 regularisation parameter (0.1, 0.5, 1, 3, 5, 10) to avoid over-fitting/-smoothing (Phillips &  
293 Dudík 2008). The final feature classes selected for both target habitat models were linear,  
294 quadratic and product features. Through trialing, hinge and threshold features were removed

295 due to lack of ecological applicability in this study; with these features turned on, the response  
296 curves produced did not make biological sense. The *D. pertusum reef* model used a  
297 regularisation parameter of 1, whilst the *P. carpenteri* model used 0.5. These parameters  
298 were chosen because they struck a balance between the model overfitting and over-  
299 generalising - this was apparent from the shape of the response curves and AUC scores. The  
300 final MaxEnt models were projected onto the study area in a raster format and constrained  
301 to sampled conditions using the MaxEnt novel climates output (i.e. areas where  
302 environmental values fall within those on which the model was trained). Environmental data  
303 layers used in the final models are plotted in Supplementary Material 5 and final model details  
304 are provided in Supplementary Material 6.

305

## 306 2.5. Evaluation of New Models

307 Both presence and pseudo-absence records were used to evaluate the MaxEnt models'  
308 performance by partitioning the data using a 70/30 split 10 times to create 10 sets of training  
309 and test data. These datasets were compiled manually rather than using the automated  
310 MaxEnt splitting tool to reduce spatial autocorrelation in the data. To achieve this, datasets  
311 were split such that whole transects fell into either a training or testing dataset. This avoided  
312 a scenario where a single transect would be split into training and testing points, leading to a  
313 within-transect testing point validating the same transect (Howell et al. 2011). The prevalence  
314 within each test and training dataset was compared to the prevalence of the full dataset and  
315 any datasets identified as having  $> \pm 1\%$  change in the amount of presence data were  
316 discarded and another random partition made until all test and train datasets satisfied the  
317 criteria. Using the partitioned data, 10 new models were built for each habitat and evaluated

318 using the 'PresenceAbsence' package (Freeman & Moisen 2008) in R, employing both  
319 threshold-independent (AUC) and threshold-dependent metrics.

320 Three thresholding techniques were used to assess model performance, as suggested in Liu  
321 et al. (2009), and recognising that different thresholding methods seek to achieve different  
322 ends. Chosen thresholds were sensitivity-specificity equality (Sens=Spec), sensitivity-  
323 specificity sum maximisation (MaxSens+Spec) and minimum distance to the top left corner in  
324 the receiver operating characteristic curve plot (MinROCDist). Using the  
325 presence.absence.accuracy() function, the thresholding techniques and resulting model  
326 performances were assessed using three widely used indices: sensitivity, specificity and  
327 percent correctly classified (PCC). True skill statistic (TSS) can be calculated from sensitivity  
328 and specificity and is used in place of Cohen's kappa as it corrects the overall accuracy of the  
329 model predictions using the accuracy expected to occur by chance (Allouche et al., 2006). For  
330 both AUC and threshold-dependent metrics the mean and standard deviation for each metric  
331 was calculated for the 10 partitioned datasets and for the full model.

332

## 333 2.6. Quantification of Habitat Distribution and Marine Protected Area Analysis

334 The thresholding technique that gave the highest average of performance across the three  
335 chosen indices was selected for use in the final models. A binary raster of predicted presence  
336 and absence was produced as well as a raster of probability of predicted presence. Model fit  
337 was visualized by plotting the match-mismatch of binary predictions (Supplementary  
338 Material 7) In addition, the relative probability maps from all ten partitioned test/training  
339 models were used to produce standard deviation rasters to convey spatial uncertainty in the  
340 model predictions (Supplementary Material 8). The number of predicted presence raster cells

341 within different MPA polygons and below 800 m were calculated and then expressed as  
342 percentages of total presences in the whole study area, UK waters, and Irish waters. Values  
343 derived from published and new models were compared.

344

### 345 **3. RESULTS**

#### 346 3.1. Original Model Validation

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

358

#### 359 3.2. New Models

360 Results of variable correlation analysis and step-by-step documentation of the variable pre-  
361 selection procedure are provided in Supplementary Material 3.0 and 4.0.

362



363 3.3. New Model Evaluation

364 Consideration of common performance indices (Table 4) allowed for selection of final  
365 thresholding methods. For both models, Sens=Spec was selected as the chosen thresholding  
366 method, providing thresholds for *D. pertusum reef* and *P. carpenteri* aggregations of 0.44 and  
367 0.37, respectively. For *D. pertusum reef*, the AUC value for the full internally validated model  
368 and all cross validation models was deemed excellent (0.9+). The 0.44 threshold determined  
369 by Sens=Spec generated good (0.8+) results for PCC, sensitivity and specificity for all models.  
370 For *P. carpenteri*, the AUC value for the full and all cross validation models was deemed  
371 excellent. When thresholded at 0.26, all threshold-dependent metrics (PCC, sensitivity and  
372 specificity) for the full and training *P. carpenteri* models were classified as excellent (0.9+ full  
373 model and training sensitivity) or good (0.8-0.9 for training PCC and specificity) when  
374 internally validated. All cross-validation models were classified as good (0.8-0.9).

375

376 3.4. New Model Variable Importance

377 When variables are considered in isolation for *D. pertusum reef*, model gain is highest for  
378 temperature (70.5% contribution), followed by rugosity (23.3%) and FBPI (6.2%) as depicted  
379 in the jackknife plot (Supplementary Material 6.0). Temperature also decreased the model  
380 gain the most when removed as a variable, further illustrating its importance as the major  
381 variable on which predictions are reliant. For the *P. carpenteri model*, when variables are  
382 considered in isolation, model gain is highest for depth (41%) followed closely by temperature  
383 (35.9%), then BBPI (20.1%) and profile curvature (3%). When omitted from the complete

384 model the variable that decreased model gain the greatest was depth, closely followed by  
385 temperature.

### 386 3.5. Old (data poor) vs. New (data rich) high resolution models

387 Model performance determined by cross-validation suggests new models (Table 4) are  
388 comparable but of lower performance than old models (Table 3). New model spatial  
389 predictions in general follow those of the Ross et al. (2015) models, however, there are some  
390 notable differences (Fig. 2). Cold-water coral reef is predicted present on all banks, seamounts  
391 and the continental slope in the region, but the distribution is more restricted than that  
392 predicted by Ross et al. (2015). As with the previous model, *P. carpenteri* is predicted present  
393 on the continental slope, Porcupine Seabight, Rosemary Bank Seamount, around the Hatton-  
394 Rockall Plateau, and particularly in the Hatton-Rockall Basin. Presence is also predicted near  
395 the Wyville-Thomson Ridge where historical records refer to “the *Holtenia* grounds” (Wyville  
396 Thomson, 1874). The most noticeable difference is in the change in predicted distribution in  
397 the south-west section of the Hatton-Rockall Basin (circled in Fig. 2 c & d). Presence is  
398 predicted for both taxa inside the existing MPA network but, following the overall trend, the  
399 predicted distribution for *D. pertusum* reef is a contracted version of the 2015 predictions  
400 (Fig. 3 a and b). Predictions for *P. carpenteri* presence inside MPAs has changed little from the  
401 2015 model.

402

### 403 3.6. Comparison of percentage area protected by 2015 MPA network

404 For both taxa there is a significant reduction in predicted extent of suitable habitat in km<sup>2</sup> in  
405 the new models when compared to the Ross & Howell (2013) and Ross et al. (2015) models

406 (Table 5). The difference is most striking for *D. pertusum* reef where the low-resolution 2013  
407 model predicts an extent 39 times larger, and the 2015 model 6 times larger, than the new  
408 model for the whole study area. Some of this reduction will be due to the removal of all *S.*  
409 *variabilis* data points from the model data, which will have led to a slight contraction in  
410 predicted depth range, however it is clear from Fig. 3 that there is a general contraction in  
411 predicted distribution between new and old models. As *D. pertusum* reefs are only found  
412 shallower than 1200m in this region, consideration of only those areas shallow than this depth  
413 reveal the same over-all trend. However, there is an increase in the estimates of the  
414 percentage of suitable habitat contained within the 2015 MPA network when calculated from  
415 the new model as compared to old models.

416

### 417 3.7. Assessment of percentage area protected by the MPA network present in 2020

418 Assessment of the proportion of suitable habitat included within the present day MPA  
419 network (Table 6) found that *D. pertusum* reef suitable environments are the most well  
420 protected within the study area (~40% contained within MPAs) with protection at national  
421 levels varying from 84% in UK to 24% in Irish waters. This is a significant increase from the 12-  
422 32% protection under the 2015 network assessed using all models (Table 5). *P. carpentieri*  
423 suitable habitat is the least well-protected of the two habitats assessed, with ~11% of  
424 predicted suitable environments included within a current MPA, with protection at national  
425 levels varying from ~49% in UK to ~4% in Irish waters. However, this again is a significant  
426 increase on the 2015 MPA network, where the new model suggests only 7% of suitable  
427 habitat was protected by the 2015 MPA network. The addition of new MPAs in UK waters  
428 between 2015 and 2020 have taken the UK from around 59% to 84% protection for *D.*

429 *pertusum* reef and from 25% to 49% protection for *P. carpenteri*. It should be noted however  
430 that the Ross et al. (2015) and new model only cover a partial extent of the UK's continental  
431 shelf limit and data are biased to those areas that have been designated as MPAs. Thus,  
432 estimates of percentage protection are likely substantial overestimates. The EU ban on  
433 bottom trawling below 800m is estimated to protect 100% of the habitat suitable for *P.*  
434 *carpenteri*, and 42% of *D. pertusum* reef suitable habitat. Measured against IUCN targets both  
435 habitats are within or above the 20-30% protection level recommended.

436

## 437 **4. DISCUSSION**

### 438 4.1. Original Model Validation

439 Habitat suitability modelling (HSM) is a potentially valuable tool in the field of marine  
440 environmental management, but there remain questions around the true accuracy and  
441 reliability of modelled maps that may serve as a barrier to growth in use. In this study we  
442 have tested the performance of four published models at two different resolutions, 750x750  
443 m (Ross & Howell 2013) and 200x200 m (Ross et al. 2015). Two for scleractinian cold water  
444 coral reef habitat and two for the sponge species *Pheronema carpenteri*. In the original  
445 published papers, all models performed well when tested using cross-validation methods,  
446 and performance was mixed when comparing low and high resolution models, according to  
447 threshold-dependent evaluation. While high-resolution *D. pertusum* reef models out  
448 performed low-resolution models, low-resolution models for *P. carpenteri* performed as  
449 well as high-resolution models according to threshold-dependent evaluation, and better  
450 than high resolution models according to threshold-independent evaluation (AUC). Our  
451 study has shown that when tested using independent data all models perform worse than

452 expected based on published cross-validation results for both threshold-dependent and  
453 independent metrics. Although models perform worse than under cross-validation, model  
454 performance is still considered good (0.9–0.8) or fair (0.8–0.7) for scleractinian cold-water  
455 coral reef habitat models, with poorer performance for the *P. carpenteri* sponge models,  
456 particularly at low resolution and when measured by sensitivity. High-resolution models  
457 out-performed low-resolution models for both taxa when assessed using independent  
458 data.

459 Our findings are in broad agreement with the very small number of comparable studies that  
460 have independently validated deep-sea sponge and coral HSM published models, with some  
461 notable differences. Rooper et al. (2016, 2018) independently validated HSM for corals and  
462 sponges in the eastern Bering Sea slope, outer shelf in Alaska and Aleutian Islands. These  
463 models were developed based on data from bottom trawl surveys at a resolution of  
464 100x100 m grid cell size and validated using camera-based surveys. These studies found that  
465 while model performance decreased when comparing cross-validation to independent AUC  
466 scores, performance was still acceptable for coral models. This taken with our own findings  
467 suggest that high resolution models (<200x200 m grid cell size) of deep-sea coral  
468 distributions can be accurate and can provide useful information for spatial management of  
469 these vulnerable taxa.

470 However, low-resolution models may not perform well. Bowden et al. (2021) recently  
471 evaluated 47 HSM from eight published studies, all focused on the area around New  
472 Zealand, using independent data. All models were at 1km or 30 arc-seconds grid cell size,  
473 and in all cases model performance was lower than in published cross-validation values.

474 Anderson et al. (2016) found that their models of the distribution of four scleractinian species

475 (not *Desmophyllum pertusum*) across the South Pacific Regional Fisheries Management  
476 Organisation area and adjoining EEZs were not successful in accurately predicting suitable  
477 habitat for reef-forming deep-sea corals when independently validated. These models were  
478 also constructed on a 30 arc-second grid (~1 km<sup>2</sup>) and data resolution was given as a  
479 possible explanation for model failure in the face of independent testing. Specifically, these  
480 authors cited the limitations of the bathymetry dataset used, which in turn affected the  
481 precision of each of the environmental predictor variables. Both studies report on models of  
482 comparable resolution to the low-resolution Ross & Howell (2013) model tested here.

483 Interestingly the Ross & Howell (2013) model appears to have performed better than the  
484 Anderson et al. (2016) models in the face of independent data. Anderson et al. (2016) cite  
485 missing critical predictor variables, particularly substrate type, lack of true absence data,  
486 spatial bias in distribution of presence records, and aspects of the topography in the study  
487 area, as possible reasons for their model's poor performance. Ross & Howell's (2013) model  
488 did make use of background data to account for spatial bias in the dataset, which may have  
489 resulted in better performance when subjected to independent testing. However, a  
490 principal difference between the Anderson et al. (2016) models and the Ross & Howell  
491 (2013) model is the focus of the models. Ross & Howell (2013) modelled scleractinian reef  
492 habitat where Anderson et al. (2016) modelled scleractinian species presence. The  
493 difference is important as the former occupies a restricted subset of the environmental  
494 niche of the latter (Howell et al. 2011), and a narrower niche width can result in a better  
495 performing model (Kadmon et al. 2003, Tsoar et al. 2007). This concept is used to explain  
496 the possible poor performance of Rooper et al.'s (2016, 2018) sponge models. These  
497 authors suggested that the difference they observed in their high-resolution (100x100 m  
498 grid cell size) coral and sponge model performance may be a result of lumping species

499 together into a large taxonomic group called 'sponge'. This essentially merged species with  
500 very different habitat preferences, ultimately giving the group a wide environmental niche.  
501 The coral group in their study was dominated by a single family (Primnoidae) and thus was  
502 less affected by this pooling action.

503 Niche width is unlikely to explain the poor performance of the *P. carpenteri* model. This  
504 hexactinellid (glass sponge) is found predominantly on fine sediments where it loosely  
505 anchors to the substrate using long spicules at the base of the organism. Aggregations in the  
506 NE Atlantic are found over a very narrow depth range from 1000 to 1300 m (Rice et al.  
507 1990) and appear to occupy a very specific niche. Cross-validation of HSMs created for this  
508 species suggested model performance was excellent (Ross & Howell 2013, Ross et al. 2015).  
509 However, independent validation suggests that while the models have fair to good PCC and  
510 specificity, they have poor sensitivity, meaning that the resulting maps may be indicating an  
511 absence where there is in fact a presence. Examination of the spatial distribution of false  
512 negatives suggests most (25 of 28 data points) are found on offshore seamounts and banks.  
513 These habitat types, and therefore this particular aspect of *P. carpenteri's* environmental  
514 niche, was not represented in the dataset used to build the published models and could  
515 help explain why the models partially fail. However, aspects of the ecology of *P. carpenteri*  
516 may also explain the poor model performance.

517 *P. carpenteri*, in common with other deep-sea sponge species that form aggregations, are  
518 thought to be associated with regions of enhanced bottom currents related to the  
519 interaction of internal waves with sloping boundaries (Rice et al. 1990, Klittgaard et al. 1997,  
520 Davison et al. 2019) and raised features like the Mid-Atlantic Ridge (van Haren et al. 2017).  
521 The causal link is suggested to be an increase in the supply of food as a result of the

522 resuspension of organic matter (Rice et al.1990). Oceanographic variables (and variability)  
523 may therefore be of critical importance in determining the distribution of *P. carpenteri*. The  
524 omission of such predictor variables from the Ross & Howell (2013) and Ross et al. (2015)  
525 models may also explain why both models partially fail when tested with independent data.  
526 The inclusion of oceanographic variables in deep-sea marine SDM has been found to  
527 improve model performance when tested with cross-validation (Rengstorf et al. 2014,  
528 Pearman et al. 2020) further supporting their inclusion in any future model development.

529 Our results suggest that for both scleractinian reef and *P. carpenteri*, the high-resolution  
530 models out-perform the low-resolution models when tested with independent data. This is  
531 an important finding as it suggests our ability to produce useful models of deep-sea benthic  
532 species and habitat distribution is dependent on availability of high-resolution  
533 environmental data including bathymetry data. Current maps of the seafloor are derived  
534 using satellite altimetry, which gives an average achievable resolution in the order of 8 km  
535 (Mayer et al. 2018). The percentage of the seafloor that has been measured by echo-  
536 sounders is considerably less than 18% and only about 9% of the seafloor is covered by high-  
537 resolution multibeam sonar data (Mayer et al. 2018). Recently an international effort has  
538 begun with the objective of facilitating the complete multibeam mapping of the world  
539 ocean by 2030. The Nippon Foundation GEBCO Seabed 2030 Project has the potential to  
540 improve significantly the quality of HSM it is possible to produce for deep-sea taxa by  
541 providing high-resolution bathymetry data. However, access to high-resolution  
542 oceanographic model output, as well as un-biased datasets of the distribution of target  
543 species and assemblages, and a good understanding of the biology and ecology of those  
544 species and assemblages, are also necessary to improve the quality of models. Targeted



545 efforts to collect these data over the next decade (Howell et al. 2020a,b) will be important  
546 in the further development of this field.

547 The good performance of the high-resolution scleractinian reef habitat model suggests that  
548 it may be a useful tool in the spatial management of cold-water coral reef in this region.  
549 Cold-water coral reef is considered a Vulnerable Marine Ecosystem (VME) under United  
550 Nations General Assembly Resolution 61/105, and, in the North East Atlantic is also classed  
551 as ‘threatened and/or declining habitat’ under the OSPAR Convention. Within European  
552 waters it is also recognised as an Annex I habitat under the EU Habitats and Species  
553 Directive (92/43/EEC). Collectively these policies require relevant management authorities  
554 to take actions to protect cold-water coral reef habitat. Specifically, UNGA 61/105 states “*In*  
555 *respect of areas where vulnerable marine ecosystems, including seamounts, hydrothermal*  
556 *vents and cold water corals, are known to occur or are likely to occur based on the best*  
557 *available scientific information, to close such areas to bottom fishing and ensure that such*  
558 *activities do not proceed unless conservation and management measures have been*  
559 *established to prevent significant adverse impacts on vulnerable marine ecosystems”*.  
560 Actions have so far been limited to those areas where cold water coral reef has been  
561 observed either through visual or physical sampling means. However, the high-resolution  
562 model provides best available scientific information on where cold-water coral reef is likely  
563 to occur in this region, and thus could be used to support decisions around further  
564 measures.

565 Similarly, the good performance of the high-resolution *P. carpenteri* model in terms of PCC  
566 and specificity, and fair AUC score, suggests it also may be a useful tool in the spatial  
567 management of the region. However, it must be noted that this is a presence / absence

568 HSM, and therefore it only indicates likely presence / absence of suitable habitat for the  
569 species (a VME indicator taxa), not the aggregation (a VME). This, together with the notable  
570 deficiencies in the model outlined above, suggests it is less useful than the scleractinian reef  
571 habitat model, but may still have value in indicating areas for further consideration given  
572 the precautionary principle.

573

#### 574 4.2. New Model performance and interpretation

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

586 In this study we have used a presence – background approach rather than a presence-absence  
587 approach since our model input data are drawn from multiple surveys using multiple gear  
588 types and spanning more than 30 years. In our opinion, absences cannot be inferred from our  
589 dataset with certainty, and so we opted to be cautious in our use of absence data. However,  
590 it should be noted that evidence suggests presence-absence models perform better than

591 presence-only models, particularly where species / assemblages occupy all suitable habitat,  
592 making absence data reliable (Brotons et al. 2004), although Maxent has been found to  
593 perform equally as well as presence-absence models (González-Irusta et al. 2014). Future  
594 modelling efforts may wish to consider use of presence-absence approaches where authors  
595 feel absence data are reliable.

596 Temperature was a significant term in both new models and is a fundamental variable that  
597 controls species distributions. *D. pertusum* has been observed living under a wide range of  
598 temperatures (4–13 °C) (Freiwald et al. 2004), with an upper thermal tolerance of 15 °C  
599 (Brooke et al. 2013). Response curves for Maxent models for *D. pertusum* reef  
600 (Supplementary Material 6.0) suggest the highest likelihood of occurrence of reef habitat in  
601 the study area is at temperatures of ~8°C, which is almost the center of the species thermal  
602 niche. There are no data available on the thermal niche of *P. carpenteri*. Howell et al. (2016)  
603 reported this species to occur over a temperature range of 2.73–20.9 °C (mean 5.17 °C,  
604 standard deviation 2.03) in the northern North Atlantic. Response curves for Maxent models  
605 for *P. carpenteri* (Supplementary Material 6.0) suggest this species occupies a narrow thermal  
606 niche, with peak likelihood of occurrence at between 6-8°C, falling sharply to no occurrences  
607 below approximately 3°C or above 10°C. The wide range reported in Howell et al. (2016) is  
608 likely a result of poor position data from the older records used in that model in order to  
609 provide whole North Atlantic data coverage.

610 New model spatial predictions in general follow those of the Ross et al. (2015) models.  
611 However, there are some notable differences, particularly in the spatial prediction for *P.*  
612 *carpenteri* in the southern region of the Hatton-Rockall Basin (Fig. 2 c, d). In this region  
613 available CTD data suggest the temperature is cooler than that at equivalent depths in the

614 Rockall Trough and on the European continental slope, making this region less suitable for *P.*  
615 *carpenteri* than predicted by the 2015 model, which did not include temperature.  
616 Interestingly the Howell et al. (2016) model, which did include temperature, also predicted  
617 this area as suitable habitat, however the thermal niche of *P. carpenteri* was likely incorrectly  
618 defined in that model as previously noted. The principal difference in the spatial predictions  
619 for the *D. pertusum reef* model is a general contraction of the 2015 predictions in the current  
620 model. This is well illustrated in Fig. 3 a and b where current model predictions are much  
621 more focused than those of the 2015 model.

622

#### 623 4.3. Re-assessment of current area closures and percentage protection targets for these VMEs

624 For both taxa there is a significant reduction in predicted extent in the new models when  
625 compared to the Ross & Howell (2013) and Ross et al. (2015) models (Table 5). The 2013  
626 low-resolution models predicted 39 times and 4 times greater extent for *D. pertusum reef*  
627 and *P. carpenteri* respectively. This difference has important implications for onward use of  
628 models in decision-making. For example, calculations of ecosystem services such as carbon  
629 sequestration (Barnes et al. 2019; Barnes et al., 2021) or nutrient cycling (Hoffman et al.  
630 2009) based on modelled extent may be grossly overestimated if based on low-resolution  
631 models. Similarly, the 2015 models predicted a greater extent of suitable habitat than the  
632 new model by 6 times and 1.4 times for *D. pertusum reef* and *P. carpenteri* respectively,  
633 suggesting that estimates of extent based on model predictions should be used with  
634 caution and considered likely overestimates.

635 In contrast, estimates of percentages of predicted suitable environments protected by the  
636 regional MPA network increased when calculated using the new model compared to the

637 2013 and 2015 models. The Convention on Biological Diversity originally set out a target of  
638 10% of marine areas to be protected by 2010 (UNEP/CBD/COP/DEC/VII/5) (later moved to  
639 2020 (UNEP/CBD/COP/10/27)), and that is now being followed up with calls for 30% by 2030  
640 (CBD, 2020). While these percentage area targets are not habitat specific, Aichi Target 11  
641 makes specific reference to 'ecologically representative and well-connected systems of  
642 protected areas' (UNEP/CBD/COP/10/27/Annex), which implies that different marine  
643 habitat types should be protected at that level. The independently validated 2015 models  
644 suggest that for the area modelled and the 2015 MPA network, both the UK and Ireland  
645 have surpassed the original 10% protection target for *D. pertusum* reef, while the UK have  
646 also surpassed this for *P. carpenteri* suitable habitat. In addition, the UK have surpassed the  
647 30% target for *D. pertusum* reef habitat in the modelled area. The picture is the same for the  
648 new model. However, in both the 2015 and new model, Ireland protects <10% of suitable  
649 habitat for *P. carpenteri*, implying that further MPAs may be required. Ireland has  
650 committed to protecting 30% of its habitat by 2030 (Marine Protected Area Advisory Group,  
651 2020) and data such as these can help guide that process.

652 The situation is broadly similar when considering the 2020 MPA network although the  
653 estimates of percentage of habitat protected in UK waters are much higher. It must,  
654 however, be noted that the current MPA network is not 'strictly protected' in line with IUCN  
655 specifications and in some cases management measures have yet to be drawn up. It is also  
656 important to remember that the modelled area in UK waters is much more limited than that  
657 modelled in Irish waters due to the limited availability of multibeam mapping in UK waters.  
658 The areas that have been mapped (and thus modelled onto) in UK waters tend to be  
659 associated with protected status, thus the UK figures are likely gross overestimates.  
660 Estimates of percentage of suitable habitat made from the low resolution 2013 model are

661 lower than all other estimates, and, reiterating the findings of Ross et al. (2015), suggests  
662 that low-resolution models result in conservative estimates in this context, which is in line  
663 with the precautionary principle and suggests low-resolution models may have a use in this  
664 area.

665 An interesting finding is that the ban on bottom trawling below 800 m in EU waters (UK is  
666 currently following) protects >30% of both habitats estimated from the new model with 100%  
667 of *P. carpanteri* suitable habitat protected. While a significant achievement, it is important to  
668 again consider the issue of representativeness in Aichi Target 11. Cold-water coral reefs  
669 occurring at different depths support different assemblages of associated species in line with  
670 the well-documented turnover of species along the depth gradient (Rowe & Menzies 1969,  
671 Howell et al. 2002, Carney 2005). In order to be representative, protection for cold-water  
672 coral reef sites must span its known depth range (thermal niche) necessitating protection of  
673 sites shallower than 800 m. In addition, the twin threats of ocean acidification and global  
674 warming mean that shallower areas of predicted suitable habitat in this region may be key  
675 refuge sites for cold-water coral reef (Jackson et al. 2014). Ocean acidification is causing the  
676 aragonite saturation horizon (ASH) to shoal exposing deep-water coral reefs to waters that  
677 are corrosive to coral skeletons (Guinotte et al. 2006). In parallel, seawater temperatures are  
678 increasingly exposing reefs to novel conditions. While live *D. pertusum* can tolerate long-term  
679 exposure to combined end-of-the-century temperature and pCO<sub>2</sub> scenarios (Hennige et al.  
680 2015, Büscher et al. 2017), the dead coral skeletons that make up the reef framework are  
681 weakened by acidified conditions and become more susceptible to bioerosion and mechanical  
682 damage (Hennige et al. 2015). This ultimately leads to crumbling, collapse, and loss of  
683 complexity of the larger habitat, and resulting ecosystem services (Hennige et al. 2020). In  
684 this region, the East Mingulay Special Area of Conservation (SAC), Wyville Thomson Ridge SAC,

685 and North West Rockall Bank SAC represent important strongholds for reef habitat (Jackson  
686 et al. 2014) and therefore the 800 m bottom-trawling ban alone will not meet the qualitative  
687 aims of Aichi Target 11.

688

## 689 **5. CONCLUSION**

690 Independent testing of four published models has shown that for the taxa considered, high-  
691 resolution models (<200x200 m grid cell size) can be accurate and can provide useful  
692 information for spatial management of these vulnerable taxa. With respect to UNGA  
693 Resolution 61/105, the high-resolution cold-water coral reef model provides best available  
694 scientific information on where this VME is likely to occur in this region, and thus could be  
695 used to support decisions around further measures. Our ability to produce useful models of  
696 deep-sea benthic species and habitat distribution is highly dependent on the availability of  
697 high-resolution environmental data including bathymetry data. To improve model  
698 performance significant research effort is needed to map the seafloor, oceanographic  
699 environment, and distribution of species and assemblages (presence, absences, density) in  
700 order to provide more, better quality, model input data. In addition, further research effort  
701 is needed to provide a more complete understanding of the importance of environmental  
702 variables to target taxa, and their interactions at a variety of scales. For well performing  
703 high-resolution models (200x200m), estimates of extent based on model predictions should  
704 be used with caution and considered likely overestimates. Low-resolution models  
705 (750x750m) may be useful in providing conservative estimates in progress towards  
706 percentage protection targets but are not recommended for use in estimates of extent. For  
707 *D. pertusum* reef and *P. carpenneri* the UK and Ireland have made good progress towards

708 the 10% CBD target for conserving habitats and species within MPAs. This together with the  
709 EU ban on bottom trawling below 800 m, provide a level of protection for both, however  
710 representativity needs to be considered in these assessments. Assessment of UK progress is  
711 limited by a lack of available multibeam data.

712

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733

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969

970 Table 1: Breakdown, total (presence/absence), of biological datasets used to build habitat  
 971 suitability models and independently validate Ross & Howell (2013) and Ross *et al.* (2015).

	Ross & Howell 2013 (GEBCO)	Ross <i>et al.</i> 2015 (200m)	Howell <i>et al.</i> 2021	Ross & Howell 2013 (GEBCO) Validation	Ross <i>et al.</i> 2015 (200m) Validation
<i>D. pertusum</i>	864 (75/789)	1,284 (116/1,168)	3,291 (227/3,064)	646 (64/582)	2,018 (122/1896)
<i>P. carpenteri</i>	864 (53/811)	1,284 (74/1,210)	3,196 (139/3,057)	597 (32/565)	1,937 (66/1871)

972

973 Table 2: Performance statistics for the published Ross & Howell (2013) models according to  
 974 original cross validation and new independent validation. Threshold values are predicted  
 975 probabilities of presence. SD = Standard deviation.

	Method	PCC (SD)	Sens. (SD)	Spec. (SD)	TSS (Sens+ Spec-1)	AUC (SD)	Thresh old values
<b><i>D. pertusum</i> reef</b>							
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 dataset.	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 dataset	Sens=Spec	0.73 (0.03)	0.74 (0.07)	0.73 (0.04)	0.47	0.79 (0.04)	0.44
<b><i>P. carpenteri</i></b>							
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 dataset.	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 dataset	MaxSens+ Spec	0.90 (0.02)	0.31 (0.12)	0.95 (0.02)	0.26	0.71 (0.07)	0.375

976

977 Table 3: Performance of the published Ross et al. (2015) models according to original cross

978 validation and new independent validation. Threshold values are predicted probabilities of

979 presence. SD = Standard deviation.

	Method	PCC (SD)	Sens. (SD)	Spec. (SD)	TSS (Sens+ Spec-1)	AUC (SD)	Thresh old values
<b><i>D. pertusum reef</i></b>							
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 dataset.		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 dataset	Sens=Spec	0.82 (0.03)	0.82 (0.07)	0.82 (0.03)	0.64	0.90 (0.03)	0.435
<b><i>P. carpenteri</i></b>							
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 dataset.		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 dataset	MaxSens+ Spec	0.84 (0.03)	0.6 (0.13)	0.86 (0.03)	0.46	0.75 (0.08)	0.175

980



Table 4: Threshold-dependent evaluation indices for training, test, and full models. Final thresholds and associated evaluation metrics shaded.

	Average Training – Internal validation			Average Test – Cross validation			Full Model – Internal validation			
Thresholding approach	PCC (SD)	Sens. (SD)	Spec. (SD)	PCC (SD)	Sens. (SD)	Spec. (SD)	PCC (SD)	Sens. (SD)	Spec. (SD)	Threshold
<b><i>D. pertusum reef</i></b>										
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
<b><i>P. carpenteri</i></b>										
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

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 MPA and NEAFC Closure network used by Ross et al. (2015) for the purpose of comparison, also broken down by national MPAs and NEAFC Closures.

		<i>D. pertusum</i> reef			<i>P. carpenteri</i>		
		Ross & Howell 2013 GEBCO Model	Ross <i>et al.</i> 2015 200m <sup>2</sup> Model	New Model	Ross & Howell 2013 GEBCO Model	Ross <i>et al.</i> 2015 200m <sup>2</sup> Model	New Model
Entire Model Extent	Predicted Suitable Habitat	185,240.25 km <sup>2</sup>	30,106.10 km <sup>2</sup>	4748.32 km <sup>2</sup>	218,725.88 km <sup>2</sup>	73,709.68 km <sup>2</sup>	54,289.48 km <sup>2</sup>
	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	57,425.06 km <sup>2</sup>	8,281.48 km <sup>2</sup>	1,244.00 km <sup>2</sup>	87,516.00 km <sup>2</sup>	9,514.00 km <sup>2</sup>	8,886.76 km <sup>2</sup>
	Predicted	29.84%	56.00%	58.95%	2.60%	11.20%	25.23%

	Suitable Habitat within MPAs/NEAFC Closures						
Model extent within Irish Shelf Claim	Predicted Suitable Habitat	48,139.31 km <sup>2</sup>	21,665.48 km <sup>2</sup>	3,412.36km <sup>2</sup>	49,343.63 km <sup>2</sup>	63,525.96 km <sup>2</sup>	43,936.44 km <sup>2</sup>
	Predicted Suitable Habitat within MPAs/NEAFC Closures	13.67%	12.60%	21.65%	1.10%	1.39%	2.86%

Table 6: Area of predicted suitable habitat for *D. pertusum* reef and *P. carpeniteri* 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 date MPA/NEAFC Closure network and the EU / UK 800m trawl ban, also broken down by nation.

		<i>D. pertusum</i> reef	<i>P. carpeniteri</i>
Entire Model Extent	Predicted Suitable Habitat	4,748.32 km <sup>2</sup>	54,289.48 km <sup>2</sup>
	800m Trawl Ban	60.11%	100.00%
	2020 MPA/NEAFC Network	40.26%	11.45%
Model extent within UK Shelf Claim	Predicted Suitable Habitat	1,244.00 km <sup>2</sup>	8,886.76 km <sup>2</sup>
	800m Trawl Ban	48.74%	100.00%
	2020 MPA/NEAFC Network	83.64%	49.30%
Model extent within Ireland Shelf Claim	Predicted Suitable Habitat	3,412.36 km <sup>2</sup>	43,936.44 km <sup>2</sup>
	800m Trawl Ban	64.25%	100.00%

	2020 MPA/NEAFC Network	24.45%	3.79%
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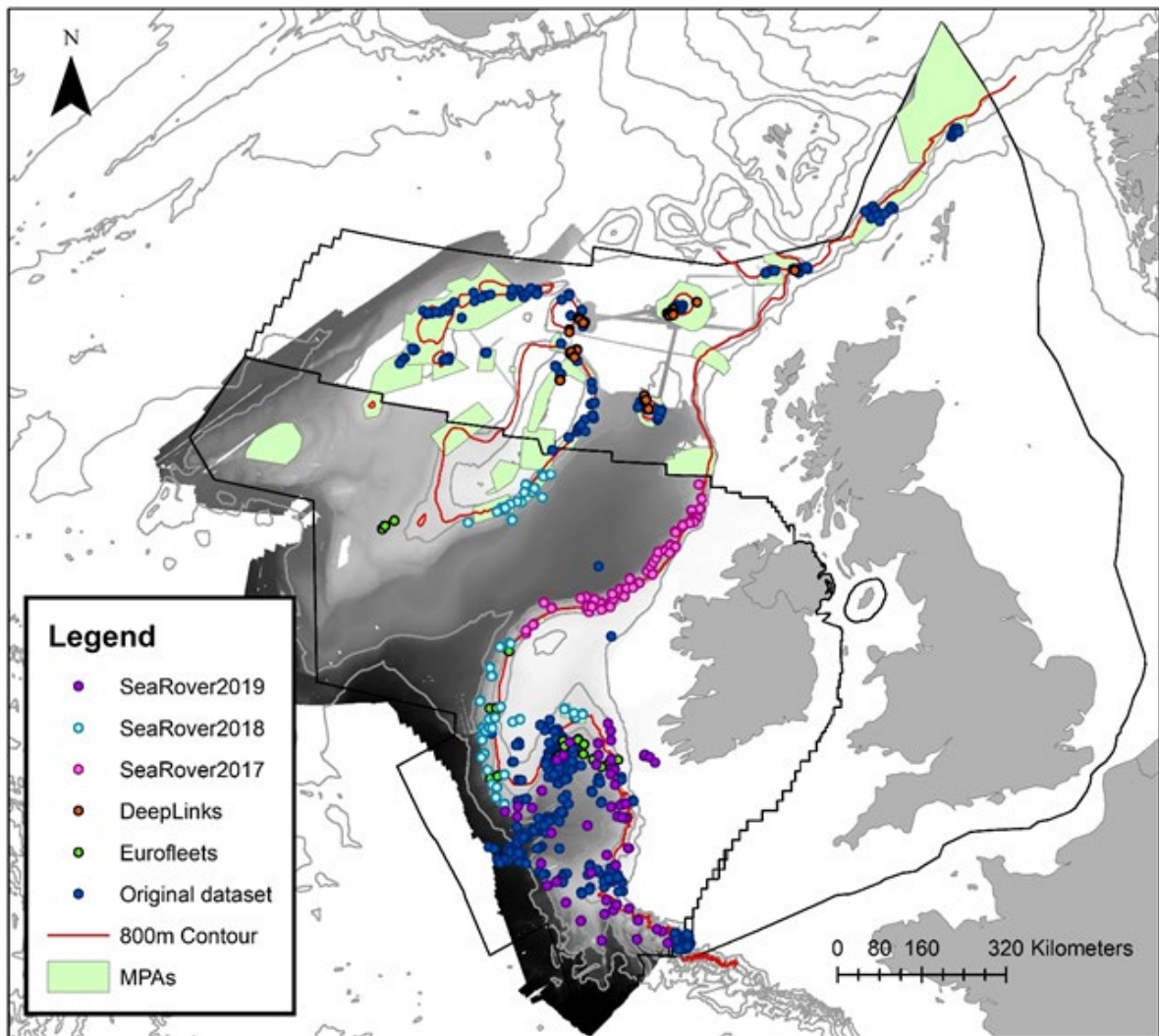


Figure 1: Map of the UK and Ireland's Continental Shelf Limits (black line) showing the original dataset from Ross & Howell (2013), and Ross et al. (2015) together with the new dataset (compiled from five different surveys over 5 years) used to independently validate the models and subsequently build new models. The current network of deep-sea Marine Protected Areas is shown, together with the 800m isobath, below which bottom trawling is prohibited. Bathymetry shown is the 200 x 200 m gridded multibeam dataset (see text below for detail) shaded for depth with contours of 200m, 500m, 1000m and intervals of 1000m thereafter shown in grey. Map projected in British National Grid for aesthetic reasons

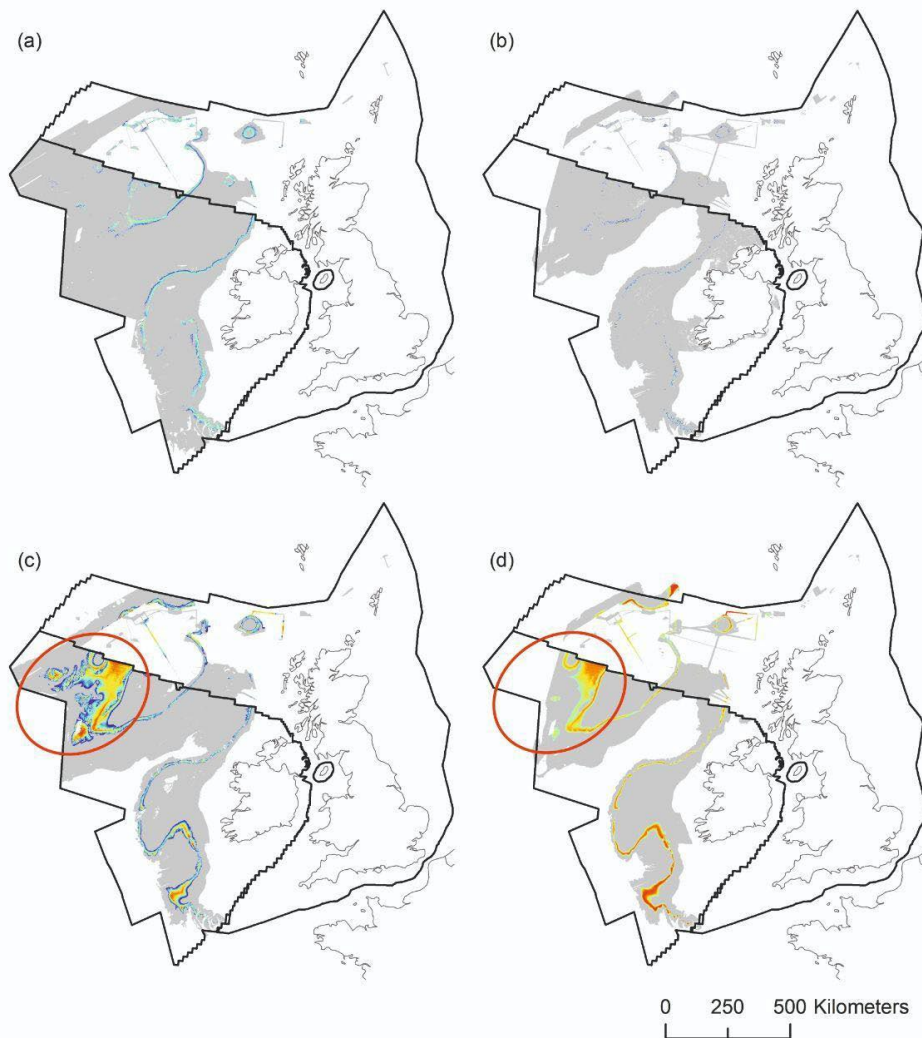


Figure 2: Above threshold full model prediction maps for: (a) scleractinian cold-water coral reef distribution from Ross *et al.* (2015); (b) *D. pertusum* reef distribution with the new dataset; (c) *P. carpenteri* aggregation distribution from Ross *et al.* (2015); (d) *P. carpenteri* aggregation distribution with the new dataset. The Hatton-Rockall Basin is circled in red in c and d. White background indicates the prediction has been masked for novel climates. Maps projected in British National Grid for aesthetic reasons.

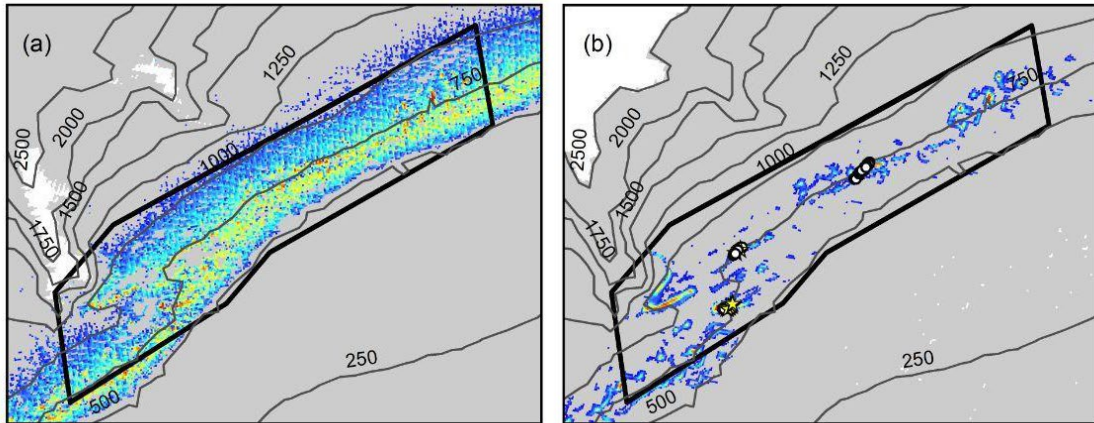


Figure 3: Examples of changes to protected area model predictions. (a) scleractinian cold-water coral reef distribution within the North-West Porcupine Bank MPA from Ross *et al.* (2015); (b) *D. pertusum* reef distribution within the North-West Porcupine Bank MPA with the new dataset. ROV transects plotted showing presences as yellow stars and absence as white circles. Maps projected in British National Grid for aesthetic reasons.