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Use of predictive habitat modelling to assess the distribution and extent of the current protection of 'listed' deep-sea habitats

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Abstract

Aim

To demonstrate the application of predictive species distribution modelling methods to habitat mapping and assessment of percentage area based conservation targets.

Location

The NE Atlantic deep sea (UK and Irish extended continental shelf limits)

Methods

MaxEnt modelling of three listed habitats (*Lophelia pertusa* (Linnaeus, 1758) reef (LpReef), *Pheronema carpenteri* (Thomson, 1869) aggregations (PcAggs), and *Syringammina fragilissima* (Brady, 1883) aggregations (SfAggs)), with some pre-selection of variables by Generalised Additive Modelling. Models are validated using repeated 70 / 30 build / test data splits using AUC and threshold dependent assessment methods. Predicted distribution maps are used to assess the adequacy of existing area closures for the protection of listed habitats and to assess percentage representation of each community within existing MPA networks.

Results

Model performances are rated as fair (LpReef), excellent (PcAggs), and good (SfAggs). Current closures are focused on the protection of cold water coral reef and incidentally capture some SfAggs suitable environments, but largely fail to protect PcAggs. Considering the wider network of MPAs in the study region approximately 23% (LpReef), 2% (PcAggs) and 6% (SfAggs) of the area predicted as suitable for each habitat respectively is contained within an MPA.

Main Conclusions

To date decisions on area closures for the protection of 'listed' deep-sea habitats have been based on maps of recorded presence of species that are taken as being indicative of that habitat. Predictive habitat modelling may provide a useful method of better estimating the extent of listed habitats, providing direction for future MPA establishment and a means of assessing MPA network effectiveness against politically set percentage targets. Given the coarse resolution of the model these figures are likely to be lower in reality.

Introduction

Global declines in biodiversity have ignited responses from local to international scales, aiming to establish management methods for the effective protection of species and ecosystems, and the limitation of human impact on the environment. Spatial management, through the use of Marine Protected Areas (MPAs) is contributing to efforts to meet these aims within the marine environment.

Decisions concerning locations to establish MPAs for conservation of biodiversity are generally taken on the basis of protecting species and/or habitats of perceived ecological importance, vulnerability, or rarity; specific examples of such species and habitats are often listed within the legislation requiring action to be taken. The designation of MPAs for the conservation of listed habitats requires extensive information on the spatial location and range extent of each habitat. In the deep-sea environment this data is patchy at best given the vast area, distance from shore, expense of exploration and resulting highly localised data availability relative to inshore waters (Howell et al., 2011). Efforts to map the distribution of listed habitats have resulted in maps of point sample data, often of indicator species rather than the habitat, with data dating back several decades or longer. While an extremely valuable first step, this approach has a number of drawbacks potentially resulting in the inappropriate placement of sites and an MPA network that is neither representative nor ecologically coherent.

Predictive modelling of species distributions (Bryan & Metaxas, 2007; Holmes *et al.*, 2007; Embling *et al.*, 2010; Howell *et al.*, 2011) provides a robust defensible means to "fill in the gaps" and provide complete coverage maps on which to base management decisions. Many species distribution models already exist for the reef-forming coral *Lophelia pertusa* (Linnaeus, 1758) in order to identify areas of conservation importance (Davies *et al.*, 2008; Dolan *et al.*, 2008; Guinan *et al.*, 2009; Tittensor *et al.*, 2009). However a recent study highlighted potential problems in using maps based on the distribution of the species, which is widespread, rather than the distribution of the habitat it forms, which is not (Howell et al., 2011). Where a habitat is the target of conservation efforts, species distribution maps produces gross overestimates of extent. It may therefore be prudent where possible to model the distribution of the habitat rather than the indicator species.

The ability to assess habitat extent can be an important tool in marine conservation efforts. Political initiatives often cite percentage targets for conservation: the 2003 IUCN Vth World Parks Congress says we must"[g]realty increase the marine and coastal area managed in marine protected areas by 2012; these networks should include strictly protected areas that amount to at least 20-30% of each habitat"; the 2006 Convention on Biological Diversity (CBD) also set a percentage target (10%) for the conservation of the world's ecological regions. Thus an important secondary use of predictive habitat maps is in the assessment of conservation efforts against specified targets.

This study focuses on creating habitat model maps for three listed deep-sea habitats in part of the NE Atlantic: *Lophelia pertusa* reefs (LpReef; a cold-water coral reef), *Pheronema carpenteri* (Thomson, 1869) aggregations (PcAggs; a sponge dominated community), and *Syringammina fragilissima* (Brady, 1883) aggregations (SfAggs; a xenophyophore community). All three habitats qualify as

Vulnerable Marine Ecosystems (VMEs) under United Nations General Assembly Resolution 61/105, while LpReef and PcAggs are also classed 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.

Lophelia pertusa is the dominant reef-building cold-water coral in the NE Atlantic with the ability to form expansive reefs and carbonate mounds up to 300m high (Roberts et al., 2006). The species may also be found as isolated colonies attached to patches of hard substrate (Wilson, 1979a; Mortensen & Buhl-Mortensen, 2004b, a; Hovland, 2005). Globally the species may be found between 39m and 3380m water depths (Thiem et al., 2006), however most reefs have been recorded between 200 and 400m at temperatures between 4 and 12°C (Freiwald *et al.*, 2004; Roberts *et al.*, 2006; Davies *et al.*, 2008). Factors driving reef formation are poorly understood but are likely to be an interplay between local hydrography and sedimentary dynamics (Thiem *et al.*, 2006; Howell *et al.*, 2011),with most reefs being found on topographic highs and sloping bathymetry (Strømgren, 1971; Genin *et al.*, 1986; Frederiksen *et al.*, 1992; Davies *et al.*, 2008) in areas of strong currents and high productivity (Mortensen *et al.*, 2001; White *et al.*, 2005; Thiem *et al.*, 2006; Kiriakoulakis *et al.*, 2007; Davies *et al.*, 2008).

Pheronema carpenteri is a glass sponge which can form aggregations on fine sediments with densities of up to 1.53 individuals m^{-2} as seen on the Goban Spur (Hughes & Gage, 2004). These aggregations are associated with an increase in abundance and richness of macrofauna within spicule mats and sponge bodies providing habitat complexity and a hard substrate for epifauna colonisation (Rice *et al.*, 1990; Bett & Rice, 1992). Aggregations are found predominantly between 1000 and 1300m depth (Rice et al., 1990) in areas of high productivity, and possibly proximate to regions of enhanced bottom tidal currents which aid in re-suspension of organic matter (Rice *et al.*, 1990; White, 2003).

Xenophyophores are found exclusively in the deep sea and can be up to 25cm in diameter (Tendal, 1972, 1996; Gooday & Tendal, 2000). *Syringammina fragilissima* is one of the largest and most commonly observed species in the NE Atlantic forming aggregations of up to 7-10 individuals m^{-2}(Roberts *et al.*, 2000; Bett, 2001). Sediments adjacent to large xenophyophore tests have been found to contain significantly more metazoan macrofauna than surrounding sediments (Levin *et al.*, 1986; Levin & Thomas, 1988) and the tests themselves can provide microhabitats for small meiofaunal-sized metazoans (Gooday, 1984) and foraminifera (Gooday & Haynes, 1983; Gooday, 1991; Shires *et al.*, 1994). Levin (1991, 1994) also suggests that xenophyophore tests may provide a structural habitat for epifauna. They are often found in areas of enhanced carbon flux, on sloped topography or near topographic features (Tendal, 1972; Levin & Thomas, 1988; Levin & Gooday, 1992; Hughes & Gooday, 2004).

This study aims to inform the development of deep-sea MPA networks by demonstrating the application of predictive species distribution models to habitat mapping and assessment of percentage area based targets.

Methods

Site Description

This study considers the NE Atlantic waters of the UK and Ireland's extended continental shelf limits, excluding the Faroe Shetland Channel as a separate biogeographic region (Bett, 2001), and the North Sea due to lack of data coverage (Figure 1). Within this region there are a number of MPAs that have been primarily designated for the protection of LpReef habitat or bedrock "reef like" assemblages. These have been achieved through three different policy mechanisms resulting in three classes of MPAs: Special Areas for conservation (SACs), OSPAR MPAs, and North East Atlantic Fisheries Commission (NEAFC) closures to bottom trawling for the protection of VMEs. While the sites cannot be considered a single coherently designed MPA network they do provide the basis of a developing network and serve as a mechanism for illustrating the potential use of habitat maps in marine management.

Biological Data

Presence/absence data was compiled for each listed habitat from 222 biological video and photographic transects obtained from several research cruises undertaken in the region between 2005 and 2011 (Howell *et al.*, 2009b; Howell *et al.*, 2009a; Stewart *et al.*, 2009; Howell *et al.*, 2011; Huvenne, 2011). Additional presence/absence data for LpReef and PcAggs models were obtained from the National Oceanography Centre, Southampton programme of activities in the Porcupine Seabight (PSB) and Porcupine Abyssal Plain (PAP) between 1977 and 2000 (Rice, 1990; Rice *et al.*, 1990; Jackson *et al.*, 1991; Rice, 1992; Bett, 1994; Billett, 2000; Bett *et al.*, 2001). PSB and PAP data were a combination of WASP photo-sled transects and semi-quantitative semi-balloon otter trawls (OTSB). Detailed technical specifications are available in the source literature.

Environmental Data

Environmental variables were selected based on their biological relevance, resolution and availability. Both topographic and oceanographic variables were trialled with preliminary models, however oceanographic variables were only available at 1 degree resolution (1 reading every 90km), severely degrading the resolution of the final models. Oceanographic variables were therefore excluded from the final study.

Five topographic variables were trialled with all models based on their expected significance in acting as proxies for environmental factors that drive species distributions in the deep-sea. Bathymetry (depth) provides a proxy for multiple other variables in the deep-sea including temperature (where biogeography is taken into account), current speed, water mass structure, food availability, and sediment type (Howell *et al.*, 2002; 2010). Bathymetric data was obtained from the General Bathymetric Chart of the Oceans (GEBCO) 2008 30 arc-second grid, as derived from quality controlled ship soundings combined with satellite derived gravity data. This dataset provides universal

coverage of the study area corresponding to a sounding every 750m at this latitude. While finer scale multibeam bathymetry is preferable, this was not available for the entire study area.

The remaining four variables were derived from the GEBCO bathymetry layer as projected into UTM zones 27N-30N. The selected derived layers isolate some of the proxy variables which may be extrapolated from bathymetry enabling better identification of variables that may be controlling habitat distribution. A review of the variables you can obtain by this method is provided by Wilson et al (2007).

Slope was generated using ArcGIS v9.3.1 (ESRI, 2009) Spatial Analyst extension. Rugosity, and bathymetric position index (BPI), at broad and fine scales, were generated using ArcGIS Benthic Terrain Modeler extension (Wright *et al.*, 2005).

Slope provides terrain gradient in degrees and serves as a proxy for the local hydrodynamic regime (Guinan et al., 2009). Enhanced current velocities and internal tides across the slope of the Porcupine Sea Bight are thought to be influential in the distribution of *Pheronema carpenteri* at this location (Rice *et al.*, 1990; White, 2003), while dense *Lophelia pertusa* has been found to tend toward areas where the bottom slope is critical to internal waves of semidiurnal frequency (Frederiksen et al., 1992). Slope is calculated as the maximum change in elevation over the distance between a cell and its eight neighbours. Rugosity is calculated as the ratio of 3D surface area to planar area derived from a neighbourhood analysis. This acts as a measure of terrain "roughness", or structural complexity, representative of geomorphology on the scale of mesohabitats (*sensu* (Greene *et al.*, 1999)), exceeding 750m in size, and substrate (Rinehart *et al.*, 2004; Dunn & Halpin, 2009). BPI (equivalent to topographic position index) uses neighbourhood analysis to calculate the relative elevation of a cell identifying topographic features such as ridges (positive BPI), valleys (negative BPI) and flat areas/ constant slope (0) (Weiss, 2001). BPI was generated at fine (BPIfine) and broad (BPIbroad) scales to provide separate layers defining small macrohabitats (*sensu* (Greene *et al.*, 1999)), such as canyons, and large macrohabitats (*sensu* (Greene *et al.*, 1999)), such as seamounts and banks. BPIfine was generated with inner radius 1, outer radius 3 (resulting in a scale factor, or sensitivity, of 2.25 km), and BPIbroad was set to inner radius 1 and outer radius 33.3 (with a scale factor of 25 km). Scales were determined relative to the features discernible from the GEBCO bathymetry.

All UTM projected derived layers were then merged to align with GEBCO as individual layers in WGS84 geographic projection (cell size 0.00833333°).

Modelling

Sample data was reduced to one data point per cell of environmental data. Due to the coarse resolution of the environmental data, a presence-only modelling technique was adopted as the primary basis of this study. While presence and absence data are available and used in initial Generalised Additive Models (GAMs) and threshold-based assessment of models, the inference of assured absence of a habitat within 750m of the video/ image transects, where the field of view may only be a few metres wide, seemed irresponsible.

Maximum entropy (MaxEnt) modelling is a presence-only modelling technique developed by Phillips et al (2004; 2006; 2008). It has been found to be amongst the highest performing modelling techniques for presence-only modelling (Elith et al., 2006) and as such was selected for use in this study. Although MaxEnt has been found to deal well with the presence of correlated variables, Elith & Leathwick (2009) highlight the importance of some expert pre-selection of variables to ensure relevance, however Elith (2011) warns that stricter pre-selection is unlikely to improve the model. Trials of MaxEnt models with and without pre-selection of variables found that pre-selection by GAMs and correlate removal yielded models with higher AUC and threshold-dependent metrics in the case of this study. Details of correlation testing and pre-selection of variables for use in MaxEnt models using GAMs can be found in Appendix S1 in Supporting Material.

Presence and absence data points in ArcGIS were overlaid with accompanying environmental variables and the data extracted for use in MaxEnt using the Marine Geospatial Ecology Tools add-on (Roberts et al., 2010).

MaxEnt was run using the samples-with-data (SWD) approach, with environmental data, comprising all presence and absence data, supplied in the same format. This method of "target-group" background sampling controls for sample bias and improves predictive performance (Phillips & Dudík, 2008). Each model was run in MaxEnt version 3.3.3. Regularisation settings were trialled to reduce over-fitting (Phillips & Dudík, 2008) resulting in a regularisation parameter of 3 for all models. Each model was then projected onto the study area environmental layer ASCIIs and constrained to sampled conditions using the MaxEnt novel climates output as a mask in ArcGIS. The MaxEnt output is a logistic probability with values between 0 (low probability) and 1 (high probability). One master model was created for each listed habitat.

Model Evaluation

Presence and absence data were used to assess the final models. For each habitat model, ten randomly generated partitions of 75% training/ 25% test data were compiled manually instead of using the MaxEnt replicates setting in order to control for spatial auto-correlation within transects (Howell et al., 2011). Training and test selections were then controlled for prevalence to be approximately equivalent to the master dataset (within a range of ±0.01).

Each model was assessed using the Presence-Absence model evaluation library (Freeman, 2007) in R. Discrimination capacity was assessed using the area under the receiver operating curve (AUC). The AUC was calculated for the full model and each of the training and test datasets along with training and test average and standard deviation AUCs. Model reliability was assessed using threshold dependent model evaluation indices (Fielding & Bell, 1997). Five thresholding methods assessed by Liu et al (2005) as "good" were considered for each model due to their tolerance to low prevalence build data: comprising sensitivity-specificity equality, sensitivity-specificity sum maximisation, and ROC-plot based approaches (Cantor et al., 1999), and prevalence, and average probability/suitability approaches (Cramer, 2003) . Each of these thresholding techniques were

evaluated against three model performance indices: Percent Correctly Classified (PCC), specificity, and sensitivity (Fielding & Bell, 1997; Manel *et al.*, 1999). Average training indices and test indices were considered with full model indices to select the final thresholding method and facilitate the interpretation of modelling results (Liu et al., 2005). Jack-knife plots and variable response curves were used to assess variable importance to the final model.

Quantification of habitat distribution

MaxEnt output probability maps were transferred to ArcGIS as raster grids and masked for novel climates. The maps were then thresholded into predicted presence/absence; the ROC-plot approach was selected for all habitats. Values below the threshold were converted to a constant absence raster; values above the threshold were allowed to retain their probabilities to better inform as to relative probability of occurrence. Confidence maps based on standard deviation of cell probabilities derived from all ten partial data models, as used in the model evaluation process, were also constructed and are provided in Figure S2.

MPA Assessment

For each listed habitat, habitat presence probability maps were converted into constant rasters for ease of assessing areas in terms of raster cells. Rasters were projected into Albers Equal Area Conic with modified standard parallels (Parallel 1: 50.2°, Parallel 2: 58.5°) in order to standardise the area of raster cells (1 cell= 750m^2). The spatial analyst extension to ArcGIS was then used to extract areas of presence within polygons of MPA and UK and Irish continental shelf extents. All MPA and continental shelf extent polygons are based on shapefiles or coordinates obtained from governing bodies. The number of presence raster cells within an MPA is expressed as a percentage of the number of presence raster cells in the study area, and at national levels for the UK and Ireland. Table S1 contains an assessment considered by MPA type.

Results

Modelling

Output habitat suitability maps can be viewed in Figure 2. Results of variable correlation analysis and pre-selection of variables using GAMs are provided in Appendix S1 and Figure S1

Model Evaluation

Table 1 and Table 2 display the AUC values and threshold dependent model evaluation metrics for all three models.

The LpReef full model AUC score was considered good (0.8-0.9), while training and test partitions were considered good (0.8-0.9) and fair (0.7-09). The threshold value assessed by minimum ROC distance yielded good (0.8-0.9) results for full model PCC and specificity, although model sensitivity was considered fair (0.7-0.8). All training metrics, and test PCC and specificity were fair (0.7-0.8), but

test sensitivity was poor (0.6-0.7). As a result this model was considered the worst of the three listed habitats, with a consistently lower sensitivity than specificity indicating that the model is more successful at predicting LpReef absence.

Full model, training and test AUC was excellent (0.9-1.0) for the PcAggs model. The threshold dependent metrics were also considered excellent (0.9-1.0) for full model, training and test partitions. As a result this model was considered the best of the three listed habitats.

The full SfAggs model AUC was considered excellent (0.9-1.0) while training and test partitions were excellent (0.9-1.0) and good (0.8-0.9). After thresholding full and training model PCC and specificity were considered good (0.8-0.9) and model sensitivity excellent (0.9-1.0), with average test model PCC considered good (0.8-0.9), sensitivity excellent (0.9-1.0) and specificity fair (0.7-0.8).

Assessment of Variable Importance

Jack knife tests of variable importance defined bathymetry as the most important variable to all models. The model build with bathymetry alone contributed the highest gain, while a global model excluding bathymetry experienced the greatest loss in gain. Bathymetry therefore contains the most information which cannot be accounted for by other modelled variables.

MaxEnt percent contribution estimates for the LpReef model rank variable importance as bathymetry (71.5%), BPIbroad (21%) and slope (7.5%). A global model excluding slope resulted in the least reduction in gain, suggesting that slope contributed the least amount of information not implicit in other variables. Response plots of models created using only single variables suggest that LpReef may be found between 500-1200m water depths on positive broad scale topographic features and positive slopes.

The PcAggs model assigned variable importance in the order of bathymetry (60.4%), BPIbroad (28.1%) and rugosity (11.5%). The importance of bathymetry was the least pronounced in this model suggesting that it is acting as a proxy for fewer unaccounted-for variables than in the other two models. Individual variable model response plots suggest that PcAggs may be found between 950-1600m water depths, on broadly flat or constant slopes of low rugosity.

Heuristic estimates of variable importance in the SfAggs model rank variables as bathymetry (84.2%), slope (12.5%), and BPIfine (3.2%). Although BPIfine has provided a marginal improvement in model gain, this is essentially a model reliant on bathymetry and slope. Individual variable model response plots indicate that SfAggs may be found at greater than 800m water depth on negative fine scale features or constant slopes of 2° or greater. The fact that no depth limit or upper slope limit is discernible suggests that the environments sampled are of insufficient range to complete the near Gaussian distribution you would expect of a habitat occurrence/variable relationship. It is also worth noting that due to the lack of PSB or PAP data the SfAggs model prediction is restricted to a depth limit of 1918m and a maximum slope of 16°; beyond these parameters the prediction has been masked to avoid un-testable assumptions.

MPA Assessment

Assessment of the proportion of listed habitat suitable environments included within current MPA network Table 3 found that LpReef suitable environments are the most well protected within the study area (23.2% contained within MPAs) with protection at national levels varying from 35.6% in UK to only 12.5% in Irish waters. PcAggs are the least well protected habitat with only 2.3% of predicted suitable environments included within a current MPA, with protection at national levels varying from 3.2% in UK to 1.1% in Irish waters. SfAggs are better protected with 6.1% contained within the existing MPA network (9.6% at UK level; 2.7% at Irish level). Measured against IUCN targets only LpReef is within the 20-30% level recommended, however it must be remembered that the current MPA network is not 'strictly protected' in line with IUCN specifications.

Discussion

Model performance and interpretation

While model performance was considered fair to excellent, all models are built on variables at the coarse resolution of GEBCO bathymetry - one depth reading every 30 arc-seconds interpreted as a cell size of 750m^2 at this latitude. As a result fine scale mesohabitats which resolve to less than 750m in size, such as carbonate mounds, iceberg plough marks, and small scours which are associated with the presence of some of these listed habitats, will not be detected. For example the LpReef areas associated with iceberg plough marks in the NW Rockall bank MPA (Wilson, 1979b) have not been predicted by this model, as iceberg plough mark features measure only tens of metres in width and could not be detected. The models produced by this study must be considered in this context, providing a reference to identify areas of search, where models can be re-built on higher resolution bathymetry suited to the scale of target features (A. Rengstorf, In Press).

All other variables must also be considered in the context of the bathymetry it is derived from, and the method in which they are calculated. Slope values, for example, will vary according to the interplay between bathymetry resolution and analysis neighbourhood (Wilson et al., 2007) so the maximum 16.59° recorded in this study should be considered as representative of a range inclusive of steeper gradients.

Predictions based on the GEBCO bathymetry are also likely to result in overestimation of distribution. C. Marshall *et al* (Submitted) found that a GEBCO (750m) resolution model and a high (50m) resolution model both predicted 90% of gorgonian species occurrence on Hatton Bank correctly, but the area of predicted suitable habitat presence in the GEBCO model was double the size of the higher resolution model. This difference in spatial efficiency must be taken into account, and proportions of habitat suitable environments within MPAs considered as maximum figures with the possibility of reduction by up to 50%.

As models are based on topographic variables and do not include other variables explicitly, models must be considered as indications of suitable environments rather than a presence of the habitat: a

site suited to LpReef may be found to actually constitute reef absence if, for example, it is not proximate to a larval supply sufficient to support a reef (Cowen et al., 2006). Furthermore if fluctuating conditions in non-topographic variables occur at any site the model should be regarded with this in mind. Inherently conditions do not vary considerably in the deep sea as a whole, but isolated areas may encounter fluctuating conditions. Within the study region parts of the Wyville Thomson Ridge experience fluctuations in temperature and salinity based on the periodic overflow of arctic water from the Faroe Shetland Channel (Sherwin & Turrell, 2005).

Further model validation maybe made in comparison to the literature (locations are labelled in Figure 1 and MPAs in Figure 3(a). Known LpReef areas are largely included within current MPAs, being the primary conservation target for MPA establishment. The LpReef model successfully predicts the presence of suitable habitat where reef has been recorded in all MPAs in Irish waters including those on the Porcupine Bank and in the PSB (Kenyon *et al.*, 1998; Foubert *et al.*, 2005; Huvenne *et al.*, 2005; Wheeler *et al.*, 2007), the Logachev Mounds (Mienis et al., 2006), and the Franken Mound and Kiel Mount sites in the NEAFC West Rockall Bank Closure (Wienberg et al., 2008) (Figure 3(b)). In UK waters successful predictions included MPAs on East Rockall Bank, Anton Dohrn seamount, and the Wyville Thomson Ridge and Hatton Bank (Narayanaswamy *et al.*, 2006; Howell *et al.*, 2007).

The LpReef model however does not predict the presence of reef in the NW Rockall MPA, SW Rockall (Empress of Britain Bank) MPA, or the East Mingulay Reef Complex where reef is known to be present (NEAFC, 2011) (Figure 3(b)). These omissions are a direct result of the coarse resolution of model bathymetry which is unable to resolve the iceberg plough marks on Rockall (Wilson, 1979b) and rocky seafloor ridges of East Mingulay (Roberts *et al.*, 2005) , respectively attributed as influential features in reef presence at these locations. For both areas a model based on finer resolution bathymetry may better predict habitat suitability at these sites.

PcAggs have been described by Rice et al. (1990) from 1250m the Porcupine Seabight, by Le Danois (1948) from Ireland to Spain in 1000-2000m water depth, by Hughes and Gage (2004) from the Rockall-Hatton Basin at 1100m, and from 1450m on Goban Spur (Duineveld *et al.*, 1997; Flach *et al.*, 1998; Lavaleye *et al.*, 2002). Historic records under its synonym *Holtenia carpenteri* also point to potential communities close to the Darwin Mounds MPA known then as the "Holtenia grounds" (WyvilleThomson, 1869, 1873). This model predicts all of these areas as suitable habitat for PcAggs, inclusive of an area extending southwest from the southernmost extent of the Darwin Mounds MPA (Figure 3(c)).

The SfAggs model is also further validated by records in the literature. SfAggs have been observed in the "tails" of the Darwin Mounds in 950m water at densities of up to 7 m-1 (Bett, 2001), on the slope of the European Continental Shelf south of the Wyville Thomson Ridge at 1108m (58°50'-59°00'N, 07°48'-08°00'W) (Roberts et al., 2000) and in the Porcupine Seabight at 1340m (Gooday, 1986; Gooday & Lambshead, 1989). The model again predicts all of these areas as suitable habitat for SfAggs (Figure 3(d)).

Assessment of current area closures for listed habitat protection

Based on known presence data and predictive model outputs, the current MPAs do capture areas of confirmed presence and modelled high probability of occurrence of LpReef habitat (Figure 3 (b)). However known reef on George Bligh (Narayanaswamy *et al.*, 2006; Howell *et al.*, 2007) is not currently protected, and the model identifies many other potential areas of suitable reef habitat including the slope of the European Continental Shelf, and the flanks of other banks, seamounts and canyons such as Rosemary, Lousy, Bill Bailey, Edoras and Fangorn Banks, the Hebrides Terrace Seamount, and Whittard Canyon.

No current MPAs within the study area protect known presence of PcAggs (Figure 3(c)). However model outputs suggest that parts of the West Rockall and Logachev Mounds MPAs may include a small proportion of suitable habitat. Apart from confirmed aggregations in the PSB and Hatton-Rockall Trough the model identifies areas of potential suitable habitat in the northern Rockall Trough spanning from George Bligh bank to the Darwin Mounds and a small area between the Hebrides Terrace Seamount and the European Continental Slope.

SfAggs suitable habitat as determined by known presence and model prediction seems to be predominantly captured where current MPAs extend beyond the base of a geomorphological feature (Figure 3(d)). These incidental captures include the deepest portions of NE Rockall, Hatton Bank, Logachev Mounds and West Rockall MPAs, and a small proportion of each of the Irish cSACs. Known aggregations in the tails of the Darwin Mounds are protected by the Darwin Mounds MPA. Many areas of high probability show some overlap with areas of high probability of PcAggs in the PSB, northern Rockall Trough and between the Hebrides Terrace Seamount and the European Continental Shelf. Further unprotected areas of high probability are found on Edoras and Fangorn Banks in Irish waters, and the deeper areas of the slope of the European Continental Shelf.

Assessment of percentage area protection targets

While there are no percentage area targets set for the protection of VMEs under UNGA 61/105, and the target of 10% set by the CBD is not habitat specific, the more aspirational IUCN Vth World Parks Congress suggests that 20-30% of habitats be held within strictly protected MPAs. It is useful therefore, in the context of assessing progress in the conservation of marine habitats, to quantify the percentage of identified listed habitats contained within areas that are managed for their protection. In offshore waters this requires area estimates based on extrapolative methods. The models presented by this study provide a relatively objective method of extrapolation; using the binary map output for each habitat to provide baseline habitat spatial distribution predictions, and allow percentage estimates to be generated. While models based on higher resolution bathymetry would provide more accurate estimates (A. Rengstorf, In Press; C. Marshall *et al*, Submitted), in the absence of large scale coverage, these GEBCO based models may provide a basic means of assessment which could be useful to marine managers.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 {Pre-selection of environmental variables}
Figure S1 {Partial-residual plots of individual variable generalised additive models}
Figure S2 {Confidence maps to accompany predictions}
Table S1 {Percentage estimates of current protection by MPA type}

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Biosketch

Rebecca Ross is a marine ecologist who currently focuses on the deep-sea. Her primary interests are in marine conservation solutions, habitat mapping, predictive modelling, the use of underwater video in ecology, and applied inter-disciplinary ecology.

Kerry Howell is a deep-sea benthic ecologist whose research interests are focused on providing the science to support sustainable management and conservation of deep-sea ecosystems. Current areas of focus are habitat mapping, predictive habitat distribution modelling, larval dispersal modelling, population connectivity and depth related patterns of faunal zonation.

Author contributions:

K.H. conceived the ideas; K.H. and R.R. collected the data; R.R. analysed the data; and R.R. led the writing with input from KH.

Table 1 Threshold independent area under the curve (AUC) indices for all three listed habitat models: LpReef = *Lophelia pertusa* (Linnaeus, 1758) reef, PcAggs = *Pheronema carpenteri* (Thomson, 1869) aggregations, SfAggs= *Syringammina fragilissima* (Brady, 1883) aggregations.

Habitat	LpReef			PcAggs			SfAggs		
Model	**Training**	**Test**	**FullModel**	**Training**	**Test**	**FullModel**	**Training**	**Test**	**FullModel**
1	0.8	0.85	0.86	0.99	0.98	0.99	0.93	0.93	0.93
2	0.84	0.69		0.99	0.99		0.92	0.92	
3	0.79	0.85		0.98	1.00		0.92	0.89	
4	0.8	0.81		0.99	1.00		0.93	0.86	
5	0.81	0.72		0.98	0.99		0.9	0.96	
6	0.83	0.74		0.99	0.97		0.93	0.89	
7	0.83	0.74		0.99	0.99		0.94	0.82	
8	0.8	0.8		0.99	1.00		0.96	0.78	
9	0.86	0.64		1.00	0.94		0.94	0.89	
10	0.84	0.69		0.99	1.00		0.92	0.94	
Average	0.82	0.75		0.99	0.99		0.93	0.89	
SD	0.02	0.07		0.00	0.02		0.01	0.05	

Table 2 Threshold dependent model evaluation metrics for (a) *Lophelia pertusa* (Linnaeus,1758) reef, (b) *Pheronema carpenteri* (Thomson,1869) aggregations, (c) *Syringammina fragilissima* (Brady,1883) aggregations. The ROC-plot based method (MinROCdist) was selected for all models, although note this always recommended the same full model threshold as the sensitivity-specificity sum maximisation approach (MaxSens+Spec). Metrics are percent correctly classified (PCC), sensitivity (sens.), and specificity (spec.).

(a)	Average Training			Average Test			Full Model			
Approach	PCC (sd)	Sens. (sd)	Spec. (sd)	PCC (sd)	Sens. (sd)	Spec. (sd)	PCC	sens.	Spec.	Threshold
Sens=Spec	0.75 (0.02)	0.76 (0.05)	0.75 (0.02)	0.70 (0.03)	0.69 (0.09)	0.70 (0.03)	0.76	0.77	0.76	0.45
MaxSens+Spec	0.79 (0.01)	0.75 (0.05)	0.80 (0.01)	0.76 (0.02)	0.69 (0.08)	0.77 (0.03)	0.82	0.75	0.82	0.48
ObsPrev	0.33 (0.02)	1.00 (0.00)	0.27 (0.02)	0.35 (0.03)	0.96 (0.02)	0.29 (0.03)	0.34	1.00	0.28	0.093939
MeanProb	0.79 (0.01)	0.75 (0.05)	0.79 (0.02)	0.48 (0.03)	0.83 (0.06)	0.44 (0.03)	0.60	0.95	0.57	0.314008
MinROCdist	0.79 (0.01)	0.75 (0.05)	0.79 (0.02)	0.75 (0.03)	0.69 (0.09)	0.75 (0.03)	0.82	0.75	0.82	0.48

(b)

Approach	Average Training			Average Test			Full Model			
	PCC (sd)	Sens. (sd)	Spec. (sd)	PCC (sd)	Sens. (sd)	Spec. (sd)	PCC	sens.	Spec.	Threshold
Sens=Spec	0.96 (0.01)	0.96 (0.03)	0.95 (0.01)	0.96 (0.01)	0.97 (0.03)	0.96 (0.01)	0.95	0.94	0.95	0.2
MaxSens+Spec	0.94 (0.01)	0.98 (0.02)	0.93 (0.01)	0.96 (0.01)	0.99 (0.01)	0.95 (0.01)	0.97	0.94	0.97	0.275
ObsPrev	0.88 (0.01)	1.00 (0.00)	0.87 (0.01)	0.90 (0.02)	0.99 (0.01)	0.90 (0.02)	0.90	0.98	0.90	0.065772
MeanProb	0.89 (0.01)	0.99 (0.01)	0.88 (0.01)	0.91 (0.02)	0.99 (0.01)	0.90 (0.02)	0.91	0.98	0.90	0.073722
MinROCdist	0.96 (0.01)	0.98 (0.02)	0.95 (0.01)	0.96 (0.01)	0.99 (0.01)	0.96 (0.01)	0.95	0.96	0.95	0.19

(c)

Approach	Average Training			Average Test			Full Model			
	PCC (sd)	Sens. (sd)	Spec. (sd)	PCC (sd)	Sens. (sd)	Spec. (sd)	PCC	sens.	Spec.	Threshold
Sens=Spec	0.84 (0.02)	0.83 (0.07)	0.84 (0.02)	0.79 (0.03)	0.78 (0.12)	0.80 (0.03)	0.85	0.85	0.85	0.39
MaxSens+Spec	0.80 (0.02)	0.95 (0.03)	0.79 (0.02)	0.78 (0.03)	0.97 (0.02)	0.76 (0.03)	0.82	0.93	0.81	0.31
ObsPrev	0.54 (0.03)	1.00 (0.00)	0.51 (0.03)	0.56 (0.04)	1.00 (0.00)	0.52 (0.04)	0.60	1.00	0.57	0.076628
MeanProb	0.70 (0.02)	1.00 (0.00)	0.68 (0.03)	0.70 (0.04)	0.97 (0.02)	0.68 (0.04)	0.73	0.98	0.71	0.191233
MinROCdist	0.83 (0.02)	0.90 (0.06)	0.83 (0.02)	0.80 (0.03)	0.92 (0.06)	0.79 (0.03)	0.82	0.93	0.81	0.31

Table 3 Percentages of predicted suitable environments for each listed habitat currently protected within the wider MPA network and by national jurisdiction (compared to predicted suitable habitat presence only within national waters). A further breakdown by MPA establishing authority is also available in the supplementary material.

Habitat	MPA wider network	MPA in UK Waters	MPA in Irish Waters
Lophelia pertusa (Linnaeus,1758) reef	23.2%	35.6%	12.5%
Pheronema carpenteri (Thomson,1869) aggregations	2.3%	3.2%	1.1%
Syringammina fragilissima (Brady,1883) aggregations	6.1%	9.6%	2.7%

Figure 1

Study Area. Black outlines and continuous greyscale bathymetry mark the study area which comprises the NE Atlantic extents of the UK and Irish extended continental shelf regions. The dotted perimeter line shows the additional extent of the UK waters into the Faroe Shetland Channel and the North Sea, which are not included in this study. Seabed features are labelled with additional features as follows: 1 – Hebrides Terrace Seamount, 2 – Anton Dohrn Seamount, 3 – George Bligh Bank, 4 – Darwin Mounds (NE Rockall Trough), 5 – Wyville Thomson Ridge, 6 – Bill Bailey's Bank, 7 – Faroe Bank. Bathymetry outside the study area is displayed as 200m isobaths to 1000m depth, then at 500m intervals. Map projected in Albers Equal Area Conic with modified standard parallels (parallel 1 = 50.2°, parallel 2 = 58.5°).

Figure 2

Full model prediction maps for (a) *Lophelia pertusa* (Linnaeus, 1758) reef, (b) *Pheronema carpenteri* (Thomson, 1869) aggregations, and (c) *Syringammina fragilissima* (Brady, 1883) aggregations. Threshold values, and medium and high probability value ranges for each habitat are as follows: (a) threshold 0.48, medium 0.48-0.58, high 0.59-0.86; (b) threshold 0.19, medium 0.19-0.55, high 0.55-0.93; (c) threshold 0.31, medium 0.31-0.57, high 0.58-0.78. Where white background is visible, prediction has been masked due to novel climates. Maps projected in Albers Equal Area Conic with modified standard parallels (parallel 1 = 50.2°, parallel 2 = 58.5°).

Figure 3

MPA Assessment. (a) Current MPAs considered during this study: 1- Hatton Bank pSAC and NEAFC Closure, 2- Darwin Mounds cSAC, 3- Wyville Thompson Ridge cSAC, 4- NW Rockall cSAC and NEAFC Closure, 5- East Rockall Bank pSAC, 6- Anton Dohrn pSAC, 7- East Mingulay cSAC (Inshore), 8- West Rockall NEAFC Closure, 9- Haddock Box NEAFC Closure, 10- SW Rockall (Empress of Britain Bank) NEAFC Closure, 11- Logachev Mounds NEAFC Closure, 12- NW Pocupine Bank cSAC, 13- SW Porcupine Bank cSAC, 14- Hovland Mound Province cSAC, 15- Belgica Mound Province cSAC. Subsequent maps, constructed from binary predictions, display only presence of predicted suitable habitat for (b) *Lophelia pertusa* (Linnaeus, 1758) reef, (c) *Pheronema carpenteri* (Thomson, 1869) aggregations, and (d) *Syringammina fragilissima* (Brady, 1883) aggregations with predicted presence within an MPA highlighted as black. Isobaths are every 200m to 1000m depth, then at 500m intervals. Maps projected in Albers Equal Area Conic with modified standard parallels (parallel 1 = 50.2°, parallel 2 = 58.5°).

Figure S1

Partial-residual plots of generalised additive models built with one of the five individual variables against the presence of (a) *Lophelia pertusa* (Linnaeus, 1758) reef, (b) *Pheronema carpenteri* (Thomson, 1869) aggregations, and (c) *Syringammina fragilissima* (Brady, 1883) aggregations, as

undertaken for variable pre-selection. Plots are centred on the no relationship zero line, with predictive capacity expressed by deviance from this line: greater than zero is a predicted presence, less than zero a predicted absence. Dotted lines are 95% confidence intervals, rugs along the x-axis mark the spread of sample values.

Figure S2

Confidence maps displaying the standard deviation of predicted presence values between the ten training/test build models for (a) *Lophelia pertusa* (Linnaeus, 1758) reef, (b) *Pheronema carpenteri* (Thomson, 1869) aggregations, and (c) *Syrinammina fragilissima* (Brady, 1883) aggregations. Low and high SD values in each model correspond with the following value ranges: (a) low 0.01-0.08, high 0.09-0.24; (b) low 0.02-0.15, high 0.16-0.26, (c) low 0.02-0.07, high 0.08-0.18.

Supporting Information

Appendix S1 *Pre-selection of environmental variables*

The statistical software environment R, version 2.13.1 (R Development Core Team, 2011) was used to run a Pearson correlation test to identify correlated variables. Rugosity and slope were considered highly correlated for all models (0.95) while BPIbroad and BPIfine were moderately correlated for all models (0.51).

Binomial Generalised Additive Models (GAMs) were run with the logit link function in R using the MGCV library (Wood, 2011), employing 4 knots and a gamma of 1.4 to reduce over fitting as advocated by Kim & Gu (2004). This process identified variables which showed no significant relationship with listed habitat occurrence. These variables were excluded from the final MaxEnt model. Partial residual plots were also examined and relationships considered for biological relevance and reliability in terms of 95% confidence intervals.

The dredge function within the MuMIn library in R (Barton, 2012) was then used to explore a variety of global GAMs containing only one of each correlate set. This process highlighted which variable combinations would produce the strongest models and further confirmed the prudence of excluding insignificant variables identified by the individual GAMs. The model containing the most variables within 2 corrected Aikike's Information Criterion, or AICc, (delta <2) of the top ranked model was employed as the variable combination used for MaxEnt.

Results of variable pre-selection process

The partial residual plots of individual variable GAMs for each habitat can be seen in Figure S1.

Individual variable GAMs found that all variables had a significant (p <0.05) relationship with *Lophelia pertusa* (Linnaeus, 1758) reef (LpAggs) occurrence. However examination of partial residual plots revealed that BPIfine, rugosity, and slope were displaying no relationship in the areas of highest confidence, while at values of low confidence 95% intervals remained inclusive of the no relationship 0-line. Dredge results indicated that a global model inclusive of bathymetry, BPIbroad, and slope would yield the highest AICc score when correlates have been removed (AICc 263.6, with next best 291.6).

All variables had a significant (p <0.05) relationship with *Pheronema carpenteri* (Thomson, 1869) aggregation occurrence with bathymetry and BPIbroad of highest significance (p=0). Examination of partial residual plots revealed possible relationships with bathymetry, rugosity and slope, while BPIbroad and BPIfine displayed wide confidence intervals with little discernible relationship to *Pheronema carpenteri* aggregation occurrence. Dredge results indicated that a model inclusive of bathymetry, BPIbroad, and rugosity would yield the highest AICc when correlates have been removed (AICc 100.5, with next best 103.9).

Bathymetry and BPIbroad had a significant ($p <0.05$) relationship with *Syringammina fragilissima* (Brady, 1883) aggregation occurrence, with slope and BPIfine ($p <0.1$), and rugosity ($p=0.208$) considered insignificant. Examination of partial residual plots revealed discernible relationships with bathymetry, BPIbroad, and a linear relationship with BPIfine. Dredge results found that a global model inclusive of bathymetry, fine scale BPI and slope yielded equal AICc to a model substituting broad scale BPI with correlates removed (AICc 197.4). Global GAMs were therefore examined further for smooth term significance. Neither BPIbroad ($p=0.65$) nor BPIfine ($p=0.99$) were considered significant terms themselves, however the fine scale model resulted in significant ($p <0.05$) terms for bathymetry and slope, while the broad scale model reduced the slope smooth term to insignificant ($p=0.0729$). Final variable selection was made on the basis of trialling both BPI models with MaxEnt. MaxEnt variable response plots indicated that the bathymetry, BPIfine, and slope construction had a greater impact on full model performance than the BPIbroad build which appeared to have no effect. The similarity in BPI models and the difference between individual variable responses and within model responses stresses the complexity of variable interactions. The difference between the results of modelling techniques is likely due to GAMs being a presence/absence models and MaxEnt a presence-only model.

Appendix S1 References

Barton, K. (2012) *MuMIn: multi-model inference.* In: R package version >= 2.12.0.

Kim, Y.-J. & Gu, C. (2004) Smoothing spline Gaussian regression: more scalable computation via efficient approximation. *Journal of the Royal Statistical Society B*, **66**, 337-356.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, **73**, 3-36.

Table S1 Percentage estimates of currently protected areas with a suitable environment for *Lophelia pertusa* (Linnaeus, 1758) Reef (LpReef), *Pheronema carpenteri* (Thomson, 1869) aggregations (PcAggs), *Syringammina fragilissima* (Brady, 1883) aggregations (SfAggs). Percentages are estimated against total predicted presence of suitable environments in the full study area (UK and Irish waters), or by national jurisdiction. MPA = marine protected area, NEAFC closure = North-East Atlantic Fisheries Commission closure, cSAC = candidate Special Area of Conservation, pSAC = possible Special Area of Conservation.

Predicted presence UK and Irish waters	LpReef	PcAggs	SfAggs
In any MPA (cSAC, pSAC or NEAFC closures)	23.2%	2.3%	6.1%
In NEAFC closures	17.1%	1.9%	3.7%

Predicted presence UK waters	LpReef	PcAggs	SfAggs
In any UK MPA (cSAC, pSAC and NEAFC closures)	35.6%	3.2%	9.6%
In UK cSACs	1.3%	0.2%	0.9%
UK pSACs	33.1%	1.8%	7.0%

Predicted presence Irish Waters	LpReef	PcAggs	SfAggs
In any Irish MPA (cSAC and NEAFC closures)	12.5%	1.1%	2.7%
In Irish cSACs	4.5%	0.0%	0.7%

Figure 1 Site Description
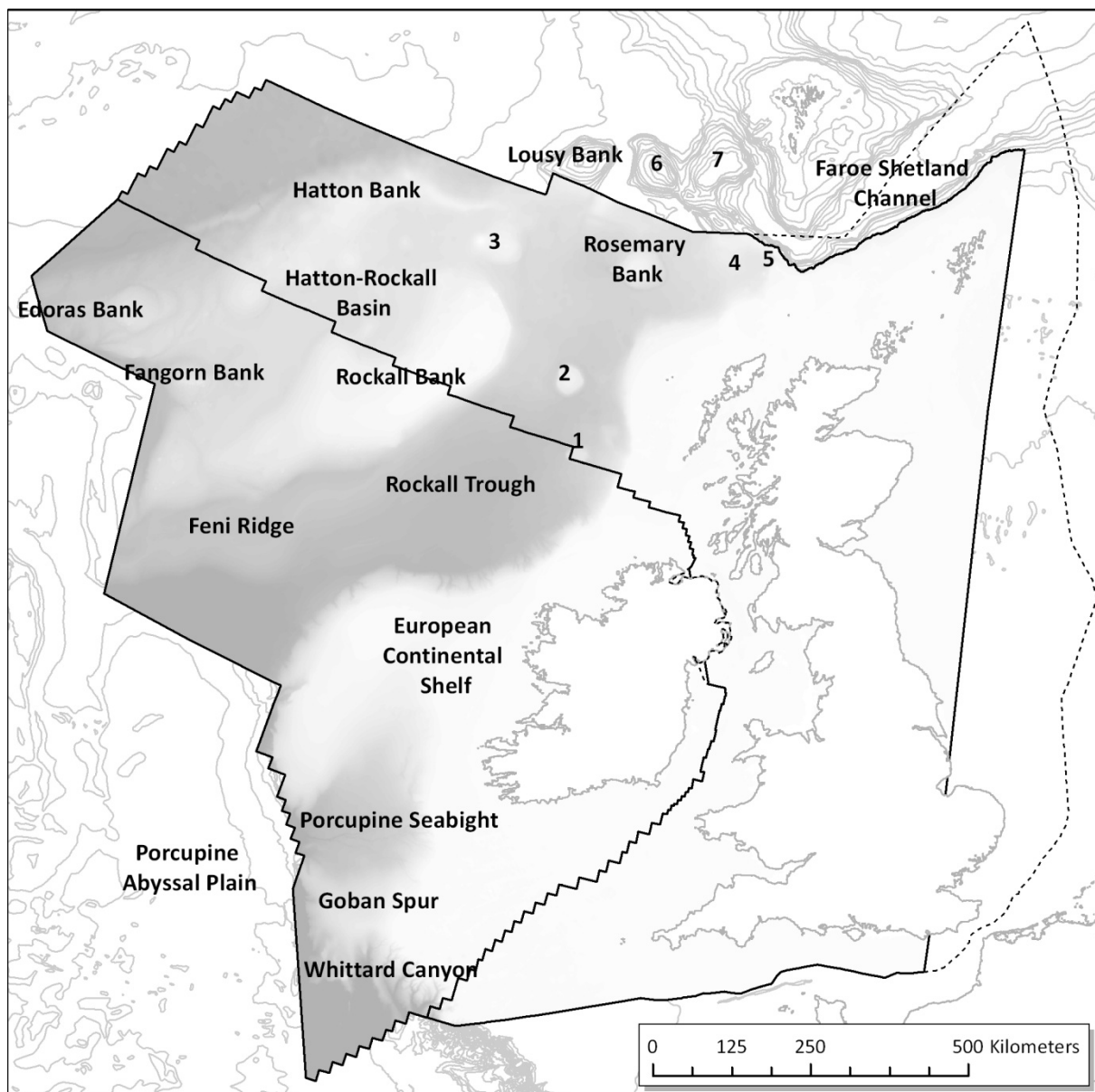
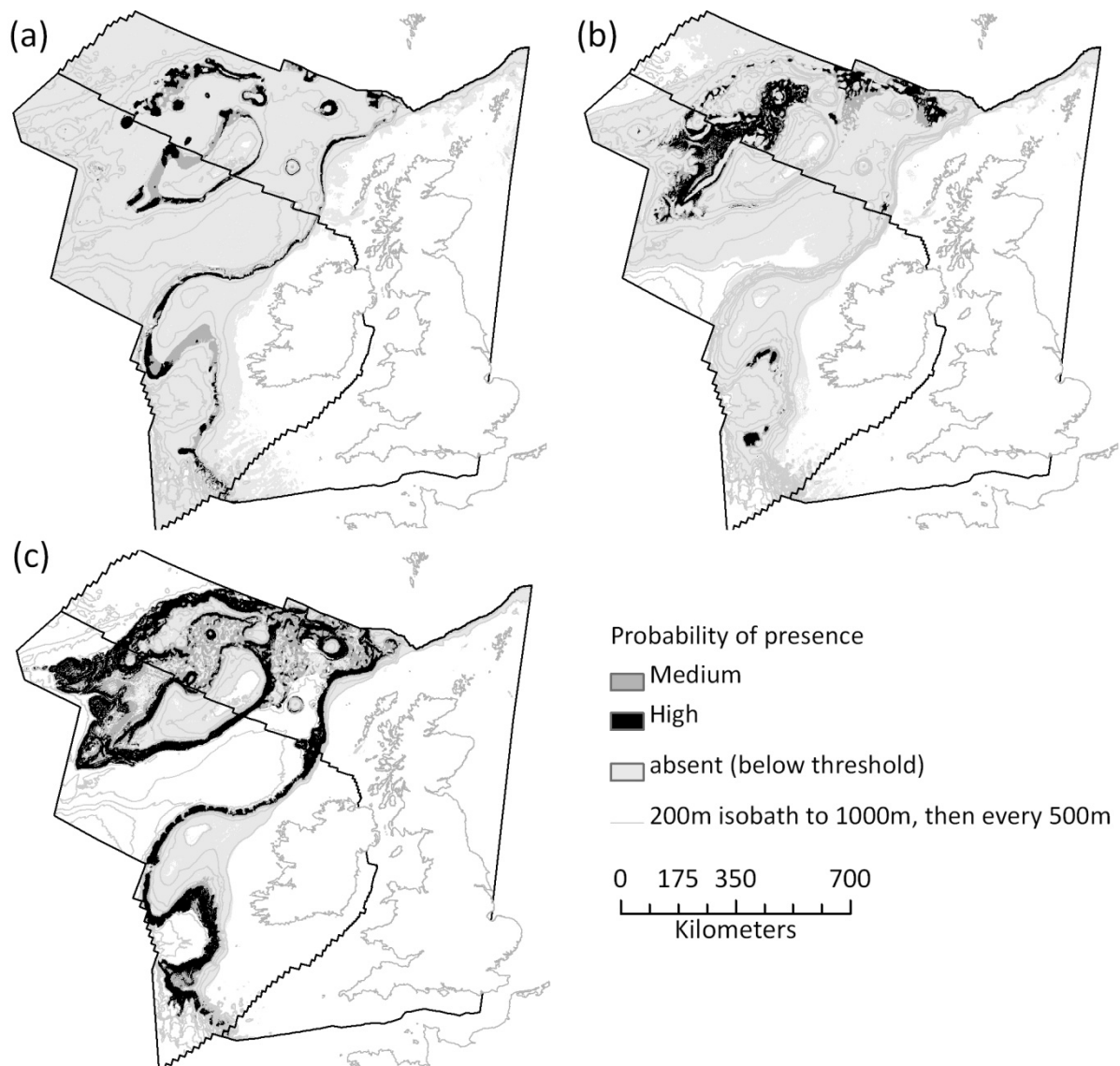Figure 2 Prediction Maps

(a)

(b)

(c)

Probability of presence

Medium

High

absent (below threshold)

200m isobath to 1000m, then every 500m

0   175 350   700

Kilometers

Figure 3 MPA Assessment Maps

(a)

candidate SAC

NEAFC closure

possible SAC

0   175 350   700

Kilometers

(b) - (d)

Suitable habitat
within an MPA

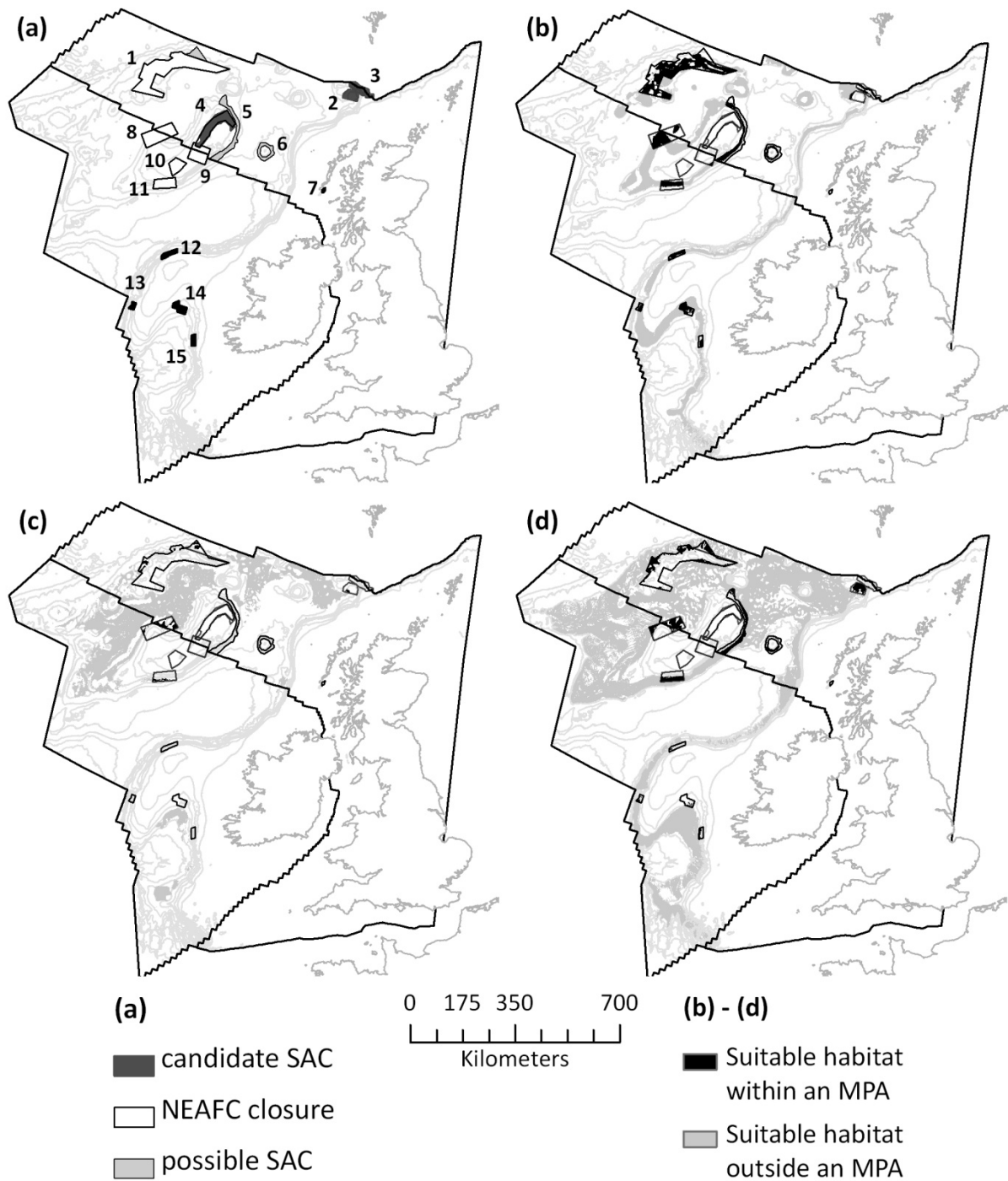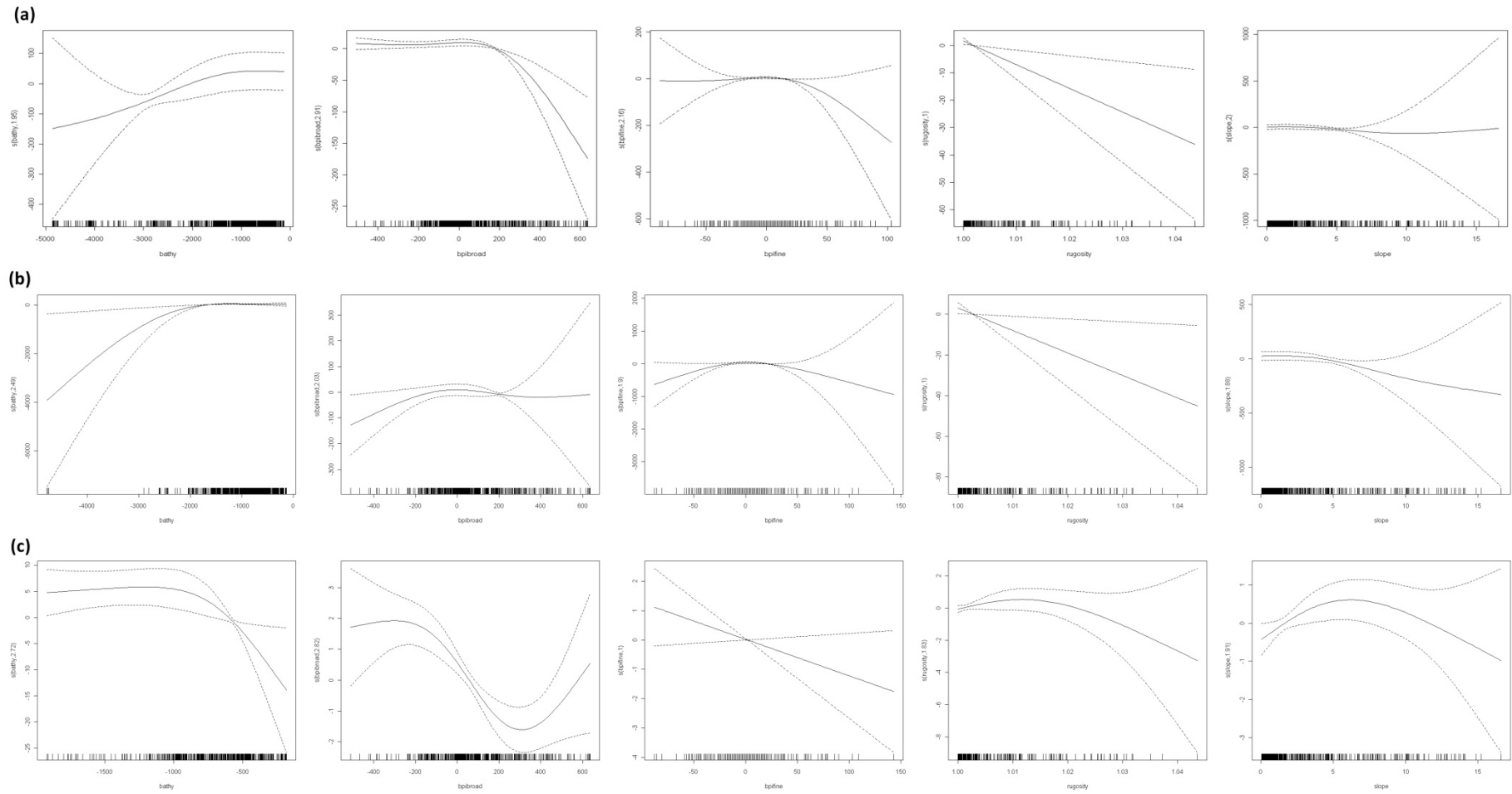Suitable habitat
outside an MPA

Figure S1 Variable pre-selection by generalised additive modelling

Figure S2 Confidence Maps

Low SD

High SD

200m isobath to 1000m, then every 500m

0   175   350   700 Kilometers