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Title: The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management.

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17 Abstract:

18 Sponge aggregations have been recognised as key component of shallow benthic
19 ecosystems providing several important functional roles including habitat building and
20 nutrient recycling. Within the deep-sea ecosystem, sponge aggregations may be extensive
21 and available evidence suggests they may also play important functional roles, however data
22 on their ecology, extent and distribution in the North Atlantic is lacking, hampering
23 conservation efforts. In this study, we used Maximum Entropy Modelling and presence data
24 for two deep-sea sponge aggregation types, *Pheronema carpenneri* aggregations and ostur
25 aggregations dominated by geodid sponges, to address the following questions: 1) What
26 environmental factors drive the broad-scale distribution of these selected sponge grounds? 2)
27 What is the predicted distribution of these grounds in the northern North Atlantic, Norwegian
28 and Barents Sea? 3) How are these sponge grounds distributed between Exclusive
29 Economic Zones (EEZs) and High Seas areas? 4) What percentage of these grounds in
30 High Seas areas are protected by the current High Seas MPA network? Our results suggest
31 that silicate concentration, temperature, depth and amount of particulate organic carbon are
32 the most important drivers of sponge distribution. Most of the sponge grounds are located
33 within national EEZs rather than in the High Seas. Coordinated conservation planning
34 between nations with significant areas of sponge grounds such as Iceland, Greenland and
35 Faroes (Denmark), Norway (coastal Norway and Svalbard), Portugal and the UK, should be
36 implemented in order to effectively manage these communities in view of the increasing level
37 of human activity within the deep-sea environment.

1. Introduction

Sponges are a key component of marine benthic ecosystems from shallow tropical coral reefs to deep-sea systems, providing a number of important functional roles. Studies in shallow waters have suggested sponge communities create complex habitats supporting high biodiversity, provide refuge for fish, are a source of novel chemical compounds, and have an important role in biogeochemical cycling (Bell 2008; Maldonado et al., 2016). Deep-sea sponge aggregations, although less studied than their shallow water counterparts, show evidence of having similar important functional roles.

Within the North Atlantic there are three widely accepted and clearly defined deep sea sponge habitat types, *Pheronema carpenneri* (Thomson 1869) aggregations (Rice et al., 1990), boreal ostur, and cold water ostur (Klitgaard and Tendal 2004). While there is no doubt other sponge aggregations do exist, these have not yet been defined in the peer reviewed literature. *P. carpenneri* is a hexactinellid (glass sponge) that can form aggregations on fine sediments with densities of up to 1.53 individuals/m² as seen on the Goban Spur (Hughes and 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 colonization, (Rice et al., 1990; Bett and Rice 1992). They are thought to be associated with areas of high productivity, and possibly proximate to regions of enhanced bottom tidal currents which aid in resuspension of organic matter (Rice et al., 1990; White et al., 2003).

Another widely recognised deep-sea sponge aggregation is 'ostur' or 'cheese bottom' as defined by (Klitgaard and Tendal 2004). These authors recognise two main types of ostur: a boreal ostur, which occurs around the Faroe Islands, Norway, Sweden, parts of the western Barents Sea and south of Iceland; and a cold water ostur, which is found north of Iceland, in most of the Denmark Strait, off East Greenland and north of Spitzbergen. Both ostur types are characterised by sponges of the genus *Geodia* Lamarck, 1815. Boreal ostur consist of

64 *Geodia barretti* Bowerbank 1858, *Geodia macandrewii* Bowerbank 1858, *G. atlantica*
65 (Stephens, 1915) and *G. phlegraei* (Sollas 1880), whilst cold water ostur is formed by *G.*
66 *hentscheli* Cárdenas, Rapp, Schander and Tendal 2010 (referred to as *G. mesotriaena*) and
67 *G. parva* (Hansen 1885) (referred to as *Isops phlegraei pyriformis* but identified as *G. parva*
68 in Cárdenas et al., (2013)) . Maps of the distribution of ostur, determined largely from
69 fisheries trawl samples, were compiled by (Klitgaard and Tendal 2004), while more recently
70 Cárdenas et al, (2013) have summarised known locations of characterising geodid species
71 on maps.

72 Deep sea sponge habitats are also thought to play a key role in nutrient recycling as a result
73 of the large quantities of water they filter (Reiswig, 1971; Reiswig, 1974). Sponges are
74 suspension feeders and recent studies have demonstrated the importance of sponge
75 feeding to benthic-pelagic coupling in the deep sea (Pile and Young 2006; Yáñez et al., 2007),
76 with sponges representing an important link between carbon in the water column in the form
77 of ultraplankton and picoplankton (Reiswig 1975), dissolved organic carbon (Yáñez et al.,
78 2003) and viral particles (Hadas et al., 2006), and the benthos. Sponges may enable carbon
79 flow to higher trophic levels through predation (Wulff 2006) and respiration rates are 9 times
80 higher on sponge grounds than surrounding sediments (Cathalot et al., 2015). In addition,
81 areas of high sponge abundance may play a key role in global Silicate cycling (Maldonado et
82 al., 2005) the importance of which might be geographically variable (Bell 2008). Further,
83 Hoffmann et al., (2009) postulated that all sponge aggregations may function as so far
84 unrecognized sinks for inorganic nitrogen.

85 The range of ecological functions provided by deep-sea sponge aggregations has resulted in
86 these habitats being considered of conservation importance under United Nations General
87 Assembly Resolution 61/105” and under Annex V of the Oslo-Paris (OSPAR) Convention for
88 the Protection of the Marine Environment of the North East Atlantic. Thus stakeholders are
89 required, in respect of areas where vulnerable marine ecosystems (VMEs) are known to
90 occur or are likely to occur based on the best available scientific information, to close such

91 areas to bottom fishing and ensure that such activities do not proceed unless conservation
92 and management measures have been established to prevent significant adverse impacts
93 on VMEs (UNGA 61/105).

94 Despite these policy provisions, progress in the protection of deep-sea sponge aggregations
95 is slow. Several nations and the Northwest Atlantic Fisheries Organization (NAFO) have
96 recently recommended or implemented area closures for the protection of sponge habitats in
97 response to UNGA Resolution 61/105. To date however, no OSPAR marine protected areas
98 (MPAs) have been designated specifically for the protection of these habitats. Part of the
99 reason for the slow progress is likely to be the more limited spatial location data for deep sea
100 sponge habitats (Rodríguez et al., 2007), although indicative maps of the distribution of
101 some types of sponge grounds have existed for some time (Klitgaard and Tendal 2004).

102 While the production of point based distribution maps are a critical first step in developing
103 environmental management strategies, predictive habitat modelling provides a means to
104 produce full coverage spatial data where distribution information is lacking (Elith and
105 Leathwick 2009; Galparsoro et al., 2009; Dambach and Rodder 2011; , , Robinson et al.,
106 2011). The resulting predictions may then be used to support conservation management
107 decisions (Kenchington and Hutchings 2012) .

108 Predictive modelling of the distribution of a biological 'habitat' such as a deep-sea sponge
109 aggregation may be achieved in a variety of ways. Where the habitat is formed by a single
110 dominant species, two different approaches have been used. The first models the
111 distribution of the species (Davies et al., 2008, Dolan et al., 2008, Guinan et al., 2009), the
112 second models the distribution of the habitat (Ross and Howell, 2013; Ross et al., 2015).
113 Where both approaches have been used results suggest that predicted habitat distribution is
114 a highly restricted subset of predicted species distribution (Howell et al., 2011, Rengstorf et
115 al., 2013). Where a 'habitat' is composed of a distinct assemblage of species, the distribution
116 of that assemblage may be modelled (Degraer et al., 2008, Gonzalez-Mirelis and Lindegarth

2012, Piechaud et al., 2015), alternatively the distribution of key indicator species may be modelled and the resulting maps overlaid highlighting areas of overlap as potential habitat distribution (Ferrier and Guisan 2006; Rinne et al., 2014)

This study uses Maximum Entropy Modelling, considering both species and habitat based approaches, to address the following questions:

- 1) What environmental factors drive the broad-scale distribution of ostur and *Pheronema carpenteri* sponge grounds?
- 2) What is the predicted distribution of these grounds in the northern North Atlantic, Norwegian and Barents Sea?
- 3) How are these sponge grounds distributed between EEZ and High Seas areas?
- 4) What percentage of these grounds in High Seas areas are protected by the current High Seas MPA network?

2. Methods

2.1. Study Area

The study is focused on the North Atlantic deep sea areas (200 to 5000 meters deep) off the Canadian coast, the Azores and the Iberian Peninsula to Baffin Bay, Greenland and Iceland, the Greenland Sea and western part of Barents Sea off the coasts of Spitzberg (Fig. 1). This region was chosen to encompass an area where sufficient data are available on presence and absence of ostur, geodids, and *P. carpenteri*. Although geodid sponges are very common in fjords (Klitgaard and Tendal 2004), coastal regions were not included as a result of both the resolution and coverage of some of the environmental layers.

2.2. Biological data

Presence data were compiled for each of six geodid sponge species *Geodia barretti*, *G. macandrewii*, *G. atlantica*, *G. hentscheli*, *G. phlegraei* and *G. parva*, for ostur habitat, and for *P. carpenteri*. All geodid presence data was derived from the same dataset as used in Cárdenas et al. (2013) and recovered from the Dryad Repository (<http://www.datadryad.org>) where it is recorded under the Dryad package identifier: <http://dx.doi.org/10.5061/dryad.td8sb>. Ostur presence data was compiled from experts identifications of the habitat (Klitgaard et al., 2001, Klitgaard and Tendal 2004), unpublished sample data held by Plymouth University and data from the NAFO NEREIDA research programme which receives support from EU, Canada, Spain, UK, Russia, Portugal. Ostur presence in the NEREIDA dataset was determined based on agglomerative clustering with average linkage on a subset of data records, with abundance values for selected VME indicator species. A group dominated by a high biomass of geodids was identified as ostur. *P. carpenteri* presence records were those used in Ross and Howell (2013) with additional data compiled from various literature sources (Table 1).

In order to control for sample bias in the model (Phillips and Dudík 2008) a background dataset was compiled from all presence data and ‘apparent absence’ data. ‘Apparent absence’ data was determined as trawling or video samples taken within the study area where the target species was not recorded as present. Trawl net mouth openings and video fields of view are at best a few meters wide. We therefore felt that absence data could not be considered reliable when used with environmental data cells of size 1km by 1km resolution. The existence of potential false absences within our dataset, a problem referred to as “imperfect detection” in (Lahoz-Monfort et al., 2014), means that rather than estimating where species occur, we are only able to estimate where they are detected, an inherent limitation of the models. Apparent absence data were compiled from various literature sources and our own data holdings from 222 biological video and photographic transects. Details of all data used in the models are provided in Table 1.

2.3. Environmental layers

Environmental variables were selected based on their biological relevance, resolution and availability. 16 variables were trialled with preliminary models (Table 2).

Bathymetric data were obtained from the General Bathymetric Chart of the Oceans (GEBCO) 2008 (<http://www.gebco.net/>) 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. The GEBCO bathymetry layer was reprojected into Goode's Homolosine (Ocean) at 1km x 1km grid cell size (the approximate size of cells over the study area) and seven further topographic variables were derived from the bathymetry layer. Slope, curvature, plan curvature, and profile curvature were created using the ArcGIS (ESRI 2009) Spatial Analyst extension. Rugosity, broad scale and fine scale bathymetric position index (BPI) were created using the Benthic Terrain Modeller extension (White et al., 2005). BPI broad was calculated with an inner radius of 5 and an outer radius of 20. BPI fine was calculated with an inner radius of 1 and an outer radius of 5. Further information on the specifics of using topographic variables as surrogates is available in existing literature (Kostylev et al., 2005; Wilson et al., 2007; Guinan et al., 2009; ; Ross and Howell 2013).

In addition seven oceanographic variables were investigated including bottom temperature, bottom salinity, bottom dissolved oxygen concentration, bottom oxygen saturation rate, bottom phosphate, nitrate, and silicate concentrations. The raw data were downloaded from the NOAA 2009 world ocean atlas (WOA, http://www.nodc.noaa.gov/OC5/WOA09/netcdf_data.html) as an ".ncdf" file and is the average of a given variable for year 2009. Each depth layer was subsampled to create a 3 dimensions (latitude*longitude*depth) Random Forest (Breiman 2001) spatial model. The accuracy of the models was evaluated by computing the correlation between extracted and predicted values on a testing set. This model was then trained on the GEBCO grid to obtain a grid of value of the variable at the seabed in each GEBCO cell. The resulting layer is at the GEBCO cell size (30 arc seconds ~ 1km*1km).

194 Finally, Particulate Organic Carbon (POC) at depth was derived from (Lutz et al., 2007).
195 All data layers were reprojected into Goode Homolosine (Ocean) projection and regridded to
196 1km*1km cell size (Table 2)

197

198 3. Modelling

199 3.1. Modelling method

200 Species / habitat sample data were reduced to one data point per cell of environmental data.
201 Using Guillera-Arroita et al's 2015 simple framework that summarizes how interactions
202 between data type and the sampling process (i.e. imperfect detection and sampling bias)
203 determine the quantity that is estimated by a habitat suitability model, we assessed that we
204 were able to model, at best, relative likelihood data using a presence-background approach.
205 While relative likelihoods are not considered appropriate for use in determining area of
206 occupancy (Guillera-Arroita et al., 2015) real world datasets on the scale at which we are
207 modelling very rarely meet the conditions required to achieve probabilities rather than
208 relative likelihoods. Our aim in this paper was to compare relative estimates of extent and
209 distribution (a measure of area of occupancy) rather than provide actual estimates of extent,
210 and thus we feel the use is justified on this occasion.

211 Maximum entropy (MAXENT) modelling is a presence-only modelling technique developed
212 by (Phillips et al., 2004; Phillips et al., 2006; Phillips and Dudík 2008). It has been found to be
213 amongst the highest performing modelling techniques for presence only modelling (Elith et al.,
214 2006) and as such was selected for use in this study. Presence and apparent absence data
215 points in ArcGIS® were overlaid with accompanying environmental variables and the data
216 extracted for use in MAXENT using the Marine Geospatial Ecology Tools add-on (Robertson
217 et al., 2010) . Pre-selection of significant variables was undertaken through preliminary
218 MAXENT runs using the samples-with-data (SWD) approach, with background data
219 comprising all presence and apparent absence data supplied in the same format.

Highly correlated variables were identified and the most ecologically relevant correlate and / or most significant in terms of preliminary model gain assessed from jack-knife plots was retained (see supplementary material – Table 1 in Supplementary material for details on correlations). The final variables selected for use in each model are given in Table 2, and the summary statistics of each given in Supplementary material - Table 2).

Each model was fitted in R with the 'dismo' package version 0.8-11 (Hijmans et al., 2012) using the MAXENT Java program version 3.3.3k (Phillips and Dudík 2008). Regularization settings were adjusted to reduce overfitting (Phillips and Dudík 2008) resulting in a regularization parameter of 2 for ostur habitat, *G.atlantica*, *G.hentscheli* *G.macandrewii*, *G.parva* and *G.phlegraei* and 3 for *G.barretti* and *P.carpenteri* models. Each model was then projected onto the environmental GIS layers covering the entire study area. Predictions were constrained to sampled conditions using a mask in ArcGIS derived from the MAXENT novel climates output, which highlights combinations in environmental conditions that were not included in the samples used to build the model. MAXENT model output is a logistic probability with values between 0 (low probability) and 1 (high probability). One master model was created for each of the following: ostur habitat, *G.atlantica*, *G.hentscheli* *G.macandrewii*, *G.parva*, *G.phlegraei*, *G.barretti* and *P. carpenteri* .

3.2. Model evaluation

Presence and apparent absence data were used to assess the final models. For each model, 100 randomly generated partitions of 75% training/25% test data were used to internally test the model. Discrimination capacity was assessed using the area under the receiver operating curve (AUC). An internal or full model (using all the available data in the training of the model) AUC and a 100 fold cross validation AUC along with training and test average and standard deviation AUCs were calculated. Model assessment and metrics calculation

was all done in R using the “dismo” library (Hijmans et al., 2012) and “PresenceAbsence” library (Freeman and Moisen 2008) in R (Team 2011).

Although AUC is a widely used statistic in measuring the performance of predictive habitat distribution models, is not without criticism (Lobo et al., 2008; Peterson and Nakazawa 2008; Jiménez-Valverde, 2012) and so the reliability of all models were also assessed using threshold-dependent model evaluation indices (Fielding and Bell 1997).

Five thresholding methods recommended by Liu et al., (2005) were considered for each model: sensitivity- specificity equality, sensitivity-specificity sum maximization, ROC-plot-based approaches (Cantor et al., 1999), prevalence, and average probability/suitability approaches (Cramer 2003). The above five methods have a high tolerance to low prevalence training data. Three model performance indices: percent correctly classified (PCC), specificity, and sensitivity (Fielding and Bell 1997; Manel et al., 1999), were calculated for each dichotomised test dataset, resulting from the different thresholding techniques. Index values were then classified on a five-point scale: excellent (1-0.9), good (0.9-0.8), fair (0.8-0.7), poor (0.7-0.6) and fail (0.6-0.5). Considering the averaged threshold-dependent metrics for the partitions together with the same metrics calculated for the full model, a final threshold was chosen to maximize final model performance. Variable importance to a final model was assessed using jack-knife plots (tests comparing model gain for each individual variable in a single variable model, and the reduction in model gain for omitting each variable in turn), as well as the variable response curves.

3.3. Quantification of habitat distribution

MAXENT output probability maps were transferred to ArcGIS as raster grids and masked to restrict prediction to the known range for environmental variables. The maps were then thresholded into predicted presence/absence. Probabilities that fell below the chosen

threshold for each species/habitat were converted to a constant absence raster (cell value of 0); probabilities above the threshold were retained to later differentiate between areas of high presence probability and low presence probability. A standard deviation of all presence probabilities from 100 partitioned models was also calculated to create a confidence map for each habitat.

The distribution of ostur grounds was assessed using 3 maps. The first was produced from the MAXENT model of ostur habitat (hereinafter referred to as the ostur habitat map), the second was produced by combining the six final presence/absence modelled maps for the *geodia* species in a single GIS raster layer indicating the number of geodid sponge species co-occurring in a cell. Where 4 or more species of *geodia* co-occur within a grid cell, the cell was classified as potential ostur presence. This map is hereinafter referred to as the combined geodia map. The third map was produced by overlaying the ostur habitat map with the combined geodia map to produce an ensemble map (hereinafter referred to as the ostur ensemble map).

3.4. Conservation and management assessment

The ArcGIS 10.1 Spatial Analyst extension was used to quantify the areas of predicted presence for both sponge ground types (ostur and *P. carpentieri*) within individual nation's EEZs and the High Seas. Additionally predicted area inside existing High Seas MPAs within the study area was calculated. Shapefiles of the boundaries of EEZs and High Seas areas were obtained from <http://www.marineregions.org> and boundaries of the High Seas MPAs as published by Northwest Atlantic Fisheries Organization. The number of presence raster cells within each management division (EEZs and High Seas) was expressed as a percentage of the total number of presence raster cells in the study area. The total number of presence-raster cells within High Seas MPAs is expressed both as a percentage of the

total number of presence-raster cells in the study area, and as a percentage of the total number of presence raster cells in the High Seas area.

4. Results

4.1. Modelling

Final habitat suitability maps for combined *Geodia*, ostur habitat, ostur ensemble and *P. carpenteri* are presented in Fig. 2. Final habitat suitability maps for the individual *Geodia* species are provided in Supplementary material – Figs. 1 to 6.

4.2. Model evaluation

Table 3 displays the AUC values and threshold-dependent model evaluation metrics for all 6 *Geodia* models plus the *P. carpenteri* and ostur models. The mean *G. hentscheli* and *G. parva* cross-validation AUC scores were considered excellent (0.9-1), while those for *G. baretti*, *G. phlegraei*, ostur, and *P. carpenteri* were good (0.8–0.9) and *G. atlantica* and *G. macandrewii* fair (0.7–0.8). The Maxent logistic output was thresholded using either minimum ROC distance for *G. barretti*, *G. hentscheli*, *G. macandrewii*, ostur and *P. carpenteri* or Maximum Sensitivity-Specificity for *G. atlantica*, *G. parva* and *G. phlegraei* as shown in Table 3. Models yielded good performances (> 0.8) for *G. hentscheli*, *G. parva*, osturs and *P. carpenteri*, fair performances (0.7-0.8) for *G. atlantica*, *G. barretti* and *G. phlegraei* and poor performances (< 0.7) for *G. macandrewii*. The best performing models according to all metrics were *G. hentscheli* and *G. parva*, with *G. atlantica* and *G. macandrewii* performing worst.

4.3. Assessment of variable importance

Jackknife plots identified silicate as the most important variable to the 3 boreal ostur species (*G. barretti*, *G. atlantica* and *G. phlegraei*) and second most important variable to *G. macandrewii* in terms of contributing the highest gain when used in isolation. Temperature was the most important variable to the two cold water ostur species *G. hentscheli* and *G. parva*, while depth was the most important variable to *P. carpenteri*, *G. macandrewii* and the ostur habitat. Variables that had the most information that wasn't present in the other variables (resulting in the highest decrease in gain when omitted) showed a similar pattern. Silicate was the most important variable to two of the boreal ostur species (*G. atlantica* and *G. phlegraei*) and temperature the most important to *G. barretti*, *G. parva* and *G. hentscheli*, *P. carpenteri* and the ostur habitat. Other important variables included POC for cold water ostur species, ostur habitat and *G. barretti* and depth for *G. atlantica*, *G. phlegraei* and *P. carpenteri*. For *G. macandrewii* silicate was also of importance. Jackknife plots and percent contributions of variables to the final models are provided in Supplementary material – Table 3.

4.4. Distribution

The model predicts that *P. carpenteri* aggregations are likely to occur on the Mid-Atlantic Ridge (MAR) south of Iceland, on the margin of Greenland and Canada, in the Hatton-Rockall Basin, throughout the Northern Rockall Trough and on the south side of the Faroes-Iceland Ridge, in the Porcupine Seabight, parts of the Bay of Biscay, along the Iberian continental slope and around Galicia Bank, around the Azores, and in most of the western Mediterranean Sea.

The distribution of ostur in the combined gGeodia map suggests this habitat is distributed in the Barents Sea, around Svalbard, along the Norwegian shelf, in the Faroe-Shetland Channel, around the Faroes and Iceland, along the Greenland Shelf edge, in the Denmark Strait, on the Flemish Cap, and off the coast of Newfoundland. The distribution suggested by

the ostur habitat map is very similar but with notable differences being predictions of presence on the northern Mid Atlantic Ridge, in the Mediterranean, Porcupine Seabight, Rockall-Hatton Plateau and parts of the North Sea, most of which are highly questionable based on our knowledge of these regions. The ostur ensemble map suggests ostur habitat distribution is again similar but more restricted with few presences on the Flemish Cap and on the Mid Atlantic Ridge, and very few off the coast of Newfoundland.

4.5. Conservation and management assessment

The majority of both types of deep-sea sponge habitats are likely to occur inside nations EEZs (Table 4). Assessed from the combined Geodia map and the ostur ensemble map, the top five territories with the highest percentage of ostur habitat within their EEZs are Norway, Svalbard, Iceland, Greenland and Canada, although the order varies between models. These same territories are in the top seven (with the addition of the United Kingdom and Ireland) when assessed using the ostur habitat map. . The top five territories with the highest percentage of the *P. carpenteri* habitat resource within their EEZs are Iceland, Italy, Spain, Azores (Portugal) and the UK.

For both sponge habitats there are some areas of suitable habitat in the High Seas (Table 5). The current High Seas MPA network contains 13.5% of the High Seas *P. carpenteri* resource (2.9% of the total resource) and between 1.5-19.5% of the High Seas ostur resource (up to 1.5% of the total resource in the ostur habitat map but only 0.07% in the ostur ensemble map).

5. Discussion

5.1. *What environmental factors drive the broad-scale distribution of ostur and Pheronema carpenteri sponge grounds?*

370 To three of the geodid species silicate was the most important explanatory variable and is in
371 the top five most important variables for all models. Dissolved silicate is needed by all
372 sponges that have siliceous spicules. This includes glass sponges (Class Hexactinellida)
373 and demosponges (Class Demospongiae). Silicate uptake is an energy demanding process
374 (Frøhlich and Barthel 1997) that is genetically controlled and regulated by silicate
375 concentrations (Krasko et al., 2000). At low concentrations, enzymes needed for spicule
376 formation are not expressed, whereas these enzymes are strongly activated by 60 μM Si.
377 Studies of silicic acid uptake by temperate sublittoral sponges have found that significant
378 uptake rates occur only at silicic acid concentrations higher than those naturally occurring in
379 the sponge habitat, suggesting that these sponge populations are chronically limited by Si
380 availability (Maldonado et al., 2005; Maldonado et al., 2011). If populations are limited by
381 silicate availability it is likely that silicate levels could play an important role in determining
382 geodid sponge habitat distribution.

383 *G. barretti* has been recorded and / or cultivated at silicate levels ranging from 2.79-4.6 μM
384 (Hoffmann et al., 2003). In our study *G. barretti* presence was recorded over a Si range of
385 5.41-24.74 μM (mean 10.52 μM , standard deviation 5.7) (Supplementary material - Table 3).
386 Silicate appeared relatively less important to *P. carpenteri* aggregations, which was
387 unexpected. The occurrence of glass sponge reefs in the relatively shallow waters around
388 British Columbia in the Pacific are thought to be related to the relatively high silicate levels
389 observed there, which do not occur at shelf depths elsewhere (Whitney et al., 2005). Silicate
390 levels observed near these reefs were in the region of 43–75 μM , while In the data set used
391 in this study, the average level of silicate is 17 μM (and 15 for *P. carpenteri* specifically with
392 a maximum of 22). In the Antarctic, siliceous sponges habitat has even higher silicate levels
393 than British Columbia coastal waters, with shelf concentrations exceeding 80 μM (Whitney et
394 al., 2005).

395 It must be noted that silicate was correlated with nitrate, phosphate and depth. Nitrate and
396 phosphate were removed from the final model but we cannot be certain which of the

correlated variables is the driving factor. Many sponge species are capable of nitrogen fixation, and (Yahelet et al., 2007) observed no significant concentration shift for nitrate between inhalant and exhalant water for 2 deep water species of glass-sponges. Therefore it is less likely that nitrate is a limiting factor. Available research also suggests uptake of phosphate by sponges is negligible and for some species a significantly higher concentration of phosphate has been observed in the exhalant current compared to the inhalant current (Yahel et al., 2007); Perea-Blazquez et al., 2012). Therefore it is again unlikely that phosphate is a limiting factor in sponge distribution. Depth acts as a surrogate for a number of environmental variables with which it is usually correlated including temperature (where biogeography is taken into account), current speed, water mass structure, food availability and sediment type (Howell et al., 2002; Howell, 2010). While in this study neither temperature nor POC were overly correlated with depth, no data were available to us on current speed and sediment type, therefore it is possible and likely that these variables are also important drivers of sponge habitat distribution (see below).

Temperature was the most important explanatory variable for the cold water geodid species *G. hentscheli* and *G. parva*. *ostur* habitat has been recorded over a temperature range of -0.5 to 8°C and a narrow salinity range of 34.8-35.5 ppt (Klitgaard and Tendal 2004; Bett 2012; Murillo et al., 2012). The cold-water species *G. hentscheli* and *G. parva* have, however, been found over a narrower temperature range of -1.76°C in eastern Greenland to 4.5°C west of Iceland and Reykjanes Ridge (Cárdenas et al., 2013). The observations included in this study had a mean temperature of 1.71°C and standard deviation of 1.35 (Supplementary material – Table 2). Although there are no data on an upper or lower physiological limit to either of these species it is likely they cannot tolerate temperatures as high as boreal geodid species like *G. barretti*. Therefore, it is highly likely that temperature limits the distribution of both *G. hentscheli* and *G. parva* within the modelled area.

In this study *G. barretti* was found over a temperature range of -0.62 to 10.75°C (mean 3.22 °C, standard deviation 1.45). While the boreal species can tolerate rapid temperature

changes of up to 7°C (Bett, 2012) a recent temperature shock event that occurred on the sill of the Kosterfjord in both 2006 and 2008 is thought to have resulted in a mass mortality in *G. barretti*. Temperature increased by approximately 4°C in a 24 hour period on both occasions to over 12°C. The coincidence of the temperature shock events with mass mortality in the species suggested an exceedance of the sponge's physiological limits, although the direct cause of the mortality is not known (Guihenet al., 2012).

Temperature was also an important variable for *P. carpenteri*. Although there are no existing data on the temperature tolerance of *P. carpenteri*, this species is found over a temperature range of 2.73 to 20.9 °C (mean 5.17 °C, standard deviation 2.03) in this study.

Depth was the most important variable to the *P. carpenteri* model. As stated previously depth provides a proxy for multiple other variables including current speed and sediment type, which were not considered in this study (Howell et al., 2002; Howell, 2010). Sediment in the water column is important as sponges, being non selective filter feeders, can get clogged if concentration gets too high (Tjensvollet al., 2013).

Current speed, or rather hydrography, is also thought to play an important role in driving the distribution of both ostur and *P. carpenteri* sponge habitat. (Klitgaard et al., 1997; Klitgaard et al., 2001) extended the theories of Frederiksen et al. (1992) to explain the distribution of ostur and Rice et al. (1990) proposed a similar explanation for the distribution of *P. carpenteri*. Accumulations of large suspension feeders show a tendency to aggregate near the shelf break in regions with a critical slope where the bottom slope matches the slope of propagation of internal tidal waves. The causal link is thought to be an increase in the supply of food related to the incidence of internal waves which results in resuspension of particulate organic matter on which the sponges feed. While recent studies support these ideas to a degree, they have suggested the forcing mechanism is not necessarily internal tides (White et al., 2003, Hosegood and van Haren 2004; Whitney et al., 2005). White et al. (2003) suggested there is some process that has a daily period and is driven by perturbations of the

density gradient that is responsible for generating the oceanographic conditions suitable for *P. carpenteri* sponge ground formation within the Porcupine Seabight. These might be associated with diurnal tidal constituents, inertial oscillations or some other process.

POC flux to the seabed was also an important explanatory variable for *P. carpenteri*, the cold water ostur species, *G. barretti*, and to a lesser degree for ostur habitat. Demosponges are generally regarded as unselective suspension feeders, filtering particles from bacterial size to about 6 µm in diameter (Reiswig 1975; Wolfrath and Barthel 1989) and recent studies of two deep water species of hexactinellid sponges has indicated that both species rely largely on free-living, non-photosynthetic bacteria and nano-planktonic protists for nutrition (Yahel et al., 2007). Therefore amount of POC is likely to be a driving factor in determining the distribution of sponge grounds. However, recent research has demonstrated that *G. barretti* is a high microbial abundance (HMA) sponge (Weisz et al., 2008; Hoffmann et al., 2009;). HMA sponges species may potentially use a higher proportion of the total pool of organic matter in seawater, making use of both POC, and DOC via their bacterial symbionts (Weisz et al., 2008). No continuous DOC bottom information was available in the North Atlantic and therefore, DOC was not considered in this study.

5.2. *What is the predicted distribution of sponge grounds in the northern North Atlantic, Norwegian and Barents Sea?*

Both the combined Geodia and ostur habitat maps suggested similar broad-scale distributions of ostur in the core areas of the Western Barents Sea, Norwegian Shelf, Faroe-Shetland Channel, around the Faroes and Iceland, in the Denmark Strait, then following the continental slope around the tip of Greenland, Labrador Basin, and down to the Flemish Cap. This distribution shows reasonable agreement with the known distribution of the habitat (Klitgaard and Tendal 2004), however, only the ostur habitat model predicts presence on the Mid Atlantic Ridge south of Iceland where ostur have been observed (Klitgaard and Tendal

2004). This model also predicts presence on Porcupine Bank, Rockall Bank, Hatton Bank and in the shallow western parts of the North Sea all of which are highly questionable given the level of past sampling in these areas with no recorded presence of ostur habitat.

There is also reasonable agreement between these two models and previously published regional models and their input data. Knudby et al. (2013) observed ostur habitat presence around the slopes of the Flemish Cap, along the edge of the Grand Banks, on the shelf from Cumberland Sound and north toward Baffin Island and on the Canadian shelf edge near the Davis Strait, which both models predict albeit in slightly different locations but with some overlap. Knudby et al. (2013) also observed ostur habitat presence along the shelf edge from Newfoundland to Resolution Island. While the ostur habitat map suggests presence here, the combined Geodia model does not.

In addition neither model predicts presence on Banquereau Bank where Knudby et al. (2013) observed ostur presence, even though the ostur habitat model predicts their presence on the slope of the bank. The models also failed to predict the presence of osturs at the depth band observed by Bett (2012) in the Faroe-Shetland Channel . Failure of one or both models to predict presence where it has been observed suggests deficiencies in the models. Both the combined Geodia and ostur habitat maps suggest presence on the Canadian Atlantic shelf where Knudby et al. (2013) observed absence. It is possible that absence may be a result of fishing activities as suggested by Knudby et al. (2013) for observed absence on parts of the Flemish Cap, or again this may suggest deficiencies in the models.

Both the Knudby et al. (2013) model and our combined Geodia map suggest presence of ostur at the base of the continental slope and extending onto the seafloor of the deep abyssal plain. This lends further support to Knudby et al. (2013) conclusions that the Newfoundland and Labrador slopes are areas where new sponge grounds are most likely to be found with future sampling efforts. We were unable to model the deeper parts of Baffin

501 Bay as these areas fell outside the range of the environmental envelope sampled, given the
502 environmental variables we used.

503 The predicted distribution of *P. carpenteri* aggregations again broadly follows the known
504 distribution of this habitat. It has been observed from the Mid Atlantic Ridge south of Iceland
505 (Copley et al., 1996), west of the Faroe Islands (Burton 1928), near the Darwin Mounds (Bett
506 et al., 2001), in the Rockall-Hatton Basin (Howell et al., 2014) Porcupine Seabight (Rice et
507 al., 1990), on Goban Spur (Duineveld et al., 1997; Flach et al., 1998; Lavaleye et al., 2002),
508 on Le Danois Bank (García-Alegre et al., 2014) and in the Mediterranean (Vacelet 1961).

509 The model predicts presence at all these locations suggesting a reasonable performance.

510 The model shows broad agreement with previously published finer scale models of *P.*
511 *carpenteri* distribution from the UK and Irish extended continental shelf limits (Ross and
512 Howell 2013; Ross et al., 2015). Both the current model and fine scale model of (Ross et al.,
513 2015) predict presence in a narrow band all along the continental slope and in the Porcupine
514 Seabight in this region, where as the (Ross and Howell 2013) model predicted a more
515 patchy distribution for these areas.

516 A regional model of Le Danois Bank off the northern Spanish coast indicated high probability
517 of suitable habitat on the southern and western sides of the bank (García-Alegre et al., 2014)
518 showing good agreement with the current model predictions. Observed presences used in
519 the Le Danois Bank model were all from this area but were not used in the building of the
520 current model again providing encouraging results for the broad-scale model performance.

521 Our model suggests new potentially large areas of presence of *P. carpenteri* sponge habitat
522 may occur in the south eastern corner of the Bay of Biscay offshore from Bilbao and
523 Bordeaux, areas around Galicia Bank, areas flanking the Nazaré and Setúbal Canyons,
524 large parts of the western Mediterranean, and also around the Azores. Interestingly our
525 model predicted very little presence in the western North Atlantic, although areas of the
526 continental slope off-shore of Boston (and at the southern limit of the model) were identified.

527

528 5.3. *Implications for conservation and management*

529 Our results suggest that for both deep-sea sponge aggregations the bulk of the suitable
530 habitat lays inside countries EEZs. 78.7% of *P. carpenteri* deep-sea sponge aggregations
531 and 92-96% of ostur habitat are likely to occur inside EEZs, therefore the effective
532 conservation and management of these habitats will depend on good integration and
533 communication between nations. Responsibility for the designation of marine protected
534 areas and management of most activities that interact with the seabed within EEZs lies at a
535 national level. Thus the development of an ecologically coherent, well managed network of
536 MPAs for the protection of deep-sea sponge aggregations will require those nations with
537 considerable sponge resource (here considered as the top 5 nations in terms of modelled
538 suitable habitat area), such as Iceland, Greenland and Faroes (Denmark), Norway (coastal
539 Norway and Svalbard), Portugal and the UK to engage with the process. Fishing activities
540 are unique in that management tends to operate at a regional level through Regional
541 Fisheries Management Organisations and thus there are opportunities for a more
542 coordinated approach to the management of fishing activities for the conservation of deep-
543 sea sponge habitat. Given the likely occurrence of these habitats, as predicted by our
544 models, within its EEZ, we recommend that the European Commission considers further
545 investigation of these areas and use of the precautionary principle as part of a risk based
546 approach to manage human pressures impacting the deep sea environment.

547 For the small percentage of ostur habitat that is likely to lay in High Seas waters much of this
548 occurs on the Mid Atlantic Ridge (MAR), in the Irminger Basin, on the Flemish Cap and in
549 the Greenland Sea and Norwegian Basin. For both the MAR and Flemish Cap areas the
550 North Atlantic Regional Management Fisheries Organisations (NEAFC and NAFO) have
551 established fishery closures to bottom trawl fishing to protect Vulnerable Marine Ecosystems
552 (VME) in part fulfilment of UNGA Resolution 61/105 for deep-sea sponge aggregations

protecting 8-15% of the likely resource. However species and habitats require effective protection measures throughout their range (Green et al., 2014) thus we suggest the High Seas area of the Norwegian and Greenland Seas, predicted by our model as likely to support ostur deep-sea sponge aggregations, are investigated for the presence of ostur habitat and, if observed, consideration given to protection of the seabed habitat in this region. For the 21.3% of *P. carpenteri* deep-sea sponge aggregations that are predicted to occur in High Seas areas much of this occurs on the MAR south of Iceland and in and around the Rockall-Hatton Plateaux including Edoras Bank. While 13.5 % of the High Seas area likely to support *P. carpenteri* aggregations is contained within the existing MPA network (shown in Fig. 1), in the case of the Hatton-Rockall Plateau this is incidental capture as these area closures were made for the protection of cold water corals. The Rockall-Hatton Basin represents a large area where our models predict *P. carpenteri* aggregations are likely to occur. The importance of the Hatton-Rockall Plateaux in this region was recently highlighted by the area being proposed as an 'Ecologically and Biologically Significant Area' (EBSA) to the Convention on Biological Diversity. Human activities occurring in the basin include bottom trawling (likely to only extend to the base of Rockall Bank) and the presence of submarine cables (Benn et al., 2010). We suggest, given the existing observations of presence of this habitat and the likely occurrence of the habitat on the basis of our model output, that areas not previously subjected to bottom trawling are considered for protection by NEAFC and the Irish and UK Governments.

6. Conclusions

Silicate concentration and temperature appear to be the most important drivers for geodid species distribution and depth is the most important for *P. carpenteri*. Depth is, however, most likely acting as a proxy for several unmeasured oceanographic parameters that correlate with depth. POC is also an important predictor for some geodids and *P. carpenteri*.

Predicted sponges distribution broadly agrees with previously published distribution maps. Sponge grounds are mainly found at the base of the continental slope and nearby deep seafloor. As most of the sponge aggregation habitat is within EEZs, conservation efforts will need to be coordinated between nations to achieve comprehensive coverage of protected areas. The precautionary principle should be applied to ensure human impact on these species and habitats is limited before a conservation strategy has been designed and implemented. Given how partial the current knowledge of deep-sea sponge ground distribution is, more research should be directed towards determining their extent and distribution through ground-truthing models. In addition research is needed to understand their ecological requirements, and how they are impacted by human activities in order to predict their response in a changing environment.

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8. References

- Bell, J.J. 2008. The functional roles of marine sponges. - *Estuar Coast Shelf S.* 79, 341-353.
- Benn, A.R., Weaver, P.P., Billet, D.S., Van Den Hove, S., Murdock, A.P., Doneghan, G.B. and Le Bas, T. 2010. Human activities on the deep seafloor in the North East Atlantic: an assessment of spatial extent. - *PloS ONE* 5: e12730.

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605
606
607
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609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630

Bett, B., Billett, D., Masson, D. and Tyler, P. 2001. RRS Discovery cruise 248. A multidisciplinary study of the environment and ecology of deep-water coral ecosystems and associated seabed facies and features (The Darwin Mounds, Porcupine Bank and Porcupine Seabight). - Cruise report 36: 52.

Bett, B.J. and Rice, A.L. 1992. The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the porcupine seabight (bathyal NE Atlantic). - Ophelia 36, 217-226.

Bett, B.J., 2012, Seafloor biotope analysis of the deep waters of the SEA4 region of Scotland's seas, JNCC Report 472, A4, 99pp.

Bowerbank, J.S. 1858. On the anatomy and physiology of the Spongiadae. - Philos. Trans. R. Soc. London 148: 279-332.

Breiman, L. 2001. Random forests. - Mach. Learn. 45, 5-32.

Burton, M. 1928. Hexactinellida. Danish Ingolf Expedition 6(4): 1-18..

Cantor, S.B., Sun, C.C., Tortolero-Luna, G., Richards-Kortum, R. and Follen, M. 1999. A comparison of C/B ratios from studies using receiver operating characteristic curve analysis. - J. Chronic Dis. 52, 885-892.

Cárdenas, P., Rapp, H.T., Schander, C. and Tendal, O.S. 2010. Molecular taxonomy and phylogeny of the Geodiidae (Porifera, Demospongiae, Astrophorida)–combining phylogenetic and Linnaean classification. Zool. Scr. 39, 89-106.

631 Cárdenas, P., Rapp, H.T., Klitgaard, A.B., Best, M., Thollessen, M. and Tendal, O.S. 2013.
 632 Taxonomy, biogeography and DNA barcodes of *Geodia* species (Porifera, Demospongiae,
 633 Tetractinellida) in the Atlantic boreo - arctic region. J. Linn. Soc. London, Zool. 169, 251-311.
 634
 635 Cathalot, C., Van Oevelen, D., Cox, T., Kutti, T., Lavaleye, M., Duineveld, G. and Meysman,
 636 F. J. 2015. Cold-water coral reefs and adjacent sponge grounds: Hotspots of benthic
 637 respiration and organic carbon cycling in the deep sea. Front. Mar. Sci. 2, 37.
 638
 639 Copley, J., Tyler, P., Sheader, M., Murton, B. and German, C. 1996. Megafauna from
 640 sublittoral to abyssal depths along the Mid-Atlantic Ridge south of Iceland. Oceanol. Acta 19,
 641 549-559.
 642
 643 Cramer, J.S. 2003. Logit models from economics and other fields. Cambridge University
 644 Press.
 645
 646 Dambach, J. and Rodder, D. 2011. Applications and future challenges in marine species
 647 distribution modeling. Aquat. Conserv. 21, 92-100.
 648
 649 Davies, A.J., Wisshak, M., Orr, J.C. and Roberts, J.M. 2008. Predicting suitable habitat for
 650 the cold-water coral *Lophelia pertusa* (Scleractinia). Deep Sea Res., Part I 55, 1048-1062.
 651
 652 Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Vincx, M. and Van Lancker, V. 2008.
 653 Habitat suitability modelling as a mapping tool for macrobenthic communities: an example
 654 from the Belgian part of the North Sea. Cont. Shelf Res. 28, 369-379.
 655

Dolan, M.F.J., Grehan, A.J., Guinan, J.C. and Brown, C. 2008. Modelling the distribution of cold-water corals in relation to bathymetric variables: adding spatial contact to deep-sea video. *Deep-Sea Res. Part 1*, 1564-1579.

Duineveld, G., Lavaleye, M., Berghuis, E., De Wilde, P., Van Der Weele, J., Kok, A., Batten, S. and De Leeuw, J. 1997. Patterns of benthic fauna and benthic respiration on the Celtic continental margin in relation to the distribution of phytodetritus. *Int. Rev. Gesamten Hydrobiol. Hydrogr.* 82, 395-424.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S. and Zimmermann, N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129-151.

Elith, J. and Leathwick, J.R. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. In: *Annual Review of Ecology Evolution and Systematics*. Annual Reviews, pp. 677-697.

Ferrier, S. and Guisan, A. 2006. Spatial modelling of biodiversity at the community level. *J. Appl. Ecol.* 43, 393-404.

Fielding, A.H. and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38-49.

683 Flach, E., Lavaleye, M., De Stigter, H. and Thomsen, L. 1998. Feeding types of the benthic
684 community and particle transport across the slope of the NW European continental margin
685 (Goban Spur). Prog. Oceanogr. 42, 209-231.

686

687 Frederiksen, R., Jensen, A. and Westerberg, H. 1992. The distribution of the scleractinian
688 coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing.
689 Sarsia 77, 157-171.

690

691 Freeman, E.A. and Moisen, G. 2008. Presence Absence: An R package for presence
692 absence analysis. J. Stat. Softw. 23, 1-31.

693

694 Frøhlich, H. and Barthel, D. 1997. Silica uptake of the marine sponge *Halichondria panicea*
695 in Kiel Bight. Mar. Biol. 128, 115-125.

696

697 Galparsoro, I., Borja, A., Bald, J., Liria, P. and Chust, G. 2009. Predicting suitable habitat for
698 the European lobster (*Homarus gammarus*), on the Basque continental shelf (Bay of Biscay),
699 using Ecological-Niche Factor Analysis. Ecol. Modell. 220, 556-567.

700

701 García-Alegre, A., Sánchez, F., Gómez-Ballesteros, M., Hinz, H., Serrano, A. and Parra, S.
702 2014. Modelling and mapping the local distribution of representative species on the Le
703 Danois Bank, El Cachucho Marine Protected Area (Cantabrian Sea). Deep Sea Res., Part II,
704 106, pp.151-164.

705

706 Gonzalez-Mirelis, G. and Lindegarth, M. 2012. Predicting the distribution of out-of-reach
707 biotopes with decision trees in a Swedish marine protected area. Ecol. Appl. 22, 2248-2264.

708

709 Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason,
710 M.G., Mumby, P.J. and White, A.T. 2014. Larval dispersal and movement patterns of coral
711 reef fishes, and implications for marine reserve network design. *Biol. Rev.* 90, pp.1215-1247..
712

713 Guihen, D., White, M. and Lundälv, T. 2012. Temperature shocks and ecological
714 implications at a cold-water coral reef. *Mar. Biodivers. Rec.* 5: e68.
715

716 Guillera-Arroita, G., Lahoz - Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E.,
717 McCarthy, M.A., Tingley, R. and Wintle, B.A. 2015. Is my species distribution model fit for
718 purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* 24, 276-292.
719

720 Guinan, J., Grehan, A.J., Dolan, M.F.J. and Brown, C. 2009. Quantifying relationships
721 between video observations of cold-water coral cover and seafloor features in Rockall
722 Trough, west of Ireland. *Mar. Ecol. Prog. Ser.* 375, 125-138.
723

724 Hadas, E., Marie, D., Shpigel, M. and Ilan, M. 2006. Virus predation by sponges is a new
725 nutrient-flow pathway in coral reef food webs. *Limnol. Oceanogr.* 51, 1548-1550.
726

727 Hansen, G.A. 1885. Spongiadae. The Norwegian North-Atlantic Expedition 1876–1878.
728 *Zoology* 13, 1-26.
729

730 Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J. and Hijmans, M.R.J. 2012. Package ‘dismo’
731 *Circles*, 9, p.1..
732

733 Hoffmann, F., Rapp, H.T., Zöller, T. and Reitner, J. 2003. Growth and regeneration in
734 cultivated fragments of the boreal deep water sponge *Geodia barretti* Bowerbank, 1858
735 (Geodiidae, Tetractinellida, Demospongiae) *J. Biotechnol.* 100, 109-118.

736

737 Hoffmann, F., Radax, R., Woebken, D., Holtappels, M., Lavik, G., Rapp, H.T., Schläppy, M.
738 L., Schleper, C. and Kuypers, M.M. 2009. Complex nitrogen cycling in the sponge *Geodia*
739 *barretti*. Environ microbiol 11, 2228-2243.

740

741 Hosegood, P. and van Haren, H. 2004. Near-bed solibores over the continental slope in the
742 Faeroe-Shetland Channel. Deep Sea Res., Part II 51, 2943-2971.

743

744 Howell, K., Huvenne, V., Piechaud, N., Robert, K. and Ross, R. 2013. Analysis of biological
745 data from the JC060 survey of areas of conservation interest in deep waters off north and
746 west Scotland. JNCC Report No. 528..

747

748 Howell, K.L., Billett, D.S. and Tyler, P.A. 2002. Depth-related distribution and abundance of
749 seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal
750 Plain, NE Atlantic. Deep Sea Res., Part I 49, 1901-1920.

751

752 Howell, K.L. 2010. A benthic classification system to aid in the implementation of marine
753 protected area networks in the deep/high seas of the NE Atlantic. Biol. Cons. 143, 1041-
754 1056.

755

756 Howell, K.L., Holt, R., Endrino, I.P. and Stewart, H. 2011. When the species is also a habitat:
757 Comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it
758 forms. Biol. Cons. 144, 2656-2665.

759

760 Hughes, D.J. and Gage, J.D. 2004. Benthic metazoan biomass, community structure and
761 bioturbation at three contrasting deep-water sites on the northwest European continental
762 margin. Prog. Oceanogr. 63, 29-55.

763

764 Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic
 765 curve (AUC) as a discrimination measure in species distribution modelling. *Glob. Ecol.*
 766 *Biogeogr.* 21, 498-507.

767

768 Kenchington, R. and Hutchings, P. 2012. Science, biodiversity and Australian management
 769 of marine ecosystems. *Ocean Coast. Manage.* 69, pp.194-199.

770

771 Klitgaard, A.B., Tendal, O.S. and Westerberg, H. 1997. Mass occurrences of large sponges
 772 (Porifera) in Faroe Island (NE Atlantic) shelf and slope areas: characteristics, distribution and
 773 possible causes. In: *Proceedings of the 30th European Marine Biological Symposium*,
 774 Southampton, UK, 5. pp. 129-142.

775

776 Klitgaard, A.B. and Tendal, O.S. 2001. "Ostur"- "Cheese Bottoms"-sponge dominated areas
 777 in the Faroese shelf and slope areas. In: Bruntse G, Tendal O.S. (Eds.) *Marine Biological*
 778 *Investigations and Assemblages of Benthic Invertebrates From the Faroese Islands*. Kaldbak
 779 Marine Biological Laboratory, Faroe Islands, pp13-21.

780

781 Klitgaard, A.B. and Tendal, O.S. 2004. Distribution and species composition of mass
 782 occurrences of large-sized sponges in the northeast Atlantic. *Prog. Oceanogr.* 61, 57-98.

783

784 Knudby, A., Kenchington, E. and Murillo, F.J. 2013. Modeling the distribution of geodia
 785 sponges and sponge grounds in the northwest atlantic. *PloS ONE* 8: e82306.

786

787 Kostylev, V.E., Erlandsson, J., Ming, M.Y. and Williams, G.A. 2005. The relative importance
 788 of habitat complexity and surface area in assessing biodiversity: fractal application on rocky
 789 shores. *Ecol. Complex.* 2, 272-286.

790

791 Krasko, A., Lorenz, B., Batel, R., Schröder, H.C., Müller, I.M. and Müller, W.E. 2000.
 792 Expression of silicatein and collagen genes in the marine sponge *Suberites domuncula* is
 793 controlled by silicate and myotrophin. Eur. J. Biochem. 267, 4878-4887.
 794

795 Lahoz-Monfort, J.J., Guillera-Arroita, G. and Wintle, B.A. 2014. Imperfect detection impacts
 796 the performance of species distribution models. Glob. Ecol. Biogeogr. 23, 504-515.
 797

798 Lavaleye, M., Duineveld, G., Berghuis, E., Kok, A. and Witbaard, R. 2002. A comparison
 799 between the megafauna communities on the NW Iberian and Celtic continental margins—
 800 effects of coastal upwelling? Prog. Oceanogr. 52, 459-476.
 801

802 Liu, C., Berry, P.M., Dawson, T.P. and Pearson, R.G. 2005. Selecting thresholds of
 803 occurrence in the prediction of species distributions. Ecography 28, 385-393.
 804

805 Lobo, J.M., Jiménez-Valverde, A. and Real, R. 2008. AUC: a misleading measure of the
 806 performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145-151.
 807

808 Lutz, M.J., Caldeira, K., Dunbar, R.B. and Behrenfeld, M.J. 2007. Seasonal rhythms of net
 809 primary production and particulate organic carbon flux to depth describe the efficiency of
 810 biological pump in the global ocean. J Geophys. Res-Oceans 112 (C10).,
 811

812 Maldonado, M., Carmona, M.C., Velásquez, Z., Puig, A., Cruzado, A., López, A. and Young,
 813 C.M. 2005. Siliceous sponges as a silicon sink: an overlooked aspect of benthopelagic
 814 coupling in the marine silicon cycle. Limnol. Oceanogr. 50, 799-809.
 815

816 Maldonado, M., Cao, H., Cao, X., Song, Y., Qu, Y. and Zhang, W. 2011. Experimental silicon
817 demand by the sponge *Hymeniacidon perlevis* reveals chronic limitation in field populations.
818 In: Ancient Animals, New Challenges. Springer, pp. 251-257.

819

820 Maldonado, M., Aguilar, R., Bannister, R.J., Bell, D., Conway, K.W., Dayton, P.K., Díaz, C.,
821 Gutt, J., Kenchington, E.L.R., Leys, D. and Pomponi, S.A., 2016. Sponge grounds as key
822 marine habitats: a synthetic review of types, structure, functional roles, and conservation
823 concerns. In: Marine Animal Forests. Springer, Berlin._24-1.

824 Manel, S., Dias, J., Buckton, S. and Ormerod, S. 1999. Alternative methods for predicting
825 species distribution: an illustration with Himalayan river birds. J. Appl. Ecol. 36, 734-747.

826

827 Murillo, F.J., Muñoz, P.D., Cristobo, J., Ríos, P., González, C., Kenchington, E. and Serrano,
828 A. 2012. Deep-sea sponge grounds of the Flemish Cap, Flemish Pass and the Grand Banks
829 of Newfoundland (Northwest Atlantic Ocean): distribution and species composition. Mar. Biol.
830 Res. 8, 842-854.

831

832 Perea-Blazquez, A., Davy, S.K. and Bell, J.J. 2012. Estimates of particulate organic carbon
833 flowing from the pelagic environment to the benthos through sponge assemblages. - PloS
834 ONE 7: e29569.

835

836 Peterson, A. and Nakazawa, Y. 2008. Environmental data sets matter in ecological niche
837 modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. Glob. Ecol. Biogeogr.
838 17, 135-144.

839

840 Phillips, S.J., Dudík, M. and Schapire, R.E. 2004. A Maximum Entropy Approach to Species
841 Distribution Modeling. In: Proceedings of the 21st International Conference on Machine
842 Learning, Banff, Canada, 2004. ACM Press, New York, pp. 655-662.

843

844 Phillips, S.J., Anderson, R.P. and Schapire, R.E. 2006. Maximum entropy modeling of
 845 species geographic distributions. *Ecol. Modell.* 190, 231-259.

846

847 Phillips, S.J. and Dudík, M. 2008. Modelling of Species Distributions with Maxent: New
 848 Extensions and a Comprehensive Evaluation. *Ecography* 31, 161-175.

849

850 Piechaud, N., Downie, A., Stewart, H.A. and Howell, K.L. 2015. The impact of modelling
 851 method selection on predicted extent and distribution of deep-sea benthic assemblages.
 852 *Earth Environ. Sci. Trans. R. Soc. Edinburgh* 105, 251-261.

853

854 Pile, A.J. and Young, C.M. 2006. The natural diet of a hexactinellid sponge: benthic–pelagic
 855 coupling in a deep-sea microbial food web. *Deep Sea Res., Part I* 53, 1148-1156.

856

857 Reiswig, H.M. 1971. Particle feeding in natural populations of three marine demosponges. -
 858 *Biol. Bull.* 141, 568-591.

859

860 Reiswig, H.M. 1974. Water transport, respiration and energetics of three tropical marine
 861 sponges. *J. Exp. Mar. Biol. Ecol.* 14, 231-249.

862

863 Reiswig, H.M. 1975. Bacteria as food for temperate-water marine sponges. *Can. J. Zool.* 53,
 864 582-589.

865

866 Rengstorf, A.M., Yesson, C., Brown, C. and Grehan, A.J. 2013. High-resolution habitat
 867 suitability modelling can improve conservation of vulnerable marine ecosystems in the deep
 868 sea. *J. Biogeogr.* 40, pp.1702-1714.

869

870 Rice, A., Thurston, M. and New, A. 1990. Dense aggregations of a hexactinellid sponge, < i>
871 *Pheronema carpeni*</i>, in the Porcupine Seabight (northeast Atlantic Ocean), and
872 possible causes. Prog. Oceanogr. 24, 179-196.
873

874 Rice, A.L., Thurston, M.H. and New, A.L. 1990. Dense aggregations of a hexactinellid
875 sponge, *Pheronema carpeni*, in the Porcupine Seabight (northeast Atlantic Ocean), and
876 possible causes. Prog. Oceanogr. 24, 179-196.
877

878 Rinne, H., Kaskela, A., Downie, A.L., Tolvanen, H., von Numers, M. and Mattila, J. 2014.
879 Predicting the occurrence of rocky reefs in a heterogeneous archipelago area with limited
880 data. Estuar. Coast. Shelf. S. 138, 90-100.
881

882 Roberts, J.J., Best, B.D., Dunn, D.C., Treml, E.A. and Halpin, P.N. 2010. Marine Geospatial
883 Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python,
884 R, MATLAB, and C++. Environ. Model. Softw 25, 1197-1207.
885

886 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P. and
887 Richardson, A.J. 2011. Pushing the limits in marine species distribution modelling: lessons
888 from the land present challenges and opportunities. Glob. Ecol. Biogeogr. 20, 789-802.
889

890 Rodríguez, E., López-González, P.J. and Gili, J.M. 2007. Biogeography of Antarctic sea
891 anemones (Anthozoa, Actiniaria): What do they tell us about the origin of the Antarctic
892 benthic fauna? Deep Sea Res., Part II 54, 1876-1904.
893

894 Ross, L.K., Ross, R.E., Stewart, H.A. and Howell, K.L. 2015. The Influence of Data
895 Resolution on Predicted Distribution and Estimates of Extent of Current Protection of Three
896 'Listed' Deep-Sea Habitats. PloS ONE 10, e0140061.
897

898 Ross, R.E. and Howell, K.L. 2013. Use of predictive habitat modelling to assess the
 899 distribution and extent of the current protection of 'listed' deep-sea habitats. Diversity and
 900 Distributions 19, 433-445.
 901

902 Sollas, W. 1880. XVII.—The sponge-fauna of Norway; a report on the Rev. AM Norman's
 903 collection of sponges from the Norwegian Coast. J. Nat. Hist. 9, 141-165.
 904

905 Stephens, J. 1915. Sponges of the Coasts of Ireland. H.M. Stationery Office.
 906

907 Team, R.D.C. 2011. R: A Language and Environment for Statistical Computing. In: R
 908 Foundation for Statistical Computing. R Foundation for Statistical Computing, Vienna,
 909 Austria.
 910

911 Thomson, W. 1869. On Holtenia, a Genus of Vitreous Sponges. Proc. R. Soc. London 18,
 912 32-35.

913 Tjensvoll, I., Kutti, T., Fosså, J.H. and Bannister, R. 2013. Rapid respiratory responses of the
 914 deep-water sponge *Geodia barretti* exposed to suspended sediments. Aquat Biol 19, 65-73.
 915

916 Topsent, E. 1928. Spongiaires de l'Atlantique et de la Méditerranée, provenant des
 917 croisières du prince Albert Ier de Monaco. Imprimerie de Monaco.
 918

919 Vacelet, J. 1961. Quelques éponges remarquables de Méditerranée. Rev. Trav. Inst. Peches
 920 Marit. 25, 351-354.
 921

922 Weisz, J.B., Lindquist, N. and Martens, C.S. 2008. Do associated microbial abundances
 923 impact marine demosponge pumping rates and tissue densities? Oecol. 155, 367-376.
 924

925 White, M., Mohn, C., de Stigter, H. and Mottram, G. 2003. Deep-water coral development as
 926 a function of hydrodynamics and surface productivity around the submarine banks of the
 927 Rockall Trough, NE Atlantic. In: 2nd International Symposium on Deep-Sea Corals. pp. 503-
 928 514.

929

930 White, M., Mohn, C., de Stigter, H. and Mottram, G. 2005. Deep-water coral development as
 931 a function of hydrodynamics and surface productivity around the submarine banks of the
 932 Rockall Trough, NE Atlantic. In: Cold-water corals and ecosystems. Springer, pp. 503-514.

933

934 Whitney, F., Conway, K., Thomson, R., Barrie, V., Krautter, M. and Mungov, G. 2005.
 935 Oceanographic habitat of sponge reefs on the Western Canadian Continental Shelf. - Cont.
 936 Shelf Res. 25, 211-226.

937

938 Wilson, S., Graham, N. and Polunin, N. 2007. Appraisal of visual assessments of habitat
 939 complexity and benthic composition on coral reefs. Mar. Biol. 151, 1069-1076.

940

941 Wolfrath, B. and Barthel, D. 1989. Production of faecal pellets by the marine sponge
 942 *Halichondria panicea* Pallas (1766). J. Exp. Mar. Biol. Ecol. 129, 81-94.

943

944 Wulff, J.L. 2006. Ecological interactions of marine sponges. Can. J. Zool. 84, 146-166.

945

946 Yahel, G., Sharp, J.H., Marie, D., Hase, C. and Genin, A. 2003. In situ feeding and element
 947 removal in the symbiont-bearing sponge *Theonella swinhoei*. Bulk DOC is the major source
 948 for carbon. Limnol. Oceanogr. 48, 141-149.

949

950 Yahel, G., Whitney, F., Reiswig, H.M., Eerkes-Medrano, D.I. and Leys, S.P. 2007. In situ
 951 feeding and metabolism of glass sponges (Hexactinellida, Porifera) studied in a deep
 952 temperate fjord with a remotely operated submersible. Limnol. Oceanogr. 52, 428-440.

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955 Table 1: Number of presence and 'apparent absence' records used in the model for each
 956 species or habitat, including references to the data sources.

Species / habitat	Number of presence	Number of pseudo- absence	References
<i>G. atlantica</i>	60	1714	(Rice et al. 1990, Bett and Rice 1992, Copley et al. 1996, Duineveld et al. 1997, Lavaleye et al. 2002, Klitgaard and Tendal 2004, Gebruk et al. 2010, Howell 2010, Tecchio et al. 2011, Cardenas et al. 2013), NEREIDA; http://www.nafo.int/science/frames/nereida.html), BioICE, http://utgafa.ni.is/greinar/BIOICE_station_list_91-04_Paper_A2.pdf
<i>G. barretti</i>	46	1708	
<i>G. hentscheli</i>	66	1694	
<i>G. macandrewii</i>	148	1648	
<i>G. phlegraei</i>	76	1705	
<i>G. parva</i>	40	1697	
<i>ostur</i>	105	2660	(Klitgaard 1995, Klitgaard and Tendal 2004, Cardenas et al. 2013), NEREIDA; http://www.nafo.int/science/frames/nereida.html), BioICE, http://utgafa.ni.is/greinar/BIOICE_station_list_91-04_Paper_A2.pdf
<i>P. carpenteri</i>	117	1944	(Topsent 1892, Topsent and ler 1904, Stephens and Branch 1915, Burton and Ingolf-Expedition 1928, Topsent 1928, Rice et al. 1990, Bett and Rice 1992, Copley et al. 1996, Duineveld et al. 1997, Lavaleye et al. 2002, Klitgaard and Tendal 2004, Fiore and Jutte 2010, Gebruk et al. 2010, Howell 2010, Tecchio et al. 2011, Cardenas et al. 2013, Narayanaswamy et al. 2013, Vacelet, 1961) , NEREIDA; http://www.nafo.int/science/frames/nereida.html), BioICE, http://utgafa.ni.is/greinar/BIOICE_station_list_91-04_Paper_A2.pdf

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959 Table 2: Summary of the environmental data layers used in this study prior to variable selection. Data sources are given.
 960 Oceanographic variables have been resampled to match the resolution of the GEBCO bathymetry with the method described in the
 961 text.

Variable	units	Manipulation	Original cell size	Source	Used in final models
Terrain variables					
Depth	m	None	0.016°	GEBCO 2008	Y
Slope	-	Created using ArcGIS Spatial Analyst Extension.	0.016°	GEBCO 2008	Y
Curvature	-	Created using ArcGIS Spatial Analyst Extension.	0.016°	GEBCO 2008	Y
Plan curvature	-	Created using ArcGIS Spatial Analyst Extension.	0.016°	GEBCO 2008	N
Profile curvature	-	Created using ArcGIS Spatial Analyst Extension.	0.016°	GEBCO 2008	N
terrain ruggedness	-	Created using ArcGIS Benthic Terrain Modeler extension (Wright et al., 2005).	0.016°	GEBCO 2008	Y
Broad-scale Bathymetric Position Index (BPI)	-	Created using ArcGIS Benthic Terrain Modeler extension (Wright et al., 2005). Inner radius 5, outer radius 20, scale factor is 20 km	0.016°	GEBCO 2008	Y
Fine-Scale Bathymetric Position Index (BPI)	-	Created using ArcGIS Benthic Terrain Modeler extension (Wright et al., 2005). Inner radius 1, outer radius 5, scale factor is 5 km	0.016°	GEBCO 2008	Y
Oceanographic variables					
Bottom temperature	°C	rescaled to 0.016° using random forest modelling	1°	WOA 2009 (Locarnini et al., 2010)	Y
Bottom salinity (PSS)	-	rescaled to 0.016° using random forest modelling	1°	WOA 2009 (Antonov et al., 2010)	Y (except <i>P. carpenieri</i>)

Bottom dissolved oxygen conc.	ml/l	rescaled to 0.016 ⁰ using random forest modelling	1 ⁰	WOA 2009 (Garcia et al., 2010a)	N
Bottom oxygen saturation rate	-	rescaled to 0.016 ⁰ using random forest modelling	1 ⁰	WOA 2009 (Garcia et al., 2010a)	N
Bottom phosphate	µmol/l	rescaled to 0.016 ⁰ using random forest modelling	1 ⁰	WOA 2009 (Garcia et al., 2010b)	N
Bottom nitrate	µmol/l	rescaled to 0.016 ⁰ using random forest modelling	1 ⁰	WOA 2009 (Garcia et al., 2010b)	N
Bottom silicate	µmol/l	rescaled to 0.016 ⁰ using random forest modelling	1 ⁰	WOA 2009 (Garcia et al., 2010b)	Y
Particulate organic carbon flux to seabed	Mg/m ² /year	None	7*7 km	derived from Lutz et al (2007)	Y

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964 Table 3: Summary of each model performance according to Area Under the Curve (AUC) and threshold dependent evaluation including
 965 Percent Correctly Classified (PCC). The full model AUC is the internal AUC of the model trained on the whole dataset. MSS (MaxSens+Spec)
 966 is the threshold value that maximizes the sum of sensitivity and specificity, ROC (MinROCdist) is the threshold values that minimizes the
 967 distance between the Receiver Operating Curve plot and the upper left corner of the unit square.

Species	mean AUC	standard deviation	full model AUC	threshold (method)	PCC	Sensitivity	Specificity
<i>G. atlantica</i>	0.774	0.062	0.865	0.450 (mss)	0.729	0.782	0.727
<i>G. baretti</i>	0.865	0.029	0.876	0.272 (roc)	0.803	0.790	0.805
<i>G. hentscheli</i>	0.942	0.030	0.94	0.238 (roc)	0.930	0.895	0.931
<i>G. macandrewii</i>	0.753	0.043	0.835	0.430 (roc)	0.689	0.743	0.687
<i>G. parva</i>	0.906	0.030	0.928	0.277 (mss)	0.904	0.823	0.907
<i>G. phlegraei</i>	0.826	0.069	0.908	0.448 (mss)	0.825	0.798	0.826
ostur	0.898	0.027	0.881	0.397 (roc)	0.811	0.829	0.810
<i>P. carpenteri</i>	0.891	0.026	0.905	0.372 (roc)	0.805	0.867	0.803

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970 Table 4: Percentage of the extent of suitable habitat predicted that is included within each
 971 nation's Exclusive Economic Zone (EEZ) and the High Seas. The nations listed are ranked
 972 in order of the nations with the highest percentage of ostur within their EEZ according to the
 973 ensemble model. The 'Rank' column provides the equivalent listing for the *P. carpenteri*
 974 model for rapid reading.

Region (Country EEZ or High Seas)	% total area combined Geodia map	% total area ostur habitat map	% total area ostur Ensemble map	% total area <i>P.carpenteri</i>	rank
Greenlandic Exclusive Economic Zone	23.99	39.98	33.47	3.63	
Norwegian Exclusive Economic Zone	16.25	12.13	25.54	0.00	
Icelandic Exclusive Economic Zone	9.06	16.87	14.83	16.29	2
Faeroe Islands Exclusive Economic Zone	6.36	6.39	10.54	2.82	
Canadian Exclusive Economic Zone	13.40	11.51	5.60	1.06	
Svalgaard	2.12	4.84	5.15	0.00	
United Kingdom Exclusive Economic Zone	8.50	2.29	3.74	6.52	6
High Seas	7.94	4.02	0.56	21.30	1
Fisheries Zone around Jan Mayen	0.16	1.86	0.39	0.00	
Portuguese Exclusive Economic Zone (Azores)	2.43	0.10	0.18	9.24	5
Portuguese Exclusive Economic Zone	0.56	0.00	0.00	0.50	
Irish Exclusive Economic Zone	5.50	0.00	0.00	3.09	
Saint-Pierre and Miquelon Exclusive Economic Zone	0.03	0.00	0.00	0.00	
French Exclusive Economic Zone	1.60	0.00	0.00	4.95	7
Spanish Exclusive Economic Zone	1.24	0.00	0.00	13.25	4
United States Exclusive Economic Zone	0.37	0.00	0.00	0.10	
German Exclusive Economic Zone	0.20	0.00	0.00	0.00	
Danish Exclusive Economic Zone	0.14	0.00	0.00	0.00	
Swedish Exclusive Economic Zone	0.06	0.00	0.00	0.00	
Italian Exclusive Economic Zone	0.05	0.00	0.00	13.50	3
Dutch Exclusive Economic Zone	0.02	0.00	0.00	0.00	
Guernsey Exclusive Economic Zone	0.00	0.00	0.00	0.00	
MonUgasque Exclusive Economic Zone	0.00	0.00	0.00	0.01	
Algerian Exclusive Economic Zone	0.00	0.00	0.00	3.18	
Tunisian Exclusive Economic Zone	0.00	0.00	0.00	0.53	

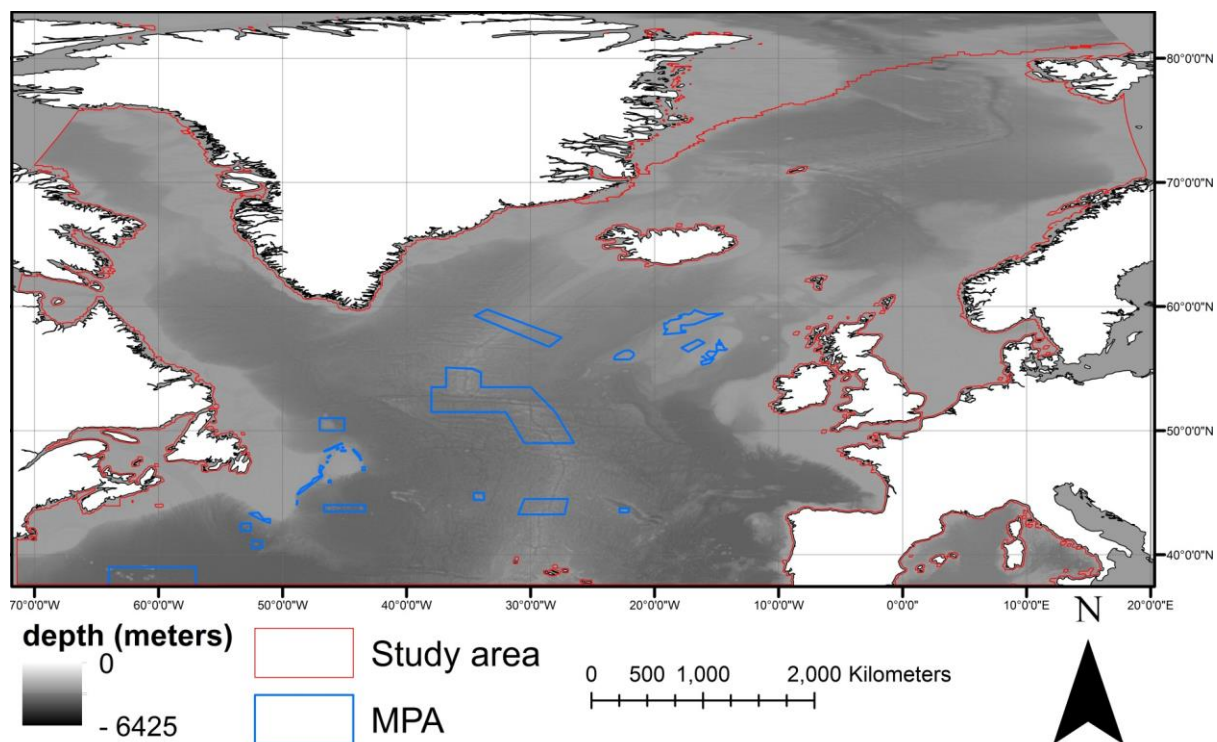
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976 Table 5: Percentage of resource according to each model within the NAFO MPA
 977 network.

	% total area Geodia4+	% total area OstH	% total area OstEns	% total area <i>P.carpenteri</i>
percentage of High Seas resource within MPA	1.50%	19.44%	13.17%	13.49%
percentage of total resource within MPAs	0.06%	1.54%	0.07%	2.87%
percentage of MPAs total surface where the resource is present	0.22%	4.46%	0.08%	8.53%

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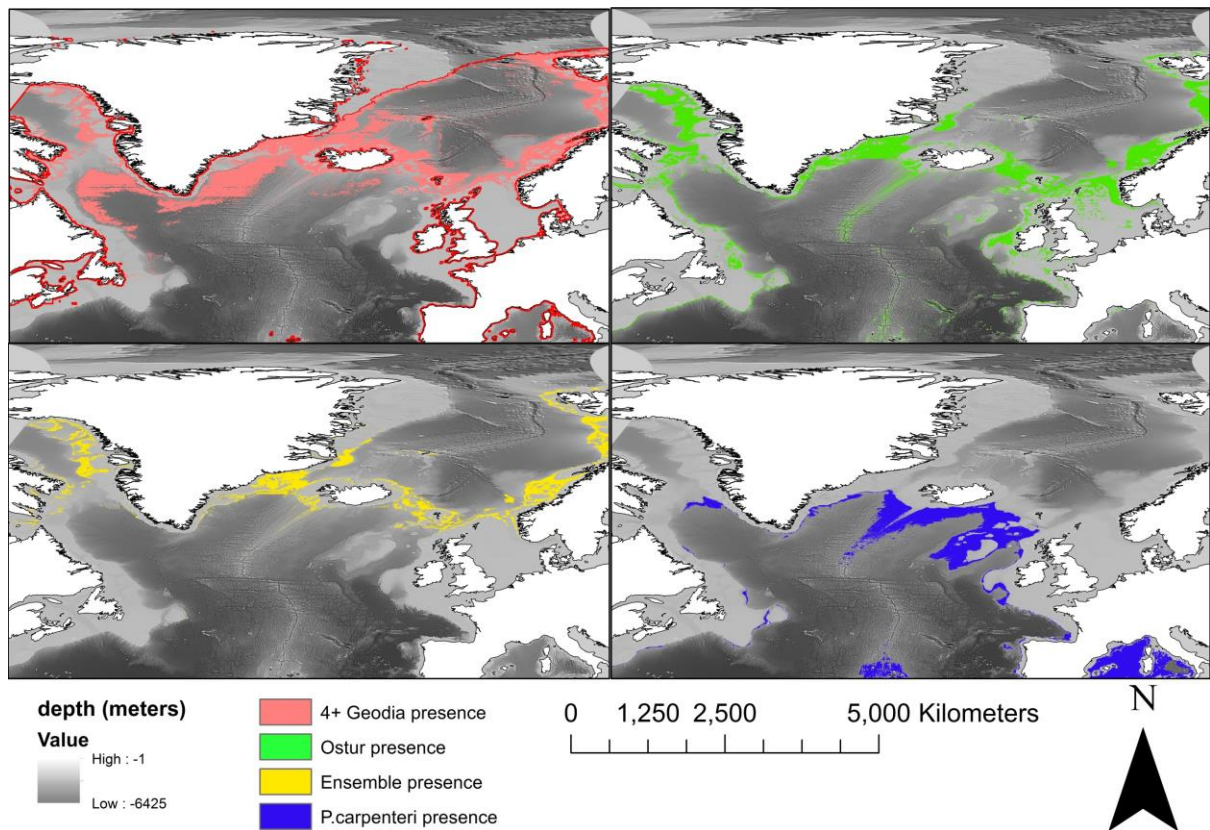


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981 Figure 1: Full extent of the study area. The red line indicates the border of the modelled area.

982 Map projected in WGS 1984.

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Figure 2: distribution maps of co-occurrence of: a) 4 or more *Geodia* species, b) presence of

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ostur habitat, c) presence of both 4 *Geodia* species and ostur habitat (ensemble model), and

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d) presence of *P. carpenteri* in the study area. Map projected in WGS 1984.