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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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Abstract:

Sponge aggregations have been recognised as key component of shallow benthic ecosystems providing several important functional roles including habitat building and nutrient recycling. Within the deep-sea ecosystem, sponge aggregations may be extensive and available evidence suggests they may also play important functional roles, however data on their ecology, extent and distribution in the North Atlantic is lacking, hampering conservation efforts. In this study, we used Maximum Entropy Modelling and presence data for two deep-sea sponge aggregation types, *Pheronema carpenteri* aggregations and ostur aggregations dominated by geodid sponges, to address the following questions: 1) What environmental factors drive the broad-scale distribution of these selected 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 Exclusive Economic Zones (EEZs) and High Seas areas? 4) What percentage of these grounds in High Seas areas are protected by the current High Seas MPA network? Our results suggest that silicate concentration, temperature, depth and amount of particulate organic carbon are the most important drivers of sponge distribution. Most of the sponge grounds are located within national EEZs rather than in the High Seas. Coordinated conservation planning between nations with significant areas of sponge grounds such as Iceland, Greenland and Faroes (Denmark), Norway (coastal Norway and Svalbard), Portugal and the UK, should be implemented in order to effectively manage these communities in view of the increasing level 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 carpenteri* (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. carpenteri* is a hexactinellid (glass sponge) that can form aggregations on fine sediments with densities of up to 1.53 individuals/m^2 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; Whiteet 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

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

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

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

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

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

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

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

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

170 Bathymetric data were obtained from the General Bathymetric Chart of the Oceans (GEBCO)
171 2008 (http://www.gebco.net/) 30 arc second grid, as derived from quality controlled ship
172 soundings combined with satellite-derived gravity data. This dataset provides universal
173 coverage of the study area. The GEBCO bathymetry layer was reprojected into Goode's
174 Homolosine (Ocean) at 1km x 1km grid cell size (the approximate size of cells over the study
175 area) and seven further topographic variables were derived from the bathymetry layer. Slope,
176 curvature, plan curvature, and profile curvature were created using the ArcGIS (ESRI 2009)
177 Spatial Analyst extension. Rugosity, broad scale and fine scale bathymetric position index
178 (BPI) were created using the Benthic Terrain Modeller extension (Whiteet al., 2005). BPI
179 broad was calculated with an inner radius of 5 and an outer radius of 20. BPI fine was
180 calculated with an inner radius of 1 and an outer radius of 5. Further information on the
181 specifics of using topographic variables as surrogates is available in existing literature
182 (Kostylev et al., 2005; Wilson et al., 2007; Guinan et al., 2009; ; Ross and Howell 2013).

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

194 Finally, Particulate Organic Carbon (POC) at depth was derived from (Lutzet 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 (Phillipset al., 2004; Phillipset al., 2006; Phillips and Dudík 2008). It has been found to be
213 amongst the highest performing modelling techniques for presence only modelling (Elithet 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 (Robertset
217 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.

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

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

237

238 3.2. Model evaluation

239 Presence and apparent absence data were used to assess the final models. For each model,
240 100 randomly generated partitions of 75% training/25% test data were used to internally test
241 the model. Discrimination capacity was assessed using the area under the receiver
242 operating curve (AUC). An internal or full model (using all the available data in the training of
243 the model) AUC and a 100 fold cross validation AUC along with training and test average
244 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. carpenteri*) 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

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

297

298 ## 4. Results

299 ### 4.1. Modelling

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

303

304 ### 4.2. Model evaluation

305 Table 3 displays the AUC values and threshold-dependent model evaluation metrics for all 6
306 *Geodia* models plus the *P. carpenteri* and ostur models. The mean *G. hentscheli and G.*
307 *parva* cross-validation AUC scores were considered excellent (0.9-1), while those for *G.*
308 *baretti*, *G. phlegraei,* ostur, and *P. carpenteri* were good (0.8–0.9) and *G. atlantica and G.*
309 *macandrewii* fair (0.7–08). The Maxent logistic output was thresholded using either minimum
310 ROC distance for *G. barretti*, *G. hentscheli*, *G. macandrewii*, ostur and *P. carpenteri* or
311 Maximum Sensitivity-Specificity for *G. atlantica*, *G. parva* and *G. phlegraei* as shown in
312 Table 3. Models yielded good performances (> 0.8) for *G. hentscheli, G. parva, osturs* and *P.*
313 *carpenteri,* fair performances (0.7-0.8) for *G. atlantica, G. barretti* and *G. phlegraei* and poor
314 performances (< 0.7) for *G. macandrewii.* The best performing models according to all
315 metrics were *G. hentscheli* and *G. parva*, with *G. atlantica* and *G. macandrewii* performing
316 worst.

317

318 ### 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.atltantica, 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

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

351

352 ### 4.5. Conservation and management assessment

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

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

366

367 ## 5. Discussion

368 ### *5.1. What environmental factors drive the broad-scale distribution of ostur and*
369 *Pheronema carpenteri sponge grounds?*

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

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

It must be noted that silicate was correlated with nitrate, phosphate and depth. Nitrate and 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 al., 2007) observed no significant concentration shift for nitrate between inhalant and exhalent 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 exhalent 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; Murilloet 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 (Cárdenaset 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; Klitgaardet 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. Knudbyet 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 Knudbyet 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

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

The predicted distribution of *P. carpenteri* aggregations again broadly follows the known distribution of this habitat. It has been observed from the Mid Atlantic Ridge south of Iceland (Copley et al., 1996), west of the Faroe Islands (Burton 1928), near the Darwin Mounds (Bett et al., 2001), in the Rockall-Hatton Basin (Howell et al., 2014) Porcupine Seabight (Rice et al., 1990), on Goban Spur (Duineveld et al., 1997; Flach et al., 1998; Lavaleye et al., 2002), on Le Danois Bank (García-Alegre et al., 2014) and in the Mediterranean (Vacelet 1961). The model predicts presence at all these locations suggesting a reasonable performance. The model shows broad agreement with previously published finer scale models of *P. carpenteri* distribution from the UK and Irish extended continental shelf limits (Ross and Howell 2013; Ross et al., 2015). Both the current model and fine scale model of (Ross et al., 2015) predict presence in a narrow band all along the continental slope and in the Porcupine Seabight in this region, where as the (Ross and Howell 2013) model predicted a more patchy distribution for these areas.

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

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

5.3. Implications for conservation and management

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

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

553 protecting 8-15% of the likely resource. However species and habitats require effective
554 protection measures throughout their range (Green et al., 2014) thus we suggest the High
555 Seas area of the Norwegian and Greenland Seas, predicted by our model as likely to
556 support ostur deep-sea sponge aggregations, are investigated for the presence of ostur
557 habitat and, if observed, consideration given to protection of the seabed habitat in this region.

558 For the 21.3% of *P. carpenteri* deep-sea sponge aggregations that are predicted to occur in
559 High Seas areas much of this occurs on the MAR south of Iceland and in and around the
560 Rockall-Hatton Plateaux including Edoras Bank. While 13.5 % of the High Seas area likely to
561 support *P. carpenteri* aggregations is contained within the existing MPA network (shown in
562 Fig. 1), in the case of the Hatton-Rockall Plateau this is incidental capture as these area
563 closures were made for the protection of cold water corals. The Rockall-Hatton Basin
564 represents a large area where our models predict *P. carpenteri* aggregations are likely to
565 occur. The importance of the Hatton-Rockall Plateaux in this region was recently highlighted
566 by the area being proposed as an 'Ecologically and Biologically Significant Area' (EBSA) to
567 the Convention on Biological Diversity. Human activities occurring in the basin include
568 bottom trawling (likely to only extend to the base of Rockall Bank) and the presence of
569 submarine cables (Benn et al., 2010). We suggest, given the existing observations of
570 presence of this habitat and the likely occurrence of the habitat on the basis of our model
571 output, that areas not previously subjected to bottom trawling are considered for protection
572 by NEAFC and the Irish and UK Governments.

573

574 ## 6. Conclusions

575 Silicate concentration and temperature appear to be the most important drivers for geodid
576 species distribution and depth is the most important for *P. carpenteri*. Depth is, however,
577 most likely acting as a proxy for several unmeasured oceanographic parameters that
578 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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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
G. atlantica	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
G. barretti	46	1708	
G. hentscheli	66	1694	
G. macandrewii	148	1648	
G. phlegraei	76	1705	
G. parva	40	1697	
ostur	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
P. carpenteri	117	1944	(Topsent 1892, Topsent and Ier 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	0.016º	GEBCO 2008	Y
Slope	-	Created using ArcGIS Spatial Analyst Extension.	0.016º	GEBCO 2008	Y
Curvature	-	Created using ArcGIS Spatial Analyst Extension.	0.016º	GEBCO 2008	Y
Plan curvature	-	Created using ArcGIS Spatial Analyst Extension.	0.016º	GEBCO 2008	N
Profile curvature	-	Created using ArcGIS Spatial Analyst Extension.	0.016º	GEBCO 2008	N
terrain ruggedness	-	Created using ArcGIS Benthic Terrain Modeler extension (Wright et al., 2005).	0.016º	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	0.016º	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	0.016º	GEBCO 2008	Y
Oceanographic variables					
Bottom temperature	ºC	rescaled to 0.016º using random forest modelling	1º	WOA 2009 (Locarnini et al., 2010)	Y
Bottom salinity (PSS)	-	rescaled to 0.016º using random forest modelling	1º	WOA 2009 (Antonov et al., 2010)	Y (except *P. carpenteri*)

Bottom dissolved oxygen conc.	ml/l	rescaled to 0.016º using random forest modelling	1º	WOA 2009 (Garcia et al., 2010a)	N
Bottom oxygen saturation rate	-	rescaled to 0.016º using random forest modelling	1º	WOA 2009 (Garcia et al., 2010a)	N
Bottom phosphate	µmol/l	rescaled to 0.016º using random forest modelling	1º	WOA 2009 (Garcia et al., 2010b)	N
Bottom nitrate	µmol/l	rescaled to 0.016º using random forest modelling	1º	WOA 2009 (Garcia et al., 2010b)	N
Bottom silicate	µmol/l	rescaled to 0.016º using random forest modelling	1º	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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Table 3: Summary of each model performance according to Area Under the Curve (AUC) and threshold dependent evaluation including Percent Correctly Classified (PCC). The full model AUC is the internal AUC of the model trained on the whole dataset. MSS (MaxSens+Spec) is the threshold value that maximizes the sum of sensitivity and specificity, ROC (MinROCdist) is the threshold values that minimizes the 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
G. atlantica	0.774	0.062	0.865	0.450 (mss)	0.729	0.782	0.727
G. baretti	0.865	0.029	0.876	0.272 (roc)	0.803	0.790	0.805
G. hentscheli	0.942	0.030	0.94	0.238 (roc)	0.930	0.895	0.931
G. macandrewii	0.753	0.043	0.835	0.430 (roc)	0.689	0.743	0.687
G. parva	0.906	0.030	0.928	0.277 (mss)	0.904	0.823	0.907
G. phlegraei	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
P. carpenteri	0.891	0.026	0.905	0.372 (roc)	0.805	0.867	0.803

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 *P.carpenteri*	ranks
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
Fishieries 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	
MonÚgasque 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	

975

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 *P.carpenteri*
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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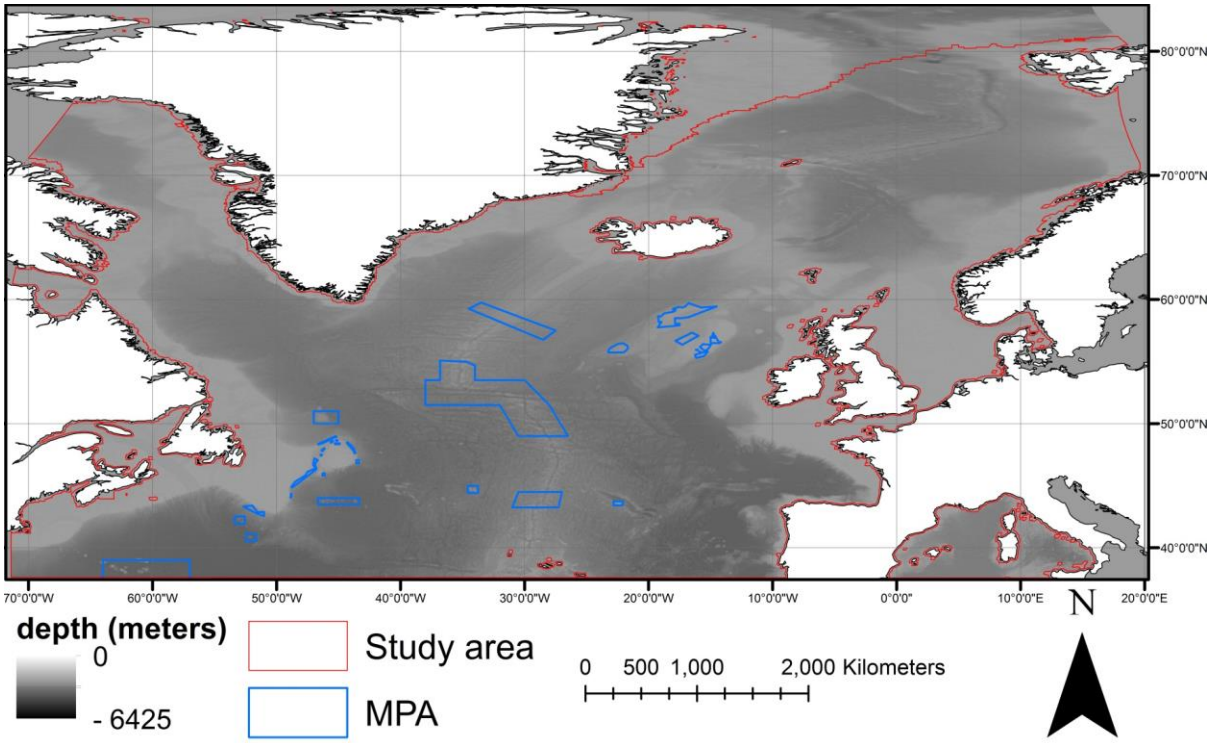

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981 Figure 1: Full extent of the study area. The red line indicates the border of the modelled area.

982 Map projected in WGS 1984.

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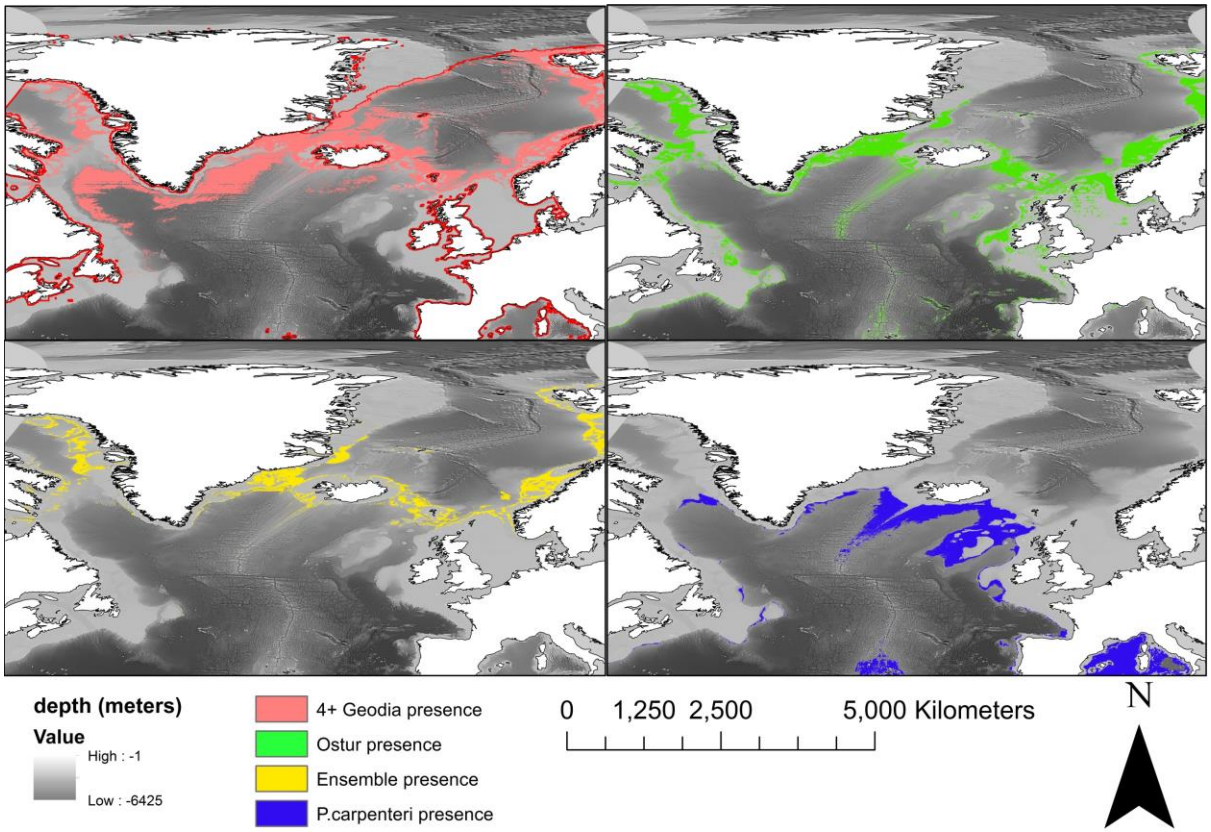

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985 Figure 2: distribution maps of co-occurrence of: a) 4 or more Geodia species, b) presence of
986 ostur habitat, c) presence of both 4 Geodia species and ostur habitat (ensemble model), and
987 d) presence of *P. carpenteri* in the study area. Map projected in WGS 1984.