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Original Article

Reconstructing baselines: use of habitat suitability modelling to predict pre-fishing condition of a Vulnerable Marine Ecosystem

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As industrialized fishing activities have moved into deeper water, the recognition of Vulnerable Marine Ecosystems (VMEs) has become important for the protection of the deep-sea. Our limited knowledge on the past and present distribution of VMEs hinders our ability to manage bottom fisheries effectively. This study investigated whether accounting for bottom fishing intensity (derived from Vessel Monitoring System records) as a predictor in habitat suitability models can (1) improve predictions of, and (2) provide estimates for a pre-fishing baseline for the distribution and biomass of a VME indicator taxon. Random Forest models were applied to presence/absence and biomass of *Geodia* sponges and environmental variables with and without bottom fishing intensity. The models including fishing were further used to predict distribution and biomass of *Geodia* to a pre-fishing scenario. Inclusion of fishing pressure as a predictive term significantly improved model performance for both sponge presence and biomass. This study has demonstrated a way to produce a more accurate picture of the current distribution of VMEs in the study area. The pre-fishing scenario predictions also identified areas of suitable *Geodia* habitat that are currently impacted by fishing, suggesting that sponge habitat and biomass have been impacted by bottom trawling activities.

Keywords: baseline, benthic habitat, bottom trawling, deep sea, habitat distribution, habitat suitability modelling, human impact, Vulnerable Marine Ecosystems

Introduction

The Vulnerable Marine Ecosystem (VME) concept is enshrined in United Nations General Assembly (UNGA) Resolution 61/105. VMEs are typically defined as interdependent communities of benthic organisms whose habitat and life histories (i.e. their anatomy, development, life span, reproductive success, and behaviour) mean they are vulnerable to impacts from fishing activities. The bottom-contact trawl fishery, given its relatively large spatial footprint, intensity and interaction with the seabed, has the potential to inflict severe, widespread, and long-lasting physical damage to VMEs. UNGA Resolution 61/105 requires member states, in respect of areas where VMEs are known, 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. As a result, several areas of seabed have been officially designated as VME and measures put in place to protect them (Bell *et al.*, 2019). However, there remains a challenge in identifying areas where VMEs are known or are likely to occur.

One approach to addressing that challenge is to predict, using habitat suitability models (HSM), where VME or VME indicator taxa are most likely to occur, based on their specific environmental preferences. HSM formalize the relationship between environmental drivers and species' distributions in a mathematical framework such that predictions of probability or likelihood of occurrence of a taxon can be made based on environmental predictor data alone. To date, most HSM on VME taxa have concentrated on the distribution (presence/absence; e.g. Bryan and Metaxas, 2007; Howell *et al.*, 2011, 2016; Knudby *et al.*, 2013; Ross and Howell, 2013; Tong *et al.*, 2013; Rengstorf *et al.*, 2014; Gonzalez-Mirelis and Buhl-Mortensen, 2015; Miller *et al.*, 2015; Ross *et al.*, 2015). Less attention has been given to predicting abundance (Rowden *et al.*, 2017) or biomass (Pham *et al.*, 2019) of taxa, although it is acknowledged that such predictions are likely to support the development of more effective management strategies (Ardron *et al.*, 2014; Anderson *et al.*, 2016). No VME modelling studies to date have implicitly considered human impacts as predictor variables on VME distribution. Yet, links between taxa and their environment preferences may be obscured by noise in the data originating from current and past human activities, confounding model estimates (Bowden *et al.*, 2021).

In addition, historic human impacts on the marine environment mean that current distribution patterns may not reflect a "baseline" state. Many marine habitats have suffered declines because of past human activities (Zu Ermgassen *et al.*, 2012). Understanding historical condition can provide a reference state against which to assess current condition and set conservation targets, as well as disentangle past drivers of change, and enable future prediction. Understanding past distribution patterns may also enable the identification of sites for potential habitat recovery and/or restoration (Swetnam *et al.*, 1999; Zu Ermgassen *et al.*, 2012). While there is no requirement to consider recovery or restoration of habitat under UNGA Resolution 61/105, there are requirements in other policy arenas to do just that, for example Sustainable Development Goal 14, and Article 8(f) of the Convention on Biological Diversity. Further, there is growing interest in the use of restoration ecology to help mitigate climate change, with a specific focus on marine habitats and their ability to effectively sequester and bury carbon (Duarte *et al.*, 2013; Da Ros *et al.*, 2019). Incorporation of human impacts into models will help both unmask the natural distribution patterns, as well as provide tools for forecasting potential impact under changed circumstances, and hindcasting distributions to pre-impact conditions.

VME are characterized by indicator taxa that tend to be drawn from two key phyla, the Cnidaria and the Porifera. The present investigation uses structure forming sponges of the genus *Geodia,* as model VME indicator taxa. *Geodia* spp. sponges are characteristic of a deep-sea VME called "Ostur", originally defined by Klitgaard and Tendal (2004). Studies show that trawling leads rapidly to severe depletion of structure forming sponges and recovery from impact is uncertain and slow (Freese, 2001; Rooper *et al.*, 2011; Pham *et al.*, 2019; Morrison *et al.*, 2020; Murillo *et al.*, 2020). This suggests that previously constructed models of *Geodia* spp. distribution could be confounded by historic and current fishing activities, and thus this group would make an excellent subject for reconstruction of an historic baseline distribution.

In this study, we (1) investigate whether inclusion of fishing intensity as a predictor variable in HSM can improve predictions of the distribution and biomass of a VME indicator taxon, *Geodia* spp., and (2) further ascertain whether aggregations of *Geodia* spp. were once present or more abundant in areas that are presently fished, by applying the models to predict the pre-fishing baseline distribution and biomass of *Geodia* spp.

Materials and methods

The study site

The Flemish Cap and Grand Banks located in the North West Atlantic are an important site for the fishing industry (Figure 1). The area has been the subject of multiple studies, most recently the international NEREIDA project 2009–2013, which established the presence of multiple VME indicator taxa at this site and resulted in a number of areas being closed to bottom trawl fishing to protect VMEs. The NEREIDA project collected multibeam echosounder (MBES) bathymetry (Durán Muñoz *et al.*, 2012), box core samples for both faunal and sediment analysis (Weitzman *et al.*, 2014), and trawl and rock dredge samples (Murillo *et al.*, 2012, Durán Muñoz *et al.*, 2009, Durán Muñoz *et al.*, 2012), providing a rich dataset for use in this study.

Data

MBES bathymetry and derivatives

MBES bathymetry data from the NEREIDA programme (Durán Muñoz *et al.*, 2012), were gridded to 75 m cell size. Some artefacts originating from the gridding process were evident in the data and were smoothed out using a 5-cell neighbourhood mean filter. Layers describing topographic attributes of the seafloor were calculated from the bathymetry data (Table 1.). Variables describing the local variability of terrain, often acting as a proxy for hard substrates, included slope, bathymetric roughness, standard deviation (within a 3-cell neighbourhood) and rugosity (within a 5-cell neighbourhood). Eastness and northness describe the main direction (aspect) of the slope. Bathymetric Position Index (BPI), which relates the elevation of each cell to the average in a specified neighbourhood, and gives an indication whether a pixel is part of an elevation or depression, was calculated for neighbourhoods with an inner radius of 1 and outer radii of 25, 50, 75, 100, 125, and 150 cells. The set of neighbourhoods were selected to represent landscape level topographic features of the seabed over scales ranging between kilometres to tens of kilometres.

Substrate variables

Layers describing sediment composition, namely the percentages of sand, clay, silt and organic carbon, were produced from 314 separate box core Particle Size Analysis (PSA) samples with an average distance between samples of 9 km. PSA sampling methodology is described in Weitzman *et al.* (2014). Universal kriging, using bathymetry, BPI150 and roughness as co-variants, was used to create layers with 75 m grid resolution to match the bathymetry. One covariant was used in each spatial model, selecting the one with highest correlation for each substrate variable. The percentages of sand and clay were modelled using roughness as covariant, whilst silt corresponded best to BPI150 and organic carbon to bathymetry.

Oceanographic variables

Model-based flow velocity (U and V) and temperature (T) at the seabed were available as monthly averages over a 10-year period (1990–2010) from a North Atlantic Ocean model developed at Bedford Institute of Oceanography (BIO; Wang and Greenan, 2014). Current speed was calculated from U and V according to the equation $\sqrt{(U^2 + V^2)}$. Current speed and temperature were summarized as mean, minimum, maximum, range, and standard

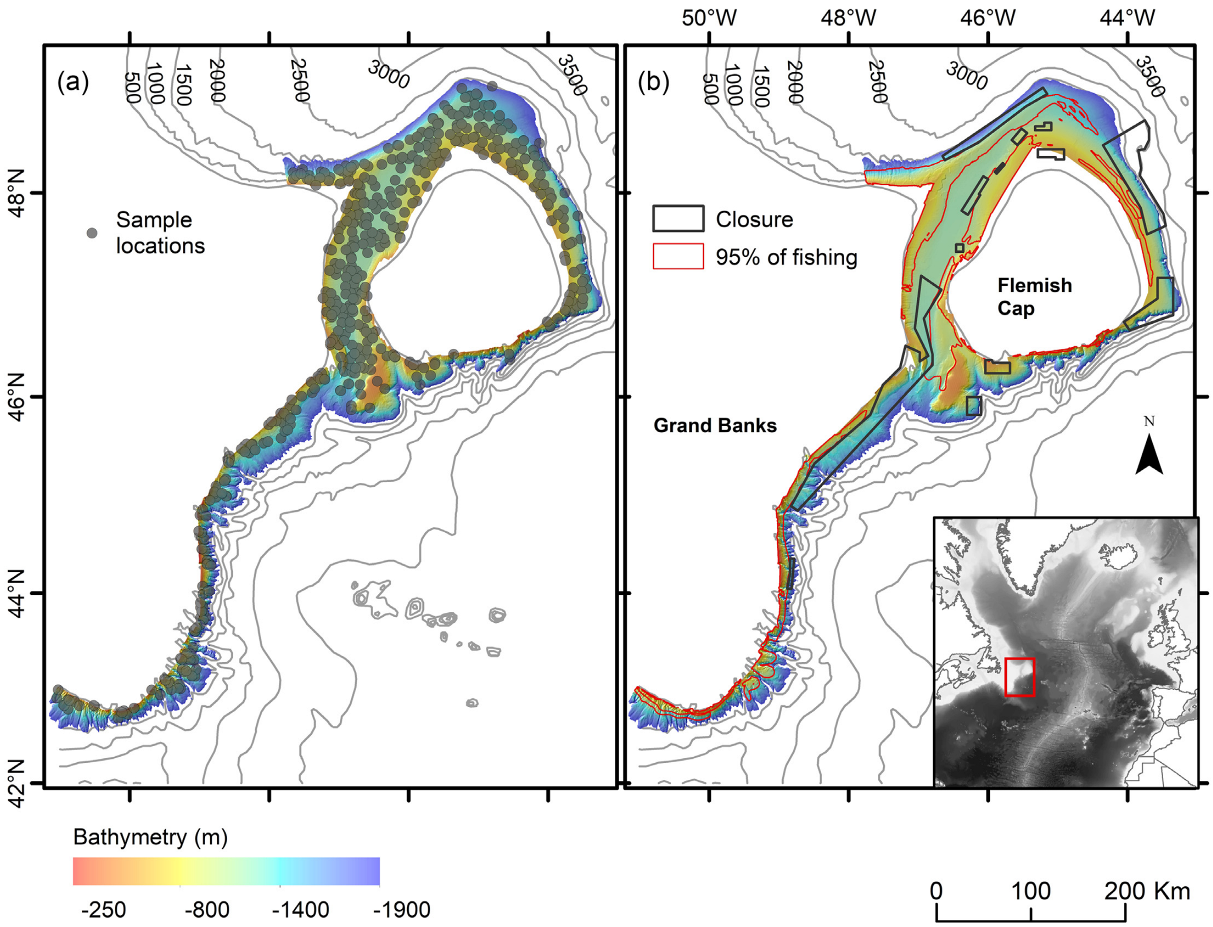

Figure 1. Study area location, extent of MBES bathymetry and locations of epifauna samples from groundfish scientific trawls and rock dredges (a), as well as area encompassing 95% of the total bottom trawling fishery, as identified from VMS records and areas closed to bottom trawling (b).

deviation at each pixel. Additionally, the mean of intra-annual variability (range of values within 1 year) and the inter-annual variability (range of annual means at each pixel) of T were calculated to describe the variability of temperature conditions. The source model exists at 1/12-degree resolution. Each data layer was interpolated to 75 m cell size using the Empirical Bayesian Kriging function in ArcGIS10.1 Geostatistical Analyst.

Bottom trawling intensity

Line features of vessel tracks, created from Vessel Monitoring System (VMS) pings filtered to bottom trawling vessels moving at fishing speed (0.5–5 knots), were available for the study area to cover bottom trawling activity for 2010–2012. A proxy of bottom trawling intensity was created by calculating line density inside a 2-km radius for each 75 m raster cell in the study area. The 2-km radius was selected to account for the spatial resolution of the VMS ping data, which is collected at hourly intervals. The trawling intensity was further categorized into percentiles at 5% intervals, to identify the area encompassing 95% of fishing activity.

Biological data

Data on the presence and biomass (kg wet weight) of the demosponges *Geodia* spp. is based on catches in 30-minute scientific groundfish survey trawls, covering ∼2 km distance, collected during 2011–2013 by EU-Spain on board RV “Vizconde de Eza” and 15-minute rock dredge tows, covering ∼600 m distance, collected by the NEREIDA project in 2009–2010 on board RV “Miguel Oliver.” The methodology for conducting groundfish survey trawls is described in Murillo *et al.* (2012) and rock dredges in Durán Muñoz *et al.* (2012). The groundfish surveys combine two types of bottom trawl gears, the “Campelen” and “Lofoten” with different dimensions and net sizes. Kenchington *et al.* (2014) determined there was no significant effect of sampling gear on community composition or catch biomass for the trawl surveys. We further investigated potential bias in the data including rock dredge samples using univariate and multivariate plotting to determine that although the largest sponge catches were obtained using the rock dredge there was no systematic bias between the trawl and rock dredge datasets. The biomass data were further square-root transformed to reduce the effect of the highest biomass samples.

Fauna in the rock dredges and a subset of the trawls were identified to genus or species. The tows with genus level taxonomy have all been used in the models. The remaining tows with identification at phylum level have been included as absences, where they show no observation of members of the phylum Porifera. The resulting dataset for modelling consisted of 416 point locations. Data have a good geographic cover of the area and span both fished and unfished areas (Figure 1).

Table 1. Environmental predictor variables included in the variable selection stage before modelling.

Variable	Description	Original resolution	Source
MBES Bathymetry		75 m	NEREIDA programme (Durán-Muñoz *et al.*, 2012)
Bathymetric Position Index (BPI)	25, 50, 75, 100, 125, and 150 m radii	75 m	Calculated from bathymetry
Slope	Percent rise	75 m	Calculated from bathymetry
Bathymetric roughness	5 × 5 cell moving window	75 m	Calculated from bathymetry
Bathymetry standard deviation	3 × 3 cell moving window	75 m	Calculated from bathymetry
Rugosity		75 m	Calculated from bathymetry
Eastness		75 m	Calculated from bathymetry
Northness		75 m	Calculated from bathymetry
Particle size composition (PSA)	% sand/clay/silt/organic carbon	1 point per 10 square km	Box core, NEREIDA programme (Durán-Munoz *et al.*, 2012).
Zonal (U) and meridional (V) velocity	Monthly means over 1990–2010	1/12 degree	North Atlantic model developed at Bedford Institute of Oceanography (BIO; Wang and Greenan, 2014)
Bottom current velocity	Annual minimum, maximum, mean, range, and standard deviation	1/12 degree	Calculated from U and V
Temperature °C	Annual minimum, maximum, mean, range, standard deviation, intra-annual variability, and inter-annual variability	1/12 degree	North Atlantic model developed at Bedford Institute of Oceanography (BIO; Wang and Greenan, 2014)
Trawling intensity	Density of trawl tracks	Lines based on hourly VMS pings	NAFO

HSM

Random Forest (RF; Breiman, 2001; Cutler *et al.*, 2007) models of the distribution and biomass of *Geodia* spp. sponges under current and pre-fishing scenarios were constructed as detailed below.

A total of three different models were built (Table 2), to assess the effect of the bottom fishing activity on the distribution of presence and biomass of the response. The basal model (BSL), included all the data points (416 observations with 36 presences) and those environmental variables that were found to be significant in the predictor variable pre-selection step (see next section), excluding the fishing pressure variable. The BSL model represents the common circumstances where the potential effect of bottom fishing is not accounted for in the model. In the second model, the same biological data points as in the BSL model were used but fishing pressure was included as a predictor variable. The fishing pressure model (FIP) presents a prediction of the current distribution/biomass, where the potential adverse effect of bottom fishing has been accounted for in the outcome. The third model does not include fishing pressure as a predictor variable but excludes data points located in the main fished area, reducing the number of total observations to 238 and presences to 35. Excluding data from areas impacted by fishing was expected to reduce noise in the model by representing "natural conditions" only (NAT). The main fished area was delineated to include 95% of all bottom fishing (determined by the 95th percentile of fishing intensity values in the VMS track density raster).

Prior to running the models, an iterative permutation procedure was used to determine predictor significance. The *boruta* algorithm in the "Boruta" package (Kursa and Rudnicki, 2010) was run in the free statistical computing software R, version 3.0.2 (R Core Team, 2013), to compare the importance of a variable as calculated by a random forest model with the importance of a random permutation of the same variables over several iterations. The variables included as predictors were further reduced by inspecting correlations among predictors. Out of a pair of correlated variables (correlation coefficient > 0.5) the one with a higher random forest importance score was retained in the model.

The models were built in R using the "randomForest" package (Liaw and Wiener, 2002). Classification trees were used for the binary presence/absence models, with predictions of probability of the presence outcome. The square-root transformed biomass was modelled using regression trees. All models were run using the default settings of the *randomForest* function, using 1000 trees. Predictor importance was investigated for each model using the decrease in end node impurity, measured by the Gini index for presence/absence and by residual sum of squares for biomass models. The importance scores were transformed into relative contributions by dividing by the total. Partial response plots (Friedman, 2001) were used to visualize the relationship between each predictor variable and the response variables in turn, while accounting for the average effect of the other predictors in the model.

Models were validated using a repeated random sub-sampling cross-validation procedure. For each response variable, 10 subsets of train and test data with an 80/20% split were randomly drawn from the full dataset, without replacement. The random sampling was stratified by presence/absence and ranges of biomass to maintain equal prevalence and spread of biomass values across the training and test datasets. The presence/absence models were validated using the "PresenceAbsence" package in R (Freeman and Moisen, 2008). A total of four validation statistics were calculated, including the area under the receiver operating curve statistic (AUC; Swets, 1988) and Sensitivity, Specificity, and Kappa statistics (Fielding and Bell, 1997). Predicted probabilities of presence are tied to the prevalence of presence and absence observations in the training dataset and are biased towards the more frequent class. The threshold used to convert the predicted probability to presence/absence represents a trade-off between the proportion of observations correctly predicted as presence (Sensitivity) and absence (Specificity) and should be optimized according to the intended use of the map output (Wilson *et al.* 2005). The threshold was selected using the "equal

Table 2. Summary of the model data and treatments.

Model	Data used in models	Fishing pressure effect	Prediction
BSL	All observations Predictor variables selected in variable selection step minus fishing pressure	Not accounted for	Current distribution without accounting for the effect of fishing
FIP	All observations Predictor variables selected in variable selection step plus fishing pressure	Outcome influenced by fishing pressure	Current distribution as influenced by fishing
NAT	Observations falling outside the area containing 95% of fishing activity only Predictor variables selected in variable selection step minus fishing pressure	Potentially affected observations are removed	Natural state

Table 3. Model validation results for Presence/Absence and Biomass models. Figures given are mean values from 10 cross-validation (cv) runs. N = number of observations, P = number of presence observations, BSL = basal model, FIP = model including fishing intensity as predictor, NAT = model excluding observations from the 95% fishing footprint. Significant differences from the BSL for FIP and NAT models (t-test on values from cv runs) are indicated with * $p < 0.05$, ** $p < 0.01$.

Response variable	Accuracy measure	BSL	FIP	NAT
Presence/Absence	**N (P)**	416 (36)	416 (36)	238 (35)
	Sensitivity	0.86 (±0.05)	0.88 (±0.08)	0.86 (±0.05)
	Specificity	0.83 (±0.04)	0.88 (±0.04)**	0.83 (±0.05)
	Kappa	0.4 (±0.09)	0.52 (±0.11)*	0.53 (±0.1)**
	AUC	0.91 (±0.03)	0.92 (±0.03)	0.91 (±0.04)
Biomass	**N**	416	416	238
	NRMSE	0.1 (±0.08)	0.1 (±0.08)	0.08 (±0.05)
	R^2	0.14 (±0.15)	0.38 (±0.16)**	0.34 (±0.14)**

sensitivity and specificity" criterion which gives equal weight to the likely accuracy of predicted presences and absences in the output (Freeman and Moisen, 2008).

Biomass models were validated using the coefficient of determination (R^2) and the root mean squared error (RMSE) value, calculated using the "caret" package in R (Kuhn and Johnson, 2013). For ease of interpretation, RMSE values were normalized to a percentage of the range of observed biomass values (NRMSE).

The influence of fishing effort on model performance was investigated by comparing the validation statistics for the model including (FIP) versus excluding (BSL) fishing pressure. A two-sample *t*-test was used on the results of the cross-validation runs between models, to ascertain if model performance significantly differed.

Pre-fishing scenario prediction

Predictions from FIP models were used to compare the current area of suitable habitat and relative biomass across the study area to the potential distribution and area under conditions without fishing. The FIP model was selected to represent the pre-fishing conditions over the NAT model, as it had the best validation scores, and included more data points across the whole study area. This pre-fishing prediction was made by replacing the fishing intensity layer with a layer consisting of zero values for the density of tows across the whole area. Areas of suitable habitat and total predicted relative biomass from each scenario were compared between fisheries closed areas, highly fished areas (95% of all fishing effort), low fishing impact areas (remaining 5% of fishing effort), and areas open to fishing but not currently utilized.

Results

Model accuracy

Random Forest models predicting the probability of *Geodia* spp. sponge presence scored high accuracy across all three models (BSL, FIP, and NAT) and four validation statistics (AUC, Sensitivity and Specificity all > 0.8, Kappa > 0.4; Table 3). The FIP model has highest overall model performance. Both Specificity and Kappa are significantly higher for the FIP model than for the BSL mode [$t(18) = -3.32$, $p = 0.004$; and $t(16.7) = -2.62$, $p = 0.02$, respectively]. Similarly, Kappa for the NAT model is significantly higher than BSL [$t(18) = -3.08$, $p = 0.007$].

Although the RMSE (average deviation of the estimates from the observed values) for all of the biomass models was within 10% of the range of observed biomass values (NRMSE ≤ 0.1), the variance explained by the BSL model was low ($R^2 = 0.14$, Table 3). Both models that accounted for the effects of fishing pressure saw a significant increase in variance explained [FIP: $R^2 = 0.38$, $t(18) = -3.38$, $p = 0.003$; NAT: $R^2 = 0.34$, $t(18) = -3.03$, $p = 0.007$].

Predictor importance

Fishing intensity was selected as a significant predictor variable by the *boruta* routine for both presence/absence and biomass models. This indicates that the performance of fishing intensity as

Table 4. Predictor contributions (as % of total) to each model. BSL = basal model, FIP = model including fishing intensity as predictor, NAT = model excluding observations from the 95% fishing footprint. BPI = Bathymetric Position Index; VMS2km = Fishing intensity.

	Presence/AbsenceA			**Biomass**		
	BSL (%)	**FIP (%)**	**NAT (%)**	**BSL (%)**	**FIP (%)**	**NAT (%)**
Bathymetry						
BPI25		7.7			24.1	
BPI50	9.3					
BPI100			11.6			14.8
Eastness	7.7	6.4	8.6			
Northness	6.6	5.8	7.0			
Roughness			13.9			23.1
Rugosity						
Max Bottom Current Speed	14.0	9.7	12.7	13.2	20.6	16.2
Mean Annual Temp. Variability	13.5	14.5	13.7	23.1	24.8	
Min. Bottom Temp.	12.6	12.2	12.3			11.9
Organic Carbon	8.0	5.5	9.2	16.2		
Sand					20.5	34.1
Silt	18.5	14.0	11.0	26.6		
Clay	9.7	10.0		20.9		
VMS2km		14.2			10.0	

a predictor is better than a random variable. All the models include maximum bottom current speed, some combination of mean intra-annual temperature variability, and/or minimum bottom temperature and a substrate variable, either sand or silt content (Table 4). All models, excluding the presence/absence BSL model, also include one or more of the topographic variables (BPI, eastness, northness, roughness, and rugosity).

In the best-performing presence/absence model (FIP), fishing intensity is the second most important predictor variable after the mean intra-annual temperature variability, contributing 14% of total predictor importance (Table 4). In the best-performing biomass model (FIP) the variable contribution of fishing intensity although less important, is still at 10% of total variable importance. The partial response curves for both presence/absence and biomass indicate a sharp negative response to fishing intensity averaged over the range of environmental conditions (Figure 2).

Distribution and biomass of *Geodia* spp. sponges under fished and unfished scenarios

The models indicate that *Geodia* spp. sponges are found in areas elevated from their surroundings at a local scale (such as ridges), with sandy sediments, low percentage of silt and clay, low intra-annual temperature variability, and high bottom current speeds (Figure 2). Bottom fishing has a strongly negative effect (Figure 2), and where trawled areas overlap with suitable habitat *Geodia* spp. sponges are largely absent, or present in low biomass (Figure 3 a and b). Prediction with the presence/absence FIP model to the unfished scenario, with an all-zero fishing intensity layer, indicate that parts of the currently fished area are within the *Geodia* spp. sponge physical habitat and could support populations (Figure 3 a). Similarly, the biomass FIP model prediction suggests that in unfished conditions some of the currently fished area could support higher biomass (Figure 3 c).

Under the unfished scenario (Figure 3 a) *Geodia* spp. sponges are predicted to be present in 45% of the study area. The majority (85%) of the potentially suitable *Geodia* spp. sponge habitat is located outside the fished area and 29% of the suitable area is currently protected by fisheries closures. Of the low fishing intensity area (last 5% of all fishing) 28% is predicted to be suitable, going down to 24% in the high fishing intensity area (95% of all bottom fishing activity). Under the current fishing scenario 37% of the total area is predicted to have *Geodia* spp. sponges present (8% less than the unfished scenario). In the low fishing intensity area approximately a third of the potential habitat has been lost, with *Geodia* spp. sponge predicted present in 18% of the area. In the high fishing intensity area approximately a sixth of the potential distribution remains, with only 4% of the area predicted to have *Geodia* spp. sponges present (Figure 4 a).

The majority of *Geodia* spp. sponge biomass is also found outside the currently fished area (Figure 4 b). Fishing occurs in 52% of the modelled area, although 28% of the area contains 95% of the fishing activity. Under the unfished scenario (Figure 3 c), 29% of potential biomass is predicted to occur in the parts of the study area that are currently fished, and 13% in the area containing 95% of all activity. Under the current fished scenario (Figure 3 b) this is reduced to only 11% of biomass within the low fishing intensity area, and 4% in the high fishing intensity area (Figure 4 b). The reduction in predicted biomass is mainly concentrated in the northern and south-western parts of the study area where suitable *Geodia* spp. sponge habitat overlaps very high fishing intensity areas (Figure 3 b and c). Conversely, the fisheries closures, which cover 18% of the modelled area, contain 22% of potential biomass predicted under the unfished scenario.

Discussion

Successful implementation of ecosystem level marine management is reliant on knowledge-based strategies that balance the requirements of sustainable use of marine resources and the protection of sensitive habitats, as well as fish stocks associated with them (Auster, 2007; Auster *et al.*, 2010). The current lack of data on the occurrence

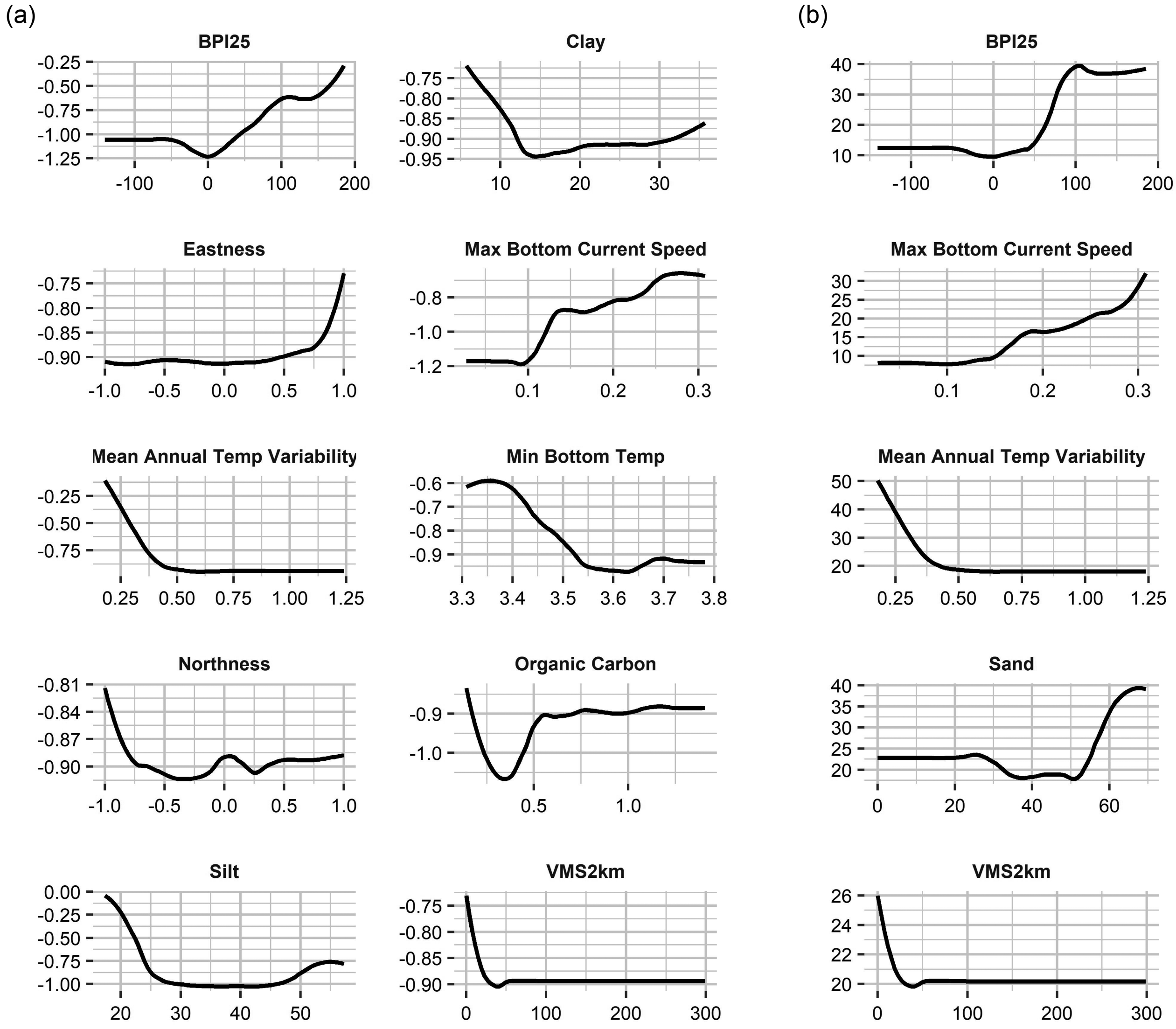

Figure 2. Partial response plots for *Geodia* spp. presence/absence (a) and biomass (b) models that include fishing pressure as a predictor variable (FIP). The plots show the predicted response to each predictor variable in turn, whilst other variables are held at their mean value. Values on the *y*-axis correspond to the logarithm of the fraction of presence votes (a) and biomass (b). BPI = Bathymetric Position Index; VMS2km = Fishing intensity.

and abundance of VME indicator taxa in the high seas, and hence poor understanding of VME distribution in large areas of the deep sea, is hampering our ability to delineate and manage these areas (Ardron *et al.*, 2014). The need for spatial data covering large areas has resulted in an increasing application of predictive spatial modelling. However, to contribute to better management and planning, models need to be as accurate and informative as possible and include predictor variables that directly relate to the requirements of the response. We investigated the benefits of including a human impact gradient into models as a predictor of distribution and abundance, and have shown that accounting for bottom trawling intensity in models is important for the VME indicator taxon *Geodia* spp. with natural distributions overlapping with a bottom fishery. Inclusion of the fishing pressure as a model predictive term significantly improved model performance for both *Geodia* spp. presence and biomass. We have further shown that when quantified in a distribution model the relationship between fishing pressure and species distribution and biomass can be used to estimate historic and potential habitat loss, given that physical conditions do not change.

Bottom trawling is considered one of the main sources of human impacts on deep-sea benthos (UNGA, 2006). Scleractinian corals, black corals, Alcyonacean corals (including those previously called Gorgonians), sea pens and sponges are all known to be very sensitive to fishing impact (McConnaughey, 2000; Sherwood and Edinger, 2009; Clark and Tittensor, 2010; Pusceddu *et al.*, 2014; Kędra *et al.*, 2017; Morrison *et al.*, 2020). The extent of impact will, however, vary between habitats on the basis of differences in physical regime and faunal composition (McConnaughey, 2000).

In their study of the NAFO regulatory area, Murillo *et al.* (2012) found the biomass of deep-water sponges was significantly higher in lightly or never trawled bottoms, but were not able to address the likelihood of whether this reflected past fishing activity or varying habitat suitability for the sponges. The impact of trawling on the benthic community at the Flemish Cap has since been confirmed

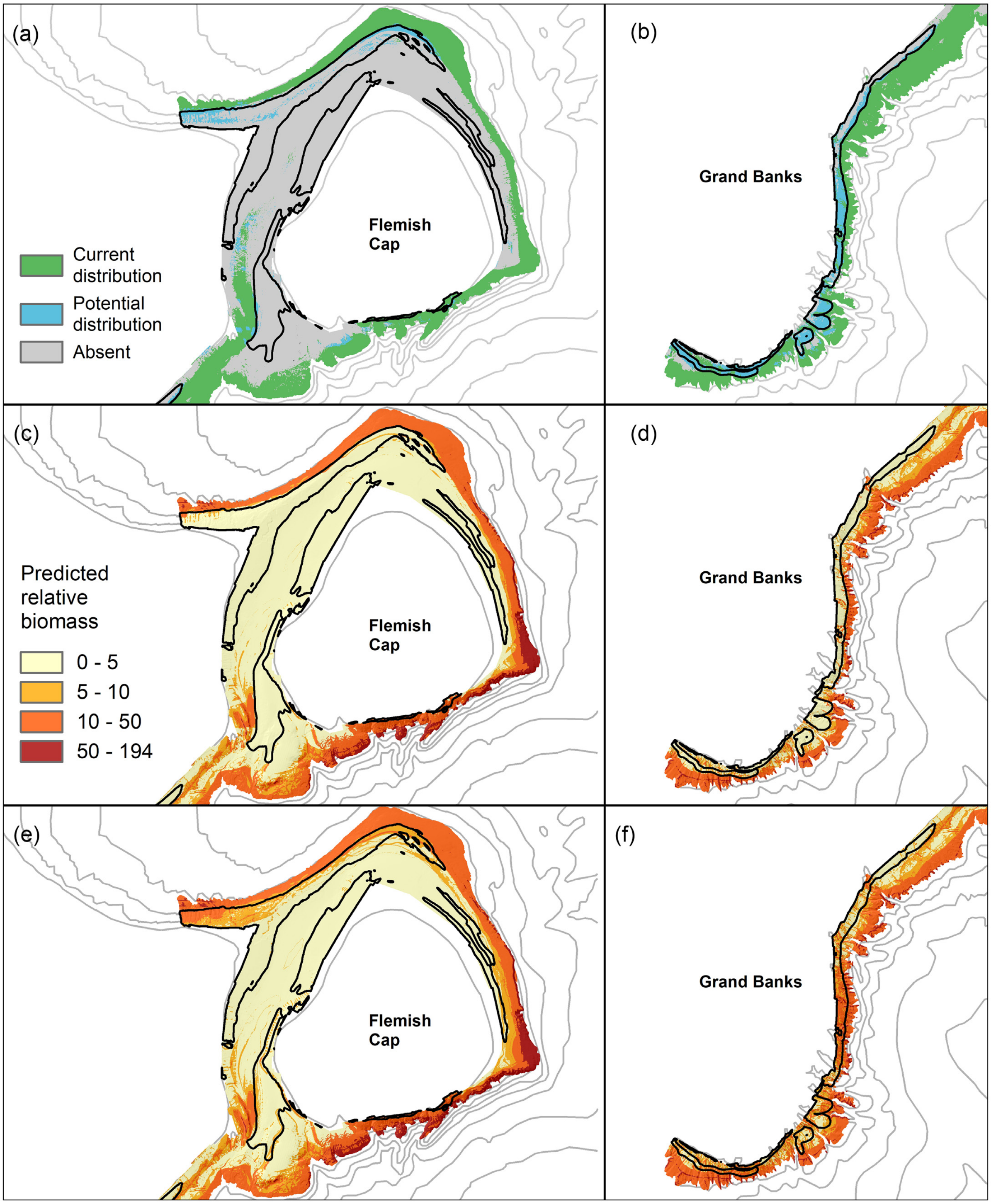

Figure 3. Predicted distribution around the Flemish Cap and the tail of the Grand Banks of *Geodia* spp. sponges for the current fishing scenario and the potential distribution under a scenario where fishing has not occurred (a and b), predicted biomass of *Geodia* spp. sponges for the current fishing scenario (c and d), and under a scenario where fishing has not occurred (e and f). The biomass values are based on square-root transformed biomass from trawls and rock dredge tows spanning more than the one pixel they are attributed to and are hence relative indicators of biomass only. Area encompassing 95% of the total bottom trawling fishery, as identified from VMS records, is shown outlined in black.

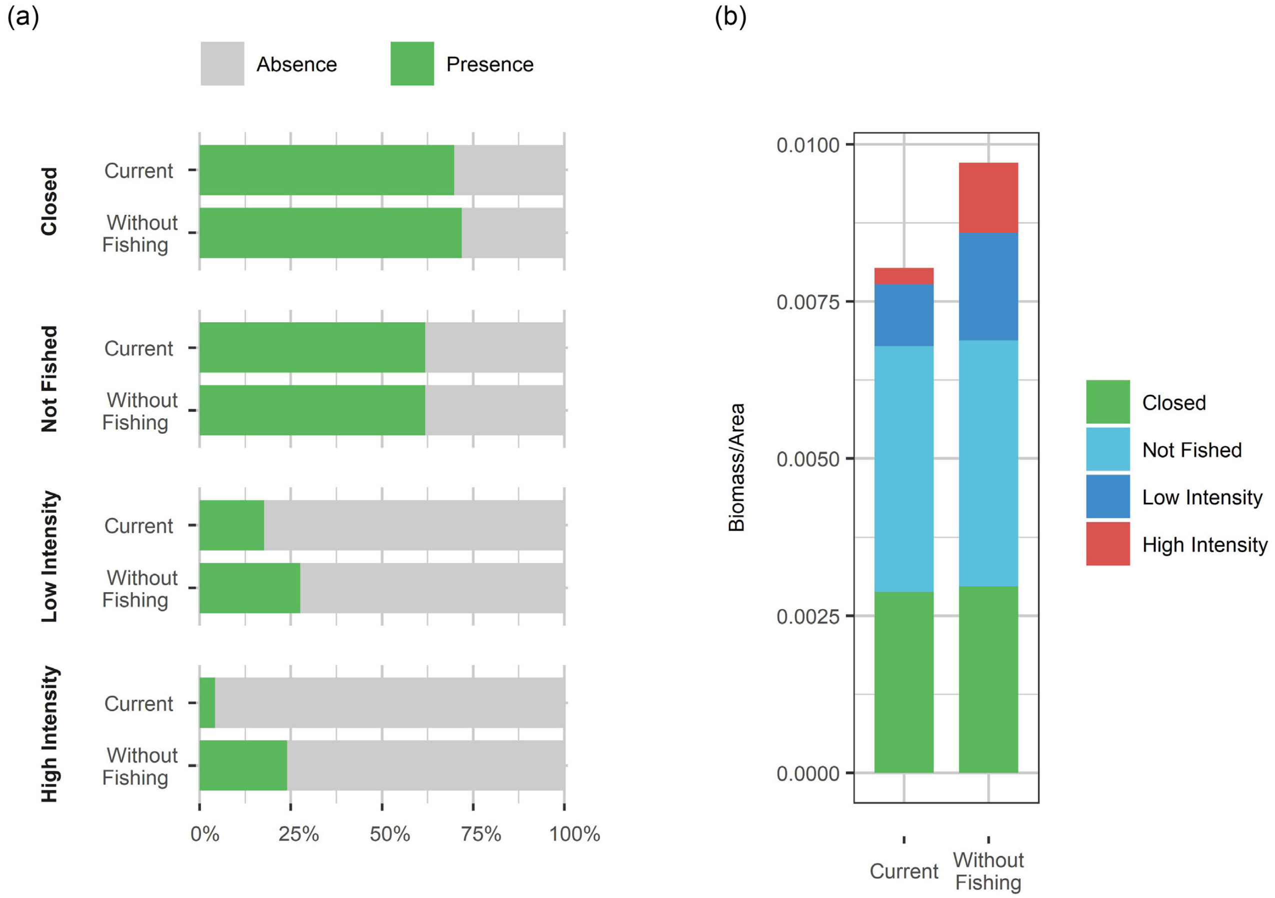

Figure 4. Predicted extent of habitat suitable for *Geodia* spp. sponges shown as percentage of the total area (a), and predicted biomass normalized to area (b) by area closed to bottom fishing, not currently fished and subject to low and high fishing intensities (lowest 5% of effort and 95% of effort, both in the current situation (FIP prediction), and under unfished conditions (ZPR prediction).

by Murillo *et al.* (2020). The impact of fishing in the form of potential removal rates of sponges in the fished part of the sponge habitat was also found to be high by Pham *et al.* (2019). Their study, conducted at broad scale, did not, however, include fishing effort as a model variable. This study has found that *Geodia* spp. sponges respond strongly to fishing intensity as a predictor of both presence and biomass and show improved modelling accuracy when impacted areas are removed from data, or alternatively, fishing intensity is included as a model predictive term. Taken together this suggests that fishing has a negative impact on the sponges, and that the sponge habitat in the area has been impacted by fishing activities. It must be noted that the negative correlation between sponge biomass and fishing activity could also stem from active avoidance of sponge grounds by fishermen or the fish targeted by the fishery as suggested by Murillo *et al.* (2020). A study investigating the use of VME habitat by fish in the study area showed that Greenland Halibut (*Reinhardtius hippoglossoides)*, a key target species of the bottom fishery in the study area, was part of the fish assemblage associated with sponge grounds based on both fish biomass and abundance (Kenchington *et al.*, 2013). Whilst avoidance by fishermen may account for the fishery not overlapping any of the area predicted to have very highest sponge biomass, there is overlap with potential habitat with lower biomass, suggesting that any avoidance behaviour by fishermen, if it exists, is likely limited to the known high biomass aggregations.

Our study is the first to use fishing pressure as a predictive term in habitat suitability modelling with the aim to predict a VME habitat baseline. Murillo *et al.* (2020) found fishing effort was strongly and negatively related to community diversity, represented by sample species density, when included as a model term, and excluding data from more intensively fished areas allowed a better fit of model. A total of two other studies have included a fishing related variable in models of VME distribution or abundance, finding no effect of fishing in their models. Rooper *et al.* (2014) used Generalised Additive Models (GAMs) to model presence–absence and abundance of corals and sponges. Their model included a variable stating whether the sample was from an area open to or closed to fishing. Miller *et al.* (2015) used Maxent to model the distribution of gorgonian corals, sea pens, and sponges including historical fishing effort data. They found weak relationships indicating gorgonian coral habitat quality was negatively related and sea pen and sponge habitat positively related to bottom trawling effort. The majority of the trawling took place outside predicted high quality gorgonian coral habitat, whilst the positive link between sponges and sea pens and fishing may reflect positive associations between these taxa and quality fishing grounds. The variable used by Rooper *et al.* (2014) does not indicate whether areas open to fishing are actively fished, whereas the model spatial resolution of 20 km used by Miller *et al.* (2015) was very coarse. It is possible that detailed and spatially accurate data on fishing, such as the high temporal resolution VMS data used in this study, is required to adequately assess the relationship between fishing and species distributions and abundance.

The study area has large sponge grounds characterized by the genus *Geodia* (Murillo *et al.*, 2012), one of the most well studied types of deep-sea sponges forming dense aggregations (Klitgaard and Tendal, 2004). Currently, aggregations of *Geodia* spp. sponges occur primarily outside fished areas. In studies investigating fisheries impact on the *Geodia* habitat, it has been found extremely vulnerable to bottom trawling suffering immediate declines through direct removal of sponges and further reductions in population densities due to delayed mortality after disturbance (Freese *et al.*, 1999; Freese, 2001). Use of the model including fishing pressure to project predictions to pre-fishing conditions enables the assessment of the effect fishing has historically had and identification of the part of the species' natural habitat that is currently impacted by the fishery.

Our study echoes the findings of Pham *et al.* (2019) that the sponge habitat has historically been impacted by bottom trawling and identifies areas where this has occurred. The presence and high biomass areas of *Geodia* spp. sponges predicted by the models generally agree with those identified by previous coarser scale models of probability of presence for Ostur grounds by (Knudby *et al.*, 2013) and co-occur with the concentrations of high biomass indicated by the kernel density analysis of Kenchington *et al.* (2014) and biomass model predictions by Pham *et al.* (2019). Highest biomass is predicted on the south-eastern and northern flanks of the Flemish cap and along the eastern flank of the Grand Banks at depths outside those currently fished.

The comparison of predictions of the *Geodia* spp. sponge model with fishing pressure (FIP) applied to the current conditions and to a theoretical no-fishing scenario, indicates that some of the currently unoccupied habitat becomes suitable under unfished conditions. The areas where higher biomass is predicted for unfished conditions include the north western-most part of the study area and the eastern flank of the Grand Banks. These sites could be considered as areas where recovery might be a possibility if fishing activities were discontinued. However, very little is known about the growth rates of deep-water sponges. Hoffmann *et al.* (2003) observed a weight increase of 40% within 1 year for *Geodia barretti* under laboratory conditions, lower than had previously been observed for shallow water species. On the other hand, the same authors stated that observations made of a specimen in the field over a 2-year period found no measurable change in size or shape suggesting *in-situ* growth rates could be very low. Similarly, Freese (2001) undertaking experimental trawling in the Gulf of Alaska on sponge and coral habitat observed that of 115 damaged sponges remaining within a trawl path, none showed signs of repair or regrowth 11 months post trawling. Using a statistical model, Rooper *et al.* (2011) suggested that intrinsic growth rates of structural sponges (including *Geodia*) in the Aleutian Islands were slow ($r = 0.107$ y-1). These authors found using these growth rates that a mortality of 67% of initial sponge biomass (the observed damage rate for bottom trawling on sponges by Freese *et al.* (1999) would result in recovery to 80% of the original biomass after 20 years in the absence of further damage or removals. This suggests that given the requirements for availability/transport of larvae are met, recovery at these sites may be possible but will likely take decades.

However, not all areas that are suitable habitat will be inhabited. Sponges have very slow dispersal due to larval attributes which tend to support local recruitment (Maldonado, 2006). Isolated areas with no known occurrences may be suitable habitat but have no current source of recruitment. Sponges are more likely to expand existing patches than establish new ones. In addition, sparser patches are more likely to be removed by the bottom fishery as fishermen are less likely to avoid them due to smaller risk of gear damage. Consequently, any historical damage, and potential recovery is likely to occur on the edges of aggregations. A recent study by Murillo *et al.* (2016) showed that sponge grounds have been present in the study area from ∼17 000 years before present. The areas where sponges are found have been very consistent across the time frame investigated. The study used the presence of sponge spicules in sections of sediment core with different ages to detect the presence of sponge aggregations. The study found no spicules in cores collected in fishing grounds, whilst most cores co-occurring with known high biomass aggregations showed evidence of sponge presence over a long time. A targeted study with cores across areas predicted to have higher biomass under unfished conditions could be useful to investigate whether the areas predicted as suitable for supporting sponge presence or higher biomass when fishing is removed have historically supported sponge populations.

Ecosystem based management endeavours to manage the marine environment as a whole, by allowing human activities to continue at levels that do not significantly harm the ecosystem functions. In this context, it is important to manage fisheries in a way that maximizes yields whilst sustaining ecosystem functions. Whilst fishing tends to occur in areas that support populations of VME taxa, VME have also been suggested to be essential for maintenance of some commercially important fish stocks (Baillon *et al.*, 2012; Miller *et al.*, 2012; Kenchington *et al.*, 2013) and damage caused to habitats may reduce the resilience of local fish populations (Miller *et al.*, 2012). Appropriate and reliable data on the distribution of VMEs are essential for the management of the interlinked habitat integrity and fishing yields. Effective spatial management requires information and the commitment of all parties to achieving a common goal. Data accuracy and availability as well as transparency between industry and conservation organizations are crucial to developing efficient collaborative management (Shelmerdine *et al.*, 2014; Wallace *et al.*, 2015). Current management practices for VME, such as the move-on rule, can in fact increase the impact by spreading fishing effort over a wider area (Auster *et al.*, 2010), where the distribution of VME is unknown.

In the absence of seabed survey data, habitat models provide the only source of information with which to objectively evaluate the likelihood of occurrence of VME. Models are also useful for linking acoustic data and point samples to extrapolate observations such as taxon abundance across the mapped area. Use of habitat suitability indices, with knowledge of the current pattern of fishing activity can provide a guide for optimal placement of spatial protection measures in previously unfished areas at risk from fisheries expanding if current fishing areas become depleted, leaving previously fished and sustainably impacted areas open to further fishing (Penney and Guinotte, 2013; Ardron *et al.*, 2014). Where management plans include the closure of areas that are already impacted by fisheries, a cost benefit analysis is required to identify whether recovery potential outweighs the benefits of continued fishing.

Our study has demonstrated a way to use all existing environmental and VME observation data together with a measure of fishing intensity to produce a more accurate picture of the current distribution of VME. This will support spatial management of the VME and local fisheries by allowing managers to identify the areas most at risk from expanding fisheries. Our methodology has the additional utility of being able to predict where the most likely historical damage caused by deep sea fisheries has occurred and the potential areas for habitat recovery on cessation of fishing activities.

Authors' contributions

A-LD and AK conceived the ideas and designed methodology; MS collated and advised on the data; A-LD analysed the data; KH and CBF provided expertise on deep sea ecology, A-LD, CBF, and KH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The data underlying this article were provided by Secretaría General del Mar (SGM) of the Ministerio de Medio Ambiente y Medio Rural Marino (Spain), Instituto Español de Oceanografía (Spain) and the Northwest Atlantic Fisheries Organization (NAFO) Secretariat by permission under the NEREIDA research programme consortium agreement. Data will be shared on a request to corresponding author with permission from the data owners.

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