

Mapping benthic ecological diversity and interactions with bottom-contact fishing on the Flemish Cap (northwest Atlantic)

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ABSTRACT

The ecological diversity of benthic invertebrates from bottom trawl surveys was mapped for the Flemish Cap, a plateau of ~200 km radius in the northwest Atlantic. Species density (SpD), the exponential Shannon diversity index ($e^{H'}$) and Heip's index of evenness (\bar{E}') were measured at different spatial scales. Continuous surfaces of each were created to 2000 m depth using predictive distribution models based on random forest (RF) algorithms. When fishing effort was included as an independent variable in the RF models, it was the most important predictor of sample SpD but unimportant in predicting $e^{H'}$ and only a minor predictor of \bar{E}' . In the absence of a historical baseline, we used a novel approach to evaluate spatial impacts of fishing on diversity by simulating and comparing spatial SpD prediction surfaces using response data associated with different levels of fishing effort. Although it is not possible to fully evaluate the precise nature of the impact of fishing on the ecological diversity, our models have identified Sackville Spur, Flemish Pass and south of Flemish Cap as the areas of greatest impact. Combining minimum bottom salinity, annual primary production range, fishing effort and biomass of sponges and small gorgonian corals, resulted in the best performing generalized additive model, explaining 73% of the total variance in SpD. Although current closures to protect vulnerable marine ecosystems from the adverse impacts of bottom fishing activities protect an important part of the ecological diversity associated with the deeper communities, unique and representative habitats on top of the Cap remain unprotected.

1. Introduction

The conservation of marine Biological Diversity of Areas Beyond National Jurisdiction (“BBNJ”) has become a high-profile international issue. In June 2015, the United Nations General Assembly (“UNGA”) adopted Resolution 69/292, calling for the development of an international, legally binding instrument under the United Nations Convention on the Law of the Sea, to address the conservation and sustainable use of BBNJ. While the governance framework has not yet been agreed, it is sure that there will be an increased need for scientific advice to support management of BBNJ, including the documentation of deep-sea biodiversity and how it may be impacted by human activities and by climate change.

Earlier UNGA resolutions have already led to protection for high-seas biodiversity associated with specific habitats. States and regional fisheries management organizations and arrangements (“RFMO/As”) have engaged in a process to identify vulnerable marine ecosystems (“VMEs”) and to protect them from destructive fishing practices through implementation of UNGA Resolution 61/105, of 2006, and subsequent resolutions – both those and their supporting implementation guidelines (FAO, 2009) stressing the value of the biodiversity within VMEs. In particular, the Northwest Atlantic Fisheries Organization (“NAFO”) has closed six seamount complexes and 15 areas on and around Flemish Cap and on the high-seas portion of Grand Bank (in the NAFO Regulatory Area: “NRA”) to protect deep-sea coral and sponge VMEs from impacts by bottom-contact fishing gears (NAFO,

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2017a), although one of those areas was re-opened to fishing in January 2019 pending reassessment in 2020. In the NRA, as elsewhere, the structure-forming mega-epibenthic species increase the number of potential niches and are therefore associated with higher species richness (Klitgaard, 1995; Buhl-Mortensen et al., 2010; Beazley et al., 2013; Beazley et al., 2015). However, VMEs contain only a subset of benthic biodiversity and some RFMO/As have broader conservation mandates. For example, the NAFO Convention on Cooperation in the Northwest Atlantic Fisheries includes commitments to the conservation of marine biodiversity in general, and to minimizing the risk of long term or irreversible, adverse effects of fishing activities (NAFO, 2017b), requiring attention to biodiversity outside the VMEs.

The distribution of benthic species is known to be influenced by abiotic factors such as depth (Carney, 2005; Rex et al., 2006), food availability (Carney et al., 1989), water mass characteristics (Hargrave et al., 2004; Beazley et al., 2015; Kenchington et al., 2017; Roberts et al., 2018) and substrates (Hargrave et al., 2004; Edinger et al., 2011), many of which are correlated with one another and act on different temporal and spatial scales (McClain et al., 2008). Spatial modelling based on environmental variables correlated to those abiotic factors can be used to interpolate between benthic sampling stations, producing maps of biodiversity in support of management decisions.

Spatial modelling to predict species richness has been commonly applied in both terrestrial (Steinmann et al., 2009; Nielsen et al., 2013) and marine (Campbell et al., 2011; Jenkins and Van Houtan, 2016) environments, most often using regression techniques. Recently, tree-based models, such as boosted regression trees (Friedman, 2002) and random forests (Breiman, 2001), which have been shown to out-perform other modelling techniques (Benito et al., 2013; Alabia et al., 2016), have been used to model diversity in both terrestrial (Revermann et al., 2016; Divíšek and Chytrý, 2018) and marine (Edgar et al., 2017) systems. Tree-based models allow fitting complex non-linear relationships between response and predictor variables by considering predictors sequentially, and thus inclusion of interactions without their explicit specification. Additionally, interpolated values are averaged between the observations, avoiding prediction of values beyond the maximum or minimum observed (Breiman, 2001). However, interpretation of maps of biodiversity must recognize that diversity metrics are scale-dependent (Tews et al., 2004). Further, species richness is constrained by the distribution and occupancy-saturation of the number of niches available, limiting the number of species that can co-exist locally (Beaugrand et al., 2018). Interpretation of observed patterns, especially recognition of anthropogenic effects, requires both an understanding of local biodiversity capacity and selection of appropriate spatial scales for assessment.

In the NRA, Murillo et al., 2016a identified 288 benthic invertebrate taxa, drawn from 11 phyla, in the catches of an extensive trawl survey of Flemish Cap. They found seven significantly different epibenthic assemblages between 138 and 1488 m depth. The present study uses the same data set to quantify the diversity of those assemblages at different spatial scales and to map benthic diversity across the bank, using environmental predictors in random-forest models. We review the effectiveness of NAFO's current closed areas for protecting diversity; identify and evaluate the abiotic and biotic environmental conditions associated with the observed patterns; and examine the impact of fishing practices on ecological diversity. This work demonstrates how diversity indicators can be transformed into direct application for fisheries management purposes to achieve policy objectives.

2. Material and methods

2.1. Study area

Flemish Cap is an isolated bank on the continental margin off Newfoundland, with a minimum depth of 122 m, and entirely in the high seas (Fig. 1A). It is considered both a bioregion and an ecosystem

production unit, based on analyses of a suite of physiographic, oceanographic and biotic variables (NAFO, 2015a), while it is treated as a discrete unit, NAFO Division 3M, for management of bottom fisheries. There are steep slopes to the east and south, below 1000 m depth, but more gradual gradients to the north and west. The Cap is separated from Grand Bank by the Flemish Pass, a 1200 m deep, saddle-shaped, mid-slope channel. Flemish Cap is influenced by two major ocean currents: the Labrador Current (LC), flowing from the north, and the North Atlantic Current (NAC), which represents the bulk continuation of the warm Gulf Stream (Stein, 2007). Flemish Cap has warmer waters than Grand Bank (Colbourne and Foote, 2000).

The Cap has been fished with other trawls since the 1950s for cod (*Gadus morhua*), redfish (*Sebastes* spp.) and American plaice (*Hippoglossoides platessoides*) and, more recently, also for Greenland halibut (*Reinhardtius hippoglossoides*) and shrimp (*Pandalus borealis*). Those species have shown major changes in abundance in recent decades (Pérez-Rodríguez et al., 2012) – most notably a collapse of cod and American plaice biomass during the early 1990s, with a simultaneous increase in shrimp abundance, the spreading of Greenland halibut onto the Cap and an increase in redfish. Since 2005, four of the five species have reverted towards their former abundance, only American plaice remaining depleted (Vazquez, 2012). In 2010 the cod fishery was reopened and in 2011 the shrimp fishery was closed. At present, three different fisheries on Flemish Cap target, respectively, Greenland halibut, redfish and cod (NAFO, 2017c).

2.2. Data sources

2.2.1. Benthic data

Records of the invertebrate epibenthos were drawn from the catches of the 2007 EU Flemish Cap bottom-trawl survey, conducted by the *Instituto Español de Oceanografía* together with the *Instituto de Investigaciones Marinas* and the *Instituto Português do Mar e da Atmosfera*. The survey sampled all of the trawlable area of Division 3M between 138 and 1488 m depth, including the Cap and the eastern side of Flemish Pass, following a depth-stratified random sampling design. It was conducted on board the Spanish research vessel *Vizconde de Eza*, with standardized sets of a Lofoten bottom trawl, which swept ≈ 0.04 km² each set. A total of 177 valid trawl sets, 176 with presence of benthic invertebrate fauna, were included in the analyses. The start position of each set was used as its location for modelling and mapping.

Murillo et al., 2016a provided details of sample processing and species identifications. In brief: all non-encrusting invertebrates other than cephalopods and pelagic shrimps were extracted from the trawl catches and identified to the lowest possible taxon, 285 discrete taxa being recorded, and the biomass (wet weight) for each was determined.

2.2.2. Environmental data

Seven environmental variables and 48 summary statistics of 15 other variables, derived from different sources and with varying spatial resolutions, were used in the modelling as predictor map layers (Table 1). The variables were chosen based on availability of data and assumed relevance to the distribution of benthic fauna. They included measures associated with food supply, depth, water mass and substrate. Minima, maxima and ranges of variables were calculated by taking the annual minimum, maximum and range at each location and averaging across years (Guijarro et al., 2016).

Depth was obtained from the Canadian Hydrographic Service Atlantic Bathymetry Compilation and was available for the entire spatial extent. Slope, and two measures describing its orientation (“easterness” and “northernness”) were derived from the depth raster projected in NAD 1983 UTM Zone 23N coordinate system using the ‘Slope’ tool in ArcMap’s Spatial Analyst toolbox for the former and the ArcGIS Benthic Terrain Modeler (Wright et al., 2012) for easternness and northernness. Sediment variables, obtained from Geological Survey of Canada records (Murillo et al., 2016a), together with the remaining

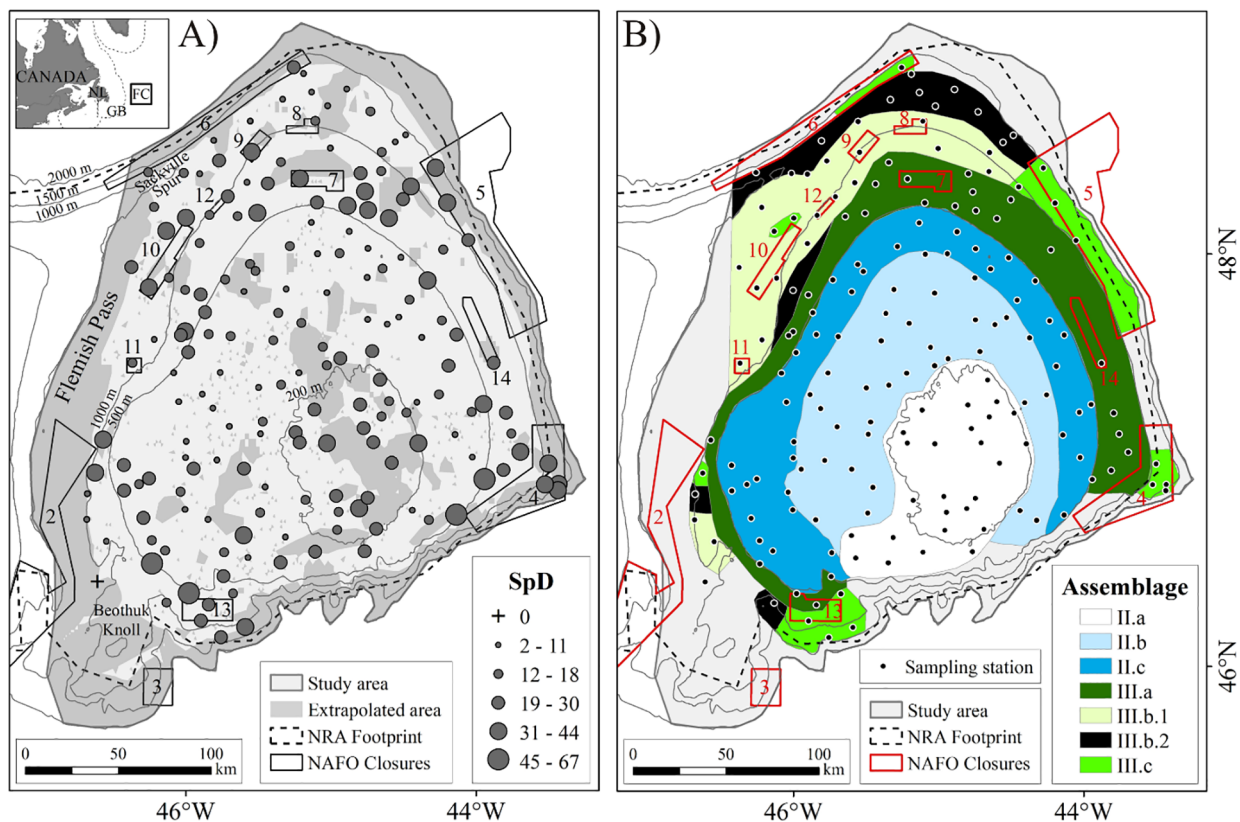


Fig. 1. A) Map showing the number of benthic invertebrate species (sample SpD) recorded from the catch of each survey set (modified from Murillo et al., 2016a). Areas closed to bottom fishing activities to protect sponge and coral concentrations and existing bottom fishing areas (NRA Footprint) are also indicated. The closed-area numbers are those used by NAFO (2017a). Area 14 was re-opened to fishing in January 2019 (NAFO, 2019) pending reassessment in 2020. Bathymetric contours were obtained from the Canadian Hydrographic Service. FC, Flemish Cap; GB, Grand Bank; NL, Newfoundland (inset). B) Map showing the location of the 7 epibenthic megafaunal assemblages identified by Murillo et al., 2016a.

variables were spatially interpolated across the study area using ordinary kriging in ArcMap 10.2.2 (ESRI, 2011), following Gujjarro et al. (2016). Each of the 55 predictor layers had a cell size $\approx 0.013^\circ$ (≈ 1 by

1.4 km horizontal resolution).

Additional depth derivatives, including ruggedness and Bathymetric Position Index, were used in preliminary runs of the models but their

Table 1

Environmental variables and summary statistics used as predictor map layers in the RF models (Max: maximum; Min: minimum; lat: latitude; long: longitude; CHS_ABC: Canadian Hydrographic Service Atlantic Bathymetry Compilation; BNAM: Bedford Institute of Oceanography North Atlantic model (Wang et al., 2017); GSC: Geological Survey of Canada; RSU-BIO: Remote Sensing Unit at the Bedford Institute of Oceanography).

| Variable | Metric | Unit | Native Resolution | Source |
|---------------------------|-----------------------|---------------------------|-------------------|---------|
| Depth | | m | 15" lat/long | CHS_ABC |
| Slope | | degrees | 15" lat/long | CHS_ABC |
| Easternness | | N/A | 15" lat/long | CHS_ABC |
| Northernness | | N/A | 15" lat/long | CHS_ABC |
| Bottom salinity | Max, Mean, Min, Range | N/A | 1/12" lat/long | BNAM |
| Bottom temperature | Max, Mean, Min, Range | C | 1/12" lat/long | BNAM |
| Bottom current speed | Max, Mean, Min, Range | $m\ s^{-1}$ | 1/12" lat/long | BNAM |
| Bottom shear | Max, Mean, Min, Range | Pa | 1/12" lat/long | BNAM |
| Gravel and coarse sands | Percentage | % | 1-32 km* | GSC |
| Medium and fine sands | Percentage | % | 1-32 km* | GSC |
| Mud | Percentage | % | 1-32 km* | GSC |
| Surface salinity | Max, Mean, Min, Range | N/A | 1/12" lat/long | BNAM |
| Surface temperature | Max, Mean, Min, Range | $^\circ C$ | 1/12" lat/long | BNAM |
| Surface current speed | Max, Mean, Min, Range | $m\ s^{-1}$ | 1/12" lat/long | BNAM |
| Fall Mixed Layer Depth | Max | m | 1/12" lat/long | BNAM |
| Winter Mixed Layer Depth | Max | m | 1/12" lat/long | BNAM |
| Spring Mixed Layer Depth | Max | m | 1/12" lat/long | BNAM |
| Summer Mixed Layer Depth | Max | m | 1/12" lat/long | BNAM |
| Fall Primary Production | Max, Mean, Min, Range | $mg\ C\ m^{-2}\ day^{-1}$ | 9 km | RSU-BIO |
| Spring Primary Production | Max, Mean, Min, Range | $mg\ C\ m^{-2}\ day^{-1}$ | 9 km | RSU-BIO |
| Summer Primary Production | Max, Mean, Min, Range | $mg\ C\ m^{-2}\ day^{-1}$ | 9 km | RSU-BIO |
| Annual Primary Production | Max, Mean, Min, Range | $mg\ C\ m^{-2}\ day^{-1}$ | 9 km | RSU-BIO |

*native resolution of the points used to create the interpolated sediment layers ranged between 1 and 32 km with a mean (\pm SD) of 10 ± 6 km.

inclusion did not improve model performance, while they led to an irregular (and apparently spurious) pattern of species density.

2.2.3. Fishing effort data

The benthic community on Flemish Cap has been exposed to fishing pressure for a long time; hence this chronic disturbance could have had an impact on benthic diversity patterns and species distributions prior to our sampling in 2007. For Division 3M, landings have been recorded from the beginning of intensive trawling but capture locations are generally only known at the scale of the bank. Higher-resolution data, derived from satellite monitoring systems (VMS), are available for the period after 2002. Although the data for 2003–07 have been mapped (NAFO, 2009), they only provide vessel locations at two-hour intervals, while the fisheries of those years exploited the resources available after the major ecosystem shift of the early 1990s, resulting in an emphasis on shrimp trawling. However, in recent years the reopening of the cod fishery and the moratoria on shrimp has steered current fishing patterns that resemble historical fisheries, and since 2008, vessels fishing in the NRA have been equipped with VMS that transmits position, heading and speed every hour. The resulting data post-date the 2007 survey but are here taken to represent the long-term spatial distribution (not the intensity) of fishing effort on Flemish Cap during the preceding six decades, hence a chronic disturbance affecting the mapped benthic diversity. From 1960 to 2006, redfish, cod and shrimp comprised, respectively, 32.9%, 31.4%, and 21.8% of the total reported landings from Division 3M (excluding pelagic species), whereas during 2008–14, they represented 32.7%, 32.1%, and 12.5% (NAFO STATLANT 21A database: <https://www.nafo.int/Data/STATLANT/>), indicating broadly similar targeting of fishing effort and, by implication, also similarity in its fine-scale spatial distribution. In contrast, the 2003–07 landings were 10.9% redfish, 0.1% cod and 78.7% shrimp, each of the first two including bycatches taken by the shrimp fishery. Confidence in the 2008–14 data as a representation of the long-term distribution of fishing effort may be increased through its similarity to maps prepared by NAFO (2009) which summarized activity in the NRA from 1987 to 2007, as a foundation for delineation of a fishing “footprint”, based on information provided by NAFO member states and drawn from various sources.

Following NAFO (2015b), the VMS data from 2008 to 14 were filtered to exclude records with vessel speed > 5 knots, trawlers moving more slowly being assumed to be fishing, and mapped as annual average fishing effort (in vessel hours) per square kilometre, at the spatial resolution of the environmental layers and trimmed to the spatial extent of the latter. The resulting map (Fig. 2) was used as a predictor layer in the models to allow assessment of the relationship between fishing impacts and benthic biodiversity.

2.3. Analysis

2.3.1. Biodiversity metrics

Diversity metrics were quantified based on the biomass data and, with one exception, following the recommendations of Kenchington and Kenchington (2013). Because the data were derived from the catches taken by standard units of sampling effort, not from collections that each contained a standard number of specimens, the count of species present in the catch from each set was a species density (SpD), rather than a species richness. In contrast to sample richness, sample SpD is not independent of the overall abundance of the catch, though asymptotic values of community richness and SpD are numerically equal (Gotelli and Colwell, 2001; Kenchington and Kenchington, 2013).

Hence, SpD, the exponential Shannon index ($e^{H'}$) and Heip's index of evenness (\bar{E}') were determined, both as measures of sample diversity, for each survey set, and as community diversities, for each of the assemblages (Fig. 1B) and regional-scale faunal groups defined by Murillo et al., 2016a, as well as for the current NAFO closures (as a combined unit) and for the whole of Flemish Cap. SpD was calculated using the

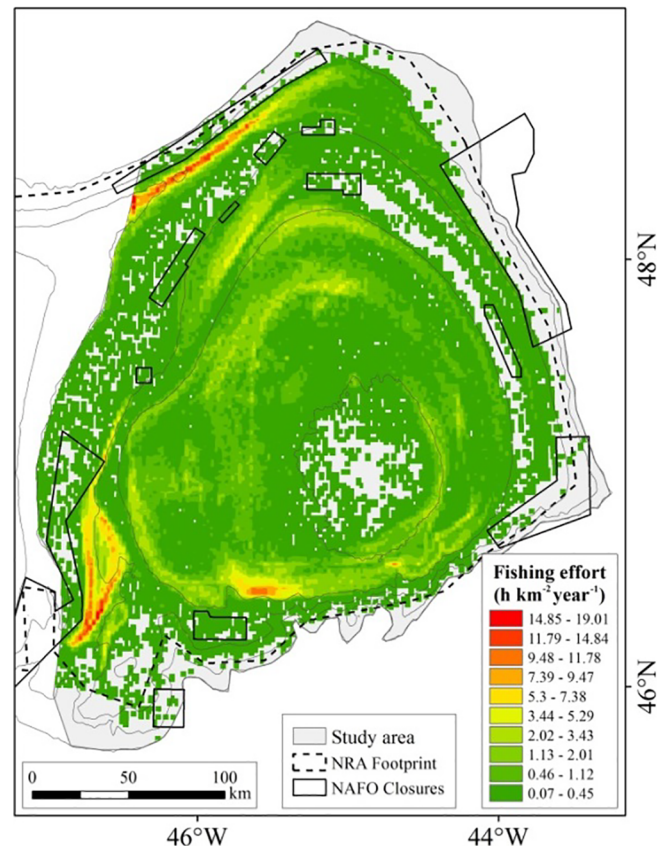


Fig. 2. Map showing annual average fishing effort between 2008 and 2014, as hours of fishing per square kilometre per year, modified from NAFO (2015b).

Chao2 estimator (Chao, 1987; Chiu et al., 2014) in the ‘vegan’ package (Oksanen et al., 2018) from the statistical computing software R 3.5.1 (R Core Team, 2018), and H' estimated using Zahl's jackknife method (Zahl, 1977) described in Heltshe and Forrester (1983). The appropriate entropy diversity measure for a single sample is Brillouin's H (Pielou, 1975; Kenchington and Kenchington, 2013) but that can only be applied to abundance data, Kenchington and Kenchington (2013) suggestion to the contrary notwithstanding, since its use with biomasses leads to values that are dependent on the chosen weight unit. Thus, we used sample H' in determining community H' and both sample and community $e^{H'}$. Throughout, the taxocene was defined as non-encrusting benthic invertebrates vulnerable to capture by the Lofoten bottom trawl.

2.3.2. Random forest modelling

We mapped sample SpD, $e^{H'}$ and \bar{E}' using regression random forest (RF) modelling (Breiman, 2001) using the ‘ranger’ package (Wright et al., 2019) in R. We used 5000 regression trees and default values for the rest of the RF parameters ($mtry$ = square root (rounded down) of explanatory variables and $nodesize$ = 5). RF modeling was performed separately using only the 55 environmental measures as predictors (Table 1) and using those plus the fishing-effort layer (Fig. 2) (56 predictors). Prediction and standard error surfaces were created for each biodiversity metric. Standard error of the predictions were estimated taking the arithmetic mean between the jackknife and infinitesimal jackknife for bagging in order to calculate an unbiased estimate of the variance statistic of the predicted mean of several random forest predictions (Wager et al., 2014). Areas of extrapolation were also identified and mapped (Fig. 1A). Goodness-of-fit of each model was evaluated by R^2 , calculated using 10-fold cross-validation repeated 10 times. Variable importance measures and partial dependence plots were created to aid ecological interpretation of the models.

Table 2

RF models of SpD based on different subsets of benthic diversity data, corresponding to different maximum levels of fishing disturbance.

| RF Model | Number of survey sets | Annual average fishing effort | Rationale |
|----------|-----------------------|--|---|
| 0 | 177 | < 20 h km ⁻² year ⁻¹ | Uses all available data |
| 1 | 165 | < 2h km ⁻² year ⁻¹ | Excludes areas of most intense fishing effort |
| 2 | 147 | < 1h km ⁻² year ⁻¹ | Inflection point in fitted relationship between observed SpD and fishing effort, see Fig. 3 |
| 3 | 112 | < 0.4 h km ⁻² year ⁻¹ | Value below which observed SpD increases with declining fishing effort |
| 4 | 69 | < 0.15 h km ⁻² year ⁻¹ | Point at which fitted relationship between SpD and fishing effort crosses mean observed SpD, see Fig. 3 |

2.3.3. Fishing interactions

The predictive maps of diversity, derived from the RF model based on the 55 environmental predictors, were overlain with the fishing effort layer. Paired values of predicted diversity and effort were extracted for each diversity metric and every mapped location. Bivariate plots of each predicted and observed diversity metric against average annual fishing effort were constructed. Kendall rank correlation coefficients (τ) were calculated between the observed values of the diversity metrics, for each survey set, and the fishing effort in the corresponding map cell.

To examine the extents and locations of fishing impacts on diversity, we constructed four additional predictive models of SpD (designated “RF Models 1 to 4”), based on the 55 environmental predictors and restricted subsets of the SpD values data that excluded survey sets made in areas with high fishing effort. Threshold fishing intensities for data inclusion in the four models (Table 2) were selected from the relationship between SpD and fishing effort fit with a LOESS smoother (Fig. 3). The resulting predictive map of SpD was compared with that from the base model using only the 55 predictors (for this purpose designated “RF Model 0”) and the differences mapped.

2.3.4. Drivers of benthic diversity

The RF models were supplemented with General Additive Models (GAMs) to further explore the drivers of sample observed SpD. The GAMs were based on the negative binomial distribution and built using the ‘mgcv’ package (Wood, 2006) in R.

The independent variables in GAM 1 comprised a subset of the 56 predictors (including fishing effort) after deletion of those which were correlated, with Spearman’s rank correlation coefficient (ρ) ≥ 0.5 , to produce an interpretable model and reduce the effect of collinearity (Graham, 2003). Model selection followed a forward, stepwise variable-selection approach, starting with the independent variable with highest importance from the base RF Model. The most parsimonious GAM was selected, following the Akaike information criterion (AIC; Akaike, 1973). GAMs 2 and 3 examined the effects on SpD of structure-forming

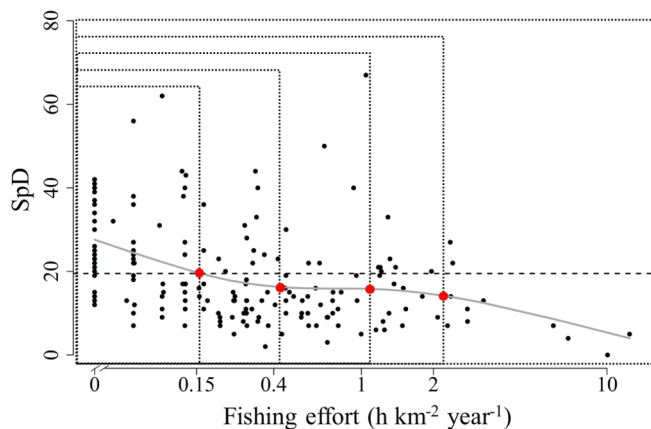


Fig. 3. Scatter plot of sample species density (SpD) against annual average fishing effort (in h km⁻² year⁻¹, plotted on a logarithmic scale, with zero offset). The solid line through the data is a LOESS smoother (LOESS span of 0.75), whereas the horizontal dashed line indicates the mean sample SpD. Dashed boxes encapsulate the sets used in RF Models 0 to 4 respectively.

epibenthos, here defined as those considered by NAFO (2017a) to be VME indicators (*viz.* sponges, sea pens, large gorgonian corals and small gorgonian corals), plus black corals and soft corals. Exploratory analysis showed two patterns in the relationship between SpD and sponge biomass, one driven by the hexactinellid *Asconema foliata* and the other by the remaining sponges. *A. foliata* was therefore considered separately. For each of those seven groups, the biomass taken by each survey set was logarithmically transformed following the procedure outlined in McCune and Grace (2002). GAM 2 used the seven transformed biomasses as independent variables, while GAM 3 used both those and the environmental and fishing variables included in GAM 1. In each model, the dependent variable comprised new sample SpDs calculated from a subset of the catch data that excluded species of corals and sponges belonging to the groups represented among the independent variables. Results from GAM 1 with the new sample SpDs (for this purpose designated “GAM 1A”) were compared with a model using the same predictors but with sample observed SpD (including all taxa) as the dependent variable (“GAM 1B”).

3. Results

3.1. Biodiversity mapping

3.1.1. Sample diversity

SpD in the catches of individual survey sets varied between 0 and 67 (Fig. 1). Predicted SpD was highest on the southeastern side of the Flemish Cap, in and near Closed Area 4, and in a ring around the Cap between 500 and 800 m depth, including near Closed Areas 7 and 13 (Fig. 4A). Relatively high values were also observed elsewhere, including on the shallow top of the Cap and in parts of the Flemish Pass. The RF model also predicted high SpD values in deep water to the south of the Cap where data were not available (area of extrapolation, Fig. 1A). Minimum predicted values of SpD were found between 200 and 500 m depth, north of Flemish Cap and south of Flemish Pass. Higher standard error of predicted SpD was found along the southeast of the Cap, at around 500 and 600 m depth, as well as south of Flemish Pass (Fig. 4D). ‘Maximum bottom salinity’ was the most important predictor for SpD followed by ‘Minimum surface salinity’ and ‘Depth’ (Fig A1A). An increase in SpD was observed at maximum bottom salinity above 34.90, reaching maximum values around 34.92 (Fig A1D).

$e^{H'}$ of individual catches varied between 1.11 and 13.86. Predicted values were highest on the top of the Cap and in the Pass (Fig. 4B) although they were associated with a high standard error there (Fig. 4E). Higher values were also found on the south of the Cap, below 700 m depth. Different statistics of bottom temperature were the top four important predictors for $e^{H'}$ (Fig A1B). An increase in $e^{H'}$ was observed when the ‘Range bottom temperature’ was higher than 0.5 °C (Fig A1E).

\bar{E}' varied between 0.003 and 0.845. Predicted values were high in a ring around the Cap between 300 and 450 m depth (Fig. 4C). Higher values were also found in the southern part of the Pass, near Closed Area 2 and Beothuk Knoll, as well as in the northeast of the Cap, where they were associated with higher standard error (Fig. 4F). Depth was the most important predictor for \bar{E}' (Fig. A1C), showing higher values associated with shallow (< 400 m) and deep (\approx > 1300 m) bottoms (Fig. A1F).

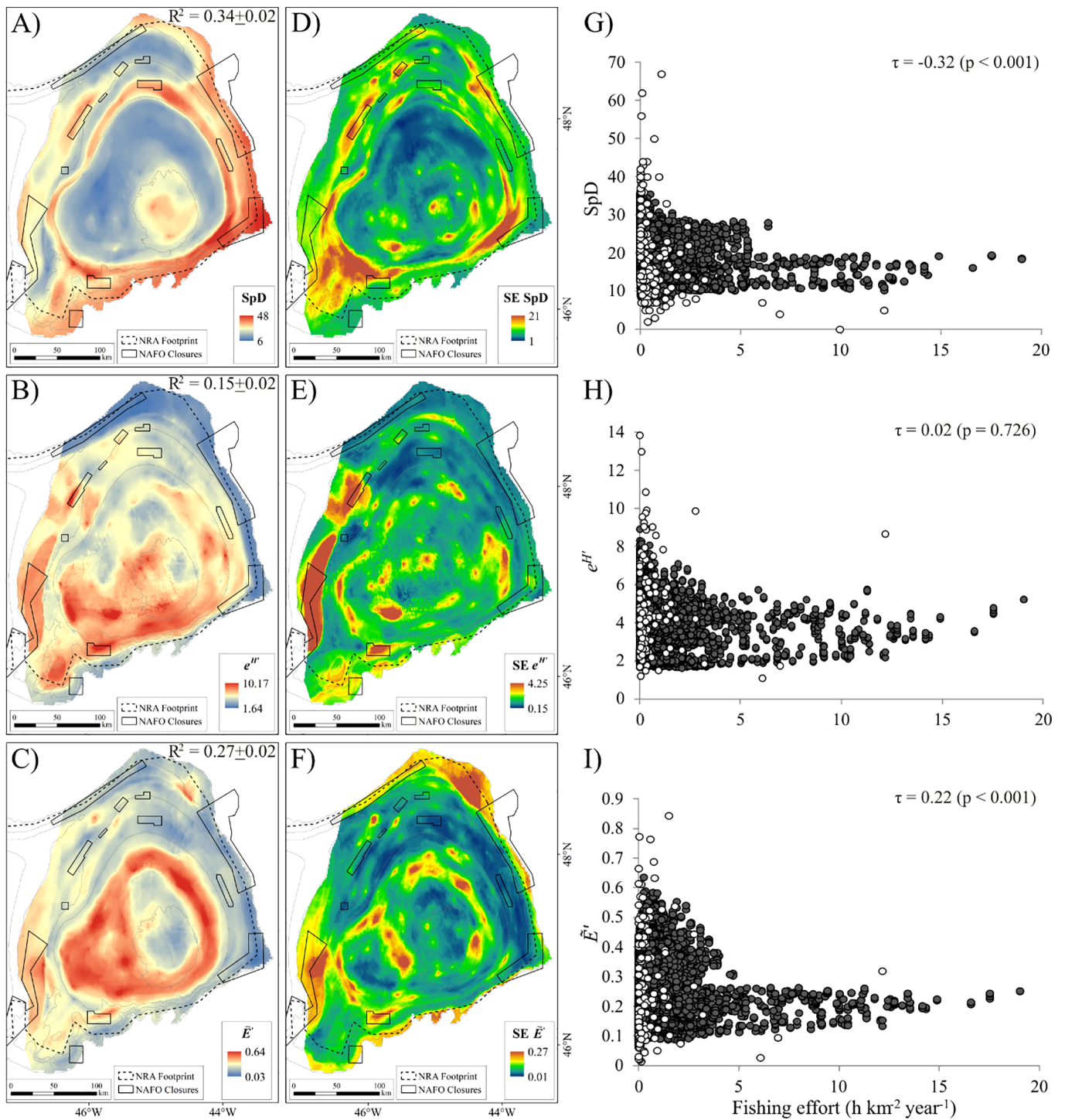


Fig. 4. A–C) Predicted maps and R^2 from random forest modelling of (A) sample SpD, (B) sample e^H and (C) \bar{E} . D–F) Standard error (SE) associated with each predicted surface. Note that fishing effort was not included as predictor in these models. G–I) Bivariate plots of corresponding metric against average annual fishing effort. White dots: observed values of metric; Grey dots: predicted values. Kendall correlation coefficient (τ) between observed values of each metric and fishing effort are indicated, with their probabilities.

3.1.2. Community diversity

Species density curves (not shown) for each of the seven assemblages defined by Murillo et al., 2016a, for their large-scale faunal groups, for the entire study area and for the NAFO closed areas all failed to reach clear asymptotes. Chao2 estimates of the number of species for each of these groups are available (Table 3). Those were high for the deep-sea coral assemblage (III.a), the shallow assemblage (II.a) and the deep-sea sponge assemblage (III.c), and lowest for the impoverished

lower slope assemblage (III.b.2). An asymptotic value (261), numerically equal to species richness, could only be determined for the Deep Flemish Cap large-scale group. e^H was high for the 300–500 m (II.c) and lower slope (III.b.1) assemblages, where it was associated with moderate values of \bar{E} . Elsewhere, evenness was low and e^H drawn down in consequence. Mean benthic biomass in the survey catches was very high in the deep-sea sponge assemblage (III.c), where fishing effort was very low, and relatively high in the coral assemblage (III.a).

Table 3

Synoptics for each of the assemblages and major large-scale faunal groups defined in Murillo et al., 2016a, for all Flemish Cap and for the combination of areas closed to bottom fishing activities by NAFO to protect sponge and coral concentrations (NAFO, 2017a). N: number of survey sets; SpN: number of species observed; $e^{H'}$: exponential Shannon diversity index; \bar{E}' : Heip's index of evenness using the Chao2 estimates; Fishing effort: average of the mapped average annual fishing efforts (in $\text{h km}^{-2} \text{ year}^{-1}$) at the locations of the N survey stations; SE: standard error. The NAFO closures included in each assemblage or faunal group are indicated, using the closure numbers of NAFO (2017a).

| Assemblage | Depth range (m) | N | SpN | Chao2 estimates \pm SE | $e^{H'} \pm$ SE | \bar{E}' | Average biomass in catch (kg) \pm SE | Fishing effort \pm SE | Closures |
|---------------|-----------------|-----|-----|--------------------------|------------------|------------|--|-------------------------|-------------|
| II.a | 138–335* | 28 | 127 | 189 \pm 26 | 11.27 \pm 0.13 | 0.054 | 0.95 \pm 0.23 | 0.45 \pm 0.13 | – |
| II.b | 171–329 | 32 | 76 | 118 \pm 21 | 10.88 \pm 0.07 | 0.084 | 0.52 \pm 0.11 | 0.45 \pm 0.06 | – |
| II.c | 298–490 | 38 | 119 | 164 \pm 19 | 20.55 \pm 0.09 | 0.120 | 0.95 \pm 0.17 | 0.65 \pm 0.10 | – |
| III.a | 416–970 | 29 | 168 | 200 \pm 12 | 12.47 \pm 0.11 | 0.058 | 6.14 \pm 1.24 | 0.42 \pm 0.13 | 4, 7, 14 |
| III.b.1 | 828–1190 | 19 | 86 | 120 \pm 15 | 20.73 \pm 0.24 | 0.166 | 2.72 \pm 0.81 | 0.85 \pm 0.36 | 8–12 |
| III.b.2 | 907–1442 | 14 | 51 | 107 \pm 30 | 3.42 \pm 0.08 | 0.014 | 0.83 \pm 0.21 | 1.85 \pm 0.92 | – |
| III.c | 673–1370 | 16 | 142 | 168 \pm 11 | 1.48 \pm 0.02 | 0.003 | 408.76 \pm 191.76 | 0.06 \pm 0.02 | 4, 5, 6, 13 |
| Major group | | | | | | | | | |
| II | 138–500 | 98 | 181 | 258 \pm 29 | 20.44 \pm 0.03 | 0.076 | 0.81 \pm 0.10 | 0.53 \pm 0.06 | – |
| III | 500–1488 | 78 | 232 | 261 \pm 11 | 1.75 \pm 0.01 | 0.003 | 86.94 \pm 42.62 | 0.71 \pm 0.20 | 3–14 |
| Flemish Cap | 138–1488 | 176 | 285 | 326 \pm 15 | 1.85 \pm 0.003 | 0.003 | 38.98 \pm 28.69 | 0.61 \pm 0.14 | 3–14 |
| NAFO Closures | 638–1370 | 16 | 155 | 201 \pm 16 | 1.47 \pm 0.016 | 0.002 | 403.97 \pm 192.40 | 0.04 \pm 0.02 | 3–14 |

*One set included in assemblage II.a is located at 538 m depth at the southeast of the Cap.

The shallow (II) and deep (III) communities on Flemish Cap showed similar Chao2 estimates. However, the large biomass of sponges taken at some deep survey stations depressed evenness of the deep community, drawing down $e^{H'}$.

The NAFO closed areas on Flemish Cap are estimated to contain species representing over 60% of the community SpD estimated for the whole of Flemish Cap. Community-scale $e^{H'}$ for the combination of those closed areas was nearly 80% of that for the whole of Flemish Cap and evenness was similar for both (Table 3).

3.2. Fishing interactions

When fishing effort was included as an independent variable in the RF models, it was the most important predictor of sample SpD but unimportant in predicting $e^{H'}$ and only a minor predictor of \bar{E}' (Fig. A2). The prediction surfaces and R^2 values differed little (Figs. 4 and A3), though predicted sample SpD was higher in Closed Areas 2 and 6 when fishing effort was included.

When the diversity metric surfaces, predicted from the 55 environmental measures, were matched with the fishing effort layer, the latter had a significant negative relationship with sample SpD (Fig. 4G) but positive relationships with $e^{H'}$ and \bar{E}' , the first being non-significant (Fig. 4H and 4I). High values of SpD were only seen where fishing effort averaged $< 5 \text{ h km}^{-2} \text{ year}^{-1}$. Most of the more-intensive fishing occurred in areas deeper than 1000 m on Sackville Spur and in Flemish Pass with SpD ≈ 15 but some was between 300 and 500 m depth on the southern slope of Flemish Cap where SpD > 20 . Two different values of \bar{E}' were likewise seen in areas with higher fishing effort (Fig. 4C). Evenness on Sackville Spur was low (≈ 0.2) but it was ≈ 0.4 in the southern more-intensively fished areas.

Predictions of sample SpD with RF Models 0 to 4 (Fig. 4A and 5) showed a generally similar pattern. RF Models 2 and 3 showed the best fit, with $R^2 = 0.42$ and 0.41 , respectively, whereas RF Model 4 had the worst. The prediction surfaces from RF Models 1 to 3 showed similar distributions to the RF Model 0 SpD surface, although they predicted higher SpD in the more-intensively fished areas of Sackville Spur and at the south end of Flemish Pass, whereas RF Model 4 predicted higher SpD in most of the deep areas.

Differences in the SpD predictions of RF Models 1 to 4 and those of RF Model 0 are shown in Fig. 6. Although only 11 data points were removed when producing RF Model 1, an increase of as much as 20 extra species were predicted for parts of Flemish Pass, and smaller increases for other areas with more-intensive fishing effort. Similar patterns emerged from comparison of RF Models 2 and 3 with RF Model 0, although the increases in predicted SpD became more widespread as the

subset of input SpD values was more restricted. In RF Models 2 to 4, an area on the southwest of Flemish Cap showed lower predicted SpD than was estimated by RF Model 0. That resulted from the removal of one survey set that took > 60 species in an area with moderate ($1 \text{ h km}^{-2} \text{ year}^{-1}$) fishing effort (Fig. 1A and 2).

3.3. Drivers of benthic diversity

GAM 1A explained 46% of the total variance in sample SpD (excluding structure-forming species) using minimum bottom salinity, minimum surface temperature, range annual primary production and fishing effort, the latter being negatively related to SpD (Table A1). Similar results were obtained when all taxa were included in the response variable (GAM 1B), although a smooth term was more appropriate for annual primary production but not for surface temperature (Table A1). The biomasses of corals and sponges were positively related to SpD (Fig. 7) and, in GAM 2, they explained 62% of the variance in sample SpD, with the biomasses of sponges (including *Asconema foliata*) and small gorgonians showing significant relationships to SpD. GAM 3, which combining environmental, fishing effort and biomass independent variables, proved to be the best model, explaining 73% of the variance. Minimum bottom salinity was significantly related to sample SpD, with higher values at salinities < 34.8 and ≈ 34.88 (Fig. A4), corresponding to depths < 200 m and ≈ 500 – 600 m, respectively. SpD was significantly and positively related to the biomasses of small gorgonians and sponges (including *A. foliata*). In contrast, SpD was negatively related to fishing effort above $\approx 2 \text{ h km}^{-2} \text{ year}^{-1}$ and reached a minimum at $\approx 9 \text{ h km}^{-2} \text{ year}^{-1}$. That relationship was only weakly significant.

The equation for GAM 3 was

$$SpD_i \sim NB(\mu_i, k)$$

$$E(SpD_i) = \mu_i \text{ and } \text{var}(SpD_i) = \mu_i + \frac{\mu_i^2}{k}$$

$$\log(\mu_i) = \alpha + f_1(\text{Minimum bottom salinity}) + f_2(\text{Fishing effort}) + f_3(A. foliata) + \beta_1 \times \text{Range annual primary production} + \beta_2 \times \text{Small gorgonians} + \beta_3 \times \text{Sponges}$$

No pattern was found in the Pearson residuals of GAM 3 and the model showed a good fit between the observed and fitted values (Fig. A5). Very low spatial autocorrelation was observed in the residuals and inclusion of latitude and/or longitude did not improve the model. No pattern was observed between the residuals and any of the covariates (Fig. A5D–K: only covariates included in the model shown).

4. Discussion

Reflecting common experience in many ecosystems, and despite the

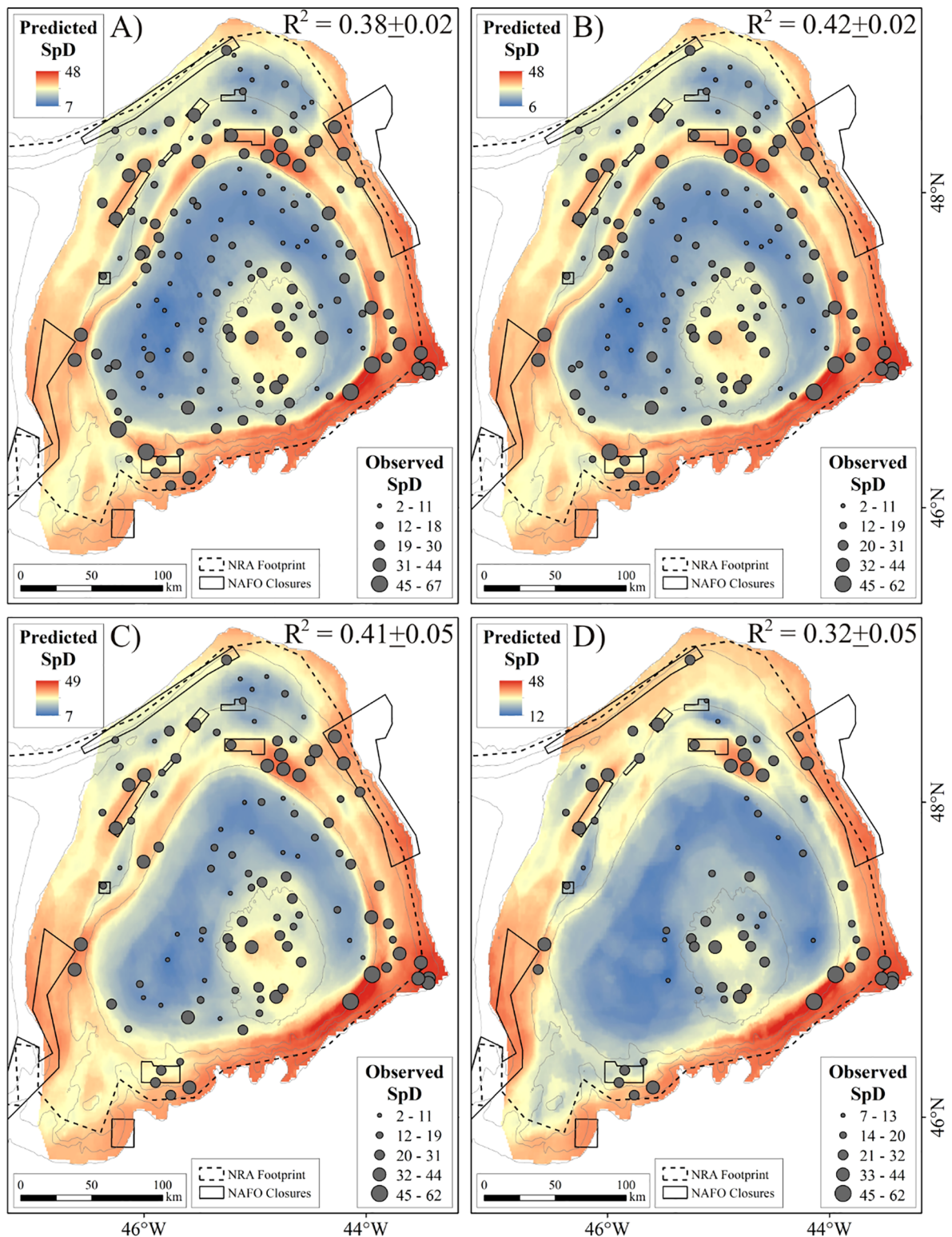


Fig. 5. Maps of predicted sample SpD from RF Models 1 to 4. A) RF Model 1 (165 sets made where fishing effort < $2 \text{ h km}^{-2} \text{ year}^{-1}$); B) RF Model 2 (147 sets made where fishing effort < $1 \text{ h km}^{-2} \text{ year}^{-1}$); C) RF Model 3 (112 sets made where fishing effort < $0.4 \text{ h km}^{-2} \text{ year}^{-1}$); D) RF Model 4 (69 sets made where fishing effort < $0.15 \text{ h km}^{-2} \text{ year}^{-1}$).

extensive survey undertaken, the catch data from 177 trawl sets on Flemish Cap were insufficient to determine asymptotic values of species richness for any of the epibenthic assemblages identified by Murillo et al., 2016a or even for the bank as a whole. Only sample diversity (measured at a scale of $\approx 0.04 \text{ km}^2$) could be mapped as a basis for management applications. Yet practical management of offshore areas

can rarely address scales even as small as 100 km^2 , while sample diversity does not provide a reliable guide to spatial patterns in community diversity at scales larger than the sample. Furthermore, as with every other study of marine diversity, the values observed, estimated and mapped here are those for a taxocene that is defined, in part, by the sampling gear used. Catchability of benthic invertebrates in fish trawls

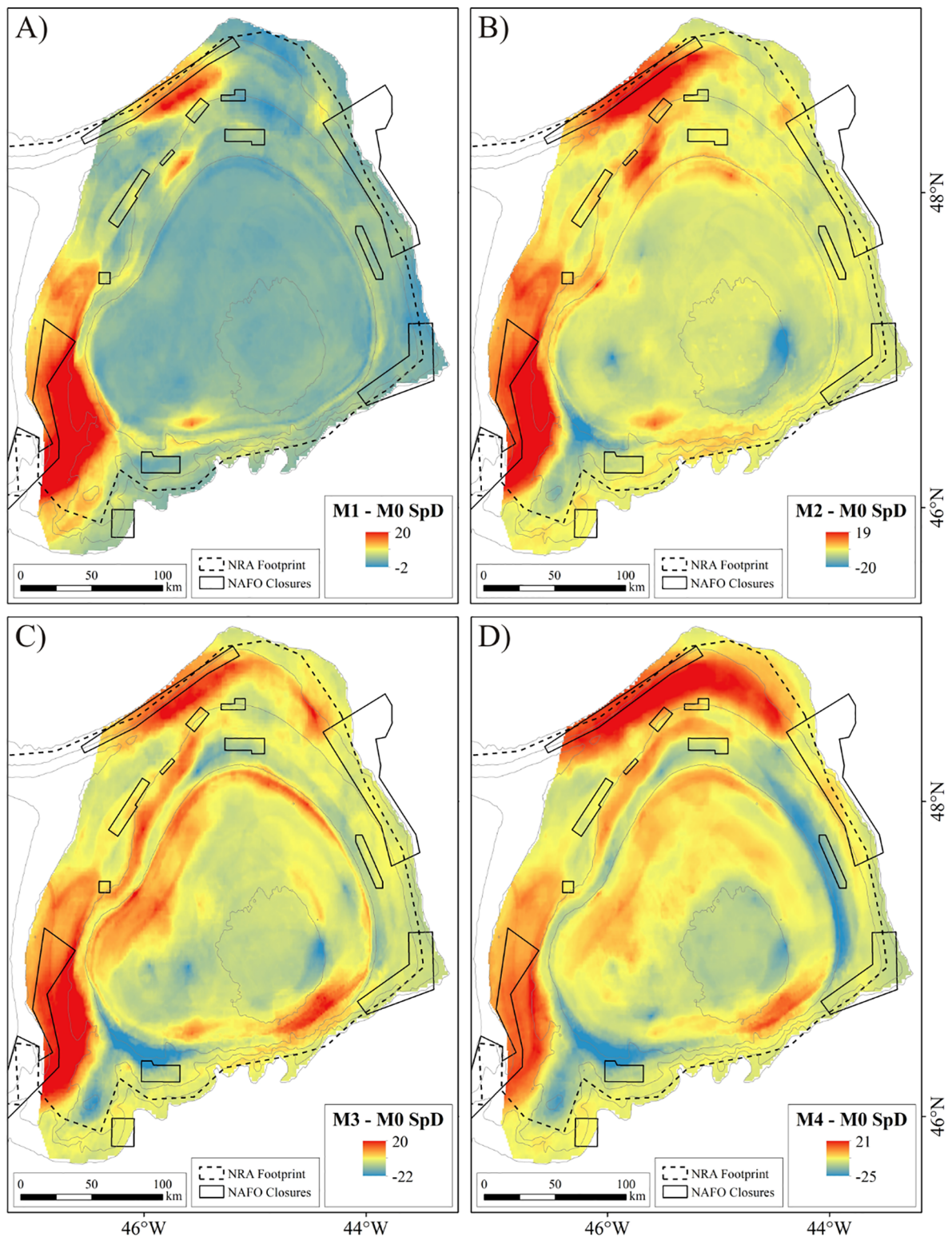


Fig. 6. Maps of the differences in predicted sample SpD between RF Model 0 and each of RF Models 1 to 4. A) RF Model 1; (B) RF Model 2; (C) RF Model 3; (D) RF Model 4.

is generally low (Moran and Stephenson, 2000; Wassenberg et al., 2002) and the VME habitats on Flemish Cap show much higher diversity when surveyed using benthic imagery (Beazley et al., 2013; Beazley et al., 2015) than they do in the present trawl-derived data. Since spatial variations in the diversity of various taxocenes within the same ecosystem are not expected to be congruent (Heino, 2010; Kenchington and Kenchington, 2013), those in the diversity of the

Lofoten trawl-vulnerable non-encrusting benthic invertebrates may not be indicative of general patterns or of patterns produced using alternative taxocenes. Additionally, biodiversity is also influenced by interspecific competition and predation, which may not be directly linked to environmental variables and in benthic invertebrates operate at smaller spatial scales. Consequently the ability to predict biodiversity patterns based on the environment alone will be greater at larger spatial

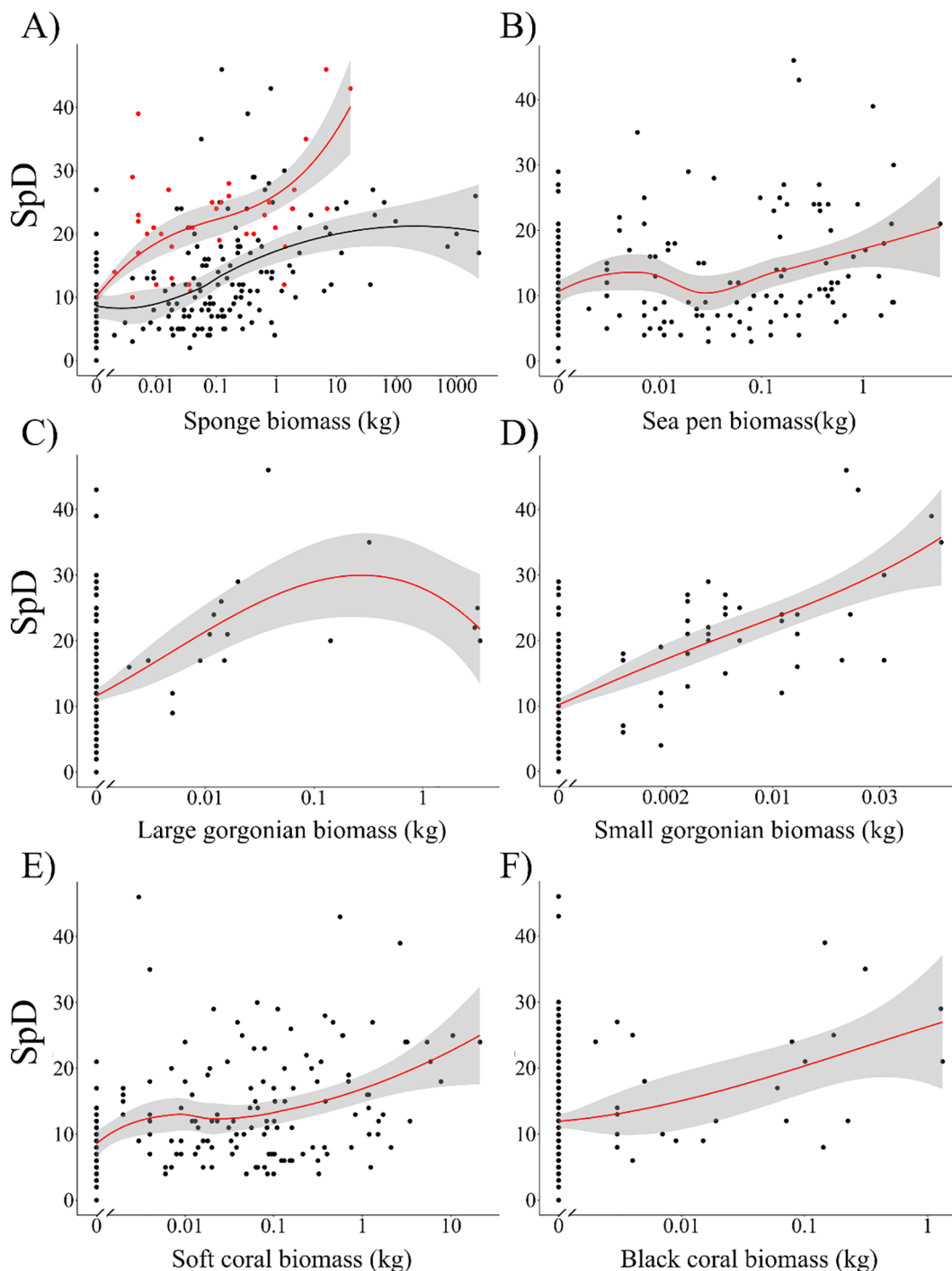


Fig. 7. Bivariate plots of sample SpD against the biomass of various groups of structure-forming epibenthos taken by the survey sets (plotted on a logarithmic scale, with zero offset). (A) presents data on the biomass of the hexactinellid *Asconema foliata* in red, overlain on the data for other sponges in black. Red and black solid lines are LOESS smoothers (LOESS span of 0.75 for A [black line], B and E. LOESS span of 1 for A [red line], C, D and F). The grey areas represent 95% confidence intervals.

scales such as the trawl swept area, where the influence of competition and predation are masked. Thus, maps of sample diversity (SpD), such as those presented here, should be interpreted properly being aware that community diversity at more relevant scales cannot be mapped without far more intensive sampling. However, our chosen taxocene and use of SpD to map diversity will facilitate monitoring of biodiversity in future from this baseline, given the ongoing research vessel multispecies surveys in this region. Further, the demonstrated GAM relationships between the structure-forming species and SpD links our results to those obtained using benthic imagery at smaller spatial scales.

Like species richness, SpD gives equal weight to every species recorded and, since assemblages almost always contain few abundant taxa but many rarities, both metrics primarily respond to the number of those rarities. $e^{H'}$ usually provides a more balanced picture of diversity, as it responds to the species' evenness as well as their number (Magurran and Henderson, 2011; Kenchington and Kenchington, 2013). However, in the Flemish Cap data, the very high biomass of large sponges taken by some sets drove \bar{E}' down, dragging $e^{H'}$ with it. Predicted $e^{H'}$ therefore responded strongly to the distribution of sponge grounds, limiting its value for other purposes. Hence, we here

emphasize SpD. While that is a poor and misleading alternative to species richness for most purposes due to its dependence on the overall abundance of the catch, it is the appropriate measure to map when planning to protect the greatest number of species within the smallest closures (Gotelli and Colwell 2001; Kenchington and Kenchington 2013). That those weaknesses remain, despite the very considerable survey effort, illustrates the inevitable challenges inherent in valid quantification of ecological diversity.

Within the limitations of the diversity measures, both the RF models and GAMs showed that their spatial distribution was congruent with those of abiotic and biotic variables, but also with the distribution of intensity of long-term trawling effort. Minimum bottom salinity was the primary driver, or correlate of drivers, but variables related to surface temperature and primary production also contributed to GAM 1 (A and B). The near-surface variables may be indicative of the amount of local primary production but are also indicators of the presence of different water masses. Sample SpD and $e^{H'}$ were higher on the southern and eastern slopes of Flemish Cap, associated with higher values of minimum surface temperature (Fig. A6). These waters are under the influence of the NAC, whereas in the north and west, the Cap is washed by LC waters. Whether the NAC supports higher diversity only by warming the bottom water or also through the transport of larvae from richer biogeographic regions in the south, northward (cf. Palardy and Witman, 2011), remains unclear.

The second class of drivers of sample SpD was the biomass of structure-forming species of sponges and small gorgonian corals, which explained a higher proportion of the variance in SpD than did the environmental predictors and fishing effort combined. The increased habitat complexity created by sponges and corals can increase local diversity (Bett and Rice, 2012; Buhl-Mortensen et al., 2010). In the Flemish Cap region, sponges are thought to have that effect. In particular, the presence of *Asconema foliata* is associated with higher diversity of epibenthic megafauna, including ophiuroids, crinoids, and other sponges, in Flemish Pass (Beazley et al., 2013). This glass sponge species reached maximum biomasses on a ring around the Cap between 500 and 700 m depth, mostly outside of the current closures (Fig. A7). However, four small catches were found in Closed Area 4 and one moderate catch of 1.4 kg inside Area 14 which is currently opened to fishing (NAFO, 2019) but will be reassessed in 2020. The results of the present study have shown that small gorgonian corals, considered VME indicators by NAFO (NAFO, 2017a), are also positively and significantly associated with SpD in this region.

The linkages between fishing effort and diversity are more complex. One primary consideration for any fisherman, when deciding where to deploy bottom gear, is the density of the target resource on the seabed. For their part, the fish respond to a similar suite of variables to that which drives the distribution of the benthos. Thus, fishing effort is apt to be found in areas with particular benthic assemblages and not necessarily ones with higher diversity. A second consideration on Flemish Cap is avoidance of high bycatches of large sponges, since they damage the fish in a trawl's codend, can damage the net and always waste valuable time while they are cleared away. Similarly, the corals are associated with complex surficial geological features (Edinger et al., 2011) which can damage bottom gear. Hence, provided that the target species can be found outside sponge- and coral-rich areas, fishing effort will mostly be directed away from those high-diversity areas. On the Cap, that avoidance is now reinforced by key sponge and coral areas being closed to bottom fishing. Where the gear is deployed, however, bottom trawling depletes the benthos (e.g., Prena et al., 1999; Hiddink et al., 2017; Sciberras et al., 2018), especially the mega-epibenthos (e.g., Althaus et al., 2009). Those species vulnerable to capture in survey trawls, the species of the present study's taxocene, are likely to be particularly affected. The effects can be short-term, reflected in the year of the trawling, but can also be accumulated over decades, through gradual depletion of long-lived species (e.g., Kenchington et al., 2007).

The RF modelling presented here showed that the intensity of

fishing effort on Flemish Cap was only weakly correlated to $e^{H'}$ and was positively, but moderately, spatially related to \bar{E}' , perhaps because of fishermen's avoidance of the lowest-evenness sponge grounds. However, fishing effort was strongly and negatively related to sample SpD. The three most-intensively fished areas showed different responses, that at intermediate depth (300–500 m) having moderate SpD, while the deep fishing ground on Sackville Spur had low \bar{E}' and only the deep ground in the southern Flemish Pass had both low SpD and moderate \bar{E}' – suggesting that sample diversity on those grounds was not driven by fishing effort alone. GAM 3 also found fishing effort to be a driver of SpD but not the major one (though that analysis may have subsumed some of its effect into those of the structure-forming epibenthic biomass, depleted by past trawling). RF modelling that excluded the data from more intensively fished areas allowed a better fit of the independent variables to sample SpD, consistent with fishing disrupting the relationships between the environment and diversity but also with fishermen selecting trawling locations where diversity is naturally low – albeit not because it is low.

In the open sea, severe anthropogenic depletions are common but extirpations of species are unusual (del Monte-Luna et al., 2007; Dulvy et al., 2009). Thus, it is unlikely that benthic community species richness has declined on Flemish Cap since the initiation of trawl fisheries there, though evenness has probably changed and with it community $e^{H'}$. Sample SpD, in contrast, is negatively affected by depletion, as the average number of individuals caught by a standard trawl set declines, reducing the number of rare species observed (Gotelli and Colwell, 2001; Kenchington and Kenchington, 2013). Consistent with that expectation, at least qualitatively, extrapolation of predicted SpD from RF modelling that excluded data from the most heavily fished areas into those areas suggested that as many as 20 species could have been deleted from sample SpD, if the lower diversity is a result, rather than a cause, of the spatial distribution of trawling. Quantitatively, however, that would be a very substantial effect from what has, in recent years, been only moderately intense fishing. Additional details can be consulted in Appendix B.

We suggest that the observed spatial relationships are best explained by a combination of two contrasting mechanisms: the abundance of structure-forming taxa and the chronic disturbance of fishing. The distribution of large geodid sponges, the dominant structure-forming taxon of the deep sponge grounds in Flemish Pass, has not greatly changed over time (Murillo et al., 2016b). Thus, the species-rich geodid grounds have apparently been avoided by most trawling, which is instead concentrated in adjacent areas, where sample SpD is naturally lower. In contrast, benthic data collected during the first years of Soviet trawling on Flemish Cap, during the late 1950s, showed sea pens, large gorgonians and black corals in a ring around the bank at 300–350 m depth (Nesis, 1963), that have not been seen in recent years. The sponge species characteristic of the shallower communities on the Cap, such as those belonging to the genus *Gellius* and *Mycale*, were also abundant when trawling began (Nesis, 1965) and have presumably been thinned by the impacts of fishing gear. Such structure-forming epibenthic species are particularly vulnerable to trawling impacts (e.g. Freese, 2001; Krieger, 2001; Heifetz et al., 2009), in part as a consequence of their growth forms. Their very high life expectancies, low recruitment rates and slow growth to the sizes and densities that provide effective structure for other species (e.g. Andrews et al., 2009; Sherwood and Edinger, 2009; Hogg et al., 2010) minimize their recovery rates, allowing the effects of repeated trawling to accumulate over decades, including the period of intensive fishing on Flemish Cap during the later 20th Century, not just the lighter exploitation of the past 20 years. Given the importance of those structure-forming species for benthic diversity, confirmed by the GAMs presented here, the consequences of their depletion have presumably included local depression of sample SpD.

The very low recovery rates of benthic biodiversity in former sponge grounds or coral aggregations mean that any recovery requires

elimination of trawling from affected areas, while protection of the remaining epibenthic structure requires continuation of the existing NAFO closures and their expansion where appropriate. The current closures were designed for conservation of VMEs. While VMEs also protect other benthic species within their boundaries from direct impacts of fishing gears, only an estimated 60% of the species in our taxocene that occur on Flemish Cap are found in those closures (Table 3). In particular, the shallower portions of the bank support distinct communities and species sponges, sea pens, and echinoderms not found at the depths of the existing closures (Murillo et al., 2016a).

5. Conclusions

We have presented an assessment of the ability of existing data from routine trawl surveys on Flemish Cap to sample common biodiversity indicators, SpD, $e^{H'}$ and \bar{E}' , at different spatial scales of both ecological and management relevance. We found that despite extensive sampling in this high seas area, only sample diversity, SpD could be assessed reliably with certain caveats which we detail. We then demonstrate how random forest modeling and spatial mapping of SpD transforms this indicator into a form that can be readily used by managers. We demonstrate how such an approach allows for an examination of fishing impacts and also provides an overview of biodiversity protection afforded by the current closed areas in the region.

Benthic biodiversity on the Flemish Cap is negatively correlated with bottom-contact fishing activities. Although it is not possible to fully evaluate the precise nature of the impact, our models have identified the areas where this impact has been the greatest. The correlation could be explained by fishing avoidance of high diversity areas which is known to occur, or through thinning of the fauna through the fishing activities making it more difficult to detect rarities. The nearby presence of areas subjected to low fishing pressure and with similar species composition to the common fishing grounds, suggests that fishing activities have altered benthic biomass and species dominance rather than producing the extinction of particular species. Species density (SpD) is the more sensitive to fishing effort than species richness, with a 40% decrease observed in the former and only 11% in the latter.

The strong influence of the mix of water masses in the area also influences the predictive biodiversity map possibly through propagating the persistence of more northern and southern species in different regions. Benthic biodiversity on Flemish Cap therefore may be sensitive to climate change and the water mass properties included herein should be also considered in future assessments.

Additionally, despite the long history of fishing in this region, there are still large extensions with presence of structure-forming sponges and corals, which play a key role in structuring such biodiversity. Although current closures to protect VMEs from the adverse impacts of bottom fishing activities protect an important part of the diversity associated with the deeper communities, on top of the Flemish Cap shallower than 500 m unique and representative habitats are not currently protected.

Data availability

Data available at the Mendeley Repository: <http://dx.doi.org/10.17632/y8wj8rvm89.1>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106135>.

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