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Marine epibenthic functional diversity on Flemish Cap (north-west Atlantic)—Identifying trait responses to the environment and mapping ecosystem functions

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Abstract

Aim: To characterize the functional diversity and selected ecological functions of marine epibenthic invertebrate communities at the ecosystem scale and to evaluate the relative contributions of environmental filtering, including bottom-contact fishing, and competitive interactions to benthic community assembly.

Location: Flemish Cap, an ecosystem production unit and fishing bank in the high seas of the north-west Atlantic Ocean.

Methods: Through the use of Hierarchical Modelling of Species Communities (HMSC), we have explored seven community response traits to the environment applied to 105 epibenthic species and evaluated the influence of such traits on the community assembly processes. Assumed bioturbation, nutrient cycling and habitat provision functions, linked to individual or a combination of biological traits, were mapped using random forest modelling.

Results: Functional richness within benthic communities reached an asymptote for trawl sets with roughly more than 30 species. Assemblages on top of the Flemish Cap (<500 m depth) were characterized by higher biomass of small- and medium-sized species with short life spans, whereas large species with longer life spans and broadcast spawners were dominant in the deeper assemblages (500–1,500 m depth). The amount of variation explained by the species' responses to the covariates mediated by the traits was relatively high (25%) indicating their relevance to community assembly. Community-weighted mean trait values changed with depth and physical oceanographic variables, indicating that environmental filtering was occurring. Interspecific interactions, as inferred from the random effect at the sample level, accounted for 16.3% of the variance in the model, while fishing effort explained only 5.2% of the variance but conferred strong negative impacts for most species.

Main conclusions: Our results suggest that while bottom-contact fishing impacts have an effect on functional diversity, changes to the physical oceanography of the

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system are likely to have more profound impacts. The maps of benthic functioning can aid assessments of ecosystem impacts of fishing.

KEYWORDS

benthic invertebrates, community assembly, deep sea, environmental filtering, Hierarchical Modelling of Species Communities, joint species distribution model, north-west Atlantic, trait composition

1 | INTRODUCTION

Benthic invertebrates provide a multiplicity of ecosystem functions and services in the marine environment. They represent a key link between benthic and pelagic ecosystems (Griffiths et al., 2017) facilitating nutrient cycling (Kutti, Bannister, & Fosså, 2013; Perea-Blázquez, Davy, & Bell, 2012), and through their physical structure, some enhance habitat complexity increasing biodiversity (Beazley, Kenchington, Murillo, & Sacau, 2013; Beazley, Kenchington, Yashayaev, & Murillo, 2015; Hawkes et al., 2019), provide nursery areas (Aldrich & Lu, 1968; Etnoyer & Warrenchuk, 2007) and modify biochemical regimes (Kaufmann & Smith, 1997; Soltwedel & Vopel, 2001). Some benthic invertebrates are also an important food source for fish and marine mammals (González, Román, & Paz, 2006; Oliver, Slattery, O'Connor, & Lowry, 1983) and can be active predators themselves (e.g., sea stars, crabs, gastropods). Furthermore, many show predictable responses to disturbance and are good indicators of the effects of fishing (Sciberras et al., 2018), oil spills (Gómez Gesteira & Dauvin, 2000) and climate change (Kortsch et al., 2012). Yet, despite their importance to healthy marine ecosystems, the functions that benthic invertebrate communities play in the marine ecosystem are rarely quantified in the deep sea or taken into account by resource managers.

The diversity of traits displayed by the species in a community can be used as a measure of functional diversity (Petchey & Gaston, 2006), providing a more direct link to ecosystem processes and functioning (Cadotte, Carscadden, & Mirotchnick, 2011) than taxonomic identity (Ricotta, 2005). Species' traits can be divided into two broad categories: effect traits, which determine how the species affect ecosystem functions, and response traits, that reveal how species respond to their environment (Lavorel & Garnier, 2002). The impact of species loss on ecosystem functioning under contemporary and future scenarios will depend in part on the degree of functional redundancy, that is, the amount of trait similarity among species (Teichert et al., 2017) and the total number of species, assuming that with more species eventually the trait distribution will become more redundant as species share similar traits. Functional redundancy is highly correlated with the genetic similarity of the taxa and can be accounted for through consideration of the phylogenetic constraints within the communities. According to the insurance hypothesis of biodiversity, the maintenance of high diversity and redundancy in functional traits will contribute to increasing the stability of biological assemblages and their associated ecological processes (Yachi & Loreau, 1999) and help ensure ecosystem recovery after disturbance (Teichert et al., 2017). This concept is particularly relevant when considering the impacts of fishing on benthic ecosystem functioning, and evaluating whether significant adverse impacts have occurred (sensu FAO, 2009), where the scale and significance of the impact will be related in part to the extent to which ecosystem functions may be altered by the impact.

Accordingly, during the last decade, ecologists have increasingly studied species' biological traits, and their subset of functional traits, as a way to connect niche-based mechanisms to community patterns, because it is recognized that species can be grouped according to common effects on ecosystem processes mediated by their functional traits, in addition to common responses to the environment (Cadotte, Arnillas, Livingstone, & Yasui, 2015; Lavorel & Garnier, 2002; McGill, Enquist, Weiher, & Westoby, 2006). Therefore, the assembly processes influencing ecological communities are a result of the combined effects of environmental filters restricting distributions, past and present biotic interactions and stochastic processes (Itter, Vanhatalo, & Finley, 2019) where the response of the species to these factors will depend on their traits, which in turn are to varying degrees constrained by phylogenetic relationships (Ovaskainen et al., 2017).

Recent advances in statistical community-level models (Ovaskainen et al., 2017; Warton et al., 2015) have allowed the incorporation of species traits into a modelling framework useful for identifying response traits that can provide functional, mechanistic and predictive perspectives on processes shaping the assembly and dynamics of ecological communities. Such models also allow the inclusion of phylogenetic information of species communities, which account for covariation within relatives displaying similar traits. Functionally important traits are often highly correlated with phylogeny, with genetically similar species often sharing the same traits, and therefore, the inclusion of phylogenetic data allows measurement of how much of the residual environmental responses of the species (after accounting for the effects of the measured traits) is explained by their phylogenetic correlations. This provides insight into the mechanisms underlying community assembly (Abrego, Norberg, & Ovaskainen, 2017) and to the impacts of anthropogenic and environmental pressures on the system.

The conservation and sustainable use of marine biological diversity in areas beyond national jurisdiction is a high priority international issue (UN, 2017). In the north-west Atlantic Ocean, the Northwest Atlantic Fisheries Organization (NAFO) has made commitments to the conservation of marine biodiversity in general, and to minimizing the risk of long-term or irreversible, adverse effects of fishing activities (Koen-Alonso, Pepin, Fogarty, Kenny, & Kenchington, 2019; NAFO, 2017). In particular, since 2006, NAFO has closed six seamount complexes and 15 areas on and around the Flemish Cap and on the high seas portion of the Grand Bank to protect deep-sea coral and sponge Vulnerable Marine Ecosystems (VMEs) from impacts by bottom-contact fishing gears (NAFO, 2018a).

Recently, the benthic diversity of the Flemish Cap ecosystem (NAFO Division 3M), based on the distributions of 288 taxa (Murillo, Serrano, Kenchington, & Mora, 2016), was mapped and the impacts of fishing evaluated (Murillo et al., 2020). However, there has been no comparable ecosystem-level assessment of the functional trait diversity of those taxa, although some habitats have been studied in detail. In particular, the association of sponge VMEs with enhanced biodiversity in this region has been described (Beazley et al., 2013, 2015) and the impact of fishing on a suite of sponge ecosystem functions (filtration, respiration, organic carbon assimilation and nitrogen cycling) on Flemish Cap has been evaluated (Pham et al., 2019). Although sponges play an important role in the Flemish Cap ecosystem (Pham et al., 2019), in order to evaluate the impact of bottom fishing on benthic ecosystem functioning, it is necessary to characterize the broader functional trait landscape considering all the species, and their contributions to overall ecosystem processes. The aims of this study were to:

1. Characterize the functional diversity of the epibenthic species and communities in the Flemish Cap area and to evaluate the relationship between functional and species diversity;
2. Identify response traits to the environment (including fishing effort) and their contribution to community assembly processes, evaluating how much of the residual environmental responses of the species is explained by phylogenetic correlations; and
3. Map selected ecological functions linked to individual or a combination of effect traits.

We address (2) through the use of Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017; Tikhonov, Øystein, Abrego, Lehikoinen, & Ovaskainen, 2019), a statistical framework which uses Bayesian inference to fit latent-variable joint species distribution models (JSDM; Warton et al., 2015).

2 | METHODS

2.1 | Study area

The Flemish Cap is an isolated bank in the high seas of the continental margin off Newfoundland, with a radius of ~200 km at the 500 m isobath and minimum depth of <150 m (Figure 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, 2014), and is treated as a discrete unit, NAFO Division 3M, for management of bottom fisheries. There are steep slopes to the east and south, below 1,000 m depth, but more gradual gradients to the north and west. It is separated from the Grand Banks by the Flemish Pass, a 1,200 m deep, mid-slope channel. Two major ocean currents influence this area: the Labrador Current (LC), flowing from the north, and the North Atlantic Current (NAC), which represents an extension of the warm Gulf Stream. When the LC reaches the Flemish Pass, it bifurcates with the major branch flowing southwards to the south-eastern slope of the Grand Bank; meanwhile, the side branch circulates clockwise around the Flemish Cap. The frontal zone between the 4°C waters around the Flemish Cap and the NAC is located about 100 km to the east of the Cap (Stein, 2007).

2.2 | Data sources

2.2.1 | Sampling and benthic data

Data used in this study were obtained from the catches of the 2007 EU Flemish Cap bottom-trawl research 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 the Flemish Cap and the eastern side of Flemish Pass between 138 and 1,488 m depth, following a depth-stratified random sampling design (Figure 1a). It was conducted on board the Spanish research vessel *Vizconde de Eza*, with standardized sets of a Lofoten bottom trawl, with a swept area of ≈0.04 km^2 each.

Details of sample processing and identification of the invertebrate epibenthos are provided in Murillo, Serrano, et al. (2016). A total of 288 taxa from 176 trawl sets were initially recorded, and the biomass (kg wet weight) for each was determined. Further taxonomic examination leads to a reduction of the total number to 285 discrete taxa.

Murillo, Serrano, et al. (2016) identified seven epibenthic megafaunal assemblages on Flemish Cap based on species co-occurrence. Those seven assemblages were nested within two major regional-scale faunal groups, one on the top of Flemish Cap in waters <500 m (Group II, Figure 1b) with assemblages II a-c and the other on the lower slope of Flemish Cap in waters >500 m (Group III referred hereafter as deep Flemish Cap, Figure 1b) with assemblages IIIa, IIIb.1, IIIb.2 and IIIc. The two large epibenthic faunal groups correspond to the two ecoregions identified by Pérez-Rodriguez, Cuff, Ollerhead, Pepin, and Koen-Alonso (2010). Details of the particular species composition of each assemblage can be found in Murillo, Serrano, et al. (2016).

2.2.2 | Trait data

We selected a suite of seven biological traits (Table 1) based on their presumed importance to the structure and functioning of benthic ecosystems (effect traits) or for their sensitivity to perturbations or changes in the environment (response traits). Trait information was based on adults

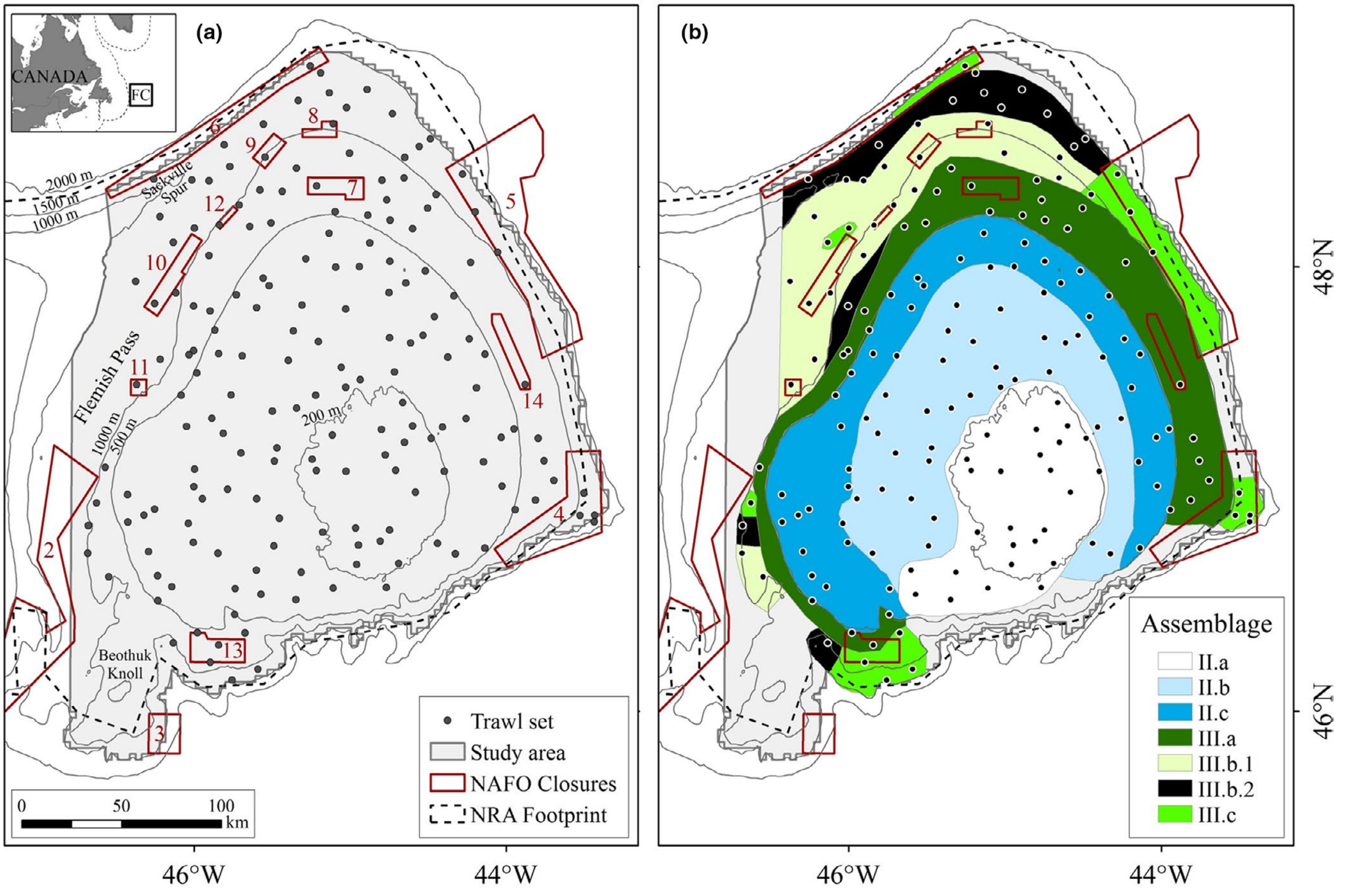

FIGURE 1 (a) Map showing the study area and the trawl sets (black dots) on Flemish Cap. Areas closed to bottom fishing activities to protect sponge and coral concentrations and existing bottom fishing areas (NAFO Regulatory Area [NRA] Footprint) are also indicated (NAFO, 2018a). Bathymetric contours were obtained from the Canadian Hydrographic Service. (b) Map showing the location of the seven epibenthic megafaunal assemblages identified by Murillo, Serrano, et al. (2016) and assessed here for functional trait diversity

of all taxa and compiled from the literature (see Appendix S1), online databases (Degen & Faulwetter, 2018; MarLIN, 2006) and from expert consultations. In cases where trait information was not available for the faunal taxon, the trait information was inferred from the closest related taxon for which data were available. Multiple categorical classifications were allowed for taxa with more than one trait category. The list of species and their respective traits are provided in Appendix S2.

2.2.3 | Explanatory variables

Six covariates derived from different sources and with varying spatial resolutions were used in the modelling (Section 2.3.2) as explanatory variables, namely depth, maximum bottom current speed, minimum bottom temperature, maximum mixed layer depth, percentage of mud in the sediment and fishing effort. They include measures associated with food supply, depth, water mass and substrate, all of which are expected to act as environmental filters influencing distributions. The variables were chosen based on availability of data and assumed relevance to the traits selected and community assembly processes (Table 2). Each of the layers had a cell size of 3 km resolution. Specific details on the methods used for the spatial interpolation of these variables are documented in Guijarro, Beazley, Lirette, Wang, and Kenchington (2016) and sources and spatial resolution provided in Appendix S5, Table S5.1.

2.3 | Data analysis

2.3.1 | Functional diversity

To quantify functional diversity (FD), we calculated two metrics for each sampling location using the 'FD' package (Laliberté, Legendre, & Shipley, 2015) from the statistical computing software R 3.5.1 (R Core Team, 2018) considering the 285 taxa, the seven biological traits and their associated categories. We calculated functional richness (FRic, Villéger, Mason, & Mouillot, 2008), recommended when the total functional range covered by the community is desired (Legras, Loiseau, & Gaertner, 2018), and functional dispersion (FDis, Laliberté & Legendre, 2010), which describes the mean distance of individual species to the centroid of all species in the community in a multivariate trait space, providing a complementary facet of functional diversity.

The computed values for each FD metric were compared with the number of species recorded for each of the two major regional-scale

TABLE 1 The species traits used in the analyses and their hypothesized relationship with factors responsible for spatial patterns in epifaunal assemblages including those traits which help to distinguish between natural and man-induced changes

Trait	Hypothesized relationship	Categories or units
Maximum adult size[a,b]	Body size is correlated with many life-history traits and influences a wide range of biological and ecological functions [1–6]. Metabolic rate scales with the 3/4-power of body mass and increases with temperature [7]. We expect small-sized species to be more prevalent in bottom-trawled areas than in similar environments not exposed to fishing impacts [8–9] and to have higher P/B ratios [10] with higher metabolic rates [7]. We expect some species to be ecosystem engineers, locally enhancing biodiversity [11–12] by increasing habitat heterogeneity and modifying the environment [13]	Small (<2 cm) Medium (2–10 cm) Medium large (10–50 cm) Large (50 cm)
Longevity[a]	Long-living species have lower relative production due to slow growth and turnover rates [14–15]. We expect that longer-lived species will be found in deeper waters where light, food availability, temperature and disturbance intensity drive highly predictable distributions [16]. As long-living species are more common in undisturbed habitats, we further expect such species, particularly those of a larger body size, to be rarer in fished areas	< 5 yrs 5 – 10 yrs 10 – 50 yrs > 50 yrs
Reproductive method[a]	We expect broadcast spawners to decrease with depth and an increase in species with other reproductive methods [17]. Asexual reproduction may be an adaptation to unfavourable environmental conditions and for species where sexual reproduction is uncertain and/or infrequent [18–19]. We expect that asexual reproduction will dominate in areas that have been disturbed by fishing over a long period of time	Asexual-budding Sexual broadcast spawner Sexual brooder-indirect development pelagic Sexual brooder-direct development demersal or viviparous
Propagule dispersal[a]	Planktotrophic larvae are associated with long pelagic duration and high dispersal capacity while lecithotrophic larvae developing from large eggs, containing a high quantity of yolk, correlate with a short pelagic duration and settlement close to parents [18]. Therefore, we expect that planktotrophic species can recolonize more easily areas that have been disturbed by fishing over a long period of time. Additionally, we expect increase of species with lecithotrophic larvae or direct development with depth [20]	Pelagic planktotrophic Pelagic lecithotrophic Benthic
Motility[a,b]	Sessile organisms are more subject to changes in the abiotic environment than motile species [21]. Motile and burrowing species are expected to have a better ability to avoid the trawl nets and can recolonize areas by migration [9, 22–23]	Burrow Crawl Swim Sessile
Degree of contagion[a,b]	We expect large-sized species that form aggregations to create habitat for other species and large spatial scales and thereby increase biodiversity [11–12]	Solitary Patchy Highly aggregated
Feeding mode (trophic position)[a,b]	The feeding mode is considered to be a proxy for energy fixation/transfer and ecosystem production [24]. Predator–prey relationships and trophic levels are indicators of community structure, and are important for monitoring ecosystem changes enabling quantification of bottom-up linkages with flow webs, top-down linkages with ingestion/production webs and trophic position. Scavengers are attracted to areas where trawling occurs and are expected to be more common in areas of high fishing intensity [9, 22, 23, 25]	Scavenger Predator Deposit-feeder Passive filter-feeder Active filter-feeder

Note: The categories and units are indicated in the last column. References are numbered in parentheses and listed in full in Appendix S3.

[a] Response trait.

[b] Effect trait.

faunal groups (top and deep Flemish Cap; Section 2.2.1). We also calculated the FRic for the whole of Flemish Cap (all trawling sets), which was compared with the FRic of the sets included in the NAFO closed areas (NAFO, 2018a). Trawling sets located inside closed Areas 7 to 12, and 14 (Figure 1a) were grouped together to assess the FRic of areas closed to protect sea pen fields and sets inside closed Areas 4–6 to assess the FRic of areas closed to protect sponge grounds. Additionally, to evaluate differences in trait composition between the seven assemblages (Figure 1b) identified by Murillo, Serrano, et al. (2016), we computed community-weighted means (CWM) using both presence/absence and biomass data to reflect the structure of trait values at the community level (Lavorel et al., 2008). Finally, the 'adiv' package (Pavoine, 2018) was used to measure the functional redundancy between communities following Ricotta et al. (2016).

2.3.2 | Statistical modelling

We used HMSC (Ovaskainen et al., 2017; Tikhonov, Øystein, et al., 2019) from the 'Hmsc' R package (Tikhonov, Ovaskainen, et al., 2019) to fit a joint species distribution model to the benthic data combining simultaneously information on traits, environmental covariates and

TABLE 2 Covariates used in the HMSC analyses with their assumed relevance and expected relationship to the selected response traits

Covariate	Relevance	Expected relationship with response trait
Depth	Benthic invertebrates of the continental margins are restricted to depth bands, which can be related to different hydrostatic pressures and food availability [1]	Size: Small (+), medium (+), medium large (−), large (−) [2] Longevity: <5 years (−), 5–10 years (−), 10–50 years (+) >50 years (+) [3] Propagule dispersal: Pelagic planktotrophic (−) [4] Pelagic lecithotrophic and benthic (+) [5–6]
Bottom current maximum	Faunal communities with specific traits are related to different current regimes. Large-size sponge grounds in the area have been related to maximum bottom current speed [7]	Feeding mode: Passive and active filter-feeder (+), deposit-feeder (−) [8–9]
Bottom temperature minimum	Low temperatures decrease the rates of protein synthesis and increase the energetic costs of such synthesis [10]. Differences in organism size at maturity at different temperatures have been explained through cell size [11]. At higher temperatures, cells will divide faster and the organism will reach maturity earlier but cellular growth will increase slower. Due to the smaller average cell size, the resulting adult will be smaller at higher temperatures	Size: Small (+), medium (+), medium large (−), large (−) [11–12]
Percentage of mud	Some suspension filter-feeders such as sea pens are associated to habitats with high mud content [13]	Feeding mode: Deposit-feeder (+) [14]
Mixed layer depth (MLD)	MLD is related to the availability of nutrients and light and hence controls biological productivity [15]. Therefore, deeper MLD has been associated with higher productivity. High levels of primary production should also result in greater quantities of organic matter sinking to the seafloor	Feeding mode: Passive filter-feeder (+), deposit-feeder (+) [16]
Fishing effort	Physical impact by fishing gears modifies the benthic communities [17–18]. Overfishing reduces abundance and can lead to changes in size structure, age structure and trophic structure and community interactions	Size: Small (+), medium (+), medium large (−), large (−) [19–20] Longevity: <5 years (+), 5–10 years (+), 10–50 years (−) >50 years (−) [21–22] Reproductive method: Asexual (+) [23] Propagule dispersal: Pelagic planktotrophic (+); Pelagic lecithotrophic (−) Mobility: Sessile (−), crawl (+) [24–25] Feeding mode: Predator (+), scavenger (+), passive and active filter-feeder (−) [24–25]

Note: References are numbered in parentheses and listed in full in Appendix S4.

phylogenetic constraints in a single model. Our response matrix was the presence–absence of epibenthic taxa per each trawl set, reduced prior to modelling by selecting those species that constituted the 95% biomass of each community of Murillo, Serrano, et al. (2016), complemented by the top 20 taxa based on occurrence to account for common species with low biomass; consequently, the analysis was based on 105 taxa.

The workflow of a typical HMSC analysis with the HMSC-R 3.0 package includes five steps (Tikhonov, Øystein, et al., 2019). The first step involves setting the model structure and fitting the model. We modelled the data using the Bernoulli distribution and the probit link function. Depth, bottom current maximum and fishing effort were previously logarithmically transformed. We included a random effect (that also model co-occurrence among species) at the level of sampling station using a latent factor approach (Ovaskainen, Abrego, Halme, & Dunson, 2016). We followed Ovaskainen et al. (2017) to partition the explained variation among the fixed and random effects. The fitted model includes parameters which measure the influences of the traits on the species-specific responses to the environmental covariates (see Ovaskainen, Roy, Fox, & Anderson, 2016), and therefore, it is possible to measure the portion of the among-species variation to responses to environmental covariates attributed to traits. The trait categories that were included in the model are described in Table 1. To account for possible phylogenetic correlations in the species' responses to the covariates, following Abrego et al. (2017), we included a phylogenetic correlation matrix in the model's covariance structure derived from the taxonomic tree that included the levels of phylum, class, order, family, genera and species, assuming an equal branch length for the six levels. This structure allowed us to evaluate how much of the residual environmental responses of the species are explained by phylogenetic correlations. The strength of the phylogenetic signal is measured by ρ, where a value of $\rho = 0$ indicates that the residual variance is independent among the species, whereas when ρ approaches 1, species' environmental niches are fully structured by their phylogeny, and therefore, related species have more similar niches than expected by random. We fitted the model to the data with Bayesian inference, using the posterior sampling scheme of Ovaskainen, Abrego, et al. (2016), extended here to account for traits and phylogenetic constraints. We used the recommended HMSC default prior distributions and model structure for our analyses (see Abrego et al., 2017; Tikhonov, Ovaskainen, et al., 2019).

After fitting the model, we examined and ensured the convergence of the Markov chain Monte Carlo simulations (step 2) and evaluated the model fit (step 3). The explanatory power of the model was evaluated by computing the R^2 for each species, and calculating the coefficient of discrimination (Tjur's R^2) for presence–absence data, defined as the difference between the average model prediction for successes and failures (Tjur, 2009). The overall explanatory power of the model was summarized as the mean R^2 across species. Additionally, a twofold cross-validation was performed to assess the predictive power of the model. Finally, the parameter estimates were explored (step 4) and predictions made (step 5). One of the main focuses of our modelling effort was to study how traits modulate responses to the environmental variables across species. For this, we predicted community-weighted means of traits based on the 105 taxa considered in the model as responses to the included environmental covariates. These predictions were used to study the 38 hypothesized relationships between trait category and the covariates considered in the model (Table 2).

2.3.3 | Mapping selected traits and ecosystem functions

The joint species distribution model fit in the previous section was used to predict the spatial probability of occurrence of each trait category (Table 1) and the probability of occurrence of selected species in the study area. We then took the next step of linking specific effect traits to three important ecological functions provided by benthic communities (Griffiths et al., 2017): (a) bioturbation; (b) nutrient cycling; and (c) habitat provision. Bioturbation was assessed using the motility category 'burrow' which included active and tube burrowers. 'Active filter feeding' mode was used as a proxy of nutrient cycling due to the high volume of water that active filters process, taking nutrients from the water column and making them available to the benthos (Ostroumov, 2005; Riisgård & Larsen, 2000). To assess the habitat provision function, taxa within trait categories medium and large for 'maximum adult size', sessile for 'motility', and patchy and highly aggregated for 'degree of contagion' were selected (excluding the Orders Actiniaria, Brisingida and Euryalida) and their biomass combined.

Continuous surfaces of the spatial distribution of these three defined ecosystem functions and the functional richness (FRic) per trawl set were created using random forest (RF) modelling (Breiman, 2001) with the 'ranger' package (Wright, Wager, & Probst, 2019) in R. We used 5,000 regression trees and default values for the rest of the RF parameters. Prediction and standard error surfaces were created for each surface. Standard error of the predictions was 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, Hastie, & Efron, 2014). The response variable was the logarithmically transformed biomass of each function or the functional richness values computed in Section 2.3.1. Seven fixed environmental variables and 45 summary statistics of 15 other environmental variables and fishing effort were used as predictors (Appendix S5, Table S5.2). These are the same predictors used previously by Murillo et al. (2020) to map the ecological diversity based on the number of species and will allow us to evaluate the relationship between functional and species diversity in the Flemish Cap area. Specific details on the methods used for the spatial interpolation of these variables are documented in Guijarro et al. (2016) and sources and spatial resolution provided in Appendix S5, Table S5.2.

3 | RESULTS

3.1 | Functional diversity

The functional richness (FRic) of sampling stations ranged between 1.5 and 39.7, following a similar trend in both the top and deep Flemish Cap major faunal groups (Figure 2a,b). After a positive linear relationship between FRic and the number of species, asymptotic values were reached for trawl sets with roughly more than 30 species. At a smaller scale, the three epibenthic assemblages from the top of Flemish Cap (Figure 2a) reached similar maximum values of FRic between 20 and 30 species. However, one of the assemblages (Figure 2b, III.b.2) from the deep Flemish Cap, characterized by a lower number of species, did not reach the maximum values of FRic found elsewhere. Assemblages with a lower number of species showed greater variation in functional dispersion (Figure 2c,d), which was mostly uniform for trawl sets with more than 20 species.

When all the trawl sets were grouped together, reflecting the overall FRic of the Flemish Cap, values increased to 45.53. Combining all trawl sets outside of the closed (protected) areas, the FRic was 44.78. Considering that FRic for all sets inside the closed areas reached a value of 45.43 suggests that the current closures protect similar amounts of the functional diversity as found in the

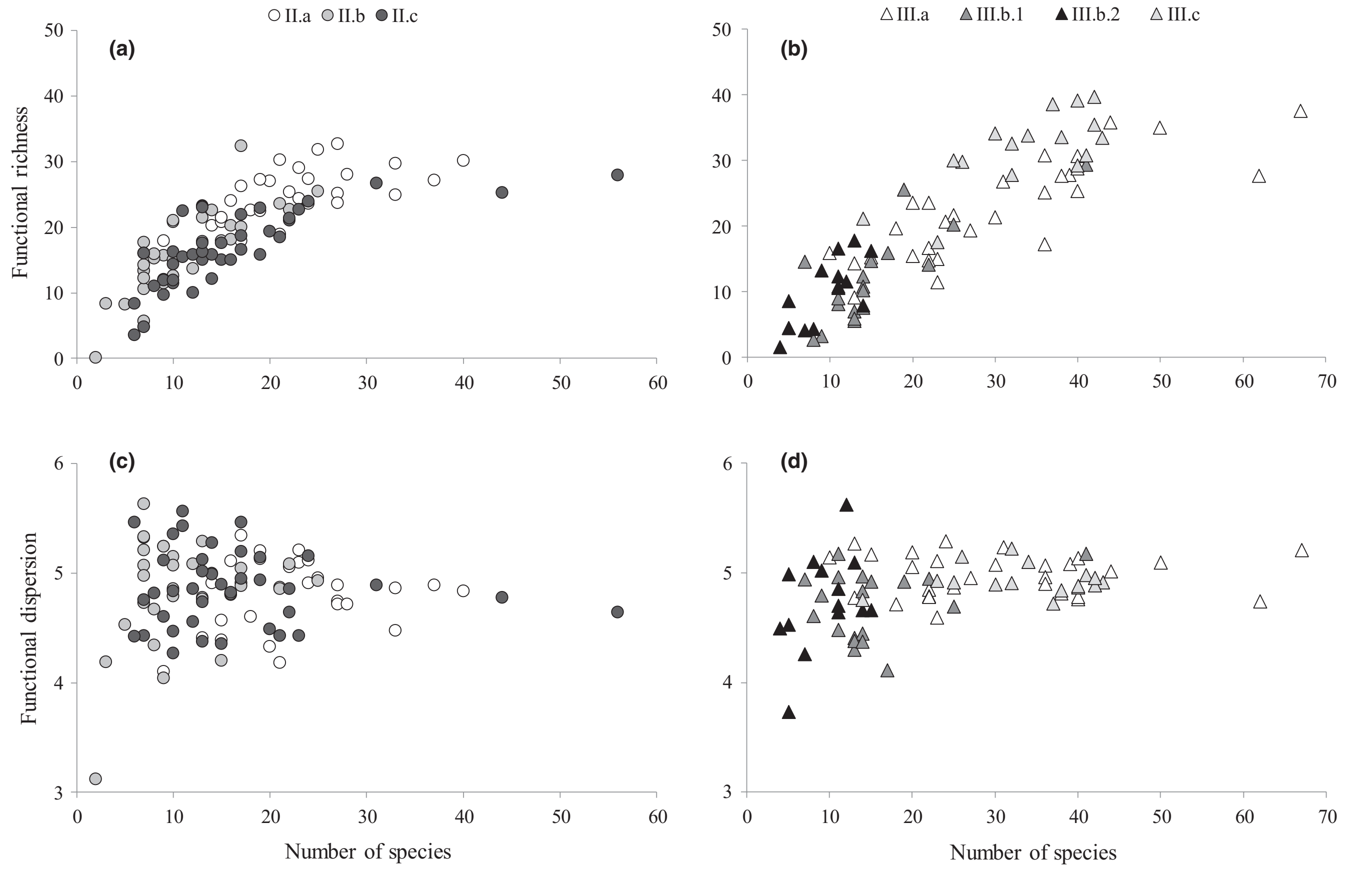

FIGURE 2 Relationship of functional richness (a, b) and functional dispersion (c, d) against the number of species per trawl set on the top (a, c) and deep (b, d) Flemish Cap major faunal groups. Trawl sets are grouped by the assemblages identified by Murillo, Serrano, et al. (2016) and detailed in Section 2.2.1

Flemish Cap as a whole. The FRic of areas closed to protect sponge was higher than the FRic of those closed to protect sea pens, with values of 43.51 and 34.46, respectively.

Predicted FRic from random forest modelling was highest on the south-eastern side of the Flemish Cap (Appendix S6, Figure S6.1a). Relatively high values were also observed elsewhere, including on the shallower part of the Cap (<200 m depth) and in parts of the Flemish Pass. The predicted surface showed a very similar pattern to that of ecological (taxonomic) diversity (Appendix 6, Figure S6.1b) and fishing effort was the most important predictor.

We plotted the CWMs of all assemblages to visualize a functional meta-composition of the seven benthic communities previously defined on the Flemish Cap based on an ecological analysis of species composition (Figure 3). In general, the benthic fauna from the Flemish Cap was characterized by a higher proportion of medium and medium-large species (Figure 3b), while medium-large and large species with long life spans counted for most of the biomass (Figure 3d). Broadcast spawners and brooders with indirect development and pelagic lecithotrophic larvae were the main reproduction method and propagule dispersal mode in both number of species and biomass. Crawlers, mainly predators, and sessile filter-feeder species were the dominant feeding types in the catches. Differences in functional composition between assemblages were better observed using biomass data than presence–absence data (Figure 3a vs. c). Deeper assemblages (Group III) were characterized by higher biomass of large species, and broadcast spawners compared to the assemblages from the shallower area of Flemish Cap (Figure 3d). One of the deep assemblages (III.b.2) was typified by solitary, crawlers, scavengers and predators species.

We observed a positive relationship between functional redundancy and total number of species per assemblage (Figure 4). Functional redundancy was maximum in the deep-sea sponge assemblage (III.c) followed by the shallower assemblage (II.a) of the Flemish Cap. The minimum value of functional redundancy was observed in the assemblage with lower number of species (III.b.2), as expected.

3.2 | Modelling

The explanatory power of the joint species distribution model was 0.27, and the cross-validation-based predictive power was 0.19. Depth explained most of that variability (38.9%), followed by environmental variables related to physical oceanography (32.1%;

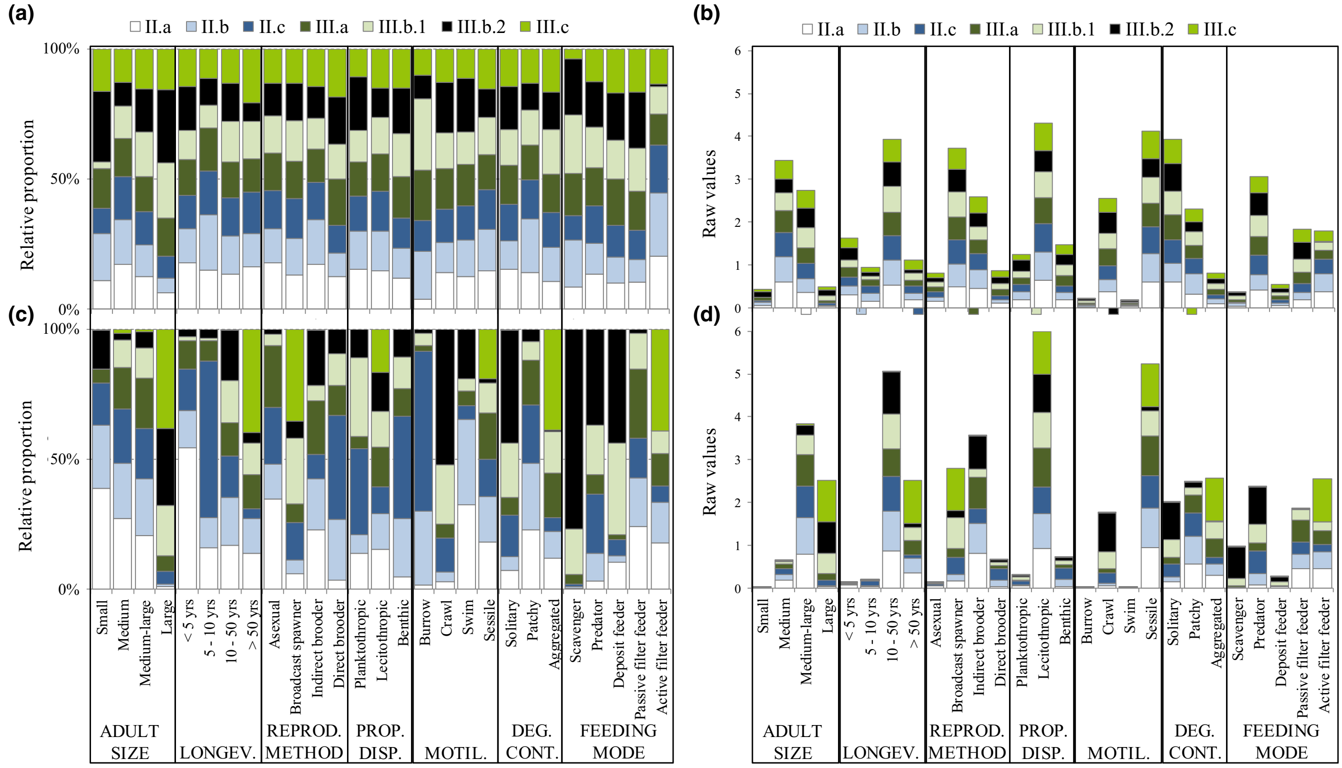

FIGURE 3 Community-weighted means (CWM) of trait category expression. (a, b) Presence–absence data; (c, d) Biomass data. Colour codes represent the epibenthic assemblages identified by Murillo, Serrano, et al. (2016) and detailed in Section 2.2.1. Traits and categories are detailed in Table 1

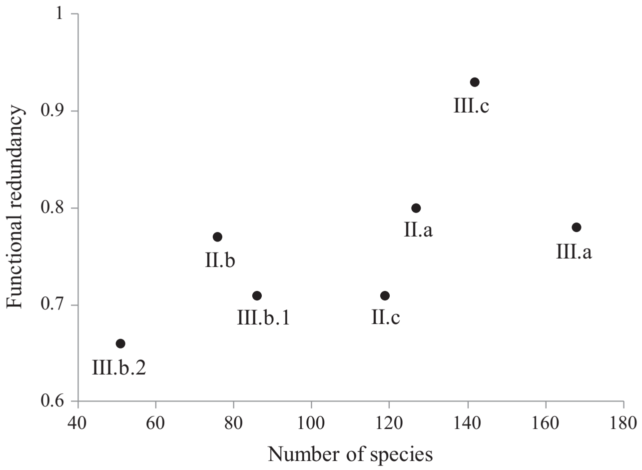

FIGURE 4 Relationship of functional redundancy against number of species per assemblage identified by Murillo, Serrano, et al. (2016) and detailed in Section 2.2.1

maximum bottom current speed, 14.7%; minimum bottom temperature, 12.1%; and maximum mixed layer depth, 5.3%), whereas sediment type (% mud) and fishing effort explained 7.6% and 5.2%, respectively. The random effect at the sample level accounted for 16.3% of the variance.

The species with the best fit were the echinothurid *Phormosoma placenta* and the glass sponge *Asconema foliata*, with R^2 of 0.66 and 061, respectively (Appendix S7). *P. placenta* had the highest probability of occurrence along the north-west of the Flemish Cap associated with muddy bottoms (Appendix S8, Figure S8.2a), while *A. foliata* showed the highest probability at the south-east of the Cap and in several discrete areas around the 500 m isobath (Appendix S8, Figure S8.2b). The most common taxa in the catches, the soft coral *Duva florida*, presented a lower fit (R^2 of 0.19) and was predicted to occur with high probability in most of the study area except for some areas in the north and west (Appendix S8, Figure S8.2c). In general, species with low prevalence fit poorly; however, the large gorgonian coral *Paragorgia johnsoni* presented a good fit (R^2 = 0.56) despite having only three records. This species had a high probability of occurrence associated with small areas in deeper slope areas (Appendix S8, Figure S8.2d).

Figure 5 shows the species–environment responses including the phylogenetic groupings. Some VME indicator taxa, such as the large sponges of the Order Tetractinellida (e.g., *Geodia barretti*, *Thenea* spp.), which are the main components of the deep-sea sponge assemblage (III.c), were positively correlated with maximum bottom current speed whereas sea pens were positively correlated with percentage of mud, corroborating what is known about the ecology of these taxa. In general, most of the species were negatively correlated with fishing effort except the gastropod *Colus islandicus*, the sea star *Pontaster tenuispinosus* and the sponge *Axinella* sp.1 which were positively correlated. The phylogenetic signal of the species' responses to environmental variation (after accounting for

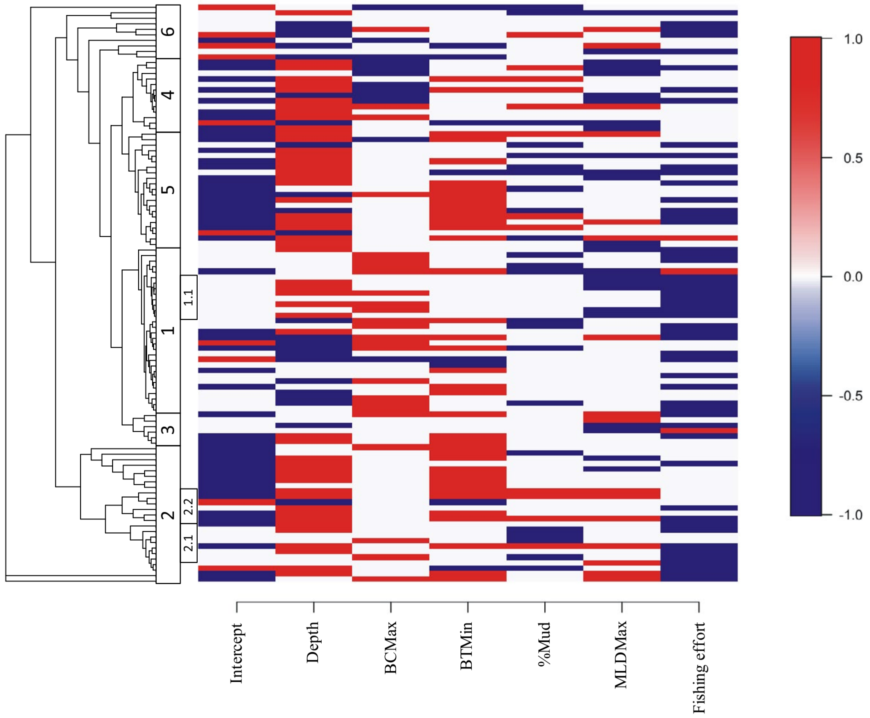

FIGURE 5 Posterior support values for species–environment responses including the phylogeny groupings (support level = 0.9). 1, Porifera; 2, Cnidaria; 3, Mollusca; 4, Arthropoda; 5, Echinodermata; 6, other phyla. VME indicator taxa such as large sponges (Order Tetractinellida, 1.1), gorgonian corals (2.1) and sea pens (2.2) are indicated. BCMax, maximum bottom current speed; BTMin, minimum bottom temperature; MLDMax, maximum mixed layer depth. Red indicates positive correlations with environmental variables, and blue indicates negative correlations

the effects of the measured traits) was 0.58, indicating that over half of the residual environmental responses of the species are explained by phylogenetic correlations.

The selected biological traits explained 25% of the variance in the model. From the 38 hypothesized relationships between trait category and the covariates considered in the model (Table 2), 25 followed the expected relationship (Figure 6). Contrary to expectation, maximum size did not follow the expected relationship with depth. The predicted probability of smaller sizes (small and medium) and short life span species (<5 and 5–10 years) shows a decrease with depth, whereas large organisms with long life spans increase (Figure 6a–h), indicating that species tend to be larger and longer-lived in deeper waters. Similarly, planktotrophic dispersal decreased with depth and lecithotrophic and benthic dispersal increased (Figure 6i–k). Both deposit-feeders and passive filter-feeders showed an increase with maximum bottom current (Figure 6l,m), whereas active filter-feeders decreased (Figure 6n). Similarly, deposit-feeders and passive filter-feeders increased with maximum mixed layer depth (Figure 6t,u). A decrease in the proportion of large and long-living species was found in relation to fishing effort (Figure 6x,y,ac). Both planktotrophic and lecithotrophic dispersal showed a decrease with fishing effort (Figure 6ae,af). Fishing effort had a positive influence on crawlers and predators (Figure 6ag,aj), whereas it was negative for sessile species and filter-feeders (Figure 6ah,ak,al). However, most predictions show high 95% credible intervals and only illustrate broad trends. Additionally, the posterior mean sign did not always follow the predicted trend, indicating that these relationships were weak and/or that they did not follow linear relationships (Figure 6).

3.3 | Mapping of selected traits and ecosystem functions

The probability of occurrence of each trait category in the study area is shown in Appendix S9 and showed spatial separation between some trait modalities in each trait category. The shallower areas of the Flemish Cap were predicted to contain a higher proportion of small- and medium-size species with shorter life span compared to the deeper areas that were dominated by larger and long-living species (Appendix S9, Figure S9.3, and S9.4). Most of the areas were predicted to have a dominance of sessile and highly aggregated species, excluding small areas north and south-west of the Cap (Appendix S9, Figure S9.7d, and S9.8c). Active filter-feeding was the dominant feeding mode on the top and south-east of the Cap, whereas passive filter-feeding dominated on a ring along the north of the Cap between 500 and 1,000 m depth, with predator species in the rest of the area (Appendix S9, Figure S9.9).

The predicted biomass of the bioturbation function was higher on a ring around the Flemish Cap between 400 and 1,100 m depth (Figure 7a), mostly associated with low standard error (Figure 7d). It was mainly driven by the sea pen *Anthoptilum grandiflorum* which was the heaviest and most common species (Appendix S8, Figure S8.2e). The biomass of nutrient cycling and habitat provision functions presented a similar pattern (Figure 7b,c), being higher in the deeper waters, in some areas between 600 and 900 m depth and in the shallower part of the Cap. The higher values of these functions overlap with the highest occurrence probability of the large sponge *Geodia barretti* (Appendix S8, Figure S8.2f). The standard error surface was also similar for both predicted surfaces (Figure 7e,f), except in the east of the Flemish Cap, where high standard error was observed for the habitat provision function, whereas it was medium for nutrient cycling.

4 | DISCUSSION

4.1 | Characterization of functional diversity

Functional diversity (FD) has been shown to respond differently to, and often perform better than, taxonomic-based diversity measures when studying ecosystem changes and functioning (Cadotte et al., 2011; Gagic et al., 2015; Törnroos & Bonsdorff, 2012) and it has been recommended that conservation efforts should focus on preserving FD rather than species richness (Cadotte et al., 2011). However, in some instances, the calculation of FD is a challenging task, subject to the number and types of biological traits selected and the index used (Legras et al., 2018), and therefore cannot be easily transferred and generalized between different systems and sites (Jax, 2005). Additionally, the lack of knowledge for many traits of deep-sea species (Tyler et al., 2012) results in many categories relying on inferences from closely related species which may or may not be accurate and which may increase the importance of phylogenetic relationships in the analyses. In the Flemish Cap area, FD showed high agreement with ecological diversity based on the number of species (Appendix S6), indicating that in this area both components of biodiversity are aligned and affected by fishing activities,

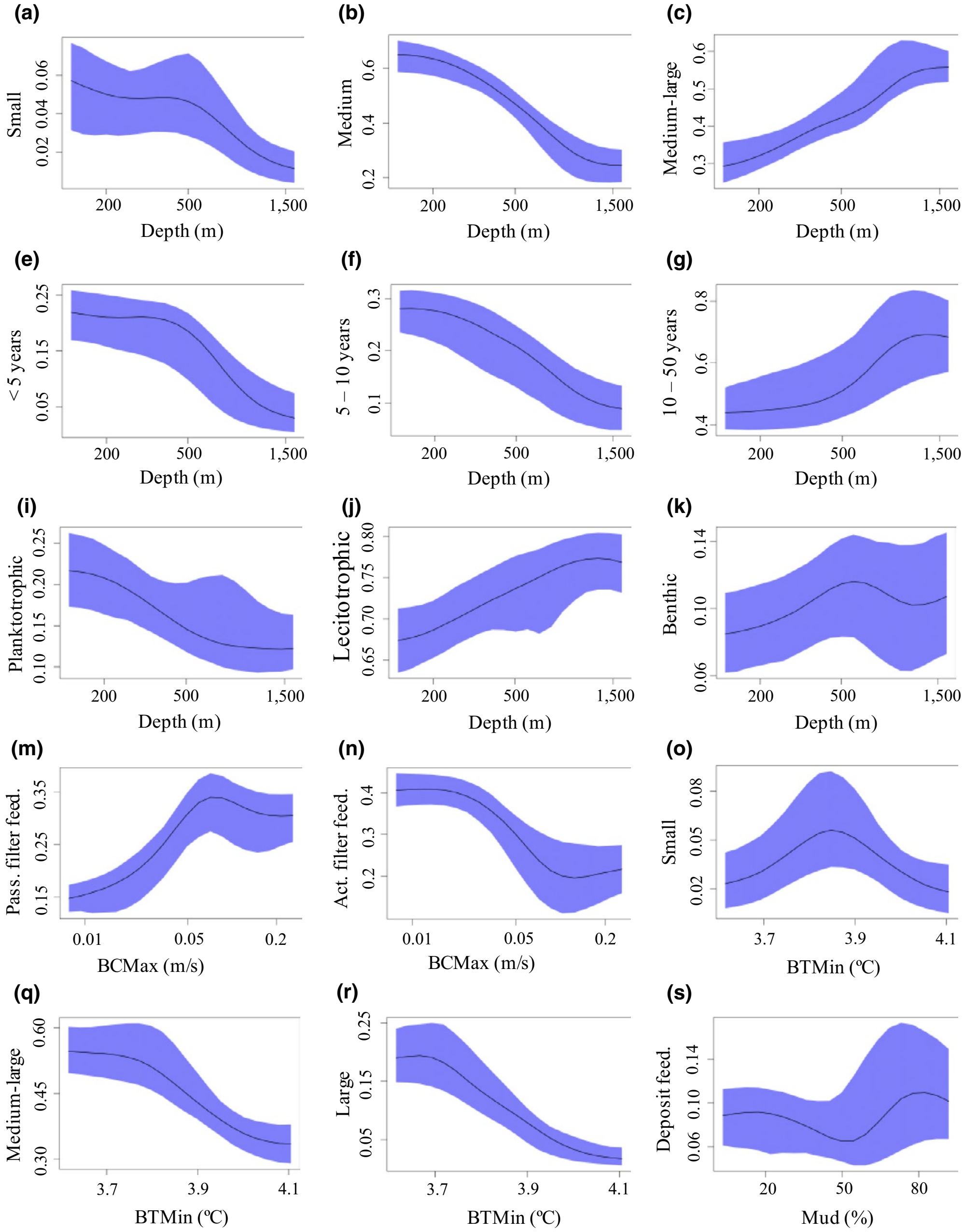

FIGURE 6 Predicted community-weighted mean of trait categories as response to covariates for the 38 hypothesized relationships indicated in Table 2. Values on panels (a)–(n) and (v)–(al) are plotted on a logarithmic scale. The blue areas represent 95% credible intervals. For description of traits, see Table 1. Act, active; BCMax, maximum bottom current speed; BTMin, minimum bottom temperature; feed, feeder; MLDMax, maximum mixed layer depth; pass, passive.

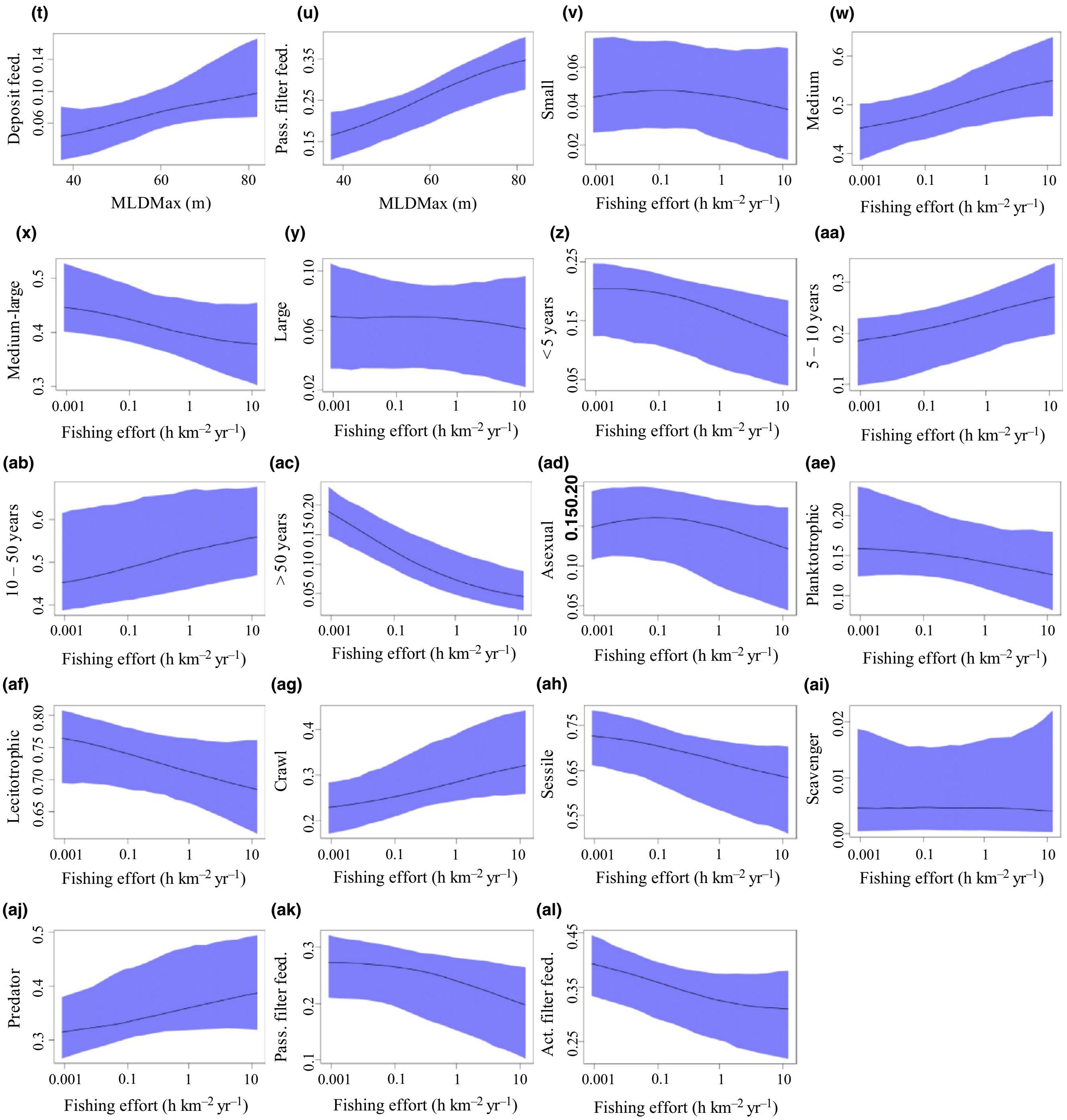

FIGURE 6 (Continued)

and could be integrated for management purposes, recognizing that conservation of rare species requires a different management approach (Bakker & Doak, 2009; Zhou, Milton, & Fry, 2012).

Functional richness (FRic) increased with the number of species observed in each assemblage comprising up to ≈30 species after which it levelled off, indicating that higher species numbers did not contribute further to higher FRic. This suggests that no new traits were added to increase the functional trait space occupied by this number of species, pointing towards functional redundancy. Another facet of functional diversity is functional dispersion (FDis). Ecosystems displaying high FDis are assumed to have a broad range of ecosystem functions (Clark, Flynn, Butterfield, & Reich, 2012). We observed high variation of FDis values in assemblages with <20 species. With increasing number of species, the variation of FDis decreased. Less variation in FDis indicates a higher functional redundancy, with higher species richness not being associated with higher FDis (Cadotte et al., 2011). Large variation of FDis in the species-poor assemblages suggests a high variation in ecosystem functioning as well as a low adaptability to environmental change.

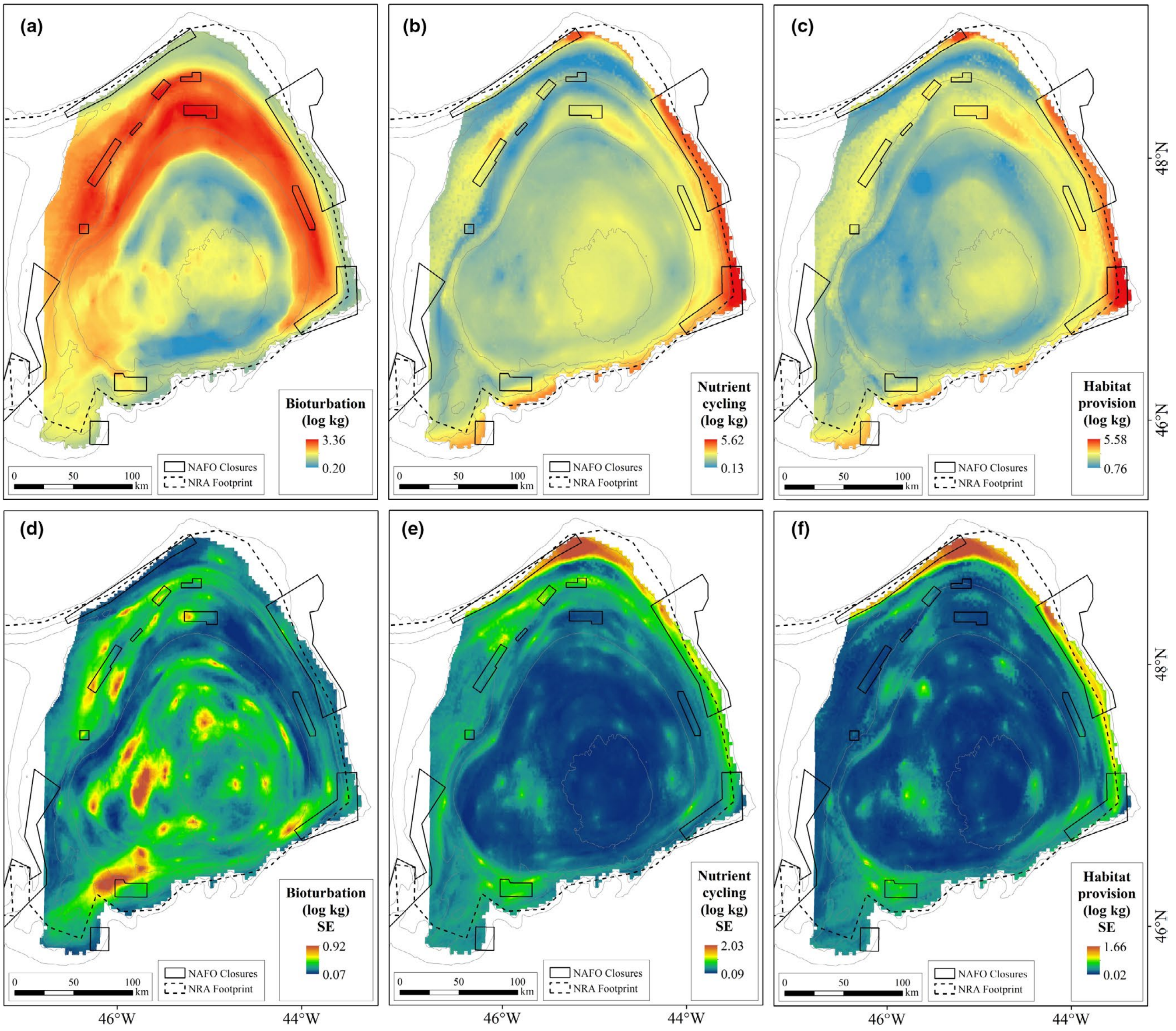

FIGURE 7 Predicted ecosystem functions from random forest modelling of (a) bioturbation, (b) nutrient cycling and (c) habitat provision. d–f) Standard error (*SE*) associated with each predicted surface. Areas closed to bottom fishing activities to protect sponge and coral concentrations and existing bottom fishing areas (NRA Footprint) are also indicated (NAFO, 2018a)

Functional redundancy is an important factor for maintaining ecosystem conditions when faced with environmental disturbances (Standish et al., 2014). In the present study, the high functional redundancy observed in the deep-sea sponge communities (assemblage III.c) could have enabled the persistence of the sponge grounds in the area for more than 17,000 years (Murillo, Kenchington, Lawson, Li, & Piper, 2016) and could help ensure their survival under future climate change conditions. However, this community and others with high redundancy in the Flemish Cap have biological traits such as large size, long life span and/or no mobility (sessile), that are very vulnerable (sensu FAO, 2009) to bottom-contact fishing activities. Therefore, the high redundancy of these communities alone would not ensure the maintenance of the function associated with these traits under such physical disturbance. Also, the phylogenetic relatedness of these sponge species imposes a risk of narrower physiological tolerance to environmental change than might be created through a suite of unrelated species.

4.2 | Response traits to the environment and degree of phylogenetic influence

Using HMSC enabled us to assess the influence of species traits through their occurrences while accounting for the phylogenetic signal in the data (Ovaskainen et al., 2017). Despite having only seven biological traits included in our model, they explained 25% of the variation in the species responses to the covariates considered in the analysis, indicating the relevance of the traits to the community assembly. Most of the community-weighted mean trait values changed with depth and physical oceanographic variables, indicating that environmental filtering was occurring. This result is common in studies at large spatial scales, where faunal zonation is aligned to the different hydrographic regimes (Neumann et al., 2013). Depth and maximum bottom current speed were the best environmental predictors, contributing 38.9% and 14.7% of the total explained variation, whereas interspecific interactions as inferred from the random effect at the sample level, and which can also account for missing environmental covariates (Zurrell, Pollock, & Thuiller, 2018), accounted for 16.3% of the variance in the model. The high value of the phylogenetic signal (more than half of the residual environmental responses of the species) suggests the existence of some traits correlated with phylogeny that were not included in our analysis.

In general, there was a good agreement between the hypothesized relationships between biological trait categories and the environmental variables considered in this study, although the relationships were weak and nonlinear in most of the cases, the latter possibly explaining the statistical results. Numerous studies have documented bathymetric size trends in recent decades. In general, the depth-size relationship has been found to be positive within-taxa and negative within faunal groups (Carney, Haedrich, & Rowe, 1983), although there are some cases of gigantism at abyssal depths (Lowry & Dempsey, 2006; Timofeev, 2001). Some authors have suggested that food limitation in the deep sea promote small sizes (Rex et al., 2006), but at the same time a larger size would increase metabolic efficiency in poor food environments (Rex, Etter, Clain, & Hill, 1999), which could explain this dichotomy. Our results indicated that medium-large and large organisms increased with depth, and the positive relationship within faunal groups found in this study is mainly related to the larger size of some deep-sea species, such as astrophorid sponges, gorgonian corals, echinoderms or arthropods. These taxa can also reach high biomass around 1,000 m depth indicating that particle flux may be supplemented by lateral current-carried supply (Kenchington, Yashayaev, Tendal, & Jørgensbye, 2017).

The relationship between larval type and their depth distribution is not as constant and direct as originally proposed. Our data confirm a trend observed by Mileikovsky (1971) of decreased pelagic (planktotrophic) development with increasing depth, which was related to the scarcity of food and increasing hydrostatic pressure.

In our study, both passive filter and deposit-feeders were associated with high current velocities. High current velocity removes sediment and organic matter (Wetzel, Werner, & Stow, 2008) which could cause a high load of suspended material providing good feeding conditions for suspension feeders whereas deposit-feeders dominate at lower flow velocities (Flach, Lavaleye, de Stiger, & Thomsen, 1998). Although high current velocities can also remove epifauna (Wetzel et al., 2008), areas dominated by suspension feeders can locally change flow velocities and cause resuspension and passive biodeposition of particles (Flach et al., 1998). Areas of high current velocities in our study were dominated by astrophorid sponges (Knudby, Kenchington, & Murillo, 2013) and the main deposit-feeders found were ophiuroids that could be taking advantage of a passive biodeposition added to the detritus provided by the sponges (De Goeij et al., 2013; Witte, Brattegard, Graf, & Springer, 1997).

Mixed layer depth (MLD), or depth at which surface vertical mixing dissipates, together with light and nutrients controls biological productivity (Yentsch, 1990). According to the dilution-recoupling hypothesis, deep winter mixing is essential for phytoplankton bloom formation which is related to maximum MLD values (Behrenfeld, 2010). It is unknown how much primary production reaches the bottom in the Flemish Cap, but the positive relationship observed between maximum MLD and organisms relying on food supply from the water column such as deposit and passive filter-feeders could be indicating a direct link between primary production and benthic biomass in this area.

The hypothesized relationships between traits and fishing effort followed the expectations for most of the cases (Figure 6). However, these relationships were only weak, likely due to the fact of analysing only presence–absence data and the patchiness of fishing effort, being higher in deep waters. The Flemish Cap has suffered the impact of bottom-trawl activities at least for 70 years (Templeman, 1966) and although the consequences for ecosystem functioning are unknown, bottom trawling reduces benthic biomass (Sciberras et al., 2018), and modifies the benthic communities towards a suppression of large, filter-feeders and long-living species, such as sponges and corals, which are replaced by small, mobile scavengers and opportunistic species (Kenchington, Kenchington, Henry, Fuller, & Gonzalez, 2007; Sciberras et al., 2018; Tillin, Hiddinkk, Jennings, & Kaiser, 2006). We have found expected (albeit weak) relationships between fishing effort and some biological traits of the benthic species. Increased fishing effort was consistent with increases in predators and decreases in the presence of both passive and active filter-feeders (Figure 6b, panels aj–al).

4.3 | Mapping of selected effect traits and ecosystem functions

NAFO has closed 14 areas in its Regulatory Area to protect deep-sea coral and sponge VMEs from the impact of bottom fishing activities (NAFO, 2018a). Collectively, the closed areas placed on Flemish Cap included almost all of the functional diversity in the area despite encompassing only 9% of the total sampling locations and being located in waters deeper than 500 m. In addition, the functional diversity was higher for the closures protecting sponges than those put in place for sea pens, representing 96% and 76% of the total FD, respectively. The sponge grounds are very important functional benthic habitat in the Flemish Cap area, in terms of both spatial extent and biomass (Murillo et al., 2012; Murillo, Serrano, et al., 2016). They group more than 90% of the total invertebrate biomass and are responsible for most of the nutrient cycling and habitat provision function in the deepest area. Sponges can transform the majority of the dissolved organic matter into particulate detritus, providing nutrients to other organisms (De Goeij et al., 2013; Witte et al., 1997). This, coupled with the biogenic habitat that sponges provide, explains the high benthic diversity associated with these grounds (Beazley et al., 2013, 2015). The sea pen habitats are important as structure formers (Baillon, Hamel, & Mercier, 2014; De Clippele, Buhl-Mortensen, & Buhl-Mortensen, 2015) and are also associated with bioturbation activity which can alter the physical and chemical properties of marine sediments (Boudreau & Marinelli, 1994), increasing sediment permeability, remineralization, or inorganic efflux, among others (Lohrer, Thrush, & Gibbs, 2004). Although their biomass is lower than the sponge grounds, they add important and different functions to areas with few other large taxa present. Large gorgonian corals also play an important role as structure formers. However, trawl catches have shown that in the sampling area they do not form large habitats that have a significant influence on diversity (Murillo et al., 2020). However, they could also be more important on hard bottoms not sampled by trawl gears. Most of the functions associated with these VME taxa are found around the slopes of Flemish Cap. However, on the shallowest water on top of Flemish Cap, <200 m depth, we have found some of these functions created by smaller sponges and scattered sea pens, where the ecological diversity based on the number of species is also high (Appendix S6) and could be linked to this sponge presence, providing food and habitat to other invertebrates.

Benthic communities from the top of Flemish Cap (<500 m) included large gorgonian corals and black corals more than 60 years ago (Nesis, 1963, 1965), not seen presently. Additionally, the sponges of the shallower part of the Cap were abundant then. Consequently, the FD of the Flemish Cap may have been modified by bottom fishing over the decades. Reduction and/or depletion of these biogenic structures will lead to a loss of biodiversity and the ecological processes associated with them, and therefore, the impact will be stronger if functions are considered together (Byrnes et al., 2014). Cod (*Gadus morhua*) juveniles and American plaice (*Hippoglossoides platessoides*) on the Flemish Cap feed mainly on benthic organisms (Gonzalez et al., 2006; Paz, Casas, & Pérez-Gándaras, 1993). How much the slow recovery of these benthic communities could impact the fish production and how the lack of recovery of species such as the American plaice could be linked to available benthic food resources remains an open but important question. Trait-based frameworks could further help to shed light on the effects that changing prey communities may have on the resource quality for their predators (Weigel & Bonsdorff, 2018). The 'NAFO Roadmap' for the development and implementation of an ecosystem approach to fisheries in the NAFO Area (Koen-Alonso et al., 2019) has tried to integrate the impacts of fishing activities on benthic communities. Significance adverse impacts (SAIs) on habitats are being evaluated through consideration of recovery potential, ecosystem function alteration and impact (FAO, 2009; NAFO, 2018b). Including the assessment of the loss of ecological functions through fishing and taking measures to enhance the recovery of benthic communities could potentially add to the rebuilding of historically important stocks that depend on benthic resources.

Although we have been able to map the spatial distribution of these three key ecosystem functions, and attribute the percentage of total functional diversity found in the closed areas, we do not know the spatial scales of influence for each of the functions. For example, the lower levels of nutrient cycling and habitat provision found over the muddy areas where bioturbation dominate may be critical if the spatial scale of influence of nutrient cycling is restricted and cannot have any influence in other areas of the Flemish Cap. The complex bottom currents in the area (Kenchington et al., 2019) indicate that retention can be quite high in some areas near bottom but that there is a rapid movement of water at the surface reaching velocities of >20 cm/s. Therefore, we cannot be confident that the high level of functional diversity found in the currently closed areas is sufficient to maintain ecosystem processes over the whole of Flemish Cap and in particular, in the shallower areas, where no closure is in place and different benthic and fish communities exist (González-Troncoso, Paz, & Cardoso, 2006; Murillo, Serrano, et al., 2016).

The use of a joint species distribution modelling approach, such as HMSC, has allowed us to reproduce some of the assembly mechanisms of the benthic communities of the Flemish Cap and to understand where key species for the function of the benthic ecosystems occur as well as to identify the likely drivers of their distribution. Our results suggest that while bottom-contact fishing impacts have an effect on functional diversity, changes to the physical oceanography of the system are likely to have much more profound impacts at the ecosystem scale. This information can also be used to predict the benthic communities in unsampled areas or to forecast their distributions under different conditions, for example, following climate change projections, and to assess the effect of trawling activities in the case of new grounds being explored. The maps of benthic functioning can aid assessments of ecosystem impacts of fishing. This integrative modelling framework provides a way to synthesize community data to answer key questions in ecology, presenting a useful framework for management and conservation.

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DATA AVAILABILITY STATEMENT

Data available at the Mendeley Repository: benthic data at http://dx.doi.org/10.17632/y8wj8rvm89.1, and explanatory variables and predicted surfaces at http://dx.doi.org/10.17632/n6vxdhhmrz.1

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BIOSKETCH

Our research involves a broad range of topics related to ecosystem dynamics, conservation and management through the use of qualitative and quantitative methods, including new modelling techniques. Additionally, we are interested in the study and conservation of deep-sea coral and sponge ecosystems from the north-west Atlantic Ocean and the biodiversity associated.

Author Contributions: FJM, BW and EK conceived the ideas and designed methodology; FJM and MBM collected the data; FJM and BW analysed the data; and FJM and EK lead the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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