Distribution models of deep-sea elasmobranchs in the Azores, Mid-Atlantic Ridge, to inform spatial planning

Diya Das [a,1,*], José Manuel Gonzalez-Irusta [a,b,1], Telmo Morato [a,c], Laurence Fauconnet [a,c], Diana Catarino [c,d], Pedro Afonso [a,c], Cláudia Viegas [a,c,e], Luís Rodrigues [a,c], Gui Menezes [a,c], Alexandra Rosa [a,c], Mário Rui Rilhó Pinho [c], Helder Marques da Silva [c], Eva Giacomello [a,c]

[a] Institute of Marine Research (IMAR), IMAR Centre of the University of the Azores, Rua Prof. Doutor Frederico Machado No. 4, 9901-862 Horta, Portugal
[b] Instituto Español de Oceanografía, Centro Oceanográfico de Santander, Promontorio San Martín s/n, 39004, Santander, Cantabria, Spain
[c] Institute of Marine Sciences - OKEANOS, Rua Prof. Doutor Frederico Machado No. 4, 9901-862 Horta, Portugal
[d] Centre for Coastal Research, Department of Natural Sciences, University of Agder, 4630, Kristiansand, Norway
[e] Marine and Environmental Sciences Centre (MARE-UC), University of Coimbra, 3004-504, Coimbra, Portugal

ARTICLE INFO

ABSTRACT

Elasmobranchs inhabiting depths beyond 200 m are extremely susceptible to overexploitation but are extracted by fisheries around the world either as target species or as bycatch. There is little information available to formulate management strategies to reduce elasmobranch-fishery interactions in the deep sea. In European Union waters, prohibiting the catches of deep-sea elasmobranchs has provided the necessary impetus to study by-catch avoidance of these threatened species. We used over 20 years of fisheries-independent and fisheries-dependent data to model the spatial distribution of 15 species of deep-sea elasmobranchs (12 sharks and 3 rays) captured frequently in the Exclusive Economic Zone of the Azores Archipelago (Mid-Atlantic Ridge) to explore spatial management to reduce unwanted catches of these species. We applied Generalised Additive Models to predict the probability of presence of 15 species, as well as the abundance of 6 of those species, within the Azores EEZ and neighbouring seamounts (up to 2000 m depth), using environmental and operational variables as predictors. Our results identified that depth is most influential in determining the distribution of these sharks and rays, in addition to seafloor topography. Distinctive bathymetric features such as seamounts and ridges were highlighted as areas where the probability of presence of the greatest number of species overlapped. Although not related to habitat, gear type influenced the capture probability of certain species, with the artisanal handline, *gorazeira*, having lower captures than bottom longline. Our results support using depth-based, area-based, and gear-based tactics to design management measures to reduce elasmobranch bycatch, for more sustainable deep-sea fisheries.

1. Introduction

The steady expansion of industrial fishing into the deep sea (beyond 200 m) has elicited concern for the conservation of this habitat and its species for some time now (Morato et al., 2006; Norse et al., 2012). Low intrinsic population growth rates of the organisms inhabiting this environment makes them extremely sensitive to disturbances like fisheries and climate change (Danovaro et al., 2017; Levin et al., 2020). Deep-sea elasmobranchs have life-history traits, including slow growth, late sexual maturity, low fecundity, and high longevity (Frisk et al., 2001; García et al., 2008; Dulvy et al., 2017), that lends them the lowest productivity (Rigby and Simpfendorfer 2015) when compared to other elasmobranch (García et al., 2008) or deep-sea teleost species (Clarke et al., 2003). This makes them susceptible to overfishing at even low rates of extraction (Frisk et al., 2001; Pardo et al., 2016), and severely limits the ability of the population to recover after fishing has ceased (Simpfendorfer and Kyne 2009). Nevertheless, they are regularly caught either intentionally (Hareide et al., 2007) or accidently (Correia and

Smith 2003; Fauconnet et al., 2019a) in deep-sea fisheries worldwide. Not surprisingly, more than one-third of the deep-sea elasmobranchs listed in the IUCN Red List of Threatened Species are in the threatened category (viz. Vulnerable, Endangered or Critically Endangered), or classified as Data Deficient (IUCN 2021) a majority of which may in fact be threatened (Walls and Dulvy 2020). The elevated risk of potentially irreversible population declines due to fisheries (Kyne and Simpfendorfer 2007; Simpfendorfer and Kyne, 2009; Dulvy et al., 2017) warrants proper management regulations for deep-sea elasmobranchs.

Though elasmobranchs feature prominently as incidental catch in most fisheries (Oliver et al., 2015), bycatch reduction research for these species has generally received less attention compared to other vulnerable and emblematic marine life such as marine mammals, sea birds, and sea turtles (Werner et al., 2006). In Europe, a discard ban or the 'Landing obligation' (LO) was implemented by the Common Fisheries Policy (Council Regulation No. 1380, 2013) as an incentive to reduce unwanted catches (Condie et al., 2014; Guillen et al., 2018). Under LO all catches of species managed by Total Allowable Catch (TAC) are required to be kept on board, landed, and deducted from their respective quotas. The fishery is closed once the quota of a single species is reached. Hence, species subject to lower TAC can rapidly 'choke' a multi-species fishery into closing prematurely as their quotas can be reached sooner. Given this scenario, deep-sea shark species that were subject to zero TAC (Council Regulation No. 1359, 2008) could theoretically 'choke' the fishery with even a single catch, necessitating a better understanding of how their catches could be avoided (Catchpole et al., 2017). Eventually the zero TAC of deep-sea sharks was revoked, and they were listed as prohibited species (Council Regulation No. 2025, 2018). This meant they were no longer subject to the LO regulation. Instead, the fishing prohibition now requires the fish to be released immediately on capture and emphasises on the need to reduce their fishing mortality. Improving the selectivity of the fishing methods (O'Neill et al., 2018) and avoidance strategies (Reid et al., 2018) such as spatial management, are particularly relevant for deep-sea elasmobranchs since post-release survival of these species is suspected to be low (Rodríguez-Cabello and Sánchez 2017; Talwar et al., 2017), although fishers believe the contrary (Fauconnet et al., 2019b).

In the waters of the Mid-North Atlantic archipelago of the Azores, bycatch of deep-water sharks occurs on a regular basis in the deep-water hooks and lines fisheries (Pham et al., 2013; Fauconnet et al., 2019a). Despite bycatch amounts being small (approximately 220 t per year, Fauconnet et al., 2019a), of the thirty-one elasmobranch species known to occur in the Azores below 200 m depth, several are classified as threatened in the European IUCN Red List (Das and Afonso 2017). The Azores region represents a transition zone for elasmobranch species, falling between the southern boundary of cold-water species and the northern boundary of tropical and sub-tropical species (Das and Afonso 2017). The importance of the Azores as a fringe habitat is expected to increase with the climate-driven shifts in species distributions (Afonso et al., 2013). There is, therefore, a strong need to identify areas with high occurrences of deep-sea elasmobranchs to promote best fisheries management practices, spatial management, as well as to promote species conservation strategies.

Distribution models are a suite of statistical tools that predict distribution of a species using occurrence data from field observations correlated with available georeferenced environmental predictors (Guisan and Thuiller 2005; Elith and Leathwick 2009). These models can be used to highlight areas of higher predicted richness or abundance of regulated species, that could be avoided to reduce unwanted catches (Reid et al., 2018). In the case of data-poor, difficult to observe and threatened species such as deep-sea elasmobranchs, these models provide crucial data to inform fisheries and management strategies (Guisan et al., 2013). In this work, we developed Generalised Additive Models (GAMs) to infer the distribution of 15 deep-sea elasmobranchs that are caught as bycatch in the Azores deep-sea hooks and lines fisheries. This study can inform conservation, spatial planning, and fisheries

management, by providing insights into spatial bycatch avoidance measures.

2. Methods

2.1. Study area

We developed predictive distribution models of deep-sea elasmobranchs for up to 2000 m depth in the Azores EEZ, from approximately 33°N to 43°N and 20°W to 36°W (Fig. 1). The Azores is a Portuguese archipelago of nine islands located around the Mid-Atlantic Ridge (MAR), with an EEZ of about one million km², narrow shelves and steep slopes, surrounded by a highly rugged and deep seabed hosting numerous distinctive bathymetric features (Peran et al., 2016). Deep-sea fisheries are central to the Azores economy (Pinho and Menezes 2005; Carvalho et al., 2011), and fishing activities – with hooks and lines gears – are concentrated on the island slopes, seamounts, and ridges (Pinho and Menezes 2005). Bottom trawling is not allowed. Although deep-sea elasmobranchs are underreported in the local fisheries statistics, they are often caught as by-catch in the hooks and lines fisheries (Fauconnet et al., 2019a).

2.2. Species selection and occurence data

Fifteen elasmobranch species with predominantly demersal and deep-water (i.e., > 200 m depth) affinities, were selected based on their relevance as bycatch in deep-sea fisheries and on the availability of spatial occurrence and abundance data (Table 1). This study included 12 species of deep-water sharks and 3 species of deep-water rays with different IUCN Red List Categories (Dulvy et al., 2014; Nieto et al., 2015) and EU fisheries regulations (Council Regulation No. 1359, 2008; Council Regulation No. 2025, 2018). We compiled species presence-absence data for all 15 species (> 30 presence records) and abundance data for the 6 most frequently caught species (> 1000 individuals caught, i.e., *Deania calcea, Deania profundorum, Etmopterus pusillus, Etmopterus spinax, Galeorhinus galeus,* and *Raja clavata*).

We obtained georeferenced presence, absence, and abundance data from scientific surveys and commercial operations (Table 1) reporting at least one deep-sea elasmobranch capture. A 20-year 'survey dataset' (1996–2017) was compiled from scientific demersal surveys using two types of bottom longlines (types LLA, 639 sets, and LLB, 27 sets), and an 'observer dataset' (2004–2018) from observer programs covering commercial fisheries operations using bottom longline (similar to type LLA, 537 sets) and vertical handline ('gorazeira', 174 sets) targeting *Pagellus bogaraveo* (details in supplementary material, Appendix A, along with maps of presence, Fig. B1). Some of the caveats to the use of data collected with longlines and handlines for predictive species distribution models have been discussed in Parra et al. (2017).

2.3. Explanatory variables

Candidate predictors were an initial set of 11 environmental variables considered relevant for explaining the spatial distribution of deep-sea elasmobranchs. All variables were projected with the Albers equal-area conical projection centred in the middle of the study area and were rescaled using bilinear interpolation to a final grid cell resolution of 1.12×1.12 km (i.e., 0.012°). We merged existing multibeam data for the Azores EEZ with bathymetry data extracted from EMODNET (EMODnet Bathymetry Consortium, 2018) to calculate depth values (down to 2000 m). Using the function *terrain* in the R package *raster* (Hijmans 2015) we computed terrain derivates such as slope (degrees) and aspect (northness and eastness) from the raster for depth. Bathymetric Position Index (BPI, a measure of a location height relative to its surroundings) was derived from the rescaled depth with an inner radius of 3 and an outer radius of 25 grid cells using the Benthic Terrain Model 3.0 tool in ArcGIS 10.1 (Walbridge et al., 2018).
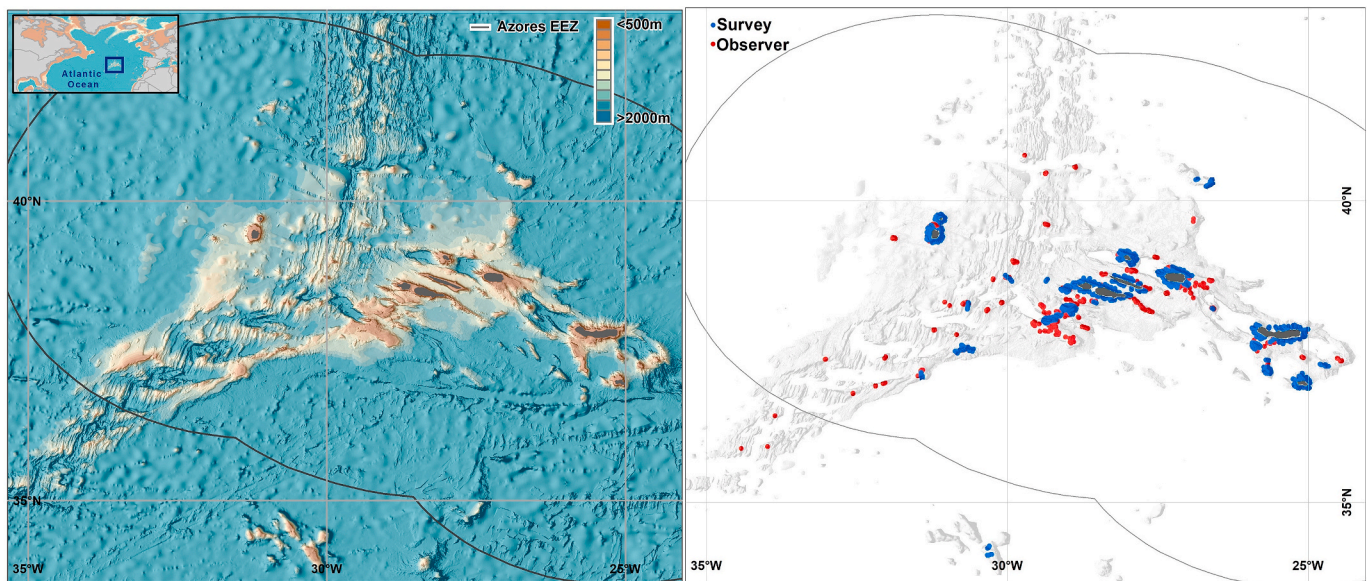
Fig. 1. Map of the Azores Exclusive Economic Zone (left panel) and distribution of data from the scientific surveys (blue) and from commercial fisheries operations (red) used for predictive modelling of 15 species of deep-sea elasmobranchs (right panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Summarised attributes of the 15 elasmobranch species selected for developing predictive distribution models and abundance models (marked by *), from the available scientific and commercial datasets in the Azores, including IUCN Red List Categories, and EU fisheries regulations status (Y for prohibited species). Taxonomy following the World Register of Marine Species (WoRMS Editorial Board, 2021).

Species	No. of occurrences		No. of individuals [a]	IUCN [b]	Prohib. spp.	Depth range (m)	Mean depth of catch (m)	Reference Year [c]
	Survey	Observer						
TRIAKIDAE								
Galeorhinus galeus *	290	51	1048	VU		12–836	232	1996
CENTROPHORIDAE								
Centrophorus squamosus	71	4	106	EN	Y	304–1442	1051	1996
Deania calcea *	614	46	1802	EN	Y	252–1481	988	1996
Deania profundorum *	1022	61	3354	DD		276–1276	743	1996
DALATIIDAE								
Dalatias licha	96	97	364	EN	Y	161–1047	557	2001
Squaliolus laticaudus	47	0	51	LC		135–997	635	2001
ETMOPTERIDAE								
Etmopterus princeps	61	1	218	LC	Y	669–1943	1358	1999
Etmopterus pusillus *	843	161	1896	DD		139–1250	692	1996
Etmopterus spinax *	991	177	5093	NT	Y	153–1196	563	1996
SOMNIOSIDAE								
Centroscymnus coelolepis	60	0	83	EN	Y	860–1812	1326	2000
Centroscymnus crepidater	205	0	276	LC	Y	622–1481	1080	1999
Centroscymnus owstonii	34	1	39	NA (VU)		226–1481	1064	1999
RAJIDAE								
Dipturus batis [d]	103	81	358	CR	Y	59–891	442	2001
Leucoraja fullonica	17	31	75	VU		182–806	483	2001
Raja clavata *	634	145	3344	NT		12–812	230	1996

[a] Presence records obtained from the 'survey' and 'observer' datasets, and the total number of individuals captured from 1996 to 2018.
[b] IUCN categories, according to the last European Red List assessment (Nieto et al., 2015), are: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NA = Not Evaluated (global status given in parenthesis).
[c] Reference year is the first year with presence records in the datasets.
[d] *Dipturus batis* is a species complex composed by two species, first identified as *D.* cf *intermedia* and *D.* cf *flossada* by Iglésias et al. (2010). Genetic identification of these species in the Azores is currently under investigation (Diana Catarino, personal communication). Here we refer to the species as *Dipturus batis* before revision.

Nitrates, phosphates, and silicates concentration (μmol·L^{-1}), dissolved oxygen (ml·L^{-1}) and percentage of oxygen saturation (%) near the ocean bottom were extracted from Amorim et al. (2017). These layers were projected and rescaled from an original resolution of 0.008° using the R function *projectRaster* (Hijmans 2015). Near-bottom temperature (°C) and near-bottom current speed (m·s^{-1}) average values were based on a MOHID hydrodynamic model application (Viegas et al., 2018) with an original resolution of 0.054°.

We used both Spearman's coefficient of correlation and the Variation Inflation Factors (VIFs) to evaluate collinearity between all candidate environmental predictor variables (Zuur et al., 2009). From the correlated variables, i.e., with Spearman's coefficient > 0.7 or resulting VIF values > 3 (Elith et al., 2006; Dormann et al., 2013), we retained the most ecologically relevant (Table A 1) for explaining the spatial distribution of deep-sea elasmobranch in the Azores: depth, slope, northness, eastness, BPI, nitrates, and near bottom currents (Fig. B 2). It should be

noted that some of these variables may be considered proxies for other habitat properties such as dominant current patterns (aspect, Wilson et al., 2007), productivity (nitrates concentration, Bristow et al., 2017; Rafter et al., 2019) and sediment type (near-bottom current speed, Forbes and Drapeau, 1989). Besides the environmental variables, we also included three operational predictors in the analysis: year, fishing effort (number of hooks) and gear type (longline LLA and LLB, and *gorazeira*). When no presence records were obtained for a certain species for a given year or gear type, those years or gears were excluded from the model of that species.

2.4. Modelling approach

We used a generalised additive model (GAM) approach to predict the probability of presence (P_p) and to predict the abundance (P_a) of deep-sea elasmobranchs in the Azores. Presence-absence data of the 15 species was used to model their P_p using GAMs with binomial distribution and logit link function, through the implementation *gam* in the package *mgcv* (Wood 2015). We applied smoothing parameters to those variables in the GAM that did not have a linear relationship with density but constrained them to 4 knots to avoid overfitting. The full binomial model for the 15 species was:

$$P_p = \beta_n + s(BPI) + s(depth) + s(fishing\ effort) + s(nitrates\ concentration) + s(eastness) + s(northness) + s(current\ speed) + s(slope) + f(year) + f(gear) + \varepsilon_n$$

where P_p is the probability of presence of the species, β_n is the intercept, s is an isotropic smoothing function specific for each variable and model, f indicates variables included as factors and ε_n is the residual error term.

We used a delta GAM modelling approach (Barry and Welsh 2002), recommended for zero-inflated data (Zuur et al., 2009), to model the abundance of the six most frequently caught species. This approach involves using the P_p as described above and the presence-only data to predict species abundances (P_a). P_a was derived using the same full model as P_p but using GAMs with negative binomial distributions and a log link function. Final predicted abundance values (F_{pa}) were computed by multiplying the P_p by the P_a. In both presence (P_p) and abundance (P_a) models, Akaike Information Criteria (AIC) determined the selection of predictor variables to include in the GAMs, using the function *dredge* from the R package *MuMIn* (Barton 2018) and a backward/forward stepwise selection process (Appendix A). We also used GAMs to test for the significance of each selected predictor variable.

The importance of the selected individual variables, i.e., the explanatory power of each variable, was the difference in the goodness-of-fit (deviance) of a model omitting that variable and the goodness-of-fit of the best model, using an analysis of deviance table (González-Irusta and Wright 2016a; 2016b). A variogram was used to analyse the spatial autocorrelation in the residuals of each model for each species. Lack of any apparent trends in the residuals for any species indicated that there was no spatial autocorrelation in the data (Fig. B 3 and Fig. B 4).

We assessed model performance with a spatial partitioning cross-validation methodology described in Guinotte and Davies (2014). In order to avoid overestimation of the evaluation metrics related with the spatial structure of the sampling method as described by Fourcade et al. (2018), training and evaluation data were separated spatially by dividing the original data into four approximately equal groups, using the *get.block* function in the *EnMEVAL* package (Muscarella et al., 2014). Three of these groups were used to predict probability of presence (or

abundance) using the best respective models for each species. This operation was run 10 times. To avoid repeating the same selection of data, only 80% of the samples of each group was randomly selected for the evaluation in each iteration. The ability of the trained presence-absence models to correctly predict the evaluation data was tested with the area under the curve of the receiver operating characteristic (AUC, Fielding and Bell 1997), sensitivity (% true positives), specificity (1 - % true negatives), and the true skill statistic (TSS, Allouche et al., 2006). The performance of abundance and delta models was evaluated with the Spearman's correlation coefficient (rho, ρ, González-Irusta and Wright 2016a; 2016b).

The binomial GAMs were used to map the spatial distribution of the probability of presence (P_p) of deep-sea elasmobranchs, on a 1000-hook bottom longline fishing set (LLA) for 13 of the 15 species, across the entire study area with individual reference years (Table 1). Predictions for *Centrophorus squamosus* and *Centroscymnus coelolepis* were made for a 500-hook bottom longline fishing set of types LLB and LLA, respectively. The extent of overlap among the predicted distribution of the 15 species was determined using Pearson's correlation coefficient computed for multi-layer raster objects. The 6 negative binomial GAMs and delta GAMs were used to map the predicted abundance (P_a, Fig. B 7) and the final predicted abundance (F_{pa}) across the entire study area. P_a was the number of individuals caught in a bottom longline set (type LLA) with elasmobranchs (n > 0), using 1000 hooks in the reference year described in Table 1, while F_{pa} was the number of individuals caught in any 1000-hook bottom longline set, with or without elasmobranchs (n $\geq$ 0) for the same reference years. We also computed the standard error associated to the binomial and negative binomial GAM predictions. Additionally, we built binary maps of presence and absence areas by converting the P_p maps using the maximisation of the sum of sensitivity and specificity (MSS) threshold (Table 2), which minimises misclassification likelihoods of false negatives and false positives (Kaivanto 2008), and a threshold that maximises Kappa (Table 2). These binary maps were used to calculate the area occupied by each species and to build a composite species richness map.

3. Results

#### 3.1. Model performance and variable importance

The binomial GAMs to predict the probability of presence of deep-sea elasmobranchs explained from 14.8% (*E. pusillus*) to 60.5% (*E. princeps*) of the variation in the species presence data (Table 2). The negative binomial GAMs explained between 31.7% (*D. profundorum*) and 54.5% (*E. spinax*) of the deviance in species abundance data (Table 2). The binomial and delta GAMs were able to predict the probability of presence and predicted abundance, respectively, to a reasonable degree of accuracy; 8 out of the 15 binomial GAMs had good performance (AUC > 0.8 and TSS > 0.6), while 4 performed moderately well (AUC $\geq$ 0.7, 0.6 $\geq$ TSS $\geq$ 0.4). Three binomial models had poor prediction power (AUC < 0.7, TSS $\leq$ 0.4) (Table 2). The six negative binomial GAMs for the predicted abundance showed Spearman's ρ correlations between trained model and evaluation data between 0.29 and 0.48, while the Delta GAMs performed better with Spearman's ρ correlations between 0.47 and 0.75 (Table 2).

Table 2

Model performance statistics for the 15 binomial GAMs for predicting the probability of presence (P_p) and 6 negative binomial GAMs and delta GAM modelling approach for predicting the abundance (P_a) and the final predicted abundance (F_{pa}) of elasmobranch species in the Azores, and the associated thresholds used to generate binary maps for each species. Species are sorted by increasing mean depth of capture.

Species	Explained deviance (P_p)	AUC	Sensitivity	Specificity	TSS	Kappa-T	MSS	Explained Deviance (P_a)	Spearman's ρ (P_a)	Spearman's ρ (F_{pa})
Raja clavata	41.4%	0.85 ± 0.05	0.89 ± 0.04	0.69 ± 0.05	0.58 ± 0.05	0.45	0.156	42.5%	0.48 ± 0.06	0.75 ± 0.04
Galeorhinus galeus	31.7%	0.86 ± 0.08	0.76 ± 0.15	0.85 ± 0.09	0.61 ± 0.14	0.10	0.017	48.2%	0.35 ± 0.07	0.70 ± 0.04
Dipturus batis	26.7%	0.78 ± 0.04	0.82 ± 0.09	0.74 ± 0.10	0.56 ± 0.06	0.11	0.050			
Leucoraja fullonica	29.6%	0.89 ± 0.07	0.84 ± 0.13	0.89 ± 0.11	0.73 ± 0.14	0.06	0.010			
Dalatias licha	21.5%	0.69 ± 0.09	0.81 ± 0.11	0.57 ± 0.22	0.38 ± 0.12	0.05	0.018			
Etmopterus spinax	23.3%	0.77 ± 0.04	0.82 ± 0.09	0.62 ± 0.06	0.44 ± 0.08	0.35	0.149	54.5%	0.44 ± 0.11	0.59 ± 0.10
Squaliolus laticaudus	20.5%	0.65 ± 0.16	0.88 ± 0.28	0.23 ± 0.36	0.11 ± 0.17	0.11	0.012			
Etmopterus pusillus	14.8%	0.66 ± 0.02	0.77 ± 0.07	0.54 ± 0.07	0.31 ± 0.03	0.08	0.045	46.6%	0.40 ± 0.05	0.47 ± 0.09
Deania profundorum	27.6%	0.80 ± 0.03	0.85 ± 0.06	0.65 ± 0.07	0.50 ± 0.06	0.15	0.069	31.7%	0.34 ± 0.06	0.62 ± 0.02
Deania calcea	41.4%	0.88 ± 0.03	0.88 ± 0.04	0.81 ± 0.03	0.70 ± 0.06	0.38	0.097	39.7%	0.29 ± 0.10	0.71 ± 0.05
Centrophorus squamosus	34.6%	0.84 ± 0.19	0.93 ± 0.10	0.71 ± 0.39	0.64 ± 0.37	0.46	0.068			
Centroscymnus owstonii	19.3%	0.81 ± 0.13	0.81 ± 0.28	0.84 ± 0.16	0.65 ± 0.24	0.06	0.004			
Centroscymnus crepidater	37.6%	0.92 ± 0.04	0.98 ± 0.04	0.58 ± 0.40	0.56 ± 0.39	0.03	0.004			
Centroscymnus coelolepis	53.3%	0.96 ± 0.04	0.94 ± 0.04	0.93 ± 0.07	0.87 ± 0.05	0.07	0.009			
Etmopterus princeps	60.5%	0.97 ± 0.04	0.95 ± 0.07	0.95 ± 0.07	0.90 ± 0.08	0.79	0.082			
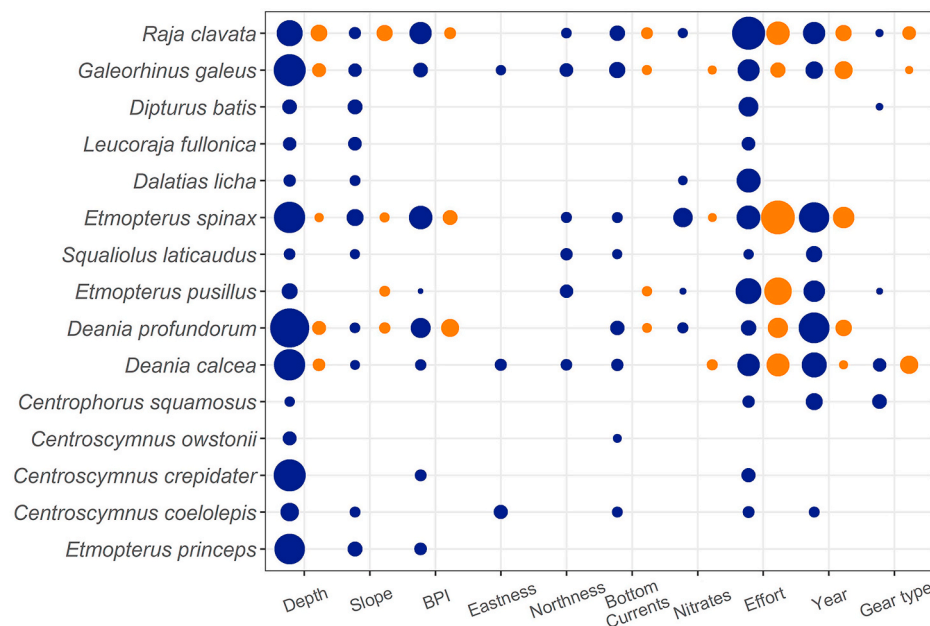
Fig. 2. The explanatory power of each predictor variable calculated as the difference in the goodness-of-fit. Blue circles (left) refer to the binomial GAMs for predicting the probability of presence (P_p) of 15 elasmobranch species while orange circles (right) refer to the negative binomial GAMs for predicting the abundance (F_{pa}) of the 6 most caught elasmobranch species. The circles' size is proportional to the variables' explanatory power. Species are sorted by increasing mean catch depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The 3 operational variables and the 7 environmental predictors used to model the presence and abundance of deep-sea elasmobranchs in the Azores varied in contributions to the different modelled species. From the operational predictors, fishing effort had an important contribution to the models of many species, being most important for the abundance models, followed closely by year of fishing (Fig. 2, Table A 2, Fig. B 6). Where significant, the artisanal handline *gorazeira* had lower probability

and abundance of catches than either gear type LLA or LLB (Fig. B 6).

Among the environmental variables explaining probability of presence, depth had the greatest contribution in 12 models of the 15 deep-sea elasmobranchs and was a significant variable in all 15 binomial models. *R. clavata* and *G. galeus* had highest probability of presence in shallow waters (< 500 m depth). *Dipturus batis, Leucoraja fullonica, Dalatias licha* and *E. spinax* showed a peak in the probability of presence

around 500 m depth, while *Squaliolus laticaudus*, *E. pusillus* and *D. profundorum* peaked in presence around 800 m and *D. calcea, C. squamosus* and *Centroscymnus crepidater* at around 1200 m depth. The three species occupying the deepest parts of the study area were *Centroscymnus owstonii*, *C. coelolepis* and *Etmopterus princeps* (Fig. B 5). We used increasing mean depth of species catch to order the model results.

When among the 3 most important environmental predictors for probability of presence (Table A 3), there was marked preference for no slope, i.e., flat areas (*D. batis*, *L. fullonica*, *D. licha*, *E. spinax* and *E. princeps*), or gentle slope (*C. coelolepis*). Preference for topographic complexity ranged from areas of low relief, i.e., BPI peak around zero (*R. clavata*, *G. galeus*), valley-like areas, i.e., negative BPI values (*E. spinax* and *C. crepidater*) and areas of slight (*E. princeps*) and high complexity, with BPI values peaking at the extremes (*D. profundorum*). Near-bottom current speed was at least the third most important environmental variable for 6 species, with preferences varying from low (*C. owstonii, S. laticaudus*) to moderate (*D. profundorum*), and high hydrodynamism (*R. clavata*, *G. galeus*, *D. calcea*) (Fig. B 5). The other environmental predictors did not contribute as much to the models in general. However, eastness (*C. coelolepis*), northness (*S. laticaudus*, *E. pusillus*), and nitrates (*D. licha*, *E. spinax*) were among the three most important environmental explanatory variables for a few species (Fig. 2, Table A 3). Response curves of each predictor variable for all models can be found in Appendix A (Fig. B 5 and Fig. B 6).

Depth (n = 3), BPI (n = 2), and slope (n = 1) had the highest contribution of the environmental predictors in the 6 abundance models as well (Table A 4). Nitrates (*G. galeus, D. calcea*) and near-bottom current speed (*E. pusillus*) were the second most important variables for some species (Fig. 2, Table A 4). In general, there was a reasonable agreement in the explanatory variables and their response curves between the presence and abundance models (Table A 3; Fig. B 5; Table A 4; Fig. B 6).

3.2. Spatial distribution of deep-sea elasmobranchs

The spatial distribution patterns of the elasmobranchs over the modelled area reflected the individual species responses to the environmental variables (Fig. 3 and Fig. 4). Moreover, species with similar predicted ecological niche, i.e., similar responses to depth and other variables, showed considerable overlap in suitable habitat (Pearson's correlation coefficient *r*, Table A 5). Predicted suitable habitat of *R. clavata* and *G. galeus* coincided for both probability of presence (P_p *r* = 0.78) and abundance (F_{pa} *r* = 0.86) around the island coast and on the shallowest seamounts (Fig. 3a and b; Fig. 4a, b). Predicted presence of *D. batis*, *L. fullonica*, *D. licha* and *E. spinax* was highly correlated (P_p *r* between 0.73 and 0.87), on relatively flat areas of shallow banks and ridges (Fig. 3c, d, e, f). *E. pusillus* and *D. profundorum* had comparable predicted habitat (P_p *r* = 0.73, F_{pa} *r* = 0.71) which overlapped with *S. laticaudus* to a certain extent (P_p *r* 0.57 and 0.63, respectively), mostly concentrated on the slopes of seamounts and ridges at intermediate depth (Fig. 3g, h, i; Fig. 4d and e). *D. calcea, C. squamosus* and *C. crepidater* (P_p *r* between 0.61 and 0.82) were jointly predicted on summits and slopes of deep seamounts and ridges (Fig. 3j, k, m), while shared suitable habitat for *C. owstonii* and *E. princeps* (P_p *r* = 0.6) was predicted mostly on ridge valleys and other deep-water habitats (Fig. 3l, o). *C. coelolepis* was least correlated with the other species (*r* < 0.3), with higher probability of presence distributed at the edge of the modelled area (Fig. 3n). The standard errors associated with the predicted P_p and P_a are in Appendix A (Fig. B 8, Fig. B 9).

The area occupied by each species, as indicated by the binary maps of P_p (Fig. B 10 and Fig. B 11), varied primarily based on the predicted suitable depth range (Fig. 5). Species peaking in P_p shallower than 1000 m (except *E. pusillus*) occupied a reduced habitat (< 10% of the modelled area) regardless of the threshold applied. *E. pusillus* along with *D. calcea, C. squamosus* and *C. crepidater* occupied a reduced (Kappa-T < 20%) to moderate (MSS < 60%) area in the Azores. The species occupying the

deepest strata, *C. owstonii*, *E. princeps* and *C. coelolepis*, were predicted over 30%–90% of the modelled area.

The deep-sea elasmobranchs shared areas of predicted suitable habitat despite these differences, mostly in the intermediate depth ranges (Fig. 6). The maximum number of species sharing the same area depended on the threshold used to build the binary maps. Nevertheless, distinctive bathymetry features such as seamounts, ridges, and submarine banks, close to the islands as well as offshore, were predicted as areas of highest overlap of species presence.

The largest contiguous area with high species richness was predicted on a complex of submarine banks south of the central group of islands (Faial and Pico), and around island slopes and ridges adjacent to the islands. Offshore seamounts both along the dorsal of the Mid-Atlantic Ridge and isolated on the Azorean Plateau were also highlighted as species-rich areas (Fig. 6). All model outputs were deposited in PANGAEA Data Publisher for Earth & Environmental Science and are publicly available for download (González-Irusta et al., 2022, https://doi.org/10.1594/PANGAEA.940808).

4. Discussion

In our model predictions, the spatial distribution of deep-sea elasmobranchs in the Azores was primarily influenced by depth, complemented by other environmental variables like seafloor topography and currents. The dominant influence of depth and terrain variables (slope and bathymetric position) is consistent with similar modelling studies (Lauria et al., 2015; Pennino et al., 2013). Although the importance of depth in determining the distribution of demersal elasmobranchs is well established (Massutí and Moranta 2003; Gouraguine et al., 2011; Bottari et al., 2014; Neat et al., 2015), our understanding of the constancy of these relationships across the species' range and life history is still limited. Effects of variables like bottom temperature that may be important in determining elasmobranch habitat use (Schlaff et al., 2014) are also likely encompassed in the extensive influence of depth, being highly correlated in the study region (Amorim et al., 2017).

Regardless of the variations in individual responses to habitat attributes, the species in our study broadly group into coherent units that showed similar spatial distributions, which could be managed jointly by fisheries. The distinct depth-based and area-based affinities shown here provide species habitat information relevant not just for Azorean fisheries management, but also address larger conservation concerns for these vulnerable species (Dulvy et al., 2017).

Ten of the 15 species selected in our study are listed as threatened or data deficient by the IUCN Red List in the European (Nieto et al., 2015) and global (only for *C. owstonii*, IUCN, 2021) assessments of marine fishes. Six of these were predicted to to peak in probability of occurrence occurrence at or shallower than 800m depth, viz. *G. galeus* (globally Critically endangered, regionally Vulnerable), *D. batis* (regionally Critically endangered), *L. fullonica* (Vulnerable), *D. licha* (Endangered), *E. pusillus* and *D. profundorum* (both Data deficient). Occurrence of these species, along with *R. clavata*, *E. spinax* (both Near threatened) and *S. laticaudus* (Least concern), occupied a very limited spatial extent of the modelled area, overlapping directly with the distribution of commercially important teleost species (Parra et al., 2017) and the deep-water bottom-fishing footprint in the Azores (Diogo et al., 2015). *D. calcea* and *C. squamosus* (both Endangered), though peaking in occurrence at around 1200 m depth which is well below the usual fishing operation depth in the Azores (Carvalho et al., 2011), are also reported frequently as bycatch in bottom-fishing gear (Fauconnet et al., 2019a). Only the species occurring at the deepest part of the study area (> 1200 m depth), viz. *C. owstonii* (listed globally as Vulnerable), *C. coelolepis* (regionally Endangered), *C. crepidater* and *E. princeps* (both Least concern) had the least recorded captures in local fisheries (Fauconnet et al., 2019a). They were predicted over larger spatial extents, across deep seamounts, troughs, and abyssal plains of the Azores EEZ, with minimal interactions with the local fishery, being *de facto* locally
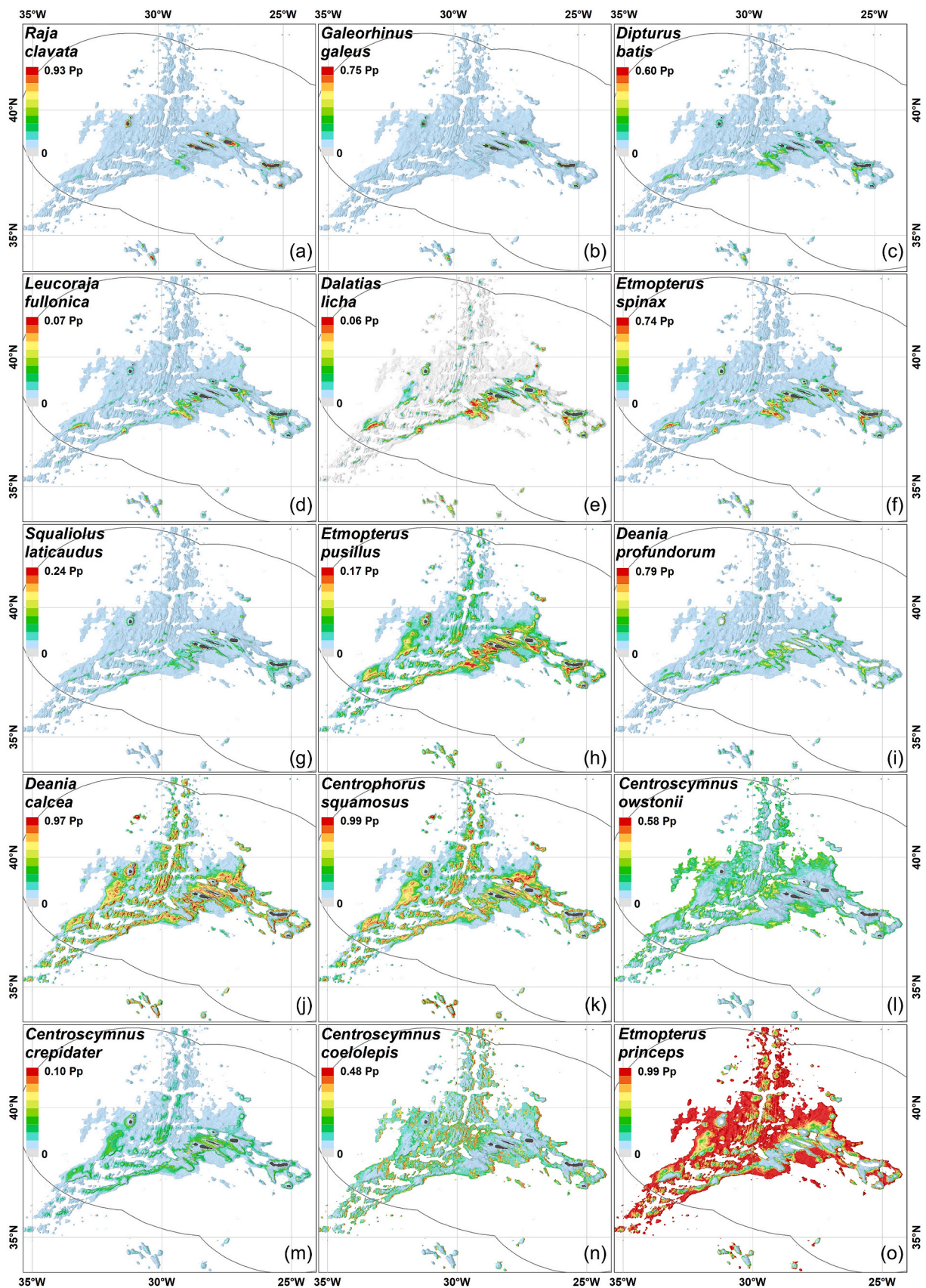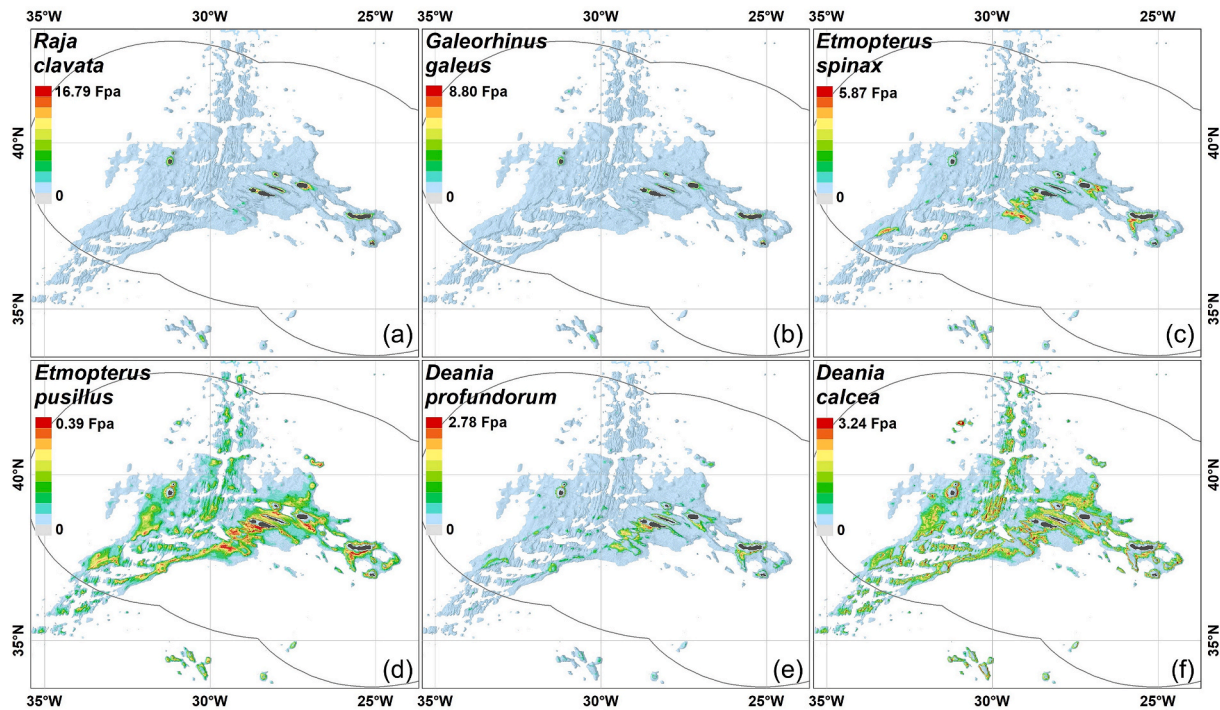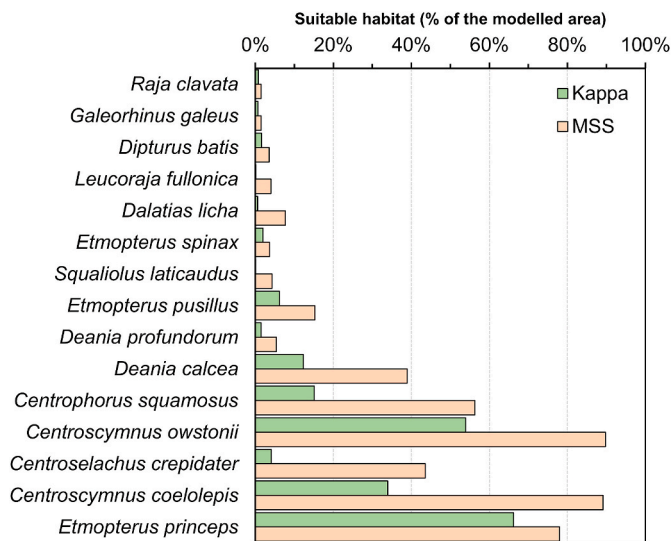
Fig. 3. Predicted probability of presence (P$_p$), resulting from binomial GAMs, of 13 elasmobranch species in the Azores on a 1000-hook bottom longline fishing set (type LLA) with reference year from Table 1. For *Centrophorus squamosus* (k) and *Centroscymnus coelolepis* (n), predictions were made for a 500-hook bottom longline fishing set of types LLB and LLA, respectively. Colour ranges are adjusted to the species maximum P$_p$ and are not comparable among species. Species are sorted by increasing mean catch depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 4. Final predicted abundance (F_{pa}) of 6 elasmobranch species in the Azores, resulting from a delta GAM modelling approach computed by multiplying the predicted abundance (P_a) by the probability of presence (P_p) of each species. Predicted abundance data is shown as the number of individuals caught in bottom longlines (type LLA) with or without elasmobranchs (n ≥ 0), using 1000 hooks and with reference year from Table 1. Species are sorted by increasing mean catch depth.

Fig. 5. Predicted suitable area for 15 deep-sea elasmobranch species in the Azores, resulting from binary maps of the predicted probability of presence (P_p) built with the maximum sensitivity and specificity (MSS, orange) and the Kappa-T (green) thresholds. Species are sorted by increasing mean catch depth.

protected. This would suggest that depth-based limits may be a simple yet effective bycatch avoidance strategy, as already recognised both by local Azorean fishers (Fauconnet et al., 2019b), and the scientific community (Clarke et al., 2015).

In contrast, depth-based limits are not a feasible avoidance strategy for species occurring regularly within the operating range of fishing activity. Preliminary estimates suggest reductions in abundance of some of the species that occur ≤ 800 m depth in the Azores (Santos et al., 2020), underscoring the need to consider alternatives like spatial

management measures to avoid catches of deep-sea elasmobranchs; as has already been advocated for some of these species (Wiegand et al., 2011; Giménez et al., 2020; Garbett et al., 2021). Distinctive underwater topographic features where the occurrence of most deep-sea elasmobranchs concentrate in our model results may effectively inform area-based management as candidates for spatial closure (Clark and Dunn 2012) to reduce and avoid unwanted catches of certain elasmobranchs, especially highly resident species (Daley et al., 2015). Additionally, our results lend support to the idea of managing networks of underwater features aggregating highest diversity or abundance of deep-sea elasmobranch species, as an integrated strategy to optimise the balance between species protection and fisheries as suggested by Clark et al. (2016).

Depth-based limits and protected areas may fall short of meeting the conservation needs for vagile species. Elasmobranchs are known to change depth strata daily (Rodríguez-Cabello et al., 2016), seasonally (Klippel et al., 2016), even spatially (Pinto et al., 2016), and can migrate over long-distances (Rodríguez-Cabello et al., 2016). Where spatial management may fail, gear restrictions can improve avoidance and discard survival of elasmobranch catches (Williams et al., 2016; Fauconnet et al., 2019b). Our model outputs show that the vertical hand-lines (*gorazeira*) had lower catches of elasmobranchs compared to bottom longlines. This is corroborated by local fishers who report that deep-sea elasmobranch bycatch and mortality are higher on longlines than on handlines (Fauconnet et al., 2019b). Due to the nature of the gear, viz. shorter soak time, fewer hooks, usually operating at shallower depths (Fauconnet et al., 2019b) than longlines, elasmobranchs captured on handlines have a greater probability of post-release survival (Ellis et al., 2017). This gear can in fact provide a compromise between species conservation and continuation of an important socio-economic activity, even within protected areas (Daley et al., 2015; Williams et al., 2016). An approach combining depth, area and gear related management measures may therefore reconcile species conservation and the continuation of fishing in the deep-sea.
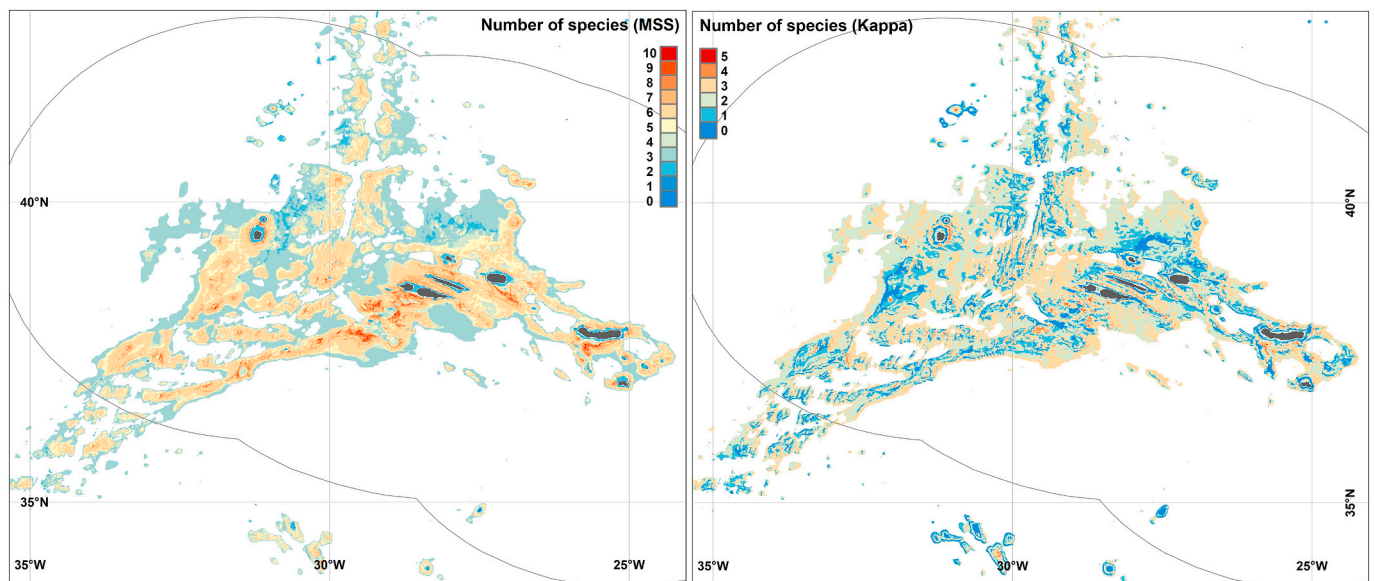
Fig. 6. Species richness maps built by stacking the binary maps of the predicted probability of presence (Pp) of 15 elasmobranch species in the Azores, resulting from binomial GAMs and the maximum sensitivity and specificity (MSS; left panel) and Kappa-T (right panel) thresholds. For visualisation purposes, the colour ranges are adjusted to the maximum species richness and are not directly comparable among panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Our study attempts to explore relationships of the occurrence of deep-sea elasmobranchs with environmental variables beyond depth (Martin et al., 2012; Pennino et al., 2013; Lauria et al., 2015; Giménez et al., 2020). In general, the performance of our models was good and comparable with similar studies (Martin et al., 2012; Lauria et al., 2015), although distribution modelling approaches come with several caveats, extensively discussed in Parra et al. (2017). A few distribution models in our study performed poorly, hence should be interpreted with caution. Models for species with broad ecological niches may show poor performance if the species are not primarily limited by the environmental variables analysed (Brotons et al., 2004; González-Irusta et al., 2015). Compagno (1984) reports *S. laticaudus* (lowest evaluation scores in our model results) and *E. pusillus* (lowest explained deviance) as occurring readily in the pelagic environment, indicating that bottom depth and seafloor topography may not be essential in determining their habitat use. For *D. licha*, the presence of midwater species in its diet (Compagno 1984) suggests that this species too ventures into the water column, possibly explaining the borderline poor evaluation scores of the model.

We further acknowledge that the data quality, quantity, and spatial coverage could be improved, including some potential uncertainty in species identification in the on-board observer dataset. Many species of deep-water sharks (e.g., species within the genus *Deania, Centroscymnus,* or *Etmopterus*) are highly similar and their identification can be challenging (Fauconnet et al., 2020). Additionally, since the deep-sea elasmobranchs were collected on baited hook gear types, the sampling method may introduce biases due to gear-related selectivity and catchability of species. The species distributions predicted here may therefore represent feeding behaviour while not capturing other essential areas for reproduction or spawning. Nonetheless, the results continue to be relevant from the perspective of fisheries management.

This work contributes to a better understanding of the distribution drivers of 15 little-known deep-sea elasmobranchs, many of which have never been modelled before. It provides habitat information that can be leveraged to reduce unwanted catches of vulnerable elasmobranch species. The resulting habitat suitability maps are potentially a decision support tool for fishers to avoid unwanted bycatch of deep-water sharks. This study is an important step to inform fisheries management and species-specific conservation actions at regional and international scales; and will contribute to marine spatial planning in the Azores archipelago.

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.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2022.103707.

References

Afonso, P., Porteiro, F.M., Fontes, J., Tempera, F., Morato, T., Cardigos, F., Santos, R.S., 2013. New and rare coastal fishes in the Azores islands: occasional events or tropicalization process? J. Fish. Biol. 83, 272–294.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232.

Amorim, P., Perán, A.D., Pham, C.K., Juliano, M., Cardigos, F., Tempera, F., Morato, T., 2017. Overview of the ocean climatology and its variability in the Azores region of the north atlantic including environmental characteristics at the seabed. Front. Mar. Sci. 4, 56. https://doi.org/10.3389/fmars.2017.00056.

Barry, S.C., Welsh, A.H., 2002. Generalized additive modelling and zero inflated count data. Ecol. Model. 157, 179–188.

Barton, K., 2018. MuMIn: Multi-Model Inference. R Package Version 1, 40 40.

Bottari, T., Busalacchi, B., Profeta, A., Mancuso, M., Giordano, D., Rinelli, P., 2014. Elasmobranch distribution and assemblages in the southern tyrrhenian sea (central mediterranean). J. Aquacult. Res. Dev. 5.

Bristow, L.A., Mohr, W., Ahmerkamp, S., Kuypers, M.M.M., 2017. Nutrients that limit growth in the ocean. Page Current Biology. Curr. Biol. 27, R431–R510. June 5.

Brotons, L., Thuiller, W., Araújo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27, 437–448. https://doi.org/10.1111/j.0906-7590.2004.03764.x.

Carvalho, N., Edwards-Jones, G., Isidro, E., 2011. Defining scale in fisheries: small versus large-scale fishing operations in the Azores. Page Fisheries Research. Fish. Res. 109 (2–3), 360–369.

Catchpole, T.L., Ribeiro-Santos, A., Mangi, S.C., Hedley, C., Gray, T.S., 2017. The challenges of the landing obligation in EU fisheries. Mar. Pol. 82, 76–86.

Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A., Rowden, A.A., 2016. The impacts of deep-sea fisheries on benthic communities: a review. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 73, i51–i69.

Clark, M.R., Dunn, M.R., 2012. Spatial management of deep-sea seamount fisheries: balancing sustainable exploitation and habitat conservation. Environ. Conserv. 39, 204–214.

Clarke, J., Milligan, R.J., Bailey, D.M., Neat, F.C., 2015. A scientific basis for regulating deep-sea fishing by depth. Curr. Biol. 25, 2425–2429. Available from. https://linkinghub.elsevier.com/retrieve/pii/S0960982215009380.

Clarke, M., Kelly, C.J., Connolly, P.L., Molloy, J.P., 2003. A life history approach to the assessment and management of deepwater fisheries in the Northeast Atlantic. Page Journal of Northwest Atlantic Fishery Science. J. Northwest Atl. Fish. Sci. 31 (November), 401–411.

Compagno, L., 1984. FAO Species Catalogue. Volume 4, Part 1: Sharks of the World, 125. FAO Fisheries Synopsis, p. 249.

Condie, H.M., Grant, A., Catchpole, T.L., 2014. Incentivising selective fishing under a policy to ban discards; lessons from European and global fisheries. Mar. Pol. 45, 287–292.

Correia, J.P.S., Smith, M.F.L., 2003. Elasmobranch landings for the Portuguese commercial fishery from 1986 to 2001. US Natl. Mar. Fish. Serv. Mar. Fish. Rev. 65 (1), 32–40.

Council Regulation (Ec) No 1359, 2008. Council Regulation (EC) No 1359/2008 of 28 November 2008 Fixing for 2009 and 2010 the Fishing Opportunities for Community Fishing Vessels for Certain Deep-Sea Fish Stocks.

Council Regulation (EU) No 1380, 2013. Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, Amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and Repealing Council Regulations (EC) No 2371/2002 and (EC. Page L 354/22. Official Journal of the European Union, European Union.

Council Regulation (EU) No 2025, 2018. Council Regulation (EU) 2018/2025 of 17 December 2018 Fixing for 2019 and 2020 the Fishing Opportunities for Union Fishing Vessels for Certain Deep-Sea Fish Stocks. Official Journal of the European Union. Page L 325/7.

Daley, R.K., Williams, A., Green, M., Barker, B., Brodie, P., 2015. Can marine reserves conserve vulnerable sharks in the deep sea? A case study of Centrophorus zeehaani (Centrophoridae), examined with acoustic telemetry. Deep-Sea Res. II Top. Stud. Oceanogr. 115, 127–136. https://doi.org/10.1016/j.dsr2.2014.05.017.

Danovaro, R., Corinaldesi, C., Dell'Anno, A., Snelgrove, P.V.R., 2017. The deep-sea under global change. Curr. Biol. 27, R461–R465. https://doi.org/10.1016/j.cub.2017.02.046.

Das, D., Afonso, P., 2017. Review of the Diversity, Ecology, and Conservation of Elasmobranchs in the Azores Region, Mid-North Atlantic. Page Frontiers in Marine Science. Mid-North Atlantic.

Diogo, H., Pereira, J.G., Higgins, R.M., Canha, Â., Reis, D., 2015. History, effort distribution and landings in an artisanal bottom longline fishery: an empirical study from the North Atlantic Ocean. Mar. Pol. 51, 75–85.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., 2014. Extinction risk and conservation of the world's sharks and rays. Elife 3, e00590.

Dulvy, N.K., Simpfendorfer, C.A., Davidson, L.N.K., Fordham, S.V., Bräutigam, A., Sant, G., Welch, D.J., 2017. Challenges and priorities in shark and ray conservation. Curr. Biol. 27, R565–R572.

Elith, J.H., Graham, C.P., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J Hijmans, R., Huettmann, F., Leathwick J, R., Lehmann, A., Li, J., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29 (2), 129–151.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.

Ellis, J.R., McCully Phillips, S.R., Poisson, F., 2017. A review of capture and post-release mortality of elasmobranchs. J. Fish. Biol. 90, 653–722.

EMODnet Bathymetry Consortium, 2018. EMODnet Digital Bathymetry (DTM 2020). EMODnet Bathymetry Consortium. Marine Information Service. https://doi.org/10.12770/18ff0d48-b203-4a65-94a9-5fd8b0ec35f6.

Fauconnet, L., Pham, C.K., Canha, A., Afonso, P., Diogo, H., Machete, M., Silva, H.M., Vandeperre, F., Morato, T., 2019a. An overview of fisheries discards in the Azores. Fish. Res. 209, 230–241.

Fauconnet, L., Frangoudes, K., Morato, T., Afonso, P., Pita, C., 2019b. Small-scale Fishers' perception of the implementation of the EU Landing Obligation regulation in the outermost region of the Azores. J. Environ. Manag. 249, 109335.

Fauconnet, L., Ribeiro, A., Catarino, D., Giacomello, E., Das, D., Morato, T., Rosa, A., Afonso, P., 2020. Guia dos Tubarões de Profundidade dos Açores. Publicações científicas Okeanos no 2. Okeanos-UAc/IMAR.

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

Forbes, D.L., Drapeau, G., 1989. Near-bottom currents and sediment transport on the inner scotian shelf: sea-floor response to winter storms during casp. Page Atmos. Ocean.

Fourcade, Y., Besnard, A.G., Secondi, J., 2018. Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. Global Ecol. Biogeogr. 27, 245–256.

Frisk, M.G., Miller, T.J., Fogarty, M.J., 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. Can. J. Fish. Aquat. Sci. 58, 969–981.

Garbett, A., Phillips, N.D., Houghton, J.D., Prodöhl, P., Thorburn, J., Loca, S.L., Eagling, L.E., Hannon, G., Wise, D., Pothanikat, L., Gordon, C., 2021. The critically endangered flapper skate (Dipturus intermedius): recommendations from the first flapper skate working group meeting. Mar. Pol. 124, 104367.

García, V.B., Lucifora, L.O., Myers, R.A., 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. Proc. Biol. Sci. 275, 83–89.

Giménez, J., Cardador, L., Mazor, T., Kark, S., Bellido, J.M., Coll, M., Navarro, J., 2020. Marine protected areas for demersal elasmobranchs in highly exploited Mediterranean ecosystems. Mar. Environ. Res. 160, 105033.

González-Irusta, J.M., Fauconnet, L., Das, D., Catarino, D., Afonso, P., Viegas, C., Rodrigues, L., Menezes, G., Rosa, A., Pinho, M.R.R., Silva, H.M. da, Giacomello, E., Morato, T., 2022. Outputs of predictive distribution models of deep-sea elasmobranchs in the Azores EEZ (down to 2,000m depth) using Generalized Additive Models. PANGAEA. https://doi.org/10.1594/PANGAEA.940808.

González-Irusta, J.M., González-Porto, M., Sarralde, R., Arrese, B., Almón, B., Martín-Sosa, P., 2015. Comparing species distribution models: a case study of four deep sea urchin species. Hydrobiologia 745, 43–57. https://doi.org/10.1007/s10750-014-2090-3.

González-Irusta, J.M., Wright, P.J., 2016a. Spawning Grounds of Haddock (Melanogrammus Aeglefinus) in the North Sea and West of Scotland, 183. Page Fisheries Research. Fisheries Research.

González-Irusta, J.M., Wright, P.J., 2016b. Spawning grounds of atlantic cod (Gadus morhua) in the north sea. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 73, 304–315.

Gouraguine, A., Hidalgo, M., Moranta, J., Bailey, D.M., Ordines, F., Guijarro, B., Valls, M., Barberá, C., de Mesa, A., 2011. Segregación espacial de elasmobranquios en el mediterráneo Occidental. Sci. Mar. 75, 653–664.

Guillen, J., Holmes, S.J., Carvalho, N., Casey, J., Dörner, H., Gibin, M., Mannini, A., Vasilakopoulos, P., Zanzi, A., 2018. A review of the European Union landing obligation focusing on its implications for fisheries and the environment. Sustainability 10, 900.

Guinotte, J.M., Davies, A.J., 2014. Predicted deep-sea coral habitat suitability for the U. S. West Coast. PLoS One 9.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Hareide, N.R., Carlson, J., Clarke, M., Clarke, S., Ellis, J., Fordham, S., Fowler, S., Pinho, M., Raymakers, C., Serena, F., Seret, B., 2007. European shark fisheries: a preliminary investigation into fisheries, conversion factors, trade products, markets and management measures. Europ. Elasmobranch Assoc. 1, 27.

Hijmans, R.J., 2015. Introduction to the ' raster ' package (version 2 . 3-24). R-CRAN Proj. 27, 1–27.

Iglésias, S.P., Toulhoat, L., Sellos, D.Y., 2010. Taxonomic confusion and market mislabelling of threatened skates: important consequences for their conservation status. Aquat. Conserv. Mar. Freshw. Ecosyst. 20, 319–333. https://doi.org/ 10.1002/aqc.1083.

IUCN, 2021. The IUCN Red List of Threatened Species. Version 2021-1. Available from. https://www.iucnredlist.org. (Accessed 24 May 2021).

Kaivanto, K., 2008. Maximization of the sum of sensitivity and specificity as a diagnostic cutpoint criterion. J. Clin. Epidemiol. 61, 517–518.

Klippel, S., Amaral, S., Vinhas, L., 2016. Development and evaluation of species distribution models for five endangered elasmobranchs in southwestern Atlantic. Hydrobiologia 779, 11–33.

Kyne, P.M., Simpfendorfer, C.A., 2007. A Collation and Summarization of Available Data on Deepwater Chondrichthyans : Biodiversity, Life History and Fisheries. Page IUCN SSC Shark Specialist Group.

Lauria, V., Gristina, M., Attrill, M.J., Fiorentino, F., Garofalo, G., 2015. Predictive habitat suitability models to aid conservation of elasmobranch diversity in the central Mediterranean Sea. Page Scientific Reports. Sci. Rep. 5 (July), 1–16.

Levin, L.A., Wei, C.-L., Dunn, D.C., Amon, D.J., Ashford, O.S., Cheung, W.W.L., Colaço, A., Dominguez-Carrió, C., Escobar, E.G., Harden-Davies, H.R., Drazen, J.C., Ismail, K., Jones, D.O.B., Johnson, D.E., Le, J.T., Lejzerowicz, F., Mitarai, S., Morato, T., Mulsow, S., Snelgrove, P.V.R., Sweetman, A.K., Yasuhara, M., 2020. Climate change considerations are fundamental to management of deep-sea resource extraction. Global Change Biol. 26, 4664–4678.

Martin, C.S., Vaz, S., Ellis, J.R., Lauria, V., Coppin, F., Carpentier, A., 2012. Modelled distributions of ten demersal elasmobranchs of the eastern English Channel in relation to the environment. Page Journal of Experimental Marine Biology and Ecology. J. Exp. Mar. Biol. Ecol. 418–419, 91–103.

Massutí, E., Moranta, J., 2003. Demersal assemblages and depth distribution of elasmobrachs from the continental shelf and slope off the Balearic Islands (western Mediterranean). ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 60, 753–766. https://doi. org/10.1016/S1054-3139(03)00089-4.

Morato, T., Watson, R., Pitcher, T.J., Pauly, D., 2006. Fishing down the deep. Fish Fish. 7, 24–34.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models . Page Methods in Ecology and Evolution. Meth. Ecol. Evol. 5, 1198–1205.

Neat, F.C., Burns, F., Jones, E., Blasdale, T., 2015. The diversity, distribution and status of deep-water elasmobranchs in the Rockall Trough, north-east Atlantic Ocean. J. Fish. Biol. 87, 1469–1488.

Nieto, A., Ralph, G.M., Comeros-Raynal, M.T., Heessen, H.J., Rijnsdorp, A.D., 2015. European Red List of Marine Fishes. Publications Office of the European Union.

Norse, E.A., Brooke, S., Cheung, W.W., Clark, M.R., Ekeland, I., Froese, R., Gjerde, K.M., Haedrich, R.L., Heppell, S.S., Morato, T., Morgan, L.E., 2012. Sustainability of deep-sea fisheries. Mar. Pol. 36 (2), 307–320. https://doi.org/10.1016/j. marpol.2011.06.008.

O'Neill, F.G., Feekings, J., Fryer, R.J., Fauconnet, L., Afonso, P., 2018. Discard avoidance by improving fishing gear selectivity: helping the fishing industry help itself. In: Uhlmann, S.S., Ulrich, C., Kennelly, S.J. (Eds.), The European Landing Obligation: Reducing Discards in Complex, Multi-Species and Multi-Jurisdictional Fisheries, pp. 279–296.

Oliver, S., Braccini, M., Newman, S.J., Harvey, E.S., 2015. Global patterns in the bycatch of sharks and rays. Page Marine Policy. Mar. Pol. 54 (August), 86–97.

Pardo, S.A., Kindsvater, H.K., Reynolds, J.D., Dulvy, N.K., 2016. Maximum intrinsic rate of population increase in sharks, rays, and chimaeras: the importance of survival to maturity. Can. J. Fish. Aquat. Sci. 73, 1159–1163.

Parra, H.E., Pham, C.K., Menezes, G.M., Rosa, A., Tempera, F., Morato, T., 2017. Predictive modeling of deep-sea fish distribution in the Azores. Deep-Sea Res. Part II Top. Stud. Oceanogr. 145, 49–60.

Pennino, M.G., Muñoz, F., Conesa, D., López-Qúlez, A., Bellido, J.M., 2013. Modeling sensitive elasmobranch habitats. Page journal of sea research. J. Sea Res. 83 (October), 209–218.

Peran, A.D., Pham, C.K., Amorim, P., Cardigos, F., Tempera, F., Morato, T., 2016. Seafloor characteristics in the Azores region (North Atlantic). Front. Mar. Sci. 3.

Pham, C.K., Canha, A., Diogo, H., Pereira, J.G., Prieto, R., Morato, T., 2013. Total marine fishery catch for the Azores (1950-2010). ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 70, 564–577.

Pinho, M., Menezes, G., 2005. Azorean deepwater fishery: ecosystem, species, fisheries and management approach aspects. In: Deep Sea 2003: Conference on the Governance and Management of Deep-Sea Fisheries, Conference Poster and Dunedin Workshop Papers. 2:974–986. Conference Poster Papers and Workshop Papers, Conference on the Governance and Management of Deep-Sea Fisheries. Part II.

Pinto, C., Thorburn, J.A., Neat, F., Wright, P.J., Wright, S., Scott, B.E., Cornulier, T., Travis, J.M.J., 2016. Using individual tracking data to validate the predictions of species distribution model. Divers. Distrib. 22, 682–693.

Rafter, P., Bagnell, A., Marconi, D., Devries, T., 2019. Global trends in marine nitrate N isotopes from observations and a neural network-based climatology. Biogeosciences 16, 2617–2633.

Reid, D.G., Calderwood, J., Afonso, P., Bourdaud, P., Fauconnet, L., González-Irusta, J. M., Mortensen, L.O., Ordines, F., Lehuta, S., Pawlowski, L., Plet-Hansen, K.S., 2018. The best way to reduce discards is by not catching them. In: Uhlmann, S., Ulrich, C., Kennelly, S.J. (Eds.), The European Landing Obligation: Reducing Discards in Complex, Multi-Species and Multi-Jurisdictional Fisheries. The European Landing Obligation, p. 257.

Rigby, C., Simpfendorfer, C.A., 2015. Patterns in life history traits of deep-water chondrichthyans. Deep-Sea Res. Part II Top. Stud. Oceanogr. 115, 30–40.

Rodríguez-Cabello, C., González-Pola, C., Sánchez, F., 2016. Migration and diving behavior of Centrophorus squamosus in the NE Atlantic. Combining electronic tagging and Argo hydrography to infer deep ocean trajectories. Deep-Sea Res. Part I Oceanogr. Res. Pap. 115, 48–62.

Rodríguez-Cabello, C., Sánchez, F., 2017. Catch and post-release mortalities of deep-water sharks caught by bottom longlines in the Cantabrian Sea (NE Atlantic). J. Sea Res. 130, 248–255.

Santos, R., Novoa-Pabon, A., Silva, H., Pinho, M., 2020. Elasmobranch species richness, fisheries, abundance and size composition in the Azores archipelago (NE Atlantic). Mar. Biol. Res. 16, 103–116.

Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2014. Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev. Fish Biol. Fish. 24, 1089–1103. https://doi.org/10.1007/s11160-014-9364-8.

Simpfendorfer, C.A., Kyne, P.M., 2009. Limited potential to recover from overfishing raises concerns for deep-sea sharks, rays and chimaeras. Environ. Conserv. 36, 97–103.

Talwar, B., Brooks, E.J., Mandelman, J.W., Grubbs, R.D., 2017. Stress, post-release mortality, and recovery of commonly discarded deep-sea sharks caught on longlines. Mar. Ecol. Prog. Ser. 582, 147–161.

Viegas, C., Juliano, M., Colaço, A., 2018. Ocean Observations- a Key Factor for Model Implementation and Validation for the Azores 3D-Hydrodynamic and Biogeochemical Model. Page European Ocean Observing System 2018. European Ocean Observing System, Brussels, Brussels.

Walbridge, S., Slocum, N., Pobuda, M., Wright, D.J., 2018. Unified geomorphological analysis workflows with benthic terrain modeler. Geosciences 8.

Walls, R.H.L., Dulvy, N.K., 2020. Eliminating the dark matter of data deficiency by predicting the conservation status of Northeast Atlantic and Mediterranean Sea sharks and rays. Biol. Conserv. 246, 108459.

Werner, T., Kraus, S., Read, A., Zollett, E., 2006. Fishing techniques to reduce the bycatch of threatened marine animals. Mar. Technol. Soc. J. 40, 50–68.

Wiegand, J., Hunter, E., Dulvy, N.K., 2011. Are spatial closures better than size limits for halting the decline of the North Sea thornback ray, Raja clavata? Mar. Freshw. Res. 62, 722–733.

Williams, A., Upston, J., Green, M., Graham, K., 2016. Selective commercial line fishing and biodiversity conservation co-exist on seamounts in a deepwater marine reserve. Fish. Res. 183, 617–624. https://doi.org/10.1016/j.fishres.2016.02.015.

Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar. Geodes. 30, 3–35.

Wood, S., 2015. Package "Mgcv" Version 1.8-7. R Package Version 1, p. 273.

WoRMS Editorial Board, . World register of marine species. Available from. http://www. marinespecies.org.at.VLIZ. https://doi.org/10.14284/170. (Accessed 18 January 2022).

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media.