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Modelling the distribution of vulnerable skate from fisheries dependent data using imperfect detection

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Abstract

Little is still known about the biology and ecology of many elasmobranchs which often inhibits species specific management measures from being implemented. The primary aim of this study was to improve the knowledge on the distribution and habitat use of the threatened and data deficient shagreen ray, *Leucoraja fullonica*, using fisheries dependent data. To model its distribution, we used Bayesian hierarchical modelling, taking into consideration imperfect capture from the non-random nature of fishing gear type and spatial autocorrelation. Our second objective was to identify the potential functional role of the high occurrence area by analysing spatial length segregation using a generalised additive mixed model.

From five environmental variables, depth, distance to coast, and seabed sediment type were used to model its habitat. *L. fullonica* was found to mainly inhabit an area of high concentration between the southern Celtic Seas and the northern Bay of Biscay. Within this area, smaller individuals were found in the deeper south-western part and larger individuals in shallower waters, closer to the coast, suggesting ontogenetic shift or spawning migration. *L. fullonica* were mainly caught by bottom trawl fishing gears. The isolated habitat occupancy of this species may increase its vulnerability, particularly since high fishing pressure has been observed in this area. These results highlight the importance of fisheries-dependent data for data-poor species and provide valuable new information on its ecology when considering management or conservation measures at a species level.

Key words: Hierarchical Bayesian model, fishery-dependent data, habitat, elasmobranch, IUCN Red List Species, data-poor species

1. Introduction

Elasmobranchs are key species to ecosystem functioning (Grubbs *et al.*, 2016; Heithaus, 2001) and have been shown to have variable top-down effects on prey depending on species, community structure, and habitat (Stevens, 2000). Their k-strategy life history traits (e.g., low fertility, slow growth and late maturity) limit their capacity to increase and maintain a viable population in the face of anthropogenic pressures (Cailliet *et al.*, 2005; Elliott *et al.*, 2020a). Overfishing and bycatch are considered as the main factors for their decline, and one in four elasmobranch species are threatened with extinction at global scale (Ferretti *et al.*, 2010; Dulvy *et al.*, 2014). 39% of elasmobranch species are considered as Data Deficient (DD) by the International Union for Conservation of Nature (IUCN), given the lack of information on their distribution and populations structures (IUCN, 2020). The International Council for the Exploration of the Sea (ICES), undertakes shark, skate and ray stock assessments in order to advise on elasmobranchs fisheries management. Unfortunately, management measures for most elasmobranchs are generic due to lack of data (ICES, 2020).

Spatio-temporal management measures have been suggested an important tool to protect vulnerable skates and rays (e.g., Dulvy *et al.*, 2003; Dedman *et al.*, 2015, Elliott *et al.*, 2020a). However, their application is hampered by incomplete knowledge of specific spatial or temporal distribution and its relationship with the environment at both adult and juvenile life history stages (Ellis *et al.*, 2010). Skates are often spatially aggregated and are known to exhibit ontogenetic shift pattern, with juveniles often occurring in different depths than egg cases or adults (Bizzarro *et al.*, 2014; Elliott *et al*, 2020a). Few studies have reported skate habitat requirements for reproduction and early life stages (Love *et al.*, 2008; Hoff, 2010). Although skates have been historically considered to inhabit soft-bottom habitats (Bizzarro *et al.*, 2014), recent video data suggest that the picture is more complex as several skate species are primarily associated with rocky substrates, including high-relief regions (Kuhnz *et al.*, 2019).

The shagreen ray, *Leucoraja fullonica*, is IUCN red-listed as vulnerable (VU) on global and European scales (2014), and data-deficient (DD) or not evaluated on national levels (IUCN red list (McCully and Walls, 2015). It is managed as part of a generic Total Allowable Catches (TACs) for 'skates and rays' with an obligation to report landings separately (ICES, 2020). A precautionary approach is advised for this species (ICES, 2020). *L. fullonica* is a demersal, benthic and oviparous species threatened by fishing (McCully and Walls, 2015). This offshore skate occurs along the edge of the continental shelf from Iceland and northern Norway to north-west Africa, including the Mediterranean Sea (Stehmann and Bürkel, 1984). It is a relatively large-bodied species, with a maximum reported size of 120 cm total length (Muus *et al*., 1999). Data on its length at maturity are scarce, and only concern males with an average of 85.5 cm total length (McCully *et al*., 2012). *L. fullonica* mainly feeds on fish and crustaceans but can also predate other elasmobranchs (Ebert and Bizzarro, 2007). The habitat requirements for *L. fullonica,* including potential ontogenetic shift patterns are not known, but as a hardnose skate, it is expected that juveniles of this species typically occur in shallower waters than egg case deposition sites or adults (Hoff, 2010). Such data gaps preclude this species from successful management and conservation.

To implement conservation or management measures adapted to vulnerable elasmobranch species, it is necessary to have a good knowledge on their distribution and their habitat. Species Distribution Models (SDM) are widely used to understand the habitat requirements of a species (e.g., Elith *et al*., 2006; Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). SDMs aim to predict a species probability of presence through different environmental variables (Elith and Franklin, 2017). When modelling species distribution, it is essential to use robust models adapted to the data and include model uncertainty for realistic distribution (Guisan and Zimmermann, 2000; Marshall *et al.*, 2014; Latimer *et al.*, 2006; Loiselle *et al.*, 2003). Currently, assessments for this species are based on commercial landing data which cannot be accurately spatialised. In addition, smaller non-exploitable individuals are often not landed (STECF, 2017). Scientific bottom trawl surveys, which are usually undertaken annually, are not used to assess skate stocks since they are not adapted to capture skates and rays (ICES, 2020).

Since 2003, an on-board French fisheries observer program (ObsMer) aims to collect fisheries data in sufficient quantity and quality required by EU fisheries regulation (EC 1639/2001; Cornou *et al.*, 2015). Fisheries observers randomly sampled targeted or incidental catches throughout the year and over a large spatial area: the English Channel, North Sea, Celtic Seas, Bay of Biscay and the Mediterranean Sea. These data, contain information on the number of individuals per species, length, weight, location, gear type, landed and/or discarded fractions (Cornou *et al.*, 2015), and constitute an important source of information for poorly studied elasmobranch species (Elliott *et al.*, 2020a). Use of fisheries dependent data, does, however, require consideration of biases linked to sampling (e.g. different fishing techniques, non-homogeneous distribution of these techniques, un-balanced sampling, the targeted nature of fishing, etc.).

The objective of this study was, as the first step, to predict the distribution of *L. fullonica* through environmental parameters from fisheries dependent data within northeast Atlantic waters. To accommodate fisheries dependent data biases, a site occupancy model in a hierarchical Bayesian framework which considers the imperfect detection and includes a spatial structure as random effect was implemented in order to take into account the spatial dependence of the data (Latimer *et al.*, 2006; Pennino *et al.*, 2013; Vieilledent, 2019). As the species was observed to be primarily aggregated spatially within one area, its potential functional role of this area was analysed using a generalised additive mixed model (GAMM) from length data. From this work insights into *L. fullonica* habitat requirements and ontogeny were acquired. In addition to the identification of gear types that bycatch this species and size ranges which are most impacted by fishing. Finally, this work provides essential information for a more effective management of this vulnerable species.

2. Material and methods

2.1 Fishery data

ObsMer data are collected by on-board observers who, randomly sample professional fishing vessels and fishing operations (FOs) within the trip (Cornou *et al*. 2015). A FO corresponds to a single fishing action, such as a haul or a net laying and lifting. Detailed descriptions of ObsMer survey methods are available in Cornou *et al*. (2015) and in the ObsMer observer manual (https://archimer.ifremer.fr/doc/00018/12895/9855.pdf). FOs catch composition was recorded on the landed fraction only or on the whole catch (i.e., landed and discarded fractions). Species were identified, weighed, and measured. FOs characteristics were also reported (e.g., date, start and end haul’s geographical coordinates, fishing gear, vessel length, target species). FOs extend in the ICES ecoregions: Celtic Seas, Greater North Sea, Bay of Biscay and the Iberian Coast, the eastern part of Oceanic Northeast Atlantic, and the western of Mediterranean Sea (Fig. 1a).

ObsMer data were obtained from the French marine fisheries and aquaculture administration (DPMA). In 2009, the ObsMer program was standardised within the implementation of the Data Collection Framework (Cornou *et al*., 2015), which establishes common EU rules on the collection, management and use of fisheries data. Data from 2009 to 2019 were therefore used. FOs where species identification was exhaustive (i.e., in both landed and discarded fractions) were used for analyses which included 39 289 FOs (Fig. 1a). The geographical coordinates used for each FOs correspond to the midpoint from a straight line between the beginning and the end of a FO. When at least one individual of *L. fullonica* was captured during a FO, it was considered as a presence and otherwise as an absence.

2.2 Data selection

To reduce zero inflation and the possibility of false zeros, the FOs selected to study the distribution of *L. fullonica* (Fig. 1b) included: (1) FOs in ICES divisions with a proven occurrence of the species (i.e., 27.2.a, 27.4.a, 27.6.a, 27.7.bce-hjk, 27.8.a-e; based on Scientific, Technical and Economic Committee for Fisheries; STECF, 2017); (2) FOs whose fishing gear types were compatible with the capture of this demersal species (i.e., otter twin trawls, otter beam trawls, trammel nets, set gillnets, bottom pair trawls, Danish seine nets, set longlines). To deal with the non-random distribution of fishing activity (i.e., fishers targeting species at the centre of their distributions; Dell *et al.*, 2011; Augustin *et al.*, 2013), FOs which targeted skates and rays were removed (1% of FOs). From the previously selected dataset, 63% of the FOs met the selection criteria.

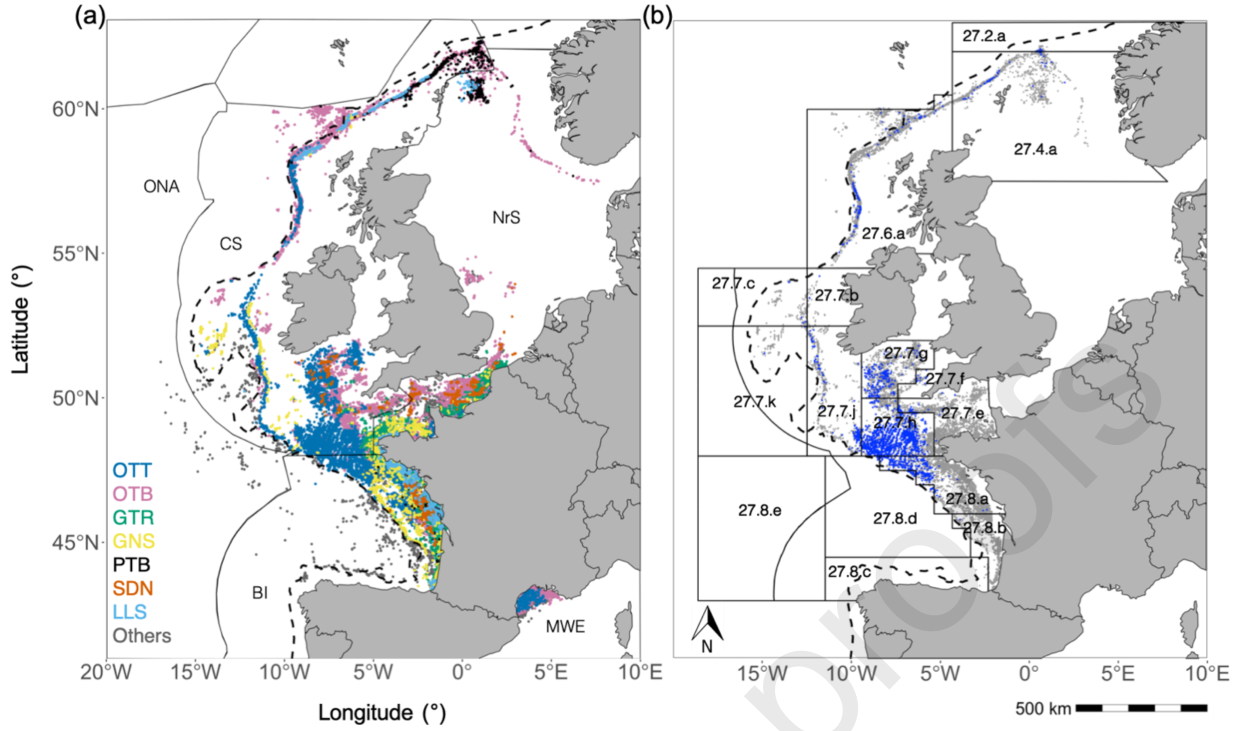

Fig. 1. Location of fishing operations (FOs). (a) All exhaustive FOs (n = 39 289) from ObsMer data from 2009 to 2019. Otter twin trawls (OTT), otter beam trawls (OTB), trammel nets (GTR), set gillnets (GNS), bottom pair trawls (PTB), Danish seine nets (SDN), set longlines (LLS), Others: Fishing gear types which did not catch of *Leucoraja. fullonica*. Black solid lines delineate ICES ecoregions. Nrs: Greater North Sea; CS: Celtic Seas; ONA: Oceanic Northeast Atlantic; BI: Bay of Biscay and the Iberian Coast; MWE: Western Mediterranean Sea. (b) Selected FOs for analyses (n = 18 782). Blue dots are *L. fullonica* presences, grey dots are absences. Black solid lines delineate ICES divisions. Dotted lines delineate the continental shelf break.

2.3 Environmental variables

Five environmental variables were considered as potential predictors of *L. fullonica* distribution (Table 1): depth (in meters), distance to coast (in kilometres), sediment type, slope, and Terrain Ruggedness Index (TRI). Since *L. fullonica* is a benthic species, we used metrics descriptive of the seafloor such as the relief (e.g., depth), the complexity (e.g., slope and TRI), the sediment classification, and the distance from the coast in relation to its offshore location. Depth and sediment type are known to be the most important explanatory variables of elasmobranchs distribution (Martin *et al.*, 2012; Pennino *et al.*, 2013; Bizzarro *et al.*, 2014). Bottom data for variables such as temperature, salinity, and chlorophyll α were not available over the entire study area and period and therefore could not be included in analyses. All the environmental variables were aggregated at 0.1° x 0.1° by averaging the values for the continuous variables (i.e., depth, distance to coast, slope and TRI) and considering the single dominant modality for the categorical variable (i.e., sediment type). The sediment type was used in 4 simplified categories based on their grain size composition (Populus *et al.*, 2017): rock (presence of rock), coarse and mixed sediment (sand: mud $\leq$ 9:1 or sand:mud $>$ 9:1 and 5% $\leq$ gravel $\leq$ 80%), sand (sand:mud $\geq$ 9:1 and gravel < 5%) and mud (1:9 $\leq$ sand: mud $<$ 9:1 and gravel $<$ 5%). Values for all environmental variables were extracted at the midpoint from a straight line between the beginning and the end of a FO.

The exploration of outliers was processed according to Zuur *et al.* (2010) and aberrant or missing values were removed. Collinearity and correlation were checked using Pearson correlation index (Pearson's *r*) and variance inflation factor (VIF). Variables which had a high significant correlation (i.e., Pearson's *r* > 0.6 or Pearson's *r* < -0.6; p < 0.01) were alternatively included to avoid two correlated variables within the same model. All variables used in the models had VIF lower than 2. Unfortunately, as of result of too few presences, seasonal life history stage migration was not considered.

Table 1. Summary of potential predictor variables. TRI: Terrain Ruggedness Index.

Predictor variables	Source	Unit or Categories	Initial spatial resolution
Depth	Bathymetry data downloaded from General Bathymetric Chart of the Oceans (GEBCO Bathymetric Compilation Group, 2020)	m	0.004° x 0.004°
Distance to coast	The *dist2line* function from 'Geosphere' R package (Hijmans, 2019) calculates the shortest distance between each points and coastal line	km	0.004° x 0.004°
Sediment type	Provided by the EMODnet broad-scale seabed habitat map for Europe (https://www.emodnet-seabedhabitats.eu)	rock coarse and mixed sediment sand mud	0.002° x 0.002°
Slope	Calculated from the GEBCO bathymetry raster with the *terrain* function from 'Raster' R package (Hijmans, 2019)	degrees	0.004° x 0.004°
TRI	Calculated from the GEBCO bathymetry raster with the *terrain* function from 'Raster' R package (Hijmans, 2019)	-	0.004° x 0.004°

2.3 Distribution model

The distribution of *L. fullonica* occurrence was modelled using Bayesian site-occupancy intrinsic conditional autoregressive (iCAR) model (MacKenzie *et al.*, 2002). This type of model takes into account both imperfect detection which leads to the consideration of false absences due to a probability of detection that is often less than 1, and spatial autocorrelation which consists in a spatial dependency between parameters and leads to inaccurate parameters estimates (Latimer *et al.*, 2006). To solve these potential biases two processes are combined: an ecological process in which the presence or absence of the species is associated with habitat suitability, and an observation process that considers the fact that the probability of detection of the species is inferior to one.

The ecological process includes the environmental variables added to an iCAR model which measure the spatial autocorrelation by assessing the spatial configuration of the eight nearest neighbouring cells (Dormann *et al.*, 2007). Specifically, the probability of presence z_i, which follows a Bernouilli distribution, can take value 1 or 0 depending on the probability that the habitat is suitable (θ_i) at site i (i.e. a 0.1° x 0.1° cell) (1):

$$z_i \sim Bernoulli(\theta_i) \tag{1}$$

$$logit(\theta_i) = X_i\beta + \rho_{j(i)} \tag{2}$$

Where θ_i is expressed as a linear model combining the matrix of environmental variables X_i, parameters β and the spatial random effect ρ of the site i for any given cell j (i.e. matrix of neighbours), using a logit link function (2).

The Gaussian iCAR model for the spatial random effect at site i is assumed by a conditional distribution (3):

$$\mathrm{p}(p_j \,|\, p_{j'}) \sim Normal(\mu_j, V_p/n_j) \tag{3}$$

Where μ_j is the mean of $p_{j'}$ in the neighbourhood of j, V_p is the variance of the spatial random effects and n_j the number of neighbours for cell j. The spatial autocorrelation in *L. fullonica* occurrences was tested using a bootstrapped Moran's I test (Moran, 1948).

As fishing technique can be a source of variation in the probability of species catch, the model of the observation process includes the type of gear used for each FO. Particularly, the random variable y_{it} represents the probability of presence of the species at site i and time t (i.e. time should be understood as the distinction of different visits within the same site). The species is observed at site i ($\sum_t y_{it} \geq 1$) only if the habitat is suitable ($z_i = 1$). The species is not observed at site i ($\sum_t y_{it} = 0$) if the habitat is not suitable ($z_i = 0$), or if the habitat is suitable ($z_i = 1$) but the probability δ_{it} of detecting the species at site i and time t is inferior to 1. Thus, y_{it} is assumed to follow a Bernoulli distribution of parameter $z_i\delta_{it}$ (4). The probability of detection δ_{it} can be expressed as a linear model combining explicative variables W_{it} and parameters γ (5):

$$y_{it} \sim Bernoulli(z_i\delta_{it}) \quad (4)$$

$$logit(\delta_{it}) = W_{it}\gamma \quad (5)$$

The model selection was performed in the following manner:

1. Identification of possible combinations including all environmental variables while ensuring there was no collinearity or strong correlations between variables
2. Run models with environmental variable combinations found in 1.
3. Select relevant environmental variables for each model and rerun
4. Select the best model according to the lowest Deviance Information Criterion (DIC)

A variable was considered relevant if the 95% credible interval (CrI) of the parameter posterior distribution did not contain zero (e.g. [-0.005; -0.00006] or [0.5; 8]). For both ecological and observation processes, uninformative priors centered at zero with a fixed variance of 100 were used, and a uniform distribution was used for the variance of spatial effect. Model convergence was assessed visually on two Markov chain Monte Carlo (MCMC) simulations, and using the potential scale reduction factor (Gelman and Rubin, 1992).

These models were fitted using *hSDM.site.occ.iCAR* function from the 'hSDM' package (Vieilledent, 2019) in the R statistical environment (version 4.0.3; http://cran.r-project.org/).

Model validation was assessed through an internal cross validation repeated 10 times, based on randomly selected training and test dataset (75% and 25% of the data respectively). The True Skill Statistics (TSS), the area under the receiver-operating curve (AUC) and the Root Mean Square Error (RMSE) were reported as performance criteria.

The probability of occurrence of *L. fullonica* was plotted for each relevant environmental variable and mapped, values ranging from 0 to 1, with higher values indicating a strong probability of occurrence. An uncertainty map of the predictions was carried out using the differences between the 2.5% and 97.5% predicted values quantiles and classified in 5 equal width classes.

2.4 Length distribution

In the area of high probability of occurrence resulting from the distribution model (from 9.5°W to 4.8°W and from 47°N to 51.4°N), a General Additive Mixed Model (GAMM) was used to understand the spatio-temporal structuring of individuals according to their length. Predictor variables tested were the same used for the distribution model alongside an interaction between latitude and longitude to understand spatial variation. As seasonal migration linked to the reproduction have already been observed for skate species (Hunter *et al*., 2005; Elliott *et al*., 2020a), a temporal scale was defined in order to consider possible variability in the length distribution over the season: spring (March, April, May), summer (June, July, August), autumn (September, October, November), and winter (December, January, February). The effect of this temporal covariate on the length distribution was tested by integrating it in the model linearly or in interaction with the other covariates. To limit biases related to temporal differences in fishing grounds exploited and fishing gear deployed or not deployed, the data used for the length distribution model are based on individuals caught by otter twin trawls (OTT) and otter beam trawls (OTB), since their distributions cover the area of high concentration for each season. We used the lowest Bayesian Information Criterion (BIC; Schwarz, 1978) to identify the model of best fit, which is more adequate when heterogeneity is present in the dataset (Brewer *et al*., 2016). The length distribution GAMM of *L. fullonica* was processed with the restricted maximum likehood (REML) smoothness selection method and takes the form as:

$$L.\,fullonica\;length = \alpha + s(latitude, longitude) + s(depth) + season \qquad (6)$$

Where α is the intercept, $s(.)$ Is a spline smoothing function of the covariate term's and comma is an interaction. A log likehood ratio test (LL) against the null hypothesis was used to test model significance. The significance of the predictors was assessed by their p value, and a Tukey test was used to test the difference between categorical variables. Predictions were mapped and their associated errors (i.e. kriging of the absolute difference between predicted lengths and data lengths).

3. Results

3.1 *L. fullonica* distribution

From the dataset, 18 782 FOs were retained for analysis with 2 186 *L. fullonica* occurrences (i.e., a presence prevalence of 0.12). The final model for *L. fullonica* distribution included distance to coast, depth and sediment type predictor variables.

Distance to coast showed a positive relationship with the occurrence of *L. fullonica* (posterior mean = 0.009; CrI = 0.002 to 0.01) until it reaches a maximum probability of occurrence at around 230 km (Fig. 2a). An increase in the probability of occurrence was observed with increasing depth (posterior mean = -0.002; CrI = -0.003 to -0.001), reaching a maximum at around 150 m and then the probability of occurrence decreased with increasing depth (Fig. 2b). Of the different sediment types, only sand discriminated from coarse and mixed sediment with a positive relevant relationship (posterior mean = 0.66; CrI = 0.14 to 1.18) in contrast to the other two comparisons with mud (posterior mean = 0.26; CrI = -0.32 to 0.81) and rock (posterior mean = -2.42; CrI = -5.40 to 0.26) sediment types. The probability of *L. fullonica* occurrence was highest on sand and lowest on rock while mud and coarse and mixed sediment did not show significant differences (Fig. 2c). The highest probability of *L fullonica* detection was for the demersal mobile gear categories otter twin trawls, followed by otter beam trawls, which had a probability of detection close to the trammel nets and set gillnets (two static net gear categories; Fig. 2d).

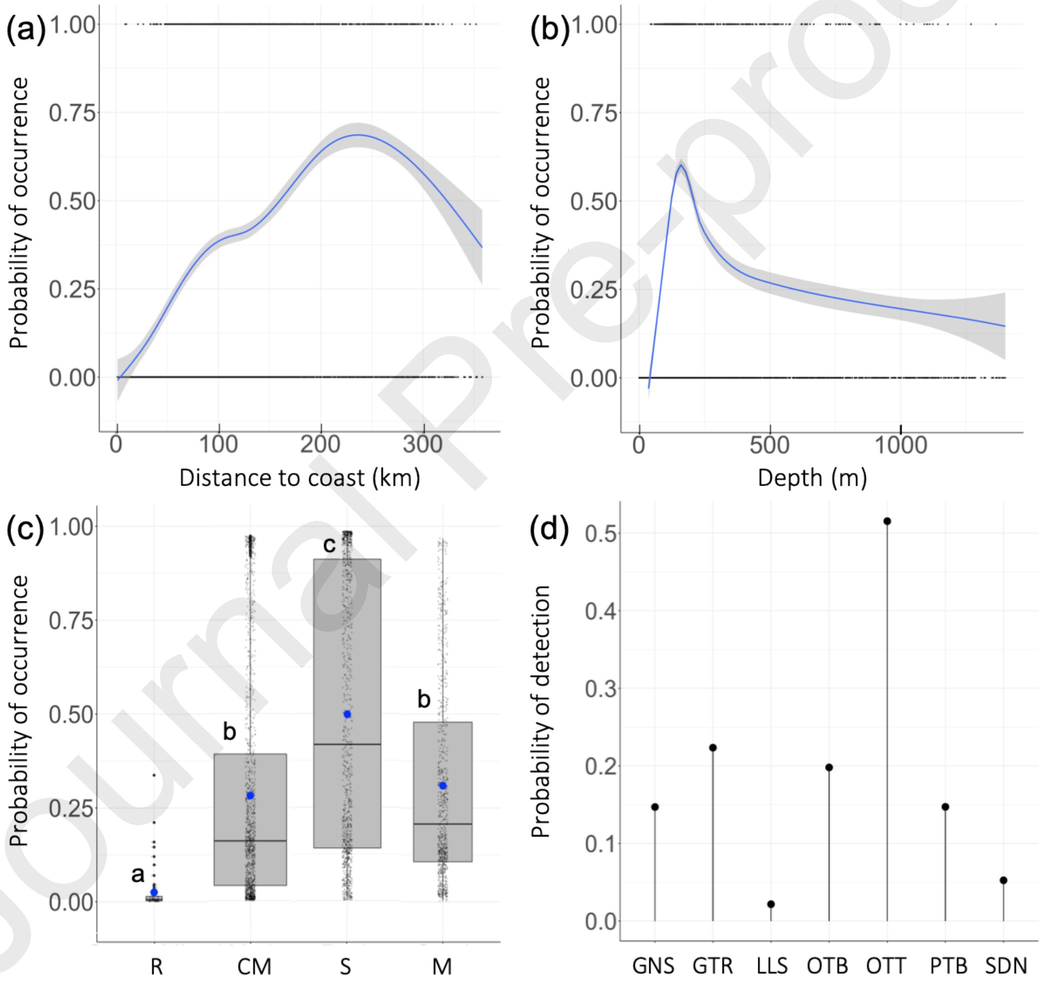

Fig. 2. Probability of *Leucoraja. fullonica* occurrence according to (a) distance to coast and (b) depth. Grey ribbon represents standard error and black dots the sample distribution. (c) Sediment categories. R: rock; CM: coarse and mixed; S: sand; M: mud. Blue dots represent means and small black dots the predictions. Letters correspond to the results of post-hoc

Tukey-test. (d) Probability of *L. fullonica* detection according fishing gear types. GNS: set gillnets; GTR: trammel nets; LLS: set longline; OTB: otter beam trawls; OTT: otter twin trawls; PTB: bottom pair trawls; SDN: Danish seine nets.

An area of high probability of *L. fullonica* occurrence, that ranges from 9.5°W to 4.8°W and from 47°N to 51.4°N, was evident in the southwest of the Celtic Seas and the north of the Bay of Biscay ICES ecoregions (Fig. 3a). The confidence of this core area is high as illustrated by the very low prediction uncertainty associated (Fig. 3b). This area extended over the continental shelf to the beginning of the slope and covered depths from 50 to 500 m approximately (Fig. 3a-e). Predictions showed that the distribution of the species appears to extend along the edge of the continental shelf but prediction uncertainty were high to very high (Fig. 3a-b). A very low or near-zero probability of occurrence of *L. fullonica* was apparent in coastal areas (e.g., western Channel Sea and/or southern Bay of Biscay ICES ecoregion) with a very low prediction uncertainty.

After the cross-validation, the model presented an excellent discrimination with an AUC value at 0.93 ± 0.005 (mean ± SD), a good fit to the data with a root mean square error (RMSE) value at 0.35 ± 0.005 and a good ability to predict true negative and true positive predictions with a TSS mean value at 0.72 ± 0.012 (sensitivity = 0.89 ± 0.01; specificity = 0.82 ± 0.01).

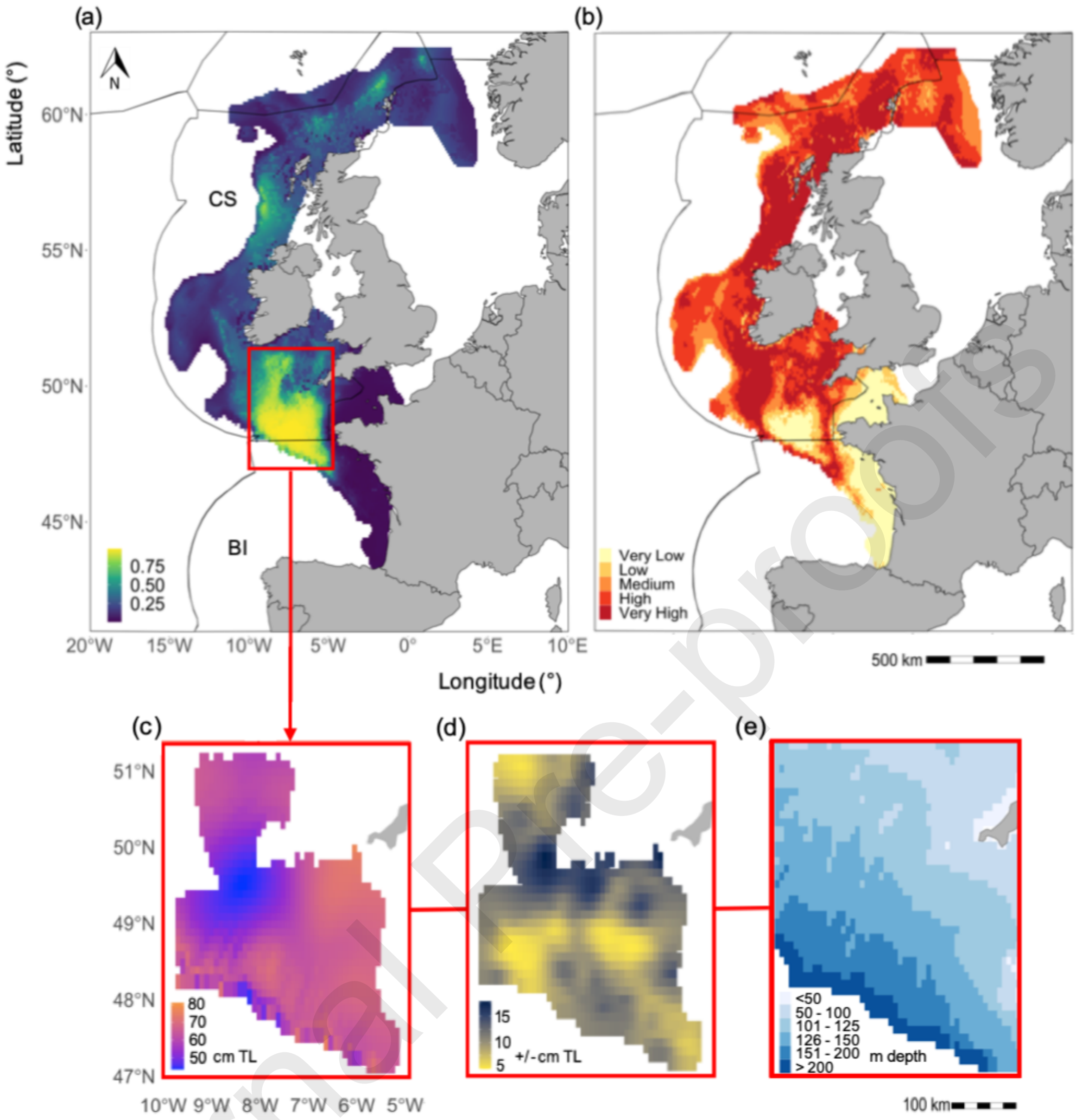

Fig. 3. (a) Predicted occurrence of *Leucoraja. fullonica*. High values indicate a strong probability of occurrence. Black solid lines delineate ICES ecoregions. CS: Celtic Seas; BI: Bay of Biscay and the Iberian Coast. (b) Prediction uncertainty for each cell based on the 95% quantiles of predicted values. (c) Predicted distribution of *L. fullonica* total lengths (TL) in cm within the area of high probability of occurrence. (d) Kriging of prediction total length errors (+/- cm TL) based on the absolute difference between predicted and data values. (e) Depths (m) of the area of high probability of occurrence.

3.2 *L. fullonica* length distribution

Data used for the length distribution model concerned 1 812 FOs conducted by OTT and OTB gears in the area of high probability of occurrence, which extends from 9.7°W to 4.2°W and from 47°N to 51.8°N within the SW Celtic Seas / North Bay of Biscay (Fig. 3a), and corresponded to 5 700 individuals measured. The total lengths ranged from 15 cm to 115 cm with a mean of 64.5 ± 16.8 cm (mean ± SD).

The best model selected by BIC (LL = -23747, DF = 39, $p < 0.01$; 14.1% of the deviance) included latitude and longitude interaction ($p < 0.01$), depth ($p < 0.01$) and season predictors ($p < 0.01$). The total length tended to decrease with increasing depth to about 150 m, beyond that the total length increased with increasing depth to about 300 m (Fig. 4a). The seasonal descriptor indicated that the smallest total lengths occur more in winter than other seasons (Fig. 4b) and did not show temporal interaction with the other predictors of the length distribution of *L. fullonica*.

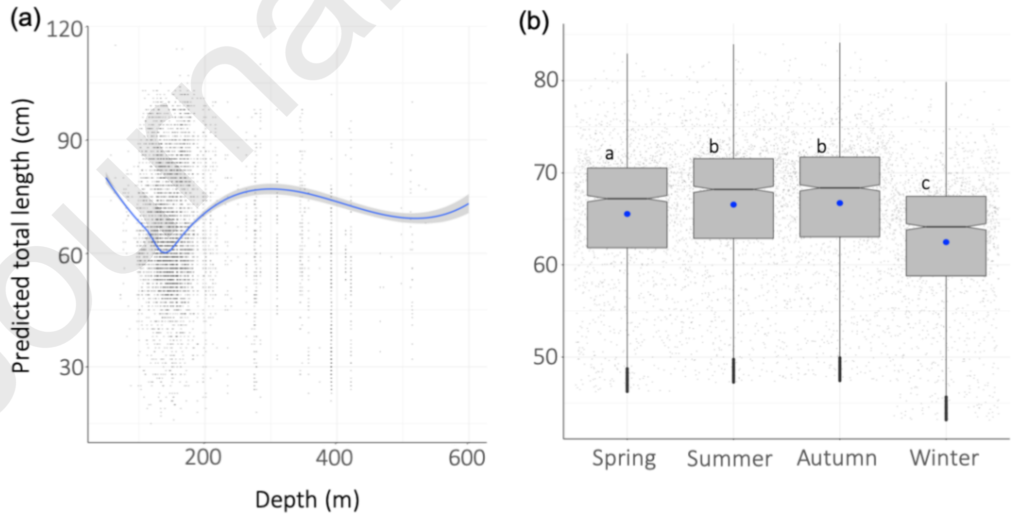

Fig. 4. Predicted total length in cm of *Leucoraja fullonica* according to (a) depth. Grey ribbon represents standard error and black dots the sample distribution. (b) seasons. Blue dots

represent means and small black dots the predictions. Letters correspond to the results of post-hoc Tukey-test.

The model results showed that smallest individuals (approximatively 45-55 cm TL) were mainly located in an area between 49°N to 50°N and 9°W to 8°W (Fig. 3c) where the depth range from 120 to 150 m (Fig. 3e). The prediction error in this area ranged from ± 10 to 18 cm TL (Fig. 3d). A small area at the edge of the continental shelf beyond 200m depth also showed lengths around 50cm TL with a prediction error of less than 10cm TL (Fig. 3c-d-e). Large individuals ($\geq$ 70 cm TL) were located to east part of the area of high concentration and near the edge of the continental shelf at depths varying from 50 to 200 m approximatively (Fig. 3c-e). The prediction error for area of large individuals was variable and highest (error range: 8 – 16 cm TL approximatively) at the limit of predictions on the eastern side where the largest individuals (80 cm TL approximatively) were located whereas it was more moderate near the edge of the continental shelf (error range: 5 – 12 cm TL approximatively).

3.3 *L. fullonica* bycatch

According to the seven fishing gear types which may bycatch *L. fullonica*, demersal mobiles gears (Table 2) were the dominant gear category with 12 740 FOs (68%). Among demersal mobile gear, *L. fullonica* was mainly caught by otter twin trawls (OTT; 1 684 occurrences) with a catch rate of 32% (Table 2). Line caught the least *L. fullonica* (catch rate < 1%).

Table 2. Summary table of *Leucoraja. fullonica* occurrence per fishing gear types. Total number of fishing operations (N_{FO}), number of *L. fullonica* occurrences (N_{occ}), *L. fullonica* percentage occurrence ($\%_{occ}$), number of individuals measured ($N_{measured}$), the minimum total length in cm

(TL_{min}), the maximal total length measured in cm (TL_{max}), the mean and the standard deviation in cm of total lengths ($TL_{mean \pm sd}$). GNS: set gillnets; GTR: trammel nets; LLS: set longline; OTB: otter beam trawls; OTT: otter twin trawls; PTB: bottom pair trawls; SDN: Danish seine nets.

Gear types	Gear categories	N_{FO}	N_{occ}	$\%_{occ}$	$N_{measured}$	TL_{min} (cm)	TL_{max} (cm)	$TL_{mean \pm sd}$ (cm)
GNS	Static net	2530	25	1.0	42	50	97	80.4 ± 10.9
GTR	Static net	2564	36	1.4	168	31	104	87.7 ± 9.8
LLS	Line	948	2	0.2	2	58	79	-
OTB	Demersal mobile	6237	401	6.4	897	22	115	66.4 ± 18.2
OTT	Demersal mobile	5315	1684	31.7	5231	15	114	64.5 ± 17.0
PTB	Demersal mobile	550	30	5.5	37	31	98	62.9 ± 12.9
SDN	Demersal mobile	638	8	1.2	12	38	63	54.0 ± 7.9

The total length (TL) of *L. fullonica* bycaught individuals ranged from 15 to 115 cm with a mean of 65.4 ± 17.4 cm (mean ± SD) (Table 2; Fig. 5). On average, static nets caught larger individuals (86.2 ± 10.4 cm TL; range = 31 - 104 cm TL) and demersal mobiles smaller individuals (64.7 ± 17.1 cm TL; range = 15 - 115 cm TL). Peak catch length densities for static nets (80 and 90 cm TL approximatively) are very close to the known length at maturity (Lm: 85.5 ± 14.8 cm TL based on two values; McCully *et al.*, 2012) whereas the peaks for demersal mobiles are much lower (60 cm TL approximatively) (Fig. 5).

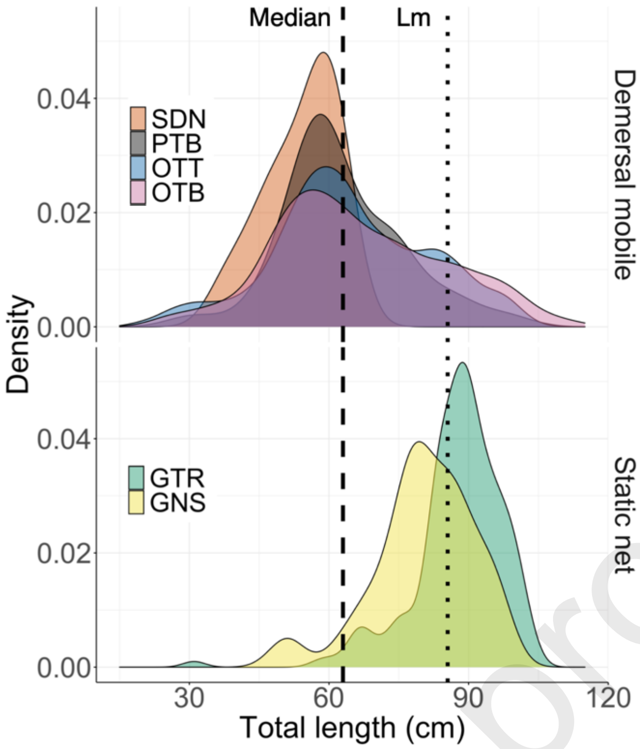

Fig. 5. *Leucoraja. fullonica* kernel smoothed probability density estimates of the total length (cm) catches by fishing gear type. SDN: Danish seine nets; PTB: bottom pair trawls; OTT: otter twin trawls; OTB: otter beam trawls; GTR: trammel nets; GNS: set gillnets. The dashed black line is the median and the dotted black line is mean length at maturity (Lm) from literature (McCully *et al.*, 2012).

4. Discussion

As a result of the availability of fisheries dependent data, the distribution and functional role of *L. fullonica*'s primary area of occurrence was modelled for the first time. Because of biases associated with fisheries dependent data, we employed a Bayesian hierarchical model to incorporate biases associated with gear detectability and spatial autocorrelation. *L. fullonica* was found to mainly occur within a localised area between the southern Celtic Seas and the northern Bay of Biscay with the edge of the continental shelf (from 9.7° W to 4.2°W and from 47°N to 51.8°N). In a descriptive study around the British Isles, Ellis *et al.* (2004) reported that the species was absent from the shallow waters of England and Wales, and catches were restricted to northern North Sea and Celtic Sea. Our study confirms that this area is of particular importance for the species given the high occurrence probability. Previous literature on *L. fullonica*, highlight its presence along the edge of the continental shelf from Iceland and northern Norway to north-west Africa, including Mediterranean Sea (Stehmann and Bürkel, 1984). We had limited data available for this species' most northerly and southerly distribution to confirm their presence here.

The main environmental variables that influenced the spatial distribution of *L. fullonica* were depth, distance to coast and sediment type. It has been already shown that depth have an important effect on the feeding habits of skates (Barbini *et al.*, 2018). These patterns may be linked to biotic factors correlated with depth, such as preferred prey species that vary with depth (Witmann and Roy, 2009). In our study, *L. fullonica* catches ranged between 44 and 1363 m depth. This observed depth range is wider than those available in the literature. For instance, Ellis *et al.* (2004) reported *L. fullonica* catches between 90 and 424 m around British Isles. According to Weigmann (2016), *L. fullonica* occurs between 30 and 600 m in north-eastern Atlantic. Specimens were caught in a depth range of 297 and 574 m in Adriatic Sea (Zupa *et al.*, 2010), and up to 800 m depth in the Mediterranean Sea (Relini *et al.*, 2010). It should, however, be noted that our results showed *L. fullonica* mainly occurred within a narrow depth range between 100 and 200 m. It is likely that the characteristics of the ObsMer data which gathers catch data throughout the year and over a large spatial area contribute to this result. Alternatively, the wide range of depths that the species were observed within may be because of miss-identification. *L. fullonica* has been miss-identified with the sandy ray

(*Leucoraja circularis*) and the small eyed ray (*Raja microocellata*) (https://www.comite-peches.fr; Iglesias *et al*, 2010).

As an offshore species (Stehmann and Bürkel, 1984; Ellis *et al.*, 2004), distance to the coast is expected to influence *L. fullonica* distribution. Surprisingly, this variable is rarely examined in skate literature. The occurrence of *L. fullonica* followed a modal curve from 0 to 350 km to the coast with a peak around 230 km. These patterns could be linked to biogeochemical factors correlated with distance to the coast. Barrón and Duarte (2015), synthesized large data sets that highlight global trends in open ocean and shelf sea. They showed that dissolved organic carbon (DOC) concentration declined significantly with increasing distance offshore from the coastline. Carr *et al.* (2019), analysed variability of dissolved organic matter (DOM) on the shelf, central shelf and shelf edge of the Celtic Sea, and showed DOM site specific trends reflecting contrasting physical and biogeochemical conditions. Such biogeochemical conditions experienced by skates is currently unknown. Research into physical and geochemical habitat of skates could help better understand the ecological process affecting their distribution.

L. fullonica was mainly observed on sand seabed types, with very low occurrence on rocky substrate, while mud and coarse and mixed sediment did not show significant differences. This pattern confirms the preference of *L. fullonica* for sandy bottoms, as demonstrated previously by Stehmann and Bürkel (1984) and Ellis *et al.* (2004). Despite its broad distribution range, the offshore nature of *L. fullonica* means there are very few published biological investigations on their seabed use (Du Buit, 1972; Consalvo *et al.*, 2009; Mnsari *et al.*, 2009). Prey and predator abundance are known to shape batoid habitat use (Vaudo, 2011). *L.*

fullonica forages on organisms buried beneath sediment and predating on a wide variety of species from crustaceans, fish, to other elasmobranchs (Ebert and Bizarro, 2007). Separately, Porcu *et al.* (2017), identified sandy bottoms (<100-150 m depth) in central-western Mediterranean as egg-laying sites of many species belonging to genus *Raja* (e.g. *R. asterias*, *R. brachyura*, *R. miraletus* and *R. polystigma*). Unfortunately, consideration of specific interaction between sex or maturity and sediment type or seasonal use for *L. fullonica* was not possible as a result of zeros inflation.

Skates are known to exhibit different distribution patterns throughout their ontogeny (Bizzarro *et al*., 2014; Elliott *et al*., 2020a). It has been further suggested that juvenile hard-nosed skates (*Raja* spp.) occur at shallower depths than egg cases or adults, whereas the opposite situation is described for *Bathyraja* spp. (Ebert *et al*, 2008; Hoff, 2010; Mull *et al*., 2010). Here, within the core area, the length distribution model of *L. fullonica* showed a spatial segregation according to size. Smaller individuals (approximately 45 - 55 cm TL) were mainly located on the continental shelf between 120 to 150 m depth, and larger individuals (≥ 70 cm TL) within a wider depth range, from 50 to 200 m depth, covering both the continental shelf and its edge. Smaller *L. fullonica* were also observed during winter indicating a potential recruitment during winter months In the case of *L. fullonica*, the spatial segregation observed may be to reduce agonistic interactions, such as predation from larger individuals, or competition for resources between individuals, and maximise juvenile survival (Elliott *et al.*, 2020a; Hoff,2010; Simpson *et al*., 2019). Unfortunately, *L. fullonica* shifts in diet with size is not available. A detailed examination of dietary variability according to size such as undertaken by Moura *et al.*, (2008) is necessary to determine the extent of trophic niche within the species.

The core area, where *L. fullonica* had the highest probability of occurrence, is known to have a very high level of fishing activity, notably from bottom trawls techniques (Sharples *et al.*, 2013; ICES, 2018). *L. fullonica* is highly susceptible to bycatch in bottom trawls fisheries and bycatch survival rate for this species is unknown (STECF, 2017; ICES, 2020). Bottom trawl gear types showed low size selectivity, with catches ranging from 15 to 115 cm TL, encompassing *L. fullonica* size range. The individuals were between 50 to 70 cm TL, which is, according to McCully *et al*. (2012), below the length at maturity. Measures to protect juveniles and nursery grounds, and to minimize fishing mortality on mature females might have tangible benefits for the stock (Apostolaki *et al*., 2006). Furthermore, several studies have shown that the survival of juveniles strongly influence the viability or recovery of elasmobranch populations (Brander, 1981; Ward-Paige *et al*., 2012; Elliott *et al*., 2020b). Since *L. fullonica*'s core area of distribution is within an area of high fishing pressure (Sharples *et al*., 2013; ICES, 2018), any management measures that decreases mortality and/or increases recruitment, facilitating population maintenance or recovery (Polunin, 2002) should be investigated.

To avoid potential displacement of fishing activity (Hilborn *et al*., 2004; Kaiser, 2005), measures that limit size selectivity should be a first step. Unfortunately, seasonal and stage specific SDMs were not possible because of too few presences. With more data, such an analysis may provide more information on potential ontogenetic migration movements. Better understanding into the key life history phases of *L. fullonica,* such as egg laying periods and avoidance of areas where juveniles occupy may help identify key periods and locations to reduce fishing whilst avoiding issues of displacement fishing activity.

Through the use of the Bayesian hierarchical model taking into account imperfect detection and spatial autocorrelation, the performance of the *L. fullonica* SDM showed a very good discrimination and a good fit of the data despite a prevalence of occurrence lower than 50% in the data as recommended by Liu *et al*. (2005). The uncertainty of prediction of *L. fullonica* occurrence showed a very low uncertainty in areas with a lot of data (i.e. southern part of the study area) and a higher uncertainty where data are scarce. Use of fisheries dependent data could be criticised due to biases associated with the targeted nature of the dataset (Hilborn and Walters, 2015). Comparative studies have, however, shown that results from fishery-dependent and fishery-independent data on species distribution and abundance analyses are consistent and complementary despite spatial and temporal differences in sampling (Pennino *et al*., 2016; Bourdaud *et al*., 2017; Elliott *et al*., 2020b).

5. Conclusion

Species specific spatio-temporal distributions and habitat use is a pitfall to protect vulnerable skates and rays (Ellis *et al*., 2010). Since expensive fishery-independent data are not designed for demersal elasmobranch species (ICES, 2020), this study highlights that already existing fishery-dependent data can fill such gaps and should be used more widely. Further, from the use of the hierarchical Bayesian modelling framework, biases associated with fishery-dependent data, can be incorporated, resulting in good prediction reliability.

Our results show that *L. fullonica* may be particularly vulnerable given its core area of distribution is restricted to one location which is subject to high fishing pressure. If more fisheries dependent data was available, further research into life history traits could be undertaken to disentangle the spatio-temporal segregation observed by *L. fullonica* within this core area. Such temporal interactions are not possible using scientific bottom trawl surveys which are usually undertaken annually. In addition, a population dynamic model such as developed by Elliott *et al*. (2020b) could provide a better understanding of whether management efforts should focus on *L. fullonica* juveniles or adults, and help support the implementation of specific spatio-temporal management measures whilst minimizing impact on the fishing industry.

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Highlights

- Fisheries-dependent data can fill gaps in knowledge of data-poor elasmobranch species
- *L. fullonica* is distributed within an area of high concentration where size segregation is present
- Its localized distribution is within an area subject to heavy fishing pressure
- *L. fullonica* is most susceptible to bycatch by bottom trawl fishing gear types
- Most of the *L. fullonica* individuals caught are immature

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: