Received: 11 January 2024 | Revised: 9 August 2024 | Accepted: 9 September 2024

DOI: 10.1002/ecs2.70050

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Coastal and Marine Ecology

Assessing the overlap between fishing and chondrichthyans exposes high-risk areas for bycatch of threatened species

Federico Maioli[1,2] | **Benjamin Weigel**[3] | **Max Lindmark**[4] | **Chiara Manfredi**[1] | **Walter Zupa**[5] | **Isabella Bitetto**[5] | **Tommaso Russo**[6] | **Michele Casini**[1,4,7]

[1]Department of Biological, Geological and Environmental Sciences, Laboratory of Marine Biology and Fisheries, University of Bologna, Fano, Italy

[2]National Institute of Aquatic Resources, Centre for Ocean Life, Technical University of Denmark, Kongens Lyngby, Denmark

[3]INRAE, EABX, Cestas, France

[4]Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, Lysekil, Sweden

[5]Fondazione COISPA ETS, Bari, Italy

[6]Department of Biology, University of Rome "Tor Vergata", Rome, Italy

[7]CoNISMa, Rome, Italy

Correspondence
Federico Maioli
Email: f.maioli@unibo.it

Handling Editor: Sean P. Powers

Abstract

Chondrichthyans (sharks, rays, skates, and chimaeras) make up one of the oldest and most ecologically diverse vertebrate groups, yet they face severe threats from fishing, necessitating improved management strategies. To effectively manage these species, we need to understand their spatial interactions with fisheries. However, this understanding is often challenged by limited data on chondrichthyan catches and species identification. In such cases, assessing potential risks from fishing activities can provide valuable insights into these spatial interactions. Here, we propose a method combining geostatistical models fitted to a fishery-independent dataset with vessel monitoring system (VMS) data to estimate the spatial overlap between chondrichthyans and fishing. Our case study focuses on the western Adriatic Sea in the Mediterranean, examining the overlap between bottom trawling (including otter bottom trawling and beam trawling) and demersal chondrichthyans. We find that the northwestern part of the basin is a hotspot where threatened chondrichthyans (classified as Vulnerable, Endangered, or Critically Endangered by the International Union for Conservation of Nature Red List) greatly overlap with bottom trawling activities. Moreover, some areas, such as the northernmost part of the Adriatic and the "area dei fondi sporchi" in the north-central offshore part, exhibit minimal overlap between threatened chondrichthyans and bottom trawling, potentially serving as refuges. We recommend prioritizing the management of otter bottom trawling in the northwestern basin to protect these threatened species, while also paying attention to the possible impacts of beam trawling on skates and chondrichthyan habitats. Despite certain limitations, our findings demonstrate that combining geostatistical models of species distributions with VMS data is a promising method for identifying areas of concern for species vulnerable to fishing. This approach can inform targeted management measures and cost-effective onboard monitoring programs.

KEYWORDS
Adriatic Sea, bottom trawl fishing, bycatch, chondrichthyans, Mediterranean Sea, SDM (species distribution models), sharks, VMS (vessel monitoring system)

INTRODUCTION

Chondrichthyans (sharks, rays, skates, and chimaeras) are among the most evolutionarily distinct and ecologically diverse groups of vertebrates (Compagno, 1990; Stein et al., 2018). This group, which includes about 1200 extant species, is now one of the most threatened among vertebrates, with one in three species considered at risk of extinction (Dulvy et al., 2021; Hoffmann et al., 2010; Weigmann, 2016). Overfishing, including targeted fisheries and bycatch, overwhelmingly poses the primary threat to their survival (Dulvy et al., 2014, 2021). Chondrichthyans are generally considered less resilient to fishing than most teleosts, partly due to their strategy of producing larger but fewer offspring (Andersen, 2019; Stevens, 2000). However, biologically sustainable fisheries can be achieved for several chondrichthyan species when strong science-based management is enforced (Simpfendorfer & Dulvy, 2017; Walker, 1998).

Spatial management of fisheries is now widely adopted to mitigate the adverse impacts of fisheries (FAO, 2023; McConnaughey et al., 2020). However, particularly for chondrichthyans, limited data on catches and species identification hinder our understanding of the spatial interactions between species and fisheries, thereby jeopardizing targeted management efforts (Cashion et al., 2019; FAO, 2022). In such cases, assessing the spatial overlap between species and fisheries becomes crucial (Queiroz et al., 2016, 2019). The vessel monitoring system (VMS), a satellite-based tool that tracks fishing vessels in real time, has emerged as a valuable tool for tracking and monitoring fishing effort (Amoroso et al., 2018; Eigaard et al., 2017). Integrating VMS data with species distribution information further constitutes a promising approach to assess the spatial overlap between fishing effort and fish distribution, aiding in identifying high-risk areas for bycatch (Queiroz et al., 2016).

The Adriatic Sea, situated in the central Mediterranean, has a long history of chondrichthyan fisheries and has witnessed the depletion of several species in recent decades (Dulvy et al., 2003; Ferretti et al., 2013; Jukic-Peladic et al., 2001; Lotze et al., 2011). Approximately 70% of the chondrichthyan species in the Adriatic Sea are regionally threatened according to International Union for Conservation of Nature (IUCN) Red List Criteria (www.redlist.org) (Soldo & Lipej, 2022). In this basin, chondrichthyans are primarily caught as bycatch in fisheries targeting more commercially valuable teleost species although certain chondrichthyan species are periodically targeted (Bradai et al., 2012; Lucchetti et al., 2023).

Among the chondrichthyan species commonly caught or observed in this region are the cathsharks (*Scyliorhinus* spp.), Brown Skate (*Raja miraletus*), Spiny Dogfish (*Squalus acanthias*), Thornback Skate (*Raja clavata*), and smoothhounds (*Mustelus* spp.) (Barausse et al., 2014; Clodia Database, 2020; Ferretti et al., 2013; Maioli et al., 2023). The Adriatic Sea is one of the most trawled regions globally (Amoroso et al., 2018; Pitcher et al., 2022), with bottom trawling being a significant and widely practiced fishing activity targeting various demersal fish species (FAO, 2022). The bottom trawling fleet in the Adriatic Sea consists of about 1900 vessels, equivalent to approximately 64,900 gross tons, with Italy owning around 70% of the total fleet (FAO, 2022). Consequently, this fishing activity significantly contributes to the bycatch of chondrichthyans, making it a major concern for the management of these species (Carpentieri et al., 2021; FAO, 2022).

Recognizing the need for action, the General Fisheries Commission for the Mediterranean (GFCM) initiated the MedBycatch project. Its goal is to develop a collaborative approach to improve the understanding of the Mediterranean multi-taxa bycatch of vulnerable species and test mitigation actions (Carpentieri et al., 2021). However, despite these efforts, there is still limited knowledge regarding the bycatch of chondrichthyan species (but see Bonanomi et al., 2018 for pelagic trawling), which hampers effective management and conservation efforts in the region (FAO, 2022).

In this study, we introduce a new approach to assess the spatial overlap between two dominant bottom trawling types—otter bottom trawling (OTB) and beam trawling (TBB)—and demersal chondrichthyans in the western Adriatic Sea. We integrate data on fishing effort from the Italian fleet, obtained through VMS, with predicted species distributions derived from geostatistical species distribution models (SDMs) based on data from a fishery-independent bottom trawl survey. Using ad hoc overlap indices, we analyze and map species distribution, species richness, and the presence of threatened species in relation to bottom trawl fishing effort. This provides valuable insights into the potential spatial impact of fishing. Our primary goal is to identify high-risk areas for bycatch and regions with minimal overlap, which could serve as refuges for these species. The results from our approach can guide the development of targeted conservation efforts and effective management strategies to protect chondrichthyan populations in this heavily exploited ecosystem. Additionally, the new provided insights can help design cost-effective onboard monitoring programs.

METHODS

Study area

The Adriatic Sea, located in the Central Mediterranean Sea between the Italian peninsula and the Balkans, is a shallow and eutrophic basin with notable morphological variations along its axes (Figure 1). In the north, it has a mean depth of about 30 m and reaches a maximum of 70 m, with a weak bathymetric gradient. This area receives significant river runoff, particularly from the Po River, contributing to its high productivity and intense fishing activity (Campanelli et al., 2011; Eigaard et al., 2017; Hopkins, 1992). The central Adriatic reaches depths of 200 m and includes two depressions, known as the Jabuka/Pomo Pits, with maximum depths of approximately 270 m. The southern Adriatic differs markedly: The northern section around the Gulf of Manfredonia has a wide continental shelf and smooth slope, whereas the southern section has a steeper slope, affecting local ecological communities and fishing methods (Di Natale et al., 2011). The western coast is regular and sandy, while the eastern coast is irregular, rocky, with numerous islands and a steeper slope (Russo & Artegiani, 1996). Water circulation is cyclonic, shaped by river runoff and atmospheric conditions, which also affect the sea's salinity and temperature (Artegiani et al., 1997).

Data

Fishery-independent survey

The complete biological dataset for this study comprised the catches from 5122 bottom trawl hauls conducted in the Italian and international waters of the Adriatic Sea during the Mediterranean International Trawl Survey (MEDITS). This survey has been conducted annually since 1994 by the Laboratory of Marine Biology and Fisheries of Fano (Italy) in the Northern and Central Adriatic Sea and by Laboratorio Provinciale di Biologia Marina of Bari (Italy) (1994–2008) and COISPA Tecnologia & Ricerca (since 2009) in the Southern Adriatic Sea. The survey is generally carried out in the late spring to summer (May–September, though occasionally it has been performed in October–December) and covers depth ranging from 10 to 800 m, following a stratified sampling scheme based on 5 different depth strata (MEDITS Working Group, 2017; Spedicato et al., 2020). The sampling gear used is the GOC-73 experimental bottom trawl, which has a horizontal opening of 16–22 m and a vertical opening of approximately 2.4 m. The trawl's codend features a 20-mm side diamond stretched mesh. Further information on the sampling procedures, data collection, and analysis can be found in the MEDITS handbook (MEDITS Working Group, 2017).

For this study, we selected and analyzed a total of 4197 hauls (Figure 1), after excluding hauls conducted prior to 1999 and those conducted during the autumn period (October–December). This exclusion was driven by two factors: The availability of the biogeochemical variables only reaches back to 1999 and the coverage of the autumn season has been inconsistent over the years. Ensuring a temporally homogenous dataset was essential due to potential seasonal redistribution of chondrichthyan species (Manfredi et al., 2010). Moreover, we excluded species that were scarcely represented in the data (i.e., those occurring in less than 3% of all the trawl hauls considered). We also grouped the Common Smoothhound (*Mustelus mustelus*) and the Blackspotted Smoothhound (*Mustelus punctulatus*) under the category smoothhounds (*Mustelus* spp.) because the morphological identification for the *Mustelus* genus is challenging (Marino et al., 2018), and the two species can be misclassified. Additionally, these species co-occur in the Northern Adriatic Sea, have similar diets (Di Lorenzo et al., 2020), inhabit similar habitats, and may hybridize (Marino et al., 2018). In total, 10 species (including one group of species) were included in further analyses (Table 1).

To determine the conservation status of each species, we used the criteria set forth by the IUCN (www.redlist.org), categorizing species as threatened if they were classified as Critically Endangered (CR), Endangered (EN), or Vulnerable (VU), and as non-threatened if they were categorized as Near Threatened (NT) or Least Concern (LC) (Table 1). Spiny Dogfish, Common Eagle Ray and smoothhounds are categorized as threatened species, whereas the remaining species are classified as non-threatened (Table 1). Species common names follow the IUCN nomenclature standards (IUCN, 2013).

Fishing effort

VMS data consist of a series of consecutive pings (signals) sent by each vessel at regular intervals, providing near real-time information on the vessel's location,

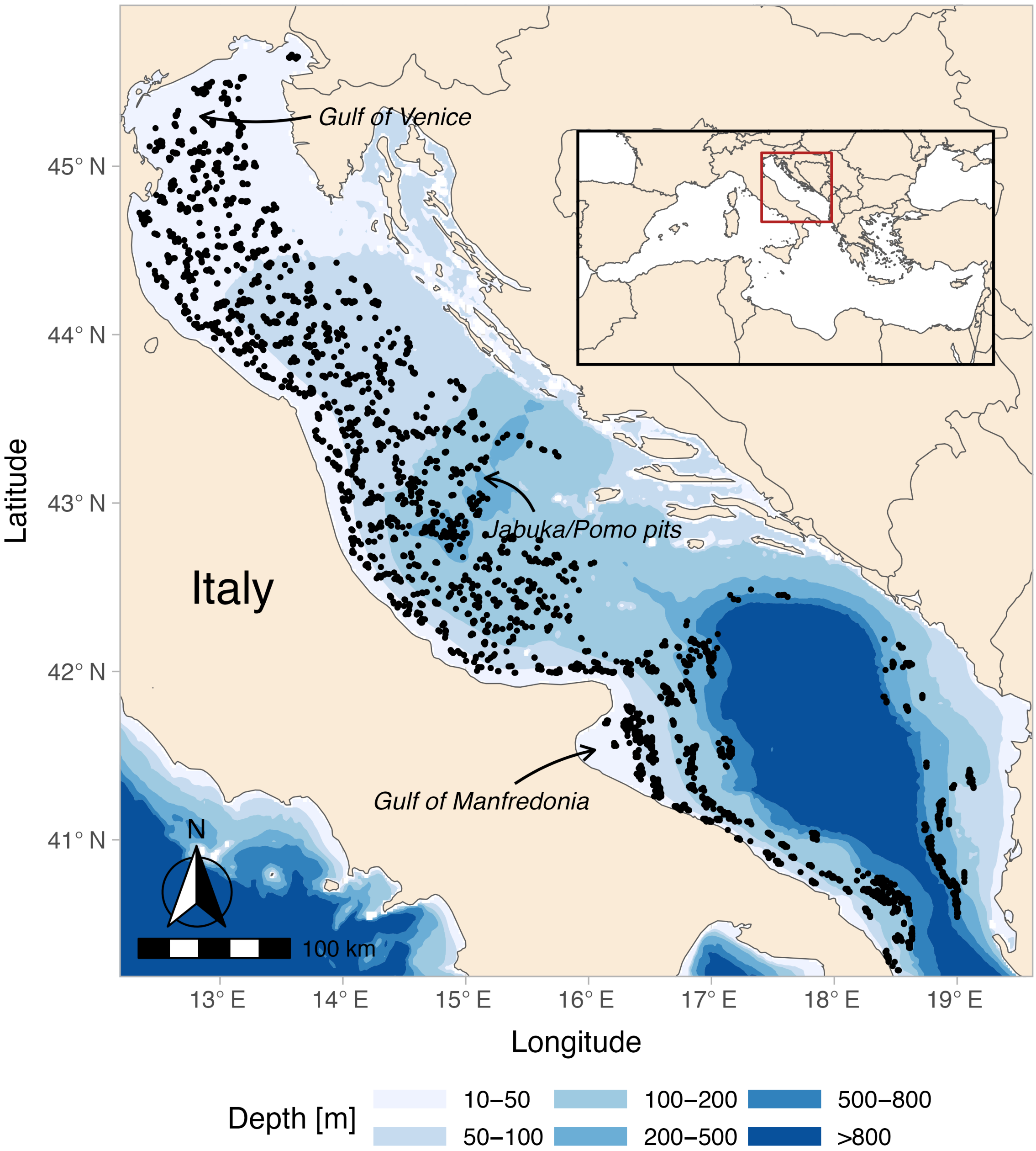

FIGURE 1 Study area location. Black points indicate the positions of Mediterranean International Trawl Survey bottom trawl hauls (1999–2021).

course, and speed. Although VMS signals are less frequent than those of the Automatic Identification System (AIS) and typically occur every 1–2 h, they offer extensive spatial coverage through the INMARSAT satellite network (Russo et al., 2016; Shepperson et al., 2018). Since 2012, vessels over 12 m are required to participate in VMS. However, vessels between 12 and 15 m are exempt if they operate exclusively within the territorial seas of the flag member state and never spend more than 24 h at sea from departure to return, in accordance with European Council (EC) Regulation Number 1224/2009.

For this study, VMS and logbook data for the bottom trawling fleet operating in the Adriatic Sea were provided by the Italian Ministry of Agriculture, Food Sovereignty and Forests (MASAF) as part of the Italian National Program for the Data Collection in the Fisheries Sector (INPDCF). We analyzed data from vessels conducting OTB and TBB, identified through logbook data and the EU Fleet Register (https://webgate.ec.europa.eu/fleet-europa/index_en). We assessed the fishing effort of these vessels from 2009 to 2021 using the R package VMSbase (version 2.2.1; Russo, Parisi, & Cataudella, 2011; Russo, Parisi, Prorgi, et al., 2011;

TABLE 1 Species included in the study and their frequency of occurrence (percentage of trawl hauls where each species was caught) from 1999 to 2021.

Species	Common name	Frequency of occurrence (%)	IUCN category	IUCN category reference	Conservation status
Scyliorhinus canicula	Smallspotted Catshark	10.8	LC	Finucci et al. (2021)	Non-threatened
Galeus melastomus	Blackmouth Catshark	10.0	LC	Abella et al. (2016)	Non-threatened
Squalus acanthias	Spiny Dogfish	8.7	EN	Ellis, Soldo, et al. (2016)	Threatened
Etmopterus spinax	Velvet Belly Lanternshark	8.2	LC	Guallart et al. (2016)	Non-threatened
Raja clavata	Thornback Skate	7.9	NT	Ellis, Serena, and Lotze (2016)	Non-threatened
Chimaera monstrosa	Rabbitfish	6.3	NT	Dagit and Hareide (2016)	Non-threatened
Raja asterias	Starry Skate	3.5	NT	Serena, Abella, et al. (2016)	Non-threatened
Myliobatis aquila	Common Eagle Ray	3.5	VU	Serena, Holtzhausen, et al. (2016)	Threatened
Raja miraletus	Brown Skate	3.3	LC	Dulvy et al. (2020)	Non-threatened
Mustelus spp.	Smoothhounds	3.1	VU	Farrell and Dulvy (2016)	Threatened

Note: Species are listed in descending order of frequency of occurrence. The International Union for Conservation of Nature (IUCN) category column shows conservation status based on the IUCN Red List: EN (Endangered), VU (Vulnerable), NT (Near Threatened), and LC (Least Concern). Species classified as EN or VU are considered threatened, while those categorized as LC or NT are non-threatened.

Russo et al., 2014). VMS pings were interpolated to increase their frequency to 10 min (Russo, Parisi, & Cataudella, 2011). The high-frequency interpolated VMS pings were then combined with the NOAA-Etopo1 database (Amante & Eakins, 2009) through the R package marmap (Pante & Simon-Bouhet, 2013) to estimate the seafloor depth for each ping. To accurately identify a vessel's fishing state, fishing set positions were isolated from other vessel states, such as steaming and resting, by applying a combination of speed and depth filters (Russo et al., 2014). We then filtered the data to include only the period consistently covered by the MEDITS survey (May–September). For a map showing the aggregated fishing effort by season, refer to Appendix S1: Figures S1 and S2. Finally, we aggregated the trawl fishing effort (i.e., the sum of fishing hours) on a grid with 4 km^2 cells by multiplying the number of fishing set positions by the interpolation frequency (10 min). For the number of unique VMS identifiers per year and by length class, refer to Appendix S1: Figure S3.

Species distribution models

Model description

We used geostatistical generalized linear mixed-effects models (GLMMs) to identify the distribution patterns of chondrichthyan species. These models were fitted to survey data using environmental covariates to capture species niches and spatial random fields to account for spatially correlated latent effects that are constant through time. We modeled the presence/absence of each included species using a Bernoulli distribution.

The models can be written as:

$$Y_{\boldsymbol{s},t} \sim \text{Bernoulli}\left(p_{\boldsymbol{s},t}\right), \tag{1}$$

$$\text{logit}\left(p_{\boldsymbol{s},t}\right) = \alpha_t + \boldsymbol{X}_{\boldsymbol{s},t}\boldsymbol{\beta} + \omega_{\boldsymbol{s}}, \tag{2}$$

$$\alpha_t \sim \text{Normal}\left(0, \sigma_\alpha^2\right), \tag{3}$$

$$\boldsymbol{\omega} \sim \text{MVNormal}\left(\boldsymbol{0}, \boldsymbol{\Sigma}_\omega\right), \tag{4}$$

where $Y_{\boldsymbol{s},t}$ is the binary response variable (presence/absence) for the observation at space $\boldsymbol{s}$ and year t, $p_{\boldsymbol{s},t}$ denotes the probability of observing the species at space $\boldsymbol{s}$ and year t, and α_t represents random intercepts by year t. The symbol $\boldsymbol{X}_{\boldsymbol{s},t}$ is the design matrix where columns are vectors of explanatory variables (see the section *Model selection* and Appendix S1: Table S1) at space $\boldsymbol{s}$ and year t and $\boldsymbol{\beta}$ represents a vector of corresponding coefficients. The latent spatial random field $\omega_{\boldsymbol{s}}$ is assumed drawn from Gaussian Markov random fields (GMRF) with covariance matrix $\boldsymbol{\Sigma}_\omega$ constrained by a Matérn covariance function (Lindgren et al., 2011; Rue et al., 2009).

Model fitting

We fit all models in R (v4.1.0; R Core Team, 2024) using the package sdmTMB (v0.6.0; Anderson et al., 2024) via maximum marginal likelihood. sdmTMB uses the Laplace approximation to integrate out random effects sourced from the TMB package (Kristensen et al., 2016) and relies on the stochastic partial differential equation (SPDE) approach to approximate Gaussian random fields as GMRFs. The SPDE method employs piecewise linear basis functions defined by a triangulation over the spatial area of interest, commonly referred to as a "mesh" (Lindgren et al., 2011). Spatial random effects are estimated at the mesh vertices, known as knots, and are then bilinearly interpolated to the data locations.

We constructed the mesh using triangles with a minimum distance of 8 km between knots (i.e., a "cutoff" of 8 km) utilizing the package fmesher (Lindgren, 2023; Appendix S1: Figure S4). We assessed model convergence by ensuring that the maximum absolute log-likelihood gradient with respect to all fixed effects was less than 0.001 and that the Hessian matrix remained positive definite (Anderson et al., 2024).

Environmental covariates

For the SDMs, we selected environmental covariates based on their availability and their assumed relevance to the distribution of the studied species (Maioli et al., 2023). We included four covariates: seafloor depth (in meters; hereafter depth), seafloor temperature (in degrees Celsius; hereafter temperature), seafloor dissolved oxygen (in milliliters per liter; hereafter oxygen), and seabed substrate (categorized into "Sandy mud," "Fine mud," "Sand" and "Muddy sand"). Depth was extracted at the haul locations using raster files with a horizontal resolution of approximately 150 m from the EMODnet Bathymetry project, funded by the European Commission Directorate General for Maritime Affairs and Fisheries (https://emodnet.ec.europa.eu/en/bathymetry). Similarly, monthly predictions for temperature and oxygen were extracted at the haul locations. These predictions were sourced from the Mediterranean Sea Physics Reanalysis and the Mediterranean Sea Biogeochemistry Reanalysis, provided by the Copernicus Marine Service (Escudier et al., 2020; Teruzzi et al., 2021). Both datasets have a horizontal resolution of approximately 4 km. Seabed substrate polygons were obtained from the EMODnet EuSeaMap 2023 (https://emodnet.ec.europa.eu/en/seabed-habitats) and matched to the haul locations using the most overlapping seabed substrate category within a 4-km buffer area around the haul position. All continuous covariates were standardized by subtracting the mean and dividing by the SD (Schielzeth, 2010).

Model selection

To evaluate the data support for different combinations of covariates, we compared models that successfully converged using the marginal Akaike information criterion (AIC; Akaike, 1974). For each species, we selected the model with the lowest AIC score to predict their distribution. When the difference in AIC scores (ΔAIC) among models was ≤2, we prioritized models based on the order presented in Appendix S1: Table S1, favoring the depth covariate over temperature and seabed substrate over oxygen.

After initial model exploration, we categorized the 10 species into three groups for testing different model subsets: common species, deep-sea species, and rare species.

The common species group includes Spiny Dogfish, Smallspotted Catshark, and Thornback Skate, which have a frequency of occurrence ≥5%. For these species, we tested the relationship with depth using two representations to account for bell-shaped relationships: log(depth) + log(depth)^2 and depth + depth^2. Additionally, we evaluated whether a linear term alone or a combination of linear and quadratic terms for temperature provided a better fit to the data. We also tested the inclusion of seabed substrate, oxygen, and the first-order interaction between oxygen and temperature. The deep-sea species group includes Blackmouth Catshark, Rabbitfish, and Velvet Belly Lanternshark. For these species, we focused on the functional form of the depth covariate, specifically testing whether depth, log(depth), depth + depth^2, or log(depth) + log(depth)^2 provided the best fit. The rare species group, which have a frequency of occurrence <5%, includes Starry Skate, Common Eagle Ray, Brown Skate, and smoothhounds. For these species, we focused on the inclusion and the functional forms of depth and temperature covariates. Appendix S1: Table S1 provides a detailed overview of the models tested for each species group. Finally, for Velvet Belly Lanternshark, we refitted the best-fitting model excluding the random year intercepts due to small effect size and convergence issues.

In total, we compared 24 different models for each common species, 4 for each deep-sea species, and 12 for each rare species. We evaluated the explanatory power of the models by computing Tjur's R^2 values (Tjur, 2009) and the area under the curve (AUC; Pearce & Ferrier, 2000). The model residuals for the best-fitting models are presented in Appendix S1: Figures S4–S8.

Prediction grid

We predicted the probability of species occurrence on a grid with 4 km^2 cells to match the resolution of the environmental covariates and ensure detailed spatial analysis. We filtered the grid to exclude locations with depths outside the range covered by the MEDITS survey, specifically those less than 10 m and greater than 800 m. Additionally, we excluded cells located on "*Posidonia oceanica* meadows" or "rock or other hard substrata" based on the EMODnet EuSeaMap 2023 layer, as survey hauls are typically not conducted on these substrates. Furthermore, we excluded the national territorial seas of Slovenia, Croatia, Montenegro, and Albania. The shapefiles for these exclusions were obtained from Flanders Marine Institute (2023).

Following the previously outlined methodology, we matched environmental covariates to the midpoint of each cell. For each cell, we averaged the monthly values of temperature and oxygen across the core survey period (May–September) to ensure the comparability of predictions across different years. The models were trained on data from 1999 to 2021, but predictions were made for the period 2009–2021, as VMS data were not available for earlier years.

Species richness

Predicted species richness was determined by summing the probabilities of occurrences for all species at each grid cell (Ovaskainen & Abrego, 2020). To estimate the associated uncertainty, we drew 1000 simulations from the joint parameter precision matrix to make predictions on the grid using the best-fitting model for each species. We then recalculated species richness at each grid cell based on these simulations and computed the SD.

Presence of threatened species

We calculated the probability of encountering at least one threatened species at each grid cell by summing the occurrence probabilities across all threatened species and simulations; then, we determined the proportion of simulations where the total probability at each grid cell was at least 1.

Spatial overlap metrics

To estimate the spatial overlap between chondrichthyans and fishing, we developed a gear- and species-specific fishing exposure index (FEI). Although we used the same terminology as Queiroz et al. (2019), our FEI is calculated differently. The computation of our FEI is as follows:

$$\mathrm{FEI}_{i,g,s,t} = \frac{p \text{ of presence}_{i,s,t} \times \text{Fishing effort}_{g,s,t}}{\mathrm{Max}\left(p \text{ of presence}_{i,t} \times \text{Fishing effort}_{g,t}\right)}. \quad (5)$$

The calculation for the FEI involves multiplying the predicted probability (p) of species i occurring in a grid cell s for a given year t by the corresponding fishing effort (measured in fishing hours) for gear type g (otter bottom trawl or beam trawl) during the same year t and grid cell s. The resulting values are subsequently divided by the maximum value obtained from the product of predicted probabilities with fishing effort for gear type g and year t. This rescaling ensures interpretability and constrains the index within a range of [0,1] and puts a strong emphasis on the spatial overlap patterns. Consequently, we presented the FEI as an average across the most recent years (2018–2021) since we consider this timeframe more relevant from a management point of view. Additionally, since 2018, a fisheries restricted area was established in the Jabuka/Pomo Pits, banning demersal fisheries (GFCM, 2021).

In addition, we employed a range overlap (RO) metric, as defined in Carroll et al. (2019), to quantify the overlap between fishing effort and chondrichthyan distribution. The RO metric measures the proportion of a species' area of occupancy where high fishing effort also occur:

$$\mathrm{RO}_{i,g,t} = A_{i,g,t}/A_{i,t}, \quad (6)$$

where $A_{i,g,t}$ is the area occupied by the species i and trawled by gear g in year t, while $A_{i,t}$ is the total area occupied by species i in year t (Saraux et al., 2014). Here, occupied cells were defined as cells with ≥75th percentile of the species maximum probability of occurrence. Similarly, to identify cells with high fishing effort, we used a threshold where the fishing effort corresponded to ≥75th percentile of the maximum fishing effort for a gear type. We also explored the sensitivity of different percentile thresholds. Yearly fishing effort was normalized within the range [0,1], which helps mitigate the limitations of VMS data as a proxy for overall fishing effort. Due to the pronounced zero-inflation in grid-cell level VMS data, caused by the spatially heterogeneous fishing effort, we calculate percentiles based only on cells with fishing effort >0. Cells with a fishing effort of zero are therefore assigned a value of zero. While an alternative approach involves computing percentiles across the entire domain and selecting a higher threshold, we find it more intuitive to interpret the percentiles of presences in this zero-inflated scenario.

Finally, we assessed the spatial overlap between the chondrichthyan community and fishing effort by creating bivariate choropleth maps using the R package biscale (Prener et al., 2022). These maps visualize the estimated species richness and probability of encountering at least one threatened species against fishing effort. Data were averaged across the most recent years (2018–2021).

RESULTS

Species distribution models

During the survey period from 1999 to 2021, Smallspotted Catshark and Blackmouth Catshark were the most dominant species, observed in approximately 10% of hauls. Spiny Dogfish, Velvet Belly Lanternshark, Thornback Skate, and Rabbitfish occurred in about 8%–6% of hauls, while Starry Skate, Common Eagle Ray, Brown Skate, and smoothhounds were less frequent (Table 1). All species models demonstrated a good fit to the data, with Tjur's R^2 values ranging from 0.13 to 0.88 (mean = 0.53) and AUC values ranging from 0.91 to 0.99 (mean = 0.97) (Appendix S1: Table S2). Among the common species models, the inclusion of seabed substrate as a covariate was supported in one case, and the interaction between temperature and oxygen was supported in another. For the rare species, temperature was included in two out of four models, once as both linear and quadratic terms and once as a linear term only. For the deep-sea species, we found consistent support for both linear and quadratic terms for depth (Appendix S1: Table S2).

Our models revealed strong spatial patterns for chondrichthyan species (Figure 2). We found that Spiny Dogfish exhibited a high average probability of occurrence across the northern and central offshore zones. Similarly, Common Eagle Ray and smoothhounds displayed higher probability of occurrence in the northernmost coastal regions (Gulf of Venice), extending into the adjacent offshore areas. Small Spotted Catshark, Thornback Skate, and Brown Skate predominantly occupied the central offshore areas and the southeastern part of the study area. In contrast, Starry Skate occurred more along the central and southern coastal zones. We also found that deep-sea species, such as Blackmouth Catshark, Velvet Belly Lanternshark, and Rabbitfish, were prevalent in the deeper southern offshore regions.

Species richness exhibited a clear contrast between the northern and deeper southern regions, which were relatively rich in species, and the coastal central and southern regions, which were relatively poor (Figure 3a). In the north, the higher predicted occurrence of Spiny Dogfish, Common Eagle Ray and smoothounds (Figure 2) contributed to the higher estimated species richness. Conversely, the deeper southern regions had higher species richness due to the prevalence of deep-sea species such as Blackmouth Catshark, Velvet Belly Lanternshark, and Rabbitfish (Figure 2). Uncertainty values for species richness were higher in the central and southern offshore areas (Figure 3b) because of greater uncertainties in single-species occurrences there (Appendix S1: Figure S9).

The probability of encountering at least one threatened species was highest in the Gulf of Venice and adjacent offshore areas (Figure 3c), due to the occurrences of Spiny Dogfish, Common Eagle Ray, and smoothounds (Figure 2). In contrast, the probability of encountering at least one threatened species was virtually zero in the central and southern regions.

Fishing effort

Fishing effort, measured in fishing hours, was substantially higher for otter bottom trawling (OTB) compared to beam trawling (TBB) due to the larger number of OTB vessels (Figure 4; Appendix S1: Figure S2). OTB was extensively practiced throughout the entire region (Figure 4a), while TBB was primarily concentrated in the northern regions and extended along the coastline toward central Italy (Figure 4c). The temporal variation of OTB over space was relatively lower, as indicated by a lower CV, than that of TBB (Figure 4b,d). This difference can again be attributed to the larger fleet size of OTB vessels (Appendix S1: Figure S2).

Single species overlap with fishing

Fishing exposure index

For the threatened species, our FEI revealed a high overlap of Spiny Dogfish, Common Eagle Ray, and smoothhounds with both OTB and TBB in the northernmost part of the study area (Figure 5). Additionally, Spiny Dogfish exhibited an intermediate level of overlap with OTB in the offshore regions of the north-central part of the basin.

The FEI for non-threatened species is reported in Appendix S1: Figures S10 and S11. Briefly, Smallspotted Catshark and Thornback Skate showed higher overlap with OTB and TBB in the northern and offshore central parts of the basin, as well as with OTB in the southern part and international waters. Brown Skate predominantly overlapped with OTB and TBB in the central offshore part and with TBB in the northern part. Starry Skate exhibited more overlap in the coastal areas of central Italy. Deep-sea species overlapped with OTB in the southernmost offshore deeper areas (Appendix S1:

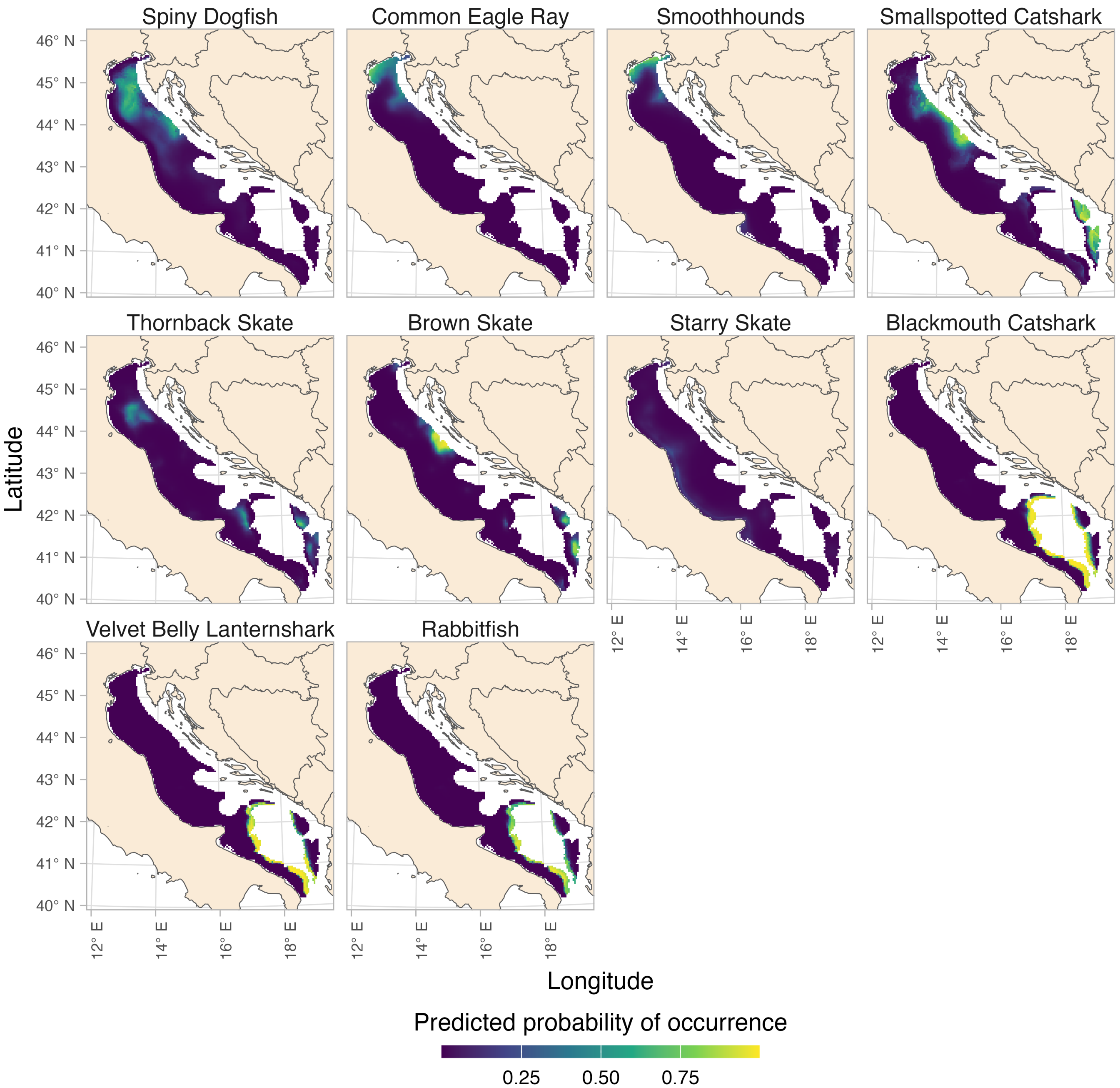

FIGURE 2 Mean predicted probability of occurrence for the included species, calculated over the period 2009–2021.

Figure S11). Despite year-to-year fluctuations, the FEI values remained relatively consistent over time, with closer years showing higher similarity (Appendix S1: Figures S12–S15).

Range overlap

Estimated RO values varied greatly among species and trawling types (Figure 6). Some species, such as deep-sea species, exhibited virtually zero RO with high TBB fishing effort (≥75th percentile), while others, such as Starry Skate, had RO values up to 0.34 (averaged across years) with high OTB fishing effort. Starry Skate, Spiny Dogfish, Velvet Belly Lanternshark, Rabbitfish, and Common Eagle Ray showed a higher overlap with high OTB fishing effort (RO ≥ 0.15, averaged across years), while Blackmouth Catshark, smoothhounds, and Brown Skate exhibited somewhat lower RO values (<0.15 and ≥0.1, averaged across years). On the other hand, Common Eagle Ray, smoothhounds, Starry Skate, and Spiny Dogfish had the highest RO with high TBB fishing effort (RO ≥ 0.1, averaged across years). RO values varied across years, with stronger fluctuations observed for

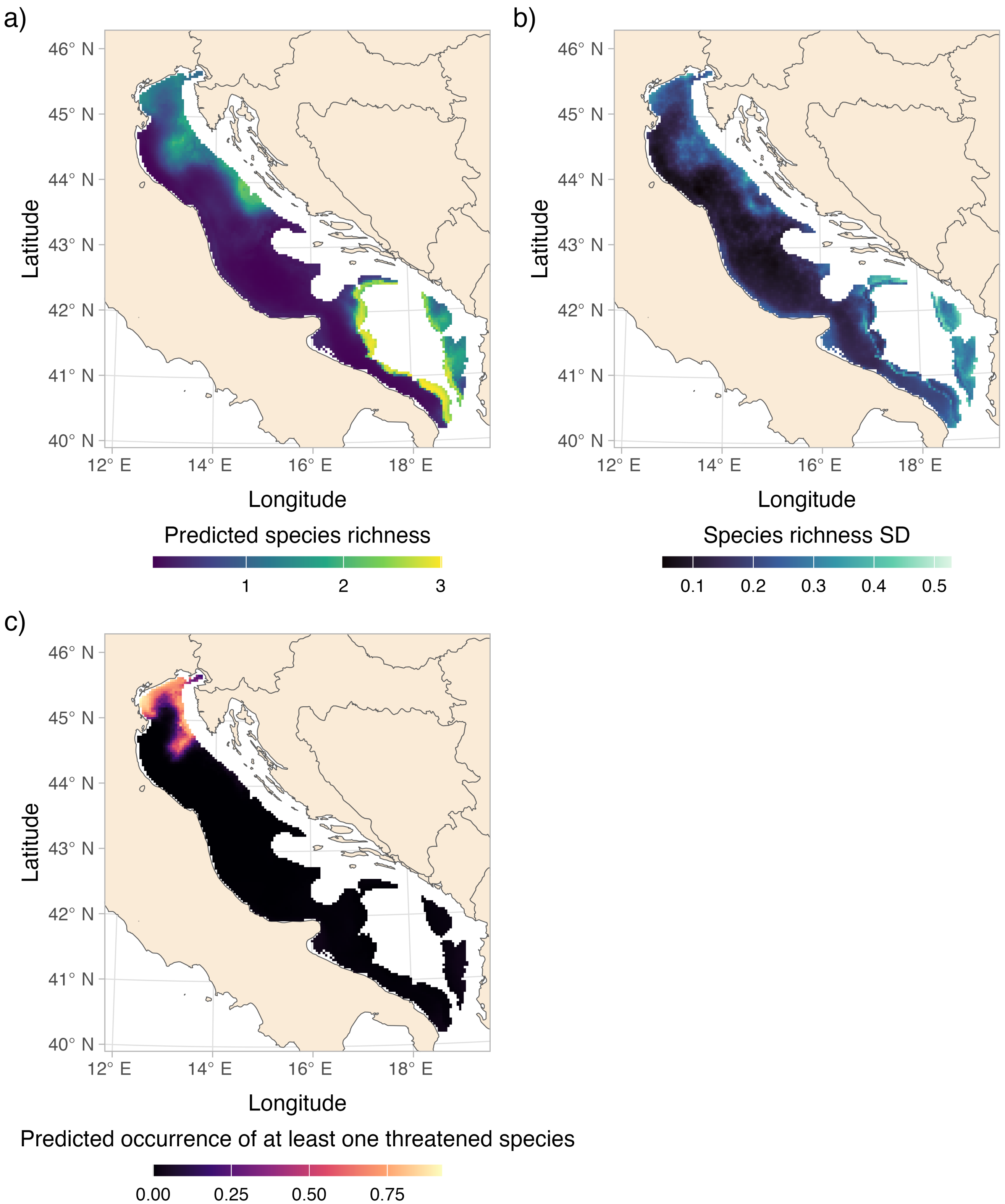

FIGURE 3 Mean and SD of species richness (a–b) and the mean probability of occurrence of at least one threatened species (c), calculated over the period 2009–2021.

Starry Skate and Spiny Dogfish with OTB (Figure 6). In general, RO values tended to increase or decrease together across species in certain years, likely in response to changes in fishing effort. ROs remained consistent relative to each other regardless of the threshold used to define a cell occupied by a species and high fishing effort, although their

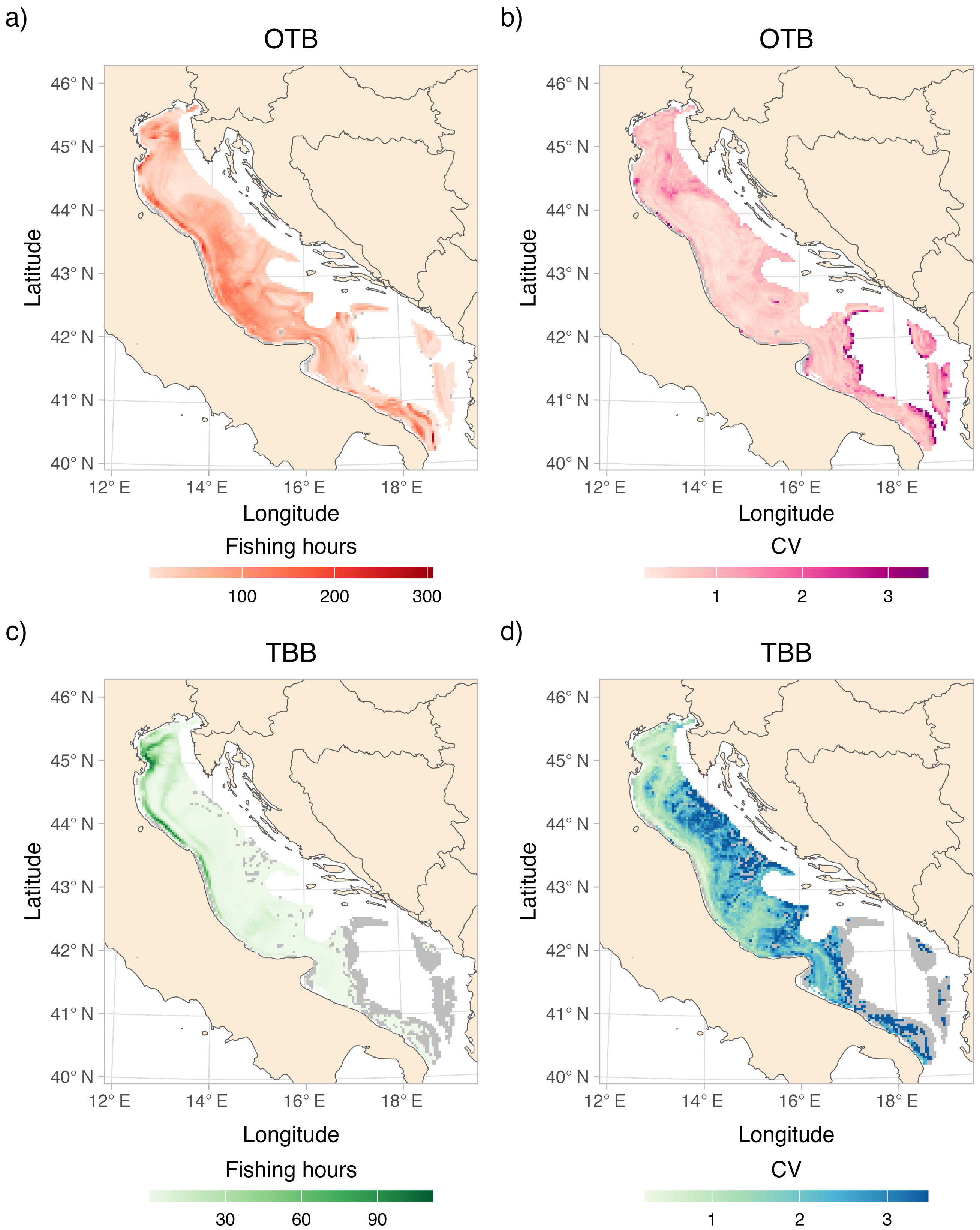

FIGURE 4 Mean fishing effort (in hours) (a–c) and corresponding CV (b–d) from vessel monitoring system signals for otter bottom trawling (OTB) and beam trawling (TBB) during May to September (2009–2021). Gray areas represent regions with estimated zero fishing effort.

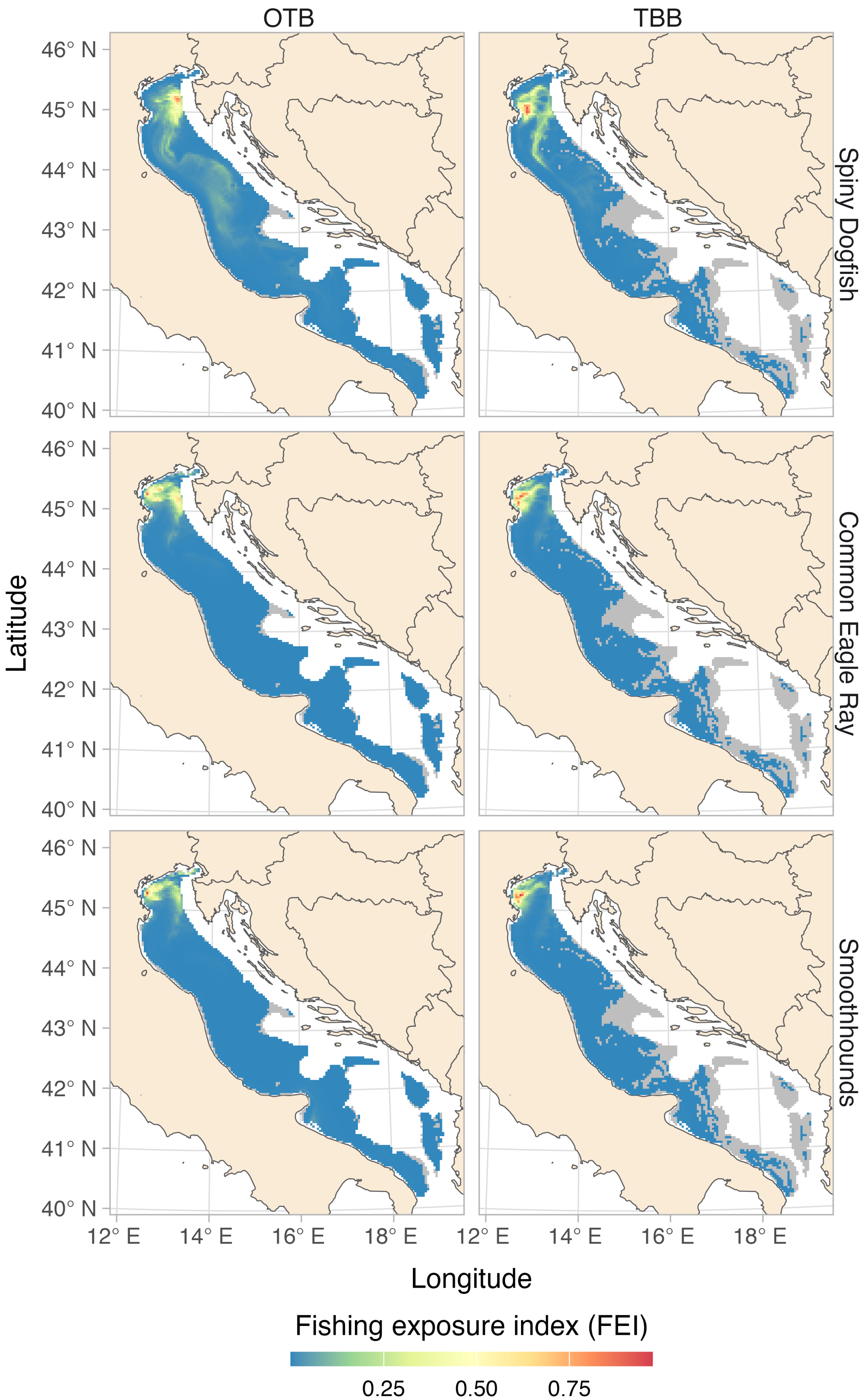

FIGURE 5 Mean fishing exposure index (FEI) for threatened species from otter bottom trawling (OTB) and beam trawling (TBB) over 2018–2021. Gray areas indicate FEI values of zero.

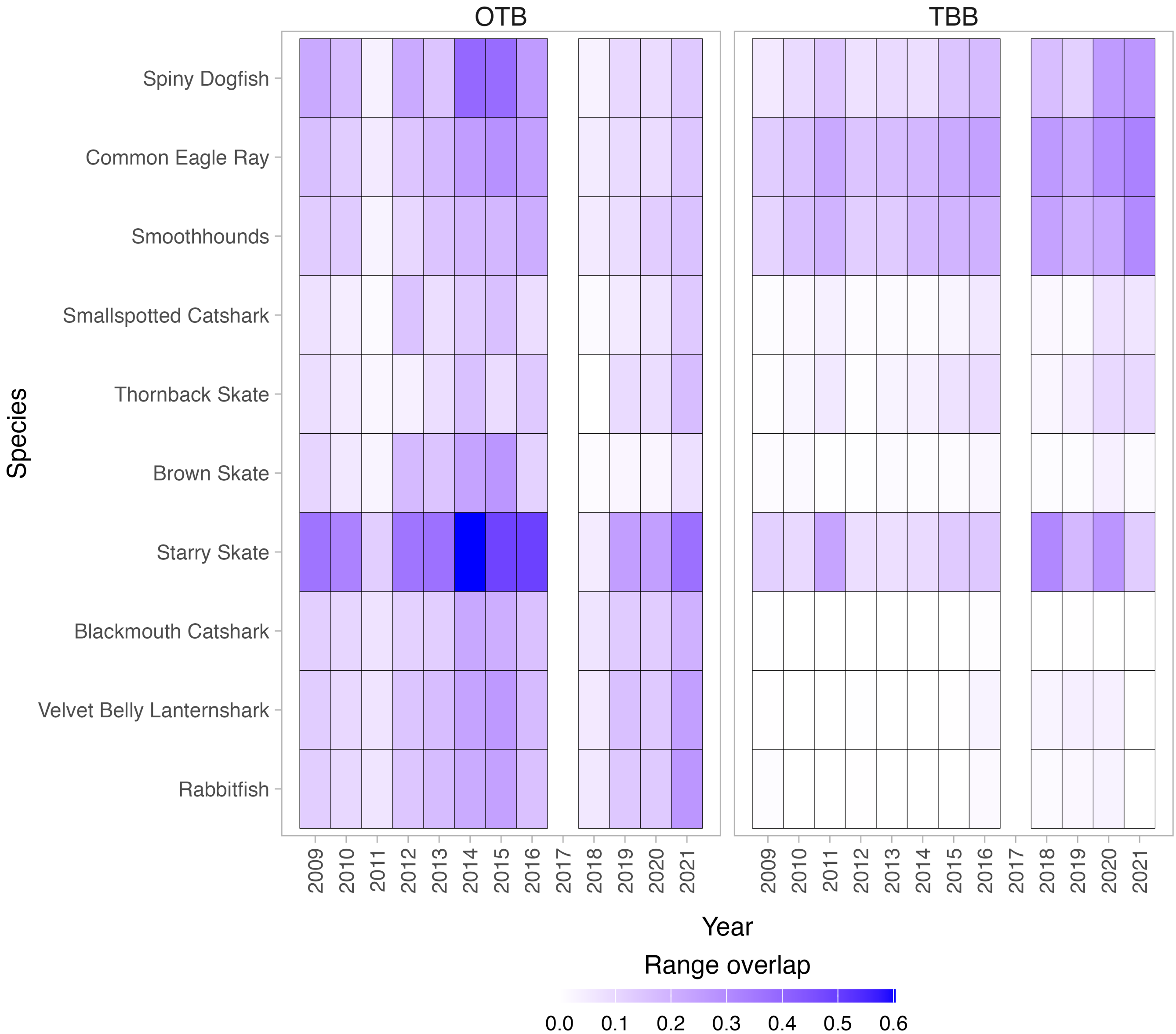

FIGURE 6 Yearly range overlap (RO) between species and otter bottom trawling (OTB) and beam trawling (TBB). A grid cell is occupied by a species if it exceeds the 75th percentile of occurrence probability and by trawling if it exceeds the 75th percentile of fishing effort. 2017 is omitted due to sampling outside the designated period.

values changed in magnitude as expected (Appendix S1: Figures S16 and S17).

Community overlap with fishing

Species richness

For both OTB and TBB, areas with high species richness and high fishing effort were highly similar in the northern part of the basin (Gulf of Venice), though high TBB effort also extended slightly southward (Figure 7). High species richness overlapped with high OTB effort also in some deeper southern areas, where TBB is practically absent. In contrast, two large areas—one in the offshore northern-central part of the basin and another in the deeper offshore southern area—had high species richness but low OTB and TBB fishing effort (Figure 7).

Threatened species

We found a high probability of encountering at least one threatened species along with high fishing effort in the northernmost part of the basin, especially on the western

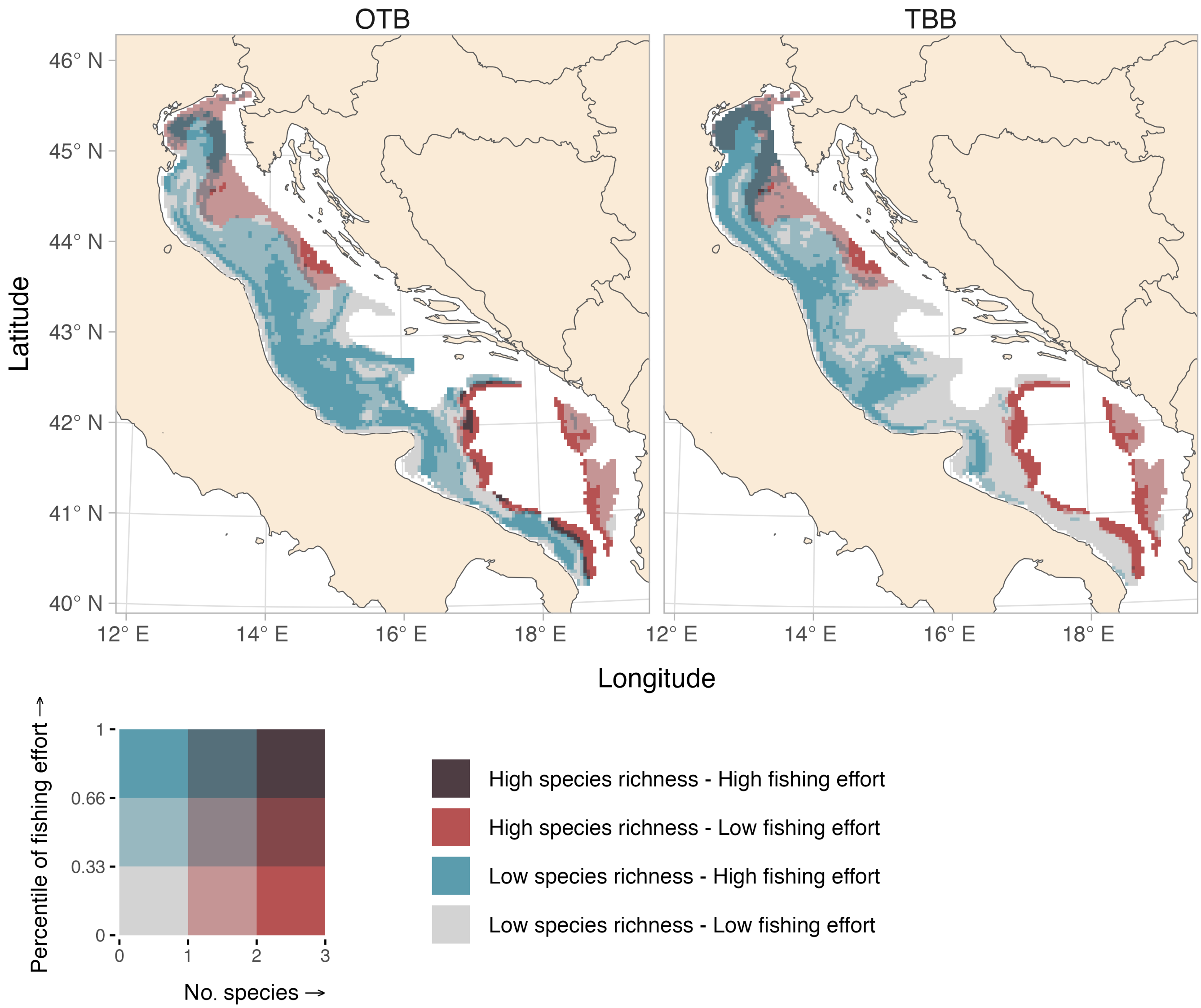

FIGURE 7 Overlap between mean species richness and fishing effort percentiles (2018–2021) for otter bottom trawling (OTB) and beam trawling (TBB).

side, for both OTB and TBB (Figure 8). However, fishing effort decreased eastward, while the probability of encountering at least one threatened species remained high. Additionally, we identified a larger area in the northern-central part of the basin characterized by a moderate-to-high probability of encountering at least one threatened species and relatively low OTB and TBB fishing effort (Figure 8).

DISCUSSION

Effective marine conservation and fisheries management require a comprehensive understanding of the spatial interactions between species and fishing activities (Douvere, 2008). For chondrichthyans, the lack of such information often hinders effective management measures (Cavanagh & Gibson, 2007; FAO, 2022). In this study, we introduce a novel approach to assess how chondrichthyan distribution overlaps with bottom trawl fishing. We combine geostatistical models fitted to fishery-independent survey data with VMS data to identify hotspot areas of overlap, indicating where chondrichthyans face higher risks of bycatch. This information can guide where to establish protected areas or impose fishing restrictions, thereby enhancing conservation and management efforts.

We applied this approach to the Adriatic Sea, a heavily fished area with a history of chondrichthyan depletion and limited data on their bycatch (Amoroso et al., 2018; FAO, 2022; Ferretti et al., 2013). Here, our findings provide new insights into the spatial overlap

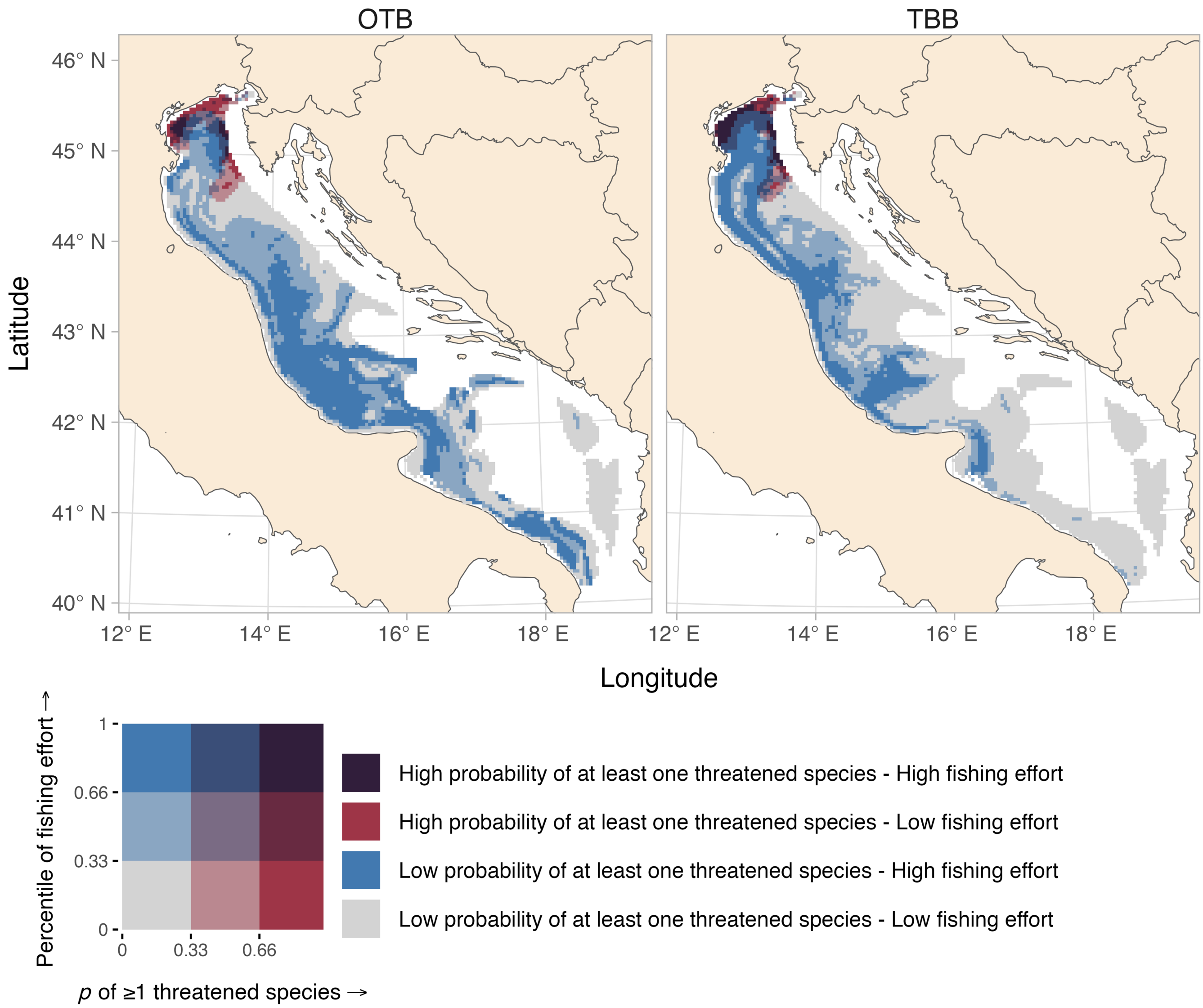

FIGURE 8 Overlap between the probability of occurrence (p) of at least one threatened species and fishing effort percentiles (2018–2021) for otter bottom trawling (OTB) and beam trawling (TBB).

between demersal chondrichthyans and the dominant bottom trawl fishing types: otter bottom trawling (OTB) and beam trawling (TBB). Our results indicate that the northwestern part of the basin is a critical hotspot where threatened chondrichthyans, such as Spiny Dogfish, smoothhounds, and Common Eagle Ray, greatly overlap with OTB and TBB. This highly productive area is crucial for chondrichthyans as it provides essential reproductive habitats (Bonanomi et al., 2018). Along with the identification of the Northwestern Adriatic as an Important Shark and Ray Area (ISRA; IUCN, 2023), this highlights the need for prioritized conservation measures in this region. We also found hotspots where high species richness overlaps with OTB in the deeper southern areas. These regions host deep-sea species like Blackmouth Catshark, Velvet Belly Lanternshark, and Rabbitfish, which likely extend to depths where bottom trawling is prohibited (GFCM, 2005). Consequently, these species are somewhat protected from trawling in part of their distribution range.

Conversely, we identified areas with minimal spatial overlap between high chondrichthyan presence and bottom trawl fishing, suggesting potential refuges. Notable examples include parts of the northernmost Adriatic Sea and the "area dei fondi sporchi" (or "dirty area") in the north-central offshore part. This latter area contains relict sand rich in epifaunal organisms, making bottom trawling difficult or impossible (Scaccini, 1967). These regions are rich in chondrichthyan species such as Spiny Dogfish, smoothhounds, Common Eagle Ray, Thornback Skate, and Smallspotted Catshark, and might serve as source habitats, promoting spillover effects.

Together with identifying hotspots of overlap, our model-based approach also calculates ROs. These results provide insights into the potential effects of relocating fishing effort. Species with narrow hotspots and low RO, like the Brown Skate with OTB, might benefit significantly from relocating fishing effort outside the hotspot, thereby reducing bycatch risk. Conversely, for species with higher RO, like the Starry Skate with OTB, merely limiting fishing in the primary overlap hotspot may be less effective in reducing bycatch risk, as the fishery spans a large portion of the species' range. This underscores the importance of considering multiple indices when implementing spatial fishing restrictions. Ultimately, understanding where fishing would increase after such an intervention, and how that would affect the total mortality rates from fishing, is one of the main challenges in designing protected areas successfully (Hilborn et al., 2004; Ovando et al., 2021).

While the spatial overlap between fishing activities and chondrichthyan distribution suggests potential interaction, it does not directly demonstrate ecological impacts or quantify the extent on chondrichthyan populations. Mediterranean chondrichthyans are generally considered highly vulnerable to trawling (Carpentieri et al., 2021; Cavanagh & Gibson, 2007; FAO, 2022), but different trawling gears have varying catchabilities. In the Adriatic Sea, official landings indicate that OTB lands about 0.8% of sharks by mass, with similar values for skates, while TBB has very low shark landings (0.05%) and about 1% for skates (STECF, 2023). Although these values underestimate total catches, they suggest that TBB catches far fewer sharks than OTB. Given these catchability differences, the maps provided should be compared within the same gear type rather than across different gears. Despite TBB's low catchability for sharks, we included its overlap in our analysis for three main reasons. First, official landings records show that beam trawlers catch skates and all the shark species in this study, indicating such catches are possible (STECF, 2023). Second, trawling, particularly beam trawling, not only directly removes chondrichthyans but also disturbs and destroys seabed habitats (ICES, 2023; Sciberras et al., 2018; Watling & Norse, 1998). These habitats are crucial for the reproduction, shelter, and foraging of many chondrichthyans (e.g., Carrier & Pratt, 1998; Heithaus et al., 2002; Simpfendorfer & Milward, 1993). Third, both OTB and TBB are focal gears addressed within the Multiannual Management Plan for demersal species in the Adriatic Sea (GFCM, 2019). This plan includes measures like fishing effort regimes and spatiotemporal closures. Considering chondrichthyan bycatch and habitat damage within this regulatory framework can optimize management strategies.

Consequently, management efforts such as spatiotemporal closures should prioritize areas where OTB is predominant, especially in the northwestern Adriatic. In contrast, TBB requires attention for its impact on skates and seabed habitats. Other mitigation measures can include gear modifications, such as excluder devices, and onboard release protocols. Although excluder devices might theoretically reduce chondrichthyan bycatch in bottom trawling, their effectiveness in reducing the bycatch of small- to medium-sized chondrichthyans in the Mediterranean Sea has been limited (Brčić et al., 2015; De Santis et al., 2024), and trawling has higher immediate and post-release mortality compared to other fishing techniques (Dapp et al., 2016).

Spatial overlap alone does not fully capture the scale of chondrichthyan bycatch. To address this, we need to increase monitoring with onboard fishery observers. Our spatial overlap data can help design cost-effective observing programs to estimate actual bycatch rates by prioritizing fishing trips in areas with high overlap. Given the current limited availability of direct and quantitative official bycatch data (but see Bonanomi et al., 2018 for pelagic trawling), our results provide an initial approach to inform conservation efforts and guide precautionary management decisions.

While our study provides novel insights into the spatial overlap between chondrichthyan distribution and bottom trawl fishing in the Adriatic Sea, certain limitations should be considered. First, our analysis relied on the availability and quality of data sources, which may introduce uncertainties and biases. VMS data serve as a good proxy for fishing effort for vessels larger than 15 m but are less reliable for vessels between 12 and 15 m and unusable for vessels below 12 m. Consequently, this may lead to an incomplete representation of fishing activities, especially for OTB. Approximately 70% of the Italian OTB fleet in the Adriatic Sea consists of vessels between 12 and 15 m, according to the EU Fleet Register (https://webgate.ec.europa.eu/fleet-europa/index_en). However, the footprint of these smaller vessels is estimated to be very similar, in terms of hotspots of effort and distribution of fishing grounds, to that of larger vessels, particularly those in the 15- to 18-m class (Russo et al., 2019). As such, our overlap metrics, which consider the relative spatial pattern rather than the absolute fishing effort, should partially mitigate this issue. Fishing effort for vessels below 12 m is about 7% in fishing days for OTB and negligible for TBB fishing in the Adriatic Sea (STECF, 2023), which should minimally affect our conclusions. Second, our data only cover the Italian fleet, while other fishing countries can operate outside the Italian territorial sea. Nonetheless, approximately 70% of the fishing fleet operating in the Adriatic Sea belongs to

Italy (FAO, 2022) and therefore we cover most of the fleet impacting chondrichthyans in the study area. Additionally, SDMs have inherent limitations, such as uncertainties in species occurrence data, model assumptions, and potential omission of relevant environmental variables. However, calculating overlap on model-predicted probabilities of occurrence has benefits, as it is less sensitive to temporal changes in sampling across space (Thorson et al., 2016). The spatial resolution of our analysis may influence the observed patterns of overlap. Fine-scale variations in fishing effort and chondrichthyan distribution may not have been fully captured, potentially leading to underestimation or overestimation of true spatial overlap. However, we chose a relatively fine resolution that aligns with the environmental covariates for the species distribution models and with the VMS data, ensuring it is relevant for management purposes. Lastly, our analysis focused on a specific period of the year (late spring to the end of summer) due to the lack of consistent autumn and winter fisheries-independent surveys. Seasonal variations in fishing effort and chondrichthyan distribution occur (e.g., Appendix S1: Figures S1 and S2; Manfredi et al., 2010), so caution is needed when extrapolating our results to other seasons, especially for management purposes. Despite these limitations, our approach represents a major advance and offers the most comprehensive information available regarding the spatial overlap of bottom trawl fishing effort with the chondrichthyan community in the Adriatic Sea.

In conclusion, our study introduces an innovative approach combining VMS data with geostatistical species distribution models. This allowed us to analyze the spatial overlap of chondrichthyan species and commercial bottom trawl fishing in the Adriatic Sea. Through this analysis, we identified areas with a likely heightened risk for bycatch where management and conservation should be prioritized, as well as areas that could serve as potential refuges for chondrichthyans. These insights support targeted conservation efforts and the development of effective spatial management measures. Additionally, they can aid in designing cost-effective onboard monitoring programs to estimate bycatch rates.

AUTHOR CONTRIBUTIONS

Federico Maioli conceptualized the study with contributions from Michele Casini. Chiara Manfredi, Walter Zupa, and Isabella Bitetto prepared the raw survey data. Tommaso Russo processed the VMS data and provided the related spatial layers. Federico Maioli conducted the statistical analysis with contributions from Benjamin Weigel, Max Lindmark, and Michele Casini. Federico Maioli wrote the initial draft. All authors reviewed the different drafts and contributed to the submitted version.

ACKNOWLEDGMENTS

This study has been conceived under the International PhD Program "Innovative Technologies and Sustainable Use of Mediterranean Sea Fishery and Biological Resources" (http://www.fishmed-phd.org/). We thank the MEDITS staff involved in the scientific sampling and analysis of biological data. We also thank Sara Bonanomi for her comments on an earlier version of the manuscript, as well as the two anonymous reviewers whose feedback significantly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

This study utilized MEDITS survey data collected through the EU Data Collection Framework (DCF-MEDITS). Access to these data is governed by EU Regulation 2017/1004. To request access, contact the Direzione Generale della Pesca Marittima e dell'Acquacoltura at the Italian Ministry of Agriculture, Food Sovereignty and Forests (MASAF). A data request template is available at the DCF-Italian website (https://dcf-italia.cnr.it/#/dati). Raw VMS data are considered confidential and are not publicly available. Requests for access to aggregated VMS data should be directed to tommaso.russo@uniroma2.it.

ORCID

Federico Maioli https://orcid.org/0000-0002-8305-1609
Benjamin Weigel https://orcid.org/0000-0003-2302-5529
Max Lindmark https://orcid.org/0000-0002-3841-4044
Michele Casini https://orcid.org/0000-0003-4910-5236

REFERENCES

Abella, A., F. Serena, C. Mancusi, N. Ungaro, N.-R. Hareide, J. Guallart, R. P. Coelho, and P. Crozier. 2016. "*Galeus melastomus* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T161398A16527793.

Akaike, H. 1974. "Information Theory and an Extension of the Maximum Likelihood Principle." In *International Symposium on Information Theory*, edited by B. N. Petrov and F. Csaki, 267–281. Budapest: Akademiai Kiado.

Amante, C., and B. W. Eakins. 2009. "ETOPO1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis." https://repository.library.noaa.gov/view/noaa/1163.

Amoroso, R. O., C. R. Pitcher, A. D. Rijnsdorp, R. A. McConnaughey, A. M. Parma, P. Suuronen, O. R. Eigaard, et al. 2018. "Bottom Trawl Fishing Footprints on the World's Continental Shelves." *Proceedings of the National Academy of Sciences of the United States of America* 115(43): E10275–E10282. https://doi.org/10.1073/pnas.1802379115.

Andersen, K. H. 2019. *Fish Ecology, Evolution, and Exploitation: A New Theoretical Synthesis*. Princeton, NJ: Princeton University Press.

Anderson, S. C., E. J. Ward, P. A. English, L. A. K. Barnett, and J. T. Thorson. 2024. "sdmTMB: An R Package for Fast, Flexible, and User-Friendly Generalized Linear Mixed Effects Models with Spatial and Spatiotemporal Random Fields." *bioRxiv* 2022.03.24.485545. https://doi.org/10.1101/2022.03.24.485545.

Artegiani, A., E. Paschini, A. Russo, D. Bregant, F. Raicich, and N. Pinardi. 1997. "The Adriatic Sea General Circulation. Part I: Air–Sea Interactions and Water Mass Structure." *Journal of Physical Oceanography* 27(8): 1492–1514.

Barausse, A., V. Correale, A. Curkovic, L. Finotto, E. Riginella, E. Visentin, and C. Mazzoldi. 2014. "The Role of Fisheries and the Environment in Driving the Decline of Elasmobranchs in the Northern Adriatic Sea." *ICES Journal of Marine Science* 71(7): 1593–1603. https://doi.org/10.1093/icesjms/fst222.

Bonanomi, S., J. Pulcinella, C. M. Fortuna, F. Moro, and A. Sala. 2018. "Elasmobranch Bycatch in the Italian Adriatic Pelagic Trawl Fishery." *PLoS One* 13(1): e0191647. https://doi.org/10.1371/journal.pone.0191647.

Bradai, M. N., B. Saidi, and S. Enajjar. 2012. *Elasmobranchs of the Mediterranean and Black Sea: Status, Ecology and Biology. Bibliographic Analysis*." Studies and Reviews No. 91. General Fisheries Commission for the Mediterranean. Rome: FAO.

Brčić, J., B. Herrmann, F. De Carlo, and A. Sala. 2015. "Selective Characteristics of a Shark-Excluding Grid Device in a Mediterranean Trawl." *Fisheries Research* 172: 352–360. https://doi.org/10.1016/j.fishres.2015.07.035.

Campanelli, A., F. Grilli, E. Paschini, and M. Marini. 2011. "The Influence of an Exceptional Po River Flood on the Physical and Chemical Oceanographic Properties of the Adriatic Sea." *Dynamics of Atmospheres and Oceans* 52(1–2): 284–297. https://doi.org/10.1016/j.dynatmoce.2011.05.004.

Carpentieri, P., A. Nastasi, M. Sessa, and A. Srour, eds. 2021. *Incidental Catch of Vulnerable Species in Mediterranean and Black Sea Fisheries – A Review*." Studies and Reviews No. 101. General Fisheries Commission for the Mediterranean. Rome: FAO. https://doi.org/10.4060/cb5405en.

Carrier, J. C., and H. L. Pratt. 1998. "Habitat Management and Closure of a Nurse Shark Breeding and Nursery Ground." *Fisheries Research* 39(2): 209–213. https://doi.org/10.1016/S0165-7836(98)00184-2.

Carroll, G., K. K. Holsman, S. Brodie, J. T. Thorson, E. L. Hazen, S. J. Bograd, M. A. Haltuch, et al. 2019. "A Review of Methods for Quantifying Spatial Predator–Prey Overlap." *Global Ecology and Biogeography* 28(11): 1561–77. https://doi.org/10.1111/geb.12984.

Cashion, M. S., N. Bailly, and D. Pauly. 2019. "Official Catch Data Underrepresent Shark and Ray Taxa Caught in Mediterranean and Black Sea Fisheries." *Marine Policy* 105: 1–9. https://doi.org/10.1016/j.marpol.2019.02.041.

Cavanagh, R. D., and C. Gibson. 2007. *Overview of the Conservation Status of Cartilaginous Fishes (Chondrichthyans) in the Mediterranean Sea*. Gland and Malaga: IUCN. vi + 42 pp.

Clodia Database. 2020. "Database of Fishery Data from Chioggia, Northern Adriatic Sea." http://chioggia.biologia.unipd.it/banche-dati/.

Compagno, L. J. V. 1990. "Alternative Life-History Styles of Cartilaginous Fishes in Time and Space." *Environmental Biology of Fishes* 28: 33–75. https://doi.org/10.1007/BF00751027.

Dagit, D. D., and N.-R. Hareide. 2016. "*Chimaera monstrosa* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T63114A16563229.

Dapp, D. R., T. I. Walker, C. Huveneers, and R. D. Reina. 2016. "Respiratory Mode and Gear Type Are Important Determinants of Elasmobranch Immediate and Post-Release Mortality." *Fish and Fisheries* 17: 507–524. https://doi.org/10.1111/faf.12124.

De Santis, L. J., S. Bonanomi, E. Bueloni, A. Petetta, O. Annibale, L. Finotto, C. Vasapollo, C. Mazzoldi, A. Lucchetti, and M. Bottaro. 2024. "Performance of Sorting Grids on Catching Elasmobranchs in a Multispecies Mediterranean Bottom Trawl Fishery." *Estuarine, Coastal and Shelf Science* 296: 108594. https://doi.org/10.1016/j.ecss.2023.108594.

Di Lorenzo, M., S. Vizzini, G. Signa, C. Andolina, G. Boscolo Palo, M. Gristina, C. Mazzoldi, and F. Colloca. 2020. "Ontogenetic Trophic Segregation between Two Threatened Smooth-Hound Sharks in the Central Mediterranean Sea." *Scientific Reports* 10(1): 11011. https://doi.org/10.1038/s41598-020-67858-x.

Di Natale, A., P. Addis, A. Cau, F. Garibaldi, C. Piccinetti, and L. Orsi Relini. 2011. "Lo stato dei grandi pesci pelagici." In *Lo Stato della Pesca e dell'Acquacoltura nei Mari Italiani*, edited by S. Cataudella and M. Spagnolo, 195–205. Rome: Ministero delle Politiche Agricole Alimentari e Forestali.

Douvere, F. 2008. "The Importance of Marine Spatial Planning in Advancing Ecosystem-Based Sea Use Management." *Marine Policy* 32(5): 762–771. https://doi.org/10.1016/j.marpol.2008.03.021.

Dulvy, N. K., S. L. Fowler, J. A. Musick, R. D. Cavanagh, P. M. Kyne, L. R. Harrison, J. K. Carlson, et al. 2014. "Extinction Risk and Conservation of the World's Sharks and Rays." *eLife* 3: e00590. https://doi.org/10.7554/eLife.00590.

Dulvy, N. K., N. Pacoureau, C. L. Rigby, R. A. Pollom, R. W. Jabado, D. A. Ebert, B. Finucci, et al. 2021. "Overfishing Drives over One-Third of All Sharks and Rays toward a Global Extinction Crisis." *Current Biology* 31(21): 4773–87. https://doi.org/10.1016/j.cub.2021.08.062.

Dulvy, N. K., Y. Sadovy, and J. D. Reynolds. 2003. "Extinction Vulnerability in Marine Populations." *Fish and Fisheries* 4(1): 25–64. https://doi.org/10.1046/j.1467-2979.2003.00105.x.

Dulvy, N. K., R. H. L. Walls, A. Abella, F. Serena, and M. N. Bradai. 2020. "*Raja miraletus* (Mediterranean Assessment) (Amended Version of 2019 Assessment)." The IUCN Red List of Threatened Species 2020: e.T124569516A176535719.

Eigaard, O. R., F. Bastardie, N. T. Hintzen, L. Buhl-Mortensen, P. Buhl-Mortensen, R. Catarino, G. E. Dinesen, et al. 2017. "The Footprint of Bottom Trawling in European Waters: Distribution, Intensity, and Seabed Integrity." *ICES Journal of Marine Science* 74(3): 847–865. https://doi.org/10.1093/icesjms/fsw194.

Ellis, J. R., F. Serena, and H. K. Lotze. 2016. "*Raja clavata* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T39399A103113598.

Ellis, J. R., A. Soldo, M. Dureuil, and S. Fordham. 2016. "*Squalus acanthias* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T91209505A16527761.

Escudier, R., E. Clementi, M. Omar, A. Cipollone, J. Pistoia, A. Aydogdu, M. Drudi, et al. 2020. "Mediterranean Sea Physical Reanalysis (CMEMS MED-Currents) (Version 1) [Data Set]."

Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1.

FAO. 2022. *The State of Mediterranean and Black Sea Fisheries 2022*. Rome: General Fisheries Commission for the Mediterranean. https://doi.org/10.4060/cc3370en.

FAO. 2023. *Report of the Expert Meeting on Fisheries-Related Other Effective Area-Based Conservation Measures in the Mediterranean*. Rome: FAO. https://doi.org/10.4060/cc4870en.

Farrell, E. D., and N. K. Dulvy. 2016. "*Mustelus mustelus* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T39358A16527988.

Ferretti, F., G. C. Osio, C. J. Jenkins, A. A. Rosenberg, and H. K. Lotze. 2013. "Long-Term Change in a Meso-Predator Community in Response to Prolonged and Heterogeneous Human Impact." *Scientific Reports* 3(1): 1057. https://doi.org/10.1038/srep01057.

Finucci, B., D. Derrick, F. C. Neat, N. Pacoureau, F. Serena, and W. J. VanderWright. 2021. "*Scyliorhinus canicula*." The IUCN Red List of Threatened Species 2021: e.T161307554A124478351.

Flanders Marine Institute. 2023. "Maritime Boundaries Geodatabase: Territorial Seas (12NM), version 4." Available online at https://www.marineregions.org/. https://doi.org/10.14284/633.

GFCM. 2005. *Recommendation GFCM/29/2005/1 on the Management of Certain Fisheries Exploiting Demersal and Deep-Water Species and the Establishment of a Fisheries Restricted Area below 1000 m*. Rome: GFCM.

GFCM. 2019. *Recommendation GFCM/43/2019/5 on a Multiannual Management Plan for Sustainable Demersal Fisheries in the Adriatic Sea (Geographical Subareas 17 and 18)*. Rome: GFCM.

GFCM. 2021. *Recommendation GFCM/44/2021/2 on the Establishment of a Fisheries Restricted Area in the Jabuka/Pomo Pit in the Adriatic Sea (Geographical Subarea 17), Amending Recommendation*. Rome: GFCM.

Guallart, J., R. P. Coelho, T. Blasdale, C. Mancusi, F. Serena, N. Ungaro, F. Litvinov, P. Crozier, and C. Stenberg. 2016. "*Etmopterus spinax* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T161388A16527777.

Heithaus, M., L. Dill, G. Marshall, and B. Buhleier. 2002. "Habitat Use and Foraging Behavior of Tiger Sharks (*Galeocerdo cuvier*) in a Seagrass Ecosystem." *Marine Biology* 140(2): 237–248. https://doi.org/10.1007/s00227-001-0711-7.

Hilborn, R., K. Stokes, J.-J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz, et al. 2004. "When Can Marine Reserves Improve Fisheries Management?" *Ocean & Coastal Management* 47(3): 197–205. https://doi.org/10.1016/j.ocecoaman.2004.04.001.

Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Böhm, T. M. Brooks, S. H. M. Butchart, K. E. Carpenter, et al. 2010. "The Impact of Conservation on the Status of the World's Vertebrates." *Science* 330(6010): 1503–9. https://doi.org/10.1126/science.1194442.

Hopkins, T. 1992. "The Structure of Ionian and Levantine Seas." *Reports in Meteorology and Oceanography* 41(II): 35–56.

ICES. 2023. "Working Group on Fisheries Benthic Impact and Trade-Offs (WGFBIT; Outputs from 2022 Meeting)." *ICES Scientific Reports* 5(16): 106.

IUCN. 2013. "Documentation Standards and Consistency Checks for IUCN Red List Assessments and Species Accounts. Version 2." Adopted by the IUCN Red List Committee and IUCN SSC Steering Committee. http://www.iucnredlist.org/documents/RL_Standards_Consistency.pdf.

IUCN. 2023. *Northwest Adriatic ISRA Factsheet*. Dubai: IUCN SSC Shark Specialist Group.

Jukic-Peladic, S., N. Vrgoc, S. Krstulovic-Sifner, C. Piccinetti, G. Piccinetti-Manfrin, G. Marano, and N. Ungaro. 2001. "Long-Term Changes in Demersal Resources of the Adriatic Sea: Comparison between Trawl Surveys Carried Out in 1948 and 1998." *Fisheries Research* 53(1): 95–104. https://doi.org/10.1016/S0165-7836(00)00232-0.

Kristensen, K., A. Nielsen, C. W. Berg, H. Skaug, and B. M. Bell. 2016. "TMB: Automatic Differentiation and Laplace Approximation." *Journal of Statistical Software* 70(5): 1–21. https://doi.org/10.18637/jss.v070.i05.

Lindgren, F. 2023. "fmesher: Triangle Meshes and Related Geometry Tools." R Package Version 0.1.5. https://cran.r-project.org/package=fmesher.

Lindgren, F., H. Rue, and J. Lindström. 2011. "An Explicit Link between Gaussian Fields and Gaussian Markov Random Fields: The Stochastic Partial Differential Equation Approach." *Journal of the Royal Statistical Society Series B: Statistical Methodology* 73(4): 423–498. https://doi.org/10.1111/j.1467-9868.2011.00777.x.

Lotze, H. K., M. Coll, and J. A. Dunne. 2011. "Historical Changes in Marine Resources, Food-Web Structure and Ecosystem Functioning in the Adriatic Sea, Mediterranean." *Ecosystems* 14(2): 198–222. https://doi.org/10.1007/s10021-010-9404-8.

Lucchetti, A., A. Petetta, M. Bdioui, G. Gökçe, M. Saber, J. Sacchi, H. Ozbilgin, A. Carlson, and P. Carpentieri. 2023. *Catalogue of Fishing Gear in the Mediterranean and Black Sea Region*." FAO Fisheries and Aquaculture Technical Papers, No. 695. Rome: FAO.

Maioli, F., B. Weigel, E. Chiarabelli, C. Manfredi, A. Anibaldi, I. Isailović, N. Vrgoč, and M. Casini. 2023. "Influence of Ecological Traits on Spatio-Temporal Dynamics of an Elasmobranch Community in a Heavily Exploited Basin." *Scientific Reports* 13(1): 9596. https://doi.org/10.1038/s41598-023-36038-y.

Manfredi, C., E. Ciavaglia, I. Isajlovic, C. Piccinetti, and N. Vrgoc. 2010. "Temporal and Spatial Distribution of Some Elasmobranchs in the Northern and Central Adriatic Sea/Distribuzione Spazio-Temporale di Alcuni Elasmobranchi in Alto e Medio Adriatico." *Biologia Marina Mediterranea* 17(1): 254.

Marino, I. A. M., L. Finotto, F. Colloca, M. Di Lorenzo, M. Gristina, E. D. Farrell, L. Zane, and C. Mazzoldi. 2018. "Resolving the Ambiguities in the Identification of Two Smooth-Hound Sharks (*Mustelus mustelus* and *Mustelus punctulatus*) Using Genetics and Morphology." *Marine Biodiversity* 48(3): 1551–62. https://doi.org/10.1007/s12526-017-0701-8.

McConnaughey, R. A., J. G. Hiddink, S. Jennings, C. R. Pitcher, M. J. Kaiser, P. Suuronen, M. Sciberras, et al. 2020. "Choosing Best Practices for Managing Impacts of Trawl Fishing on Seabed Habitats and Biota." *Fish and Fisheries* 21(2): 319–337. https://doi.org/10.1111/faf.12431.

MEDITS Working Group. 2017. *MEDITS-Handbook, 106*. MEDITS Working Group.

Ovando, D., J. E. Caselle, C. Costello, O. Deschenes, S. D. Gaines, R. Hilborn, and O. Liu. 2021. "Assessing the Population-Level Conservation Effects of Marine Protected

Areas." *Conservation Biology* 35(6): 1861–70. https://doi.org/10.1111/cobi.13782.

Ovaskainen, O., and N. Abrego. 2020. *Joint Species Distribution Modelling: With Applications in R*. Ecology Biodiversity and Conservation. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/9781108591720.

Pante, E., and B. Simon-Bouhet. 2013. "marmap: A Package for Importing, Plotting and Analyzing Bathymetric and Topographic Data in R." *PLoS One* 8(9): e73051. https://doi.org/10.1371/journal.pone.0073051.

Pearce, J., and S. Ferrier. 2000. "Evaluating the Predictive Performance of Habitat Models Developed Using Logistic Regression." *Ecological Modelling* 133(3): 225–245. https://doi.org/10.1016/S0304-3800(00)00322-7.

Pitcher, C. R., J. G. Hiddink, S. Jennings, J. Collie, A. M. Parma, R. Amoroso, T. Mazor, et al. 2022. "Trawl Impacts on the Relative Status of Biotic Communities of Seabed Sedimentary Habitats in 24 Regions Worldwide." *Proceedings of the National Academy of Sciences of the United States of America* 119(2): e2109449119. https://doi.org/10.1073/pnas.2109449119.

Prener, C., T. Grossenbacher, and A. Zehr. 2022. "Biscale: Tools and Palettes for Bivariate Thematic Mapping." R Package Version 1.0.0. https://CRAN.R-project.org/package=biscale.

Queiroz, N., N. E. Humphries, A. Couto, M. Vedor, I. da Costa, A. M. M. Sequeira, G. Mucientes, et al. 2019. "Global Spatial Risk Assessment of Sharks under the Footprint of Fisheries." *Nature* 572: 461–66. https://doi.org/10.1038/s41586-019-1444-4.

Queiroz, N., N. E. Humphries, G. Mucientes, N. Hammerschlag, F. P. Lima, K. L. Scales, P. I. Miller, L. L. Sousa, R. Seabra, and D. W. Sims. 2016. "Ocean-Wide Tracking of Pelagic Sharks Reveals Extent of Overlap with Longline Fishing Hotspots." *Proceedings of the National Academy of Sciences of the United States of America* 113(6): 1582–87. https://doi.org/10.1073/pnas.1510090113.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Rue, H., S. Martino, and N. Chopin. 2009. "Approximate Bayesian Inference for Latent Gaussian Models by Using Integrated Nested Laplace Approximations." *Journal of the Royal Statistical Society Series B: Statistical Methodology* 71(2): 319–392. https://doi.org/10.1111/j.1467-9868.2008.00700.x.

Russo, A., and A. Artegiani. 1996. "Adriatic Sea Hydrography." *Scientia Marina* 60: 33–43.

Russo, T., L. D'Andrea, A. Parisi, and S. Cataudella. 2014. "VMSbase: An R-Package for VMS and Logbook Data Management and Analysis in Fisheries Ecology." *PLoS One* 9(6): e100195. https://doi.org/10.1371/journal.pone.0100195.

Russo, T., L. D'Andrea, A. Parisi, M. Martinelli, A. Belardinelli, F. Boccoli, I. Cignini, M. Tordoni, and S. Cataudella. 2016. "Assessing the Fishing Footprint Using Data Integrated from Different Tracking Devices: Issues and Opportunities." *Ecological Indicators* 69: 818–827. https://doi.org/10.1016/j.ecolind.2016.04.043.

Russo, T., S. Franceschini, L. D'Andrea, M. Scardi, A. Parisi, and S. Cataudella. 2019. "Predicting Fishing Footprint of Trawlers from Environmental and Fleet Data: An Application of Artificial Neural Networks." *Frontiers in Marine Science* 6: 670. https://doi.org/10.3389/fmars.2019.00670.

Russo, T., A. Parisi, and S. Cataudella. 2011. "New Insights in Interpolating Fishing Tracks from VMS Data for Different Métiers." *Fisheries Research* 108(1): 184–194. https://doi.org/10.1016/j.fishres.2010.12.020.

Russo, T., A. Parisi, M. Prorgi, F. Boccoli, I. Cignini, M. Tordoni, and S. Cataudella. 2011. "When Behaviour Reveals Activity: Assigning Fishing Effort to Métiers Based on VMS Data Using Artificial Neural Networks." *Fisheries Research* 111(1–2): 53–64. https://doi.org/10.1016/j.fishres.2011.06.011.

Saraux, C., J.-M. Fromentin, J.-L. Bigot, J.-H. Bourdeix, M. Morfin, D. Roos, E. Van Beveren, and N. Bez. 2014. "Spatial Structure and Distribution of Small Pelagic Fish in the Northwestern Mediterranean Sea." *PLoS One* 9(11): e111211. https://doi.org/10.1371/journal.pone.0111211.

Scaccini, A. 1967. "Dati Preliminari sulle Zoocenosi Bentoniche e sulla Biomassa in una Zona dell'Alto e Medio Adriatico." Note del Laboratorio di Biologia Marina di Pesca Fano 2.

Schielzeth, H. 2010. "Simple Means to Improve the Interpretability of Regression Coefficients: Interpretation of Regression Coefficients." *Methods in Ecology and Evolution* 1(2): 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x.

Sciberras, M., J. G. Hiddink, S. Jennings, C. L. Szostek, K. M. Hughes, B. Kneafsey, L. J. Clarke, et al. 2018. "Response of Benthic Fauna to Experimental Bottom Fishing: A Global Meta-Analysis." *Fish and Fisheries* 19(4): 698–715. https://doi.org/10.1111/faf.12283.

Serena, F., A. Abella, R. H. L. Walls, and N. K. Dulvy. 2016. "*Raja asterias* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T63120A16527773.

Serena, F., J. Holtzhausen, D. A. Ebert, and C. Mancusi. 2016. "*Myliobatis aquila* (Mediterranean Assessment)." The IUCN Red List of Threatened Species 2016: e.T161569A16527996.

Shepperson, J. L., N. T. Hintzen, C. L. Szostek, E. Bell, L. G. Murray, and M. J. Kaiser. 2018. "A Comparison of VMS and AIS Data: The Effect of Data Coverage and Vessel Position Recording Frequency on Estimates of Fishing Footprints." *ICES Journal of Marine Science* 75(3): 988–998. https://doi.org/10.1093/icesjms/fsx230.

Simpfendorfer, C. A., and N. K. Dulvy. 2017. "Bright Spots of Sustainable Shark Fishing." *Current Biology* 27(3): R97–R98. https://doi.org/10.1016/j.cub.2016.12.017.

Simpfendorfer, C. A., and N. E. Milward. 1993. "Utilisation of a Tropical Bay as a Nursery Area by Sharks of the Families Carcharhinidae and Sphyrnidae." *Environmental Biology of Fishes* 37(4): 337–345.

Soldo, A., and L. Lipej. 2022. "An Annotated Checklist and the Conservation Status of Chondrichthyans in the Adriatic." *Fishes* 7(5): 245. https://doi.org/10.3390/fishes7050245.

Spedicato, M. T., E. Massutí, B. Mérigot, G. Tserpes, A. Jadaud, and G. Relini. 2020. "The MEDITS Trawl Survey Specifications in an Ecosystem Approach to Fishery Management." *Scientia Marina* 83(S1): 9. https://doi.org/10.3989/scimar.04915.11X.

STECF (Scientific, Technical and Economic Committee for Fisheries). 2023. *The 2023 Annual Economic Report on the EU Fishing Fleet (STECF 23-07)*, Vol. 2023. Edited by R. Prellezo, E. Sabatella, J. Virtanen, M. T. Martorell, and J. Guillen. Luxembourg: Publications Office of the European Union. https://doi.org/10.2760/423534.

Stein, R. W., C. G. Mull, T. S. Kuhn, N. C. Aschliman, L. N. K. Davidson, J. B. Joy, G. J. Smith, N. K. Dulvy, and A. O. Mooers. 2018. "Global Priorities for Conserving the Evolutionary History of Sharks, Rays and Chimaeras." *Nature Ecology & Evolution* 2(2): 288–298. https://doi.org/10.1038/s41559-017-0448-4.

Stevens, J. 2000. "The Effects of Fishing on Sharks, Rays, and Chimaeras (Chondrichthyans), and the Implications for Marine Ecosystems." *ICES Journal of Marine Science* 57(3): 476–494. https://doi.org/10.1006/jmsc.2000.0724.

Teruzzi, A., V. Di Biagio, L. Feudale, G. Bolzon, P. Lazzari, S. Salon, G. Coidessa, and G. Cossarini. 2021. "Mediterranean Sea Biogeochemical Reanalysis (CMEMS MED-Biogeochemistry, MedBFM3 System) (Version 1) [Data Set]." Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_BGC_006_008_MEDBFM3.

Thorson, J. T., M. L. Pinsky, and E. J. Ward. 2016. "Model-Based Inference for Estimating Shifts in Species Distribution, Area Occupied and Centre of Gravity." *Methods in Ecology and Evolution* 7(8): 990–1002. https://doi.org/10.1111/2041-210X.12567.

Tjur, T. 2009. "Coefficients of Determination in Logistic Regression Models – A New Proposal: The Coefficient of Discrimination." *The American Statistician* 63(4): 366–372. https://doi.org/10.1198/tast.2009.08210.

Walker, T. I. 1998. "Can Shark Resources Be Harvested Sustainably? A Question Revisited with a Review of Shark Fisheries." *Marine and Freshwater Research* 49: 553–572. https://doi.org/10.1071/MF98017.

Watling, L., and E. A. Norse. 1998. "Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting." *Conservation Biology* 12(6): 1180–97. https://doi.org/10.1046/j.1523-1739.1998.0120061180.x.

Weigmann, S. 2016. "Annotated Checklist of the Living Sharks, Batoids and Chimaeras (Chondrichthyes) of the World, with a Focus on Biogeographical Diversity." *Journal of Fish Biology* 88(3): 837–1037. https://doi.org/10.1111/jfb.12874.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Maioli, Federico, Benjamin Weigel, Max Lindmark, Chiara Manfredi, Walter Zupa, Isabella Bitetto, Tommaso Russo, and Michele Casini. 2024. "Assessing the Overlap between Fishing and Chondrichthyans Exposes High-Risk Areas for Bycatch of Threatened Species." *Ecosphere* 15(11): e70050. https://doi.org/10.1002/ecs2.70050