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ARTICLE TYPE

Estimating the spatial distribution of the white shark in the Mediterranean Sea via an Integrated Species Distribution Model accounting for physical barriers

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Summary

Conserving oceanic apex predators, such as sharks, is of utmost importance. However, scant abundance and distribution data often challenge understanding the population status of many threatened species. Occurrence records are often scarce and opportunistic, and fieldwork aimed to retrieve additional data is expensive and prone to failure. Integrating various data sources becomes crucial to developing species distribution models for informed sampling and conservation purposes. The white shark, for example, is a rare but persistent inhabitant of the Mediterranean Sea. Here, it is considered *Critically Endangered* by the IUCN, while population abundance, distribution patterns, and habitat use are still poorly known. This study uses available occurrence records from 1985 to 2021 from diverse sources to construct a spatial log-Gaussian Cox process, with data-source specific detection functions and thinning, and accounting for physical barriers. This model estimates white shark presence intensity alongside uncertainty through a Bayesian approach with Integrated Nested Laplace Approximation (INLA) and the `inlabru` R package. For the first time, we projected species occurrence hot spots and landscapes of relative abundance (continuous measure of animal density in space) throughout the Mediterranean Sea. This approach can be used with other rare species for which presence-only data from different sources are available.

KEYWORDS:
SDM, integrated species distribution modeling, Spatial Log–Gaussian Cox Process, white shark, Mediterranean Sea, conservation, ecology, Barrier model

1 | INTRODUCTION

Species abundance and distribution patterns are essential components of conservation studies. Assessing population baselines, status, and spatiotemporal trends (IUCN 2001), identifying critical habitats (Darin 2000), and characterizing ongoing threats (Gordon et al. 2019) and interactions with human activities (T. D. White et al. 2019) are the building blocks of conservation assessments. Scientists and decision-makers need robust and reliable occurrence data to estimate species distributions to promote management and conservation.

Species Distribution Models (SDMs) are quantitative tools that combine species occurrence or abundance data with environmental parameters to describe and predict species distribution throughout their habitat (Elith & Leathwick 2009; Nephin et al. 2023). Hence, they are valuable and largely utilized to identify and plan effective conservation measures (Jetz, McPherson, & Guralnick 2012). Unfortunately, obtaining occurrence data for rare and elusive species at the necessary spatial and temporal scales is often challenging. These species are often assumed to be highly threatened, and data paucity hampers any further effort to draw rigorous conclusions about their population dynamics (Thompson 2013) and conservation status.

This is particularly true for marine top predators, such as sharks, which face strong declines due to a constantly increasing anthropogenic impact (McCauley et al. 2016; O'Hara, Frazier, & Halpern 2021), with large-scale ecosystem consequences not yet completely understood (Hammerschlag et al. 2019; Steneck 2012). To address these information gaps, field surveys are often planned to gather additional abundance indices. However, sampling highly mobile and elusive species in large marine ecosystems can be difficult and expensive. Planning efficient fieldwork and sampling activities relies on a fundamental understanding of the studied species' ecology, including knowledge of aggregation sites, nursery areas, and migratory patterns.

Such ecological information is often lacking for endangered shark species both globally (Jorgensen et al. 2022), and specifically in the Mediterranean Sea (Serena et al. 2020). Here, the paucity of quantitative population assessments has hindered shark conservation (Cashion, Bailly, & Pauly 2019), making Mediterranean sharks the most threatened worldwide (Dulvy, Allen, Ralph, & Walls 2016). This condition is particularly true for large pelagic species, where observations typically stem from opportunistic occurrence records rather than systematic monitoring programs (Bargnesi, Moro, Leone, Giovos, & Ferretti 2022). Opportunistic occurrence records have often served as the primary data source for prior assessments, projecting temporal trends in relative population abundance and consequently evaluating the extinction risk for various species (Colloca, Enea, Ragonese, & Di Lorenzo 2017; Ferretti, Myers, Serena, & Lotze 2008). Temporal and aggregated population index trajectories have prevailed over more in-depth spatially disaggregated assessments, which can often reveal important biological and ecological processes.

This is also the case of the white shark, which represents one of the most iconic and studied species of shark in the world, though its distribution pattern and ecological characteristics remain largely unknown in some sectors where the species is present (Huveneers, Apps, et al. 2018). For example, the Mediterranean white shark is among the least known and most endangered white shark populations in the world (Dulvy et al. 2016; Moro et al. 2020). The species have been sporadically but regularly sighted in the Mediterranean basin throughout history (Boldrocchi et al. 2017; De Maddalena & Heim 2012; Moro et al. 2020), though the available records are sparse and highly scattered both in space and time (Boldrocchi et al. 2017; De Maddalena & Heim 2012; I. K. Fergusson 1996; Moro et al. 2020). This makes it difficult to estimate the species distribution due to the very low population density (Moro et al. 2020).

A recent analysis suggests that the population declined between 52% and 96% from historical levels in different sectors of the Mediterranean Sea (Moro et al. 2020). However, the authors investigated the spatial distribution of white sharks in the Mediterranean Sea based on a very coarse spatial resolution.

Here, for the first time, we assess the spatial distribution of white sharks in continuous space in the Mediterranean Sea. By using all opportunistic occurrence data available for Mediterranean white sharks, we develop a Point Process SDM. Fitting SDM to opportunistic data has two major challenges: 1) occurrence data often indicates where the species is observed but not where the species is absent, so they must be considered "presence-only" data (Pearce & Boyce 2006); and 2) the data lack standardized sampling protocols, meaning that sampling effort is uncontrolled and likely uneven over time and space. These two aspects must be considered carefully when modeling opportunistic data. Point processes are a natural way to analyze presence-only data (Renner et al. 2015). In the case of opportunistic data, the observed point process is subject to degradation (thinning) due to the varying sampling effort (see for instance Martino et al. 2021). Our study provides a spatial model in continuous space for presence-only data[1], accounting simultaneously for imperfect detection and physical barriers. Starting from data collected in Moro et al. (2020), integrated with recent records collected by ongoing monitoring projects (i.e., MEDLEM Mancusi et al. (2020), and sharkPulse Bargnesi et al. (2022)), we used Point Process Models to account for the imperfect detection of white shark occurrence data in the Mediterranean Sea. We denote the resulting model as an integrated SDM (ISDM) (see definition in e.g. Paradinas, Illian, Alonso-Fernändez, Pennino, & Smout 2023). In terms of model development, we build on Martino et al. (2021), choosing a Spatial Log-Gaussian Cox Process, including physical barriers (Bakka, Vanhatalo, Illian, Simpson, & Rue 2019), like islands, peninsulas, or other complex coastal systems. Barriers must always be considered when modeling the spatial distribution of marine animals to avoid distortion of species' distributional range when the model smooths over land (Bakka et

[1]Relative abundance should be understood as in, for example, Curtis et al. (2014). Hence, all results must be interpreted considering the large amount of uncertainty affecting the abundance estimates, mostly due to data sparsity. For example, abundance maps should be taken to point out hotspots but not as a measure of the abundance in itself. An element adding to the uncertainty is that detection functions cannot account for all possible confounding factors, as described Nephin et al. (2023)

al. 2019; Sangalli, Ramsay, & Ramsay 2013).

Model estimation is carried out in the Integrated Nested Laplace Approximation with Stochastic Partial Differential Equation (INLA-SPDE)(Lindgren, Rue, & Lindström 2011; Rue, Martino, & Chopin 2009) with `inlabru` (Bachl, Lindgren, Borchers, & Illian 2019) in a full-Bayesian framework. Several recent studies used Bayesian hierarchical models with INLA-SPDE to study species distributions (Cosandey-Godin, Krainski, Worm, & Flemming 2015; Martino et al. 2021; Munoz, Pennino, Conesa, López-Quílez, & Bellido 2013; Quiroz, Prates, & Rue 2015; Rufener, Kinas, Nóbrega, & Oliveira 2017). However, using SPDE-approach based on a relatively small number of locations can be challenging, as in any other spatial statistics model, and lead to inappropriate inference if external meaningful information is not added to the model. Here, we add environmental covariates (depth and temperatures) from different sources (COPERNICUS n.d.; GEBCO n.d.) while describing each data source with a specific detection function. As indices of observation effort, we considered two different layers: 1) landscapes of fishing intensity produced by using Synthetic Aperture Radar (SAR, Sentinel I) detections (Paolo et al. 2024), and 2) vessel density estimates based on Automatic Identification Systems (AIS), referring to pleasure and passenger boats (Falco, Pittito, Adnams, Earwaker, & Greidanus 2019; Martín Míguez et al. 2019).

This study will characterize landscapes of white shark relative abundance and identify hot spot areas to be monitored and further investigated, as it already happens in other oceanic sectors of the white shark distribution (Bruce & Bradford 2012; Francis, Duffy, Bonfil, & Manning 2012; Huveneers, Watanabe, Payne, & Semmens 2018; Jorgensen et al. 2010; Kock et al. 2022; Skomal, Braun, Chisholm, & Thorrold 2017). This information is crucial to building effective conservation plans and preventing species' local extinction. The paper is organized as follows. Section 2 introduces the data and model used in this work. Within Section 2 we provide details on the study area, available sighting data, and observation effort data that will be used in the model. The second part of Section 2 presents a detailed description of the model built in this study, focusing on the barrier model and its implementation within the INLA-SPDE framework. In Section 3, we discuss the obtained results. A final discussion is presented in Section 4.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is the entire Mediterranean basin, including the Marmara Sea. The area covers almost 2.500.000 km^2, and it is the deepest enclosed sea in the world (maximum depth 5267 m in the Calypso Pit). The Mediterranean Sea connects westward to the Atlantic Ocean via the Strait of Gibraltar and eastward to the Black Sea via the Turkish Strait System formed by the Marmara Sea, the Bosporus Strait, and the Strait of the Dardanelles. Since 1869, it has also been connected with the Red Sea due to the construction of the Suez Canal digging. The Mediterranean Sea accounts for <1% of the total water surface area of the planet, but it is one of the 25 main regions in the world for biodiversity (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent 2000). It is a complex marine ecosystem that hosts about 4-8% of the world's marine biodiversity (Coll et al. 2010) and about 6% of the global elasmobranchs' biodiversity (Serena et al. 2020). Unlike other marginal seas, large Mediterranean Sea sectors are classified as deep sea (average depth 1500m). However, the area displays unique characteristics which strongly differ from the nearby Atlantic waters. It is considered an oligotrophic basin, with an average net primary production much lower than typical oceanic sectors (Bosc, Bricaud, & Antoine 2004), though a west-east gradient for both temperature (Coll et al. 2010) and productivity (Bosc et al. 2004) is present. The eastern Mediterranean basin is considered one of the most oligotrophic areas in the world (Psarra, Tselepides, & Ignatiades 2000; Tselepides, Papadopoulou, Podaras, Plaiti, & Koutsoubas 2000). Despite this apparent paucity of nutrients, a substantial homeothermic state is recorded from 200-300 m to the bottom, favoring the nutrients' recycling over the entire water column in winter (Emig & Geistdoerfer 2005).

2.2 | Data sources and environmental covariates

We considered all documented sightings of white sharks in the Mediterranean since 1985, assuming that the spatial distribution of the population has not significantly changed in the last decades. This is reasonable considering the long lifespan of the species (around 70 years, Hamady, Natanson, Skomal, and Thorrold (2014)) and the high generation time (53 years, Rigby et al. (2019)). The data were collected from various sources using multiple search strategies (Moro et al. 2020). Depending on their source, we divided the data into two categories: 1) data from fishing captures, referred to as *catches* (N=144), and 2) data from observations of free-swimming specimens, referred to as *sightings* (N=125) Figure 1 .

FIGURE 1 Available data. Catches are in red and sightings in green.

As species distribution predictors, we considered the following environmental variables: depth, slope (i.e. seabed morphology and depth gradients), sea surface temperature (SST), and chlorophyll A concentration. These constitute the typical environmental parameters used in SDMs for marine megafauna (Garcia-Baron et al. 2020; McClellan et al. 2014) and SST and chlorophyll A have been used before to predict the distribution of juvenile white sharks in California (C. F. White et al. 2019).

Depth data were obtained from GEBCO (General Bathymetric Chart of the Ocean - `https://www.gebco.net`). The slope was computed from depth data through the terrain() function of the R package "terra" (Hijmans & Van Etten 2021). SST and chlorophyll A were retrieved from the COPERNICUS platform (`https://marine.copernicus.eu/`) and recorded as monthly averages. Only depth and temperature range were significant out of all the tested covariates.

2.3 | Detection data

Detection processes differ between the two occurrence data categories, *catches* and *sightings*. *Catches* were assumed to be related to the level of fishing activities occurring in a region. Estimating the fishing effort is not trivial and estimates usually are based on AIS data (Kroodsma et al. 2018). AIS is a mandatory anti-collision system for all vessels larger than 500 GT, vessels above 300 GT traveling across countries, and all passenger vessels (ferries, cruise ships, etc.). Hence, fishing activities detected with AIS can be a reliable estimate of industrial fishing occurring on the European side of the Mediterranean Sea and for large-scale industrial fishing fleets. By contrast, AIS usage off the northern African and Middle Eastern countries is virtually null as local fisheries are mainly small-scale and composed of fishing vessels untracked with AIS or other satellite tracking devices (Supplementary Figure 2). To control for this bias and obtain a comprehensive representation of the fishing effort in the area, we relied on the Synthetic Aperture Radar (SAR) detection provided by the Global Fishing Watch (`https://globalfishingwatch.org/`) to estimate fishing intensity. This database provides SAR detection matching with AIS tracks as well as the probability of being a fishing vessel for unmatching detections. A detailed description of the dataset and the methodology used to classify the SAR detections can be found in Paolo et al. (2024). In the areas where the AIS underestimates the fishing effort, SAR detections can complement AIS tracks to identify untracked fishing vessel activities. In this paper, we used this integrated dataset to estimate fishing intensity as a proxy of observation effort. Among all the new records available, we considered the coordinates of points representing all vessels matching with AIS detection and all vessels with a probability of being a fishing vessel greater than 0.95. This represents a standard interval for the model's uncertainty level. Since SAR detections are represented by points, we then estimated the intensity of the effort through a Spatial Log-Cox process. The estimated mean log-intensity is represented in Figure 2 (upper panel); additional information on the estimated model can be found in the Supplementary Materials (Section S2a). This section emphasizes the importance of considering SAR data when estimating intensity. Supplementary Figure 2 demonstrates the underestimation of fishing boat intensity in the northern Mediterranean when only AIS data is considered.

The detection of *sightings* data was described using an index of private boating. We used vessel density estimates from EMODnet (European Marine Observation and Data Network; Martín Míguez et al. (2019), Falco et al. (2019)) to estimate this observation effort index. These data were chosen because most observations in this category originate from private boats. Therefore, we selected the "passenger vessels", "sailing boats", and "pleasure craft" categories as they predominantly represent private boating activities. Details are reported in Supplementary Materials (Section S2b). Figure 2 (lower panel) depicts the median of the log vessel intensity used for catching sightings data. The same coverage issues affecting fishing effort data may affect vessel density information. However, the two datasets impact the relative abundance estimates differently. Indeed, where AIS data for fishing activities are underrepresented, several catches are reported, implying their potential strong impact on intensity estimates. By contrast, where vessel density information is lacking, no sightings are available, implying no effect on intensity estimates.

2.4 | Model

We aim to predict shark presence intensity in the Mediterranean Sea using different data sources. We use a Spatial Log–Gaussian Cox Process (LGCP) (Renner et al. 2015) thinned with different detection functions to manage possible detection biases in each dataset (Martino et al. 2021). We assumed that the sighting pattern, i.e., locations of sharks in space ($s \in \mathbb{R}^2$) are properly described by a point process whose intensity function $\lambda(s)$ is additive on the log-scale. Hence, for all data sources, we assume the following "true" (unthinned) intensity:

$$\log(\lambda(s)) = \mathbf{X}^T(s)\boldsymbol{\beta} + \omega(s) \tag{1}$$

where $\mathbf{X}(s)$ is a set of covariates detected at location s with linear effect $\boldsymbol{\beta}$ to be estimated, $\omega(s)$ is a zero-mean Gaussian process describing the residual spatial variation. Although it would have been theoretically possible to consider a complex spatio-temporal model (Yuan et al. 2017), $\omega(s,t)$, the limited number of sightings each year did not provide enough information to allow robust estimates. Therefore we chose to estimate a purely spatial model (see supplementary section 1 for further details). For each data source (*catches* and *sightings*) the observed intensity is defined as:

$$\lambda_j^*(s) = g_j(s)\lambda(s), \quad j = 1,2 \tag{2}$$

where $g_j(s)$ is the detection function that determines the thinning of the original process (Martino et al. 2021). More precisely, $g_j(s)$ is the probability that a point present in location s is included in the dataset j. The detection functions were formalized as follows:

$$g_j(s) = \Phi\left(\frac{d_j(s)}{\xi_j} - \mu_j\right), \quad j = 1,2 \tag{3}$$

where Φ is the normal cumulative distribution function (cdf) with μ and ξ as location and scale parameters, respectively. $d_j(s)$ represents the log-intensity of the fishing vessels for *catches* and pleasure vessel log-intensity for *sightings*. The normal cdf was selected as we required $g_j(s)$ to be between 0 and 1, in addition it should be close to 1 when the vessel log-density is high, and close or equal to zero when it is small (or null). This reflects our working hypotheses that the probability of sightings is higher where the density of vessels is also higher.

Model evaluation was performed using goodness-of-fit measures, following the approach of Sicacha-Parada, Steinsland, Cretois, and Borgelt (2021). We used the deviance information criterion (DIC) (Spiegelhalter, Best, Carlin, & Van Der Linde 2002) to evaluate the model's fit and choose the final set of covariates. After considering these measures, we selected the model incorporating depth and temperature range as covariates (Figure 3).

Therefore, the model for the unthinned log intensity was formalized as:

$$\log(\lambda(s)) = \beta_0 + \beta_{depth}depth(s) + \beta_{sst}sst(s) + \omega(s), \quad s \in S \tag{4}$$

where $S \subset \mathbb{R}^2$ is the study area.

Point Process estimation is based on the methodology introduced by Simpson, Illian, Lindgren, Sørbye, and Rue (2016) and successfully applied, among others, by Sicacha-Parada et al. (2021); Yuan et al. (2017). The SPDE (Stochastic Partial

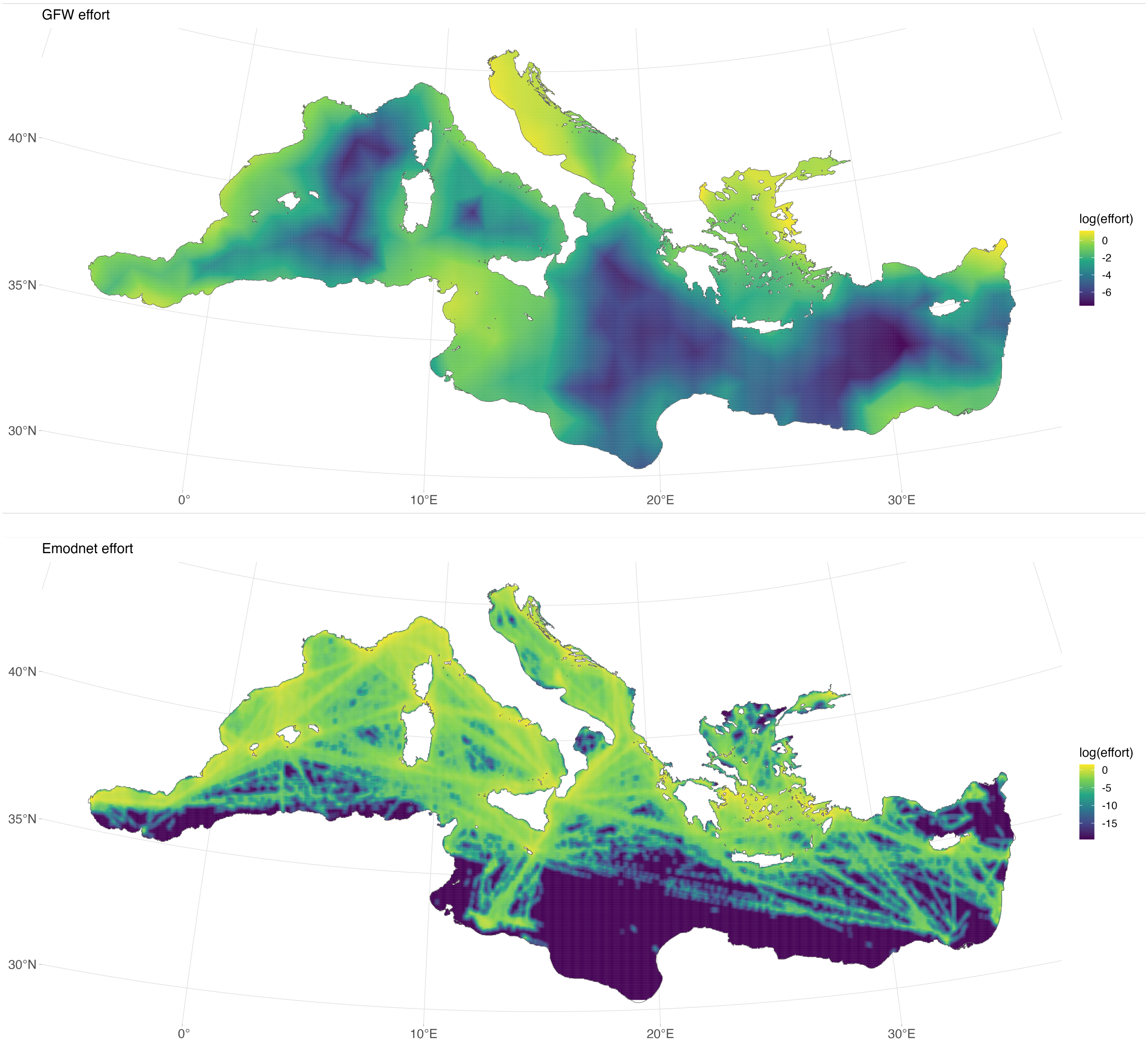

FIGURE 2 The final estimate of the median vessel log intensity from SAR data is shown in the top figure, while the log vessel density of EMOdnet is depicted in the lower figure.

Differential Equation) representation of Gaussian fields (GFs), pioneered by Lindgren et al. (2011), provided us with several computational advantages. This approach allows for efficient computation and inference on spatial models, making it particularly well-suited for handling large datasets and complex spatial structures. The SPDE approach relies on a mesh (the one we used is depicted in Supplementary Figure 4) to discretize the spatial domain. On the other hand, and contrary to what happens when one uses a grid discretization, the locations of the points do not need to be approximated (for example at the grid cell centroids) but the exact occurrences coordinates can be directly used. See Simpson et al. (2016) for more details about fitting point processes with the SPDE approach.

We accounted for the presence of islands and the Italian peninsula in the Mediterranean Sea, using the so called Barrier model introduced in Bakka et al. (2019). The characteristic of such non-stationary GF is that spatial correlations do not necessarily follow the shortest path between two points but are allowed to follow the topography of the study area so that if two locations at sea are separated by, say, an island, the correlation paths would travel around the island.

The model is built in Bakka et al. (2019) by defining the non-stationary Matern GF as the solution of a system of stochastic partial differential equations:

$$
\begin{aligned}
\omega(s) - \nabla \cdot \frac{r^2}{8} \nabla \omega(s) &= r\sqrt{\frac{\pi}{2}}\sigma_u W(s), \quad \text{for } s \in \Omega_n \\
\omega(s) - \nabla \cdot \frac{r_b^2}{8} \nabla \omega(s) &= r_b\sqrt{\frac{\pi}{2}}\sigma_u W(s), \quad \text{for } s \in \Omega_b
\end{aligned}
\tag{5}
$$

Here $\omega(s)$ $s \in \mathbb{R}^2$ is the GF of interest, $\nabla = \left(\frac{\partial}{\partial x}, \frac{\partial}{\partial y}\right)$ and $W(s)$ denotes white noise. Ω_n represents the domain of interest (in our case, the sea) while Ω_b is the barrier (in our case, the land). The parameter σ_u is the marginal variance of the Matern covariance function while r and r_b are the ranges of the Matern covariance, respectively, on the sea and land. The parameter r_b is taken to be a fixed fraction of the range, e.g., $r_b = r/10$ to create the barrier effect. This ensures the desired behaviour of the correlation functions for areas that are close to the barrier areas. For more details on the model and the implementation see Bakka et al. (2019).

We specified priors for all model parameters to finalize the model in a Bayesian framework. For the parameters in the spatial field $\omega(s)$ in (1), we chose Penalized Complexity priors (PC priors) (Simpson, Rue, Riebler, Martins, & Sørbye 2017). PC priors are advantageous in Bayesian modeling as they effectively handle model complexity and aid in model selection. By penalizing complex models and promoting simplicity, PC priors improve the efficiency and interpretability of the analysis (Simpson et al. 2017).

For computational efficiency, we used INLA (Rue et al. 2009) to fit the model in a Bayesian framework. The model above does not directly fall under the latent Gaussian model framework for the INLA estimation software because the parameters μ_j and ξ_i of the detection function in (3) do not enter the model in a log-linear way. We used, therefore, the methodology introduced in Yuan et al. (2017) and implemented in the `inlabru` R package (Bachl et al. 2019) that allows fitting models with some non-linear elements. This is done by linearizing the model via Taylor approximation and using a line search to optimize the linearization point. This method has already been successfully used in several studies (for example Arce Guillen et al. 2023; Martino et al. 2021; Serafini, Lindgren, & Naylor 2023; Yuan et al. 2017)). Details on the optimization method can be found in the vignettes of the GitHub repository `https://inlabru-org.github.io/inlabru/`. The method is implemented in the `inlabru` package available on CRAN and from the repository above. Besides the computational advantages, `inlabru` allows for a user-friendly implementation of LGCP with ad-hoc functions for generating posterior samples and prediction maps. The proposed approach enables the joint estimation of all model components, including parameters in the detection functions, thereby accounting for all uncertainties consistently (refer to section S3 in the Supplementary Materials for prior specifications and implementation details).

3 | RESULTS

A total of 269 white shark occurrence records were collected over approximately 40 years, with a decreasing trend in the sighting rate. It went from about 10 specimens per year recorded in 1985-1995 to about 4 specimens in the last decade. Occurrences were not homogeneously distributed around the Mediterranean Sea since, as expected, most of the records were located in the northern Mediterranean sectors. The final selection of environmental covariates was determined by evaluating various combinations using goodness-of-fit measures of the model, in particular DIC, and indicated that depth and temperature range (Figure 3) significantly affected relative white shark abundance (at the 95% level, Table 1). Maps showing covariates used within the model are shown in Figure 3 (depth and range temperature). Depth was inversely related to relative abundance, while temperature range had a positive effect. Depth clearly increased moving from coastal to more pelagic habitats (Figure 3), though extended continental shelves are located in the Adriatic, the Sicilian Channel, and the Aegean Sea. Specific areas of these sectors also showed the largest annual ranges in temperature(Figure 3). In fact, the Italian side of the northern Adriatic Sea, the northern Aegean Sea, and the Gulf of Gabes exhibited variations in temperature around 15-20°C across the year.

The combined effect of the environmental variables indicates that relative white shark abundance increases in shallow coastal waters, which are linked to more variable environmental conditions. However, sea surface temperature can be linked to different drivers and local factors (i.e., winds, up-welling phenomena, water circulation), affecting all the area's environmental conditions.

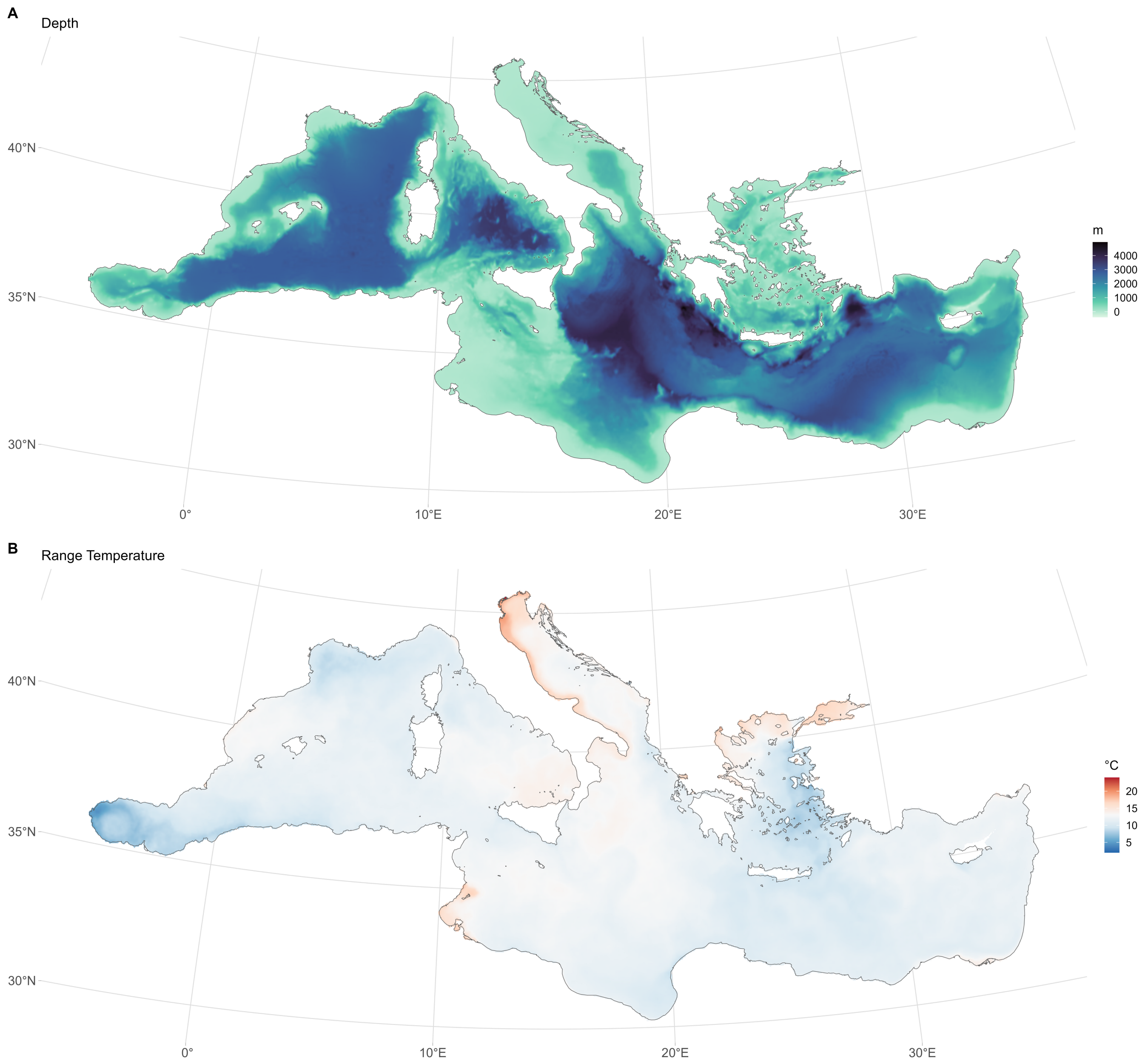

FIGURE 3 Bottom depth (panel A) and Temperature Range (panel B).

In any case, most records are located in coastal areas, and thus, the model estimates in pelagic areas (characterized by deep waters) are more uncertain.

The highest intensity of white shark occurrence is in the Sicilian Channel (Figure 4); due to a large amount of data and effort, a rather low standard deviation was also expected in this area. Conversely, the variance is high in the southeastern Mediterranean Sea. Here, the low observational effort increased uncertainty. Accounting for the observational effort is crucial for opportunistic observations. In this study, the effect of this process is particularly evident in the Adriatic area, where numerous observations are recorded together with a very high effort. Figure 5 , which refers to the no-effort model where $\lambda^*(s) = \lambda(s)$, confirms the importance of the detection function in estimating observation intensity. The anomalies surrounding the Adriatic Sea and the area between Corsica and Italy are resolved by considering effort intensity. In general, it is possible to observe that in the case of the absence of detection, the intensity estimate is entirely driven by the observations. In areas with a higher density of observations, the estimate tends to be higher. However, relying solely on this approach leads to distorted estimates as it does

Parameter	Posterior mean	Posterior 0.025 quantile	Posterior 0.975 quantile
β_0	1.371	0.345	2.210
β_{depth}	-0.413	-0.650	-0.184
β_{sst}	1.011	0.553	1.456
Range of Matérn field (Km) (ρ)	583.879	396.271	849.899
Standard deviation of Matérn field(σ)	1.312	0.232	1.903
ξ_1	0.064	0.034	0.108
μ_1	-1.324	-2.418	-0.490
ξ_2	0.406	0.305	0.535
μ_2	-0.790	-1.116	-0.499

TABLE 1 Posterior mean and 95% credible intervals for the parameters in Equation 4 and Equation 3.

not consider the sampling effort. In reality, the higher likelihood of observations in heavily trafficked areas does not necessarily indicate a higher presence of sharks. Instead, it is a result of increased human activity in those regions.

In this study, modeling the occurrence records considering geographic barriers was fundamental as it allowed us to correct the covariance distortion due to model propagation inland. This correction is particularly evident along the Italian coast of the Tyrrhenian, where if we do not consider the barrier effect, the presence of many sightings in the Adriatic increases the intensity (see Supplementary Figure 5 for model estimates without barriers).

4 | DISCUSSION

Modeling the spatial distribution of rare and elusive marine species is often challenging as mainly relies on using opportunistic occurrence records. These are widely scattered in their temporal and spatial dimension, limiting the scope of possible analyses. Their opportunistic nature also results in different sources of biases, often discouraging their use. For example, the imperfect detection of individuals must always be controlled when estimating SDMs. However, this is often overlooked in the literature, especially when data are scarce (Cosentino & Maiorano 2021; Elith & Leathwick 2009). Similar to Martino et al. (2021)'s approach, our model considers imperfect detection and, given its hierarchical nature, includes all sources of uncertainty, returning a rigorous evaluation of prediction uncertainty. Hence, this study illustrates how to use this data and obtain relative abundance estimates consistent with the observation process and avoid, as much as possible, artifacts generated by underestimating uncertainty.

Building on Martino et al. (2021) and Pace et al. (2022) approaches, we developed two main innovations. First, we included geographic barriers such as landmasses, islands and archipelagos, and wide peninsulas, which represent discontinuities in the marine environment and a crucial factor for species dispersal (Longhurst 2010; Steele 1991). Therefore, ignoring their presence can affect the robustness of SDMs' results (Robinson et al. 2011). In our case, differences between models that do not use barriers and the proposed detection function were particularly evident in the Adriatic Sea, the Sicilian Channel, and the Tuscan Archipelago (see Supplementary materials Figure 5). Previous attempts to use the method led to limited success (Martínez-Minaya, Conesa, Bakka, & Pennino 2019), while in this study, the use of barriers allowed us to reduce the error in estimating the distribution near, for example, the Italian coast. Introducing barriers avoids circular propagation of covariance functions across the land, linking, for example, the Ligurian Sea with the Adriatic.
Second, we developed a better index of observation effort by integrating AIS data with SAR's detections (Paolo et al. 2024). SAR data compensates for underestimating fishing activities that usually characterize AIS data. AIS detection can vary highly between oceanic regions because of the different fleet compositions, regulations, intensity of vessel activity and satellite coverage(Kroodsma et al. 2018; Paolo et al. 2022) as well as the intensity of illegal fishing since fishers tend to turn off the AIS

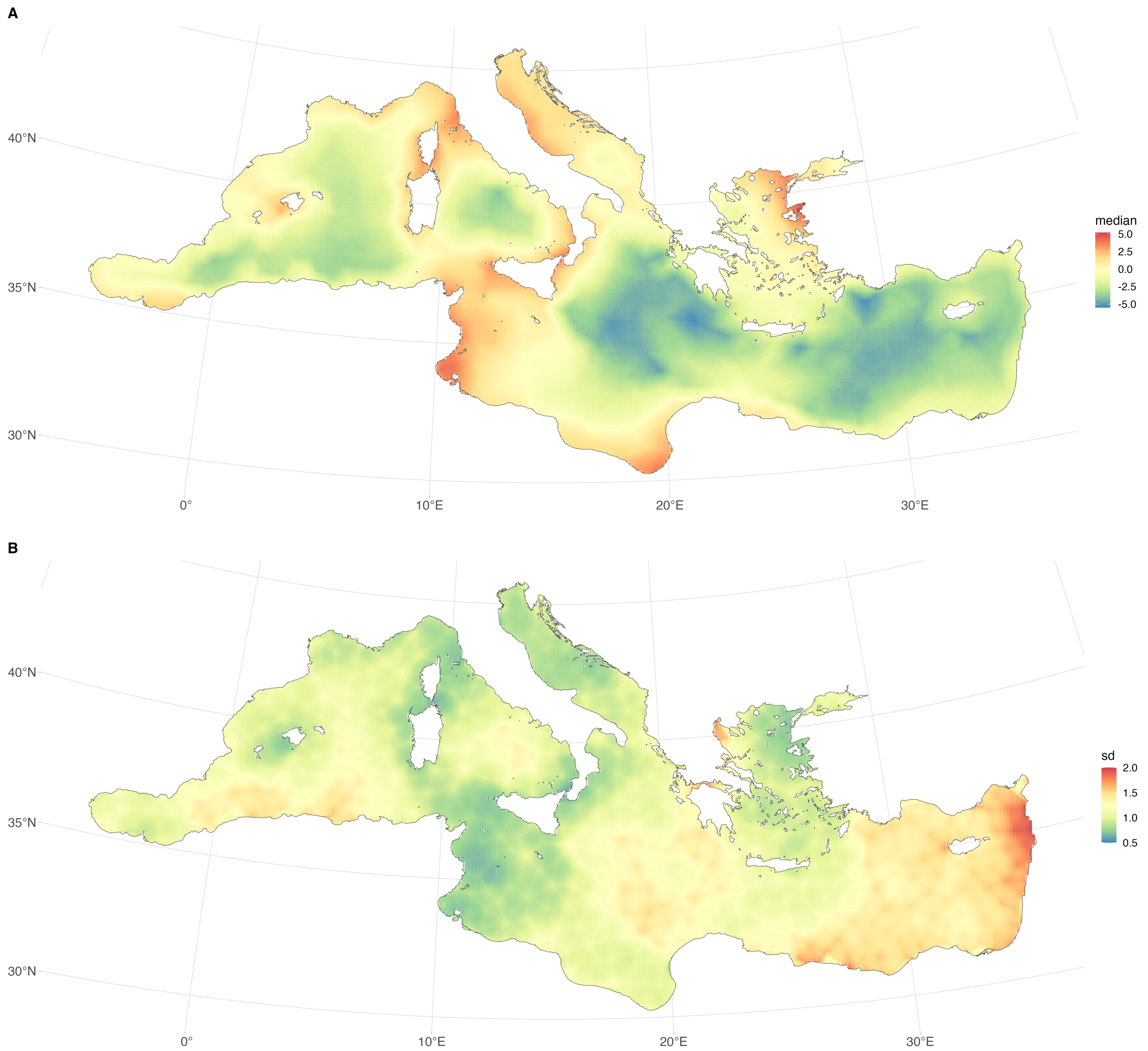

FIGURE 4 The posterior estimates of the median (panel A) and the standard deviation (panel B) of the log intensity of the white shark occurrence.

when acting illegally (Park et al. 2020). Combining AIS and SAR data resulted in better estimates of the fishing effort and allowed us to characterize and detect hidden fishing activities from regions with low AIS coverage. This aspect is particularly important in the Mediterranean Sea, where small-scale and artisanal fisheries are highly developed (Quetglas et al. 2016), and especially off the North African coast, where AIS is virtually unused. In these areas, AIS data vastly underestimate fishing intensity, overestimating white shark presence.

With this approach, for the first time, we estimated a spatial model for the Mediterranean white shark in continuous space at a very fine resolution. Unfortunately, the number of white shark sightings was insufficient for complete space-time modeling. White sharks exhibit complex seasonal migrations in other ocean sectors, highly varying by sex, age, and region (Bradford et al. 2020; Francis et al. 2012; Kock et al. 2022; Skomal et al. 2017). We do not know whether Mediterranean white sharks show similar spatio-temporal patterns. Our small sample size hampered the possibility of capturing possible temporal dynamics in

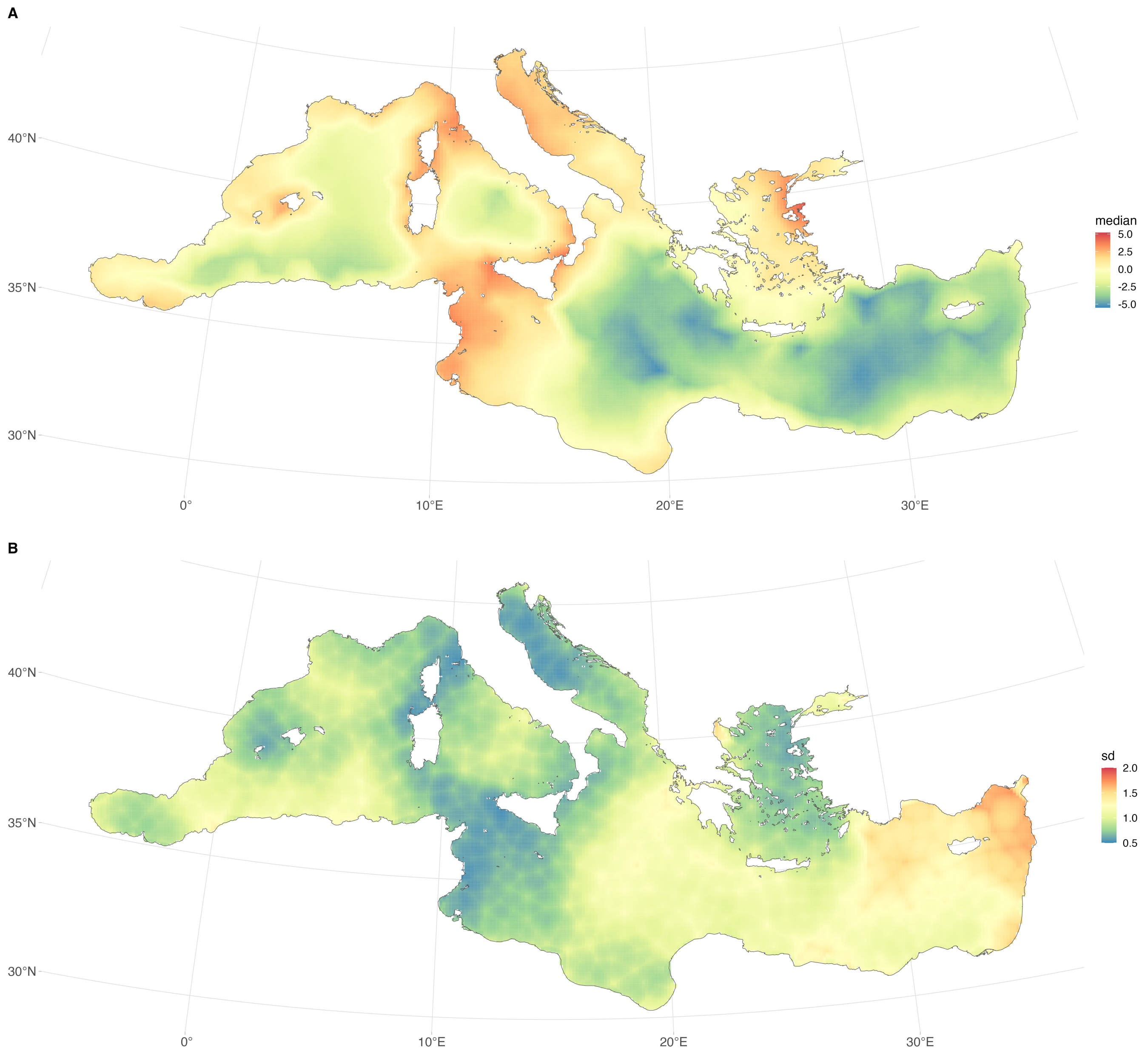

FIGURE 5 The posterior estimates of the median (panel A) and the standard deviation (panel B) of the log intensity of the white shark occurrence using the model without detection functions.

the area, which now needs deeper investigations. Therefore, our final estimate can only pinpoint areas with higher intensity of white sharks at a finer scale than previously done, testing the effect of some important environmental predictors.

Our results confirmed that white sharks have distinct spatial distribution patterns in the Mediterranean Sea. Overall, relative abundance decreased from coastal to more pelagic habitats, as confirmed by the strong negative effect of depth. In line with Moro et al. (2020)'s prediction of a population spatial contraction, hot spots of relative abundance are now restricted in specific central Mediterranean sectors. Yet, It is unclear whether these patterns reflect the entire population or mainly juvenile distribution. Around 62% of the specimens with known length (75%) were juveniles (> 300 cm in length, Bruce and Bradford 2012). To reduce the sampling bias, we restricted our analyses to all occurrences recorded after 1985. This minimized the influence of tuna trap catches, which, historically, almost exclusively caught adult white sharks (Moro et al. 2020), and between the 1960s and 1980s were gradually discontinued due to the development of offshore industrial fisheries (Fromentin & Powers 2005). The two major abundance hot spots highlighted by our results are hypothesized white shark nurseries and breeding grounds: the Sicilian Channel (De Maddalena & Heim 2012; I. Fergusson 2002) and the north-east Aegean Sea (Kabasakal 2020). Although the coastal distribution of records can be associated with most human activities being concentrated close to the shores, we attempted to control this factor with the estimated index of observation effort. In other ocean sectors, adult white sharks spend part of the year in oceanic waters, while smaller specimens are largely restricted to coastal habitats with short travels in more pelagic waters (Bruce, Harasti, Lee, Gallen, & Bradford 2019; Duffy, Francis, Manning, & Bonfil 2012; Jorgensen et al. 2010). We do not know whether these dynamics also occur in the Mediterranean Sea. Oceanic sectors are limited in the region, and our analyses did not show gradients of relative abundance suggesting a connection with outer Atlantic waters, nor could detect seasonal shifts in relative abundance suggestive of systematic migrations. This aspect would need further investigation.

Although the Sicilian Channel was expected to be an important area for the species (Boldrocchi et al. 2017; Bradai & Saidi 2013; I. K. Fergusson 1996; Jenrette et al. 2023; Moro et al. 2020), the high spatial resolution of our model allowed us to reveal more insightful distribution patterns than previously done. For example, relative abundance increased from the Italian to the Tunisian side of the sector, confirming how the Tunisian Plateau may represent an important habitat for the species (Bradai & Saidi 2013; Rafrafi-Nouira, Diatta, Diaby, & Capapé 2019; Saidi, Bradai, Bouain, Guelorget, & Capapé 2005; Zaouali, Rafrafi-Nouira, Amor, Amor, & Capapé 2020)]. The Tunisian Plateau is characterized by a more extended continental shelf with extensive seagrass meadows, which might represent a suitable habitat for the species, particularly for juvenile white sharks (Anderson et al. 2021; Harasti, Lee, Bruce, Gallen, & Bradford 2017; Spurgeon, Anderson, Liu, Barajas, & Lowe 2022). In particular, the waters of the Gulf of Gabes are known to host nurseries for other shark species (Enajjar, Saidi, & Bradai 2015) as well as abundant demersal species (El Lakhrach, Hattour, Jarboui, Bradai, & Ramos Esplá 2019; Lasram, Hattab, Halouani, Romdhane, & Le Loc'h 2015) that are primary prey-items for juvenile white sharks (Hussey et al. 2012; Spurgeon et al. 2022). Further investigations are required to highlight whether differences in the distribution of juveniles and adults are present (e.g., via a marked-point process (Jacobsen & Gani 2006)) and whether these abundance patterns may also reflect a greater level of exploitation than those estimated by our fishing intensity index.

The western Mediterranean Sea showed higher relative abundance values than the eastern Mediterranean. This pattern aligns with previous hypotheses (Boldrocchi et al. 2017; De Maddalena & Heim 2012; I. K. Fergusson 1996) and analyses (Moro et al. 2020). Our model results suggest that temperature gradients may explain this pattern. The Mediterranean Sea is warmer than other oceanic regions where white sharks occur (Rohling, Marino, & Grant 2015). While, its average annual Sea Surface Temperature (SST) is within the white shark optimal temperature range (10-23°C) (Boustany et al. 2002; Bruce & Bradford 2012; Domeier & Nasby-Lucas 2008; Francis et al. 2012; Skomal et al. 2017; Weng et al. 2007), Mediterranean SST can reach 29-30°C peaks during the summer in the central (Di Lorenzo, Sinerchia, & Colloca 2018) and eastern sectors (Rohling et al. 2015). Although we cannot completely exclude the emerging pattern is associated with an underestimation of the observation effort, considering the paucity of both historical and more recent occurrences from the eastern Mediterranean sectors, the warmer and less productive waters of that basin (Bosc et al. 2004; Coll et al. 2010) may be a sub-optimal habitat for the species (Moro et al. 2020).

5 | CONCLUDING REMARKS

In this work, we proposed a spatial log-Gaussian Cox process incorporating different detection functions and thinning for each data source and accounting for physical barriers. Estimates are obtained in a fully Bayesian framework using INLA and `inlabru`. Here, we showed how to obtain a reliable estimate of white shark abundance in the Mediterranean. The latter is critical to understanding its ecology and informing effective conservation management decisions. In the future, a combination of different data collection methods, including citizen science initiatives and molecular approaches (Jenrette et al. 2023), can enhance our knowledge of the species distribution and behavior in the region. Future research should target areas with high shark presence, such as known or hypothesized feeding or breeding sites and use standardized protocols to facilitate data collection, comparison, and integration. A better understanding of white shark ecology in the Mediterranean will help preserve a key apex predator for this large marine ecosystem. Our approach contributed to this objective and laid the ground for deeper investigations in the suggested abundance hot-spots. It also contributes to refining the analytical approach to investigate the spatial ecology of rare and elusive species, which are often understudied and highly threatened with extinction, but for which there is an increasing amount of opportunistic records from the public and citizen science approaches.

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