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COMMUNITY STRUCTURE AND DYNAMICS OF SHARKS AND THEIR RELATIVES IN THE ADRIATIC SEA

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I believe Richard McElreath, the author of ‘Statistical Rethinking,’ once said that while science is great, academia itself isn’t. I agree with this sentiment. However, it is within academia that I have met some of the most exceptional people I know.

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List of publications

This thesis draws upon the research presented in the following papers, referenced using Roman numerals throughout the text:

I. **Maioli, F.**, Weigel, B., Chiarabelli, E., Manfredi, C., Anibaldi, A., Isailović, I., Vrgoč, N., & Casini, M. (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

II. **Maioli, F.**, Weigel, B., Lindmark, M., Manfredi, C., Zupa, W., Bitetto, I., Russo, T., & Casini, M. (2023). Assessing the overlap between fishing and chondrichthyans exposes high-risk areas for bycatch of threatened species. [Manuscript submitted][1]

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[1] The preprint version is available at https://doi.org/10.1101/2023.10.25.563919

Abstract

Chondrichthyans—sharks, rays, and chimaeras—represent one of the most evolutionarily distinct and ecologically diverse groups of vertebrates. However, overfishing poses a severe threat to this group, with one-third of global chondrichthyan species at risk of extinction. The Mediterranean Sea is a critical hotspot for this risk.

In my research, I address the urgent need for comprehensive knowledge about chondrichthyan species distribution and their interaction with fisheries in the Adriatic Sea—a heavily exploited basin within the Mediterranean.

By analyzing long-term fishery-independent monitoring data and employing state-of-the-art distribution modeling techniques, I uncover key insights.

The chondrichthyan community exhibits strong depth and spatial sorting. Some viviparous species are abundant in the shallower northern Adriatic, while there is a west-to-east gradient of increasing abundance and species richness.

Over time, dominant chondrichthyan species have increased in abundance, yet at different rates, except for the threatened spurdog, which continues to decline. Consequently, the community now displays a lower community-weighted age at first maturity and fraction of viviparous species compared to the 1990s.

To estimate the spatial overlap between bottom trawling and chondrichthyans, I introduce a novel approach that combines Vessel Monitoring System data (representing fishing effort) with geostatistical species distribution models.

By employing diverse overlap metrics that capture different levels of organization—from individual species to the entire community—I estimate substantial spatial overlap between intensive trawling, areas of high species richness, and the presence of threatened chondrichthyans (i.e. assessed as Vulnerable, Endangered and Critically Endangered by the IUCN Red List). These areas of high overlap are primarily concentrated in the northern and central offshore sectors of the western Adriatic, highlighting specific areas of conservation concern.

In summary, this thesis contributes innovative statistical frameworks and ecological insights and may help in guiding conservation efforts to sustain chondrichthyan populations in the Adriatic Sea and beyond.

1 Introduction

1.1 Sharks and their relatives

Sharks and their relatives, which encompass rays, skates, and chimeras (class Chondrichthyes; referred to herein as ‘chondrichthyans’), occupy a remarkable position in the evolutionary history of jawed vertebrates, spanning over 400 million years (Stein et al., 2018). This diverse and successful group comprises approximately 1200 living species and spans widely along the trophic chain (Weigmann, 2016). From filter-feeding species like the whale shark (*Rhincodon typus*) (Cárdenas-Palomo et al., 2018), to mesopredators such as the grey reef shark (*Carcharhinus amblyrhynchos*) (Roff et al., 2016), and apex predators such as the iconic white shark (*Carcharodon carcharias*) (Heupel et al., 2014), their ecological roles vary considerably across different ecosystems (Ferretti et al., 2010). Chondrichthyans also hold significant cultural and societal importance globally, having been subject to fishing for millennia (Dell’Apa et al., 2014; Drew et al., 2013; Leeney & Poncelet, 2015; Mojetta et al., 2018). In more recent times, their value extends beyond consumption, embracing aspects such as shark tourism (Cisneros-Montemayor et al., 2013; Healy et al., 2020).

Despite enduring through at least 5 mass extinctions (Raup & Sepkoski, 1982), these ancient creatures now face significant challenges. Over the past few decades, alarming declines have been observed in several oceanic and coastal chondrichthyan populations (e.g. Pacoureau et al. (2021); Colloca et al. (2017); Ferretti et al. (2013); Shepherd & Myers (2005); Simpfendorfer et al. (2023)). Currently, approximately one-third of the world's chondrichthyans species are at risk of extinction, being classified as Vulnerable, Endangered and Critically Endangered by the IUCN Red List (IUCN, 2023). These population declines have been almost entirely driven by overfishing (Dulvy et al., 2014, 2021).

While chondrichthyans exhibit considerable variability in life-history traits, many chondrichthyan species display characteristics of a 'K-selected' strategy. Their late age at maturity and low fecundity make them more vulnerable to fishing than most teleosts (Stevens et al., 2000; Walker, 1998). Despite this vulnerability, there is potential for sustainable fishing of certain chondrichthyan populations when robust, science-based management strategies are implemented. Ideed, many of these species have the capacity to sustain fisheries that operate within well-defined ecological limits (Simpfendorfer & Dulvy, 2017; Walker, 1998).

The Mediterranean Sea ecosystem contributes to about 7% of the chondrichthyan global diversity, encompassing more than 80 species (Ebert & Dando, 2021; Serena et al., 2020). Of these, 73 have undergone assessment by the IUCN, with more than half (53%) of these species facing the risk of extinction (Dulvy, Allen, et al., 2016). Many of these species exhibit a worsening regional status compared to their global status (Otero et al., 2019), making the Mediterranean Sea a hotspot for extinction risk (Dulvy et al., 2014). Specifically, in the exploited Adriatic Sea, located in the heart of the Mediterranean, chondrichthyans face the highest level of threat within the region. Recent assessments indicate that 70% of Adriatic species are regionally threatened according to the IUCN Red List criteria (Soldo & Lipej, 2022).

1.2 The Adriatic Sea

1.2.1 Bathymetry and hydrography

The Adriatic Sea, located in the Central Mediterranean Sea between the Italian peninsula and the Balkans, constitute the largest continental shelf of the Mediterranean Sea and is primarily a shallow and eutrophic basin. The Adriatic Sea displays distinct bathymetric variations along both its longitudinal and latitudinal axes.

The northern part of the Adriatic Sea is extremely shallow, with an average depth of around 30 m, reaching a maximum of 70 m and with a relatively gentle bathymetric gradient following the latitudinal axis (Figure 1). This region receives a significant influx of freshwater from the Po river and other northern Italian rivers, contributing to approximately 20% of the total Mediterranean river inflow (Hopkins, 1992). This influx of freshwater also brings substantial nutrient loads, making the Northern Adriatic Sea one of the most productive areas in the Mediterranean (Campanelli et al., 2011; Colloca et al., 2017). Consequently, it is among the busiest fishing grounds in Europe (Eigaard et al., 2017).

Moving towards the Central Adriatic Sea, depths increase to about 200 m except for two depressions, known as the Jabuka/Pomo Pits, which reach a maximum depth of around 270 m (Figure 1).

The Southern Adriatic Sea exhibits marked differences between its northern and southern parts. In the northern part, a wide continental shelf stretches approximately 45 nautical miles from the coast to the 200 m isobath, featuring a gradual slope. Conversely, in the southern part, depth increases more rapidly. These marked morphological differences between the two areas have direct implications for the local ecosystems, fisheries resources, and fishing techniques employed in the region (Anonymous, 2011).

The western coast of the Adriatic Sea is characterized by a generally uniform, sandy shoreline with a gentle slope. In contrast, the eastern coast displays irregularities, numerous islands, and steeply sloping rocky bathymetry.

The Adriatic Sea experiences a cyclonic water circulation pattern, with water masses flowing into the basin from the Eastern Mediterranean in a north-westward direction along the eastern coast and exiting through a south-eastward flow along the west coast. This circulation, as well as the composition of water masses in the Adriatic Sea, is significantly influenced by river runoff and atmospheric conditions, which, in turn, impact the water's salinity and temperature (Artegiani et al., 1997).

For fisheries management purposes, the Adriatic basin is divided into two distinct areas known as Geographical Sub-Areas (GSA). GSA 17, encompassing the Northern and Central Adriatic, is bordered by Italy, Slovenia, Croatia, and

Bosnia-Herzegovina. GSA 18, covering the Southern Adriatic, is bordered by Italy, Albania, and Montenegro (Figure 1).

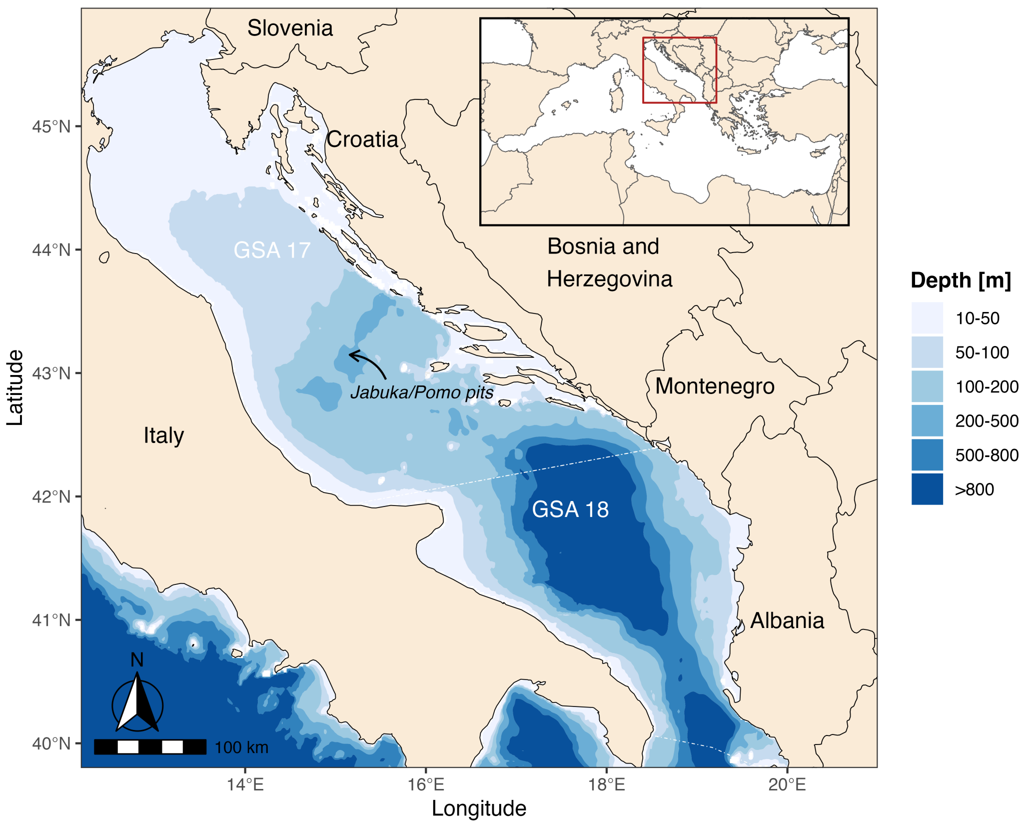

Figure 1: Map of the Adriatic Sea. Geographical Sub-Areas (GSAs) are delimited by a white dotted line.

1.2.2 Fish and fisheries

Small pelagic fish species are widely distributed in the Adriatic Sea, playing a critical role for the commercial fisheries of the countries bordering its coast. The primary species of small pelagics include sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) with additional catches of Atlantic mackerel (*Scomber* *scombrus*), chub mackerel (*Scomber japonicus*), and sprat (*Sprattus sprattus*). Fishing methods for these species include mid-water pair trawls and purse seines (Lucchetti et al., 2023).

The demersal fisheries in the Adriatic, much like Mediterranean fisheries in general, are characterized by the exploitation of a high number of species, rendering them markedly multi-specific. The primary targets of demersal fisheries in the Adriatic include European hake (*Merluccius merluccius*), red mullet (*Mullus barbatus*), breams (*Pagellus* spp.), whiting (*Merlangius merlangus*), anglerfish (*Lophius* spp.), flatfish (such as *Solea vulgaris*, *Psetta maxima*, *Scophthalmus rhombus*), mollusks like *Eledone* spp., common cuttlefish (*Sepia officinalis*), squids (*Loligo vulgaris* and *Illex coindetii*), and crustaceans such as Norway lobster (*Nephrops norvegicus*) and deepwater rose shrimp (*Parapenaeus longirostris*).

In this basin, demersal fishing spans the entire continental shelf and a portion of the continental slope in the Southern Adriatic. Trawlers predominantly engage in fishing activities using classical bottom trawls while beam trawl, the “rapido”, is used to catch flatfishes and Norway lobsters, clams and other mollusks (Lucchetti et al., 2023). The use of fixed gear is typically confined to areas unsuitable for trawling.

The Adriatic Sea hosts a fleet of over 10,000 fishing vessels (FAO, 2022). Approximately 80% of this fleet consists of small-scale vessels, followed by demersal trawlers and beam trawlers at around 13%, purse seiners and pelagic trawlers at about 3%, and other less significant segments making up approximately 6% of the total fleet. The demersal fisheries, particularly relevant for this thesis on demersal chondrichthyans, encompass a fleet of over 1,900 vessels, with a total gross tonnage of around 64,900 tonnes. Italy accounts for about 70% of the vessels authorized for these fisheries in the Adriatic Sea.

From 2018 to 2020, the total landings averaged 163,400 tonnes per year. During this period, purse seiners and pelagic trawlers accounted for approximately 60%, demersal trawlers and beam trawlers contributed around 20%, and small-scale vessels made up roughly 7%. Over the past 15 years, there has been an overall increase in validated stock assessments for commercial species in various Mediterranean subbasins, including the Adriatic. However, a persistent concern emerges due to consistently high levels of fishing mortality observed in these assessed stocks (FAO, 2022). In 2020, an alarming 73% of the assessed commercial stocks were deemed overexploited, although this marked a 10% reduction compared to the situation in 2012 (FAO, 2023).

Within the Adriatic Sea, only three out of the twelve assessed commercial demersal stocks are being sustainably exploited. However, four of these twelve species exhibit high relative biomass levels, indicating potential for stock recovery and sustainable management (FAO, 2023).

Nevertheless, the intensive fishing in this highly productive area implies a significant bycatch of chondrichthyans (Cavanagh & Gibson, 2007; FAO, 2022), with current catch rates posing a threat to the long-term survival and conservation of certain species, thereby jeopardizing their overall conservation status (FAO, 2022).

1.2.3 Chondrichthyan community

The chondrichthyan community in the Adriatic Sea comprises approximately 60 species (Soldo & Lipej, 2022). This community has endured multiple population depletions linked to fishing exploitation, dating back to at least the early 19th century (Fortibuoni et al., 2010; Lotze et al., 2011), likely starting with the decline of large predatory sharks (Ferretti et al., 2008; Fortibuoni et al., 2010). Throughout the 20th century, numerous pelagic and demersal sharks, once widespread, experienced declines or even disappeared entirely in this basin (Barausse et al., 2014; Dulvy et al., 2003; Ferretti et al., 2013; Jukic-Peladic et al., 2001). Currently, 39 species are regionally threatened, and three are considered Regionally Extinct according to the IUCN Red List criteria (Soldo & Lipej, 2022). For a detailed list of the chondrichthyan species analyzed in this thesis and their conservation status, refer to Table 1.

Table 1: Chondrichthyans analyzed in this thesis, along with their current conservation status according to the International Union for the Conservation of Nature (IUCN). All assessments refer to the Mediterranean subregion, except for the small-spotted catshark, which is assessed at the European level. The reference for each IUCN latest assessment is provided in the rightmost column.

Common name	**Scientific name**	**IUCN Status**	**Reference**
Small-spotted catshark	*Scyliorhinus canicula*	Least Concern	Serena et al. (2015)
Blackmouth catshark	*Galeus melastomus*	Least Concern	Abella et al. (2016)
Spurdog	*Squalus acanthias*	Endangered	Ellis, Soldo et al. (2016)
Velvet belly lanternshark	*Etmopterus spinax*	Least Concern	Guallart et al. (2016)
Thornback skate	*Raja clavata*	Near Threatened	Ellis, Dulvy et al. (2016)
Rabbitfish	*Chimaera monstrosa*	Near Threatened	Dagit & Hareide (2016)
Starry skate	*Raja asterias*	Near Threatened	Serena, Abella et al. (2016)
Common eagle ray	*Myliobatis aquila*	Vulnerable	Serena, Holtzhausen et al. (2016)
Brown skate	*Raja miraletus*	Least Concern	Dulvy et al. (2020)
Smooth-hound	*Mustelus* spp.	Vulnerable	Farrell & Dulvy (2016); Dulvy, Farrell et al. (2016)
Marbled torpedo	*Torpedo marmorata*	Least Concern	Notarbartolo di Sciara et al. (2016)
Nursehound	*Scyliorhinus stellaris*	Near Threatened	Ellis, Serena, et al. (2016)

Official statistics from the Food and Agriculture Organization (FAO) show that landings of chondrichthyans in the Adriatic Sea peaked in the 1980s but declined sharply in the late 1990s and early 2000s. While there was a resurgence in the mid-2000s, landings have generally remained low since then (Figure 2). However, FAO data underestimate catches due to its focus on official landings, excluding instances of bycatch discarded back into the sea and providing only limited taxonomic detail (Cashion et al., 2019).

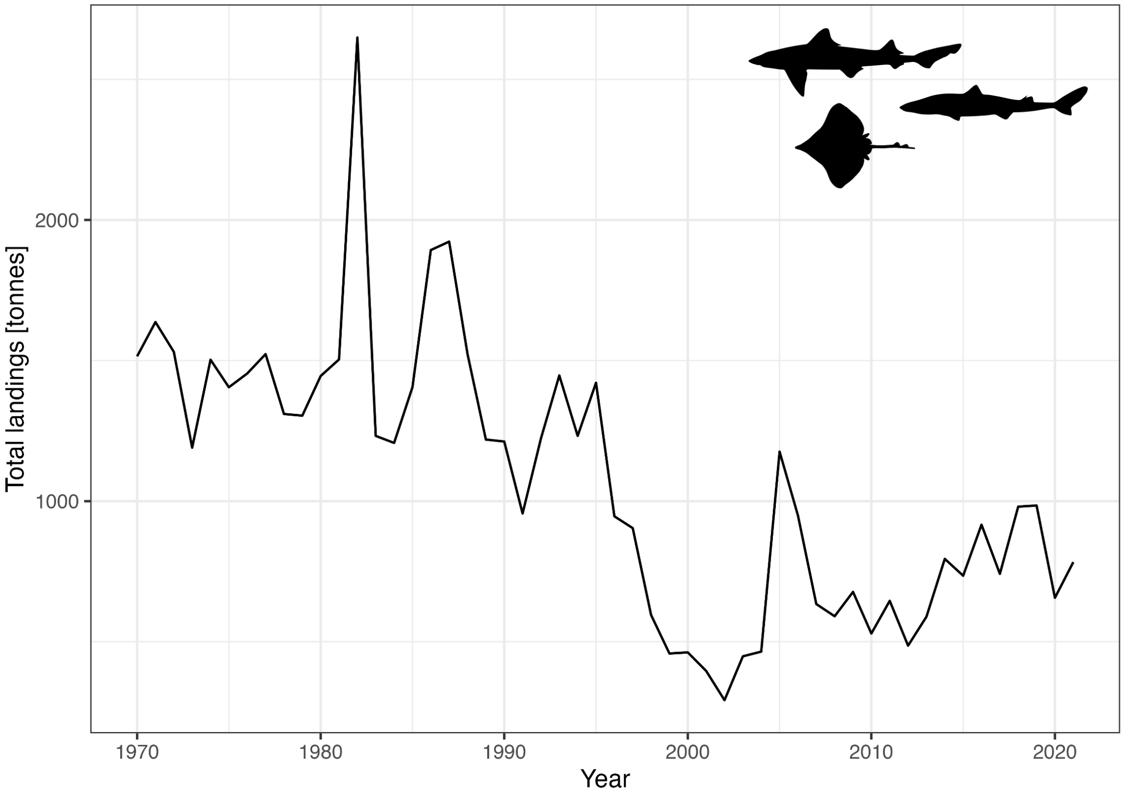

Figure 2: Total landing of chondrichthyans in the Adriatic Sea over time. Source: General Fisheries Commission for the Mediterranean (GFCM) capture production (https://www.fao.org/fishery/statistics-query/en/gfcm_capture/gfcm_capture_quantity). Species silhouettes sourced from PhyloPic (https://www.phylopic.org/).

Historically, fisheries targeting chondrichthyans have played a significant role in this basin (Fortibuoni et al., 2016). However, more recently, while a few species are still intentionally targeted for food consumption, the majority of shark and ray catches result from incidental catches in fisheries that primarily focus on more economically valuable teleost species (Bradai et al., 2012; Carpentieri, 2021; Ferretti & Myers, 2006). Demersal chondrichthyans are primarily affected by interactions with bottom trawlers, gillnets and longlines (Carpentieri, 2021; Farrugio et al., 2015). Additionally, pelagic and midwater trawlers are implicated in the Northern Adriatic Sea (Bonanomi et al., 2018). Fisheries have historically developed at different rates in the eastern and western parts of the basin. High-capacity fishing fleets in Italian waters have exerted significant pressure on chondrichthyan populations, while fishing exploitation in former Yugoslavian waters was lighter and only expanded from the 1990s onwards (Ferretti et al., 2013; Fortibuoni, 2010). This pattern likely contributes to the west-to-east increasing gradient in the abundance and richness of chondrichthyans (Ferretti et al., 2013).

1.2.4 Conservation and management of chondrichthyans

To date, the Adriatic Sea hosts three designated Fisheries Restricted Areas (FRAs) established by the General Fisheries Commission for the Mediterranean (GFCM; https://www.fao.org/gfcm/en/). A FRA constitutes a ‘geographically defined area in which all or certain fishing activities are temporarily or permanently banned or restricted to improve the exploitation and conservation of harvested living aquatic resources or the protection of marine ecosystems'. The three FRAs are:

1. The large deep-water FRA, which borders the Southern Adriatic Sea, established in 2005, which prohibits towed dredges and trawl nets below 1,000 m depth (GFCM, 2005). This measure aims to safeguard deep-sea fish habitats and fish stocks, including chondrichthyans.
2. The Jabuka/Pomo Pit FRA in the Central Adriatic Sea, positioned between Italy and Croatia, introduced by the GFCM in 2017. Within this FRA, specific fishing activities, including bottom-set nets, bottom trawls, set longlines or traps, as well as recreational fisheries, are strictly prohibited in a core area. Additionally, these activities are strictly regulated in the surrounding adjacent areas (GFCM, 2017).
3. The most recent (2021) Bari Canyon FRA was established in the southern Adriatic Sea (GSA 18) off the coast of Bari, Italy (GFCM, 2021a). This FRA was designed to protect vulnerable marine ecosystems within the canyon. Among other functions, the canyon serves as a crucial nursery for some deep-sea chondrichthyan species.

Moreover, to address issues related to the multispecies demersal fishery in the Adriatic Sea, a multiannual management plan was adopted in 2019 (GFCM, 2019). This plan is designed to promote sustainable fishing of key demersal species, including European hake, Norway lobster, common sole, deep-water rose shrimp, and red mullet but is expected to yield beneficial effects also on demersal chondrichthyans. The objective of this management plan is to curtail fishing effort by implementing yearly fishing effort quotas, fostering a progressive and linear annual reduction in fishing mortality (F) toward the target of maximum sustainable yield (FMSY) by 2026. For instance, in 2022, specific reductions in fishing effort were set, with a 7 % decrease in fishing days for bottom otter trawls and a 3 % decrease for beam trawls.

Additionally, recent direct mitigation measures have been implemented to enhance the conservation of chondrichthyans in the Mediterranean Sea, including the Adriatic, specifically addressing species listed in Annex III of the Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean (SPA/BD Protocol; https://www.rac-spa.org/sites/default/files/protocole_aspdb/protocol_eng.pdf). These species include smooth-hound sharks and spurdog, both of which are threatened species analyzed in this thesis. To mitigate bycatch, vessels incidentally capturing these species are subject to restrictions. These limitations aim to ensure that the bycatch is within a specified maximum percentage of the total catch in weight or, alternatively, to no more than three specimens per fishing trip and per vessel (GFCM, 2021b).

1.3 Conservation challenges and research gaps

To effectively manage marine resources, it is imperative to understand how species and communities respond to both environmental changes and human activities (Doney et al., 2012; Halpern et al., 2015; Johnston et al., 2022; Queiroz et al., 2019; Smale et al., 2019). The current emphasis on Ecosystem Based Management (EBM) underscores the importance of decision-making that considers the interplay between biological, environmental, and human elements within an ecosystem (FAO, 2003). Within this framework, the utilization of marine spatial planning (MSP) has become instrumental (Douvere, 2008). MSP serves as a valuable tool for realizing EBM objectives by striving to strike a balance between conflicting human demands and conservation goals. This planning approach is designed to achieve ecological, economic, and social objectives while explicitly incorporating the spatial and temporal dimensions. To transition from conventional, single-species-focused management to the multi-species and spatially detailed approach essential for EBM and MSP, comprehensive monitoring and analysis of all components of the community are imperative.

In the context of the Adriatic Sea, a robust body of knowledge exists regarding the spatial and temporal variation of commercially relevant demersal resources (FAO, 2022). However, this understanding is notably lacking for less commercially important fish resources, such as chondrichthyans, for which analytical assessments are also absent (FAO, 2022). This knowledge gap encompasses both the lack of information regarding species- and community-level spatial and temporal patterns. Integral to the processes within EBM and MSP is the identification of existing and potential threats to species, along with the formulation of conservation and enhancement measures required to eliminate or minimize these threats. The primary threat to the long-term survival of chondrichthyans is fishing (Dulvy et al., 2021). In the Mediterranean Sea, including the Adriatic Sea, effective chondrichthyan management is hindered by limited knowledge about fisheries and their interactions chondrichthyans (Carpentieri, 2021).

Closing these knowledge gaps is fundamental for informed decision-making and effective management of this vulnerable marine species (Bradai et al., 2012; Farrugio et al., 2015).

1.4 Aims of the thesis

The primary objectives of this PhD thesis are twofold. Firstly, it aims to provide a comprehensive understanding of the spatiotemporal changes demersal chondrichthyans have undergone in the Adriatic Sea during the past three decades in relation to environmental drivers, while also analyzing the relationship between traits and the environment and phylogenetic constraints of species responses to the environment. Secondly, it seeks to explore the recent overlap between demersal chondrichthyans and bottom trawl fisheries in the Adriatic Sea to expose the bycatch risk of these species over their distribution range. Employing state-of-the-art modeling techniques and leveraging long-term monitoring efforts, this thesis seeks to bridge existing knowledge gaps and shed light on the structure, dynamics and fishing threats to this important and vulnerable community.

In **Paper I**, I investigate the spatiotemporal changes in the community structure and dynamics of chondrichthyans. I analyze critical environmental drivers, such as depth, temperature, and seabed substrate, to better comprehend the underlying environmental drivers shaping chondrichthyan distribution and abundance patterns. To gain a comprehensive understanding of community-level responses, I incorporate species' traits such as reproductive strategies, age at first maturity, and trophic level to model species' responses to environmental covariates. The inclusion of these fundamental characteristics enhances our understanding of the ecological roles and functional diversity of chondrichthyans in the Adriatic Sea, offering insights that extend beyond the species level (Cadotte et al., 2015; Mcgill et al., 2006).

In **Paper II**, I estimate the overlap between chondrichthyans and the two dominant bottom trawling gear types (otter bottom trawl and beam trawl) in the heavily exploited western Adriatic Sea. By analyzing the overlap between model-based chondrichthyan distribution, species richness, and the presence of threatened species (i.e., assessed as Vulnerable, Endangered, or Critically Endangered by the IUCN Red List) with bottom trawl fishing activities, I aim to identify areas at high risk of chondrichthyan bycatch.

This PhD thesis, as a whole, contributes to our understanding of chondrichthyan communities, their distribution, assembly processes, and fishing threats. It also offers valuable insights for policymakers, conservation organizations, and fisheries management agencies, promoting sustainable conservation and management of these iconic marine species in the Adriatic Sea and beyond.

2 Methods

2.1 Theoretical framework

2.1.1 From species to communities

Understanding the factors that influence species abundance and distribution is a central focus of ecology (Smith, 1966). Effective ecosystem management hinges upon a profound understanding of these factors. While the monitoring and analysis of individual species provide valuable insights, a holistic approach focusing on entire communities is often indispensable. Environmental fluctuations or anthropogenic disturbances, for instance, can impact not only single population abundance but also species richness, diversity, and community composition, thus shaping the overall community structure (e.g. Smale et al. (2019)). The community assembly rules framework is one of the leading standing theories in community ecology. According to this theory, community structure, which is determined by the presence and abundance of species in a given location, results from an interplay of stochastic and deterministic processes collectively known as community assembly processes. These assembly processes can be described as 'filters' operating at different scales (Keddy, 1992; Zobel, 1997). Initially, species must reach an environment through phylogeographic processes such as selection, speciation and large-scale migration. Subsequently, they must adapt to abiotic factors (i.e., local environmental conditions) and survive and persist against biotic factors (i.e., species interactions, such as competition and predation). These forces can interact; for instance, environmental filters may modify species interactions and vice versa. Stochastic processes, including colonization, extinction, ecological drift, and environmental stochasticity, introduce additional variation in local communities and may generate divergence among communities occupying similar environments (Chase & Myers, 2011). From a practical standpoint, exploring community assembly provides crucial insights into various ecological mechanisms. For example, anticipating the ecological impact of global warming necessitates an understanding of how entire communities respond to temperature, not only single species, which in terms requires simultaneously accounting for the resulting biotic interactions in addition to associated environmental changes.

2.1.2 Species traits matter

To attain a more mechanistic understanding of the assembly processes shaping communities, it is crucial to account for species-specific trait information (Mcgill et al., 2006). In this context, traits are defined as measurable organism characteristics which play a role in shaping their geographic distribution and abundance (Green et al., 2022).

Traits assume a pivotal role in determining where species live and how they interact with each other (Cadotte et al., 2015). For instance, environmental constraints can filter out species lacking well-adapted traits for specific local conditions and biotic interactions can be shaped by the trait composition of species (Keddy, 1992; Zobel, 1997). Furthermore, traits themselves are influenced by phylogenetic relationships (Webb et al., 2002). This implies that closely related species may exhibit a similar subset of traits, even when inhabiting diverse environments - a phenomenon known as phylogenetic niche conservatism (Harvey & Pagel, 1991; Wiens et al., 2010). By leveraging traits, one can gain profound insights into community dynamics, understanding the drivers behind species co-occurrence, interactions, and responses to environmental changes, leading to a more comprehensive understanding of the complex relationships between species and their environment. Practical applications include analyzing trait composition along environmental gradients, offering a nuanced perspective on community structure and functioning.

2.2 Modelling framework

Within the array of analytical tools available to ecologists for exploring community composition and dynamics, species distribution models (SDM), also known as habitat suitability models or niche models, are widely employed (Guisan et al., 2017). Generally, SDMs are correlative models designed to establish a statistical relationship between species and their habitats.

When dealing with ecological data, one is often faced with information with inherent spatial attributes. That is, data points are associated with geographic positions. This spatial aspect introduces spatial dependences, which is often referred to as Tobler's first law of geography, which posits that "*everything is related to everything else, but near things are more related than distant things*" (Tobler, 1970). In the context of ecological data modeling, addressing and accounting for these spatial dependencies is instrumental for making valid inference (Legendre & Fortin, 1989) and improving predictions (e.g. Shelton et al. (2014); Thorson et al. (2015)).

In my PhD thesis, I employed state-of-the-art SDM approaches based on generalized linear mixed-effects models (GLMM). Although **Paper I** and **Paper II** differ in their model frameworks—specifically, their hierarchical structures—both approaches are fundamentally geostatistical. That is, they account for spatial variation in density by estimating a smoothed surface, acknowledging that population densities at nearby locations are more similar than those at geographically distant sites. Additionally, the GLMM which are at the core of these approaches are spatially explicit, meaning they estimate interpretable parameters that define the extent of spatial variation and the rate of correlation decay with distance.

In **Paper I**, where my focus was on characterizing the chondrichthyan community patterns, I employed joint species distribution models (JSDMs; Warton et al. (2015)). These models offer the advantage of accounting for correlations among species, and more recently, they allow for the incorporation of trait and phylogenetic information (Ovaskainen & Abrego, 2020). One direct advantage of modeling species jointly lies in its ability to 'borrow strength' from one species to another by capturing correlations among taxa. For instance, including more common species that share similar environmental responses with rare species allows the model to leverage this information, improving estimates for rare species (Ovaskainen & Soininen, 2011). Nevertheless, fitting correlated responses of multiple species presents a considerable challenge, both in terms of model complexity and the computational resources required.

However, the hierarchical structure of JSDMs provides a framework for gaining several ecological insights. It facilitates the visualization of species responses to environmental factors (i.e., their realized niches) and trait-environment relationships through the extraction of the slope parameters. Furthermore, it enables the assessment of the relative importance of environmental covariates and traits by partitioning the explained variation among fixed and random effects, while also evaluating the strength of the phylogenetic signal.

Here, I utilized a hurdle approach in the model fitting process, employing two distinct submodels—one for modeling species presence-absence and another for modeling species abundance conditional on presence. To gain deeper insights into community spatiotemporal changes, I used the fitted models to predict expected species abundance on a spatial grid, calculated indices of abundance, and computed community-weighted mean traits. To address spatial dependencies, these models were fitted with spatial random effects via Gaussian processes, effectively addressing the spatial autocorrelation in the data (Tikhonov et al., 2020). Additional details can be found in the methods section of **Paper I**.

In **Paper II**, I employed an alternative formulation of GLMM for modeling the distribution of individual species, which fit predictive-process stochastic partial differential equation (SPDE) based spatial and spatiotemporal SDMs (Anderson et al., 2022). Within this framework, both spatial and spatiotemporal random effects are utilized to capture spatially correlated latent effects that are constant through time or that vary through time, respectively. Individual species distribution models were aggregated to derive community metrics, such as the proportion of threatened species and species richness (Ovaskainen & Abrego, 2020). Notably, the models in **Paper II** exhibited substantially faster fitting times compared to those in **Paper I**. Additionally, they allowed greater flexibility in terms of the choice of distribution families and accommodated extra flexibility with spatiotemporal random effects when modeling interannual differences in species distributions. This was crucial for predicting the bycatch risk of species.

For estimating the fishing effort in **Paper II**, I employed Vessel Monitoring System

(VMS) data. This dataset comprises a sequence of consecutive pings (signals) sent by each vessel at regular intervals. To correctly assess the fishing activity of the primary trawling gear types in the Adriatic Sea —bottom otter trawl (OTB) and beam trawl (TBB)— the fishing set positions were isolated from other vessel states, such as steaming and resting. This isolation was achieved through a combination of speed and depth filters (Russo et al., 2014).

Finally, diverse metrics spanning various organizational levels, from individual species to the entire community, were employed to assess the potential overlap between fisheries and chondrichthyans. Additional details can be found in the methods section of **Paper II**.

2.3 Fish data

Fishery-independent surveys play a critical role in monitoring fish population abundances and in gathering biological parameters of species, serving as a cornerstone in fishery stock assessment and the formulation of scientifically robust advice (Pennington & Strømme, 1998). This is even more important for species that are not the primary focus of commercial fisheries, as fishery-dependent data, such as landings, are frequently afflicted by issues like incomplete time series, insufficient spatial coverage, or misreporting (Cotter et al., 2009). This issue is particularly pronounced in the case of chondrichthyans in the Mediterranean Sea, including the Adriatic Sea (Cashion et al., 2019).

In the Mediterranean Sea, the MEDiterranean International Trawl Survey (MEDITS) program has been pivotal for evaluating the status and distribution of the demersal resources, including chondrichthyans (Spedicato et al., 2020). In the Adriatic Sea, this survey was initiated in 1994 for Italy and subsequently expanded to encompass Albania, Croatia, and Slovenia in 1996, with Montenegro joining in 2008. The MEDITS is the longest-running systematic survey of demersal communities in the entire Adriatic Sea that remains ongoing.

The survey employs a depth-stratified sampling scheme, with random positioning of hauls within each stratum. The number of hauls in each stratum is proportionally determined based on strata area, with standardized haul durations set at 30 minutes for depths less than 200 m and extended to 60 minutes for greater depths. The designated sampling gear for this survey is the GOC-73 experimental bottom trawl, featuring a horizontal opening ranging from 16 to 22 m and a vertical opening of approximately 2.4 m. The trawl's codend is equipped with a 20 mm side diamond stretched mesh. Further details on sampling procedures, data collection and analysis can be found in the MEDITS handbook (Anonymous, 2017).

3 Results and discussion

Chondrichthyans, including sharks and their relatives, represent an evolutionarily distinct and ecologically diverse group of vertebrates. Despite their significance, they are globally threatened due to widespread depletion caused by fishing activities. In this thesis, I delve into the dynamics and vulnerability of demersal chondrichthyans in the exploited Adriatic Sea, addressing key aspects relevant to both basic and conservation ecology. Firstly, I conducted a comprehensive assessment of the spatiotemporal changes in the chondrichthyan community across three decades in the Adriatic, considering environmental drivers, key ecological traits, and phylogeny (**Paper I**). Secondly, I delved into the recent overlap between demersal chondrichthyans and bottom trawl fishing in the western Adriatic Sea, exposing the bycatch risk of these species across their distribution range (**Paper II**).

3.1 Spatial patterns of the chondrichthyan community

The model-based distribution maps presented in **Paper I** reveal a pronounced west-to-east gradient with increasing abundance and richness of chondrichthyans, except for the northernmost part, which exhibits relatively high abundance for certain species (Figure 3). This pattern aligns with existing literature (e.g., Ferretti et al. (2013); Jukic-Peladic et al. (2001)). Previous studies have linked this spatial pattern to historical and recent differences in fishing efforts between Italian and Croatian (formerly Yugoslavian) fleets (Barausse et al., 2014; Ferretti et al., 2013; Fortibuoni, 2010). My findings further indicate that the community is strongly sorted by depth, with minor influence from bottom temperature and seabed substrate. The spatial patterning was also evident when mapping community-weighted mean traits, where trait values are weighted by local species abundances. Notably, higher trophic levels and late-maturing species tended to concentrate along the deeper and less exploited eastern coastal areas (Figure 4). Additionally, a significant proportion of viviparous species was observed in the northernmost part. Despite the lower richness and abundance of species in the western coastal areas (Figure 3), a higher community-weighted trophic level was detected.

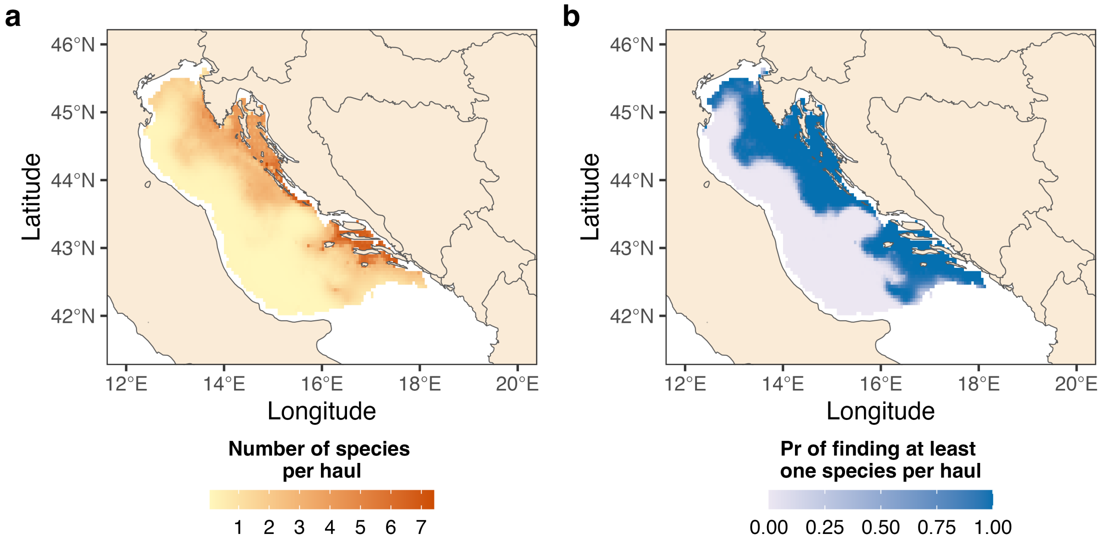

Figure 3: Model-based predicted community features across the study area. Panel (a) shows the posterior mean number of species per haul and panel (b) the posterior probability (Pr) of finding at least one species per haul. Predictions refer to the year 2019.

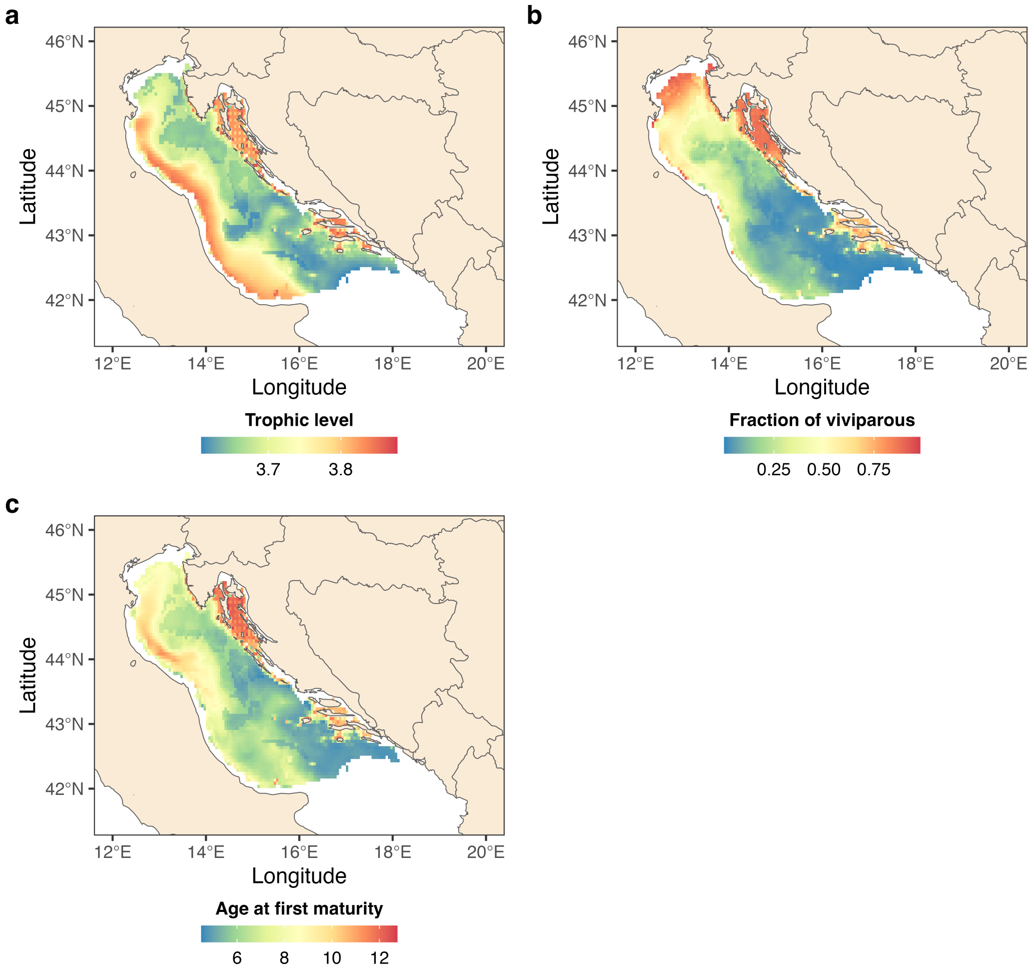

Figure 4: Model-based predicted community-weighted mean traits. Panel (a) shows the posterior mean estimate of the trophic level, panel (b) the posterior mean estimate of the fraction of viviparous species, and panel (c) the posterior mean estimate of the age at first maturity. Predictions refer to the year 2019.

3.2 Influence of traits in shaping the structure of the chondrichthyan community

Despite including only three ecological traits in the species distribution model, they collectively explained around half of the variation in the species' responses to environmental covariates. This may indicate that trait-mediated environmental filtering was at play. Furthermore, I found indications of a phylogenetic signal in the model considering species abundances, i.e., the abundances of species in relation to the observed environment is phylogenetically structured, suggesting there may be additional phylogenetically correlated traits not included in the model, which play a role in species responses.

Examining the relationships between traits and environmental factors, I demonstrate a general association of viviparous species with shallower depths. This association can be attributed to various factors, including the reproductive strategy of viviparous species, which involves giving birth to live offspring that are larger in size. This strategy may be less effective in deeper waters where prey availability is limited to support the growth and development of larger offspring. Additionally, shallower waters provide more favorable conditions for the development and survival of the young, including warmer temperatures and hiding places to protect them from predators (Wourms, 1977). Furthermore, viviparous chondrichthyans, on average, have larger bodies than their oviparous relatives (Goodwin et al., 2002);

this larger size grants them greater active dispersal ability and wider home ranges, enhancing their ability to persist in heavily exploited shallow areas (Goodwin et al., 2005).

3.3 Dynamics of the chondrichthyan community over time

Paper I of the thesis addressed a crucial knowledge gap by examining trends and changes in the demersal chondrichthyan community in the Adriatic Sea over three decades. The findings revealed significant shifts in species abundances, accompanied by modifications in trait composition. The analysis indicated an overall increase in the abundance of dominant chondrichthyan species from the late 1990s onwards, except for the threatened spurdog, which continues to decline (Figure 5). The overall increase in abundance for most species, particularly the more resilient ones, is a trend observed not only in the Adriatic but also mirrored in other European regions (Falsone et al., 2022; Geraci et al., 2021; Ramírez-Amaro et al., 2020; Sguotti et al., 2016). This promising pattern is likely linked to the recent reduction in fishing effort following the EU's fleet decommissioning scheme (Sabatella et al., 2017; Villasante, 2010). Nevertheless, the spurdog, listed as Endangered in the Mediterranean Sea by the IUCN (Ellis, Soldo, et al., 2016), stands out as a species without signs of recovery, calling for better management. Furthermore, when focusing on traits rather than specific species, the study revealed an overall decline in community-weighted age at first maturity and the

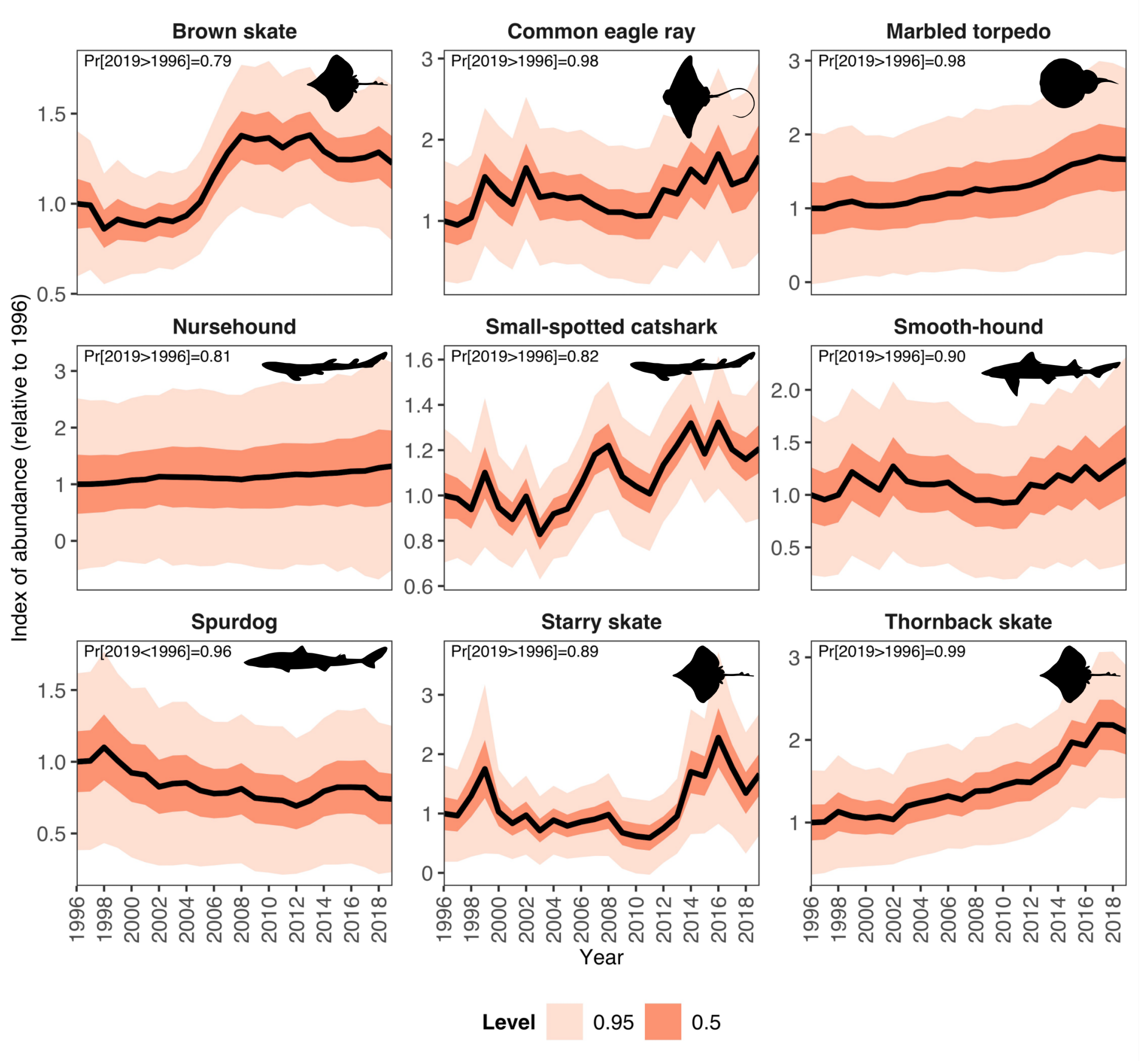

Figure 5: Indices of abundance. Black lines represent the posterior mean estimate while the dark and light red areas represent 50% and 95% credible interval levels, respectively. For each species, the abundance index is scaled to 1996 posterior mean values (i.e., a value of 2 on the *y*-axis indicates 2 times higher abundance than in 1996). In the top-left part of each panel, in case of increasing trend, the probability (Pr) by which the last year (2019) has higher estimated abundance compared to the first year of the survey (1996) is reported; in case of decreasing trend, the probability by which the last year has lower estimated abundance compared to the first year. Species silhouettes sourced from PhyloPic (https://www.phylopic.org/).

proportion of viviparous species, while the decline of community-weighted trophic level was negligible (Figure 6). This underscores the strong link between these life-history traits and species resilience. Notably, the vulnerability of chondrichthyan species is recognized to be associated with life history traits; for instance, species with late maturation and viviparity are often the most susceptible to exploitation (Frisk et al., 2001; García et al., 2008; Stevens et al., 2000; Walker, 1998). The strong increase in oviparous or early-maturing species, such as the thornback skate and the common eagle ray, since the late 1990s, alongside the decline of the late-maturing viviparous spurdog, aligns with these expectations.

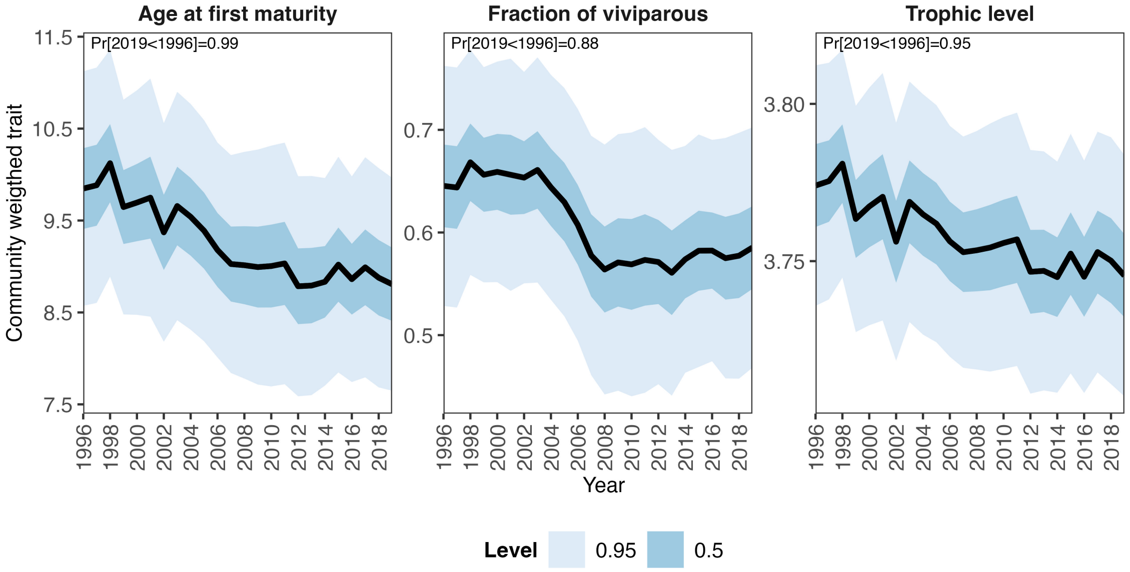

Figure 6: Predicted community-weighted trend of trait categories. Black lines represent the posterior mean estimate, while the dark and light blue areas represent 50% and 95% credible interval levels, respectively. In the top-left part of each panel is reported the probability (Pr) by which the last year (2019) has a lower estimated community-weighted mean trait value compared to the first year (1996). Note the different scale of the y-axes.

3.4 Overlap between chondrichthyans and bottom trawling

By focusing on the western and more exploited part of the Adriatic Sea, the model-based analysis in **Paper II** has revealed specific hotspots of overlap between chondrichthyans and bottom trawling. One primary hotspot is located in the northern central part of the western Adriatic Sea. This area is characterized by a high species density and intense bottom trawling activity, involving both otter bottom trawling (OTB) and beam ('rapido') trawling (TBB). A second hotspot is identified in specific areas of the Southern Adriatic, primarily affected by OTB (Figure 7). However, while the southern part of the study area is predominantly occupied by non-threatened deep-sea species (Figure 8), the northern central part is rich in threatened chondrichthyans (classified as Vulnerable, Endangered, and Critically Endangered by the IUCN). Similarly, the northern central part of the Adriatic is recognized as bycatch hotspot for these species by the pelagic fleet (Bonanomi et al., 2018) and was recently acknowledged as Important Sharks and Rays Areas (ISRA) due to its critical role in harboring threatened species and serving as essential reproductive habitats (IUCN SSC Shark Specialist Group, 2023). Consequently, my study strengthens the urgent need for addressing and prioritizing conservation efforts in this area.

In **Paper II**, my model-based approach not only produces overlap maps but also enables the calculation of range overlaps (see Figure 5 in **Paper II**)—indicating the extent to which fishing activities occupy a species' distributional range. This metric,

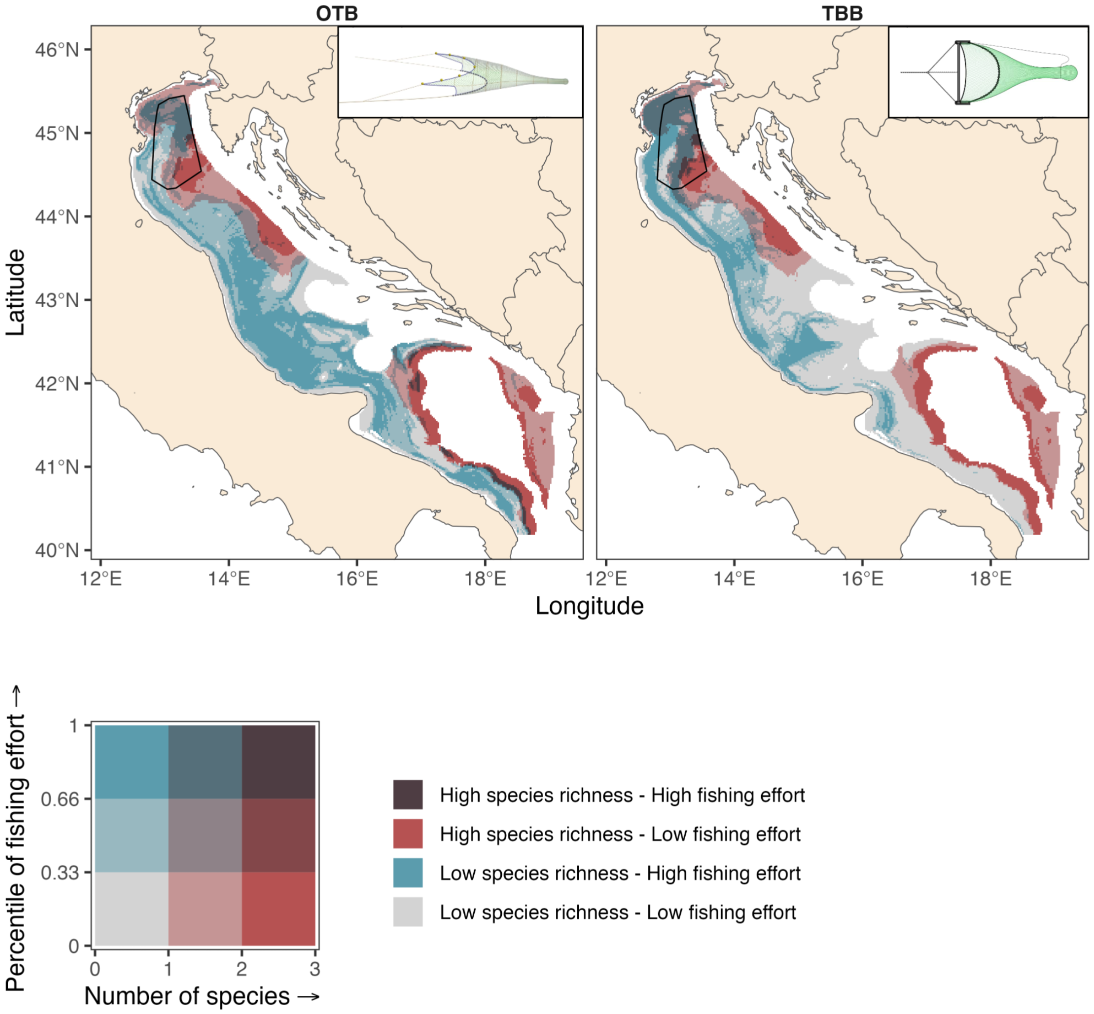

Figure 7: Bivariate plot illustrating the relationship between mean species richness and the percentile of fishing effort for the period 2018-2021 for otter bottom trawling (OTB) and beam trawling (TBB). The region enclosed by the black polygon represents the Northwest Adriatic Important Sharks and Rays Area (ISRA). Dark red areas indicate locations with the highest mean predicted number of species and higest fishing effort. Light red areas correspond to regions characterized by high species richness and low fishing effort. Conversely, dark blue areas represent locations with high fishing effort but a low number of species, whereas gray areas depict regions where both fishing effort and number of species are low. Gear sketches sourced from SeaFish (https://www.seafish.org/).

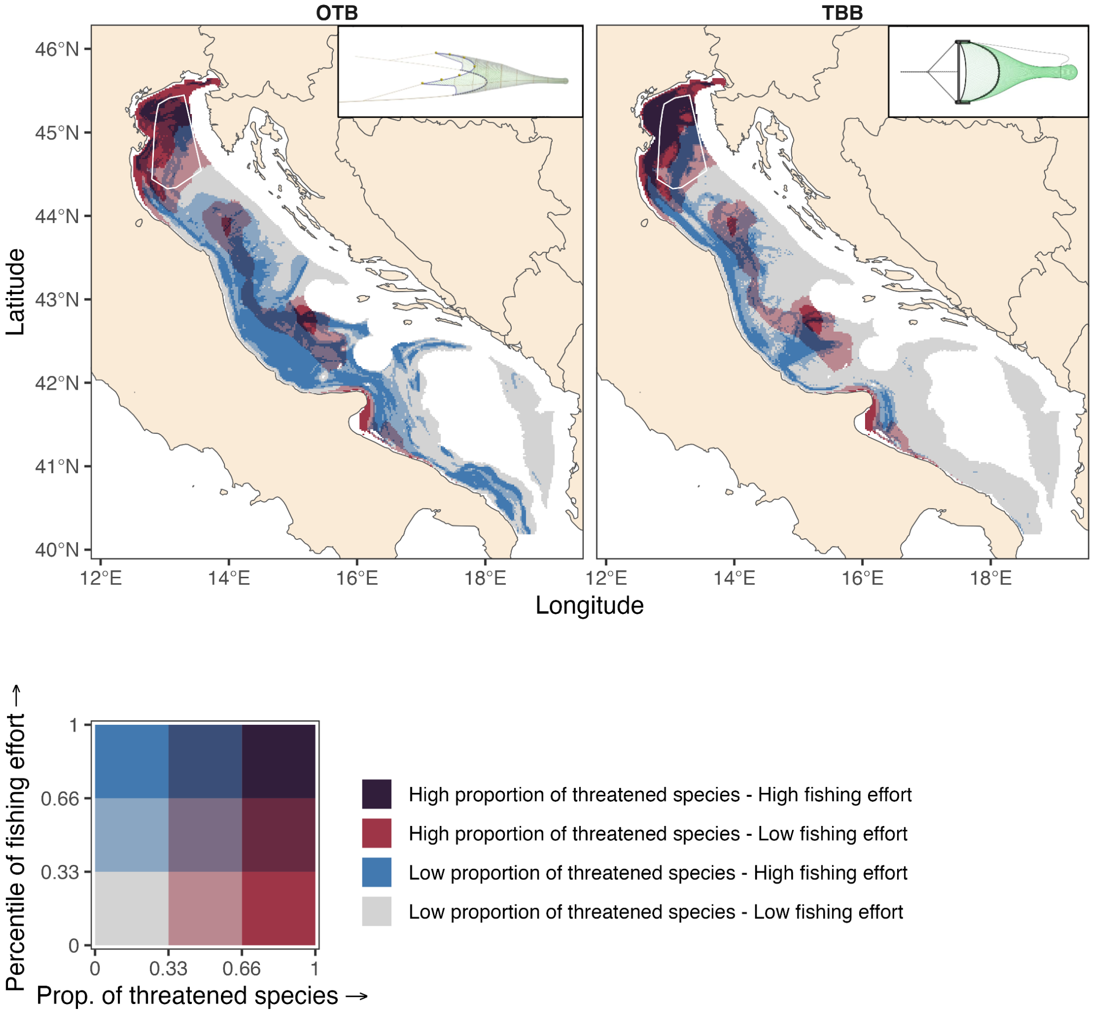

Figure 8: Bivariate plot illustrating the relationship between the mean proportion (prop.) of threatened species and the percentile of fishing effort for the period 2018-2021 for otter bottom trawling (OTB) and beam trawling (TBB). The region enclosed by the white polygon represents the Northwest Adriatic Important Sharks and Rays Area (ISRA). Dark red areas indicate locations with the highest mean predicted proportion of threatened species and fishing effort. Light red areas correspond to regions characterized by a high proportion of threatened species and low fishing effort. Conversely, dark blue areas represent locations with high fishing effort but a low proportion of threatened species, whereas gray areas depict regions where both fishing effort and the proportion of threatened species are low. Gear sketches sourced from SeaFish (https://www.seafish.org/).

when combined with the identification of overlap hotspots and distribution models, provides insights into the potential impacts of relocating spatial fishing efforts. For example, for species with distinct spatial hotspots and low range overlap, relocating fishing effort could significantly reduce mortality from incidental bycatch within that specific area. However, for species with high range overlap, simply limiting fishing in the 'hottest spot' area may have negligible effects if the fishery covers the entire species range and the region with high overlap is large. Understanding where fishing activities might increase after the implementation of a spatially restricted area and how this affects total mortality rates from fishing is a key challenge in designing successful protected areas (Hilborn et al., 2004; Ovando et al., 2021). The implications of **Paper II** extend beyond this case study. By developing a generalizable approach to examine model-based spatial exposure of species to fisheries, along with creating ad hoc indices, I've provided a robust tool that can assist in planning spatial fisheries restrictions. This tool can be particularly valuable for managing species of conservation concern.

4 Conclusions

My thesis and the two included papers make substantial contributions to ongoing initiatives aimed at understanding, safeguarding, and managing chondrichthyan populations in the heavily exploited Adriatic Sea. Additionally, they provide new ecological insights into chondrichthyan community assembly processes and their underlying drivers.

By integrating long-term survey catch data with state-of-the-art spatiotemporal models, this research offers valuable insights for effective conservation and management strategies. It tackles current challenges and establishes a foundation for future studies. The findings deepen our understanding of chondrichthyans' status, dynamics, and vulnerability to fisheries in the Adriatic Sea, providing robust scientific evidence to inform ecosystem-based fishery management and marine spatial planning.

For instance, the maps generated in **Paper I** illustrate the distribution of key species of the demersal chondrichthyan community of the Adriatic Sea and identify density hotspots. Additionally, the mapping of community metrics, which includes species richness and community-weighted mean traits, serves as a valuable tool for prioritizing conservation areas. Specifically, a higher fraction of viviparous species, an elevated community-weighted trophic level, and age at first maturity can be associated with lower species resilience, emphasizing the significance of considering a broader spectrum of ecological indicators in conservation planning.

Moreover, in **Paper II** I focused on identifying areas of overlap between threatened chondrichthyans and bottom trawling, emphasizing the pressing need for conservation interventions in the Northwest Adriatic (Bonanomi et al., 2018; IUCN SSC Shark Specialist Group, 2023). By analyzing metrics at different community organizational levels, this research also facilitates mapping potential trade-offs when exploring various area-closure strategies.

The modeling frameworks employed throughout this thesis contribute novel insights to the existing literature on chondrichthyans. The integration of trait-based approaches, as showcased in **Paper I**, proved to be instrumental in explaining community patterns, showing a promising avenue for future chondrichthyan community analyses. In **Paper II**, I introduce an innovative model-based approach to estimate areas of overlap between chondrichthyans and fisheries. This strategy becomes particularly crucial when dealing with limited catch data, highlighting the versatility and practical utility of the modeling frameworks developed in this research.

4.1 Future perspectives

This thesis has explored essential aspects of shark and their relatives' ecology, including interactions with key Adriatic Sea fisheries. However, further research is needed for a comprehensive understanding of their ecology and to inform effective management policies for sustainable use and conservation.

A specific focus should involve disaggregating survey catch data into juvenile and adult categories, identifying essential fish habitat (EFH), including nursery areas, and understanding their overlap with fisheries.

Another unexplored dimension is predicting the impact of climate change on the future distribution of chondrichthyans in the Adriatic Sea. Understanding this aspect is pivotal for marine spatial planning, as it has the potential to reshape conflicts between chondrichthyans and fisheries in the area.

Moreover, this study primarily focused on analyzing the most prevalent demersal chondrichthyans in the Adriatic Sea. However, it's crucial to acknowledge the existence of numerous less common species. For instance, in the Mediterranean, over one-third of the species are categorized as Data Deficient or Not Evaluated by the IUCN (Serena et al., 2020). Looking ahead, I anticipate that modeling, incorporating diverse data sources such as additional surveys, catch data, and opportunistic records, will play a key role in refining estimates of the distribution of these less common chondrichthyans in both the Adriatic Sea and the broader Mediterranean region.

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Paper I

scientific reports

OPEN

Influence of ecological traits on spatio-temporal dynamics of an elasmobranch community in a heavily exploited basin

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Elasmobranchs, which include sharks and batoids, play critical roles in maintaining the integrity and stability of marine food webs. However, these cartilaginous fish are among the most threatened vertebrate lineages due to their widespread depletion. Consequently, understanding dynamics and predicting changes of elasmobranch communities are major research topics in conservation ecology. Here, we leverage long-term catch data from a standardized bottom trawl survey conducted from 1996 to 2019, to evaluate the spatio-temporal dynamics of the elasmobranch community in the heavily exploited Adriatic Sea, where these fish have historically been depleted. We use joint species distribution modeling to quantify the responses of the species to environmental variation while also including important traits such as species age at first maturity, reproductive mode, trophic level, and phylogenetic information. We present spatio-temporal changes in the species community and associated modification of the trait composition, highlighting strong spatial and depth-mediated patterning. We observed an overall increase in the abundance of the dominant elasmobranch species, except for spurdog, which has shown a continued decline. However, our results showed that the present community displays lower age at first maturity and a smaller fraction of viviparous species compared to the earlier observed community due to changes in species' relative abundance. The selected traits contributed considerably to explaining community patterns, suggesting that the integration of trait-based approaches in elasmobranch community analyses can aid efforts to conserve this important lineage of fish.

Elasmobranchs (hereafter also sharks and rays), which include sharks and batoids, play crucial roles in maintaining the integrity and stability of marine ecosystems, often being at, or near, the top of the food chain[1,2]. Sharks and rays grow relatively slowly, take many years to mature, and produce relatively few offspring compared to teleosts[3]. These characteristics make elasmobranchs inherently vulnerable to fishing[1,3,4]. Over the past 50 years, oceanic shark and ray populations have decreased by more than 70%[5]. Similar declines are also documented for coastal elasmobranchs[6–10]. It has been estimated that over one-third of all species are now threatened with extinction, mainly as a result of overfishing[11]. Habitat loss and degradation, climate change and pollution are also compounding factors of this decrease[11,12]. Despite the critical role that elasmobranchs play in regulating marine ecosystems, our current understanding of their biology and ecology remains incomplete. This is further complicated by the issue of unregulated, misidentified, unrecorded, aggregated, or discarded catches, which makes obtaining accurate, species-specific landing information challenging[13–15]. As a result, understanding the structure (i.e., the types and numbers of species present) and dynamics (how communities change over time and vary in space) of elasmobranch communities remains a major research topic in conservation ecology[12].

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The establishment and persistence of species in a particular location are the results of the combined effects of environmental filters (which correspond to those abiotic factors which prevent the establishment or persistence of species in local communities)[16], biotic interactions[17] and stochastic processes (e.g., dispersal[18]). In turn, the response of species to these factors is mediated by their traits[19] and constrained by phylogenetic relationships[20] such that for instance closely related species might display a similar subset of traits even though they may live in very different habitats. As a result of these processes, we observe variation in the number, abundance, composition, and traits of species present in different communities over time and space. Understanding the ecological processes underlying changes in natural communities has been challenging in part because of the lack of a coherent statistical framework enabling to infer actual assembly processes from community data. A promising framework for modeling community structures and dynamics is joint species distribution modeling[21], which allows to simultaneously explore community-level patterns in how species respond to environmental gradients, estimate interaction across species and, more recently, link such patterns to species traits and phylogenies[22]. There are several advantages modeling multiple species jointly. One significant advantage is the ability to capture correlations in abundance among taxa and to use this information to improve estimates for rare species. This phenomenon is known as "borrowing strength" and occurs when more common species that share similar environmental responses with rare species are included in the model. Furthermore, incorporating species traits into the modeling process provides mechanistic insights into the processes that shape ecological communities and their dynamics[19,23]. Traits can be used to identify the drivers of species co-occurrence, interactions, and responses to environmental changes, leading to a more comprehensive understanding of the complex relationships between species and their environment[22].

Accordingly, here we use such an approach to assess the demersal elasmobranch community of the North-Central Adriatic Sea, a heavily exploited basin[24] where elasmobranchs have been depleted historically[25,26]. Elasmobranchs in this basin face the highest level of threat when compared to the other areas in the Mediterranean Sea. Recent assessments indicate that 70% of Adriatic species are regionally threatened, with 42 out of 59 species at risk[27]. Elasmobranch fisheries have been historically significant in this basin, and while a few species are still intentionally fished for food consumption, the majority of shark and ray catches are incidental captures in fisheries targeting more valuable teleost species[28]. Demersal elasmobranchs are primarily affected by interactions with bottom trawlers and trammel nets, although recent reports have also implicated pelagic and midwater trawlers in the northern Adriatic Sea[29]. Fisheries have developed at different rates in the eastern and western parts of this basin; high-capacity fishing fleets in Italian waters have put significant pressure on elasmobranch populations, while fishing exploitation in former Yugoslavian waters has been much lighter and only later expanded[30].

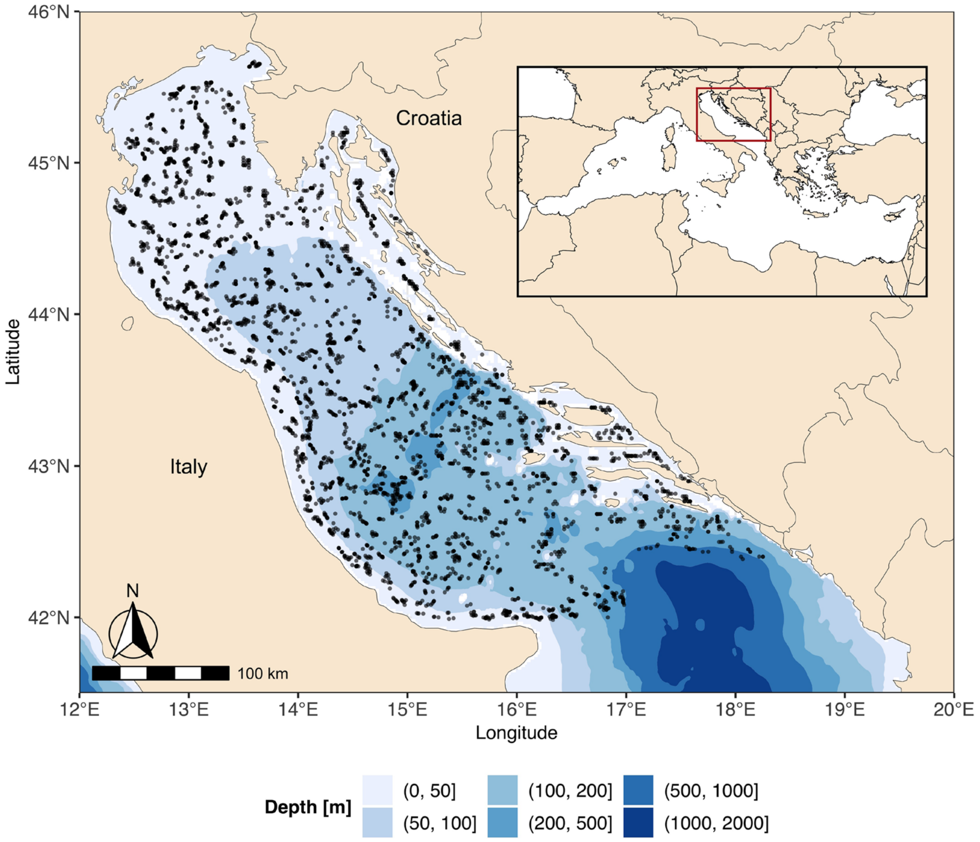

Figure 1. Map showing the location of the study area and the positions of all the analyzed MEDITS bottom trawl hauls for the period 1996–2019.

However in the last 20 years the fishing capacity decreased as effects of the decommissioning scheme adopted by the EU[31]. As a result, the number of trawl vessels has decreased by 36% between 2004 and 2015, with a similar decrease in Gross Tonnage and a reduction in days at sea by more than 50%[32] (for an illustration of the recent trend in fishing effort, see Supplementary Fig. S1). Moreover, fisheries management plans have implemented various measures to protect the fish stocks, such as temporal and spatial fishing restrictions[33].

Whereas several studies documented elasmobranch community depletion in the North-Central Adriatic Sea[7,34–36] no attempts have been made to relate traits to community assembly, specifically examining to what extent spatiotemporal variation in occurrence and abundance patterns can be related to traits (but see Ferretti et al.[7] for species intrinsic rebound potential, which is a measure of species ability to recover from exploitation). In fact, despite their comparative traits, shark and ray species exhibit fine differences in life-history traits[3,37] and trophic level[38,39] which likely influence the outcomes of biotic and abiotic filtering on species occurrence and abundance across space and time. Identifying the importance of these species' ecological characteristics offers the potential to gain community-level insights as well as predict community dynamics. This knowledge can then be leveraged to develop targeted conservation strategies, such as implementing stricter fishing regulations or establishing protected areas and ultimately aid efforts for the conservation of this important lineage of fish.

Here, we assess elasmobranch community changes in the North-Central Adriatic Sea by considering key life-history traits (i.e., age at fist maturity and reproductive mode), trophic level, phylogeny, and environmental factors. Specifically, we aimed at (a) understanding the spatiotemporal changes of the elasmobranch community in relation to environmental factors, (b) quantifying how much of the responses of the species to their environment can be ascribed to traits or explained by phylogenetic correlations. We employed Hierarchical Modeling of Species Communities (HMSC)[40,41], a statistical framework that uses Bayesian inference to fit latent-variable joint species distribution models (JSDM) to data collected by a scientific bottom trawl survey conducted between 1996 and 2019 (Fig. 1). We fitted separate models to analyze the presence-absence of the species and the abundance conditional on species presence (hereafter conditional abundance), and visualized their response to environmental factors (i.e., their niches) and trait-environment relationships by extracting the slope parameters. We determined the relative importance of environmental covariates and traits by partitioning the explained variation among fixed and random effects and assessed the strength of the phylogenetic signal. To gain further insight into community changes, we used the fitted models to predict expected species abundance on a spatial grid, calculated indices of abundance, and computed community-weighted mean traits.

Results

Between 1996 and 2019, more than 4000 bottom trawl hauls were conducted in the North-Central Adriatic Sea, which led to the identification of 29 elasmobranch species. However, further analysis revealed that only 11 of these species were sufficiently represented in the data, and from those, only 9 were ultimately included in the analysis (for more details on the criteria for species selection, refer to the Methods section). These retained species have varying ages at first maturity, ranging from 2.5 to 15 years (mean: 7.1 years, s.d.: 4.4), and a mid-ranking trophic level (mean: 3.78, s.d.: 0.26). Four of the species exhibited viviparity, giving birth to live young, while the other five displayed oviparity, laying eggs as their reproductive mode (Table 1). Considering the entire survey period, the most dominant species were the small-spotted catshark being recorded in one-fourth of all hauls, followed by brown skate, spurdog, thornback skate and smooth-hound, which occurred in roughly 10% of the hauls. The remaining species occurred more sporadically (Table 1).

Species modeling.

The presence-absence (PA) and the conditional abundance (ABU) models showed a satisfactory fit to the data. The mean Tjur's R^2 (AUC) was 0.29 (0.92) considering the PA model, whereas the explanatory power R^2 for the ABU model was on average 0.39 (Supplementary Fig. S2). Both species presence-absence and species conditional abundances were influenced by environmental variables. Variance partitioning

Species	Frequency of occurrence (%)	Total number of individuals	Age at first maturity	Reproductive mode	Trophic level
Small-spotted catshark (*Scyliorhinus canicula*)	25.75	12,628	5.0[75]	Oviparous[75]	3.60[38]
Brown skate (*Raja miraletus*)	13.33	3124	2.5[73]	Oviparous[75]	3.67[76]
Spurdog (*Squalus acanthias*)	11.68	3068	15.0[73]	Viviparous[75]	3.90[38]
Thornback skate (*Raja clavata*)	10.74	1188	7.5[73]	Oviparous[75]	3.69[76]
Smooth-hound (*Mustelus* spp.)	7.75	1970	10.5[73]	Viviparous[75]	3.80[38]
Common eagle ray (*Myliobatis aquila*)	6.07	1065	3.0[73]	Viviparous[75]	3.33[39]
Marbled torpedo (*Torpedo marmorata*)	2.94	150	12.0[73]	Viviparous[75]	4.24[39]
Starry skate (*Raja asterias*)	2.62	169	3.5[73]	Oviparous[75]	3.82[75]
Nursehound (*Scyliorhinus stellaris*)	2.62	255	5.0[75]	Oviparous[75]	4.00[37]

Table 1. Frequency of occurrence (percentage of trawl hauls where the species was caught), total number of individuals caught in all the trawl hauls, as well as traits values and classifications of the elasmobranchs included in the study. Species are sorted in descending order according to their frequency of occurrence.

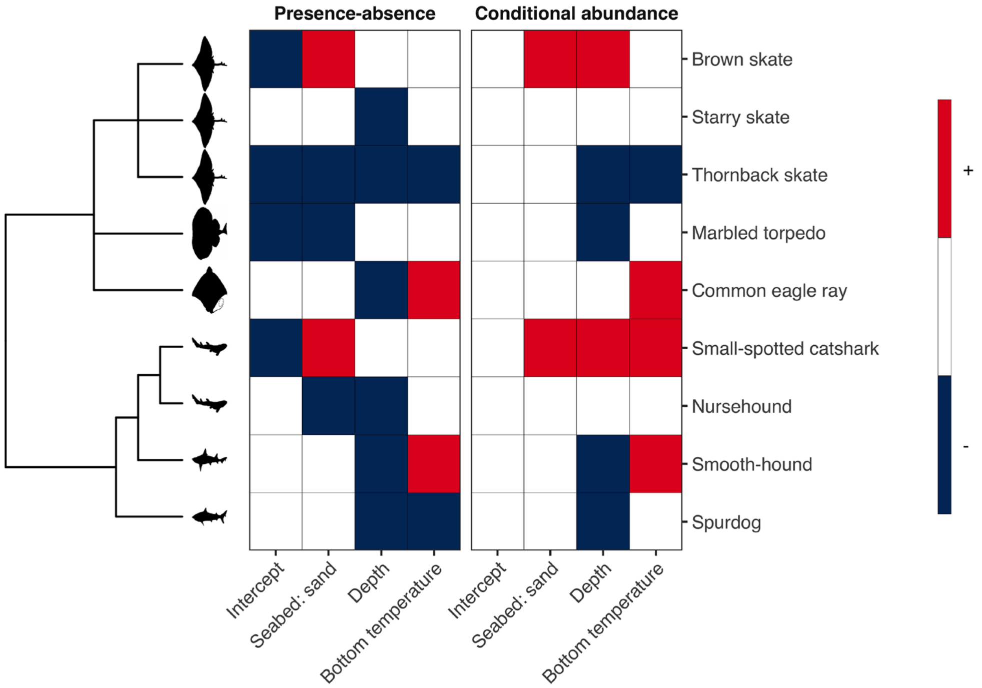

Figure 2. Heatmap of the estimated β parameters linking the responses of species to environmental covariates. Responses that are positive with at least 95% posterior probability are shown in red, responses that are negative with at least 95% posterior probability are shown in blue, while responses that did not gain strong statistical support are shown in white. The intercept represents the average value of the response variable for the reference group of the seabed substrate covariate (i.e., seabed characterized by mud to muddy sand). For the seabed covariate, colors represent contrasts between mud to muddy sand and sand substrates such that red indicates species preferring the sand substrate over the mud to muddy sand, while blue the opposite. Species are ordered according to their phylogeny as illustrated by the phylogenetic tree shown on the left. Icon credits: PhyloPic (phylopic.org).

over the explanatory variables included in the models showed that depth explained a substantial amount of variation (17% averaged over the species) among the fixed effects in the PA model, whereas in the ABU model, depth and bottom temperature explained on average 30% and 14% of all variation, respectively (Supplementary Fig. S3). Haul-level spatial random effects accounted for the largest portion of variance in both the PA and in the ABU models, explaining on average 69% and 32% of the variance, respectively. Temporal random effects, on the other hand, explained on average 9% of the total variation for the PA model and 12% for the ABU model (Supplementary Fig. S3).

We found strong support for species-specific responses to the environmental covariates that in part differed between explaining the presence of a species (PA model) and the abundance of a species (ABU model) (Fig. 2). For instance, seabed type was important for determining if a species was present or not, while bottom temperature had a similar effect on both presence and abundance. Certain elasmobranchs species were more likely to occur in specific seabed types, such as brown skate and small-spotted catshark on sand seabeds and thornback skate, marbled torpedo, and nursehound on mud and muddy sand bottoms. Generally, most species had a lower occurrence probability with increasing depth. Warmer bottom temperature seemed to negatively affect certain species, while positively affecting others (Fig. 2). The species responses to environmental covariates showed a weak phylogenetic signal in the PA model ($E[\rho] = 0.46$; $Pr[\rho > 0] = 0.71$) and a strong signal in the ABU model ($E[\rho] = 0.86$; $Pr[\rho > 0] = 0.97$).

The models' predictions identified a clear spatial pattern in the elasmobranch community of the North-Central Adriatic Sea (Fig. 3). Specifically, species diversity was significantly lower in the western part of the study area, while the central and southern Croatian coasts in the eastern part exhibited higher diversity (Fig. 3a). The level of uncertainty in the models' predictions was higher in the eastern part of the study area but overall relatively low, with a margin of error of less than one species (Fig. 3b). Likewise, species had higher probability of occurrence and were more abundant along the Croatian coasts (Fig. 3c, Supplementary Fig. S4). Notably, the northernmost part of the basin showed a relatively high abundance of common eagle ray and smooth-hound, despite lower overall species diversity in this area (Supplementary Fig. S4, Fig. 3a)

Over the study period, we predicted the relative temporal changes in species abundances (Fig. 4). The abundance index showed a general upward trend for the majority of the species. In particular, the thornback skate recorded the highest abundance increase (110%) comparing 1996 to 2019, followed by common eagle ray (80%), marbled torpedo (66%), and starry skate (66%). Whereas spurdog was the only elasmobranch decreasing (– 26%).

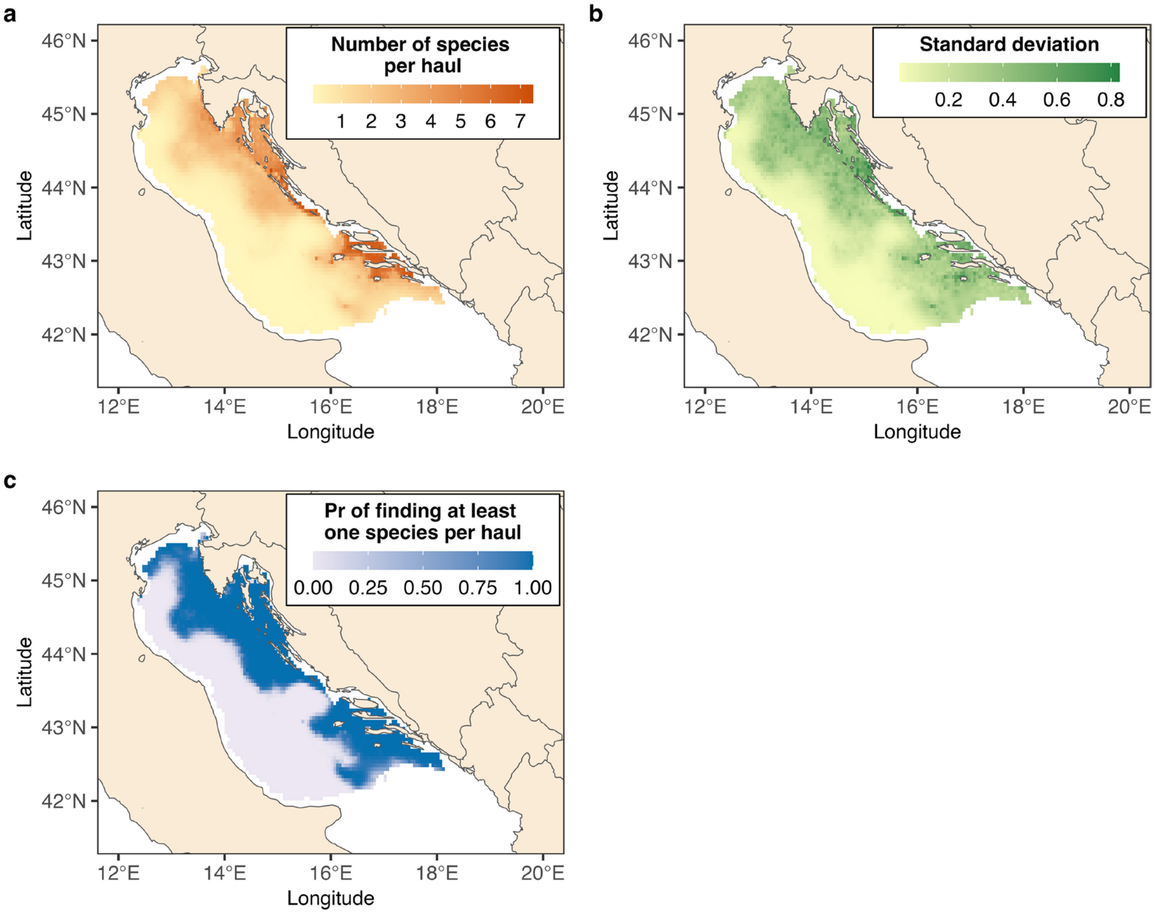

Figure 3. Predicted community features across the study area. Panel (**a**) shows the posterior mean number of species per haul, panel (**b**) the posterior standard deviation of the mean number of species per haul, and panel (**c**) the posterior probability (Pr) of finding at least one species per haul. Predictions refer to the year 2019. In the predictions, the swept area is set to a constant value equal to the mean of the trawl hauls used in the study (i.e., 0.047 km^2).

Traits modeling. The selected ecological traits (i.e., age at fist maturity, reproductive mode, and trophic level) explained 44% of the variation in species occurrence and 40% of the variation in species abundance. Considering species niches (i.e., species responses to environmental covariates), traits explained 52% (PA model) and 66% (ABU model) of the species response to depth, 28% (PA model) and 20% (ABU model) of the species response to the seabed substrate, 19% (PA model) and 30% (ABU model) of the species response to bottom temperature. Considering the PA model, the γ parameters (i.e., the parameters linking species traits to species niches) indicated that viviparity is negatively correlated with depth (with at least 95% posterior support; Supplementary Fig. S5). This relationship became more obvious once clustering the species responses to depth (β_{depth}) by reproductive mode which shows that viviparous are more negatively affected by depth (i.e., lower β_{depth} values) (Fig. 5). Contrastingly, we found no significant relationship between trait and environmental covariates for the ABU model (Supplementary Fig. S5).

To generate community-weighted mean (CWM) trait maps we weighted trait values by species relative abundances. These maps indicate higher CWM trophic level along the Italian and Croatian central and southern coastal areas (Fig. 6). Also, the shallow areas along the northern and eastern coasts encompassed a higher fraction of viviparous species compared to the deeper southern areas that were dominated by oviparous species such as thornback skate, brown skate, and small-spotted catshark (Supplementary Fig. S4). Finally, the predicted CWM age at first maturity was higher along the Croatian coast, whereas lower values were present in the deeper southern areas.

Our modeling results estimated an overall decline in community-weighted mean traits values considering age at first maturity, fraction of viviparous species and trophic level over time. Examining the magnitude of the decline, CWM age at first maturity declined by 11%, the fraction of viviparous species by 9%, while CWM trophic level declined by less than 1%, from 1996 to 2019 (Fig. 7).

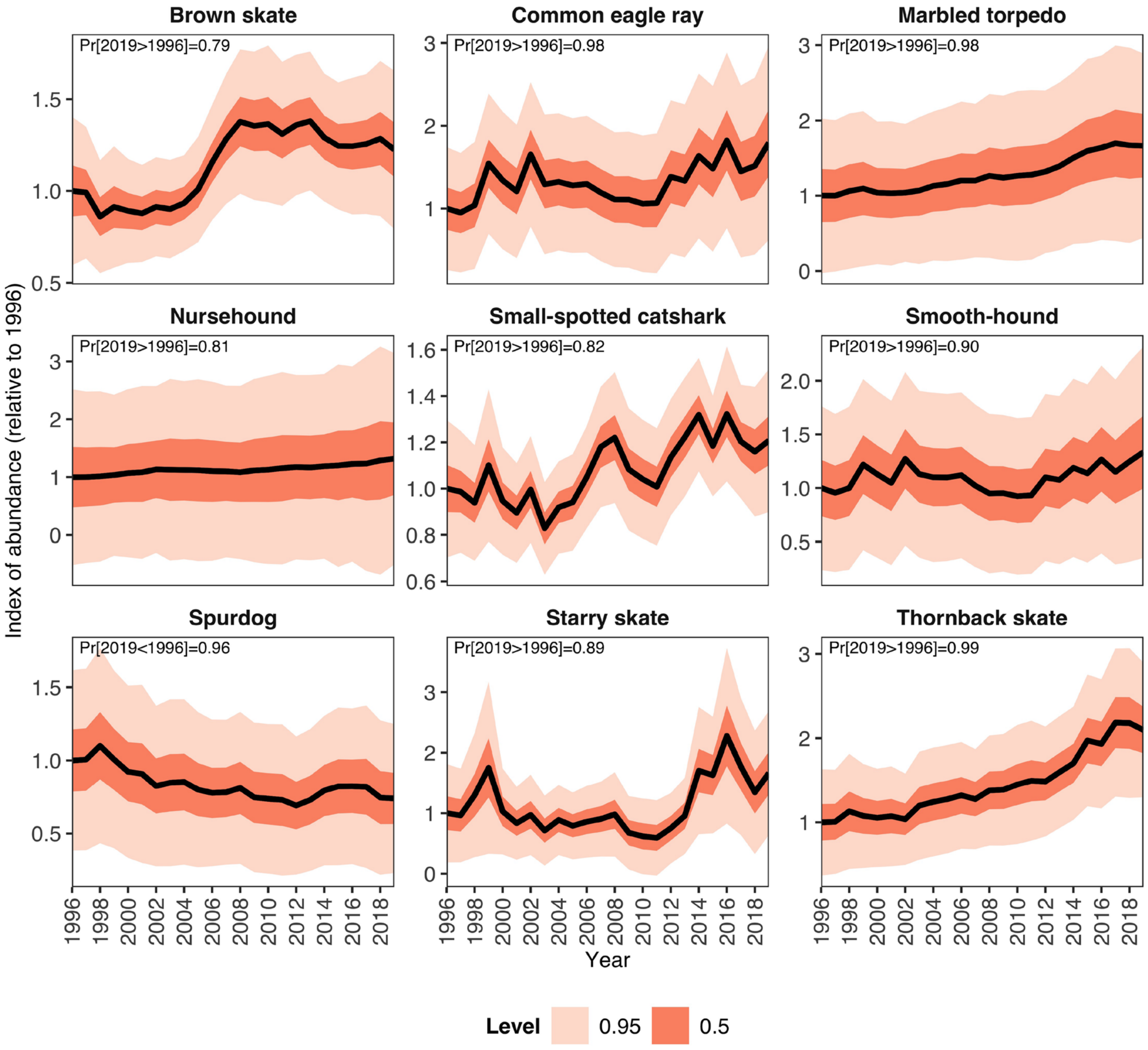

Figure 4. Indices of abundance. Black lines represent the posterior mean estimate while the dark and light red areas represent 50% and 95% credible interval levels, respectively. For each species, the abundance index is scaled to 1996 posterior mean values (i.e., a value of 2 on the *y*-axis indicates 2 times higher abundance than in 1996). In the top-left part of each panel, in case of increasing trend, the probability (Pr) by which the last year (2019) has higher estimated abundance compared to the first year of the survey (1996) is reported; in case of decreasing trend, the probability by which the last year has lower estimated abundance compared to the first year.

Discussion

A growing body of literature reports the decline of elasmobranchs in coastal and oceanic ecosystems worldwide[5,8,42]. However, understanding changes in community composition is challenging due to multiple factors that influence populations, such as environmental conditions, biotic interactions, and stochastic events such as colonization, extinction, ecological drift, and environmental stochasticity. Insights into community dynamics can be gained from the incorporation of traits, phylogeny, and by explicitly acknowledging co-occurence patterns among species. Our study takes a leap forward towards a mechanistic understanding of the spatio-temporal changes of an elasmobranch community over two decades in the North-Central Adriatic Sea. Here, by fitting joint species distribution models we show that the Adriatic elasmobranch community is primarily sorted by space and depth, which is in agreement with studies performed in other areas[43]. We show that the eastern part of the basin has higher abundance and diversity compared to the western part. Secondly, we present species-specific abundance trends which show an increase for all species analysed but spurdog, which declined in abundance. Thirdly, we highlight that the included ecological traits (i.e., trophic level, age at first maturity and reproductive mode) explain about half of the variation in species occurrence and abundance as well as of the response to environmental covariates, suggesting that the use of traits is beneficial in modelling these rare species.

Our results show a higher abundance and diversity of elasmobranchs in the eastern Adriatic Sea, supporting previous findings[7,35]. This spatial pattern has been linked in literature to past and recent differences in the fishing effort between the Italian and Croatian fleets[7] (see Supplementary Fig. S6 for a spatial effort projection), although depth, temperature, seafloor morphology and sea bed type have been suggested as well to be important factors influencing elasmobranch distribution in the Mediterranean Sea (e.g., this study,[7,44]). Previous studies[7,35]

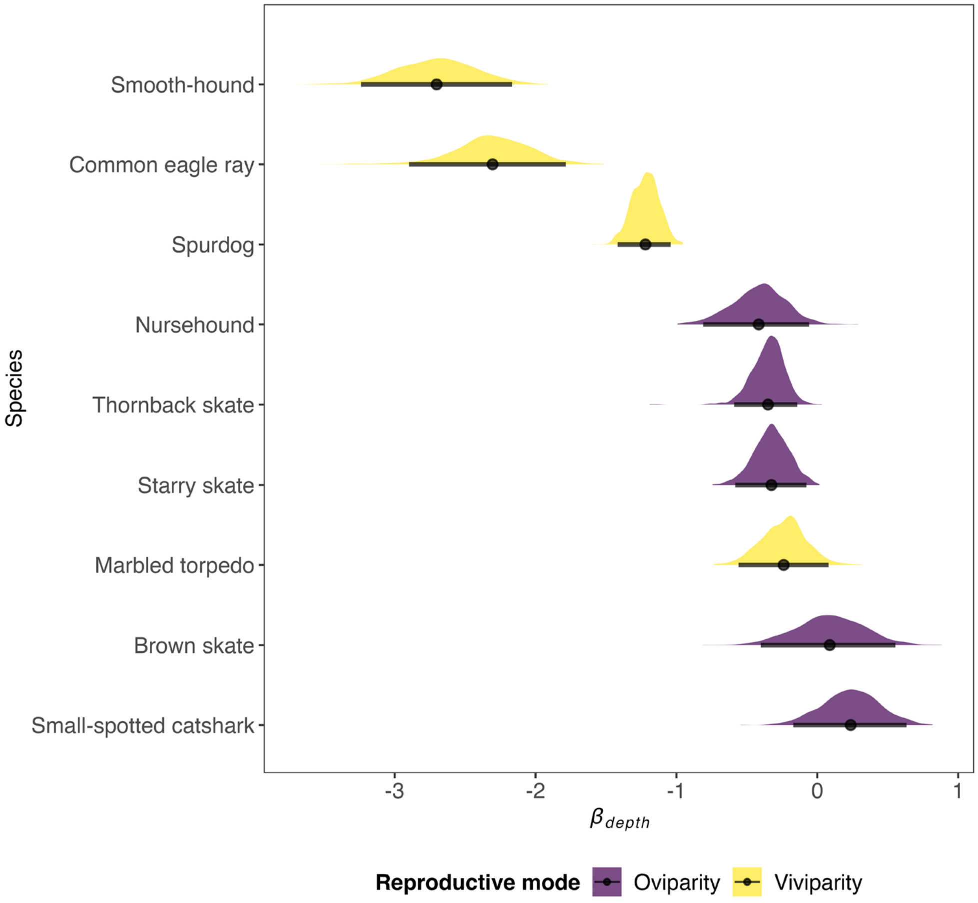

Figure 5. Posterior distribution of the β_{depth} parameters linking species occurrences to log-transformed depth. The point intervals represent the mean values and the 95% credible intervals. Above the point intervals the probability density functions are plotted (oviparous and viviparous species shown in violet and yellow, respectively). Lower values indicate stronger species preferences for shallower waters. Species are ordered according to mean values in ascending order.

covering large parts of the Adriatic Sea depicted a decline of more than 90% in elasmobranch abundance comparing the late 1940s with the early 2000s levels. The most dramatic decline was recorded for the thornback skate and the small-spotted catshark[7]. Yet, few species showed departures from this general trend such as brown skate, common eagle ray, marbled torpedo, and spurdog, which instead increased[7]. With our data covering the period 1996-2019, we extend by 14 years the previous analysis[7] which presented elasmobranch trends estimated from the MEDITS trawl survey for the period 1994-2005. We found a strong rebound of the thornback skate, which doubled in abundance comparing the 1996 with the 2019. This is consistent with recent trends observed by fishers in the Adriatic basin, who have reported an increase in the occurrence of *Raja* spp. over the last decade[27]. These observations are further corroborated by an increase in the abundance of this species complex in commercial landings at Chioggia harbor[45], which is among the primary fishing ports in the Adriatic Sea. In continuation with what was previously detected[7], we estimated an increase in abundance for the common eagle ray (1.8 times) and the marbled torpedo (1.7 times). We found also an increase, although less pronounced, in the abundance of the starry skate, the smooth-hound, the nursehound, the brown skate, and the small-spotted catshark. These species showed either a continuous positive trend from the mid 1990s or an increase in the most recent years. Similarly to our results, recent increase in abundance for thornback skate and small-spotted catshark were also detected in the South of Sicily[46,47], in the Western Mediterranean[48], and in the North Sea[49], suggesting convergent patterns in historically heavily exploited areas that have experienced recent reduction in fishing effort. A negative trend since 1994 was previously detected for spurdog[7] and our results show that its abundance remained steady at a low level in the past two decades. Yet, this species is listed as Endangered in the Mediterranean by the International Union for Conservation of Nature (IUCN)[50] and alarmingly our study reveals that it has not shown signs of recovery in the Adriatic Sea. A decline in abundance for spurdog was also evident in the North Sea[49] from the late 1970s, which may indicate that the current level of fishing effort in the European waters did not allow for the rebound of this species.

Despite including only 3 ecological traits in the presence-absence (PA) model and in the abundance conditional on presence (ABU) model, they explained 44% and 40% of the variation in the species responses to the covariates considered in the analysis, respectively. Although this might be suggestive of the relevance of the traits

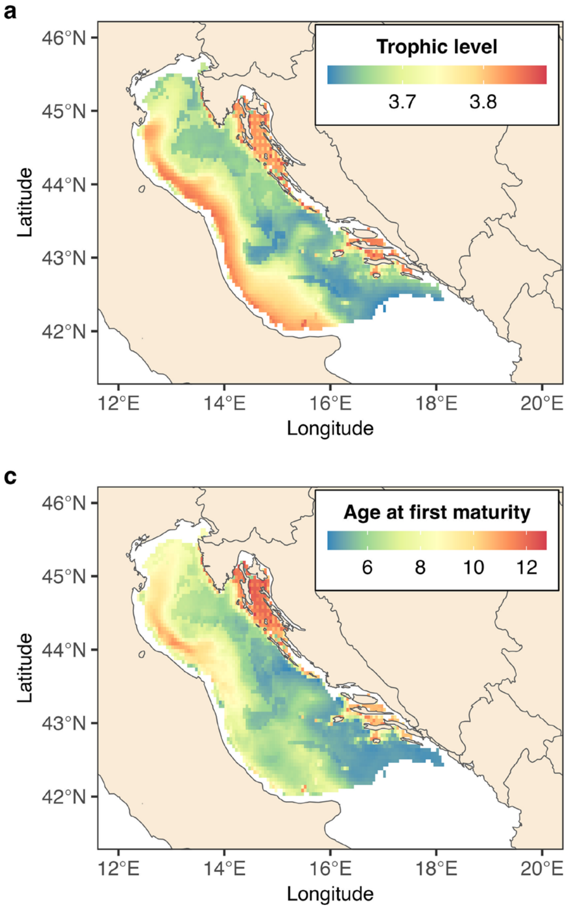

Figure 6. Predicted community-weighted mean traits. Panel (**a**) shows the posterior mean estimate of the trophic level, panel (**b**) the posterior mean estimate of the fraction of viviparous species, and panel (**c**) the posterior mean estimate of the age at first maturity. Predictions refer to the year 2019.

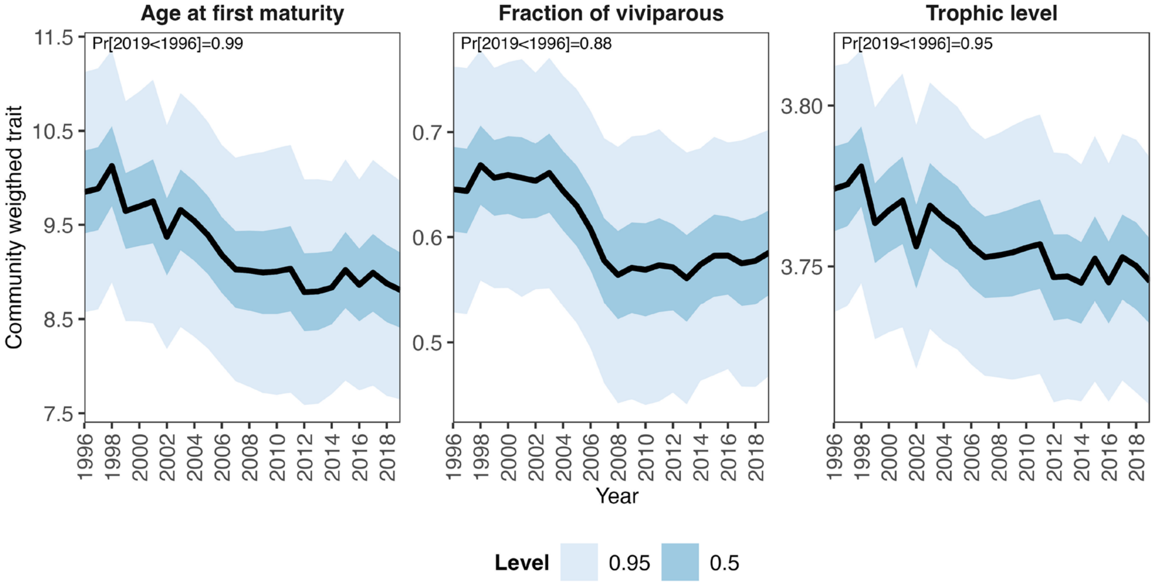

Figure 7. Predicted community-weighted trend of trait categories. Black lines represent the posterior mean estimate, while the dark and light blue areas represent 50% and 95% credible interval levels, respectively. In the top-left part of each panel is reported the probability (Pr) by which the last year (2019) has a lower estimated community-weighted mean trait value compared to the first year (1996). Note the different scale of the *y*-axes.

included to the community assembly processes we also note that life-histories (such as reproductive mode and age at first maturity included in the analysis) are constrained by trade-offs which mainly co-vary along a 'fast-slow continuum'[51]. At the fast extreme, species develop quicker, are more productive but have shorter life spans; whereas at the slow extreme, species have higher survival rates, develop slower and live longer. It follows that, for instance, age at first maturity is linked with other relevant life-history traits such as total length, average adult life expectancy and species growth rate[3]. However, among the trait-environment relationships we examined, the reproductive mode was tightly linked with depth which may indicate that environmental filtering was at play. Our study indicates that viviparous elasmobranch species are typically found in shallower waters compared to oviparous species, likely due to several factors. Firstly, the reproductive strategy of viviparous species involves giving birth to live offspring that are larger in size, which may be less effective in deeper waters where there is limited prey availability to support their growth and development. Additionally, shallower waters provide more favorable conditions for the development and survival of the young, including warmer temperatures and hiding places to protect them from predators[52]. Furthermore, viviparous elasmobranchs are on average larger bodied than oviparous relatives[53], which enable greater active dispersal ability and wider home ranges[54] , enhancing their ability to persist in heavily exploited shallow areas. Based on our findings, we observed that the elasmobranch community in the Adriatic Sea is segregated along a depth gradient, with viviparous species such as spurdog, smooth-hound, and common eagle ray primarily occupying coastal shallow areas, while oviparous species reside also in the deeper areas. Additionally, we identified a strong spatial pattern in the predicted community-weighted mean traits, showing a decreasing gradient of viviparous species from the northern and eastern coastal to offshore areas. Furthermore, we found that higher trophic levels and late-maturing species tend to concentrate along the eastern costal areas, but also in the western coastal areas despite the low diversity and abundance of species in this region. Among the included traits, we found a noticeable decline over time of the community-weighted age at first maturity, the fraction of viviparous species and the trophic level, although the decline of the latter was minor. The degree of vulnerability of shark and rays species is known to be associated with life history traits, such that for instance species exhibiting late maturation and viviparity are often the most vulnerable to exploitation[1,3,4,55]. The strong increase from the late 1990s of oviparous or early-maturing species such as the thornback skate and the common eagle ray, as well as the decline of the late-maturing viviparous spurdog, found in our study are in accordance with this expectation. However, it is important to note that the CWM traits are primarily influenced by the most abundant species, such as the small-spotted catshark, brown skate, thornback skate, and spurdog, rather than rare ones like the marbled torpedo, which is also a late-maturing viviparous species that has experienced a substantial increase. This pattern suggests that the EU's fleet decommissioning scheme, aimed at promoting sustainable European fisheries[31,32], may have benefited more resilient species, while less resilient ones may have struggled to recover. Nonetheless, other factors such as historical removal of large predators of these elasmobranchs[56] or the availability of open ecological niches resulting from the disappearance of other elasmobranch species[7] could also have played a role in driving the observed changes in the community.

The high value of the estimated phylogenetic signals in the ABU model suggests the existence of some traits correlated with phylogeny that were not considered in our analysis, and which may therefore contribute to explain the abundance of species in a certain environment. Therefore, we suggest that further research is needed to identify other traits than those considered here.

In conclusion, our study including ecological traits provided a helpful framework for predicting the structure and dynamics of an elasmobranch community in the Adriatic Sea over the past three decades. Our findings indicate a lower age at first maturity and a decreased fraction of viviparous species in the current community compared to the community observed in the late 1990s. Furthermore, we observed a concerning and persistent decline in the threatened spurdog population, while most other elasmobranch species in the basin experienced an increase. The elasmobranch community in the Adriatic Sea has been subjected to multiple population depletions over time[26], starting with the decline of large predatory sharks in the 19th and 20th centuries[25,56]. During the 20th century, numerous pelagic and demersal sharks, which were once widespread, experienced declines or even disappeared altogether in this basin[7,57]. Therefore, caution is necessary when interpreting recent increases in the abundance of some species as an early indication of recovery, since their recent rebounds are still far from their historical baselines.

Methods

Study area.

The North-Central Adriatic Sea is a semi-enclosed basin corresponding to the FAO - Geographical Sub-Area 17 (GSA 17) located in the Central Mediterranean, between the Italian peninsula and the Balkans (Fig. 1). This basin is a shallow and mainly eutrophic sea with clear morphological differences along both the longitudinal and the latitudinal axes. Most of the basin is characterized by a wide continental shelf where depth gradually increases from north to south. However, the central area is characterized by meso-Adriatic depressions (Pomo/Jabuka Pit), where the depth reaches ~ 270 m. The sea bottom is mostly covered with recent muddy and coastal sandy sediments supplied by rivers and dispersed southward by currents while no present sedimentation affects the offshore seabed in the Northern Adriatic, which is characterized by relict sand[58]. The eastern coast is rocky and presents numerous islands, whereas the western coast is flat, alluvial, and characterized by heavy river runoff. The Po and other northern Italian rivers contribute to approximately 20% of the whole Mediterranean river runoff[59] and introduce large fluxes of nutrients[60], making this basin the most productive area of the Mediterranean Sea[61], and consequently one of the most intensively fished areas in Europe[62]. The general pattern of water circulation is cyclonic with water masses inflow from the Eastern Mediterranean along the eastern side of the Adriatic Sea and outflow along the western side. The Adriatic Sea circulation and water masses are also strongly influenced by river runoff and atmospheric conditions which in turn affect salinity and temperature[63]. Pronounced seasonal fluctuations in environmental conditions, cause high seasonal variations in coastal waters, where bottom temperatures range from 7° in winter to 27°C in summer[64]. Contrarily, the thermal variability of the deeper areas is less pronounced, with values ranging between 10°C in winter and 18°C in summer at a depth of 50 m[64].

Survey data. The whole dataset comprised 4231 bottom trawl hauls performed during the Mediterranean International Trawl Survey (MEDITS)[65], which is jointly performed by the Laboratory of Marine Biology and Fisheries of Fano (Italy) and the Institute of Oceanography and Fisheries of Split (Croatia) on an annual basis since 1996 generally in the late spring-summer period (May to September). Hauls were located from 10 to 500 m of depth, following a random-stratified sampling scheme where strata were defined according to depth. The sampling gear utilized was the GOC-73 experimental bottom trawl, which featured a horizontal opening of 16-22 meters and a vertical opening of approximately 2.4 meters. The codend of the trawl was equipped with a 20mm side diamond stretched mesh. It should be noted, however, that potential biases in capturing elasmobranchs may exist for bottom trawls. For instance, skates, have a body morphology that keeps them close to the sea bed making them more likely to avoid the trawl entrance[66]. Additionally, some species of medium to large-sized sharks such as spurdog and smooth-hound are known for their fast swimming speeds and pelagic behavior[67]. These characteristics make them less likely to be captured by bottom trawl survey gear, which may result in an underestimation of their absolute abundance. Furthermore, the interpretation of trends in spurdog abundance may be complicated by their tendency to aggregate. However, the survey area have been overall covered consistently over the years, and our aim was to analyse the relative changes in species abundances and community composition, therefore we consider the results robust to these sampling caveats that are common in any trawl survey. Further details on sampling procedures, data collection and analysis can be found in the MEDITS handbook[68]. For this study, we excluded those hauls which have occurred in the autumn-winter period (October to December) due to the potential redistribution of elasmobranch among seasons[69], leading to a total of 4050 trawl hauls analysed. The abundance (i.e., the number of fish per trawl haul) of 29 elasmobranch species was recorded totally. However, we excluded those species scarcely represented (i.e., that occurred in less than 2% of the trawl hauls or with less than 150 individuals in the whole dataset). The common smooth-hound *Mustelus mustelus*, and the blackspotted smooth-hound *Mustelus punctulatus* were grouped together under the category smooth-hound. The morphological identification for the *Mustelus* genus is not trivial[70], and the common smooth-hound and the blackspotted smooth-hound can be often misidentified. Also, the two species co-occur in the North-Central Adriatic Sea, have a similar diet[71], share similar habitats, and the chance of hybridization is not excluded[70,72]. The blackmouth shark *Galeus melastomus*, was excluded from the analysis because it inhabits deeper water[73] and its distribution range is likely not adequately covered by the survey. As a result, our final dataset comprised the recorded abundance of nine elasmobranch species (Table 1).

Environmental covariates. As explanatory covariates, we included log-transformed depth, and bottom temperature as linear fixed effects and seabed substrate as a binary categorical variable (sand, mud to muddy sand). Additionally, we accounted for the variability in the sampling effort including the log-transformed swept area of each haul as a predictor. To account for any underlying linear temporal trends that may have been present but not captured by the included covariates, we also added survey year as a linear fixed effect. We ensured that covariates were not strongly correlated with each other ($r < 0.7$) (Supplementary Fig. S7). We chose environmental variables based on the availability of the data and assumed relevance to the community assemblages. We extracted the monthly mean bottom temperature from the Copernicus Marine Service Data[74] and derived seabed substrate from the European Marine Observation Data Network (EMODnet) Geology Project (http://www.emodnet-geology.eu/), using the Folk 5 classification. To integrate these environmental variables with the trawl hauls data, we associated each trawl haul with the nearest spatial point of the variables. In the case of bottom temperature, we also matched the data in time. For the grid of the spatio-temporal predictions, we followed the same approach but we used the mean values of bottom temperature over the survey period (May to September) in each cell. This step enabled us to standardize the effects of bottom temperature across different years.

Traits and phylogeny. As species traits, we compiled data on three ecological traits related to life-histories and feeding habits that we expected to influence the spatio-temporal dynamics of the elasmobranchs, that were comparable across sharks and rays, and for which information was available in the literature. Included traits were age at first maturity, reproductive mode and trophic level (Table 1). Age at first maturity data were retrieved from a field guide to the Mediterranean elasmobranchs[73] and complemented with a publicly available dataset on marine fish traits[75]. If data were disaggregated by sex we kept the female age at first maturity, and in case data were available as a range we took the median value. Wherever age at first maturity information was not available at the species level we used inferred data from the genus level (i.e., for small-spottedcatshark and nursehound). Considering trophic level, we sourced data from standardised diet studies[38,39,76]. For smooth-hound, we used trait data of *Mustelus mustelus*. We provide detailed references in Table 1. We further ensured that traits were not highly correlated ($r < 0.7$) (Supplementary Fig. S8). To account for phylogenetic dependencies, we included a phylogenetic correlation matrix in the model's covariance structure. However, since true phylogenetic information of species was not available, we used the as.phylo function in the ape R-package[77] to build a phylogenetic tree of the included species based on their taxonomic structure including phylum, class, order, family, genus and species, and assuming equal branch length of 1 between each node. This allowed the model to estimate how much of the residual environmental responses of the species were explained by phylogenetic correlations. The strength of the phylogenetic signal is measured by the parameter ρ which is constrained between 0 and 1. A value of $\rho = 0$ indicates that the residual variance in species' environmental niches is independent among the species, while when $\rho = 1$, species' environmental niches are fully explained by their phylogeny.

Statistical analysis. Using the 'Hmsc' R-package[22,41] version 3.0-12 we fitted joint species distribution models (JSDMs) to the elasmobranch community abundance data while also including information on traits, environmental covariates and phylogenetic constraints. To account for the spatial and temporal stochasticity of the data, as well as to model residual co-occurrence among species, we employed spatially[78] and temporally structured latent variables. These variables allowed us to incorporate hierarchical structures in our model and account for any unexplained variation in the data. We implemented spatially structured latent variables through the predictive Gaussian process for big spatial data[79]. The response matrix was the number of individuals of each elasmobranch species per trawl haul. Due to the zero-inflated nature of the data, we applied a hurdle approach, i.e., one model for presence-absence (PA) and another model for conditional abundance (ABU). We employed probit regression in the PA model and a log-linear regression for the abundance data in the ABU model. The abundance data in the ABU model were scaled to zero mean and unit variance within each species to better accommodate default priors, which are reported in the 'Hmsc' R-package paper[41]. For additional information on the model equations, please refer to the Supplementary Information. For each model, we sampled the posterior distribution with four Markov chains Monte Carlo (MCMC) simulations, each of which was run for 37,500 iterations, the first 12,500 being discarded as burn-in. The chains were thinned by 100, resulting in 250 posterior samples per chain, returning 1000 posterior samples in total. After fitting the model, we examined and ensured the convergence of the MCMC simulations by examining the potential scale reduction factors[80] (Supplementary Figs. S9–S10). The explanatory power of the model was evaluated by computing the coefficient of discrimination Tjur's R^2[81] and the Area Under the Curve (AUC)[82] for the PA model, which measures how well the model discriminates between presences and absence, and by computing the R^2 for the ABU model. The overall explanatory power of each model was then summarized as the mean explanatory power across species. To visualize the species niches, we extracted from the models fit the so-called β parameters (regression slopes) which represent species-specific responses to environmental covariates. To visualize the trait-environment relationships, we extracted from the models fit the so-called γ parameters which measure the influences of the traits on the species' responses to the environmental covariates. To determine the relative importance of the environmental covariates and to measure how much of the variation in species occurrences and abundances are explained by their traits we partitioned the explained variation among the fixed and random effects[22,83]. We then used the parameterized model to predict the expected species abundance on a 0.05° latitude x 0.05° longitude grid. The abundance of each species was computed as the product of occurrence probability (from the PA model) and abundance conditional on presence (from the ABU model). In these predictions, we fixed the swept area value to the mean of the trawl hauls used in this study (i.e., 0.047 km^2). To functionally characterize the elasmobranch community, we then computed community-weighted mean traits (i.e., haul-level trait values weighted by species abundances) on predicted abundances. Indices of abundance were computed by raising the predicted abundance to the cell area and summing across the grid cells. The mean and the credible intervals were reported as summary statistics. All analysis was performed in R[84] version 4.0.4.

Data availibility

The survey data that support the findings of this study were collected within the EU Data collection Framework (DCF - MEDITS) and are available upon official request to the Direzione Generale della Pesca Marittima e dell'Acquacoltura of the Ministero dell'Agricoltura, della Sovranità Alimentare e delle Foreste (MASAF) and to the Croatian Ministry of Agriculture.

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Author contributions

F.M. conceptualized the study with significant contributions from M.C.; C.M., A.A., I.I., and N.V. prepared the raw data; E.C. and F.M. collected and selected the traits data; F.M. and B.W. conducted the statistical analysis with contribution from M.C.; F.M. wrote the initial draft and all authors reviewed the different drafts and contributed to the final version.

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Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to F.M. or M.C.

Supplementary Information

Influence of ecological traits on spatio-temporal dynamics of an elasmobranch community in a heavily exploited basin

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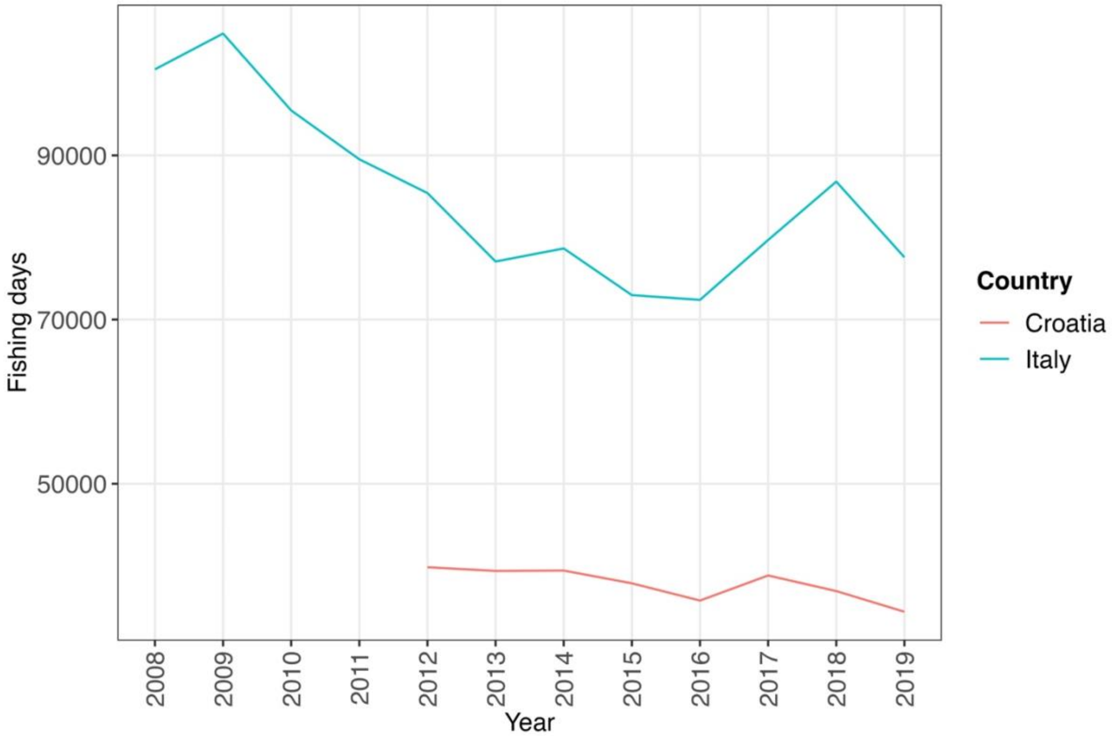

Figure S1. Trend in fishing effort in the North-Central Adriatic Sea from 2008 to 2019. Data are obtained from the Scientific, Technical and Economic Committee for Fisheries (STECF; https://stecf.jrc.ec.europa.eu/reports/economic). The data are filtered for beam trawlers (TBB), and demersal trawlers (DTS). Fishing effort is expressed as the number of days fishing vessels spent fishing.

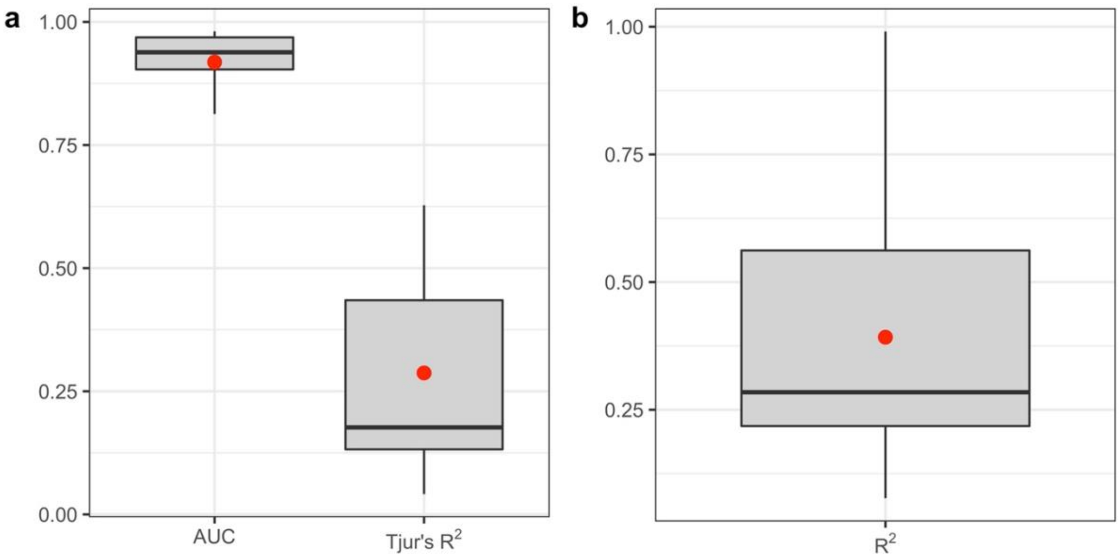

Figure S2. Boxplots showing the explanatory power. The panels show the results (a) for the presence-absence (PA) model and (b) for the conditional abundance (ABU) model. Data point represents species-specific values. Red dots represent mean values.

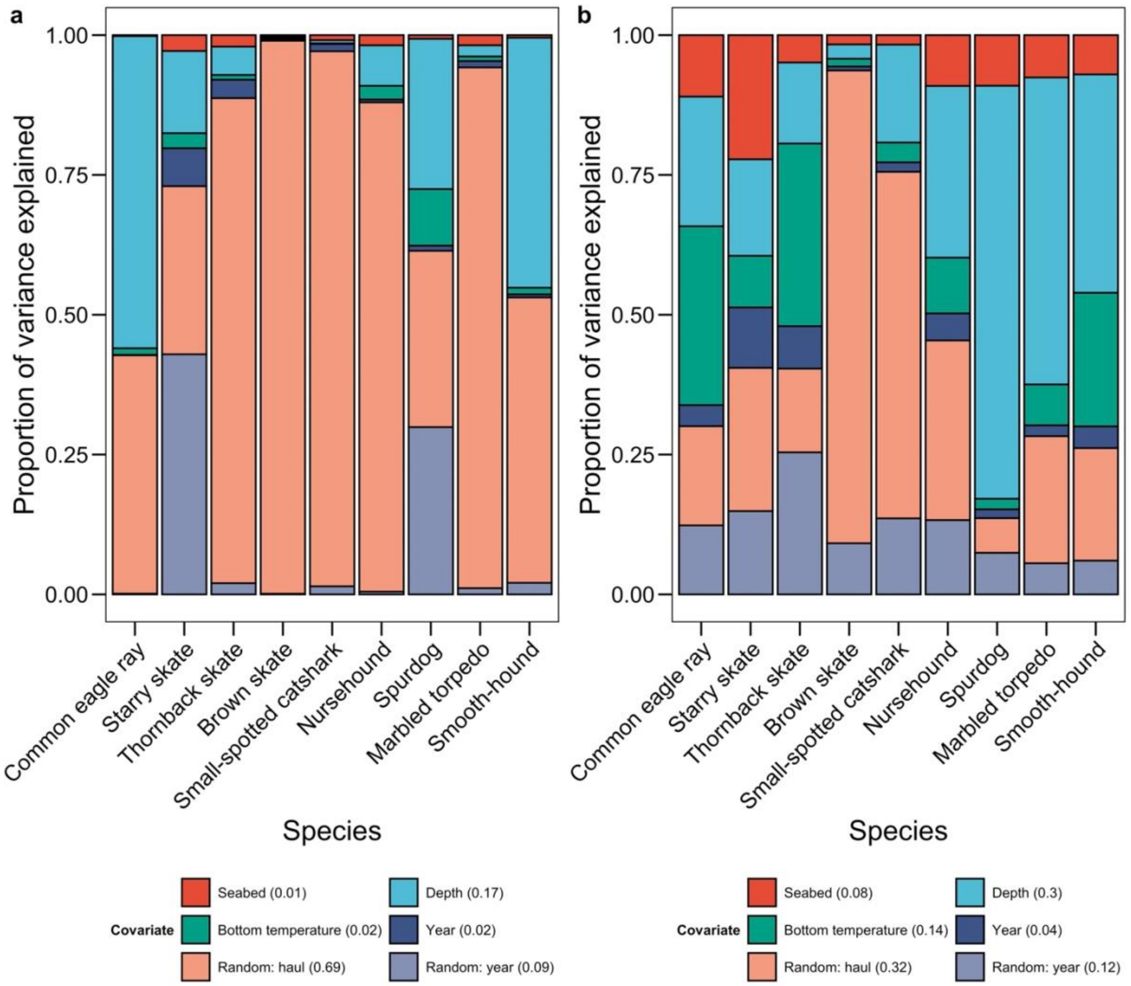

Figure S3. Variance partitioning among the explanatory variables included in the models. The panels show the results (a) for the presence-absence model and (b) for the conditional abundance model. The explanatory power is measured by Tjur R^2 for the presence-absence (PA) model and R^2 for the conditional abundance (ABU) model. The mean variance proportions averaged over the species are reported in brackets alongside the legend. **‘**Random: haul’ indicates haul-level spatial random effects, while ‘Random: year’ represents temporal random effects.

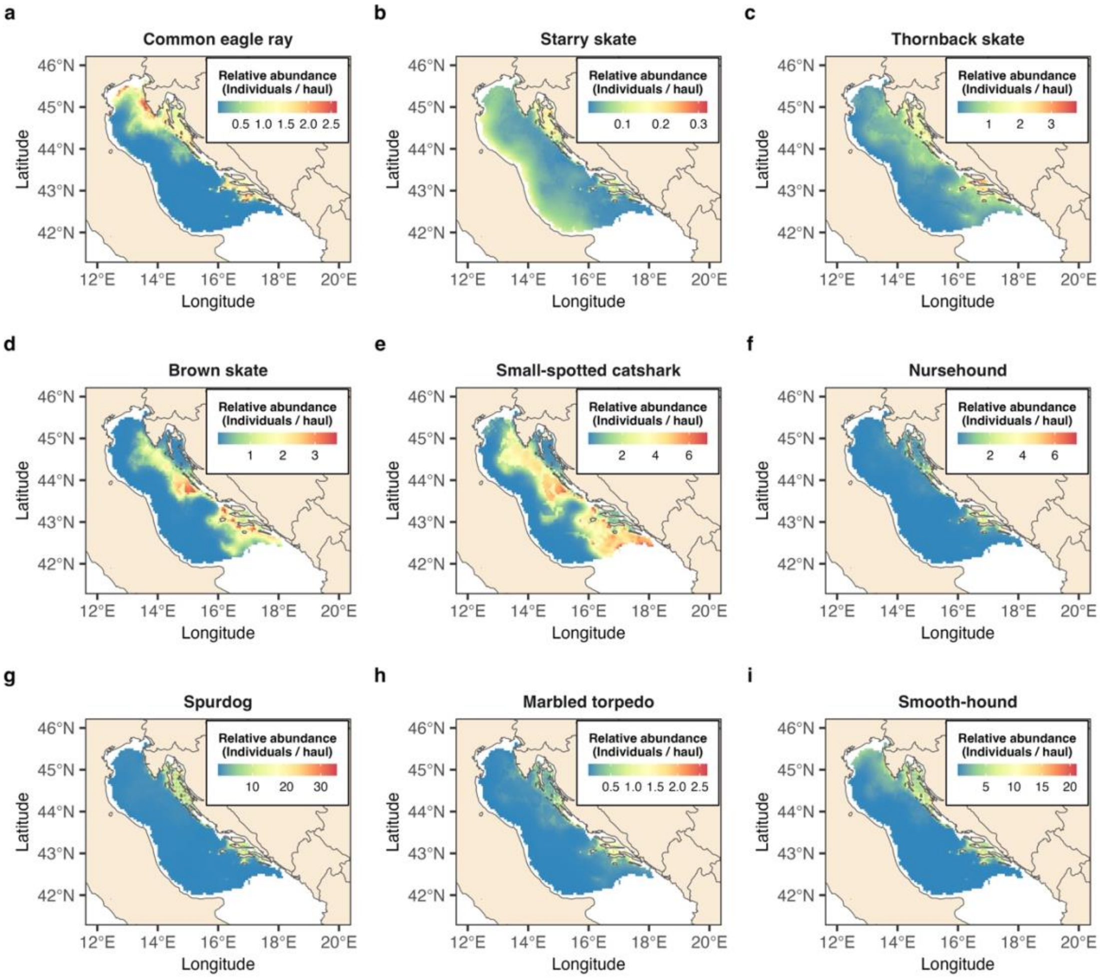

Figure S4. Predicted species mean abundance across the study area. Predictions refer to the year 2019. In the predictions, the swept area value is fixed to the mean of the trawl hauls used in the study (i.e., 0.047 km^2).

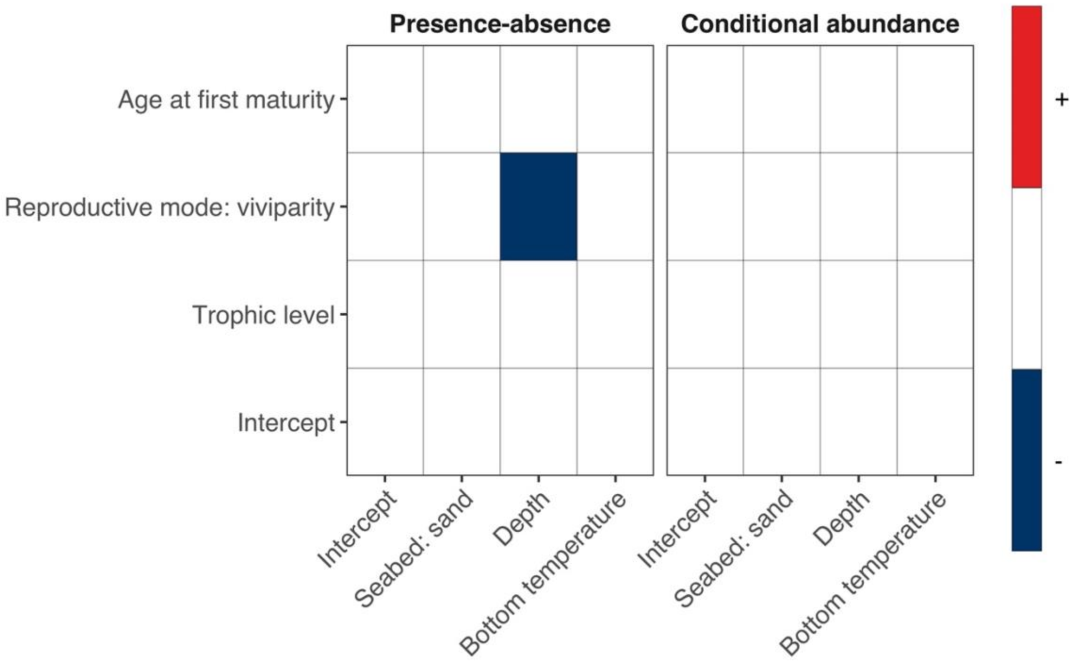

Figure S5. Heatmap of the estimated γ parameters (regression slopes) which link species traits to species niches. The left panel represents the presence-absence (PA) model while the right panel the conditional abundance (ABU) model. Blue color indicates parameters that are estimated to be negative with at least 95% posterior probability, while responses that did not gain strong statistical support are shown in white. No parameter is estimated to be positive with at least 95% posterior probability.

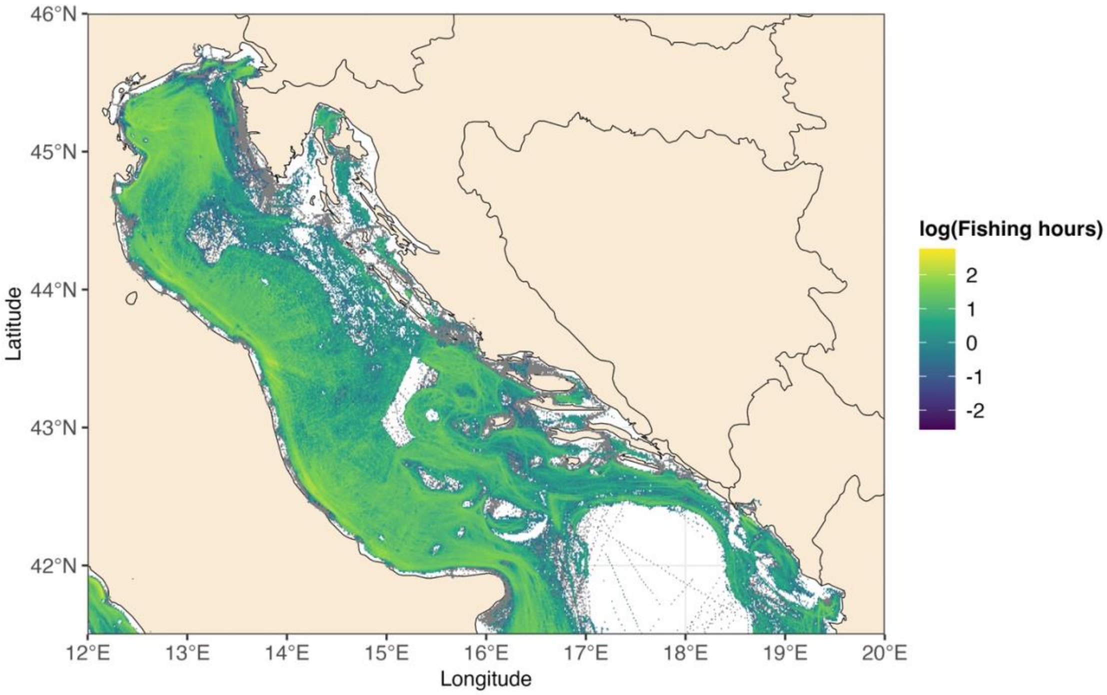

Figure S6. Map showing the estimated spatial distribution of fishing effort in the North-Central Adriatic Sea during the year 2019. Data are obtained from the Automatic Identification System (AIS) and analyzed using Global Fishing Watch (https://globalfishingwatch.org/). The map specifically shows trawlers as the gear type used. Fishing effort is expressed in fishing hours.

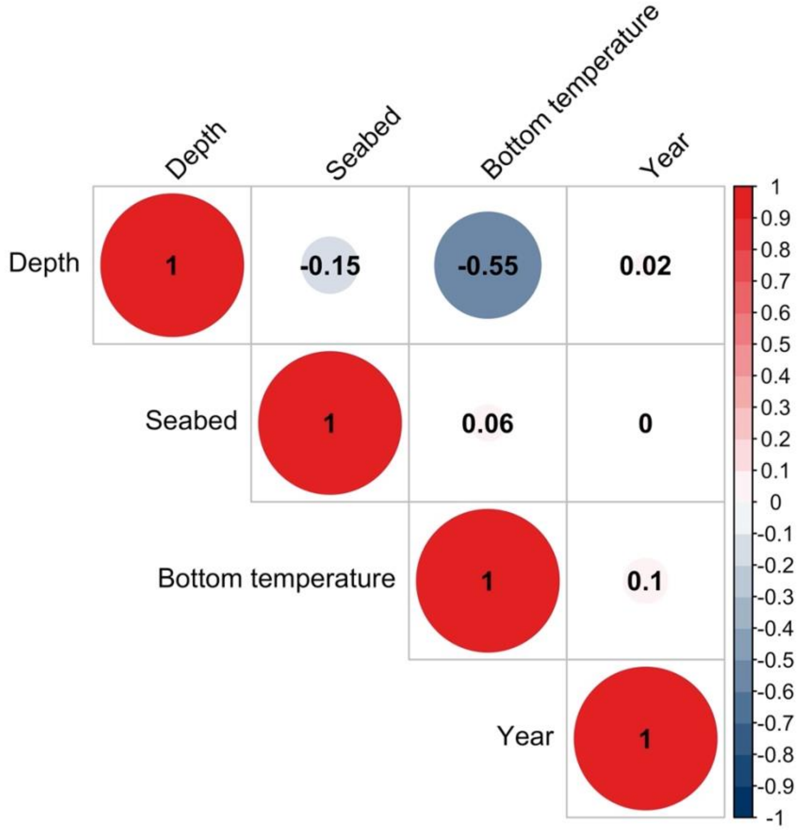

Figure S7. Pearson pairwise correlation coefficients for the environmental covariates included in the analysis. Red (blue) colour indicates positive (negative) coefficients, which are reported inside the circles.

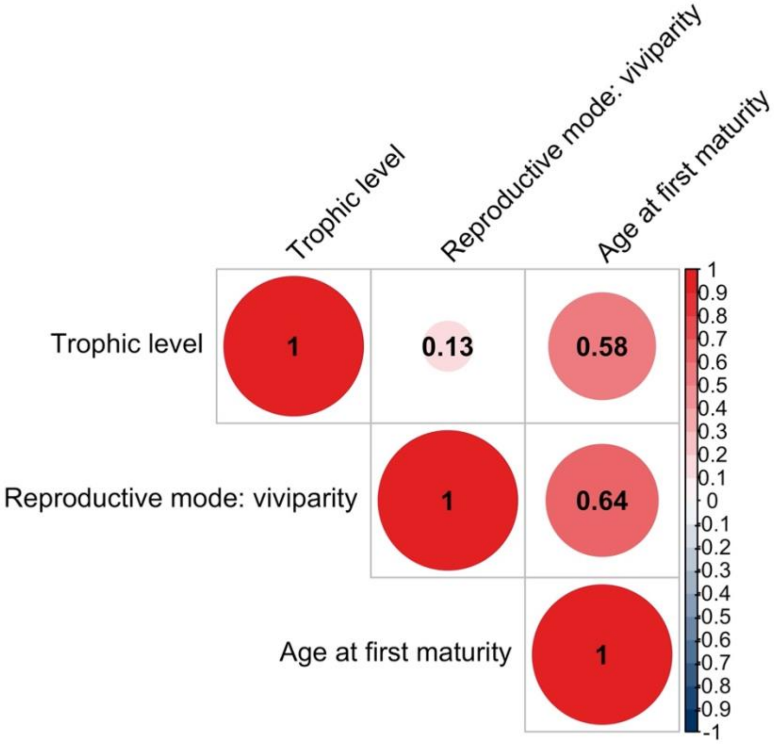

Figure S8. Pearson pairwise correlation coefficients for the traits included in the analysis. Red colour indicates positive coefficients, which are reported inside the circles.

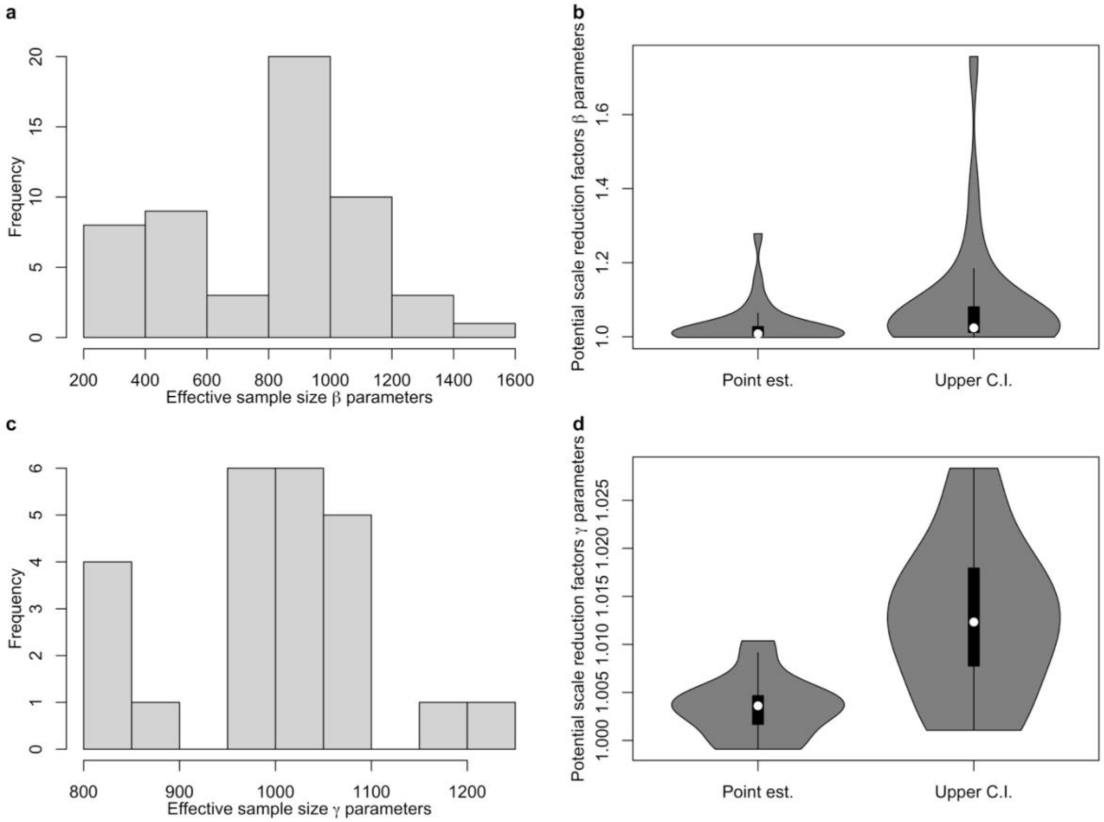

Figure S9. Model diagnostics for the presence-absence (PA) model. The panels correspond (a-b) to the β parameters and (c-d) to the γ parameters. The panels on the left measure MCMC in terms of the effective sample size and the panels on the right in terms of the potential scale reduction factor.

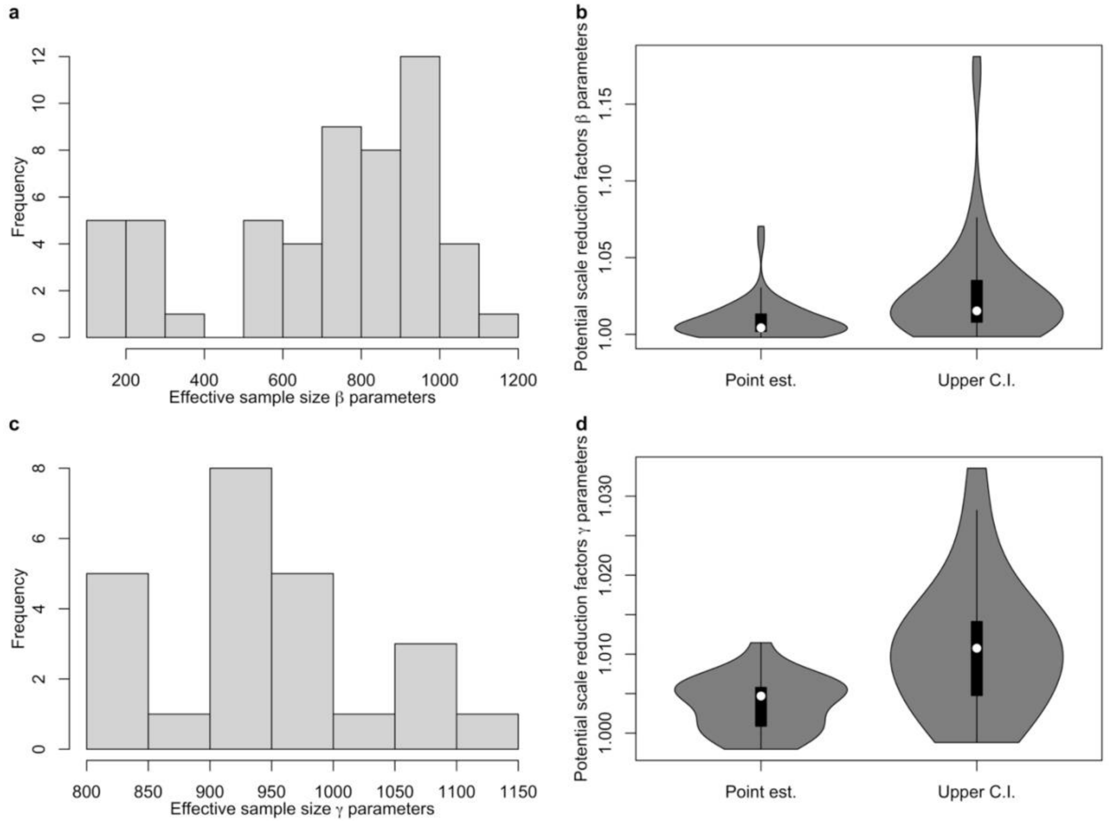

Figure S10. Model diagnostics for the conditional abundance (ABU) model. The panels correspond (a-b) to the β parameters and (c-d) to the γ parameters. The panels on the left measure MCMC in terms of the effective sample size and the panels on the right in terms of the potential scale reduction factor.

Models' equations

We modeled the occurrence and abundance of each species (denoted as j) in each sampling unit (denoted as i) using a generalised linear model

$$y_{ij} \sim D\left(L_{ij}, \sigma_j^2\right) \qquad (1)$$

where D is the statistical distribution (i.e., probit for the presence-absence model and normal for the conditional abundance), L_{ij} is the linear predictor, and σ_j^2 is the variance term (which is excluded for the probit model).

The linear predictor L_{ij} is modeled as the sum of fixed and random effects

$$L_{ij} = L_{ij}^F + L_{ij}^R \qquad (2)$$

The fixed effects were modeled as a regression

$$L_{ij}^F = \sum_k x_{ik}\,\beta_{jk} \qquad (3)$$

Here, x_{ik} represents the covariate k measured at site i, and β_{jk} represents the response of species j to covariate k, where $x_{i1} = 1$ denotes the intercept.

The species' response to covariates is assumed to follow a multivariate normal distribution

$$\beta_{..} \sim N(\mu_{..}, V \otimes [\rho C + (1 - \rho) I]) \qquad (4)$$

Here, $\beta_{..}$ denotes the vector of regression coefficients for all species' response to the covariates, which can be interpreted as species environmental niches. The symbol $\otimes$ denotes the Kronecker product, and $0 \leq \rho \leq 1$ measures the strength of the phylogenetic signal.

The expected niche μ_j models the influence of species-specific traits on species' responses, with

$$\mu_{jk} = \sum_l t_{jl}\,\gamma_{lk} \qquad (5)$$

where t_{jl} is the value of trait l for species j (with $t_{j1} = 1$ denoting the intercept), and γ_{lk} measures the effect of trait l on the response to covariate k. In this equation, C denotes the phylogenetic covariance matrix, and I denotes the identity matrix. When $\rho = 0$, the residual variance is independent among the species, implying that closely related species do not have more similar environmental niches than distantly related ones. When ρ approaches $\rho = 1$, species' environmental niches are fully structured by their phylogeny, with related species having more similar niches than expected by chance, implying niche conservatism.

The random effects are modeled as

$$L_{ij}^R = \sum_{r=1}^{n_f} L_{ij}^{r,R} \qquad (6)$$

where $L_{ij}^{r,R}$ is the linear predictor related to the random effect r. In this case, $r = 1$ represents the random effect of haul, and $r = 2$ represents the random effect of year.

We define “units” as the sampling units at the haul and year level and denote the unit behind sampling unit i as $u^r(i)$. The random effect number r is then defined as

$$L_{ij}^{r,R} = \sum_{h=1}^{n_f^r} \eta_{u^r(i)h} \lambda_{hj}^r \qquad (7)$$

Here, the summation goes over n_f^r, which are the number of factors included for random effect r. The $\eta_{u^r(i)h}$ are the “unit loadings,” and the λ_{hj}^r are the “species loadings”. The unit loadings $\eta_{u^r(i)h}$ have an exponentially decaying correlation structure, where

$$\eta_{.h}^r \sim N(0, \Sigma) \qquad (8)$$

and

$$\sum_{u_1^r u_2^r} = exp\left(-d_{u_1^r u_2^r} / \alpha_h^r\right) \qquad (9)$$

Here, $d_{u_1^r u_2^r}$ is the distance in space or time between the units u_1^r and u_2^r, and α_h^r is the spatial or temporal scale associated with the factor number h of the random effect r.

Paper II

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

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Abstract

Sharks, rays, and chimaeras (chondrichthyans) represent one of the most evolutionarily distinct and ecologically diverse groups of vertebrates. However, their widespread decline due to overfishing is a pressing concern, making it essential to understand the spatial interactions between chondrichthyans and fisheries for sound conservation and management. Limited data on landings, bycatch, and species identification in many regions challenge our grasp of these interactions. In such cases, an alternative approach to understanding vulnerability to fishing involves evaluating the potential risks posed by fishing activities.

To address this, we present a generalizable approach that combines Vessel Monitoring System (VMS) data with spatiotemporal species distribution models to estimate the spatial overlap between commercial fishing effort and chondrichthyan.

As a case study, we analyze the overlap between two common bottom trawling gear types (otter bottom trawl and beam trawl) and bottom-dwelling (demersal) chondrichthyan populations in the heavily exploited western Adriatic Sea within the Mediterranean.

By analyzing the overlap between model-based chondrichthyan distribution, species richness, and the presence of threatened species (i.e., assessed as Vulnerable, Endangered, or Critically Endangered by the IUCN Red List) with bottom trawl fishing activities, we identify areas with a high risk of chondrichthyan bycatch.

Our findings show that many of these species are at-risk across a large portion of their distribution within the study area, highlighting the vulnerability of these species to fishing pressure. We find a substantial spatial overlap between intensive trawling, areas of high species richness and presence of threatened chondrichthyans, primarily in the northern and central offshore sectors of the western Adriatic. Furthermore, differences in the degree of overlap between distinct fishing gears underscore the importance of considering specific fishing practices when formulating management strategies.

While not without caveats, our findings suggest that the general approach of combining spatiotemporal models of threatened species distributions and VMS data is promising for identifying areas of conservation concern for species exposed to fishing activities and can thus contribute to the development of targeted conservation and spatial management measures.

Introduction

Chondrichthyans (sharks, rays and chimaeras) make up one of the oldest and most ecologically diverse vertebrate radiations (Compagno, 1990; Stein et al., 2018). This group, which includes about 1,200 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, is overwhelmingly the main threat to their survival (Dulvy et al., 2014, 2021). The late age at maturity and low fecundity of many chondrichthyans species make them more vulnerable to fishing than most teleosts (Stevens, 2000). Yet, biologically sustainable fisheries are possible 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 negative impacts of fishing activities (FAO, 2023; McConnaughey et al., 2020). However, particularly for chondrichthyans, limited data on incidental catches, landings, and species identification hinder our understanding of the spatial overlap between species distribution and fishing effort, thereby jeopardizing targeted management efforts (Cashion et al., 2019; FAO, 2022). In such cases, assessing the potential overlap between species and fishing effort becomes crucial (Queiroz et al., 2016, 2019).

Vessel Monitoring Systems (VMS) satellite-based tools that track fishing vessels in real-time, have 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 fish bycatch (Queiroz et al., 2016).

The Adriatic Sea, situated in the central Mediterranean, has a long history of chondrichthyans fisheries and has experienced depletion of several species in the last few decades (Dulvy et al., 2003; Ferretti et al., 2013; Jukic-Peladic et al., 2001; Lotze et al., 2011). Among the chondrichthyan species commonly caught or observed in this region are the catsharks (*Scyliorhinus* spp.), brown skate (*Raja miraletus*), spurdog (*Squalus acanthias*), thornback skate (*Raja clavata*), and smooth-hound (*Mustelus* spp.) (Barausse et al., 2014; Clodia database, 2020; Ferretti et al., 2013; Maioli et al., 2023). Presently, 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).

This basin is recognized as 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 1946 vessels, equivalent to approximately 64,900 gross tonnes, with Italy owning around 70% of the total fleet (FAO, 2022). This fishing activity significantly contributes to the incidental capture of chondrichthyans, making it a major concern for the conservation of these species (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, 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 gear types—otter bottom trawl and beam trawl—and demersal chondrichthyans in the western Adriatic Sea. We integrate data on fishing effort from the Italian fleets obtained through VMS with predicted species distributions derived from geostatistical Species Distribution Models (SDMs) fitted to data from a fishery-independent bottom trawl survey. Additionally, we analyze and map species richness and the proportion of threatened species. This enables us to assess the overlap between this community and bottom trawl fishing activities, providing insights into the potential impact of fishing. Our goal is to identify high-risk areas for bycatch, where the potential impact of fishing on chondrichthyan populations and communities is the highest, thus guiding the development of targeted conservation efforts and management strategies to protect chondrichthyan populations in this heavily exploited ecosystem.

Methods

Study area

The Adriatic Sea, located in the Central Mediterranean between the Italian peninsula and the Balkans, is primarily a shallow and eutrophic basin (Supplementary Information: Figure S1). It displays distinct morphological variations along both its longitudinal and latitudinal axes. In the northern part of the Adriatic Sea, there is an extremely shallow mean depth of approximately 30 m up to a maximum of 70 m, and the bathymetric gradient along the major axis of the basin is quite weak (Supplementary Information: Figure S1). This region experiences a strong river runoff, with the Po River and other northern Italian rivers contributing around 20% of the entire Mediterranean river outflow (Hopkins, 1992). These rivers introduce significant amounts of nutrients, making the Northern Adriatic Sea the most productive area in the Mediterranean (Campanelli et al., 2011) and one of the most heavily fished regions in Europe (Eigaard et al., 2017).

The central zone of the Adriatic Sea reaches depths of about 200 m. However, it is also characterized by two depressions known as the Jabuka/Pomo Pits, which have a maximum depth of approximately 270 m.

The Southern Adriatic Sea exhibits significant differences between its northern and southern areas. In the northern region, specifically around the Gulf of Manfredonia, a wide continental shelf can be found, with a distance of about 45 nautical miles between the coast and the 200-meter isobath. This area is characterized by a smooth slope. On the other hand, in the southern region, the isobaths are much closer together, with a distance of only 8 nautical miles. These distinct morphological variations between the two areas have direct implications for the biocenoses, fisheries resources, and prevalent fishing techniques employed in the region (Anonymous, 2011).

The western coast of the Adriatic Sea is generally regular, sandy, and gently sloping, while the eastern coast is characterized by irregularities, numerous islands, and steeply sloping rocky bathymetry (Russo & Artegiani, 1996).

The water circulation pattern in the Adriatic Sea is cyclonic, with water masses flowing into the basin from the Eastern Mediterranean following a north-westward flow on the east oat and exiting trough a south-eastward flow on the west coast. The circulation and water masses in the Adriatic Sea are strongly influenced by river runoff and atmospheric conditions, which, in turn, impact the salinity and temperature of the water (Artegiani et al., 1997).

Data

Fishing effort data

Vessel Monitoring Systems (VMS) data consists of a series of consecutive pings (signals) sent by each vessel at regular time intervals. Compared with other tracking devices like the Automatic Identification System (AIS), the temporal frequency of these pings is relatively low, usually with 1-2 hours between successive pings. However, the VMS data offers unparalleled spatial coverage as it relies on the INMARSAT satellite network (Russo et al., 2016; Shepperson et al., 2018). The main limitation of VMS is related to its limited coverage of the fleets since VMS is mandatory only for fishing vessel with a length-over-all larger than 12 m, which means that smaller vessels may not be included in the data.

For this study, VMS and logbook data for the trawling fleet operating in the Adriatic Sea were provided by the Italian Ministry of Agriculture, Food Sovereignty and Forests (MASAF) within the scientific activities related to the Italian National Program for the Data Collection in the Fisheries Sector (INPDCF). We extracted a subset of VMS data from 538 vessels utilizing bottom otter trawl (OTB) and beam trawl (TBB) gear types, which are two common fishing methods used along the Italian Adriatic coast. These bottom trawlers were identified through cross-analysis involving logbook data and the EU Common Fleet Register (https://webgate.ec.europa.eu/fleet-europa/index_en).

This subset of data was then used to assess the fishing activity of these vessels from 2009 to 2021 using the R package VMSbase (version 2.2.1; Russo et al., 2014; Russo et al., 2011a; Russo et al., 2011b). VMS pings were partitioned into fishing trips by vessel and interpolated to increase their temporal frequency to 10 minutes (Russo et al., 2011a). The high-frequency interpolated VMS pings were then joined with the NOAA-Etopo1 database (Amante, Christopher & Eakins, 2009) through the R package marmap (Pante & Simon-Bouhet, 2013) to estimate the bottom sea depth for each ping. Finally, to identify fishing activities accurately, 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).

Thereafter, we filtered the data to include only the period covered by the MEDITS survey (May to September, see below). Subsequently, we computed the yearly aggregated value of trawl fishing effort (i.e. the sum of the fishing hours) for each cell in a 2 x 2 km square grid multiplying the number of fishing set positions by the interpolation frequency (10 minutes).

We then filtered this grid by excluding depths not covered by the MEDITS survey, specifically excluding depths < 10 m and > 800 m. Additionaly we excluded the national territorial seas of Slovenia, Croatia, Montenegro and Albania. The shapefiles for the exclusion of the territorial seas was obtained from www.marineregions.org (2023).

Survey data

The complete biological dataset considered for this study consisted of the catches of 5,122 bottom trawl hauls that were performed 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-summer period (May to September, although in some years it has been performed in October-December), and the hauls are located at depths ranging from 10 to 800 m, following a random-stratified sampling scheme based on 5 different depth strata (Anonymous, 2017; Spedicato et al., 2020). The GOC-73 experimental bottom trawl is used as the sampling gear, which has a horizontal opening of 16-22 m and a vertical opening of approximately 2.4 m. The codend of the trawl is equipped with a 20 mm side diamond stretched mesh. Further information on the sampling procedures, data collection, and analysis can be found in the MEDITS handbook (Anonymous, 2017).

We selected and analyzed a total of 4,216 hauls in this study (Supplementary Information: Figure S1), after excluding hauls conducted prior to 1999 and hauls conducted during the autumn period (October to December). The decision to exclude these hauls was driven by two factors. Firstly, the availability of the biogeochemicals variables (see section

Environmental covariates and model selection) only reaches back to 1999. Secondly, the coverage of the autumn season has been inconsistent over the years. Ensuring a seasonally homogenous dataset was essential, considering the potential redistribution of chondrichthyan species across seasons (Manfredi et al., 2010). Moreover, we excluded species scarcely represented in the data (i.e., those that occurred in less than 3% of all the trawl hauls considered). Further, we grouped the common smooth-hound (*Mustelus mustelus*) and the blackspotted smooth-hound (*Mustelus punctulatus*) together under the category smooth-hound (*Mustelus* spp.) because the morphological identification for the *Mustelus* genus is not straightforward (Marino et al., 2018), and the two species can therefore be misclassified. Additionally, the two species occur together in the Northern Adriatic Sea, display a similar diet (Di Lorenzo et al., 2020), inhabit similar habitats, and the chance of hybridization is not excluded (Marino et al., 2015, 2018). In total, 10 species/genera were included in further analyses (Table 1).

Species distribution models

We utilized geostatistical generalized linear mixed-effect models (GLMMs) as SDMs to capture the distribution patterns of chondrichthyan species (Table 1). These models combined survey data and environmental covariates, while also considering the influence of spatial and spatiotemporal correlations using Gaussian random fields.

Specifically, we modelled the presence/absence of each species using a Bernoulli distribution:

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

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

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

$$\omega_{\boldsymbol{s}} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\omega) \tag{4}$$

$$\boldsymbol{\delta}_{t=1} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon) \tag{5}$$

$$\boldsymbol{\delta}_{t>1} = \rho\boldsymbol{\delta}_{t-1} + \sqrt{1 - \rho^2}\,\epsilon_t, \epsilon_t \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon) \tag{6}$$

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, α_t represents random intercepts by year t. $\boldsymbol{X}_{s,t}$ represents the vector of the environmental covariates (see the section *Environmental covariates and model selection* and Supplementary Information: Table S1) at space $\boldsymbol{s}$ and year t and $\boldsymbol{\beta}$ represents a vector of corresponding coefficients. $\omega_{\boldsymbol{s}}$ and $\epsilon_{\boldsymbol{s},t}$ are the spatial and spatiotemporal random fields with estimated covariance matrices $\boldsymbol{\Sigma}_\omega$ and $\boldsymbol{\Sigma}_\epsilon$, respectively. Spatiotemporal random effects are here assumed to follow a stationary AR1-process where ρ represents the correlation between subsequent spatiotemporal random fields.

To overcome convergence issues encountered during the initial analysis, for the deep-sea species (blackmouth catshark, rabbitfish, and velvet belly lanternshark) and the rare species (with a frequency of occurrence ≤ 5%: starry skate, common eagle ray, brown skate, smooth-hound) we did not include spatiotemporal random fields ($\epsilon_{\boldsymbol{s},t}$) in the models and relied exclusively on the spatial random fields ($\omega_{\boldsymbol{s}}$).

To optimize computational efficiency, we utilized a predictive process modeling framework (Anderson & Ward, 2019; Latimer et al., 2009) for fitting all models. In this framework, we employed the Stochastic Partial Differential Equation (SPDE) approximation (Lindgren et al., 2011) and a triangulated mesh (Supplementary Information: Figure S2), generated using the R-package R-INLA (Rue et al., 2009), to represent spatial random fields. Random effects are estimated at the knots (the vertices of the mesh) and are then bilinearly interpolated to data locations. The optimal knot locations were determined using a *k*-means clustering algorithm, which minimized the total distance between knots and data points. We selected 200 knots for our models after an initial exploration, as this balance between accuracy and computational time was deemed appropriate (Supplementary Information: Figure S2). The models were fitted using TMB (Kristensen et al., 2016) through the R-package sdmTMB (version 0.2.1) (Anderson et al., 2022 [preprint]) with maximum marginal likelihood and the Laplace approximation to integrate over random effects. We assessed convergence of the models and ensured that the maximum absolute gradient with respect to all fixed effects was < 0.001, and that the Hessian matrix was positive-definite (Anderson et al., 2022 [preprint]). The model residuals are presented in the Supplementary Information: Figures S3-S6.

Environmental covariates and model selection

For the SDMs, we selected environmental covariates based on data availability and their assumed relevance to the distribution of the studied species (Maioli et al., 2023). We included four covariates: depth (m), seafloor temperature (°C; hereafter temperature), seafloor dissolved oxygen (ml/L; hereafter oxygen), and seabed substrate (categorized into "Sandy mud", "Fine mud", "Sand" and "Muddy sand"). We extracted monthly mean temperature and oxygen values from the Copernicus Marine Service (Escudier et al., 2020; Teruzzi et al., 2021), wich have a spatial resolution of approximately 4 km. We obtained seabed substrate and depth data from the EMODnet Seabed Habitats project (https://www.emodnet-seabedhabitats.eu) and the EMODnet Bathymetry project (https://www.emodnet.eu/en/bathymetry), respectively. To integrate these environmental covariates with the trawl hauls data, we associated each trawl haul with the nearest spatial point of the variables. In the case of temperature and oxygen variables, we also matched the trawl hauls data with the nearest available measurements in time. Inter-annual variations were accounted for by including year as random intercept.

We then asked which combination of covariates resulted in the most parsimonious model, as estimated by the Akaike Information Criterion (AIC). To investigate the relationship with depth, for the most common species (spurdog, small-spotted catshark, and thornback skate), we explored 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. Finally, we tested the inclusion of substrate type and of the interaction term between oxygen and temperature.

To address convergence issues encountered during the initial analysis, we narrowed down our model selection process for the deep sea species and for the rare species. For the deep sea species we focused on the functional form of the depth covariate. For the rare species, we focused on the functional forms of both depth and temperature covariates. Specifically, for depth, we considered the following options for both deep sea species and rare species: depth, log(depth), depth + depth^2, and log(depth) + log(depth^2) (Supplementary Information: Table S1).

Moreover, for the small-spotted catshark, the velvet belly lanternshark and the thornback skate, we refitted the best candidate model excluding the random year intercepts, as their effect sizes were small and yielded convergence issues. For the common eagle ray we set Normal(0,10) weakly informative priors for the linear and quadratic terms of the depth covariate, as the initial estimates were unreasonably high, and consequently, we refitted the best candidate model using a penalized likelihood framework.

In total, we compared 16 different models for each common species, 4 for each deep sea species, and 8 for each rare species. To facilitate comparison of effect sizes between the included covariates and to compare them to the marginal standard deviation of spatial variation, we rescaled all covariates to have a mean of 0 and a standard deviation of 1 (Schielzeth, 2010). Finally, the explanatory power of the models was evaluated by computing the R^2 values (Nakagawa et al., 2017; Nakagawa & Schielzeth, 2013) and the Area Under the Curve (AUC; Pearce & Ferrier, 2000).

Prediction grid

We predicted the probability (*p*) of chondrichthyan species occurrence onto the same 2 x 2 km grid used for the assessment of the trawl fishing effort, using the best-fitting models. We followed the previously mentioned methodology by matching environmental covariates to the midpoint of each cell. For this particular step, we utilized the average values of temperature and oxygen spanning the core survey period, which extends from May to September. By considering the mean values over this period for each cell, we standardized the effects of temperature and oxygen, making our predictions comparable across different years. We restricted the predictions to the period between 2009 and 2021, as VMS data were unavailable for earlier years.

Species richness

To estimate the species richness, we predicted onto the grid by drawing 1000 simulations from the joint precision matrix of the best-fitting model for each species. This allowed us to obtain an estimate of species richness by summing the number of species in each grid cell (Ovaskainen & Abrego, 2020).

Proportion of threathened species

To characterize the chondrichthyan community as a whole, we calculated the proportion of threatened species. This was done for each cell of the prediction grid, weighing the species-specific conservation status by the predicted proportion of each species in each cell. To determine the conservation status of each species, we used the criteria set forth by the IUCN (www.redlist.org), categorizing species as threatened (1) if they were classified as Critically Endangered (CR), Endangered (EN), or Vulnerable (VU), and as nonthreatened (0) if they were categorized as Near Threatened (NT) or Least Concern (LC) (Table 1). Spurdog, common eagle ray and smooth-hound are categorized as threatened species, whereas the remaining species are classified as nonthreatened (Table 1).

Spatial overlap metrics

To evaluate the relationship between the distribution of chondrichthyans and fishing activities, we developed a species-specific Spatial Overlap Index (SOI).

$$\mathrm{SOI}_{i,g,\boldsymbol{s},t} = \frac{p\ \text{of presence}_{i,\boldsymbol{s},t} \times \text{Fishing effort}_{g,\boldsymbol{s},t}}{\mathrm{Max}\left(p\ \text{of presence}_{i,t} \times \text{Fishing effort}_{g,t}\right)} \tag{7}$$

The calculation for the SOI involves multiplying the predicted probability (*p*) of species *i* being present in a specific grid cell ***s*** for a given year *t* by the corresponding fishing effort (measured in fishing hours) for gear type *g* 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 stronger emphasis on the spatial overlap patterns. Consequently, we presented the SOI as an average across the most recent years (2018-2021) since we consider this timeframe more relevant from a conservation point of view. Also, 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 metric (RO) as defined in Carroll et al. (2019) to quantify the overlap between chondrichthyan species and trawling activities. The RO metric estimates the proportion of a species' area of occupancy where also trawling activities occur:

$$RO_{i,g,t} = A_{i,g,t}/A_{i,t} \tag{8}$$

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 trawling activities, we used a threshold where the fishing effort corresponds to ≥ 75th percentile of the maximum fishing effort for a gear type. Here, we normalized yearly fishing effort within the range [0,1]. This normalization helps address the potential limitation of VMS data as an accurate 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 0 are therefore assigned a value of 0. 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. To ensure the robustness of the chosen threshold, we also explored the sensitivity to different set thresholds.

Finally, we explored the chondrichthyans community overlap with fishing effort, using the estimated species richness and the proportion of threatened species. To visualize these relationships, we employed the R-package biscale (Prener et al., 2022) to generate bivariate choropleth maps. To this end, we used fishing effort, species richness, and the the proportion of threatened species as averages across the most recent years (2018-2021).

Results

Fishing effort

Overall we processed an average of 445 unique VMS identifiers for otter bottom trawlers (OTB) and 93 for beam trawlers (TBB) per year (Supplementary Information: Figure S7). Otter trawling was extensively practiced throughout the entire region (Figure 1a). On the other hand, beam trawling was primarily concentrated in the northern regions, extending along the coastline towards the central part of Italy (Figure 1c). Fishing effort (fishing hours in our study) was substantially higher for OTB compared with TBB. The temporal variation over space of OTB was relatively lower (lower coefficient of variation, CV) compared with TBB (Figures 1b, 1d), which can be attributed to the lower fleet size of the latter (Supplementary Information: Figure S7).

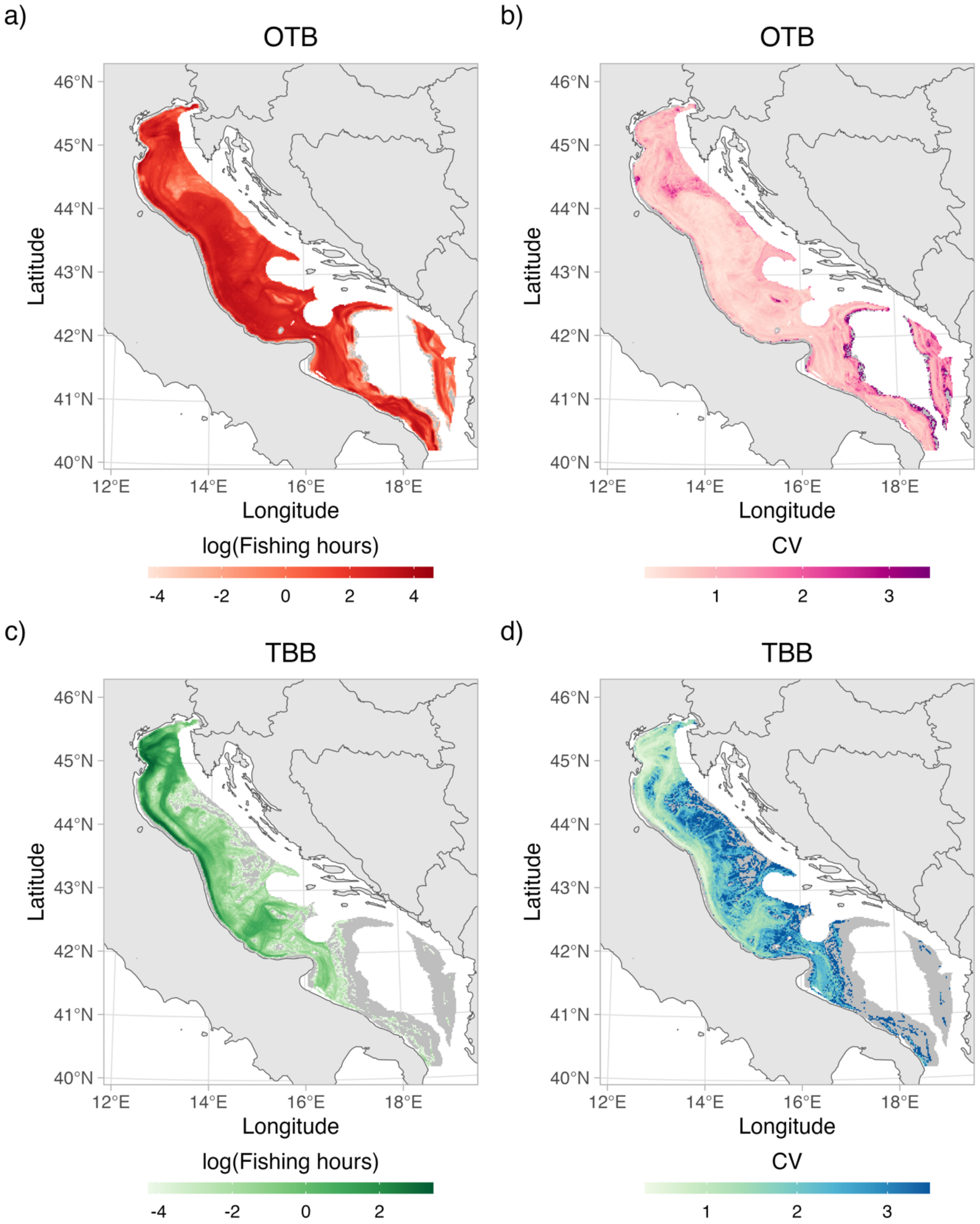

Figure 1. Mean fishing effort (fishing hours) derived from VMS signals. Mean fishing effort for otter bottom trawlers (OTB) (a) and beam trawlers (TBB) (c). Coefficient of variation (CV) of fishing effort for OTB (b) and TBB (d). Gray areas represent regions with estimated 0 fishing effort. The plots represent the sum of effort from May to September averaged over the period 2009 to 2021.

Species distribution models

Considering the entire survey period (1999-2021), the most dominant species were small-spotted catshark and blackmouth catshark being observed in ~ 10% of the hauls, followed by spurdog, velvet belly lanternshark, thornback skate, and rabbitfish being recorded in ~ 8% to 6% of the hauls, while starry skate, common eagle ray, brown skate, and smooth-hound occurred more sporadically (Table 1).

All species models demonstrated a good fit to the data, with conditional R^2 values ranging from 0.54 to 0.93, and AUC values ranging from 0.91 to 0.99 (Supplementary Information: Table S1). Overall, the inclusion of the linear and quadratic terms for depth provided better support to the models (i.e. lower AIC) across species. Specifically, half of the species models showed a better fit using log-transformed depth while the other half performed better without the transformation (Supplementary Information: Table S1). Three species models exhibited better fitting when using the linear temperature term, another three benefited from employing both the linear and quadratic termperature terms, and for 1 species model, the inclusion of temperature was not supported. Among the three species for which the interaction term between temperature and oxygen was considered, the inclusion of this term led to better model fitting in 2 cases (Supplementary Information: Table S1).

The models' predictions revealed a distinct spatial pattern in the chondrichthyan community (Figure 2). Specifically, among the threatened species, spurdog exhibited an elevated average probability of occurrence (p) across the northern and central offshore zones. Similarly, common eagle ray and smooth-hound displayed higher average p values in the northern coastal regions, extending into the offshore area below (Figure 2).

Conversely, for nonthreatened species, the small spotted catshark, thornback skate, and brown skate predominantly occupied the central offshore areas and the southeastern part of the study area (Supplementary Information: Figure S8). Deep-sea species such as the blackmouth catshark, velvet belly lantern shark, and rabbitfish were prevalent in the deeper southern central regions. The starry skate, on the other hand, showed a more prevalent distribution along the central and southern coastal zones (Supplementary Information: Figure S8).

Table 1. Species/genera selected for this study and the corresponding frequency of occurrence (percentage of trawl hauls where the taxon was caught) for the period 1994-2021. Species are sorted in descending order of occurrence. The IUCN Status column indicates the conservation status of each species: EN (Endangered), VU (Vulnerable), NT (Near Threatened), and LC (Least Concern). In this study, species are categorized as nonthreatened (0) if classified as LC or NT and threatened (1) if classified as EN or VU.

Species	**Common name**	**Frequency of occurrence (%)**	**IUCN Status**	**IUCN Status reference**	**Threatened**
Scyliorhinus canicula	Small-spotted catshark	10,7	LC	Finucci et al. (2021)	0
Galeus melastomus	Blackmouth catshark	10,0	LC	Abella et al. (2016)	0
Squalus acanthias	Spurdog	8,7	EN	Ellis, Soldo, et al. (2016)	1
Etmopterus spinax	Velvet belly lanternshark	8,2	LC	Guallart et al. (2016)	0
Raja clavata	Thornback skate	7,8	NT	Ellis, Dulvy, et al. (2016)	0
Chimaera monstrosa	Rabbitfish	6,2	NT	Dagit & Hareide (2016)	0
Raja asterias	Starry skate	3,6	NT	Serena, Abella, et al. (2016)	0
Myliobatis aquila	Common eagle ray	3,5	VU	Serena, Holtzhausen, et al. (2016)	1
Raja miraletus	Brown skate	3,5	LC	Dulvy et al. (2020)	0
Mustelus spp.	Smooth-hound	3,1	VU	Farrell & Dulvy (2016)	1

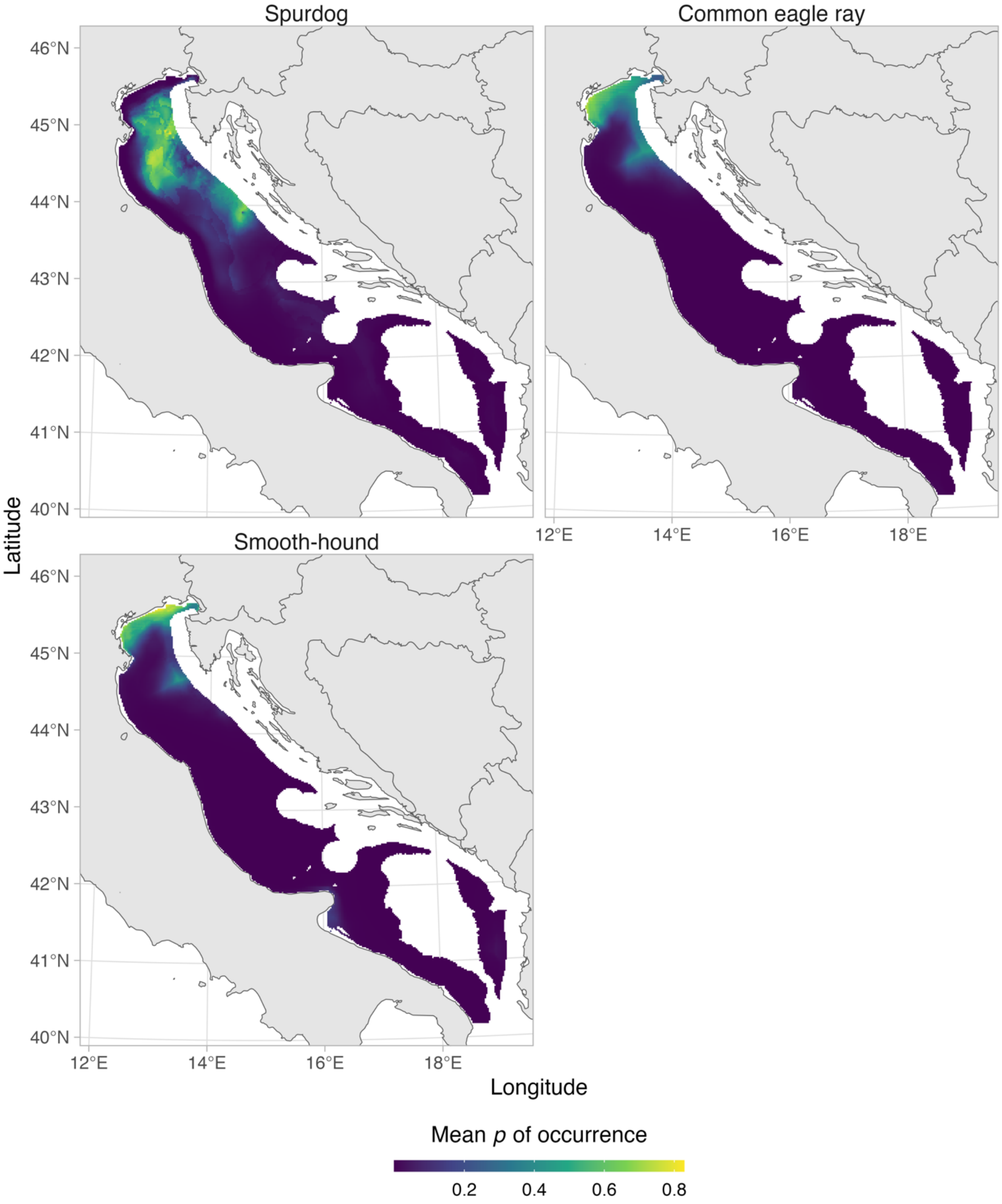

Figure 2. Mean predicted probability (p) of occurrence for the threatened species. Means are computed over the period 2009 to 2021.

Species richness exhibited a distinct contrast between the coastal central and southern regions, which were relatively poor in species, and the northern and deeper southern regions, which were rich in species (Figure 3a). In the northern areas, the relatively high probability of occurrence of spurdog, smooth-hound, and common eagle ray (Figure 2) contributed to the observed higher species richness. On the other hand, the higher species richness observed in the deeper southern regions was driven by the local high probability of occurrence of deep-sea species such as blackmouth catshark, velvet belly lanternshark, and rabbitfish (Supplementary Information: Figure S8). Although the overall level of uncertainty in the mean predicted species richness was relatively low (SD < 0.4), it exhibited higher values in the central and southern offshore areas, suggesting greater temporal variations (Figure 3b). The proportion of threatened species was found to be highest in the northernmost part of the study area and lowest along the central and southernmost coasts (Figure 3c). This pattern was influenced by the relatively high local probability of occurrence of spurdog, smooth-hound, and common eagle ray in the northern regions, all of which are classified as threatened species (Figure 2). The overall level of uncertainty in the mean proportion of threatened species remained relatively low (SD < 0.2), exhibiting lower values in the northern and central coastal regions as well as in the southern and southeastern offshore areas. This suggests that these specific areas experienced lower temporal fluctuations (Figure 3d).

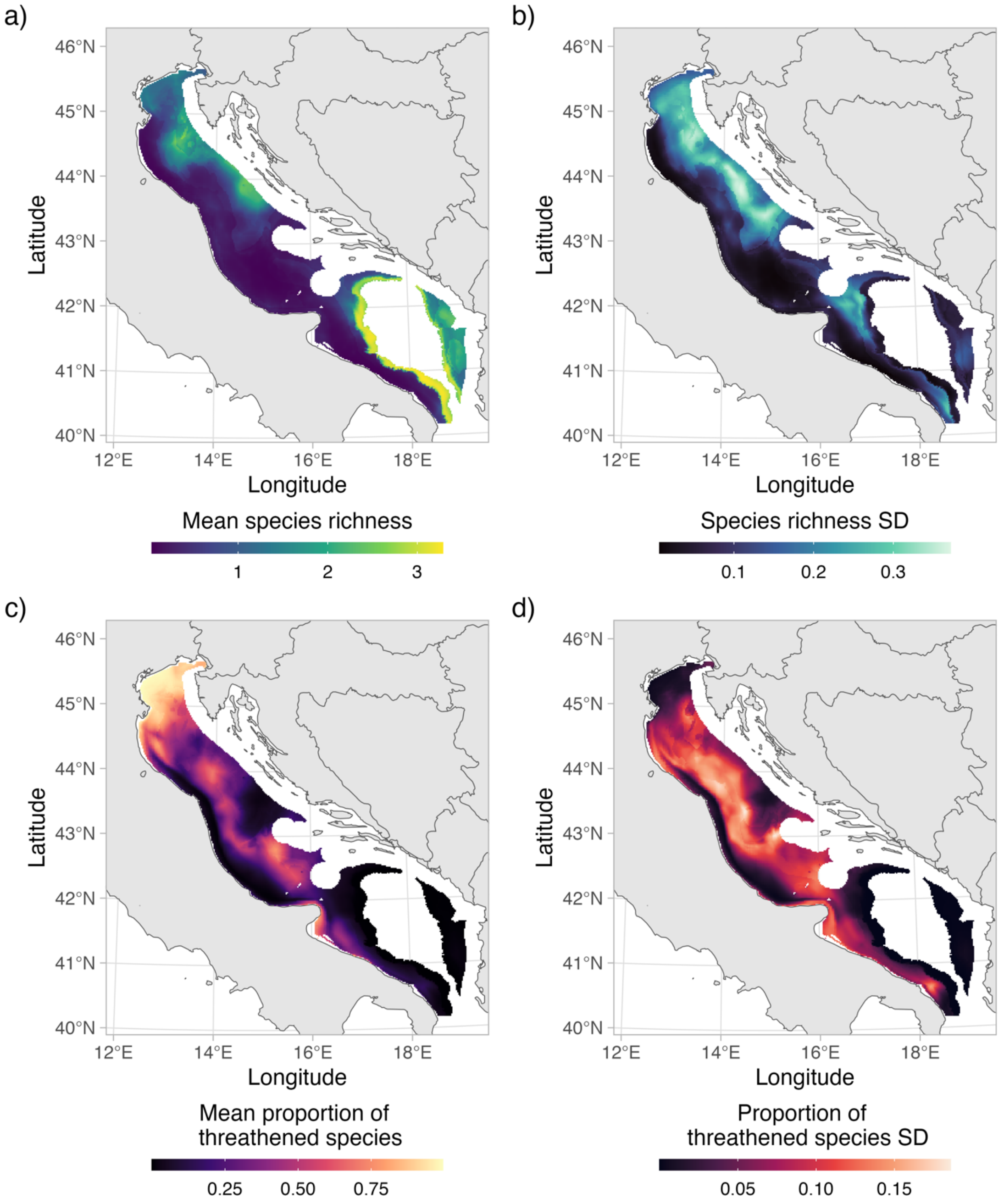

Figure 3. Mean and standard deviation (SD) of species richness (a-b). Mean and SD of proportion of threatened species (c-d). Metrics are computed over the period 2009 to 2021.

Single species overlap with fishing effort

Spatial Overlap Index

For the threatened species, the analysis of the Spatial Overlap Index (SOI) between species and fishing effort across the most recent years (2018-2021) revealed high mean overlap scores for the spurdog, common eagle ray, and smooth-hound in the northernmost part of the study area, both for OTB and TBB (Figure 4). Additionally, spurdog exhibited a notable level of overlap with OTB along the offshore regions in the northern-central part of the basin. The SOI for the nonthreatened species is reported in Supplementary Information: Figures S9-S10. Despite year-to-year fluctuations, the SOI values remained relatively consistent over time, with closer years showing higher similarity (Supplementary Information: Figures S11-S14).

Range overlap

For several species, there was a high potential risk of bycatch extending across a significant portion of their distribution within the study area, as indicated by high range overlap values (RO). Among the species analyzed, starry skate, spurdog, and velvet belly lantern shark were found to share a significant overlap with regions of intensive OTB fishing effort, as indicated by higher RO values (≥ 0.15, averaged across years). Rabbitfish, common eagle ray, blackmouth catshark, smooth-hound, and brown skate exhibited somewhat lower but still significant RO values (< 0.15 and ≥ 0.1, averaged across years) (Figure 5).

On the other hand, common eagle ray, smooth-hound, spurdog and starry skate had the highest overlap with regions affected by TBB activities (≥ 0.1, averaged across years) (Fig. 3). The RO metrics exhibited variations across years, with significant fluctuations observed for certain species, including spurdog, common eagle ray, and smooth-hound, in both OTB and TBB contexts (Figure 5). Temporal patterns were also evident, with RO values increasing or decreasing together in certain years, likely in response to changes in fishing effort.These findings remained consistent regardless of the threshold used (Supplementary Information: Figures S15-S16).

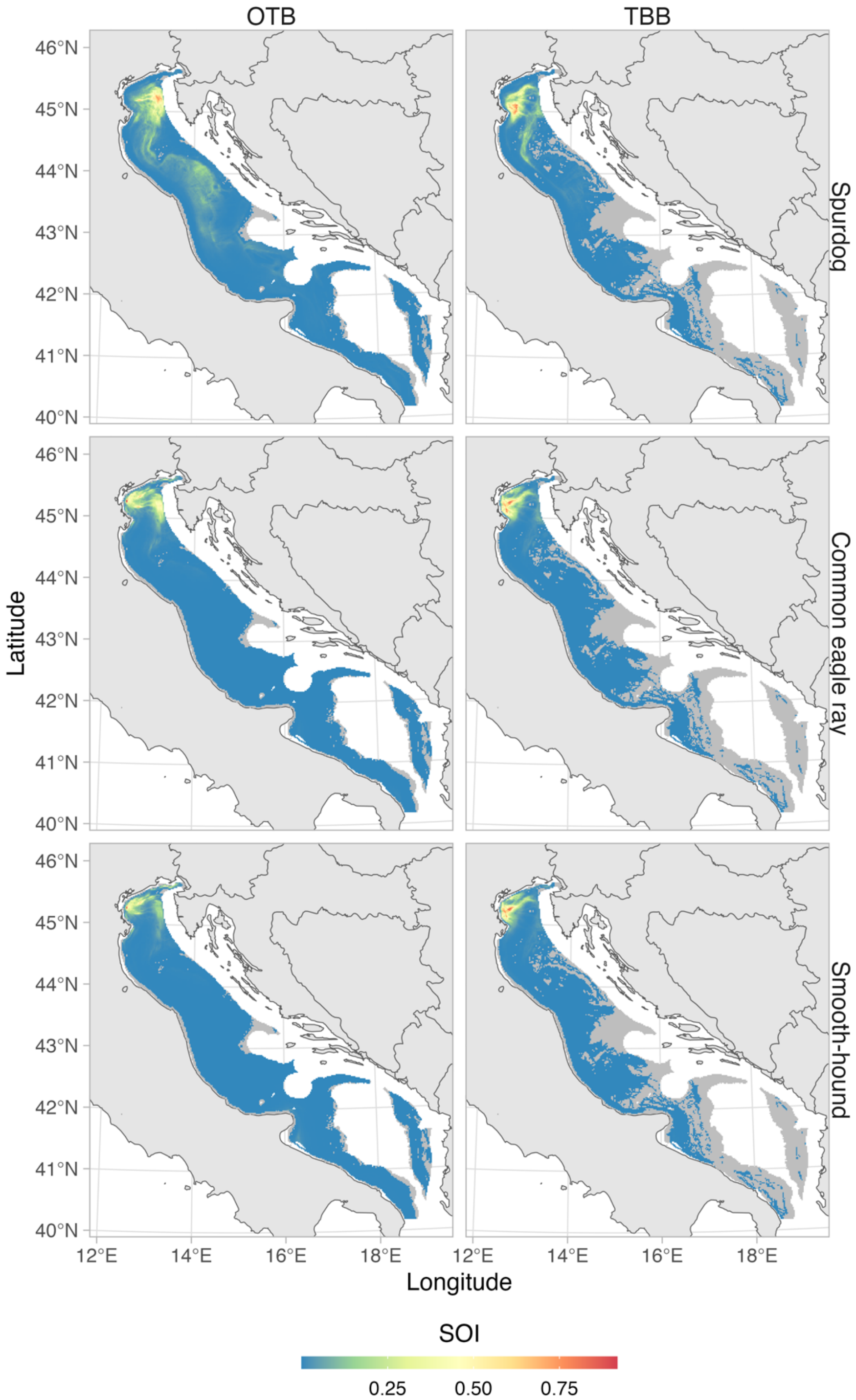

Figure 4. Mean Spatial Overlap Index (SOI) for threatened species and otter bottom trawling (OTB) and beam trawling (TBB) computed over the period 2018-2021. SOI values of 0 are displayed in gray.

Community overlap with fishing effort

Species richness

In general, the areas exhibiting simultaneous high species richness and high OTB fishing effort were predominantly found in the northernmost section of the basin and in some areas along the outer edge of the continental shelf in the southernmost region (Figure 6). On the other hand, for TBB, our analysis revealed significant overlap between regions of high species richness and fishing effort in the northernmost area of the basin and the northern central region (Figure 6). Additionally, we identified two distinct zones in the northern-central part of the basin and in the deeper offshore southernmost areas, characterized by high species richness and comparatively low fishing effort of OTB and TBB (Figure 6).

Proportion of threathened species

The analysis of OTB revealed distinct patterns in the spatial overlap between fishing effort and the proportion of threatened species. Specifically, in the northernmost regions of the study area, high fishing effort coincided with a higher proportion of threatened species (Figure 7). However, towards the central and southern portions of the study area, the proportion of threatened species gradually diminishes, in combination with the consistently high levels of OTB fishing activity. Regarding TBB, a clear spatial pattern emerges. The northern part of the study area exhibits a pronounced overlap between fishing effort and the proportion of threatened species. However, this overlap rapidly diminishes southward (Figure 7). Moreover, we identified distinct areas in both the northernmost and northern-central parts of the basin, which were characterized by a medium-to-high proportion of threatened species and relatively low fishing effort of OTB and TBB (Figure 7).

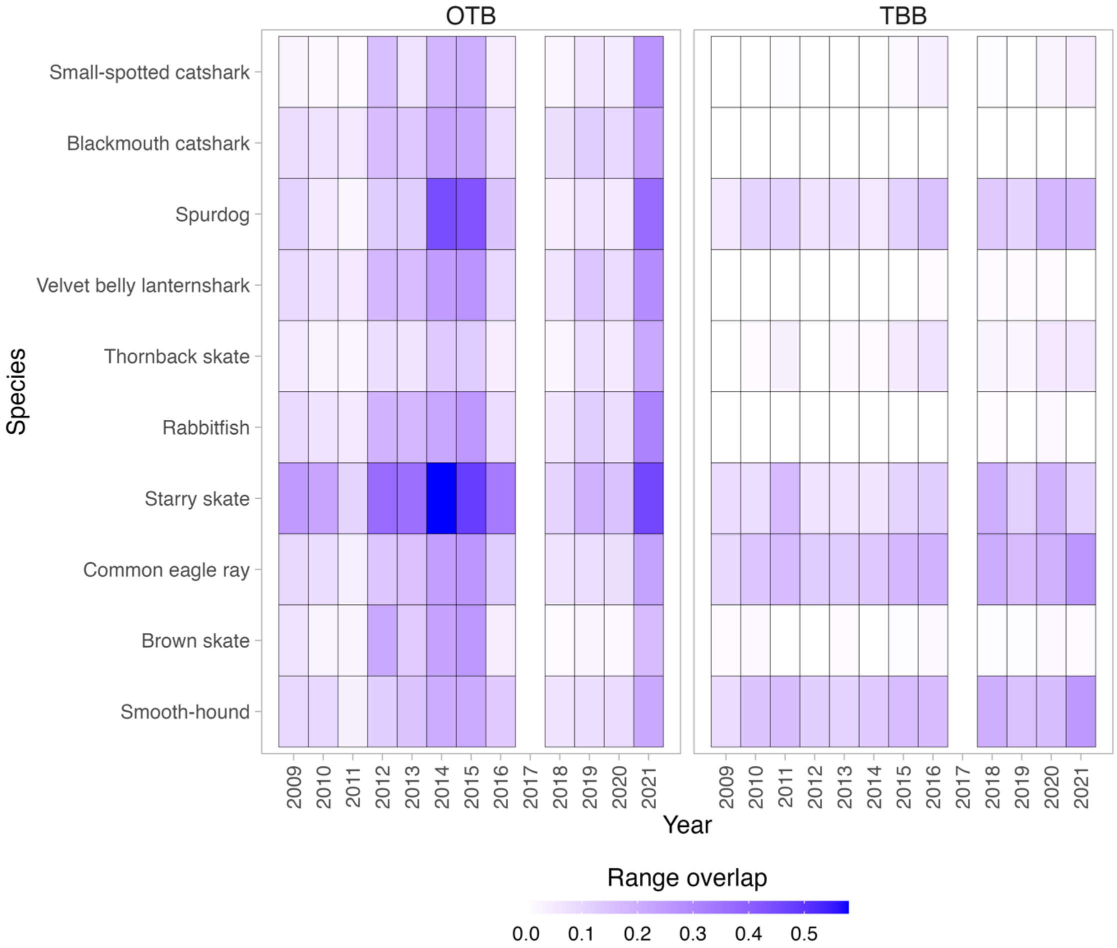

Figure 5. Yearly range overlap (RO) between species and otter bottom trawling (OTB) and beam trawling (TBB) fishing gears. A grid cell is considered to be occupied by a species with ≥ 75th percentile of the probability of occurrence, and by trawling activities with ≥ 75th percentile of fishing effort. The year 2017 is omitted due to sampling occurring outside the designated sampling period (May to September; see the section Survey data in Methods).

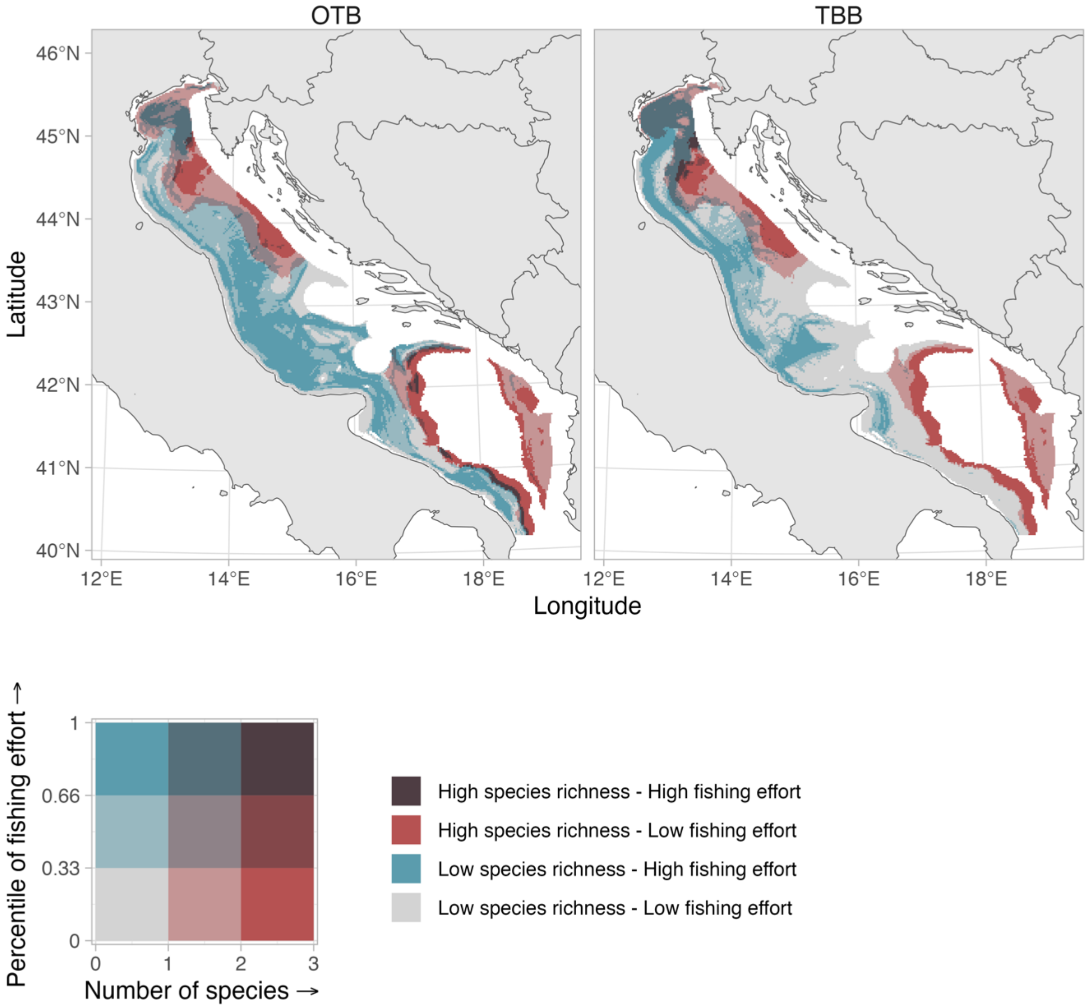

Figure 6. Bivariate plot illustrating the relationship between mean species richness and the percentile of fishing effort for the period 2018-2021 for otter bottom trawling (OTB) and beam trawling (TBB). Dark red areas indicate locations with the highest mean predicted number of species and higest fishing effort. Light red areas correspond to regions characterized by high species richness and low fishing effort. Conversely, dark blue areas represent locations with high fishing effort but a low number of species, whereas gray areas depict regions where both fishing effort and number of species are low.

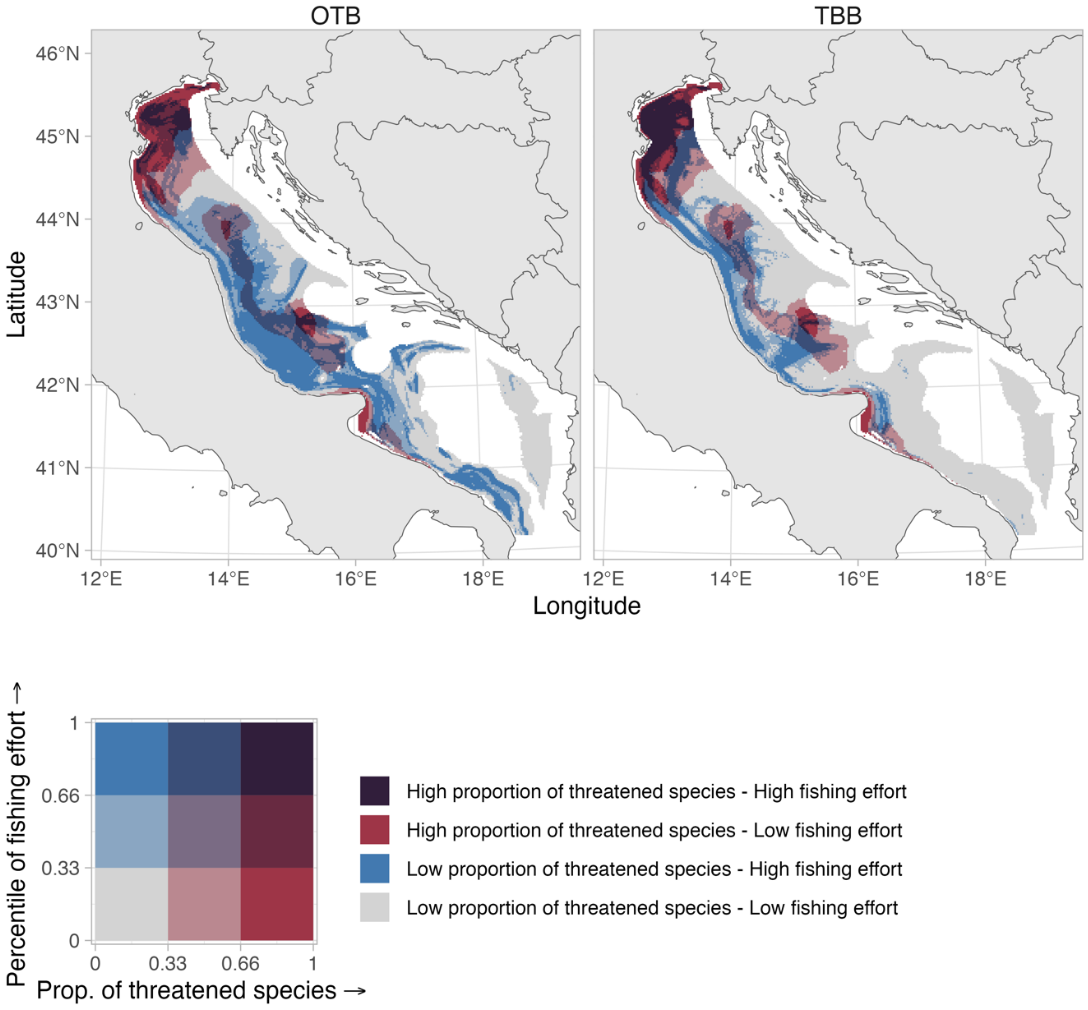

Figure 7. Bivariate plot illustrating the relationship between the mean proportion (prop.) of threatened species and the percentile of fishing effort for the period 2018-2021 for otter bottom trawling (OTB) and beam trawling (TBB). Dark red areas indicate locations with the highest mean predicted proportion of threatened species and fishing effort. Light red areas correspond to regions characterized by a high proportion of threatened species and low fishing effort. Conversely, dark blue areas represent locations with high fishing effort but a low proportion of threatened species, whereas gray areas depict regions where both fishing effort and the proportion of threatened species are low.

Discussion

Effective marine conservation and fisheries management requires a comprehensive understanding of the spatial overlap between species distribution and fishing activities (Douvere, 2008). Especially for chondrichthyans, the deficiency of such information is often recognized as a key factor contributing to the failure to implement suitable management measures (Cavanagh & Gibson, 2007; FAO, 2022). Bottom trawl fishing is known to result in incidental bycatch of nontarget species, including chondrichthyans (Carpentieri et al., 2021). In addition to the direct removal of chondrichthyans, bottom trawl fishing also poses a threat to their habitats. The use of weighted nets dragged along the seabed can cause disturbance and destruction of benthic habitats and removal of the associated biota (ICES, 2023; Sciberras et al., 2018; Watling & Norse, 1998), which are crucial for the reproduction, sheleter and foraging of many chondrichthyans (e.g. Carrier & Pratt, 1998; Heithaus et al., 2002; Simpfendorfer & Milward, 1993).

In this study, we propose an innovative approach that produces model-based overlap between chondrichthyan distribution and bottom trawl fishing, leveraging high-resolution Vessel Monitoring System (VMS) and the spatial distribution of species derived from geostatistical models fitted to fishery-independent survey data. This information may serve as a critical tool for identifying areas that require protection and implementing conservation measures, such as establishing protected zones or imposing fishing restrictions. Such measures can play a crucial role in safeguarding vulnerable chondrichthyan species and communities, thus promoting their conservation and recovery. We applied this integrated approach to the Adriatic Sea, an highly exploited area (Amoroso et al., 2018) characterized by a long history of chondrichthyan depletion (Ferretti et al., 2013) and limited data on their incidental catches (FAO, 2022). We addressed the latter knowledge gap providing novel insights into the potential interaction between chondrichthyans and bottom trawl fishing in this basin.

Our findings reveal significant spatial overlap between chondrichthyans and bottom trawl fishing hotspots in the western part of the Adriatic Sea. This overlap raises concerns about the vulnerability of chondrichthyans, that also includes threatened shark and ray species, to fishing pressure, particularly in regions with high fishing intensity. Our results show distinct spatial patterns of overlap, highlighting both areas of concern and potential refuge for chondrichthyan populations.

We detected two distinct species richness hotspots within the study domain. One hotspot, situated in the northern and central offshore region of the basin, featured primarily threatened species like spurdog, smooth-hound, and common eagle ray, as well as some non-threatened species including thornback skate and small-spotted catshark. The second hotspot, located in the southern and deepest regions, was characterized by the presence of non-threatened deep sea species such as blackmouth catshark, velvet belly lanternshark, and rabbitfish.

In the northwestern part of the Adriatic Sea, we observed a pronounced overlap between the distribution of several threatened chondrichthyan species such as spurdog, smooth-hound, and common eagle ray, and locations of intense bottom trawl fishing activity. These same areas were identified as bycatch hotspot for these species by the pelagic fleet, as confirmed through direct onboard observations (Bonanomi et al., 2018) and are recognized as Important Sharks and Rays Areas (ISRA) due to their significance in harboring threatened species and serving as essential reproductive habitats for these species (IUCN SSC Shark Specialist Group, 2023).

Notably, this significant spatial overlap persisted over a considerable portion of these species habitat, despite some year-to-year fluctuations. These areas of high spatial overlap suggest potential risks for threatened chondrichthyan populations.

Conversely, we also identified areas with minimal spatial overlap between high chondrichthyans probability of occurrence and bottom trawl fishing, indicating potential refuge areas. One such area, known as "area dei fondi sporchi" (or "dirty area") by local fishers, located in the northern-central part of the basin, contains relict sand rich in epifaunal organisms that make trawling difficult or even impossible (Scaccini, 1967).

Furthermore, our analysis revealed localized differences in spatial overlap between different fishing gears, such as otter bottom trawling (OTB) and beam trawling (TBB), along the central and southern Adriatic coastline. These differences highlight the significance of taking specific fishing gears, and their respective potential impacts, into account when evaluating spatial overlap and formulating effective management strategies. Notably, both OTB and TBB are the focal gears addressed within the Multiannual Management Plan (GFCM, 2019) for demersal species in the Adriatic Sea including hake (*Merluccius merluccius*), red mullet (*Mullus barbatus*), common cuttlefish (*Sepia oficinalis*), Norway lobster (*Nephrops norvegicus*) and common sole (*Solea solea*) (Sea Around Us, 2006). This Management Plan combines different measures and among them, fishing effort regimes and spatio-temporal closures. Tailoring conservation measures, within this management context, related to these fishing gears and their interactions with chondrichthyan populations, can optimize conservation efforts and minimize unintended bycatch or habitat damage.

In addition to identifying hotspots of overlap between species or proportion of threatened species with fishing, our model-based approach also allows calculation of range overlaps. This is an important metric along identifying hotspots of overlap, because together with distribution models, it provides information about potential effects of relocating spatial fishing effort. For instance, for species with clear spatial hotspots and low range overlap, relocating fishing effort might reduce mortality from incidental bycatch substantially within the domain. However, for species with high range overlap, simply limiting fishing in “the hottest spot” might have neglible effects, if the fishery over the entire species range and the area with high overlap is large. This illustrates the need to develop a suite of indices before implementing spatial fisheries-restrictions. Understanding where fishing would increase after such an intervention, and how that affects 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 our study provides novel insights into the spatial overlap between chondrichthyan distribution and bottom trawl fishing in the western part of the Adriatic Sea, there are certain limitations that should be considered when interpreting the results. Firstly, our analysis relied on the availability and quality of data sources, which may introduce uncertainties and biases. For instance, VMS data is considered a good proxy for fishing effort for the fleet segment larger than 15 meters in overall length, while their reliability decreases for vessels between 12 and 15 meters in length, and miss the fishing effort of the fleet below 12 meters. This may result in only a partial representation of fishing activities, potentially leading to an incomplete understanding of the spatial overlap between fishing and chondrichthyan distribution for smaller vessels. Secondly, 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 the majority of the fleet that should have the major impact on the chondrichthyans in the study area. Additionally, SDMs are subject to inherent limitations, such as uncertainties in species occurrence data, model assumptions, and potential omission of relevant environmental variables. However, the approach described here, calculating overlap on model-predicted probabilities of occurrence also has benefits, primarily in that it is not as sensitive to temporal changes in sampling across in space (Thorson et al., 2016). Lastly, the spatial resolution of our analysis may influence the observed patterns of overlap. While we aimed to use the finest available resolution of the data, the accuracy and precision of VMS data and species occurrence records can vary spatially. Fine-scale variations in both fishing effort and chondrichthyan distribution may not have been fully captured in our analysis, potentially leading to underestimation or overestimation of the true spatial overlap. Despite these mentioned constraints, the approach presented here, to the best of our knowledge, offers the most comprehensive information available regarding the overlap of bottom trawl fishing effort with the chondrichthyan community in the Adriatic Sea.

Our analysis focused on a specific period of the year (from the late spring to the end of summer) due to the lack of consistent autumn and winter fisheries-independent surveys during the last twenty years. Seasonal variations in fishing effort and chondrichthyan distribution may occur though, and therefore caution must be taken in extrapolating our results to other seasons, especially for conservation and management purposes.

While spatial overlap between fishing activities and chondrichthyan distribution indicates potential interaction, it does not directly provide evidence of actual biological impacts or quantify the extent of such impacts on chondrichthyan populations. Nevertheless, Mediterranean chondrichthyans are widely acknowledged to be highly vulnerable to trawlers (Carpentieri et al., 2021; Cavanagh & Gibson, 2007; FAO, 2022). Given the limited availability of direct and quantitative official bycatch data, our results may offer an initial and valid approach to inform conservation efforts and guide precautionary management decisions.

In conclusion, our study introduces an innovative approach that combines VMS data with geostatistical species distribution models, allowing us to analyze the spatial co-occurrence of chondrichthyan species and commercial bottom trawl fishing practices in the Adriatic Sea. Through this analysis, we identified areas of heightened risk for bycatch and thus of potential impacts on chondrichthyan populations, as well as areas that could serve as potential refuge. These findings provides therefore new knowledge that may support the implementation of targeted conservation efforts and the development of effective spatial management measures in the region.

Author Contributions

F.M. conceptualized the study with contributions from M.C.; C.M., W.Z. and I.B. prepared the raw survey data. T.R. prepared the VMS data. F.M. conducted the statistical analysis with contributions from B.W., M.L. and M.C.; F.M. wrote the initial draft and all authors reviewed the different drafts and contributed to the submitted version.

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Open research statement

The study was based on the MEDITS survey data collected through the EU Data Collection Framework (DCF-MEDITS). Access to these data is currently governed by EU Regulation 2017/1004. To request access to this data, contact the Italian Direzione Generale della Pesca Marittima e dell'Acquacoltura of 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).

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Supplementary Information to

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

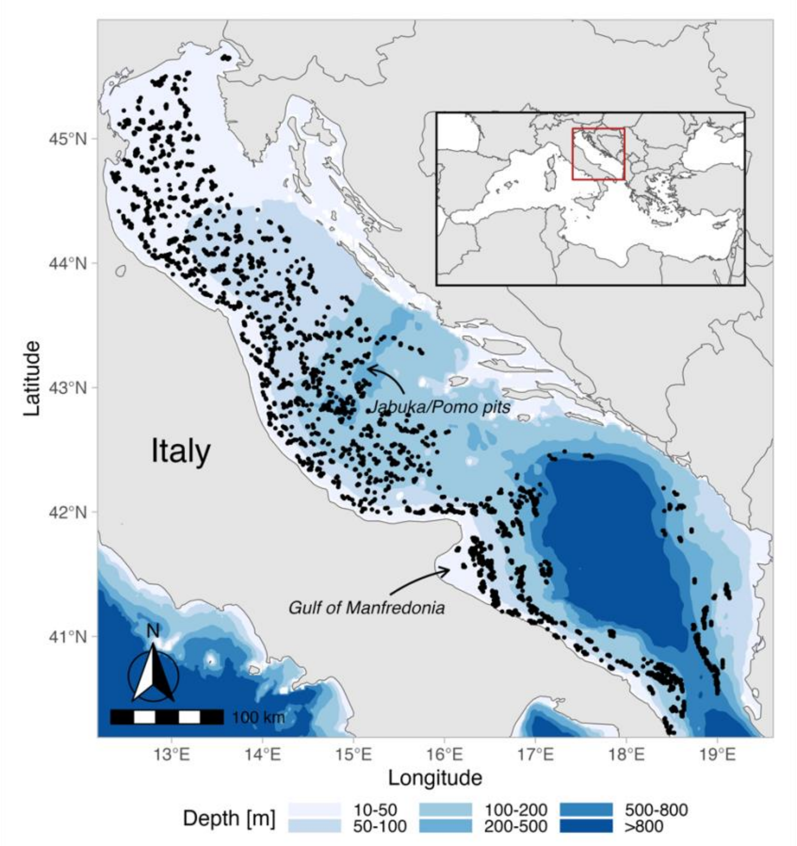


Figure S1. Location of the study area and the positions of MEDITS bottom trawl hauls swept during the period 1999–2021 selected and analyzed in this study.

Table S1. Environmental covariates included in the best fitting model for each species, along with their respective explanatory power. Species are ordered according to model selection similarities. Green cells represent the combinations of covariates tested during model selection, while the '+' sign indicates the terms that were retained by the best fitting model, as selected by Akaike Information Criterion. T = temperature; Oxy = oxygen; T:Oxy = interaction term between T and Oxy; AUC = Area Under the Curve.

Species	Depth	log(Depth)	Depth + Depth^2	log(Depth) + log(Depth^2)	T	T + T^2	Substrate	Oxy	T:Oxy	Conditional R2	AUC
Spurdog			🟩	+	🟩	+	+	+	+	0,89	0,98
Small-spotted catshark			+	🟩	+	🟩	+	+	+	0,84	0,97
Thornback skate			🟩	+	🟩	+	+	+	🟩	0,76	0,96
Blackmouth catshark	🟩	🟩	+	🟩						0,86	0,99
Velvet belly lanternshark	🟩	🟩	+	🟩						0,92	0,99
Rabbit fish	🟩	🟩	+	🟩						0,88	0,99
Starry skate	🟩	🟩	🟩	+	🟩	+				0,54	0,91
Common eagle ray	🟩	🟩	+	🟩	+	🟩				0,86	0,98
Smooth-hound	🟩	🟩	🟩	+	+	🟩				0,76	0,98
Brown skate	🟩	🟩	🟩	+	🟩	🟩				0,92	0,98

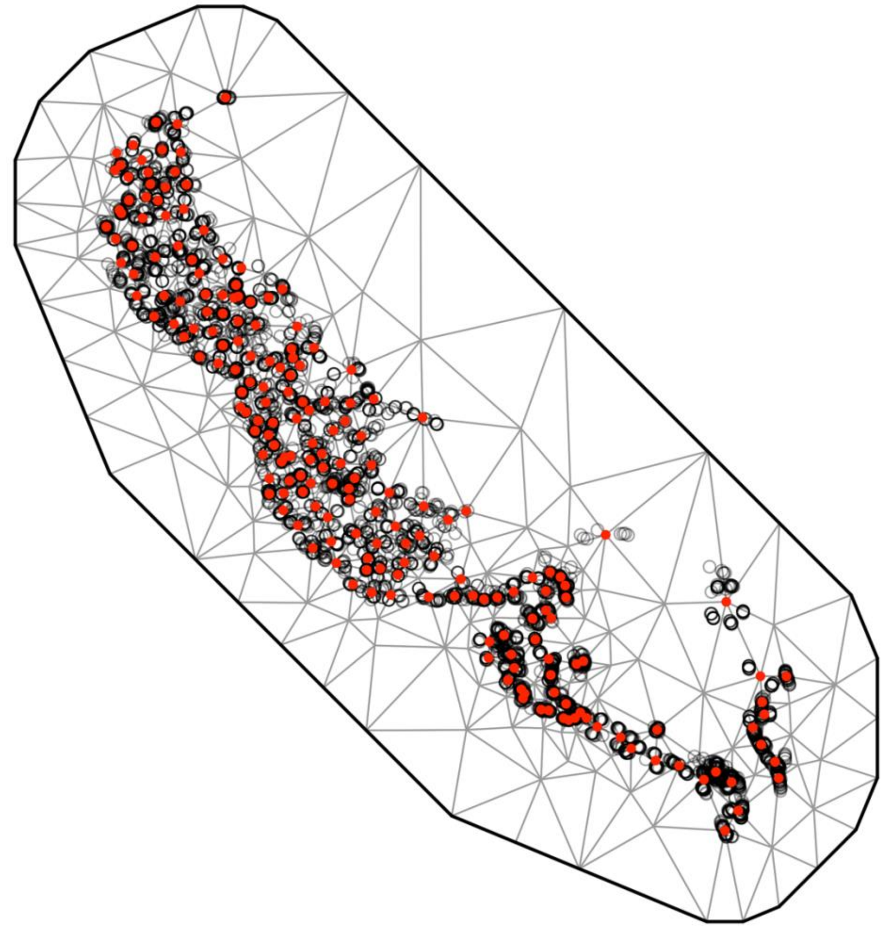


Figure S2. Stochastic Partial Differential Equation (SPDE) mesh for the species distribution models. The knots (n=200) are displayed in red, and the haul positions are represented as open circles.

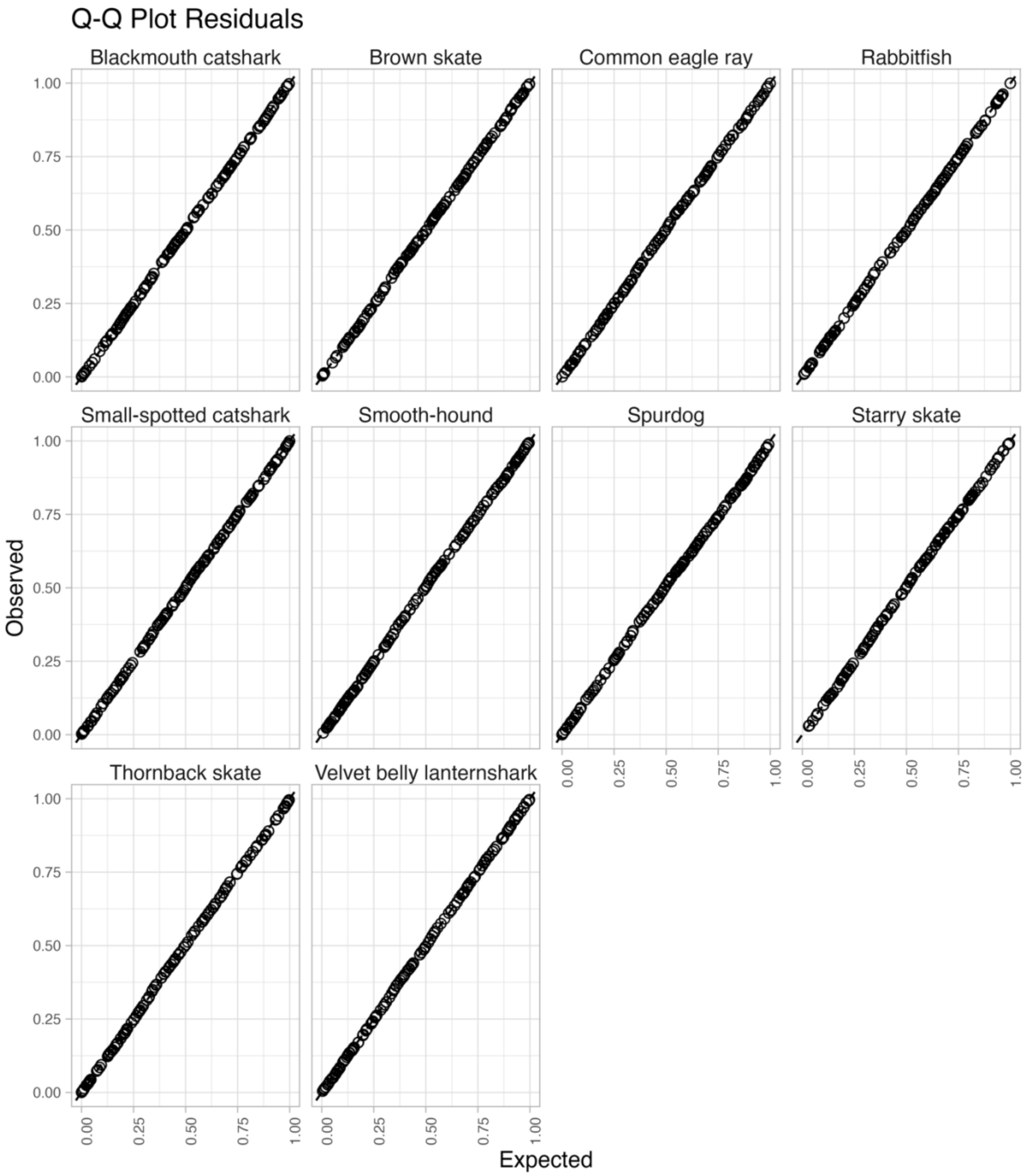


Figure S3. Quantile-quantile plot illustrating randomized quantile residuals of the species distribution models. To enhance clarity, a random sample of 1000 points was selected and visualized.

Figure S4. Quantile regression of the residuals of the species distribution models. Solid lines represent the theoretical expectations for the 0.25, 0.5, and 0.75 quantiles, while dashed lines represent the observed values. To enhance clarity, a random sample of 1000 data points was selected and displayed.

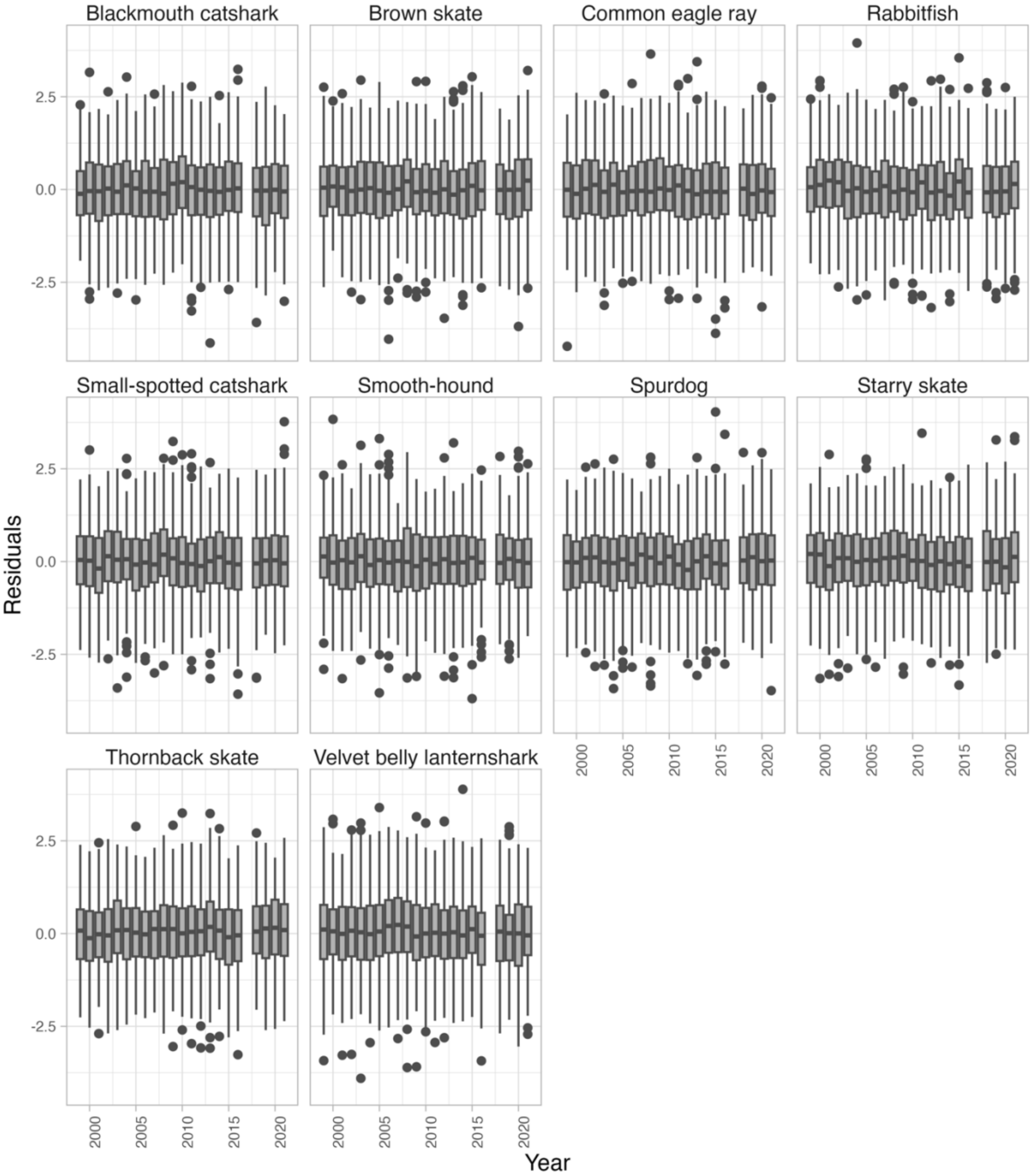


Figure S5. Residuals of the species distribution models aggregated by year. The year 2017 is omitted due to sampling occurring outside the designated sampling period (May to September; see the section *Survey data* in *Methods*).

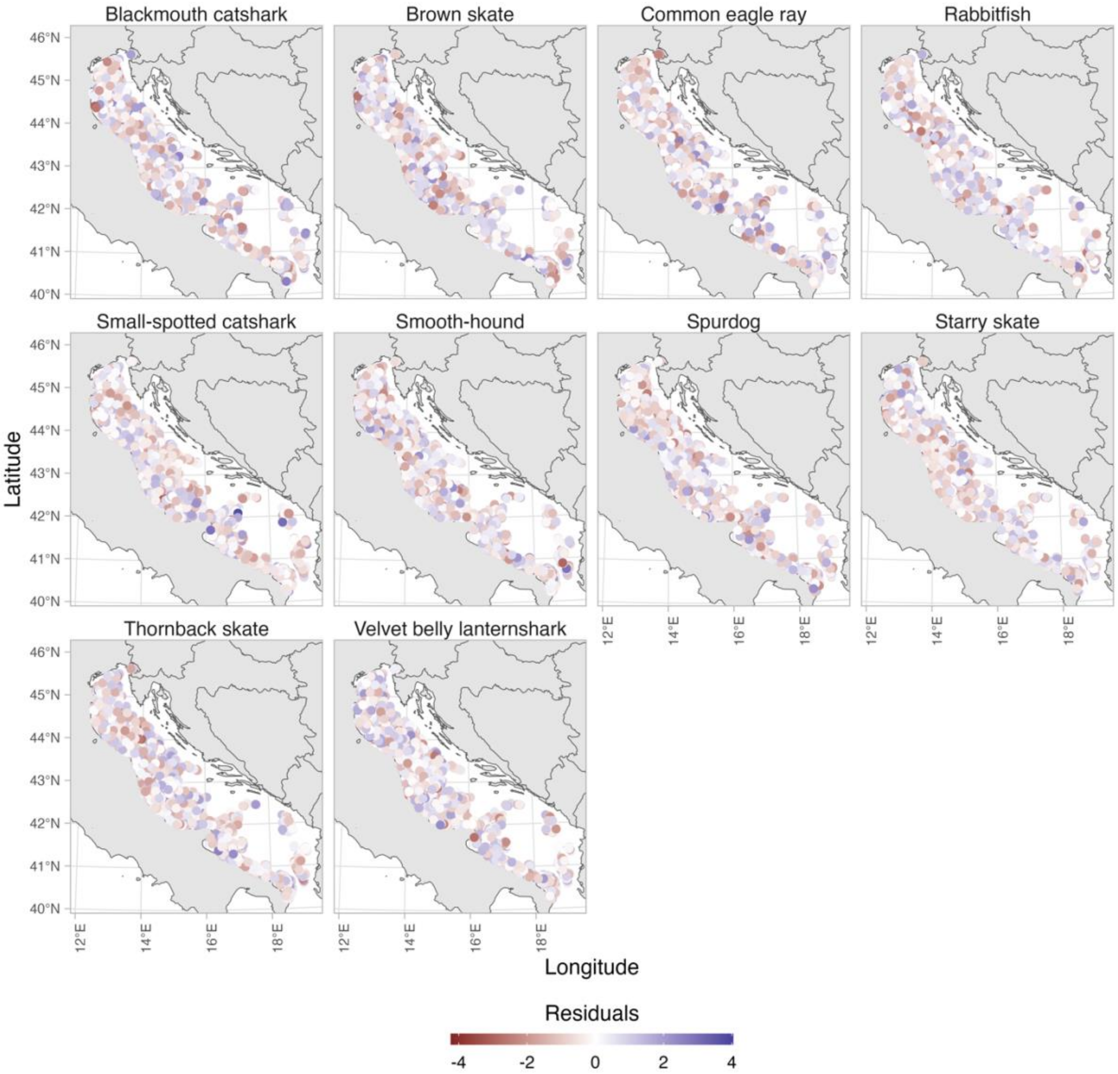


Figure S6. Residuals of the species distribution models plotted in space.

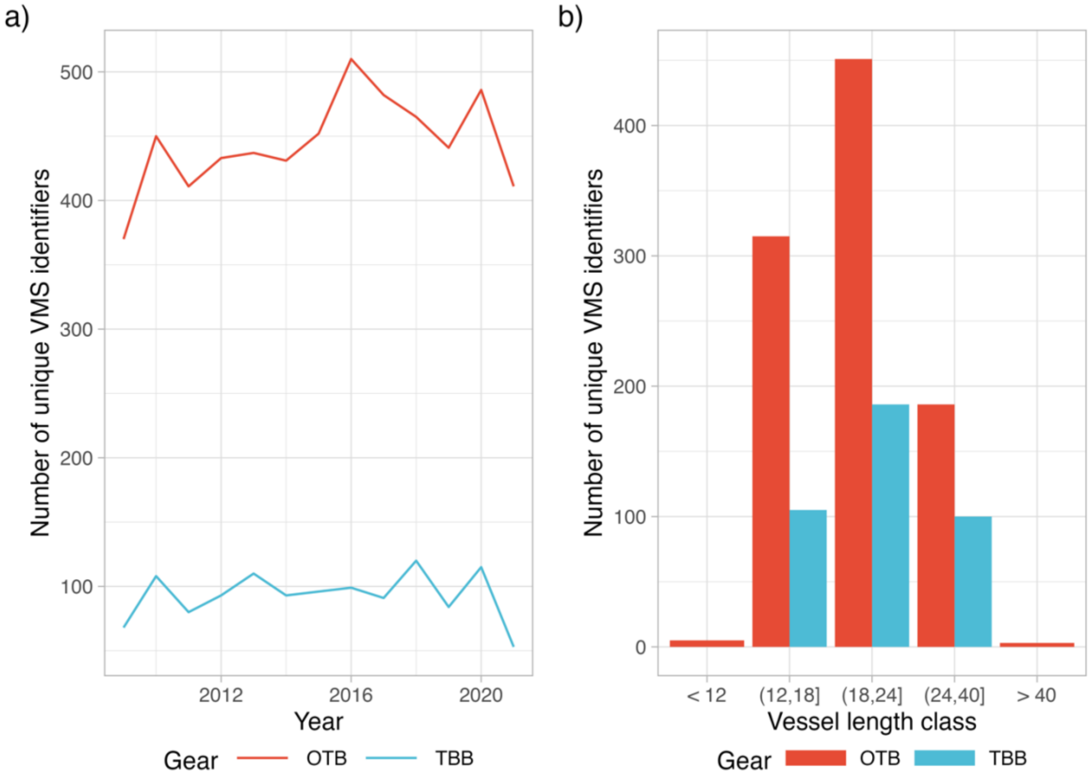


Figure S7. Number of unique VMS identifiers per year separated into otter bottom trawling (OTB) and beam trawling (TBB) (a). Number of unique VMS identifiers categorized by vessel length class (b).

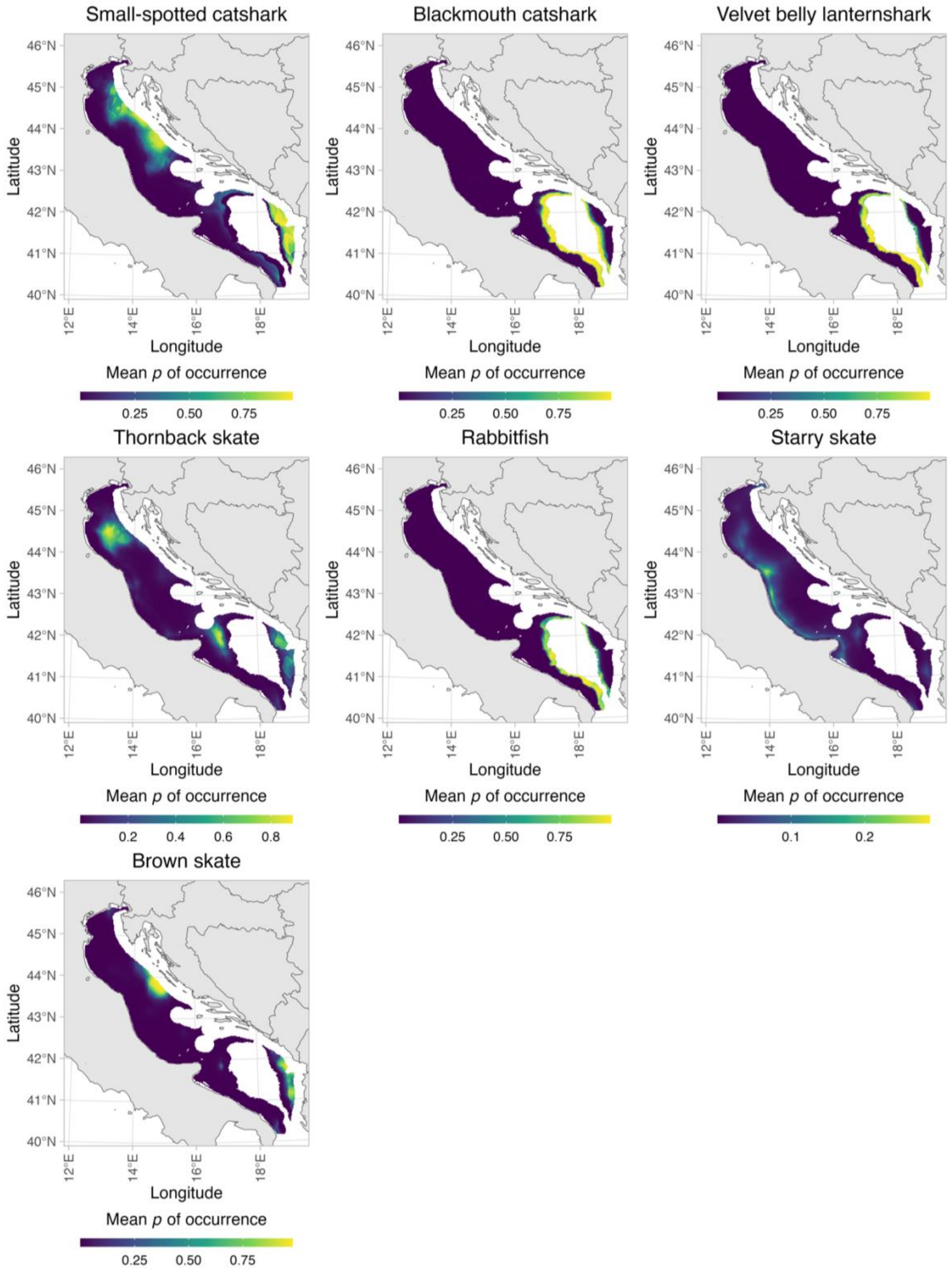


Figure S8. Mean probability (p) of occurrence for the nonthreatened species. Means are computed over the period 2009 to 2021.

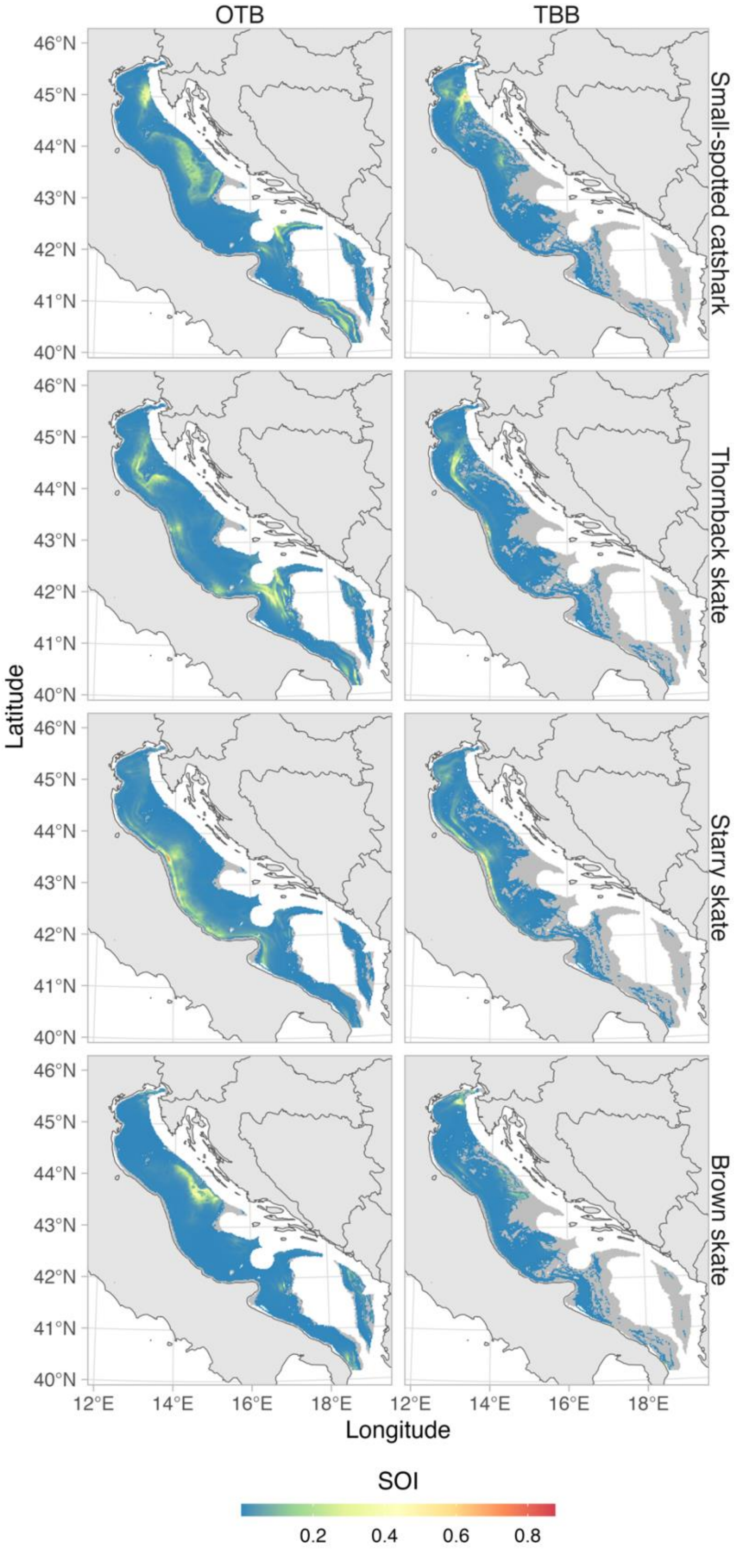


Figure S9. Mean Spatial Overlap Index (SOI) for nonthreatened species computed over the period 2018-2021. SOI values of 0 are displayed in gray.

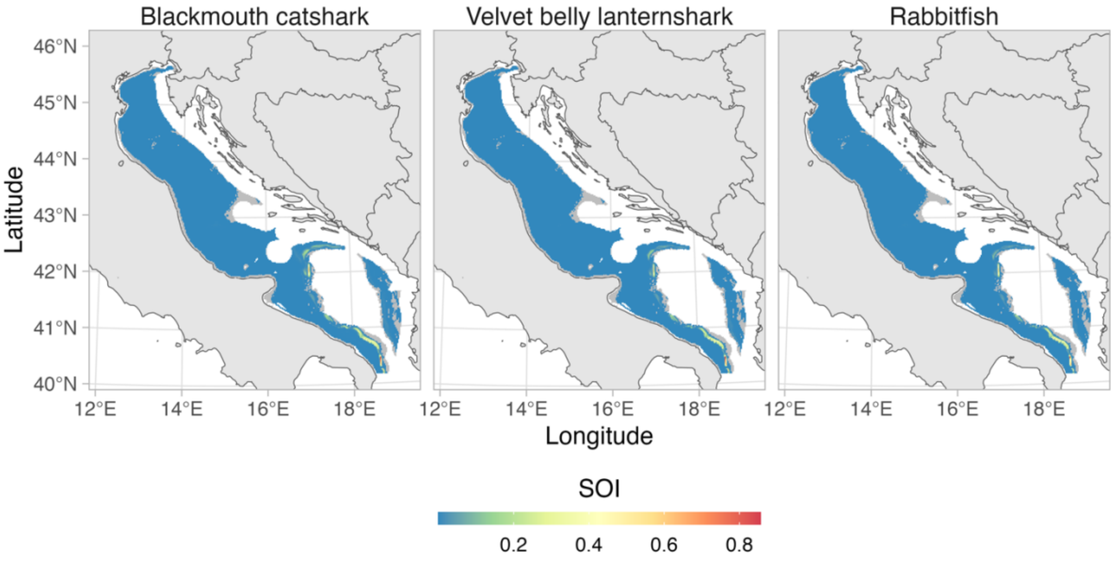
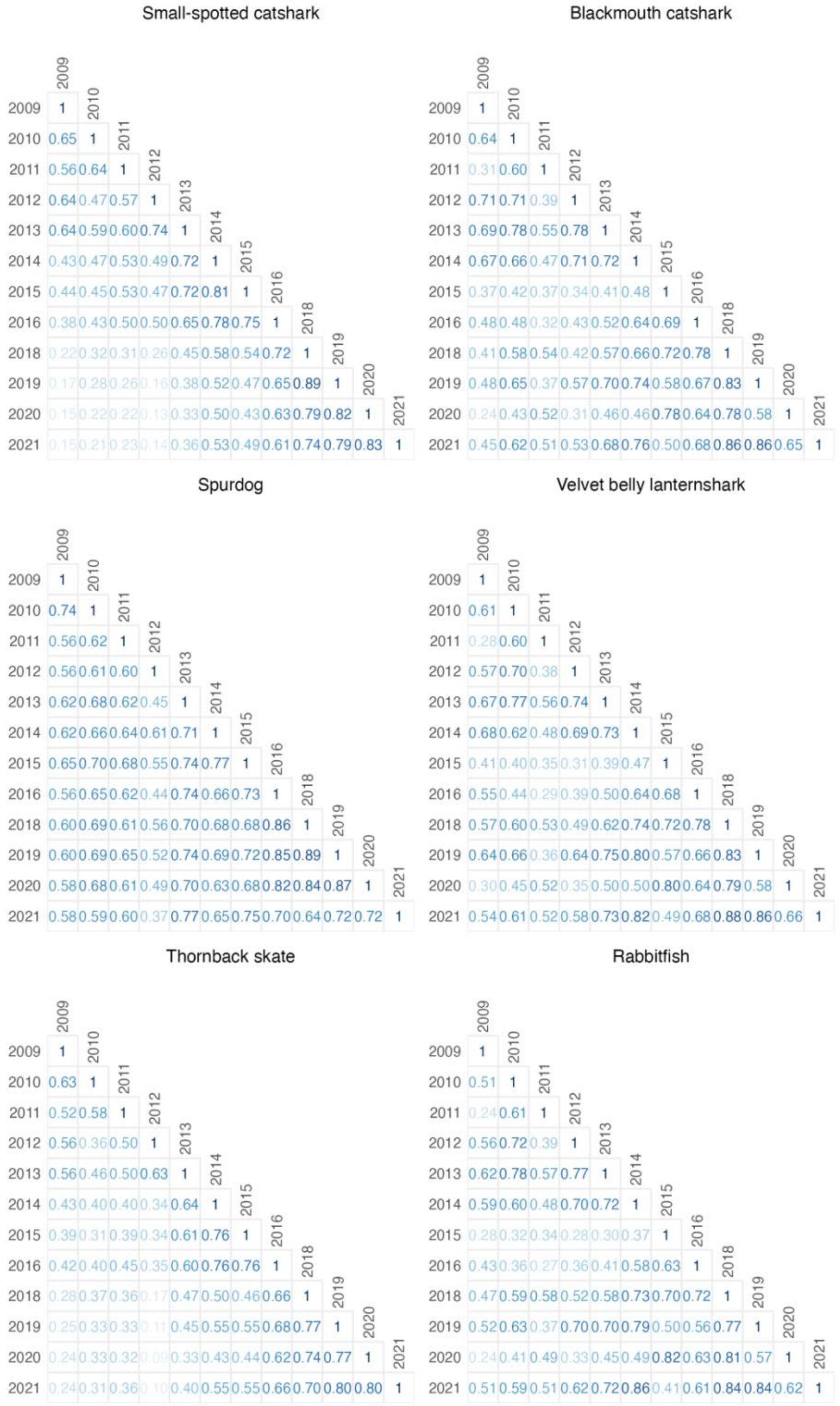


Figure S10. Mean Spatial Overlap Index (SOI) between for the remaining nonthreatened species and OTB for the years 2018-2021. SOI values of 0 are displayed in gray. For simplicity, only SOI with OTB is shown due to virtually 0 overlap of these deep-sea species with TBB.



Small-spotted catshark

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.65	1										
2011	0.56	0.64	1									
2012	0.64	0.47	0.57	1								
2013	0.64	0.59	0.60	0.74	1							
2014	0.43	0.47	0.53	0.49	0.72	1						
2015	0.44	0.45	0.53	0.47	0.72	0.81	1					
2016	0.38	0.43	0.50	0.50	0.65	0.78	0.75	1				
2018	0.22	0.32	0.31	0.26	0.45	0.58	0.54	0.72	1			
2019	0.17	0.28	0.26	0.16	0.38	0.52	0.47	0.65	0.89	1		
2020	0.15	0.22	0.22	0.13	0.33	0.50	0.43	0.63	0.79	0.82	1	
2021	0.15	0.21	0.23	0.14	0.36	0.53	0.49	0.61	0.74	0.79	0.83	1

Blackmouth catshark

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.64	1										
2011	0.31	0.60	1									
2012	0.71	0.71	0.39	1								
2013	0.69	0.78	0.55	0.78	1							
2014	0.67	0.66	0.47	0.71	0.72	1						
2015	0.37	0.42	0.37	0.34	0.41	0.48	1					
2016	0.48	0.48	0.32	0.43	0.52	0.64	0.69	1				
2018	0.41	0.58	0.54	0.42	0.57	0.66	0.72	0.78	1			
2019	0.48	0.65	0.37	0.57	0.70	0.74	0.58	0.67	0.83	1		
2020	0.24	0.43	0.52	0.31	0.46	0.46	0.78	0.64	0.78	0.58	1	
2021	0.45	0.62	0.51	0.53	0.68	0.76	0.50	0.68	0.86	0.86	0.65	1

Spurdog

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.74	1										
2011	0.56	0.62	1									
2012	0.56	0.61	0.60	1								
2013	0.62	0.68	0.62	0.45	1							
2014	0.62	0.66	0.64	0.61	0.71	1						
2015	0.65	0.70	0.68	0.55	0.74	0.77	1					
2016	0.56	0.65	0.62	0.44	0.74	0.66	0.73	1				
2018	0.60	0.69	0.61	0.56	0.70	0.68	0.68	0.86	1			
2019	0.60	0.69	0.65	0.52	0.74	0.69	0.72	0.85	0.89	1		
2020	0.58	0.68	0.61	0.49	0.70	0.63	0.68	0.82	0.84	0.87	1	
2021	0.58	0.59	0.60	0.37	0.77	0.65	0.75	0.70	0.64	0.72	0.72	1

Velvet belly lanternshark

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.61	1										
2011	0.28	0.60	1									
2012	0.57	0.70	0.38	1								
2013	0.67	0.77	0.56	0.74	1							
2014	0.68	0.62	0.48	0.69	0.73	1						
2015	0.41	0.40	0.35	0.31	0.39	0.47	1					
2016	0.55	0.44	0.29	0.39	0.50	0.64	0.68	1				
2018	0.57	0.60	0.53	0.49	0.62	0.74	0.72	0.78	1			
2019	0.64	0.66	0.36	0.64	0.75	0.80	0.57	0.66	0.83	1		
2020	0.30	0.45	0.52	0.35	0.50	0.50	0.80	0.64	0.79	0.58	1	
2021	0.54	0.61	0.52	0.58	0.73	0.82	0.49	0.68	0.88	0.86	0.66	1

Thornback skate

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.63	1										
2011	0.52	0.58	1									
2012	0.56	0.36	0.50	1								
2013	0.56	0.46	0.50	0.63	1							
2014	0.43	0.40	0.40	0.34	0.64	1						
2015	0.39	0.31	0.39	0.34	0.61	0.76	1					
2016	0.42	0.40	0.45	0.35	0.60	0.76	0.76	1				
2018	0.28	0.37	0.36	0.17	0.47	0.50	0.46	0.66	1			
2019	0.25	0.33	0.33	0.11	0.45	0.55	0.55	0.68	0.77	1		
2020	0.24	0.33	0.32	0.09	0.33	0.43	0.44	0.62	0.74	0.77	1	
2021	0.24	0.31	0.36	0.10	0.40	0.55	0.55	0.66	0.70	0.80	0.80	1

Rabbitfish

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.51	1										
2011	0.24	0.61	1									
2012	0.56	0.72	0.39	1								
2013	0.62	0.78	0.57	0.77	1							
2014	0.59	0.60	0.48	0.70	0.72	1						
2015	0.28	0.32	0.34	0.28	0.30	0.37	1					
2016	0.43	0.36	0.27	0.36	0.41	0.58	0.63	1				
2018	0.47	0.59	0.58	0.52	0.58	0.73	0.70	0.72	1			
2019	0.52	0.63	0.37	0.70	0.70	0.79	0.50	0.56	0.77	1		
2020	0.24	0.41	0.49	0.33	0.45	0.49	0.82	0.63	0.81	0.57	1	
2021	0.51	0.59	0.51	0.62	0.72	0.86	0.41	0.61	0.84	0.84	0.62	1

Figure S11. Inter-year correlations of Spatial Overlap Index for some species and OTB. Values in blue inside the plot represent Pearson correlation coefficients.

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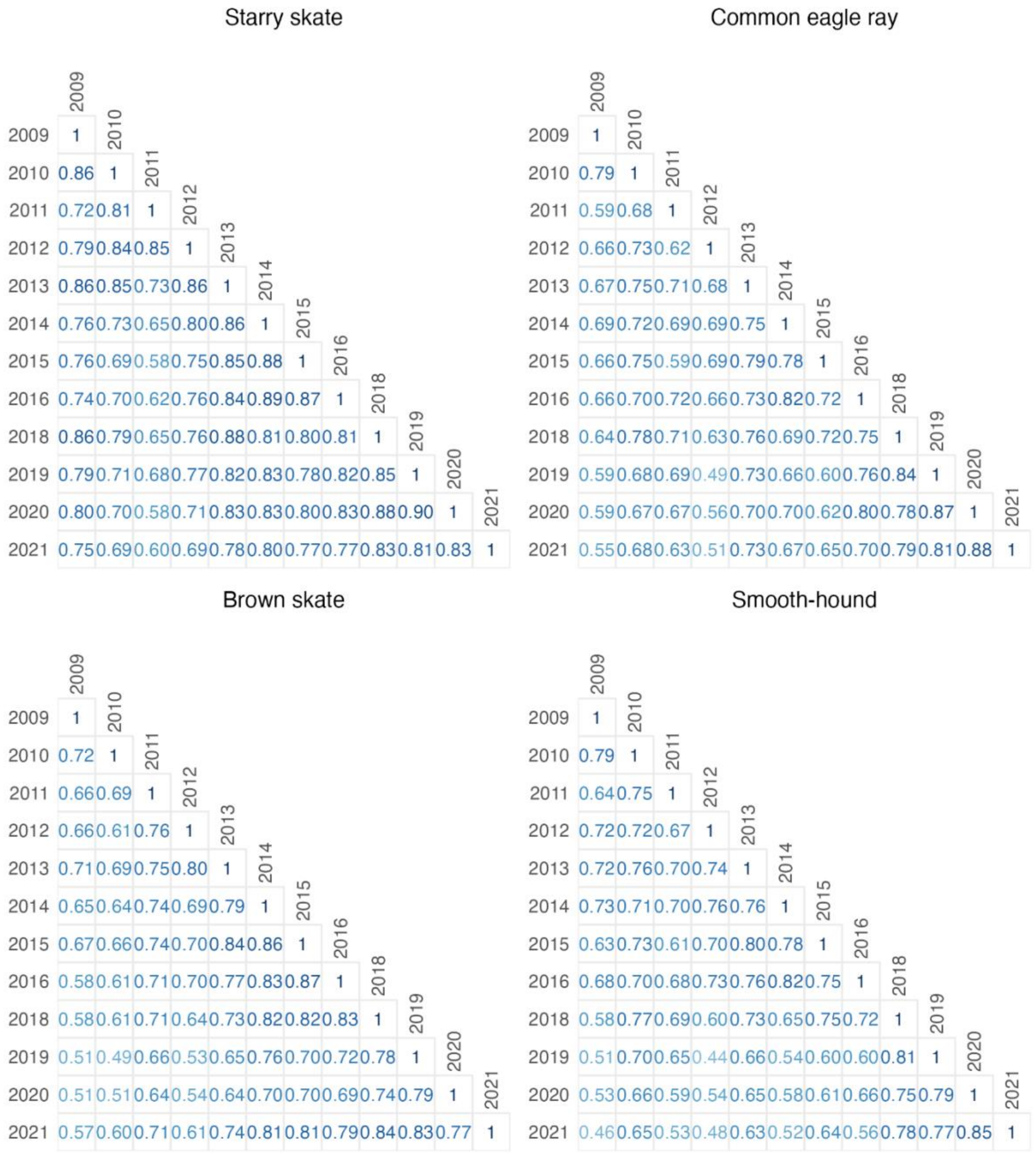


Starry skate

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.86	1										
2011	0.72	0.81	1									
2012	0.79	0.84	0.85	1								
2013	0.86	0.85	0.73	0.86	1							
2014	0.76	0.73	0.65	0.80	0.86	1						
2015	0.76	0.69	0.58	0.75	0.85	0.88	1					
2016	0.74	0.70	0.62	0.76	0.84	0.89	0.87	1				
2018	0.86	0.79	0.65	0.76	0.88	0.81	0.80	0.81	1			
2019	0.79	0.71	0.68	0.77	0.82	0.83	0.78	0.82	0.85	1		
2020	0.80	0.70	0.58	0.71	0.83	0.83	0.80	0.83	0.88	0.90	1	
2021	0.75	0.69	0.60	0.69	0.78	0.80	0.77	0.77	0.83	0.81	0.83	1

Common eagle ray

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.79	1										
2011	0.59	0.68	1									
2012	0.66	0.73	0.62	1								
2013	0.67	0.75	0.71	0.68	1							
2014	0.69	0.72	0.69	0.69	0.75	1						
2015	0.66	0.75	0.59	0.69	0.79	0.78	1					
2016	0.66	0.70	0.72	0.66	0.73	0.82	0.72	1				
2018	0.64	0.78	0.71	0.63	0.76	0.69	0.72	0.75	1			
2019	0.59	0.68	0.69	0.49	0.73	0.66	0.60	0.76	0.84	1		
2020	0.59	0.67	0.67	0.56	0.70	0.70	0.62	0.80	0.78	0.87	1	
2021	0.55	0.68	0.63	0.51	0.73	0.67	0.65	0.70	0.79	0.81	0.88	1

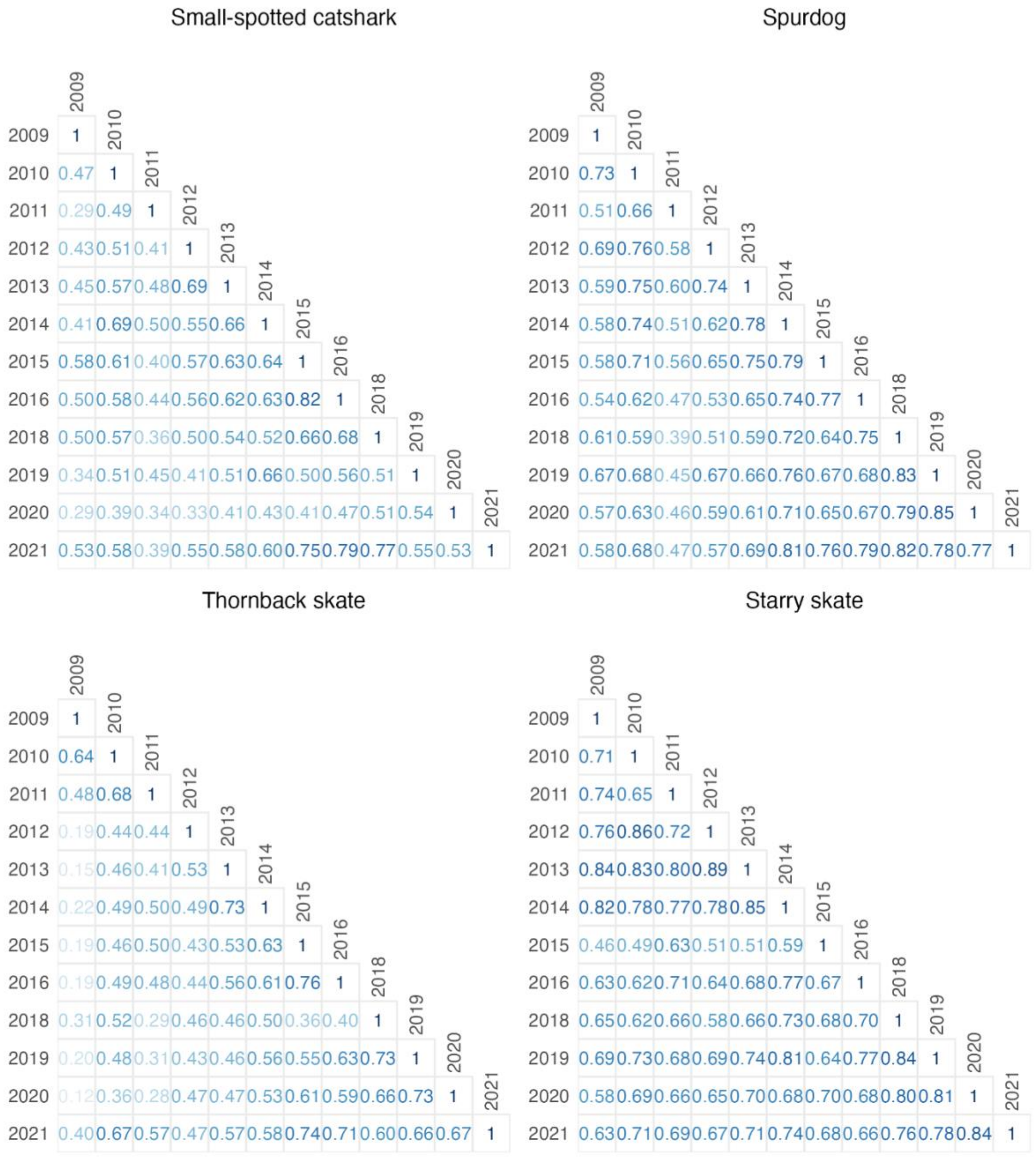
Brown skate

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.72	1										
2011	0.66	0.69	1									
2012	0.66	0.61	0.76	1								
2013	0.71	0.69	0.75	0.80	1							
2014	0.65	0.64	0.74	0.69	0.79	1						
2015	0.67	0.66	0.74	0.70	0.84	0.86	1					
2016	0.58	0.61	0.71	0.70	0.77	0.83	0.87	1				
2018	0.58	0.61	0.71	0.64	0.73	0.82	0.82	0.83	1			
2019	0.51	0.49	0.66	0.53	0.65	0.76	0.70	0.72	0.78	1		
2020	0.51	0.51	0.64	0.54	0.64	0.70	0.70	0.69	0.74	0.79	1	
2021	0.57	0.60	0.71	0.61	0.74	0.81	0.81	0.79	0.84	0.83	0.77	1

Smooth-hound

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.79	1										
2011	0.64	0.75	1									
2012	0.72	0.72	0.67	1								
2013	0.72	0.76	0.70	0.74	1							
2014	0.73	0.71	0.70	0.76	0.76	1						
2015	0.63	0.73	0.61	0.70	0.80	0.78	1					
2016	0.68	0.70	0.68	0.73	0.76	0.82	0.75	1				
2018	0.58	0.77	0.69	0.60	0.73	0.65	0.75	0.72	1			
2019	0.51	0.70	0.65	0.44	0.66	0.54	0.60	0.60	0.81	1		
2020	0.53	0.66	0.59	0.54	0.65	0.58	0.61	0.66	0.75	0.79	1	
2021	0.46	0.65	0.53	0.48	0.63	0.52	0.64	0.56	0.78	0.77	0.85	1

Figure S12. Inter-year correlations of Spatial Overlap Index for the remaining species and OTB. Values in blue inside the plot represent Pearson correlation coefficients.



Small-spotted catshark

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.47	1										
2011	0.29	0.49	1									
2012	0.43	0.51	0.41	1								
2013	0.45	0.57	0.48	0.69	1							
2014	0.41	0.69	0.50	0.55	0.66	1						
2015	0.58	0.61	0.40	0.57	0.63	0.64	1					
2016	0.50	0.58	0.44	0.56	0.62	0.63	0.82	1				
2018	0.50	0.57	0.36	0.50	0.54	0.52	0.66	0.68	1			
2019	0.34	0.51	0.45	0.41	0.51	0.66	0.50	0.56	0.51	1		
2020	0.29	0.39	0.34	0.33	0.41	0.43	0.41	0.47	0.51	0.54	1	
2021	0.53	0.58	0.39	0.55	0.58	0.60	0.75	0.79	0.77	0.55	0.53	1

Spurdog

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.73	1										
2011	0.51	0.66	1									
2012	0.69	0.76	0.58	1								
2013	0.59	0.75	0.60	0.74	1							
2014	0.58	0.74	0.51	0.62	0.78	1						
2015	0.58	0.71	0.56	0.65	0.75	0.79	1					
2016	0.54	0.62	0.47	0.53	0.65	0.74	0.77	1				
2018	0.61	0.59	0.39	0.51	0.59	0.72	0.64	0.75	1			
2019	0.67	0.68	0.45	0.67	0.66	0.76	0.67	0.68	0.83	1		
2020	0.57	0.63	0.46	0.59	0.61	0.71	0.65	0.67	0.79	0.85	1	
2021	0.58	0.68	0.47	0.57	0.69	0.81	0.76	0.79	0.82	0.78	0.77	1

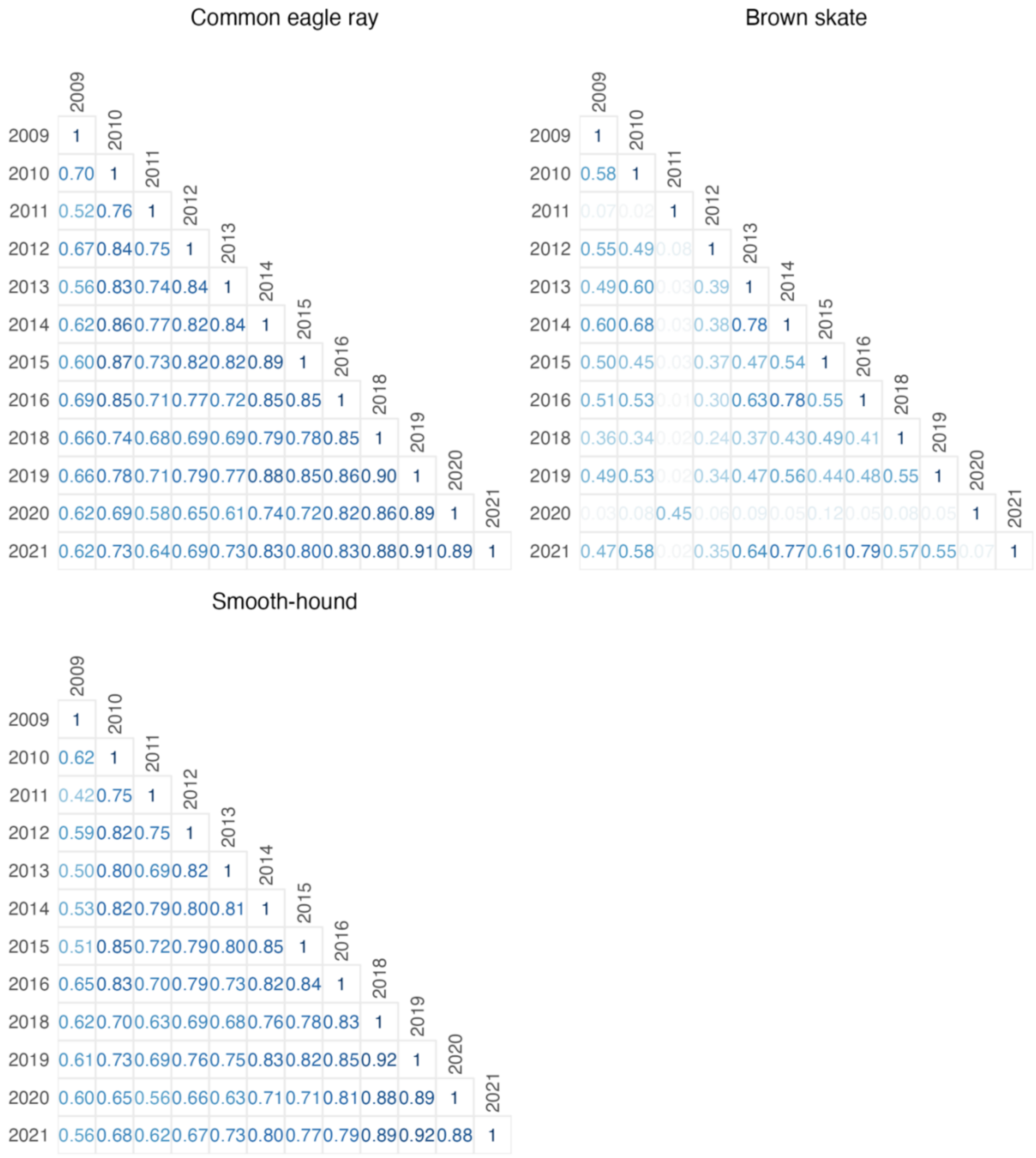
Thornback skate

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.64	1										
2011	0.48	0.68	1									
2012	0.19	0.44	0.44	1								
2013	0.15	0.46	0.41	0.53	1							
2014	0.22	0.49	0.50	0.49	0.73	1						
2015	0.19	0.46	0.50	0.43	0.53	0.63	1					
2016	0.19	0.49	0.48	0.44	0.56	0.61	0.76	1				
2018	0.31	0.52	0.29	0.46	0.46	0.50	0.36	0.40	1			
2019	0.20	0.48	0.31	0.43	0.46	0.56	0.55	0.63	0.73	1		
2020	0.12	0.36	0.28	0.47	0.47	0.53	0.61	0.59	0.66	0.73	1	
2021	0.40	0.67	0.57	0.47	0.57	0.58	0.74	0.71	0.60	0.66	0.67	1

Starry skate

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.71	1										
2011	0.74	0.65	1									
2012	0.76	0.86	0.72	1								
2013	0.84	0.83	0.80	0.89	1							
2014	0.82	0.78	0.77	0.78	0.85	1						
2015	0.46	0.49	0.63	0.51	0.51	0.59	1					
2016	0.63	0.62	0.71	0.64	0.68	0.77	0.67	1				
2018	0.65	0.62	0.66	0.58	0.66	0.73	0.68	0.70	1			
2019	0.69	0.73	0.68	0.69	0.74	0.81	0.64	0.77	0.84	1		
2020	0.58	0.69	0.66	0.65	0.70	0.68	0.70	0.68	0.80	0.81	1	
2021	0.63	0.71	0.69	0.67	0.71	0.74	0.68	0.66	0.76	0.78	0.84	1

Figure S13. Inter-year correlations of Spatial Overlap Index for some species and TBB. Values in blue inside the plot represent Pearson correlation coefficients.



Common eagle ray

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.70	1										
2011	0.52	0.76	1									
2012	0.67	0.84	0.75	1								
2013	0.56	0.83	0.74	0.84	1							
2014	0.62	0.86	0.77	0.82	0.84	1						
2015	0.60	0.87	0.73	0.82	0.82	0.89	1					
2016	0.69	0.85	0.71	0.77	0.72	0.85	0.85	1				
2018	0.66	0.74	0.68	0.69	0.69	0.79	0.78	0.85	1			
2019	0.66	0.78	0.71	0.79	0.77	0.88	0.85	0.86	0.90	1		
2020	0.62	0.69	0.58	0.65	0.61	0.74	0.72	0.82	0.86	0.89	1	
2021	0.62	0.73	0.64	0.69	0.73	0.83	0.80	0.83	0.88	0.91	0.89	1

Brown skate

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.58	1										
2011	0.07	0.02	1									
2012	0.55	0.49	0.08	1								
2013	0.49	0.60	0.03	0.39	1							
2014	0.60	0.68	0.03	0.38	0.78	1						
2015	0.50	0.45	0.03	0.37	0.47	0.54	1					
2016	0.51	0.53	0.01	0.30	0.63	0.78	0.55	1				
2018	0.36	0.34	0.02	0.24	0.37	0.43	0.49	0.41	1			
2019	0.49	0.53	0.02	0.34	0.47	0.56	0.44	0.48	0.55	1		
2020	0.03	0.08	0.45	0.06	0.09	0.05	0.12	0.05	0.08	0.05	1	
2021	0.47	0.58	0.02	0.35	0.64	0.77	0.61	0.79	0.57	0.55	0.07	1

Smooth-hound

	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019	2020	2021
2009	1											
2010	0.62	1										
2011	0.42	0.75	1									
2012	0.59	0.82	0.75	1								
2013	0.50	0.80	0.69	0.82	1							
2014	0.53	0.82	0.79	0.80	0.81	1						
2015	0.51	0.85	0.72	0.79	0.80	0.85	1					
2016	0.65	0.83	0.70	0.79	0.73	0.82	0.84	1				
2018	0.62	0.70	0.63	0.69	0.68	0.76	0.78	0.83	1			
2019	0.61	0.73	0.69	0.76	0.75	0.83	0.82	0.85	0.92	1		
2020	0.60	0.65	0.56	0.66	0.63	0.71	0.71	0.81	0.88	0.89	1	
2021	0.56	0.68	0.62	0.67	0.73	0.80	0.77	0.79	0.89	0.92	0.88	1

Figure S14. Inter-year correlations of Spatial Overlap Index for the remaining species and TBB. Inter-year correlations of deep-sea species (blackmouth catshark, velvet belly lanternshark and rabbitfish) and TBB are not shown as their overlap is virtually 0. Values in blue inside the plot represent Pearson correlation coefficients.

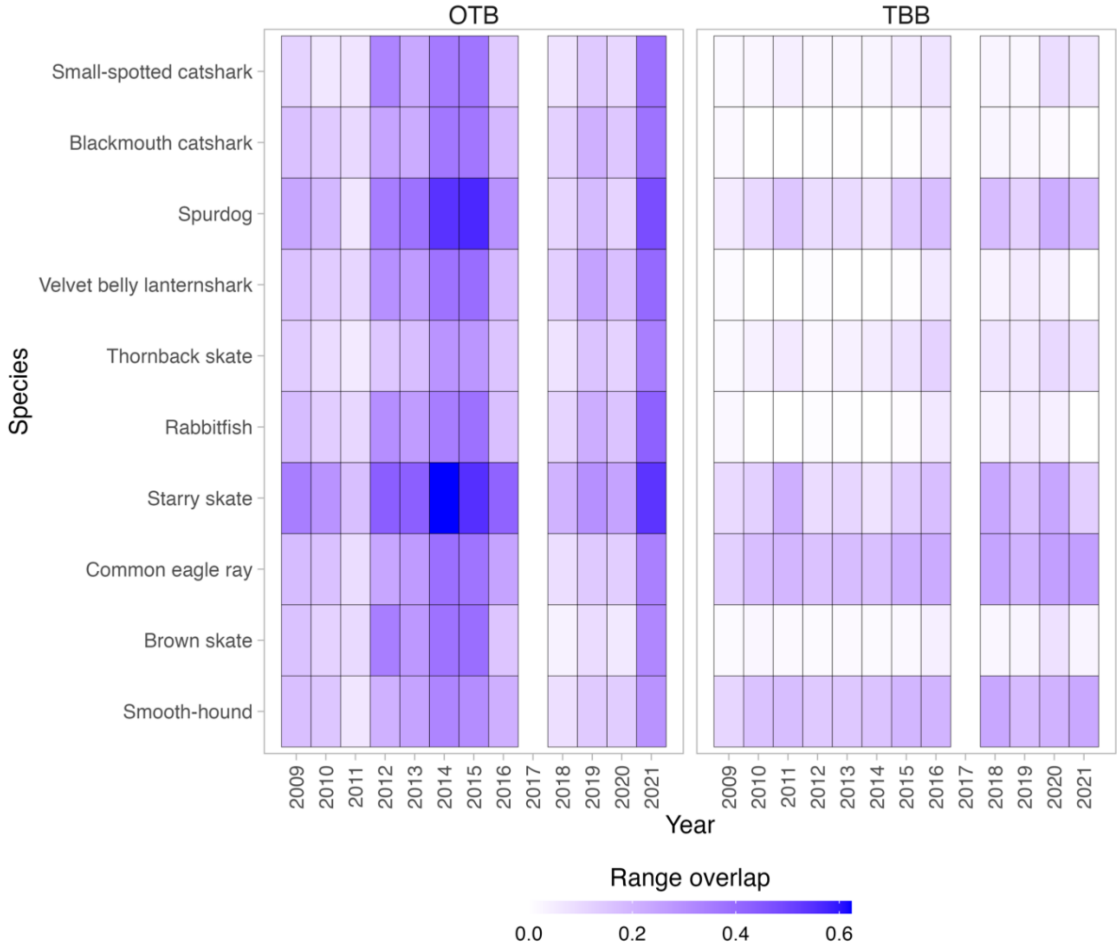


Figure S15. Yearly range overlap between species and otter bottom trawling (OTB) and beam trawling (TBB) fishing gears. The analysis considered a grid cell to be occupied by a species if it exceeded the 65th percentile of the probability of occurrence, and by trawling activities if it exceeded the 65th percentile of fishing effort. The year 2017 is omitted due to sampling occurring outside the designated sampling period (May to September; see the section *Survey data* in *Methods*).

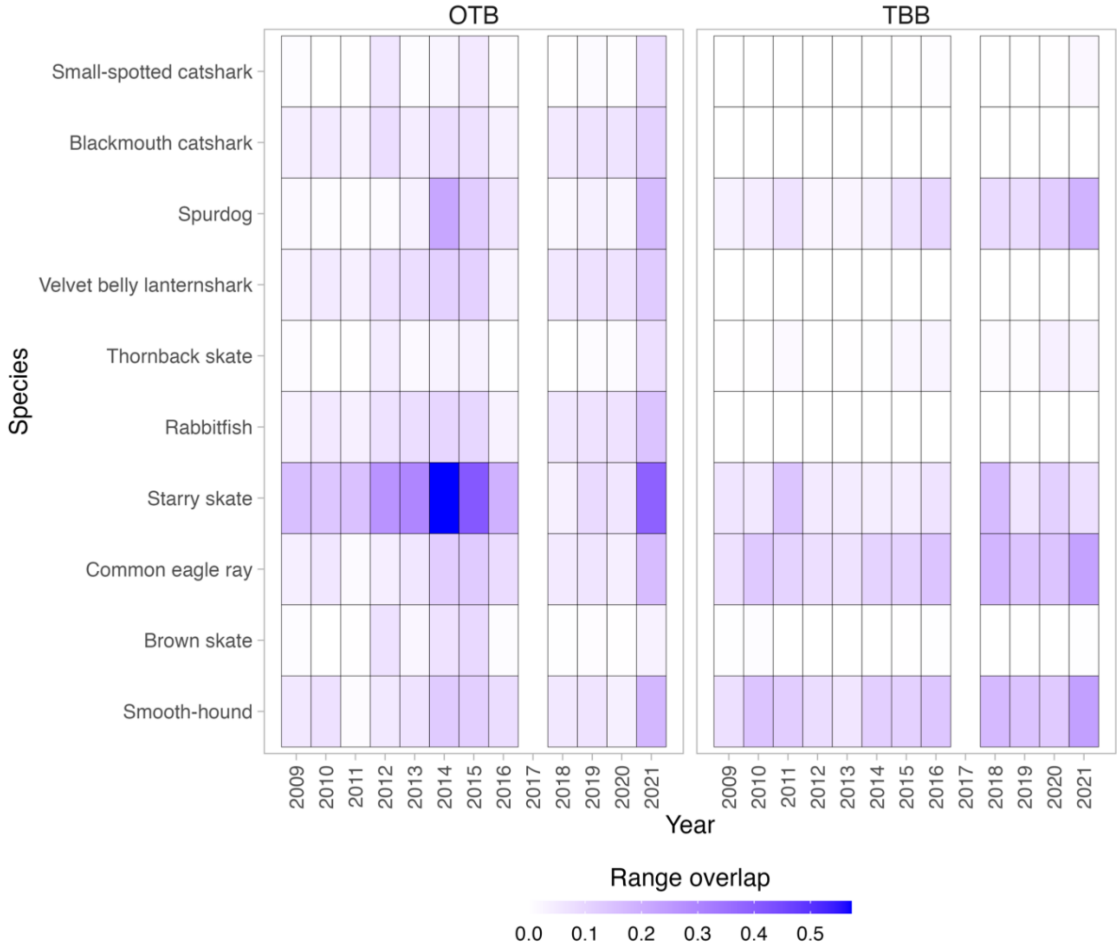


Figure S16. Yearly range overlap between species and otter bottom trawling (OTB) and beam trawling (TBB) fishing gears. The analysis considered a grid cell to be occupied by a species if it exceeded the 85th percentile of the probability of occurrence, and by trawling activities if it exceeded the 85th percentile of fishing effort. The year 2017 is omitted due to sampling occurring outside the designated sampling period (May to September; see the section *Survey data* in *Methods*).