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Identifying Spatial Patterns of Egg Nursery Habitat for a Demersal Shark in the Northwestern Mediterranean Sea: Conservation and Management Implications

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ABSTRACT

Aim: Oviparous elasmobranchs lay benthic eggs with long incubation periods, many of which also require habitat-forming sessile organisms for their development. However, they are threatened by bottom-trawling fishing impacts. Here, we aimed to identify the suitable habitat distribution of small-spotted catshark (*Scyliorhinus canicula*) egg nursery areas, assess their current protection extent by an existing no-take MPA network and their coverage by other delimited spatial-based conservation areas.

Location: Balearic Sea, northwestern Mediterranean.

Methods: Egg cases were collected over 5 years (2018–2022) by a bottom-trawling monitoring programme along the eastern coast of the Iberian Peninsula. We used these occurrences and various environmental variables (bathymetry, slope, sea bottom temperature, sea bottom dissolved oxygen and seabed type) to model the habitat suitability of egg nurseries for the species using maximum entropy modelling.

Results: Sea bottom temperature was the most important variable explaining habitat suitability of egg nurseries. Small-spotted catshark eggs were found either attached to or in the same samples as various species of habitat-forming sessile organisms. We found only 3.6% (381 km^2) of the modelled suitable egg nursery habitat in the Balearic Sea to be currently covered by an implemented no-take MPA network. At the same time, 52% of said MPAs are inadvertently protecting suitable egg nursery habitats (and their associated benthic community), as they were not initially planned with elasmobranchs as conservation targets. Important shark and ray areas (ISRA-IUCN) were also observed to cover egg nursery habitat (4502 km^2 or 15.52%) within their boundaries.

Main Conclusions: While half of the current MPA surface is providing protection to this elasmobranch species' egg nursery areas and their associated benthic communities, they are not sufficient for their conservation. However, mapping the distributions of these essential fish habitats can help towards the 2030 European conservation target of 'strictly protecting' 10% of marine environments.

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1 | Introduction

Elasmobranchs (sharks and batoids) are an essential component of healthy marine ecosystems, as they play a key ecological role in the trophic dynamics and ecological functioning of the systems they inhabit (Heithaus et al. 2010; Ferretti et al. 2010). However, they are strongly affected by human activities, particularly fishery overexploitation, which has led to a third of their species being classified as threatened globally (Dulvy et al. 2021). The Mediterranean Sea, which has been under intense fisheries pressure for over a century (Osio 2012), is both a hotspot of elasmobranch biodiversity and human threats (Dulvy et al. 2014), highlighting the need for the implementation of concrete protection and conservation measures for these species.

Oviparous elasmobranchs (around 40% of all elasmobranch species; Dulvy and Reynolds 1997) are particularly at risk from the threat of human activities. While fishing pressure on bentho-demersal habitats may remove them from the ecosystem during their juvenile, immature and adult stages, it can also affect their recruitment and reproductive cycles. Fishing gears may capture elasmobranch eggs before hatching and also damage or extract their egg-laying habitats and structures (e.g., sessile organisms such as kelp, Wheeler et al. 2020; cold-water octocorals or hydrozoans, *this study*). Many oviparous elasmobranchs lay their eggs within egg nurseries—that is, specific locations with certain habitat conditions which are used repeatedly throughout the years, and where eggs are laid in high-density aggregations, in contact with the benthos or certain fixed structures (Hoff 2016). Thus, egg nurseries are key areas in their reproductive cycle since they offer a fixed place during incubation and beneficial conditions for the development of the embryos, such as increased water flow in the case of shark eggs (Etnoyer and Warrenchuk 2007; Hoff 2016; Cau et al. 2017) or even help maintaining genetic diversity in the case of batoids (Spies et al. 2021). As oviparous elasmobranchs do not provide parental care, their eggs are effectively exposed to external threats for long periods of time (i.e., several months to several years; Hoff 2008), and nursery habitats may as well offer protection from direct predation by gastropods, octopus and other sharks (Guallart et al. 2015; Schröder et al. 2021). Preventing human impacts on these elasmobranch egg nursery areas is not easy, as little is known about their location and extent in the Mediterranean Sea.

Among the demersal oviparous elasmobranchs, the small-spotted catshark *Scyliorhinus canicula* (Linnaeus, 1758) is the most abundant and frequently encountered in the bottom trawling fishery along the western Mediterranean Sea (Ramírez-Amaro et al. 2020; Follesa et al. 2020). Due to its well-known biology, relative high abundance, wide distribution, ease of sampling (e.g., discarded bycatch from bottom-trawling fisheries) and relatively straightforward identification compared to other elasmobranchs, the small-spotted catshark and its eggs are a valuable proxy for understanding data-deficient and vulnerable oviparous elasmobranchs with similar reproductive behaviours (e.g., *Scyliorhinus stellaris*, Finucci, Derrick, and Pacoureau 2021). Furthermore, scyliorhinid egg nursery habitats have been found associated with ecologically important areas such as forests of endangered benthic colonial species (e.g., the black coral *Leiopathes glaberrima*, Cau et al. 2017) and soft corals (e.g., *Eunicella cavolini* and *Paramuricea clavata*; De Sabata and Clò 2013). This suggests additional potential for the small-spotted catshark to serve as an umbrella species (Caro 2010) of endangered bentho-demersal habitats and habitat-forming sessile organisms. Thus, helping recent efforts in mapping some of them (e.g., *Leiopathes glaberrima*, Lauria et al. 2021; *Isidella elongata*, González-Irusta et al. 2018). Habitat-forming benthic organisms are of particular importance for the ecosystem functioning of areas such as the western Mediterranean Sea, where wide expanses of the seabed are flat muddy bottoms with low three-dimensionality. Here, chronic and intensive trawling activity over the last century has further reduced the structural complexity of the seabed by removing them from the ecosystem (Maynou and Cartes 2011), a common result of high-impact fisheries worldwide (Hall-Spencer et al. 2002; Althaus et al. 2009; Bo et al. 2014).

The decline of fish populations and habitat loss in the marine environment have led to a growing interest in implementing management measures such as no-take marine protected areas (no-take MPAs), that is, areas where extractive activities are generally not allowed (Sala and Giakoumi 2018). The necessity to protect and restore bentho-demersal habitats from overfishing and other human pressures is being reflected on new international policy measures such as the European Union's recently passed Nature restoration law, which is set to restore 20% of all of the EU sea areas 'in need of restoration' by 2030 (European Commission 2024), and the EU Biodiversity Strategy for 2030 which requires a minimum of 30% of the sea to be under protection and 10% under strict protection (European Commission 2020). Management measures that involve restrictive spatial closures such as no-take MPAs, even when set to protect and recover mainly commercially important species, effectively protect both the habitat and the whole bentho-demersal community located within their boundaries. No-take MPAs are generally considered the most effective way of preserving biodiversity (Costello and Ballantine 2015; Sala and Giakoumi 2018), including elasmobranch species (Giménez et al. 2020; Albano et al. 2021). Unintended conservation benefits for demersal sharks arising from protected areas designed for other species have been documented in other regions (e.g., New Zealand; Heldsinger et al. 2023), which suggests that an evaluation effort of both currently active no-take MPAs and proposed areas is needed to identify if similar processes are happening elsewhere.

Improving the conservation of the marine environment requires knowledge-based management measures that consider the distributions and extents of suitable habitats for the species and/or communities that need protection, in order to make informed decisions. Accurate habitat suitability maps, which are based on available occurrence data, outline the geographic area of adequate environmental conditions for the presence of species or their local populations—that is, the species' realised niche or parts of it (Phillips, Anderson, and Schapire 2006). They provide managers and governments with valuable information on which areas to prioritise and where to focus available resources to maximise conservation/protection efforts, for example, during the planning and the establishment of protected areas. Information on elasmobranch egg nurseries in the Mediterranean Sea is very scarce, with only a few published reports (e.g., Treude et al. 2011; Cau

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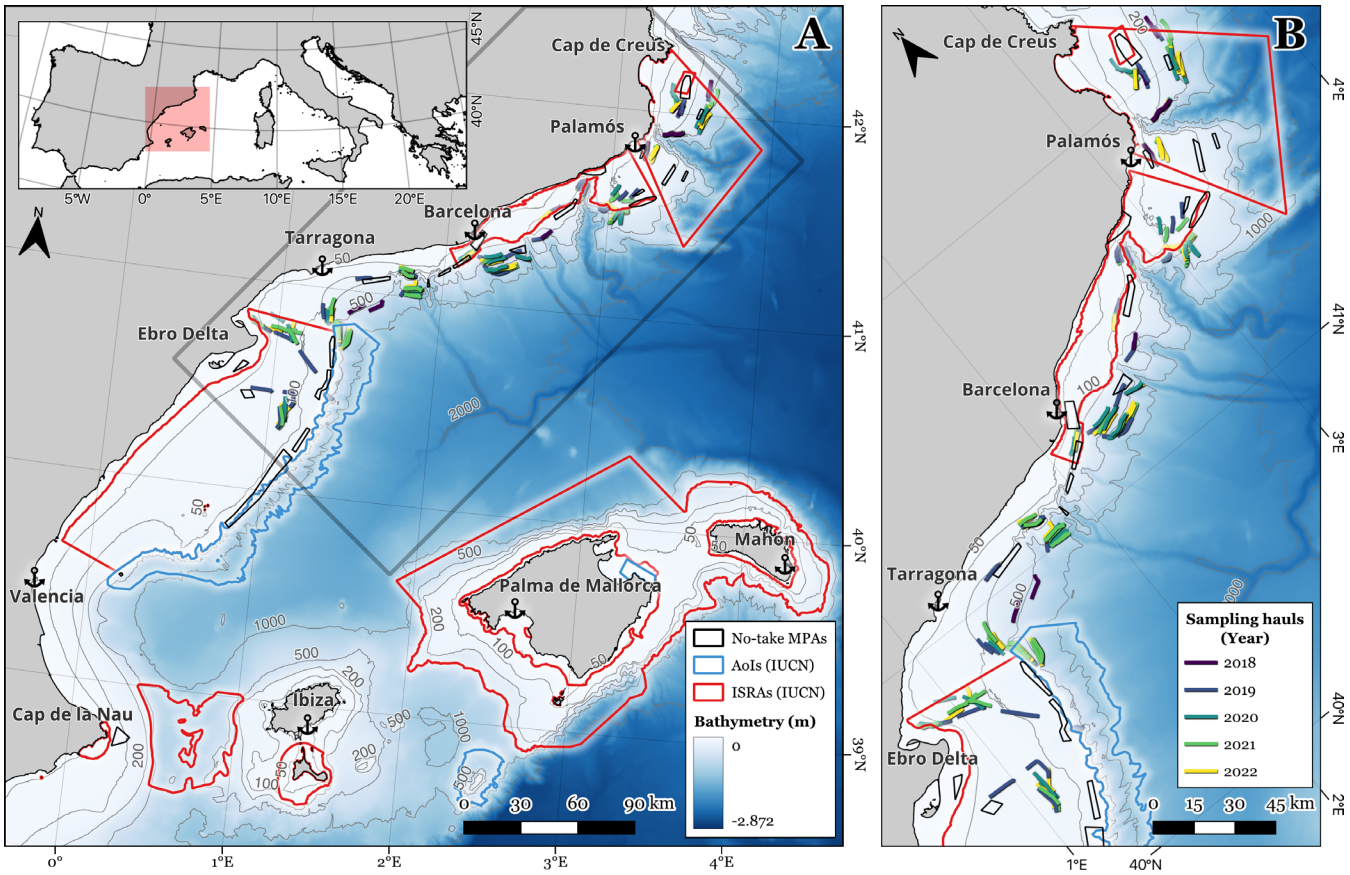


FIGURE 1 | (A) Study area in the northwestern Mediterranean Sea. No-take MPAs are outlined in black, important shark and ray areas (ISRAs) are outlined in red, and areas of interest (AoI) for future ISRAs are outlined in blue (IUCN-SSG 2022). (B) shows a close-up pointing out the fishing hauls where small-spotted catshark eggs were caught. See Figure 2 for the names of the MPAs, ISRAs and AoIs.

et al. 2017). To the authors' knowledge, no mapped distributions of egg nursery habitats exist in the Mediterranean Sea, although some studies have been done in other areas such as the Bering Sea (e.g., Rooper et al. 2019).

In the present study, we focused on the northwestern Mediterranean Sea, a highly impacted area within the Mediterranean basin (Ramírez et al. 2018). Here, a network of no-take MPAs was recently implemented in 2020 as a spatial-based management measure aimed at mitigating the impact of fisheries (Ministerio de Agricultura, Pesca y Alimentación 2020). Moreover, in 2023, multiple important shark and ray areas (ISRA) and areas of interest (AoI) were proposed by the shark specialist group (International Union for Conservation of Nature, SSC-IUCN) to help policy-makers in future conservation efforts (IUCN SSC-SSG 2022; Kyne et al. 2023). Specifically, we mapped and presented five consecutive years of small-spotted catshark egg presence data with the aim of locating areas of recurrent use for the reproduction of the species. These occurrences were then used to fit a Maximum Entropy (MaxEnt) model with the following aims: (i) to identify the environmental variables driving the habitat suitability of small-spotted catshark eggs in the northwestern Mediterranean Sea, and map their egg nursery suitable habitat in the area; (ii) to assess the extent to which egg nursery habitat might be protected by an already established no-take MPA network; (iii) to determine the overlap extent of currently identified ISRAs and AoIs with the modelled egg nursery habitats.

2 | Material and Methods

2.1 | Study Species

The small-spotted catshark (*Scyliorhinus canicula*) is a demersal elasmobranch inhabiting the Atlantic Ocean from the northern coast of Mauritania to Norway and the entire Mediterranean Sea (Soares and Carvalho 2019; Follesa et al. 2020). In the Mediterranean Sea, the species is present between 10 and 800 m depth (Follesa et al. 2020), but it is most abundant between 100 and 500 m (ICATMAR 2023). Small-spotted catshark egg laying occurs continuously throughout the year (Ellis and Shackley 1997; Capapé et al. 2008), while eggs go through long incubation periods that can last over 7 months before hatching (Ballard, Mellinger, and Lechenault 1993). Female small-spotted catsharks carry two formed eggs (one per oviduct) which are attached to living organisms such as macroalgae, hydrozoans, deep-sea corals, bryozoans or sponges, as well as other non-biological structures (Figure S1; Ellis and Shackley 1997; Rodríguez-Cabello, Velasco, and Olaso 1998; Subías-Baratau et al. 2022). Eggs are composed of a hard shell or casing covering the developing embryo, its yolk and the jelly that covers and protects the egg contents, as well as four slits that eventually

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open to facilitate sea water to enter the egg case (but see Ballard, Mellinger, and Lechenault (1993) for a full description of the egg and its developmental stages).

2.2 | Study Area and Biological Sampling

The study was conducted in the Balearic Sea, within the northwestern Mediterranean basin (Figure 1A). To identify nursery areas for small-spotted catsharks, we used a data set comprising egg occurrences from fishing hauls collected directly on-board commercial trawling vessels from November 2018 to December 2022 along the continental shelf and slope of the Catalan coast in Spain (Figure 1). The sampling is part of the monitoring programme of the ICATMAR (ICATMAR 2023), overseeing local recreational and commercial fishing activities. Small-spotted catshark eggs were detected in 202 of 417 bottom trawl hauls, with sampling location being determined by the centroid of the vessels' GPS track. Briefly, when trawling the seabed, the capture including small-spotted catshark eggs ends up in the codend (the end portion of the trawling net), which after each fishing haul is taken to the lab for identification and quantification. When the capture is too abundant, only a fraction of it is taken and quantified, to which a subsample ratio is then applied to calculate the total assumed capture (see Ribera-Altimir et al. (2023) for details).

A network of permanent no-take MPAs was recently established in 2020 alongside the Spanish peninsular coast to safeguard demersal fishery resources (Ministerio de Agricultura, Pesca y Alimentación 2020), 23 of them being located within the extent of the study area (Figure 1, Table 2), but none including small-spotted catshark as a protection target species. In relation to the IUCN classification, the study area has multiple ISRAs and AoIs, with only two of them (Central Catalonia and Ebro Delta) having small-spotted catshark as one of their considered targets (Figure 1, Table 2).

2.3 | Environmental Variables

Five environmental variables were considered to model the spatial distribution of small-spotted catshark egg nursery habitat suitability. The variables represented different characteristics of the seabed (Table S1; Figure S2) and included bottom depth, seabed slope, substrate type, sea bottom temperature and dissolved oxygen. Bottom depth (in meters) was extracted from the GEBCO database at a resolution of 0.0042° (GEBCO Compilation Group 2023). Seabed slope (in degrees) was computed using QGIS v3.34 'raster terrain analysis' tool (QGIS Development Team 2024) from GEBCO's bathymetry layer (GEBCO Compilation Group 2023). Seabed substrate type was extracted from EMODnet's data set, including seven classes: Mud, sandy mud, muddy sand, sand, coarse-grained, mixed sediment and rock and boulders. Sea bottom temperature (°C) and dissolved oxygen (mmol/m^3) were extracted from Copernicus Marine Physics and Biogeochemistry reanalysis data, respectively, and averaged for the summer 2018 to summer 2021 time period at a resolution of 0.042°. All variables were reprojected to metres (EPSG: 3035) for the analyses. In addition, to understand the distribution of environments similar to the locations where eggs occurred (Figure S2F), an 'environmental similarity' layer was calculated from the continuous environmental variables (all but seabed type) using the 'similarity' function in the R v4.3 (R Core Team 2023) package 'ENMeval' v.2.0.4 (Kass et al. 2021).

2.4 | Habitat Suitability Modelling

Habitat suitability modelling was carried out using Maxent (Phillips, Anderson, and Schapire 2006), coded in the R package 'ENMeval' v.2.0.4 (Kass et al. 2021). Maxent is a commonly used approach to model species' suitable habitat or using presence-only spatial records and their assigned environmental values (i.e., samples of the species' realised niche) to estimate probabilities of distribution for 'unsampled' background locations of known environmental variables (Phillips, Anderson, and Schapire 2006). The centroid of each of the 202 trawling hauls from the period 2018–2022 were used as occurrence location data. Removing duplicates located in the same grid cells of any of the environmental variable layers is standard procedure when fitting Maxent models. This resulted in the removal of 56 occurrence points to avoid replications, leaving a total of 146 occurrence points.

The calibration area used to train the model spanned the Balearic Sea basin (Figure 1A), with background points/locations set in suitable areas for the potential occurrence of the species, determined by the dispersal capabilities of adult small-spotted catsharks. Points were roughly restricted a priori to depths where the small-spotted catshark is known to occur, specifically limited to bottom depths shallower than 1500 m. After restricting the suitable area, 50,000 background locations (enough to evenly cover all of the study area) were randomly set using the R package 'dismo' v1.3–14 (Hijmans et al. 2023) and the 'randomPoints' function.

A cross-validation approach, splitting the data into five random training and testing folds was followed using the function 'cv_spatial' from the R package 'blockCV' v3.1–3 (Valavi et al. 2019) with a checkerboard hexagonal pattern and 2000 iterations to find evenly dispersed folds—that is, the folds include a similar number of presences–absences (see Valavi et al. (2019) for information on fold strategies).

Five Maxent models were trained with the following feature classes: 'linear', 'linear quadratic', 'linear quadratic hinge', 'hinge' and 'linear quadratic hinge product'. These features allowed evaluating the best model fitting between the environmental covariates and the egg occurrence data. Then, to test for overfitting, five regularisation multipliers (RMs) 1:5 were used for each of the models (Elith et al. 2011), resulting in 25 fitted models in total.

With regard to variable selection, priority was given to the biological importance of variables to the habitat distribution of small-spotted catshark. Correlation between the bottom dissolved oxygen and bottom temperature variables (Pearson = 0.80) and between bottom dissolved oxygen and depth (Pearson = 0.74) was detected. However, Maxent is known to be robust to variable collinearity as demonstrated by De Marco and Nóbrega (2018) using simulated datasets and by Feng et al. (2019) with real-world data. Therefore, all initial variables were left in the final model. The importance of each environmental variable used in

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the model was calculated with the function 'varImp' and 1000 permutations with the R package 'SDMtune' v.1.3.1 (Vignali et al. 2020).

2.5 | Area-Based Calculations

A quantitative threshold of presence–absence in the study area was calculated with the final model. We used the function 'thresholds' from the R package 'SDMtune' (Vignali et al. 2020), which defines a value within the habitat suitability range (between 0 and 1) allowing dividing the continuous gradient into suitable/unsuitable categories. The value that maximised training sensitivity and specificity was selected, resulting in a threshold of 0.54, which was then used to obtain a dichotomised suitable egg nursery habitat distribution. This was then used to calculate the area (in km^2) that is currently covered by the permanent no-take MPA network, as well as the area covered by the IUCN's ISRAs and AoIs in the study area using the union algorithm in QGIS v3.34 (QGIS Development Team 2024).

3 | Results

3.1 | Model Performance

Of the 25 models, the five with lowest Akaike information criterion corrected for small sample sizes (AICCc) ranging from 3435.2 to 3462.3 were selected. All of them had a similar area under the curve of validation folds (AUCval) of ~0.85 (presence-only models can only have a maximum AUC close 1; Phillips, Anderson, and Schapire 2006) and similar Continuous Boyce Index (CBIval) values, a commonly used metric for assessing transferability of the model to a different area than used in the model fit (Hirzel et al. 2006). Due to similar performance metrics, the simplest model (i.e., with the lowest number of coefficients) was selected, which included the linear, quadratic and hinge classes, and had a regularisation parameter of 2, with an AICc of 3442.7, an average AUCval of 0.865 and a CBI of 0.657.

3.2 | Egg Presence and Habitat Description

A total of 3046 eggs were collected from 202 trawling hauls conducted between 2018 and 2022, covering a swept area of 31.47 km^2, with a median capture of 39.87 eggs/km^2 (Table 1). Small-spotted catshark eggs were present in most of the sampled area during the whole sampling period (Figure 1B) and were generally found attached to benthic species such as the critically endangered tall sea pen *Funiculina quadrangularis* (Salvati et al. 2014), the soft coral *Alcyonium palmatum* or the hydrozoan *Lytocarpia myriophyllum* (Figure S1). Furthermore, the benthic community of the locations where small-spotted catshark eggs were observed also included dead fragments of the critically endangered *Isidella elongata* (Bo et al. 2015; Figure S1), multiple species of sea-pens from various genus such as *Pennatula rubra*, *Pennatula phosphorea*, *Pteroeides griseum*, *Veretillum cynomorium*, *Virgularia mirabilis* and *Kophobelemnon stelliferum*, as well as the gorgonians *Eunicella* spp. and *Leptogorgia sarmentosa*.

Mud bottom was the most common seabed type with 87.7% of the egg occurrences, followed by sandy mud (10.3%), mixed sediment (8.22%), muddy sand and sand (3.43%) and rock and boulders (0.68%). No eggs were found over coarse-grained sediment. Eggs were found between 22 and 673 m depth, at a median depth of 181 m. The median value for the slope where eggs were located was 2.6° (range of 0°–39°). Eggs were found at median bottom sea temperature of 13.75°C (range of 13.29°C–17.01°C). Median sea bottom dissolved oxygen (DO) was 232.6 mmol/m^3 where eggs were found (range of 222.4–244.7 mmol/m^3; Table S2).

3.3 | Habitat Suitability of Small-Spotted Catshark Egg Nurseries

The environmental variable explaining the highest variability in the final model was sea bottom temperature (47.16%), followed by sea bottom dissolved oxygen (DO) (24.58%), bottom depth (15.02%), seabed substrate (11.1%) and lastly bottom slope (2.16%). The optimal temperature for occurrences peaked at around 14°C, with the suitable habitat probability falling abruptly as temperature increased (Figure S3). Higher DO corresponded with higher probabilities of suitable habitat for small-spotted catshark eggs, with values around 240 DO mmol/m^3 showing the highest probability (Figure S3). Greater depths showed higher probabilities of suitable habitat than shallower depths, with a sharp decrease of probability of presence above 400 m (Figure S3). Seabed type was second to last in explaining egg nursery habitat suitability, but still played a role defining suitable and unsuitable areas. A negative relationship was found

TABLE 1 | Sampling data on captured small-spotted catshark eggs.

Year	Number of hauls	Total swept area in km^2	Total eggs captured (Median value)	Maximum eggs/haul	Median eggs/km^2 (range)
2018	7	1.27	159 (9)	76	44.12 (8.64–390.26)
2019	47	7.05	851 (6)	140	43.63 (6.06–1088.71)
2020	42	6.35	367 (4)	80	30.67 (3.12–639.95)
2021	55	8.62	746 (6)	87	45.81 (5.53–1458.02)
2022	51	8.18	923 (6)	138	35.56 (3.70–1493.73)
Total	202	31.47	3046 (6)	140	39.87 (3.12–1493.73)

Note: Sampling in 2018 only occurred during the months of November and December, while all months were sampled during 2019–2022.

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between 'Sand' and 'Coarse-grained sediments' and habitat suitability for small-spotted catshark eggs. Bottom slope was of less importance than the other variables, and optimal probability of suitable habitats for small-spotted catshark eggs was at around 5° with decreasing probabilities for lower and higher slopes (Figure S3).

From Cap de Creus to the Ebro Delta, the depths of 100–500 m seem to provide suitable habitat for small-spotted catshark egg nurseries (Figure 2)—that is, for the most part, these depths show modelled suitability values of >0.60 and >0.80. Between the Ebro Delta and the area offshore from Valencia, most of this suitable area is located within a narrower fraction between 200 and 500 m deep, located within the Castellón Slope AoI and offshore Cap de la Nau (Figure 2). The Balearic Archipelago, particularly around the Islands of Mallorca and Menorca (included within the ISRA area of the Balearic Islands), has a relatively narrow area of suitable habitat for small-spotted catshark egg nurseries, similar to the area within the Castellón Slope but with lower overall suitability values. There is an almost total absence of suitable habitat south of both islands. Around the Ibiza-Formentera archipelago, the area shows a more extensive surface suitable for the species' reproduction (values >0.60 and >0.80), particularly in the north between the 200 and 500 m depths (Figure 2).

3.4 | Potential Nursery Areas and Protection Status

The egg nursery habitat presence–absence distribution was mapped using a threshold value of 0.54 on the habitat suitability range. Our model resulted in 10,456 km^2 or 7.9% of the study area as having a suitable habitat for small-spotted catshark egg nurseries (Figure 3). Of this suitable habitat, only 3.65% (382 km^2) is currently included within the no-take MPA boundaries included here, while 44.06% (4502 km^2) is located within the IUCN's ISRAs and 8.01% (838 km^2) within AoIs. When considering the 23 permanent no-take MPAs located within the study area, around 382 km^2 (51.74%) of their surface area include small-spotted catshark suitable habitat (Table 2, Figure 3). The rest of the area covered by MPAs (356 km^2) falls under this threshold, thus modelled as unsuitable for small-spotted catshark egg nurseries (see Figure S6 for individual MPAs).

The Central Catalonia ISRA covered a total of 1010 km^2 (61.82%) of suitable egg nursery habitat, while the Ebro Delta ISRA covered 1135 km^2 (12.93%). Other ISRAs, even if not aimed at small-spotted catshark conservation, cover suitable habitat for its egg nurseries (Table 2; Figures 3 and S5). The ISRA of roses covers 71.64 km^2 (100% of its surface area) of small-spotted catshark egg nursery habitat, followed by the Costa Brava Canyons ISRA, which is covering 1400 km^2 (39.13%) of suitable habitat for small-spotted catshark egg nurseries. The Balearic Islands and the Ibiza Channel Slope ISRAs are covering an area of 524 km^2 (4.30%) and 359.73 km^2 (18.21%), respectively, of suitable habitat. In total, 4502 km^2 (15.52%) of the ISRAs area in the Balearic Sea is covering small-spotted catshark suitable egg nursery habitat. With regard to the IUCNs AoIs, only the Castellon Slope appears to cover small-spotted catshark egg nursery habitat with 838 km^2 (25.86%) (Figure S4, Table 2), or 21.7% of the total 3861.7 km^2 of AoI surface in the study area.

4 | Discussion

4.1 | Egg Nursery Habitat Description

Elasmobranch egg nursery locations are generally considered to have particular habitat characteristics that help in the development of the embryos (Hoff 2016; Rooper et al. 2019). For small-spotted catsharks, sea bottom temperature was a key variable in delimiting areas suitable for the deposition of eggs and was the most influential factor in predicting suitable egg nursery areas. Average bottom temperatures higher than ~14°C lead to lower habitat suitability for egg nursery areas in the Balearic Sea. Higher water temperature in laboratory conditions accelerate both embryogenesis growth rates and the depletion of yolk energy reserves of small-spotted catsharks, resulting in smaller hatchlings which could lead to higher predation rates in their natural environment (Musa et al. 2020). This favouring of colder water coupled with apparent preference towards deeper bottoms for spawning, in time, could result in a shift in the optimal distribution shown in the current study. As the Mediterranean Sea warms, this could induce a deepening of the suitable habitat of small-spotted catshark nursery areas, as has been predicted to happen for this and other elasmobranch species (Coulon et al. 2024).

During embryo development, small-spotted catsharks go through different stages where both metabolic requirements and gas exchange levels vary (Musa, Czachur, and Shiels 2018), which suggests that nursery areas with higher dissolved oxygen may be more advantageous for the species. Sea bottom dissolved oxygen (DO, egg occurrences between 222.4 and 244.7 mmol/m^3) was the second most important predictor, and areas with higher DO areas appear to be better suited for small-spotted catshark egg nurseries. Dissolved oxygen concentration was the third most important variable in Rooper et al.'s (2019) model of skate nursery habitat, with increasing concentrations leading to higher probability of suitable egg locations. Scyliorhinids such as the small-spotted catshark lay their eggs on elevated structures above the seabed, which allows for better water flow and oxygenation even when the eggs are densely aggregated (Flammang, Ebert, and Cailliet 2007, 2011).

The methodology we used inherently constrained the range of depths sampled, as bottom trawling is prohibited at depths of less than 50 m in the Mediterranean Sea (or three nautical miles from coast on the Ebro Delta platform). However, bottom depth was also a relevant variable for small-spotted catshark nursery habitat in the study area. In the Mediterranean, a small-spotted catshark nursery location was reported in Sardinia, at around 200 m depth Cau et al. (2017). Our model shows that, within the Balearic Sea, the optimal depths vary, but most suitable habitats fall deeper than 100 m, with the notable exception of the Ebro Delta shelf and parts of the Catalan coast where it lies between 50 and 100 m, with some shallower MPAs partly covering them and serving as protection. Mediterranean small-spotted catsharks appear to lay eggs in areas much deeper than, for example, coastal egg-laying small-spotted catsharks in southern Ireland, where eggs have been found at depths of up to 5 m (Wearmouth et al. 2013). The wide egg nursery bathymetric range shown by this species throughout their distribution may be explained by the aforementioned importance of sea bottom

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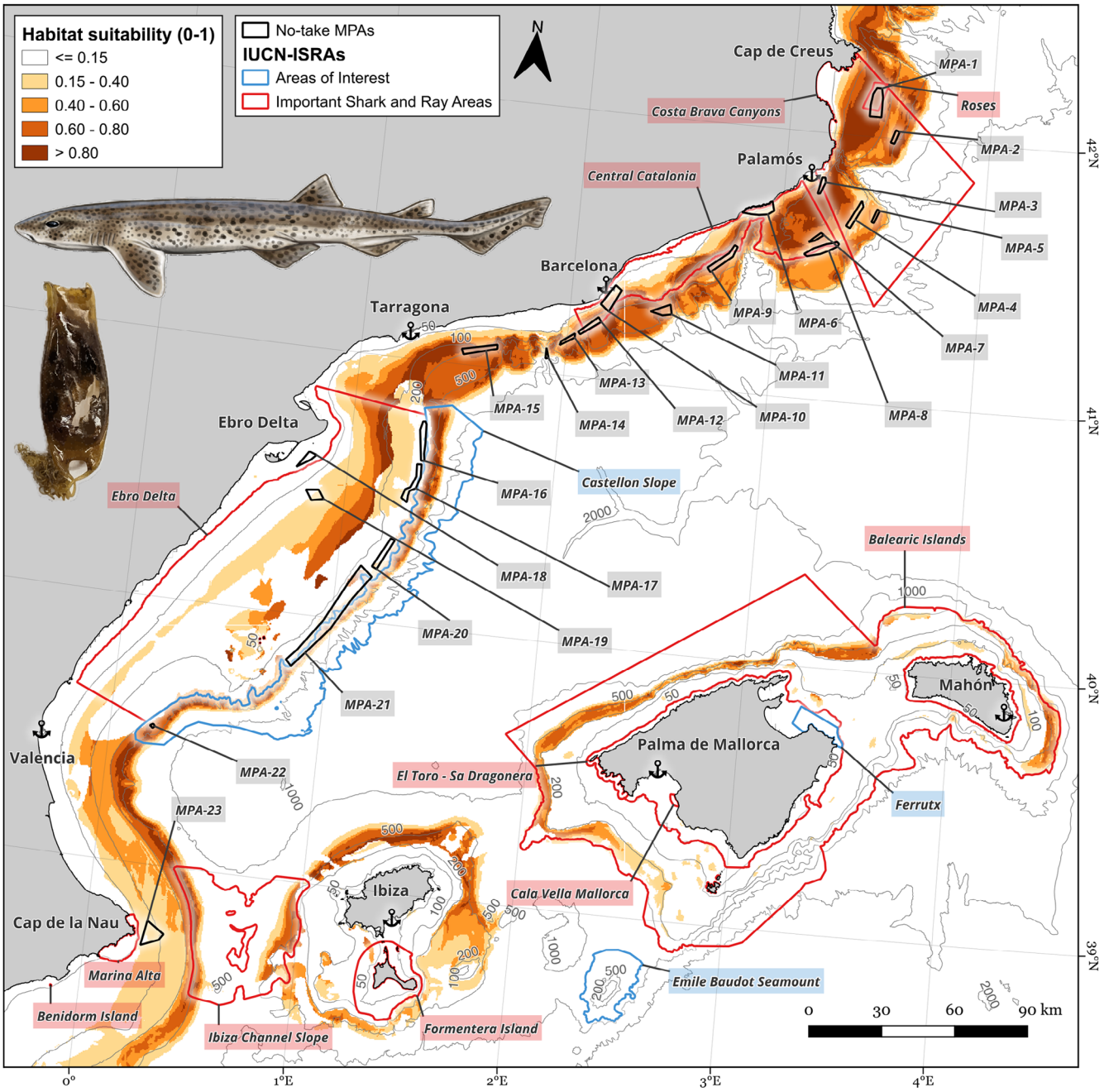


FIGURE 2 | Habitat suitability range for small-spotted catshark nurseries in the continental shelf and the slope of the Balearic Sea (northwestern Mediterranean) based on the final Maxent model and relevant area-based management delimitations. No-take MPAs are shown in black, important shark and ray areas (ISRAs) are shown in red, and areas of interest (AoIs) are shown in blue (IUCN-SSG 2022). Small-spotted catshark illustration by Alex Mascarell.

temperature; as in the Balearic Sea, average sea bottom temperatures of lower than 14°C are generally found at greater depths than in the north Atlantic. Small-spotted catshark distribution (Navarro et al. 2016) and present results suggest that, in the Balearic Sea, both adults and pre-hatched egg stages may share the same depth ranges, as the higher temperature of shallower depths in the area makes it unsuitable for egg nurseries.

Seabed type, while fourth in terms of variable importance, seems to be a key indicator as a habitat predictor. Coarser grained seabed sediments appear to be unsuitable for small-spotted catshark eggs in the area, and most eggs were captured over thinner, muddy substrates, with mixed sediments being relevant as well. As mentioned before, maps of sessile communities were not available and thus, not used as model predictors. However, this substrate preference could be reflecting the suitable distribution of varied Mediterranean communities of habitat-forming organisms that live on muddy substrates at differing depths such as *Funiculina quadrangularis*, *Alcyonium spp.* or *Lytocarpia myriophyllum*. These colonial organisms appear to be the preferred spawning locations for scyliorhinids, tightly attaching their eggs to their branches or main bodies both in the Mediterranean (De Sabata and Clò 2013; Cau et al. 2017) and the Atlantic (Etnoyer and Warrenchuk 2007; Flammang, Ebert,

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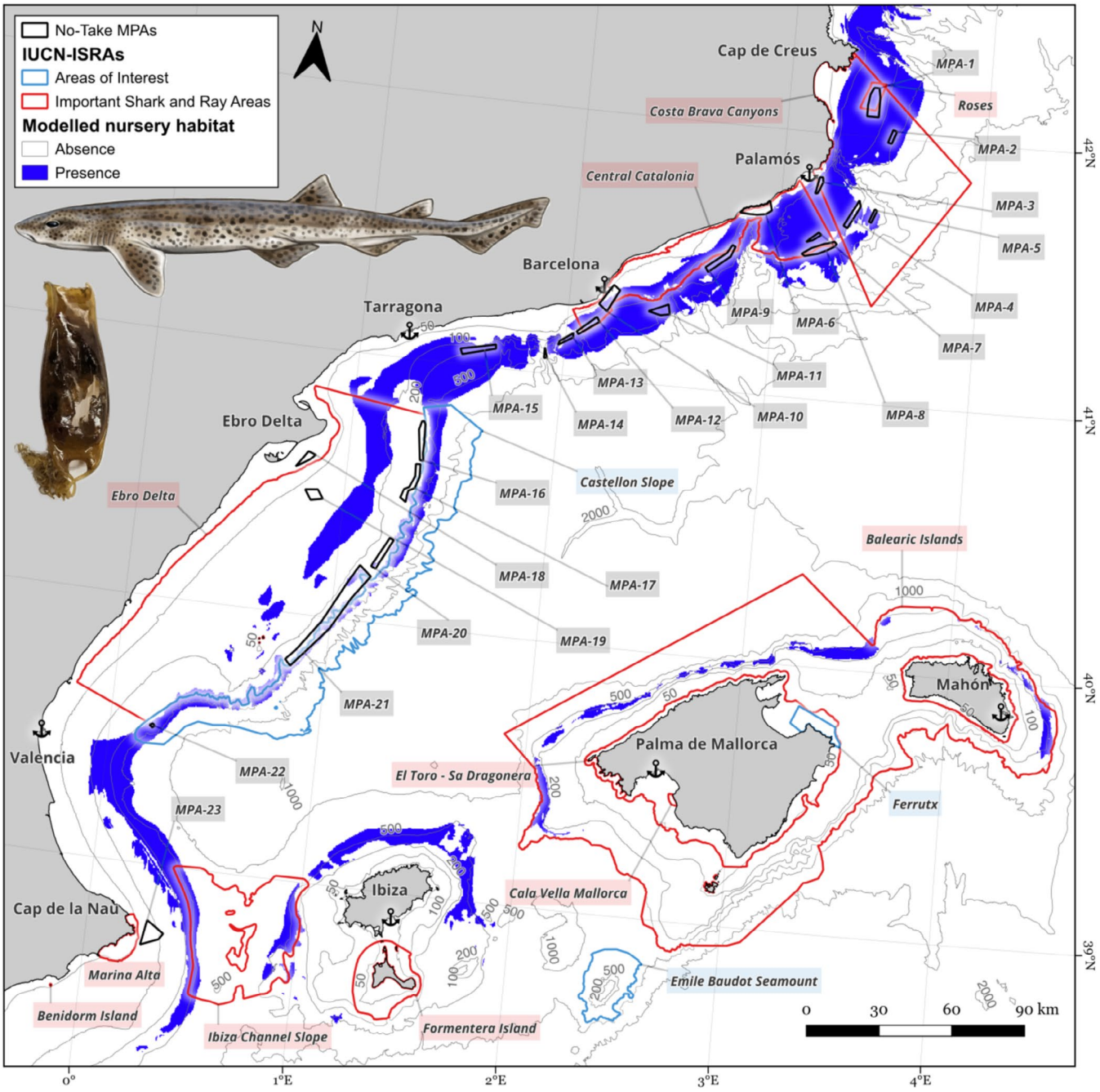


FIGURE 3 | Modelled small-spotted catshark nursery habitat (dark blue) in the Balearic Sea (northwestern Mediterranean) and relevant area-based management delimitations. No-take MPAs are shown in black, Important Shark and Ray Areas (ISRAs) are shown in red, and Areas of Interest (AoIs) are shown in blue (IUCN-SSG 2022). Small-spotted catshark illustration by Alex Mascarell.

and Cailliet 2011). Even if potential bias might arise from the fact that the trawling fleet operates mostly over muddy bottoms, these are the predominant seabed type of the depths where small-spotted catshark occurs in the Balearic Sea. Here, rocky bottoms are uncommon, and benthic habitat-forming species that grow over them, when present, occur over small isolated rocky shoals also surrounded by muddy bottoms with thin sediment (Bo et al. 2012; Cau et al. 2017).

The bottom slope appears to be the least important predictor for suitable small-spotted catshark egg habitat. Eggs were generally found at relatively low slopes and the most optimal values in terms of suitable habitat probability reflected this. Higher slopes had an increasingly lower probability of suitable habitat for the species. This less optimal spawning habitat could either reflect the distribution of the species itself or, again, be directly influenced by the habitat distribution of the colonial organisms previously mentioned. Rooper et al. (2019) found slope to be the most important variable predicting egg-laying sites for skates (family Rajidae) on the Bering Sea. However, the relatively low importance of slope in the habitat suitability of small-spotted catshark egg-laying sites compared to Rajidae possibly reflects the essentially different egg laying behaviours. Skates normally lay their eggs unattached on the seabed substrate, which suggests

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TABLE 2 | Predicted small-spotted catshark egg nursery habitat extent within the current no-take MPAs and the IUCN important shark and ray areas and areas of interest.

Type	Name	Target species	Habitat coverage (km²)	Total area (km²)
No-take Permanent MPAs	MPA-01 (Área de Repoblación Blanes-Palamós)	*Merluccius merluccius*	51.35 (100%)	51.35
	MPA-02 (Área de Interés Pesquero Roses-Palamós)		9.15 (100%)	9.15
	MPA-03 (Núcleo mar d'Enterra)		10.37 (100%)	10.37
	MPA-04 (Bol de terra a vapor de Palamós)		12.30 (58.22%)	21.13
	MPA-05 (Área cigala de Palamós)	*Nephrops norvegicus*	5.13 (79.93%)	6.41
	MPA-06 (Bol de Tossa)		0.49 (1.21%)	40.76
	MPA-07 (Zona Bol de les bruixes de Blanes)		6.75 (100%)	6.75
	MPA-08 (Área de repoblación Blanes—Palamós)		35.45 (99.3%)	35.70
	MPA-09 (Zona merluza de Arenys)	*Merluccius merluccius*	31.33 (99.91%)	31.35
	MPA-10 (Área bol del port de Barcelona)		19.15 (48.83%)	39.22
	MPA-11 (Área cigala de Barcelona)	*Nephrops norvegicus*	21.68 (99.87%)	21.71
	MPA-12 (Área merluza de Barcelona)	*Merluccius merluccius*	16.53 (90.75%)	18.22
	MPA-13 (Área merluza de Vilanova)	*Merluccius merluccius*	6.46 (73.57%)	8.78
	MPA-14 (Área cigala de Vilanova)	*Nephrops norvegicus*	0.00 (0%)	2.78
	MPA-15 (Área Tarragona)		29.58 (100%)	29.58
	MPA-16 (Zona Cambrils)		0.28 (0.92%)	30.52
	MPA-17 (Zona l'Ametlla)		0.39 (1.21%)	32.58
	MPA-18 (Zona de exclusión de Sant Carles de la Ràpita)		15.44 (100%)	15.44
	MPA-19 (Área Barques, la Ràpita)		0.00 (0%)	21.85
	MPA-20 (Zona fora, la Ràpita)		2.66 (9.45%)	28.13
	MPA-21 (Veda permanente de Castellón)		105.32 (46.73%)	225.41
	MPA-22 (Área les Moletes)		1.81 (100%)	1.81
	MPA-23 (Roca dels Feliu)		0.00 (0%)	48.58
All no-take MPAs			381.62 (51.74%)	737.58

(Continues)

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TABLE 2 | (Continued)

Type	Name	Target species	Habitat coverage (km²)	Total area (km²)
Important Shark and Ray Areas (ISRAs)	Roses	*Raja polystigma*	71.64 (100%)	71.64
	Costa Brava Canyons	*Prionace glauca*	1400.61 (39.13%)	3579.20
	Central Catalonia	*Scyliorhinus canicula*, *Raja asterias*	1010.25 (61.82%)	1634.22
	Ebro Delta	*Scyliorhinus canicula*, *Raja asterias*	1135.45 (12.93%)	8779.31
	Balearic Islands	*Centrophorus uyato*, *Dalatias licha*, *Etmopterus spinax*, *Oxynotus centrina*, *Cetorhinus maximus*, *Galeorhinus galeus*, *Mustelus mustelus*, *Galeus melastomus*, *Prionace glauca*, *Scyliorhinus stellaris*, *Aetomylaeus bovinus*, *Myliobatis aquila*, *Bathytoshia lata*, *Dasyatis pastinaca*, *Gymnura altavela*, *Mobula mobular*, *Leucoraja circularis*, *Raja polystigma*, *Raja radula*, *Rostroraja alba*, *Torpedo marmorata*	524.42 (4.30%)	12195.54
	Cala Vella Mallorca	*Dasyatis pastinaca*, *Raja radula*	0.00 (0%)	10.56
	El Toro – Sa Dragonera	*Gymnura altavela*	0.00 (0%)	68.76
	Ibiza Channel Slope	*Hexanchus griseus*, *Somniosus rostratus*	359.73 (18.21%)	1975.23
	Formentera Island	*Raja radula*, *Rostroraja alba*	0.00 (0%)	562.63
	Benidorm Island	*Myliobatis aquila*	0.00 (0%)	0.22
	Marina Alta	*Gymnura altavela*, *Raja asterias*, *Raja polystigma*, *Raja radula*	0.00 (0%)	134.24
All ISRAs			4502.09 (15.52%)	29011.54
Areas of Interest (potential ISRAs)	Castellon Slope	*Centrophorus uyato*	837.94 (25.86%)	3240.00
	Ferrutx	*Dasyatis pastinaca*, *Rostroraja alba*, *Gymnura altavela*, *Bathytoshia lata*	0.00 (0%)	124.21
	Emile Baudot Seamount	*Mobula mobular*, *Centrophorus uyato*	0.00 (0%)	497.50
All AoIs			837.94 (21.70%)	3861.7

Note: Geospatial calculations were performed with QGIS and presence–absence distribution shown in Figure S4.

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a stronger influence of the seabed's degree of inclination on egg nursery areas than compared to catsharks.

4.2 | Current Distribution and Protection of Egg Nursery Habitat

Current MPA establishment efforts are generally lacking in their implementation and biodiversity protection targets, while MPA area coverage is not sufficient by itself to measure present protection levels (Pike et al. 2024). To match the ongoing push towards increasing MPA coverage globally in the short and medium term, information about biodiverse areas such as benthic communities, as well as important areas for the reproduction and growth of marine species, is needed to advice decision makers. Having clear delimitations of these key areas can help achieve a more efficient implementation of new MPAs or a redesign of current MPA networks. Here, we used a threshold approach to delimitate areas suitable for small-spotted catshark spawning. However, we acknowledge that thresholding ecological processes to clear-cut presence/absence outputs is inherently problematic (Merow, Smith, and Silander 2013), as the complexity of ecological processes results in some flexibility in said values. For this reason, the thresholding results are presented together with the continuous distribution values of probable habitat suitability. Both outputs, together with actual observations, should ideally be used jointly when taking informed decisions for the management and conservation of elasmobranch nursery areas.

The repeated use of specific locations to lay fertilised eggs in high abundances is clearly shown the by the continuous, year-round egg presence over 3–4 years throughout the Catalan coast, a requirement for an area to be defined as an elasmobranch egg nursery (Hoff 2016). This observed recurrent presence of small-spotted catshark eggs confirms the north-western Mediterranean Sea as an essential reproduction and habitat location for the small-spotted catshark. Particularly the northern part of the Balearic Sea, which concentrates both the densest areas suitable for egg nurseries, and the highest protected surface area by means of no-take MPAs, although most of the suitable habitat still remains outside of any protected areas. Due to the shared habitat between small-spotted catshark egg nurseries and important benthic colonial organisms in the area, this species' egg nurseries could be considered as 'umbrella areas/species' (Caro 2010) of essential habitats and bentho-demersal communities in current need of protection. Furthermore, while the analysis presented here is species-specific, other shark and batoid species might have an overlapping habitat in terms of environmentally suitable areas for spawning, such as the nursehound *Scyliorhinus stellaris*, currently classified as vulnerable and decreasing in population by the IUCN's Red List (Finucci, Derrick, and Pacoureau 2021). Currently, only 3.65% of the area modelled as suitable for small-spotted catshark egg nurseries in the Balearic Sea is under protection. This sharply contrasts with the need to increase conservation efforts to protect local elasmobranch stocks, with the recent classification of different parts of the Balearic Sea as Important Shark and Ray Areas (IUCN-ISRAs; https://sharkrayareas.org), and with the need to protect important benthic ecosystems at the European level (e.g., Directive 2008/56/EC).

Apart from the aforementioned considerations, our work is not without limitations. We did not have egg presence data from the whole Balearic Sea or inside the no-take MPAs that were closed in 2020 to fit the model; still, reproductively active adult small-spotted catsharks are known to be present throughout it (Navarro et al. 2016; Ramírez-Amaro et al. 2020). This suggests that the predictions shown here are informative of the realised niche of small-spotted catshark egg nurseries over the Balearic Sea, but are nevertheless only a partial representation of the species' full distribution. It is possible that the creation and enforcement of the no-take MPAs in the area could have a positive bias on habitat suitability, mainly due to the recovery of the associated benthic species required for incubation, which should ideally be considered in the analyses. However, the protection status of areas where eggs were sampled was not taken into account in the model, mainly due to the sampling design and constraints (bottom trawling hauls were located outside of the no-take MPAs). Moreover, current MPAs have only been in place for around 5 years, while bottom trawling impact is long-lasting and the recovery of these species after it stops is known to be very slow (Althaus et al. 2009; Clark et al. 2019). Lastly, another potential limitation was the use of a single modelling framework (Maxent) for the habitat suitability predictions. Fine-tuned ensemble models (a combination of multiple model outputs) generally perform better than Maxent, but they come at the cost of being much more time-intensive to both produce and run, while in some cases only offering small improvements to the predictions (Valavi et al. 2022). Even though this is an important consideration, we decided on using a single and easily tuned model such as the one presented here with the aim of updating it when new data are available from monitoring programmes in the area.

Although small-spotted catshark distribution in the western Mediterranean is relatively well known (Navarro et al. 2016; Follesa et al. 2020), few studies have described scyliorhinid egg nurseries in the Mediterranean (Cau et al. 2017), making it difficult to take informed decision towards how these areas can be defined and protected. We used occurrences from invasive sampling methods (i.e., bottom trawling), but as bottom trawling activities inside no-take MPAs are permanently banned, MPA monitoring strategies such as video recording should ideally be implemented to validate that these areas are being used as nursery locations for the species. Current sampling efforts have shown constant egg presence for at least 3–5 years in many areas along the north-western Mediterranean Sea. However, future research should target in situ and ideally non-invasive sampling methods that not only confirm the non-sampled, predicted areas but also allow future monitoring and longer time series.

Protecting known recruitment hotspots may result in enhanced results when establishing MPAs for fish, especially when including them inside a no-take MPA network (Wen et al. 2013). The results shown here are in support of future increases of some of the already implemented no-take MPAs, and the establishment of new ones in locations where there are none in place (e.g., north of the Balearic archipelago), particularly when considering the relationship between scyliorhinids' spawning locations and habitat-forming sessile, fragile and endangered organisms. Furthermore, they offer additional support to the already defined ISRAs and AoIs within this area of the western Mediterranean,

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in particular based on their Criterion C1: Reproductive Areas (Hyde et al. 2022). The marine environment is currently facing the fast deployment of new human activities, such as offshore renewable energy (European Commission 2023), that compete for available space and that need to be spatially and sustainably managed together with both existing ones and with nature. At the same time, future expansions of the MPA networks that consider demersal elasmobranchs and their associated benthic biodiversity are needed to reach current conservation aims, such as the European Union's target of 'strictly protecting' 10% of the European waters by 2030. Our results give clear and easily interpretable spatial information for decision makers and stakeholders to help with this process, from assessing current no-take MPAs in the north-western Mediterranean Sea to guiding future marine spatial planning frameworks.

5 | Conclusions

The threat to elasmobranchs is essentially multifactorial and requires protecting them at different stages of their development. In this study, we showed for the first time in the Mediterranean Sea a habitat map of egg nurseries of an iconic demersal elasmobranch which requires a diversity of habitat-forming colonial organisms to successfully lay eggs. The habitat overlap of small-spotted catshark eggs and threatened benthic communities of colonial organisms such as sea pens and soft corals suggests these results might serve two purposes: First, as a much needed distribution map of key locations where oviparous elasmobranchs such as the small-spotted catshark close their reproductive cycle through benthic egg-laying behaviour; and second, as a proxy of areas with ecologically important benthic communities.

Our area-based calculations clearly show that no-take MPAs originally designed to recover commercially important species such as Norway lobster or European hake have potential cascading benefits that go well beyond their initial single-species objectives. These closures partly cover habitats of slow-growing deep-sea colonial organisms, which in turn facilitate successful hatching of elasmobranch eggs. The only way to conserve these fragile ecosystems from high impact activities such as bottom trawling is through permanent spatial closures such as no-take MPAs. These deep-sea habitats, if intact, are known to provide extended benefits to the fishery sector by serving as resilient nursery areas for juvenile fish stages. In the current push for further protection of the sea and the restoration of impacted ecosystems, our results serve as useful information for the assessments of current MPAs. Furthermore, they could help identify under-protected areas for the demersal community and guide future protection efforts and MPA design strategies.

Author Contributions

Miguel López: conceptualization, data curation, methodology, formal analysis, investigation, visualization, writing – original draft, writing – review and editing. **Morane Clavel-Henry:** conceptualization, supervision, writing – review and editing. **Nixon Bahamon:** conceptualization, supervision, writing – review and editing. **Maria Vigo:** conceptualization, writing – review and editing. **Marc Balcells:** data curation, writing – review and editing. **Antoni Sánchez-Márquez:** conceptualization, writing – review and editing. **Joan Navarro:** conceptualization, supervision, funding acquisition, writing – review and editing. **Joan B. Company:** conceptualization, supervision, funding acquisition, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Scyliorhinus canicula egg occurrence locations used in this study are available as a .csv file in the Data S2. Bathymetry data are available online at GEBCO's database (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). Seabed type data are available online at EMODnet (https://emodnet.ec.europa.eu/geoviewer/). This study has been conducted using E.U. Copernicus Marine Service Information, and dissolved oxygen and bottom temperature data are available online at Copernicus Marine Service (https://marine.copernicus.eu/).

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