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# Diversity, Abundance and Distribution of Sharks in a Multispecies Nursery Area in the Eastern Central Atlantic

Adam Whiting[1,2] | Francesco Garzon[3,4] | Ze Luis Monteiro[3,†] | Zeddy T. A. Seymour[3] | João Lima[3] | Cintia Lima[3] | Sam Owen[2] | Rachel T. Graham[2]

[1]Centre for Ecology and Conservation, University of Exeter, Penryn, UK | [2]MarAlliance, Panama City, Panama | [3]MarAlliance, Sal Rei, Boa Vista, Cabo Verde | [4]Faculty of Health and Life Sciences, Hatherly Laboratories, University of Exeter, Exeter, UK

**Correspondence:** Francesco Garzon (f.garzon@exeter.ac.uk) | Rachel T. Graham (rachel@maralliance.org)

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## ABSTRACT

Shark nursery habitats are priority targets for area-based conservation as they protect key age classes that exhibit restricted area use. However, the lack of detailed, species-specific biological and ecological data often undermines the efficacy of coastal management strategies. This study employed complementary Baited Remote Underwater Video (BRUV) and longline surveys to assess the diversity, distribution and seasonal use of shark species in a possible multispecies nursery in the Bay of Sal Rei (Cabo Verde), a critical but understudied habitat within the Eastern Central Atlantic (ECA). A total of 132 sharks were identified in BRUV footage, and 198 individuals were caught, measured and tagged for recapture. Size estimates from BRUV footage and maturity assessments from longline surveys revealed possible nursery use by at least 6 shark species. Size ranges indicate that the BSR is likely a primary nursery for milk (35–125 cm), blacktip (60–175 cm), scalloped hammerhead (35–54 cm) and spinner (60–126 cm) sharks, and a secondary nursery for common smoothhounds (61–100 cm) and Atlantic weasel sharks (58.5–135 cm). Possible altered space use between age classes was identified, with spatial and temporal differences in habitat partitioning between the primary and secondary nursery. These results, co-created with local fishers and practitioners, identify the Bay of Sal Rei as a critical habitat for shark populations in the Eastern Central Atlantic and provide a robust scientific basis for implementing targeted, spatial and seasonal management that both engages and includes local communities.

## 1 | Introduction

As apex predators, sharks occupy key trophic roles in ecosystems, contributing to the maintenance of biodiversity and ecosystem stability (Ferretti et al. 2010; Dedman et al. 2024). However, their K-selected life history traits (low fecundity, late maturity, slow growth) make them particularly vulnerable to exploitation (Frisk et al. 2005). Subsequently, sharks are among the most threatened vertebrate groups globally, with over a third of shark and ray species classified as critically endangered, endangered or vulnerable by the IUCN red list criteria (Dulvy et al. 2021, 2024). In response, area-based conservation strategies have been proposed as a key element in the safeguarding of shark populations, with initiatives such as the IUCN's Important Shark and Ray Areas (ISRA) striving to identify discrete regions critical for shark survival on which to focus conservation efforts (Hyde et al. 2022). Nursery areas, typically occurring in delimited, accessible shallow coastal habitats, are a clear target for conservation, given their crucial role in shark life-history (Heupel et al. 2007; Heupel et al. 2018) and the relative ease of monitoring and enforcement of these areas compared with offshore habitats.

Shark nurseries are defined as areas (i) where juveniles occur in relatively higher densities than the surroundings, (ii) where juveniles tend to remain or return for extended periods and

†Deceased.

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(iii) that are used repeatedly across years (Heupel et al. 2007). Nurseries can further be distinguished between primary shark nurseries (areas in which sharks are born and spend the initial stage of their lives) and secondary shark nurseries (areas inhabited by older individuals yet to reach maturity) (Bass 1978). Both nursery types can occur in the same geographic area and likely serve to reduce the risk of predation (Bass 1978; Heithaus 2007), offer increased feeding opportunities for juveniles (Yates et al. 2015; Heupel et al. 2018) and reduce the overall natural mortality (Simpfendorfer and Milward 1993; Merson and Pratt 2001; Heupel et al. 2004; Heupel and Simpfendorfer 2011). Neonate and juvenile age classes are considered the most crucial in determining population recruitment (Cortés 1998) and are hence a critical demographic target for shark conservation, but their restricted area-use and reliable catchability within coastal nurseries might expose them to high fishing pressure. As such, protection and management of nursery areas have been widely advocated for whenever such sites have been identified.

Despite the bias towards protecting nursery habitats due to their defined spatial boundaries and implementation feasibility, their shallow, coastal waters make them particularly susceptible to temperature increases associated with anthropogenic climate change, leading to documented shifts in nursery use by some species due to altered habitat suitability (Bangley et al. 2018; Crear et al. 2020). Habitat suitability varies between shark species, and the simultaneous examination of habitat use across multiple coastal shark species remains relatively limited, hindering the development of comprehensive spatial and temporal conservation models regarding multispecies nurseries (Kinney and Simpfendorfer 2009). The failure to incorporate movement patterns and ontogenetic shifts in habitat use into management strategies can further inhibit positive conservation outcomes if protected areas exclude key behaviours/life histories such as seasonal migratory movements, diel space use patterns or ontogenetic shifts in habitat use (Speed et al. 2010). As such, the long-term monitoring of seasonal use patterns and habitat partitioning of nurseries can help to predict how the suitability of these areas may be altered due to climate change, whilst identifying susceptible species and life stages.

The Eastern Central Atlantic (ECA), despite its ecological significance, remains a data-deficient region, whilst facing documented threats to marine biodiversity due to overharvesting of marine resources (Polidoro et al. 2017). Within this region, the archipelagic islands of Cape Verde have emerged as a particularly important area, supporting high concentrations of endangered species (Rosa et al. 2023; Seymour et al. 2024). Boa Vista, the easternmost island of the archipelago, faces intensification of extractive activities due to an influx of tourism (Varela et al. 2025). The Bay of Sal Rei, located to the Northwest of Boa Vista Island (Figure 1), consists of shallow, sandy habitat protected from wave action by a small islet (Ilheu de Sal Rei). The Bay of Sal Rei is, based on local anecdotal knowledge, known to support various juvenile shark species and is used as an artisanal fishery for '*caçao*', which typically refers to any small shark resembling the milk shark (*Rhizoprionodon acutus*) or common smoothound (*Mustelus mustelus*). Longline and gillnet surveys have also confirmed multiannual, seasonal nursery use by nurse (*Ginglymostoma cirratum*), blacktip (*Carcharhinus limbatus*), scalloped hammerhead (*Sphyrna lewini*) and Atlantic weasel sharks (*Paragaleus pectoralis*) (Seymour and Graham 2016; Rosa et al. 2023), as well as their relative higher abundance compared with other sites in the island (Rosa et al. 2023). Together, these surveys appear to fulfil the requirements for nursery area identification described above, and have prompted discussions regarding the establishment of protection in the Northeastern portion of the bay (Seymour and Graham 2016). However, management uncertainty persists, largely due to unresolved ecological measures regarding residency, species distributions, habitat associations and seasonal variations in life stage composition.

This study employed complementary baited remote underwater video (BRUV) and scientific longline surveys to characterise the nursery function of the Bay of Sal Rei by quantifying shark species and life stage composition, spatial distribution and seasonal presence and nursery use. Specific objectives were (i) to determine species-specific abundance and distribution patterns within the bay; (ii) to identify pupping seasonality through the presence of neonates; (iii) to document which life stages utilise the nursery throughout the year.

## 2 | Methods

### 2.1 | Study Area

The bay exhibits a range of habitat types across various depths, including rocky reefs and sand plains (average depth ~10 m), whilst the North-East region consists of a shallow (< 5 m), sandy channel, protected from wave action by a small islet (Figure 1).

### 2.2 | Survey Methods

Following recommendations for multimethod approaches to studying coastal elasmobranch species, two complementary methods were employed to assess shark populations in the Bay of Sal Rei: Baited Remote Underwater Video systems (BRUVs) to provide standardised abundance estimates and species distributions, and fishing surveys, which enable detailed biological sampling and individual identification to confirm residency and maturity. All fieldwork for the study was conducted under multiannual research permits provided by Direccion Nacional do Ambiente do Cabo Verde (2016–2019).

BRUVs are a noninvasive method effective for assessing biodiversity, abundance and distribution patterns of marine megafauna whilst eliminating catchability bias (Whitmarsh et al. 2017). However, the time-limited nature of video capture compounded by the time-intensive nature of the analysis typically restricts BRUV sampling to discrete periods, potentially underestimating abundance of mobile species (Speed et al. 2010; Seymour et al. 2024). In contrast, scientific longline surveys can be conducted over extended timeframes and provide immediate data with additional benefits that include captured animals' precise length measurements, confirmation of maturity status through umbilical scarring and individual identification through tagging and recapture (Daly et al. 2018). Conversely, fishing surveys suffer from selectivity bias resulting from hook size, bait and fishing method selection. Given these complementary strengths, this dual-method approach provided a more



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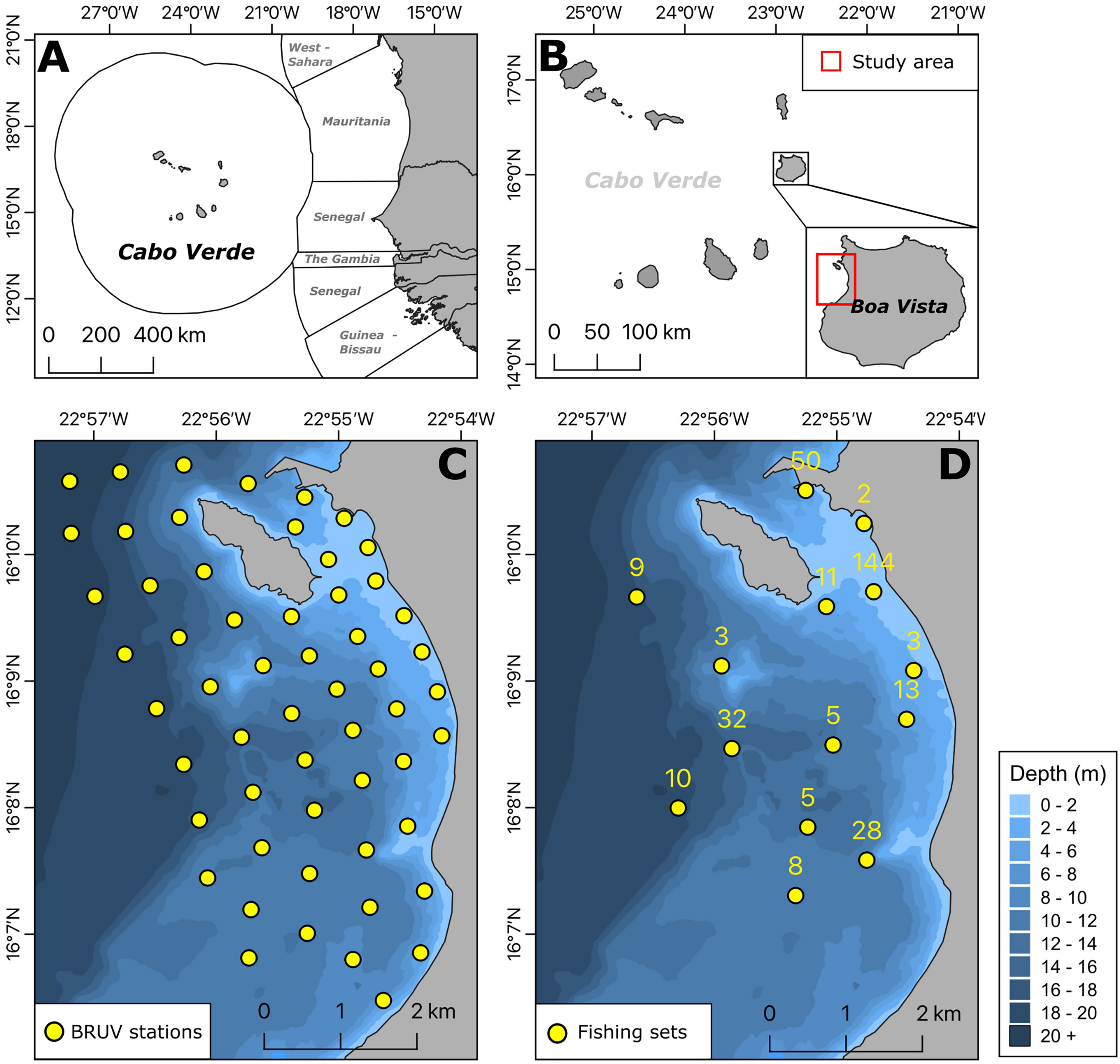


**FIGURE 1** | Distribution of survey effort. (A,B) Location of the study area (Bay of Sal Rei) in Cabo Verde and survey locations for BRUV surveys during June and August of 2019 (D), and fishing surveys from 2016 to 2019 (D). Numeric labels in D denote the number of fishing sets conducted at each station.

comprehensive assessment of shark populations in the Bay of Sal Rei, following recommendations for multimethod approaches in elasmobranch research to reduce selectivity bias of methods (White et al. 2013).

BRUV sampling was conducted across 56 fixed stations in the Bay of Sal Rei during June and August 2019, resulting in 112 total deployments. Stations were positioned approximately 2 km apart to ensure homogeneous coverage and replication whilst avoiding bait plume overlap between stations (Exeter et al. 2025) (Figure 1c). Sampling occurred in June (2–8th) and August (12–18th), with these months selected to target pre- and post- pupping periods (based on local anecdotal knowledge). BRUV surveys were conducted during daylight hours only. Each sampling day, 9–13 randomised deployments were conducted, achieving complete coverage of all stations in each period. Bottom depth, temperature and deployment time were recorded during each BRUV deployment. Following standardised methodology (Graham 2012; Seymour et al. 2024), each deployment used a single horizontal-facing camera (GoPro, 2k resolution, 60 fps) and 1.0 kg of crushed Frigate tuna (*Auxis thazard*) or similar oily fish as bait across all deployments. The bait receptacle extended 1.0 m from the frame and was positioned 70 cm above the seafloor. A 30-cm t-bar attached to the bait cage enabled size estimation of sharks that approached the bait and could be viewed laterally. Two trained observers independently analysed 60-min video segments, with analysis beginning 5 min after BRUV settlement to allow for the boat to depart and ambient conditions to resume. Sharks were identified to the lowest possible taxonomic



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level, and abundance was quantified using MaxN—a standard metric used in BRUV surveys that equates to the maximum number of individuals of each species visible in a single frame (Willis and Babcock 2000; Cappo 2003). Total length estimates were obtained for sharks that were fully visible laterally against the 30-cm t-bar reference. Inter-observer size discrepancies were resolved through post analysis discussions, and size estimates for which variation exceeded 30 cm were excluded from analyses.

Between 2016 and 2019, 328 fishing surveys were conducted, predominantly between May and October, at various sites within the bay (Figure 1). Fishing effort was unevenly split between years, with 31, 2, 157 and 189 fishing surveys conducted in 2016, 2017, 2018 and 2019, respectively. Sharks were captured using either short demersal longline sets (10–15 hooks) or handlines fitted with 4/0 or 6/0 circle hooks and baited with dead mackerel or other oily fish. Lines were set predominantly at dusk/night and were left to soak for an average of 30 min between checks to maximise shark survival post-release (Horton et al. 2023). Longline sets in 2019 were placed at a sample of BRUV stations to offer a comparison in species sightings between methods. Fishing surveys were often targeted at tag-and-release operations and so were biased towards locations and timings that offered the highest chances of catches (according to fishers' knowledge). Upon capture, sharks were secured close to the boat by a tail rope or if very small to conduct the procedure more rapidly were brought onboard. Gill irrigation was not possible when onboard; therefore, handling procedures and biological sampling were limited to a maximum duration of 2 min per individual to minimise physiological stress (Horton et al. 2023). For each shark, precaudal and total length were recorded, as well as sex, presence of an umbilical scar and clasper length and calcification stage to assess maturity for male sharks (Stehmann 2002). Identification tags (spaghetti tag) were applied at the base of the first dorsal fin of each individual, and a fin clip taken from either the anal or the second dorsal fin for storage and future genetic analysis.

## 2.3 | Data Analysis

### 2.3.1 | BRUV Metrics

Three metrics were calculated across all BRUV deployments for each species: (1) total sightings (N), defined as the sum of MaxN values; (2) relative abundance (%RA), calculated by dividing N by the number of BRUVs deployed per season; (3) frequency of occurrence (%FO), expressed as the percentage of BRUVs where the species was observed.

### 2.3.2 | Temporal and Spatial Patterns of Size Distributions

For species with multiple individual measurements in BRUV footage, length-frequency distributions were plotted by season, whilst length-frequency distributions were plotted for all seasons and years from longline efforts. Published size-at-maturity estimates were used to infer maturity status of individuals (Branstetter 1987; Castro 1996; Saïdi et al. 2008; Ba et al. 2013). To calculate differences in sizes over season from caught sharks, catches of each species were grouped into season (Spring: April–May; Summer: June–August; Autumn: September–October) and compared using ANOVA followed by post hoc Tukey's test comparisons following confirmation of normality. For species with sufficient measurement data, depth-driven patterns of size distribution were investigated using linear models following confirmation of normality. Linear models and ANOVAs were performed using Program R (Version 2024.04.2+764), with the MASS (V7.3.65; Venables and Ripley 2002) and Vegan (Oksanen 2017) packages. The tidyverse (V2.0.0; Wickham et al. 2019) package was used throughout.

### 2.3.3 | Species Distribution Patterns

Spatial structure of shark sightings (relative abundance) was analysed through kernel density distributions of BRUV deployments, weighted by MaxN values for each deployment location. Analyses were performed using QGIS (version 3.34.12). Kernel densities were calculated separately for each species on combined data from both seasons (sum of MaxN), with a radius of 1.4 km selected based on optimal representation of the underlying spatial distribution patterns. Distributions could not be inferred from catch data due to the opportunistic nature of the sampling method.

### 2.3.4 | Environmental Drivers of Abundance

Generalised linear mixed models (GLMMs) were used to examine the effects of depth (meters), season (June/August) and sun height (minutes relative to solar noon) on MaxN of each species. Depth is known to influence the distribution of coastal shark species (Speed et al. 2010). Seasonality is known to influence the movement patterns and pupping behaviours of sharks (Bres 1993). The effect of sun height was included in the full model as it is known to influence the movement and activity patterns of coastal sharks (Speed et al. 2010). To calculate sun height (H), the deployment time was converted into minutes relative to sunrise, following Equations (1) and (2).

$$H = T_{\text{dep}} - T_{\text{rise}} \quad \text{for } T_{\text{dep}} \leq T_{\text{noon}} \tag{1}$$

$$H = \left(T_{\text{noon}} - T_{\text{rise}}\right) - \left(T_{\text{dep}} - T_{\text{noon}}\right) \quad \text{for } T_{\text{dep}} > T_{\text{noon}} \tag{2}$$

where $T_{\text{dep}}$ is the deployment time, $T_{\text{rise}}$ is the time of sunrise, and $T_{\text{noon}}$ is the time at solar noon (all units in minutes). For times after solar noon, the number of minutes past midday is subtracted to account for the sun's descent during the afternoon.

This approach standardised time relative to the sun's position throughout the day, whilst accounting for differences in day length across sampling periods. Predictors were tested for collinearity prior to modelling using linear models; temperature displayed a significant negative association with depth ($b = -3.05 \pm 0.87$, $p < 0.001$) and thus only depth was retained for modelling.

A Poisson error family with a log link was applied to the count data (MaxN), switching to a negative binomial distribution if overdispersion was detected using DHARMa residuals (Zeileis



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et al. 2008). Station was included as a random effect to account for repeated deployments at the same locations but retained only if it significantly improved model fit (likelihood ratio test). Models were compared with the null model using ANOVA (chi-squared). Model selection was guided by Akaike's information criterion (AIC), and residual diagnostics ensured goodness-of-fit. Interaction effects between depth and time (an a priori assumption of shallower depth use at night was assumed to discern diel movement) were tested by comparing models with interactions against reduced models without interactions using likelihood ratio tests (chi-squared; Zeileis et al. 2008). Only significant interactions ($p < 0.05$) were retained. Analyses were conducted in R (Version 2024.04.2+764) using the MASS (V7.3.65; Venables and Ripley 2002), DHARMa (V0.4.7; Hartig et al. 2024) and glmmTMB packages (V1.1.11; Brooks et al. 2017).

## 3 | Results

### 3.1 | Sightings and Catch Statistics

All BRUVs ($N=56$, 56 for June, August) successfully recorded video, yielding 112 h of footage. Species level identification was achieved for all sharks, leading to the identification of 132 individuals across eight species. Milk shark (*R. acutus*) were the most abundant species, followed by Atlantic weasel (*P. pectoralis*), blacktip (*C. limbatus*), spinner (*Carcharhinus brevipinna*), smooth-hound (*M. mustelus*), nurse (*G. cirratum*), scalloped hammerhead (*S. lewini*) and tiger sharks (*G. cuvier*) (Table 1). All species, excluding *G. cirratum* and *G. cuvier*, were also caught during fishing efforts, totalling 198 catches. Species across both survey types generally displayed similar relative abundances, with the exception of *P. pectoralis*, of which catches were proportionally lower than BRUV sightings (Table 1). A single *M. mustelus* and *C. brevipinna* were recaptured, each 1 month after initial tagging.

**TABLE 1** | Species composition of BRUV sightings and scientific fishing catches. Comparison of relative abundance (RA%) between BRUV surveys ($N=122$) and scientific fishing surveys ($N=328$).

| | BRUV | | | Fishing | |
|---|---|---|---|---|---|
| **Species** | **MaxN** | **FO (%)** | **RA (%)** | **N** | **RA (%)** |
| *Rhizoprionodon acutus* | 53 | 34 | 40 | 135 | 68 |
| *Paragaleus pectoralis* | 26 | 20 | 20 | 9 | 4 |
| *Carcharhinus brevipinna* | 18 | 5.3 | 13 | 32 | 16 |
| *Carcharhinus limbatus* | 17 | 13 | 12 | 15 | 8 |
| *Mustelus mustelus* | 7 | 4.5 | 5 | 3 | 2 |
| *Ginglymostoma cirratum* | 6 | 5.4 | 5 | — | — |
| *Sphyrna lewini* | 4 | 2.7 | 3 | 4 | 2 |
| *Galeocerdo cuvier* | 1 | 0.9 | 1 | — | — |

### 3.2 | Size Distribution

A total of 120 size measurements were made from BRUV footage. Neonates and young of the year (inferred by comparing to published average sizes at birth and maturity) of *R. acutus*, *C. limbatus*, *S. lewini* and *C. brevipinna* were observed, whilst *P. pectoralis* and *M. mustelus* were of an older average inferred age but yet to reach maturity (Figure 2).

Individuals of *S. lewini* of typical neonate size were exclusively observed during August, *M. mustelus*, *C. limbatus* and *C. brevipinna* displayed decreased average total lengths during August, whilst *P. pectoralis* length estimates were lower in June. *M. mustelus* were recorded solely in June across both BRUV and fishing effort (Figure 2).

During fishing efforts, length measurements and maturity estimates were achieved for all but two sharks (Figure 3). Neonates represented all *S. lewini* and the majority of *R. acutus* and *C. limbatus* catches, whilst catches of *C. brevipinna* were dominated by juveniles. *P. pectoralis* and *M. mustelus* caught in longlines were exclusively juveniles and adults (no neonates recorded), with *P. pectoralis* juveniles of subadult size. *M. mustelus* were caught during the summer months, whereas *S. lewini* were exclusively caught in August. Significant seasonal variations in size were detected in *R. acutus* (ANOVA (2,125), $p < 0.001$) and *C. brevipinna* (ANOVA (2,29), $p < 0.005$) (Figure 3), with average total lengths of *R. acutus* significantly smaller in both summer (mean TL = 48 cm) and autumn (mean TL = 47 cm) compared with those caught in spring (mean TL = 79 cm, Tukey's HSD, $p < 0.005$), whilst *C. brevipinna* were significantly smaller in Autumn (mean TL = 79 cm) than those caught in Summer (mean TL = 104 cm, Tukey's HSD, $p < 0.005$).

*R. acutus* total lengths derived from longline surveys furthermore displayed a significant positive association with depth ($b = 2.21 \pm 0.16$, $p < 0.001$), with larger individuals more commonly caught in deeper water.

### 3.3 | Spatial Distribution and Drivers of Abundance

Shark species displayed distinct spatial distributions within the bay (Figure 4). *R. acutus* were observed throughout the Bay of Sal Rei, whereas *P. pectoralis* exhibited a bimodal pattern, with higher abundances to the NW and SE of the bay. Both *S. lewini* and *C. limbatus* were most abundant within the shallow, sandy channel between Ilheu de Sal Rei and Sal Rei, with *C. limbatus* displaying a greater range north and south of the islet. *C. brevipinna* were also observed in the channel but were distributed throughout the north of the Bay of Sal Rei. *M. mustelus* distributions were limited to a discrete region to the west of Ilheu de Sal Rei.

Generalised linear mixed effect models indicated that the abundance of all species excluding *P. pectoralis* was influenced by depth (Table 2). Both *M. mustelus* ($b = 1.04 \pm 0.018$, Chi(1) < 0.01, $p < 0.01$) and *C. brevipinna* ($b = 1.01 \pm 1.01$, Chi(1) < 0.01, $p < 0.01$) displayed significant positive relationships with depth; however, *M. mustelus* had a considerably



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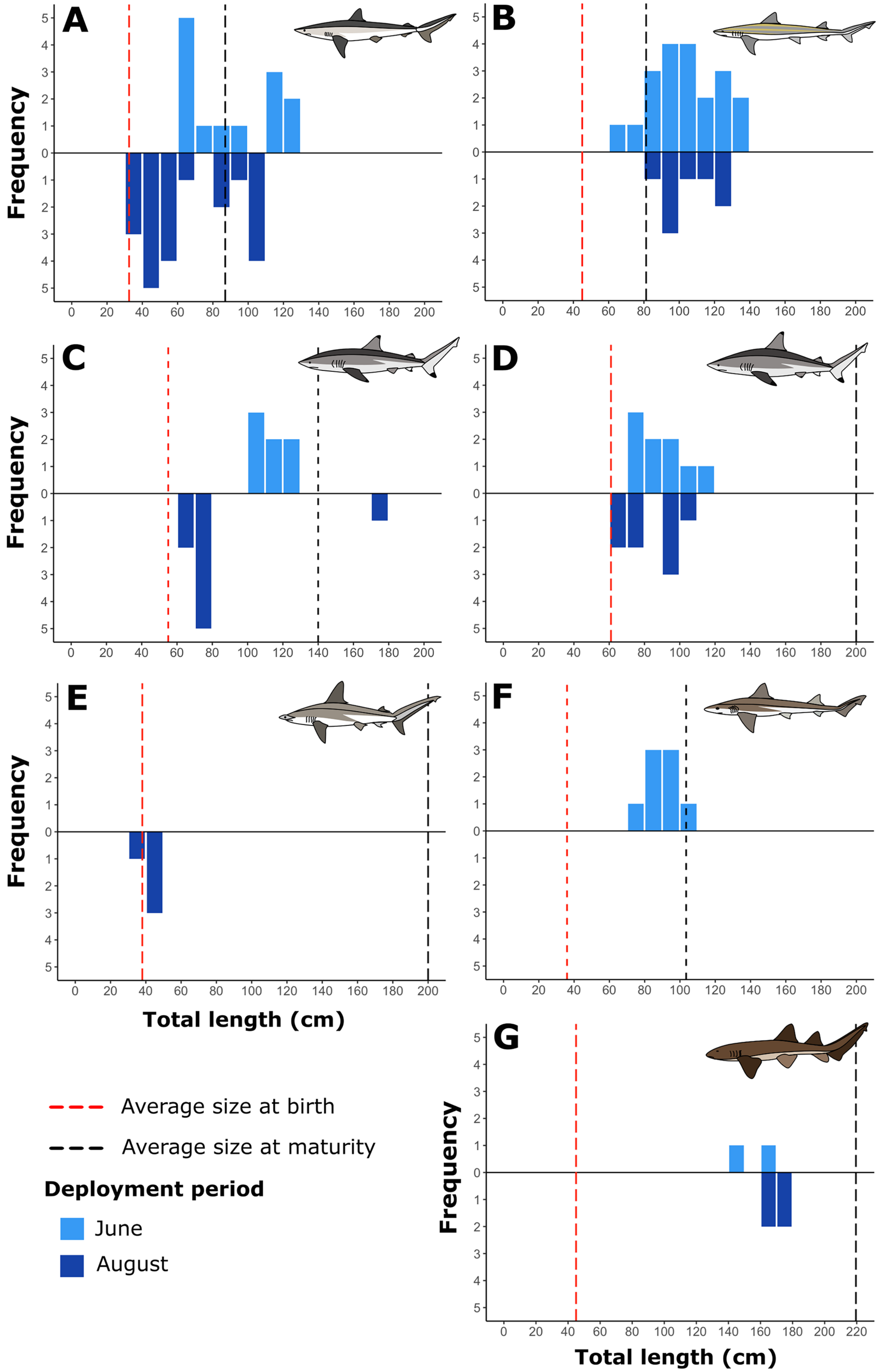


**FIGURE 2** | Legend on next page.



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**FIGURE 2** | Size distribution of shark species sighted in BRUV surveys. Seasonal length frequency distributions of sharks for which total length estimates could be estimated from BRUV footage. Vertical black dashed lines represent the mean size at maturity derived from literature, and vertical red dashed lines indicate average species specific sizes at birth. Light blue = June, dark blue = August. A = *Rhizoprionodon acutus* ($N = 35$), B = *Paragaleus pectoralis* ($N = 27$), C = *Carcharhinus limbatus* ($N = 15$), D = *Carcharhinus brevipinna* ($N = 17$), E = *Sphyrna lewini* ($N = 4$), F = *Mustelus mustelus* ($N = 8$), G = *Ginglymostoma cirratum* ($N = 6$).

lower intercept (−136.2), indicating that they typically appear at greater depths than *C. brevipinna* (−12.21). *C. limbatus* MaxN was instead predicted to be significantly higher, on average, in shallow water ($b = -1.04 \pm 1.06$, Chi(1) < 0.01, $p < 0.05$). The effect of season (June vs. August, categorical predictor) had a significant positive influence on *R. acutus* MaxN, indicating higher abundances in August ($b = 2.52 \pm 1.37$, $p < 0.01$). In addition, the interaction between sun height and depth was also significant ($b = -1.0 \pm 1.0$, $p < 0.01$) for this species, suggesting a preference for deeper water at times nearer to sunrise or sunset (Table 2).

## 4 | Discussion

### 4.1 | Bay of Sal Rei as a Nursery Area

In the context of declining shark populations due to exploitation and human-induced habitat loss, protecting nursery areas is a key strategy to promote recruitment and safeguard threatened shark species. Cabo Verde, in the Eastern Central Atlantic, is home to a range of elasmobranchs (Seymour et al. 2024) and likely to host a number of shark nurseries in the sheltered, shallow coastal waters surrounding the islands (Rosa et al. 2023; Varela et al. 2025). The Bay of Sal Rei, flanking the western edge of Sal Rei, the main city of Boavista, is known to host juvenile sharks of numerous species, including the critically endangered Scalloped hammerhead (*S. lewini*; Seymour and Graham 2016; Rosa et al. 2023). Based on population size-structure, seasonality and spatial use, the results of BRUVs and fishing surveys presented in this study indicate that the Bay of Sal Rei is likely a primary and secondary shark nursery, used by at least 6 shark species: scalloped hammerhead sharks at the initial stage of their lives, milk (*R. acutus*), blacktip (*C. limbatus*) and spinner sharks (*C. brevipinna*) from birth to sub-adult stage, and common smoothhound (*M. mustelus*) and Atlantic weasel sharks (*P. pectoralis*) as subadults. Adult Atlantic nurse sharks (*G. cirratum*) and tiger sharks (*G. cuvier*) were also recorded in the bay. Previous estimates of shark diversity in the bay reported the presence of five species (Rosa et al. 2023), which the results of this study increase to eight by demonstrating the presence of *G. cuvier*, *M. mustelus* and *C. brevipinna* in the area (likely a result of the combination of different survey methods and longer sampling timeframes). All but one species are of conservation concern: Atlantic nurse sharks, spinner sharks, blacktip sharks and milk sharks are listed as Vulnerable in the IUCN Red List (Rigby, Carlson, et al. 2020; Rigby, Harry, et al. 2020; Carlson et al. 2021; Rigby et al. 2021), the common smoothhound and Atlantic weasel shark are listed as Endangered (Jabado, Chartrain, Cliff, et al. 2021; Jabado, Chartrain, De Bruyne, et al. 2021), and the scalloped hammerhead shark is considered Critically Endangered (Rigby et al. 2019). Tiger sharks are listed as Near Threatened on a global scale (Ferreira and Simpfendorfer 2019), though lack of data for the species may be masking similar population declines to those observed for most shark populations in West Africa (Sall et al. 2021).

Given the diversity of species recorded, their conservation status and the diversity of life stages recorded, the Bay of Sal Rei represents a key area for the conservation of elasmobranch populations in Cabo Verde and the wider central Atlantic. The bay is, however, also used for a wide range of recreational (e.g., sailing, surfing, snorkelling) and extractive activities (recreational and subsistence fishing), with unknown overlap and unquantified potential impacts on sharks. A deeper understanding of the spatio-temporal patterns of shark presence in the bay is therefore needed in order to inform management of human activities (e.g., introduction of spatial or temporal closure areas, identification of critical monitoring/enforcement periods) and build engagement for the safeguarding of this critical habitat.

### 4.2 | Space Use of Sharks in the Nursery

The simultaneous examination of habitat use between species is a key element when developing conservation models for multispecies nurseries (Kinney and Simpfendorfer 2009), to highlight hotspots of occupancy or species-specific needs to take into account in spatial planning of area-based conservation measures. Within the Bay of Sal Rei, individual species appeared to exhibit distinct distribution patterns. Species for which neonates were the predominant age class (i.e., *C. limbatus*, *S. lewini* and *C. brevipinna*) were distributed nearer to the coast, whilst sharks of an older average age (as inferred by estimated size; that is, *R. acutus*, *G. cirratum* and *P. pectoralis*) were observed further offshore, and generally exhibited more dispersed distributions within the Bay of Sal Rei. Furthermore, the latter also showed possible higher levels of species separation, whilst species for which neonates and juveniles were the predominant age class displayed strong overlaps in distributions, particularly in the north-east of the bay.

A potential explanation for the differences in space use between age classes may be related to their primary use of the nursery (i.e., maximise feeding opportunities or minimise predation). Whilst some nurseries can be associated with areas of high productivity, whereby juveniles will exhibit spatial partitioning to reduce competition for resources (Kinney et al. 2011), distribution patterns of some juvenile shark species within nurseries are more consistent with predator avoidance than prey availability, leading to shared occupancy (Heithaus 2007). In this optic, it is plausible that that deeper, more productive habitats of the Bay of Sal Rei are used by some species for their better foraging opportunities, whilst the



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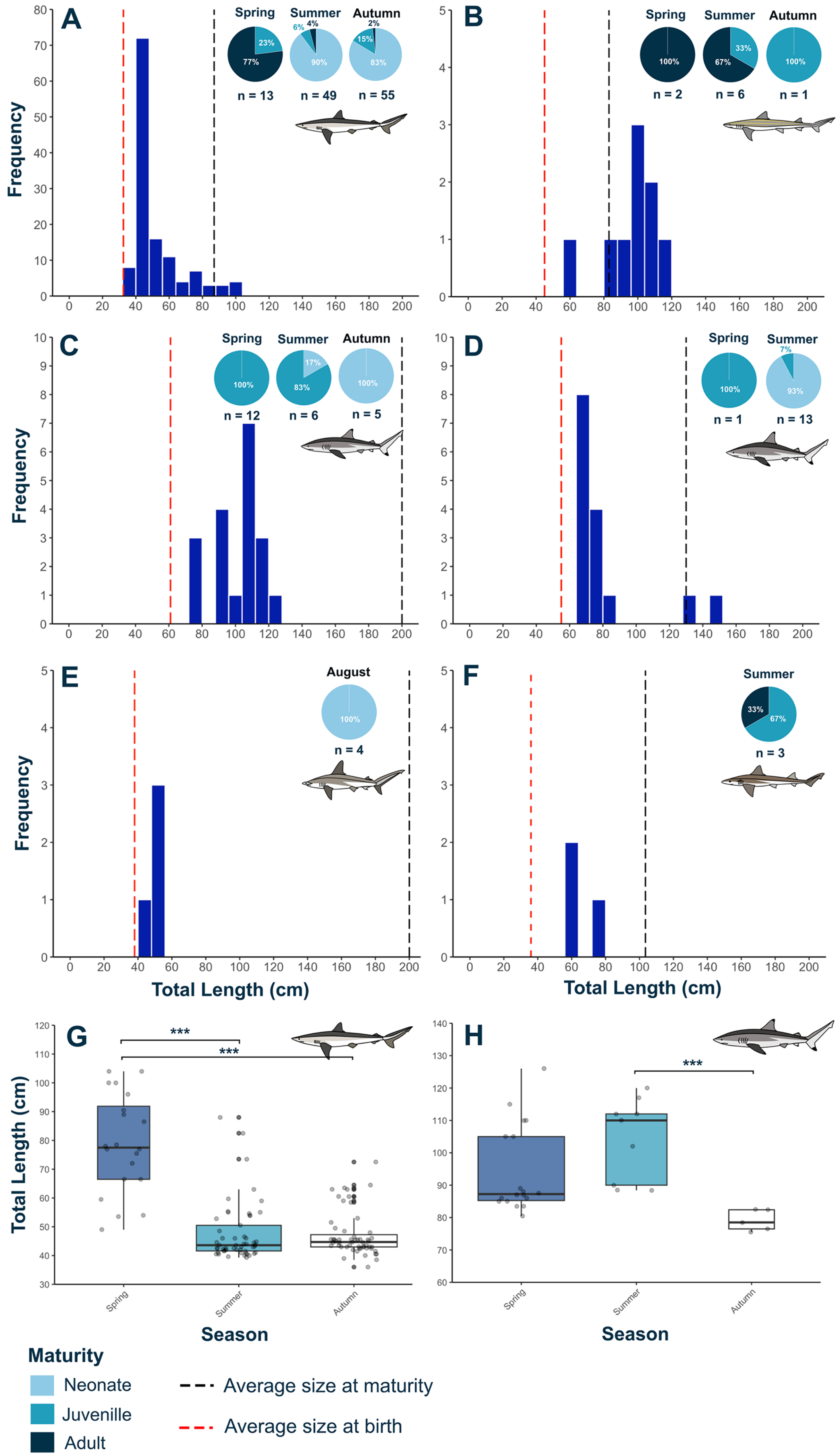


**FIGURE 3** | Legend on next page.



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FIGURE 3 | Size distribution of shark species caught in fishing surveys. Length frequency distributions of sharks caught during scientific fishing surveys. Pie charts indicate maturity estimates caught during spring, summer and autumn. Vertical dashed black lines represent average size at maturity, and vertical red dashed lines indicate average size at birth. Boxplots denote total lengths of individuals caught across season, *** = $p < 0.001$. A = *Rhizoprionodon acutus*, B = *Paragaleus pectoralis*, C = *Carcharhinus limbatus*, D = *Carcharhinus brevipinna*, E = *Sphyrna lewini*, F = *Mustelus mustelus*, G = *R. acutus*, H = *C. brevipinna*.

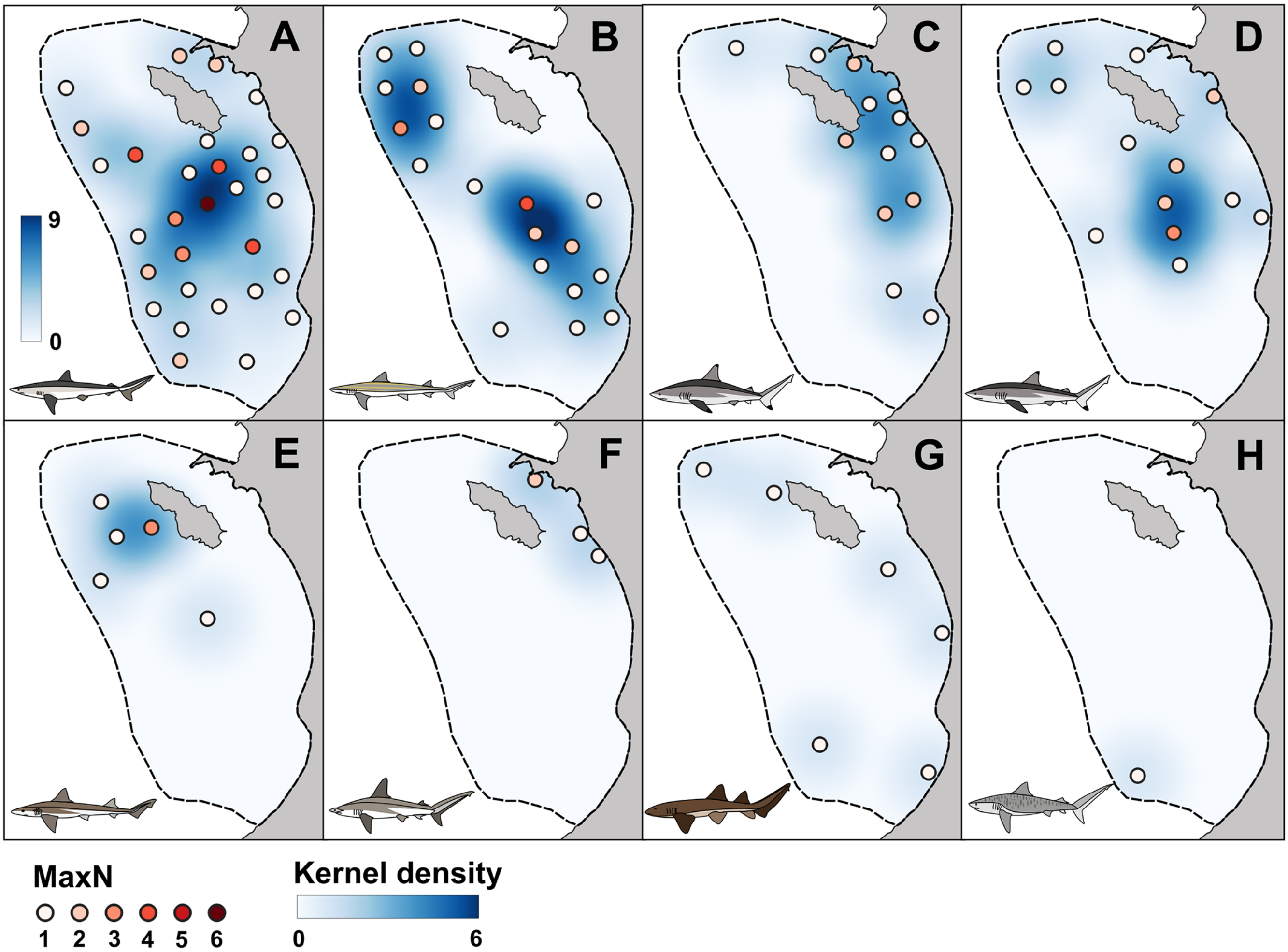


FIGURE 4 | Distribution of shark species within the Bay of Sal Rei. MaxN (coloured dots) and kernel density (blue shading) of shark species sighted in BRUV surveys conducted in the bay of Sal Rei. Darker shading indicates higher measured or estimated abundance. Note the different kernel density scale in A. A = *Rhizoprionodon acutus*, B = *Paragaleus pectoralis*, C = *Carcharhinus limbatus*, D = *Carcharhinus brevipinna*, E = *Mustelus mustelus*, F = *Sphyrna lewini*, G = *Ginglymostoma cirratum*, H = *Galeocerdo cuvier*.

shallow areas, characterised by higher surface temperatures, high turbidity and sand as the dominant benthic substrate (a habitat traditionally associated with low primary productivity and low dissolved oxygen levels; Heupel and Hueter 2002) may provide refuge from larger sharks, which tend to avoid hypoxic environments (Waller et al. 2024).

An alternative mechanism to reduce predation risk whilst partitioning resources is diel movement. *R. acutus* displayed higher abundances in deep water during sunrise and sunset, indicating diel movement to deeper waters at night. The shallow, coastal waters of the bay are likely resource limited, therefore diel movement as a strategy to partition resources is a possibility. Diel movement has been well documented in *S. lewini* and *C. limbatus*, but given their low abundance within the Bay of Sal Rei, coupled with the brief residency of *S. lewini*, the design of this study may have underestimated the abundances of these species due to diel movement during survey periods. Continuous, structured surveys within the Bay of Sal Rei will reveal movement patterns and true abundance of species to implement meaningful conservation strategies. To this effect, the installation of an acoustic tracking network would offer an invaluable complement to visual and fishery-based surveys in investigating species movements in the bay.



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**TABLE 2** | Selected GLMM model of relative abundance (MaxN) for BRUV sightings. Estimates and standard errors are back transformed, and model selection was based on testing against the null model. Significant effects are denoted in bold text.

| | | Output | | | | Selection | |
|---|---|---|---|---|---|---|---|
| Species | Factor | Estimate | SE | *z* | *p* | AIC | Chi squared |
| *Mustelus mustelus* | Intercept | −136.20 | 2.98 | −4.50 | < 0.001 | 52.57 | < 0.01 |
| | Depth | 1.04 | 0.018 | 2.64 | **< 0.01** | | |
| *Carcharinus brevipinna* | Intercept | −12.21 | 1.56 | −5.64 | < 0.001 | 128.98 | < 0.01 |
| | Depth | 1.01 | 1.01 | 3.07 | **< 0.01** | | |
| *Carcharinus limbatus* | Intercept | −2.60 | 1.50 | −2.37 | < 0.05 | 100.95 | < 0.01 |
| | Depth | −1.04 | 1.06 | −2.27 | **< 0.05** | | |
| *Rhizoprionodon acutus* | Intercept | −66.92 | 3.28 | −3.54 | < 0.001 | 202.28 | < 0.01 |
| | Depth | 1.09 | 1.03 | 3.27 | **< 0.05** | | |
| | Sun height | 1.01 | 1.00 | 2.19 | **< 0.05** | | |
| | Season (August) | 2.52 | 1.37 | 2.94 | **< 0.01** | | |
| | Depth:sun height | −1.00 | 1.00 | −2.71 | **< 0.01** | | |

### 4.3 | Phenology of Shark Presence and Pupping in the Area

Pupping of sharks in the Bay of Sal Rei displayed clear seasonality, with occupation of smaller sharks during the late summer to early autumn months (late July to early October), indicating pupping during the summer. Temporal differences in pupping were also observed, with *S. lewini* and *C. brevipinna* pupping in late summer to early August, whilst *R. acutus* likely pupping in mid-summer.

Previous studies of *S. lewini* neonates have described their tendency to inhabit primary coastal nurseries for 3–4 months before migrating to deeper waters (Klimley and Nelson 1984). It is likely that neonates in the Bay of Sal Rei display similar behaviour; however, tagging effort in the present study was insufficient to quantify site fidelity or residency times. Likely due to the abundance of individuals within the Bay of Sal Rei, few individuals were recaptured during tagging efforts. Nonetheless, the recapture of juvenile *M. mustelus* and *C. brevipinna* months after initial tagging provides some anecdotal evidence that species exhibit residency within the Bay of Sal Rei. Future efforts should focus on the use of electronic tagging as a means to confirm residency.

### 4.4 | Methodological Comparisons

Multi-method sampling is crucial to evaluate population trends in coastal regions, as differing sampling methods can yield significant differences in elasmobranch diversity, abundance and habitat use (Elston and Murray 2024). Nonetheless, methods should be evaluated to assess whether replacement or complementary noninvasive methods are more appropriate to reduce the exploitation of vertebrates (Grunow and Strauch 2023). The results of this study indicate that scientific fishing and BRUV surveys exhibit broad comparability regarding relative abundances of species, size estimations and changes in size across seasons. Some key differences were observed, namely in relative abundance of *P. pectoralis* and species diversity estimates across methods. These differences are likely explained by the opportunistic nature of fishing surveys, in which sampling was biased towards the North-East region of the bay.

Fishing surveys provide comprehensive, immediate biological data; however, differing catchability of species may lead to underreporting species diversity. In the present study, fishing surveys suggested a lower diversity of species than that obtained from BRUVs, which were not limited by the catchability of species (hook size, bait type). Fishing surveys also yielded lower abundances of *P. pectoralis* than estimates from BRUV footage. Fishing surveys were biased towards shallow water and conducted at dusk, predominantly to the east of the islet, though BRUV footage revealed that the species were distributed in deeper waters, accounting for the method underestimating the abundance of the species.

Comparisons between longlines and size estimations from BRUV footage were similar, though the limited number of size estimations, combined with likely high error rates associated with visual size estimates from footage, hindered the ability to conduct statistical analyses in BRUV footage. One possible method to obtain accurate, reliable size estimates in a noninvasive manner is stereo BRUVs. However, the high cost, calibration needs and higher analytical burden of this method can represent a barrier for long-term monitoring in small organisations and engagement of local fishers turned community shark monitors.

### 4.5 | Future Research Needs and Conservation Focus

The reliable catchability and restricted area use of elasmobranchs in coastal nurseries may predispose juveniles and neonates to higher rates of fishing. Given the importance of these



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life stages in shark life history (Heupel et al. 2007), measures directed at alleviating or eliminating anthropogenic pressures on nursery grounds should be prioritized when possible.

Although the total domestic value created by the fishing sector is ~1% of GDP in Cabo Verde, small scale fisheries contribute 60% to sector GDP (Fortes 2019). Therefore, management strategies should prioritise life stages crucial for population recruitment whilst simultaneously ensuring livelihoods in the community. The Bay of Sal Rei is often utilised as an artisanal fishery for '*caçao*', an ambiguous term referring to the dried meat of any juvenile or small bodied shark resembling *R. acutus*. Gillnets and handlines are the preferred fishing methods in the area (ZLM pers. comm.; Rosa et al. 2023; Seymour and Graham 2016), most often used to catch small teleost fish but also targeting small sharks when they are most abundant. Gillnet surveys indicate a high catchability of *S. lewini* within the Bay of Sal Rei, as well as other endangered species (Rosa et al. 2023), raising concerns as to the long-term sustainability of the fishery. Given the distinct spatio-temporal patterns of shark presence in the bay described here, it is possible that dynamic management of fisheries in the bay may offer benefits to both shark populations and fisheries. *R. acutus* were the most abundant species in the Bay of Sal Rei, exhibiting overlaps in distribution with all other shark species in all sites but the southeast. Given the conservation status of species with lower abundances to the northeast of the bay, possible restrictions on fishing to the SE could be explored, to reduce the bycatch of endangered species whilst benefiting stakeholders. Furthermore, given the limited and predictable time frame of neonate presence, seasonal restrictions on artisanal fishing during late summer to autumn months could be adopted to reduce the bycatch of neonates and juveniles and increase their recruitment to deeper waters, where they are less likely to be caught.

Warm shallow coastal habitats such as the nursery presented in this study are likely to be disproportionately affected by the increase in global temperatures caused by climate change. The altered suitability of coastal habitats may lead to changes in nursery selection, as Elasmobranchs are highly sensitive to temperature changes, and juvenile sharks actively seek to remain within their thermal optimum (Skelton et al. 2023). It is unclear how warming temperatures may affect the Bay of Sal Rei, where temperatures in the primary nursery were found to already be significantly higher than in deeper parts of the bay, or whether juveniles will be able to adapt to the increase in temperature. Evidence suggests some species are altering their nursery use in response to increased temperatures (Crear et al. 2020), and it is possible that these changes in nursery use may even lead to range expansion into unprotected areas. Therefore, delineating protection to nurseries that meet current criteria (residency, used over multiple years, seen more frequently than in other areas) may not be a sustainable long-term approach. Understanding the fine scale movements of individuals and the influence of environmental factors on nursery dynamics is therefore key to establishing sustainable, long-term protection. Moreover, monitoring the survival rates within nurseries will inform whether hypothesised altering of habitat use may influence the future efficacy of nurseries as a means of protection from predation.

While the Bay of Sal Rei is included in planned expansions of the island's marine protected area network (Coastal and adjacent Sea Management Plan (POOCM), 2020), management plans are focused on the shallow, south-easterly region of the bay which correspond with turtle nesting beaches, and do not explicitly reference elasmobranchs. For these species, explicit MPA zoning and targeted seasonal gear restrictions could have higher conservation impact and should be considered in planning scenarios. Furthermore, the proximity of two tourism development zones in the north-eastern region of the bay may pose a risk to the future safeguarding of the nursery. Long-term monitoring of the effectiveness of the nursery, particularly by collecting data regarding survival rates whilst engaging coastal traditional fishers, is therefore critical to inform the implementation of effective conservation strategies adopted by coastal stakeholders.

### Author Contributions

**Sam Owen:** data curation. **João Lima:** investigation. **Ze Luis Monteiro:** conceptualization, investigation. **Cintia Lima:** project administration. **Zeddy T. A. Seymour:** conceptualization, investigation, funding acquisition, project administration. **Adam Whiting:** data curation, formal analysis, visualization, writing – original draft, writing – review and editing. **Francesco Garzon:** funding aquisition, investigation, project administration, data curation, writing – original draft, writing – review and editing. **Rachel Graham:** conceptualization, funding aquisition, project administration, investigation, writing – original draft, writing – review and editing.

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### Ethics Statement

All fieldwork for the study was conducted under multiannual research permits provided by Direccion Nacional do Ambiente do Cabo Verde (2016–2019).

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

All data presented in the study are supplied in Supporting Information. Raw video data that are too large to store online are available upon request to the authors.

### References

Ba, A., C. T. Ba, K. Diouf, P. I. Ndiaye, and J. Panfili. 2013. "Reproductive Biology of the Milk Shark *Rhizoprionodon acutus* (Carcharhinidae) off the Coast of Senegal." *African Journal of Marine Science* 35, no. 2: 223–232. https://doi.org/10.2989/1814232X.2013.796892.



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Bangley, C. W., L. Paramore, D. S. Shiffman, and R. A. Rulifson. 2018. "Increased Abundance and Nursery Habitat Use of the Bull Shark (*Carcharhinus leucas*) in Response to a Changing Environment in a Warm-Temperate Estuary." *Scientific Reports* 8, no. 1: 6018. https://doi.org/10.1038/s41598-018-24510-z.

Bass, A. 1978. "Problems in Studies of Sharks in the Southwest Indian Ocean." In *Sensory Biology of Sharks, Skates and Rays*, 545–594. Arlington: Office of Naval Research, Department of the Navy.

Branstetter, S. 1987. "Age and Growth Estimates for Blacktip, *Carcharhinus limbatus*, and Spinner, *C. brevipinna*, Sharks From the Northwestern Gulf of Mexico." *Copeia* 1987, no. 4: 964–974. https://doi.org/10.2307/1445560.

Bres, M. 1993. "The Behaviour of Sharks." *Reviews in Fish Biology and Fisheries* 3, no. 2: 133–159. https://doi.org/10.1007/BF00045229.

Brooks, M., K. Kristensen, K. J. van Benthem, et al. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9, no. 2: 378–400. https://digitalcommons.unl.edu/r-journal/675.

Cappo, M. 2003. "Potential of Video Techniques to Monitor Diversity, Abundance and Size of Fish in Studies of Marine Protected Areas." In *Aquatic Protected Areas-What Works Best and How Do We Know*, 455–464. World Congress on Protected Areas.

Carlson, J., P. Charvet, M. P. Blanco-Parra, et al. 2021. "Ginglymostoma cirratum." *IUCN Red List of Threatened Species* 21: e.T144141186A3095153. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T144141186A3095153.en.

Castro, J. I. 1996. "Biology of the Blacktip Shark, *Carcharhinus limbatus*, off the Southeastern United States." *Bulletin of Marine Science* 59, no. 3: 508–522.

Cortés, E. 1998. "Demographic Analysis as an Aid in Shark Stock Assessment and Management." *Fisheries Research* 39, no. 2: 199–208. https://doi.org/10.1016/S0165-7836(98)00183-0.

Crear, D. P., R. J. Latour, M. A. M. Friedrichs, P. St-Laurent, and K. C. Weng. 2020. "Sensitivity of a Shark Nursery Habitat to a Changing Climate." *Marine Ecology Progress Series* 652: 123–136. https://doi.org/10.3354/meps13483.

Daly, R., M. J. Smale, S. Singh, et al. 2018. "Refuges and Risks: Evaluating the Benefits of an Expanded MPA Network for Mobile Apex Predators." *Diversity and Distributions* 24, no. 9: 1217–1230. https://doi.org/10.1111/ddi.12758.

Dedman, S., J. H. Moxley, Y. P. Papastamatiou, et al. 2024. "Ecological Roles and Importance of Sharks in the Anthropocene Ocean." *Science* 385, no. 6708: adl2362. https://doi.org/10.1126/science.adl2362.

Dulvy, N. K., N. Pacoureau, J. H. Matsushiba, et al. 2024. "Ecological Erosion and Expanding Extinction Risk of Sharks and Rays." *Science* 386, no. 6726: eadn1477. https://doi.org/10.1126/science.adn1477.

Dulvy, N. K., N. Pacoureau, C. L. Rigby, et al. 2021. "Overfishing Drives Over One-Third of All Sharks and Rays Toward a Global Extinction Crisis." *Current Biology* 31, no. 21: 4773–4787.e8. https://doi.org/10.1016/j.cub.2021.08.062.

Elston, C., and T. Murray. 2024. "Multi-Method Approach Identifies a South African Estuary as an Important Elasmobranch Habitat and Potential Nursery Ground." *African Journal of Marine Science* 46, no. 2: 91–102. https://doi.org/10.2989/1814232X.2024.2326814.

Exeter, O. M., A. C. Broderick, X. A. Harrison, et al. 2025. "Application of Spatially Robust Stereo-BRUV Sampling for Quantifying Fish Assemblages in UK Marine Protected Areas." *Ecological Applications* 35, no. 6: e70104. https://doi.org/10.1002/eap.70104.

Ferreira, L.C. and C. Simpfendorfer. 2019 "'Galeocerdo Cuvier', The IUCN Red List of Threatened Species." p. e.T39378A2913541.

Ferretti, F., B. Worm, G. L. Britten, M. R. Heithaus, and H. K. Lotze. 2010. "Patterns and Ecosystem Consequences of Shark Declines in the Ocean." *Ecology Letters* 13, no. 8: 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x.

Fortes D.M. 2019. "Assessment of Economic Viability of the Artisanal Fisheries in Cabo Verde: Recommendations for Improvement". Iceland: United Nations University Fisheries Training Program. Final project. http://www.unuftp.is/static/fellows/document/Delvis18prf.pdf.

Frisk, M., T. Miller, and N. Dulvy. 2005. "Life Histories and Vulnerability to Exploitation of Elasmobranchs: Inferences From Elasticity, Perturbation and Phylogenetic Analyses." *Journal of Northwest Atlantic Fishery Science* 37: 27–45. https://doi.org/10.2960/J.v35.m514.

Graham R. 2012. "Rapid Shark Assessment the Swan Islands, Honduras Technical Report."

Grunow, B., and S. M. Strauch. 2023. "Status Assessment and Opportunities for Improving Fish Welfare in Animal Experimental Research According to the 3R-Guidelines." *Reviews in Fish Biology and Fisheries* 33, no. 4: 1075–1093. https://doi.org/10.1007/s11160-023-09781-8.

Hartig, F., L. Lohse and M. de Souza Leite. 2024. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." Accessed: February 16, 2026. https://cran.r-project.org/web/packages/DHARMa/index.html.

Heithaus, M. 2007. "Nursery Areas as Essential Shark Habitat: A Theoretical Perspective." American Fisheries Society Symposium, pp. 3–13. Accessed February 16, 2026. https://www.academia.edu/58382842/Nursery_areas_as_essential_shark_habitat_a_theoretical_perspective.

Heupel, M. R., J. K. Carlson, and C. A. Simpfendorfer. 2007. "Shark Nursery Areas: Concepts, Definition, Characterization and Assumptions." *Marine Ecology Progress Series* 337, no. Nmfs 2006: 287–297. https://doi.org/10.3354/meps337287.

Heupel, M. R., and R. E. Hueter. 2002. "Importance of Prey Density in Relation to the Movement Patterns of Juvenile Blacktip Sharks (*Carcharhinus limbatus*) Within a Coastal Nursery Area." *Marine and Freshwater Research* 53, no. 2: 543–550. https://doi.org/10.1071/MF01132.

Heupel, M. R., S. Kanno, A. P. B. Martins, and C. A. Simpfendorfer. 2018. "Advances in Understanding the Roles and Benefits of Nursery Areas for Elasmobranch Populations." *Marine and Freshwater Research* 70, no. 7: 897–907. https://doi.org/10.1071/MF18081.

Heupel, M. R., and C. A. Simpfendorfer. 2011. "Estuarine Nursery Areas Provide a Low-Mortality Environment for Young Bull Sharks *Carcharhinus leucas*." *Marine Ecology Progress Series* 433: 237–244. https://doi.org/10.3354/meps09191.

Heupel, M. R., C. A. Simpfendorfer, and R. E. Hueter. 2004. "Estimation of Shark Home Ranges Using Passive Monitoring Techniques." *Environmental Biology of Fishes* 71, no. 2: 135–142. https://doi.org/10.1023/B:EBFI.0000045710.18997.f7.

Horton, T. W., O. Exeter, F. Garzon, et al. 2023. "Best Practices for Catch-and-Release Shark Angling: Current Scientific Understanding and Future Research." *Fisheries Research* 267: 106760. https://doi.org/10.1016/j.fishres.2023.106760.

Hyde, C. A., G. Notarbartolo di Sciara, L. Sorrentino, et al. 2022. "Putting Sharks on the Map: A Global Standard for Improving Shark Area-Based Conservation." *Frontiers in Marine Science* 9: 968853. https://doi.org/10.3389/fmars.2022.968853.

Jabado, R.W., E. Chartrain, and G. Cliff, et al. 2021. "'Mustelus Mustelus', the IUCN Red List of Threatened Species." p. e.T39358A124405881. https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T39358A124405881.en.




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Jabado, R.W., E. Chartrain, G. De Bruyne, et al. 2021. "Paragaleus pectoralis." The IUCN Red List of Threatened Species 2009, p. e.T161707A124531152. https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T161707A124531152.en.

Kinney, M.J., N.E. Hussey, A.T. Fisk, A.J. Tobin, and C.A. Simpfendorfer. 2011. "Communal or Competitive? Stable Isotope Analysis Provides Evidence of Resource Partitioning Within a Communal Shark Nursery." *Marine Ecology Progress Series* 439: 263–276. https://doi.org/10.3354/meps09327.

Kinney, M. J., and C. A. Simpfendorfer. 2009. "Reassessing the Value of Nursery Areas to Shark Conservation and Management." *Conservation Letters* 2, no. 2: 53–60. https://doi.org/10.1111/j.1755-263X.2008.00046.x.

Klimley, A. P., and D. R. Nelson. 1984. "Diel Movement Patterns of the Scalloped Hammerhead Shark (*Sphyrna lewini*) in Relation to El Bajo Espiritu Santo: A Refuging Central-Position Social System." *Behavioral Ecology and Sociobiology* 15, no. 1: 45–54. https://doi.org/10.1007/BF00310214.

Merson, R. R., and H. L. Pratt. 2001. "Distribution, Movements and Growth of Young Sandbar Sharks, *Carcharhinus plumbeus*, in the Nursery Grounds of Delaware Bay." *Environmental Biology of Fishes* 61, no. 1: 13–24. https://doi.org/10.1023/A:1011017109776.

Oksanen J. 2017. "Vegan: Community Ecology Package. R Package Version 2.4-3."

Polidoro, B. A., G. M. Ralph, K. Strongin, et al. 2017. "The Status of Marine Biodiversity in the Eastern Central Atlantic (West and Central Africa)." *Aquatic Conservation: Marine and Freshwater Ecosystems* 27, no. 5: 1021–1034. https://doi.org/10.1002/aqc.2744.

Rigby, C.L. J. Carlson, and D. Derrick, et al. 2021. "'Carcharhinus Limbatus', the IUCN Red List of Threatened Species." p. e.T3851A2870736. https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T3851A2870736.en.

Rigby, C.L., J. Carlson, and J. J. Smart, et al. 2020. "'Carcharhinus Brevipinna', the IUCN Red List of Threatened Species." p. e.T39368A2908817 https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T39368A2908817.en.

Rigby, C. L., N. K. Dulvy, R. Barreto, et al. 2019. "Sphyrna lewini." *IUCN Red List of Threatened Species* 2019: T39385A2918526.

Rigby, C.L., A.V. Harry, and N. Pacoureau, et al. 2020. "Rhizoprionodon acutus." The IUCN Red List of Threatened Species, p. e.T41850A68642326. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T41850A68642326.en.

Rosa, R., E. Nunes, V. Pissarra, et al. 2023. "Evidence for the First Multi-Species Shark Nursery Area in Atlantic Africa (Boa Vista Island, Cabo Verde)." *Frontiers in Marine Science* 10: 1077748. https://doi.org/10.3389/fmars.2023.1077748.

Saïdi, B., M. N. Bradaï, and A. Bouaïn. 2008. "Reproductive Biology of the Smooth-Hound Shark *Mustelus mustelus* (L.) in the Gulf of Gabès (South-Central Mediterranean Sea)." *Journal of Fish Biology* 72, no. 6: 1343–1354. https://doi.org/10.1111/j.1095-8649.2008.01801.x.

Sall, A., P. Failler, B. Drakeford, and A. March. 2021. "Fisher Migrations: Social and Economic Perspectives on the Emerging Shark Fishery in West Africa." *African Identities* 19, no. 3: 284–303. https://doi.org/10.1080/14725843.2021.1937051.

Seymour, A. T. A. and R. T. Graham. 2016. "Building Capacities and Knowledge to Underpin the Conservation of Threatened Sharks in Rays in Cabo Verde, West Africa. Sal Rei, Boa Vista, Cabo Verde: MarAlliance." https://maralliance.org/research-publications/.

Seymour, Z. T. A., Z. L. Monteiro, A. Monteiro, I. E. Baremore, F. Garzon, and R. T. Graham. 2024. "Baseline Assessment of the Coastal Elasmobranch Fauna of Eastern Cabo Verde, West Africa." *Aquatic Conservation: Marine and Freshwater Ecosystems* 34, no. 9: e4206. https://doi.org/10.1002/aqc.4206.

Simpfendorfer, C. A., and N. E. Milward. 1993. "Utilisation of a Tropical Bay as a Nursery Area by Sharks of the Families Carcharhinidae and Sphyrnidae." *Environmental Biology of Fishes* 37, no. 4: 337–345. https://doi.org/10.1007/BF00005200.

Skelton, Z. R., T. S. Prinzing, P. A. Hastings, and N. C. Wegner. 2023. "Laboratory-Based Measures of Temperature Preference and Metabolic Thermal Sensitivity Provide Insight Into the Habitat Utilisation of Juvenile California Horn Shark (*Heterodontus francisci*) and Leopard Shark (*Triakis semifasciata*)." *Journal of Fish Biology* 102, no. 4: 829–843. https://doi.org/10.1111/jfb.15307.

Speed, C. W., I. C. Field, M. G. Meekan, and C. J. A. Bradshaw. 2010. "Complexities of Coastal Shark Movements and Their Implications for Management." *Marine Ecology Progress Series* 408: 275–293. https://doi.org/10.3354/meps08581.

Stehmann, M. F. W. 2002. "Proposal of a Maturity Stages Scale for Oviparous and Viviparous Cartilaginous Fishes (Pisces, Chondrichthyes)." *Archive of Fishery and Marine Research* 50, no. 1: 23–48.

Varela, J., C. P. Santos, E. Nunes, et al. 2025. "Sharks in Cabo Verde, Canarias, Madeira and Azores Islands: Species Richness, Conservation Status and Anthropogenic Pressures." *Frontiers in Marine Science* 12: 1490317. https://doi.org/10.3389/fmars.2025.1490317.

Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics With S. Fourth Edition*. Springer ISBN 0-387-95457-0.

Waller, M. J., N. E. Humphries, F. C. Womersley, et al. 2024. "The Vulnerability of Sharks, Skates, and Rays to Ocean Deoxygenation: Physiological Mechanisms, Behavioral Responses, and Ecological Impacts." *Journal of Fish Biology* 105, no. 2: 482–511. https://doi.org/10.1111/jfb.15830.

White, J., C. A. Simpfendorfer, A. J. Tobin, and M. R. Heupel. 2013. "Application of Baited Remote Underwater Video Surveys to Quantify Spatial Distribution of Elasmobranchs at an Ecosystem Scale." *Journal of Experimental Marine Biology and Ecology* 448: 281–288. https://doi.org/10.1016/j.jembe.2013.08.004.

Whitmarsh, S. K., P. G. Fairweather, and C. Huveneers. 2017. "What Is Big BRUVver Up to? Methods and Uses of Baited Underwater Video." *Reviews in Fish Biology and Fisheries* 27, no. 1: 53–73. https://doi.org/10.1007/s11160-016-9450-1.

Wickham, H., M. Averick, J. Bryan, et al. 2019. "Welcome to the Tidyverse." *Journal of Open Source Software* 4, no. 43: 1686. https://doi.org/10.21105/joss.01686.

Willis, T. J., and R. C. Babcock. 2000. "A Baited Underwater Video System for the Determination of Relative Density of Carnivorous Reef Fish." *Marine and Freshwater Research* 51, no. 8: 755–763. https://doi.org/10.1071/MF00010.

Yates, P. M., M. R. Heupel, A. J. Tobin, and C. A. Simpfendorfer. 2015. "Ecological Drivers of Shark Distributions Along a Tropical Coastline." *PLoS ONE* 10, no. 4: e0121346. https://doi.org/10.1371/journal.pone.0121346.

Zeileis, A., C. Kleiber, and S. Jackman. 2008. "Regression Models for Count Data in R." *Journal of Statistical Software* 8: 1–25.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** BRUV effort data. **Data S2:** BRUV sightings data. **Data S3:** Longline capture data.



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