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Drivers of behaviour and spatial ecology of the small spotted catshark (*Scyliorhinus canicula*)

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Abstract

1. Shark populations have suffered dramatic declines across the world as a result of overfishing.
2. Marine protected areas (MPAs) can help restore overfished populations; however, their effectiveness largely relies on understanding the ecology of the targeted species.
3. This study investigated the spatial ecology of the intensely harvested but understudied small spotted catshark (*Scyliorhinus canicula*) through acoustic telemetry in the Cíes Islands, a small MPA in the north-west of the Iberian Peninsula.
4. There were significant effects of diel, seasonal cycles, biotic (sex and total length) and abiotic (bottom sea temperature) variables on the spatial behaviour of *S. canicula*. The mean residency index was low (0.27) and movement patterns suggested a strong connection with inshore waters. While the probability of presence in the study area was mainly driven by sex (i.e. greater for females), a drastic increase in activity was observed at night (compared with daytime hours). The activity space decreased with larger body sizes. Warmer waters were related to higher activity levels and larger activity spaces.
5. This study provides essential knowledge of the spatial behaviour of *S. canicula*, with significant implications for the conservation and management of this species. The results indicate that small MPAs may fail to protect the whole range of movements of *S. canicula*, but suggest a larger protection potential for females.
6. To be effective for *S. canicula* conservation, MPAs should be appropriately sized and designed for the ranging behaviour of the target species in order to provide total protection. Temporal restrictions on fishing at night mirroring the peak activity pattern of *S. canicula* could be implemented to limit the probability of its capture.

KEYWORDS
acoustic telemetry, diel patterns, elasmobranch, marine protected area, *Scyliorhinus canicula*, sharks, spatial ecology

1 | INTRODUCTION

Sharks are one of the most endangered groups of species on the planet (Lucifora, García & Worm, 2011). Over the last 50 years, the global abundance of oceanic sharks and rays has decreased by 71% (Pacoureau et al., 2021) and today, one out of three shark species is considered endangered or threatened with extinction (Dulvy et al., 2021). Sharks' high extinction risk has two major drivers: their life history strategy and their exposure to fishing (Dulvy et al., 2014). Most shark species follow a K-strategy (Smallegange, Flotats & Eustache, 2020) with extended gestation periods, low fecundity and long life span (Dulvy et al., 2008), ultimately resulting in slow intrinsic population growth. Sharks are being heavily harvested all over the world for their meat, fins, gill plates and liver oil (McClenachan, Cooper & Dulvy, 2016). Shark landings increased by 227% from 1950, reaching a peak in 2003 with ∼900,000 tonnes (Musick & Musick, 2011; FAO, 2013). Although a 15% drop in subsequent shark landings was recorded in 2011, this decrease was mainly the result of population decline (FAO, 2013; Davidson, Krawchuk & Dulvy, 2015).

Globally decreasing shark populations have sparked a growing interest in setting up new marine protected areas (MPAs) and assessing whether existing MPAs can assist in their recovery (Knip, Heupel & Simpfendorfer, 2012; Mizrahi et al., 2019; Jacoby et al., 2020). MPAs are the cornerstone of marine conservation (Giakoumi et al., 2018). Covering 7.9% of the world's ocean (UNEP-WCMC and IUCN, 2022), MPAs are intended to help rebuild overharvested fish stocks and conserve biodiversity through a total or partial reduction of fishing within their borders (West et al., 2009). Because of their typically small size, MPAs tend to be more effective in protecting sedentary species (Wood et al., 2008), with reduced benefits for species that move over larger areas, such as many shark species. However, recent studies have demonstrated the ecological importance of MPAs also for species with large activity ranges (Casselberry et al., 2020). For MPAs to be effective in granting protection, their design should be based on the biology, especially the spatial ecology, of the targeted populations (Gilmour et al., 2022).

For most aquatic animals, including sharks, long-term behavioural data essential to measure residency, activity space and the drivers of movement are lacking (Heupel et al., 2019; Dwyer et al., 2020). Unveiling the spatial ecology of marine animals can prove challenging since animals cannot be readily observed and technology such as GPS does not operate in aquatic environments (Cui et al., 2006). Acoustic telemetry is now recognized as a powerful tool for tracking marine animals in their natural environments over large spatial and temporal scales (Hussey et al., 2015; Harcourt et al., 2019). Ecological insight into animals' habitat preferences, home range and activity patterns can be gained from acoustic telemetry (Block et al., 2011; Raymond et al., 2014). In response to growing anthropogenic pressures (Bindoff et al., 2019), identifying the biotic and abiotic drivers of shark movements is vital if protection of key habitats is to be achieved (Gilmour et al., 2022).

The small spotted catshark, *Scyliorhinus canicula* (Linnaeus, 1758), is one of the most common elasmobranchs in coastal areas of the north-east Atlantic and the Mediterranean Sea. Characterized as a small-sized demersal shark, its geographical distribution extends from the Senegalese coast to the west coast of Norway (Compagno, Dando & Fowler, 2011). Often found over sandy, gravelly or muddy substrates, *S. canicula* depth distribution ranges from the shallow sublittoral to the upper regions of the continental slope (400 m; Ellis et al., 2009). *Scyliorhinus canicula* is an opportunistic scavenger and active predator that interacts with the substratum to feed on a diverse array of benthic species (Martinho et al., 2012). As with most Scyliorhinidae species, females produce egg cases throughout the year by internal fertilization (Kousteni, Kontopoulou & Megalofonou, 2010), which are later attached to macroalgae and sessile erect invertebrates (Ellis & Shackley, 1997). Although classified as 'Least Concern' by the Red List of the IUCN (International Union for Conservation of Nature; Ellis et al., 2009), *S. canicula* is frequently captured as by-catch across its distribution range (Alonso-Fernández, Otero & Bañón, 2021). Often caught by bottom trawls and fixed bottom nets, it has been characterized by Osio & Cardinale (2013) as an overexploited shark in Europe. In 2018, it was estimated that 1,035 tonnes of *S. canicula* were caught in the Cantabrian Sea and Atlantic Iberian waters (ICES, 2019) of which landings by the small-scale fishing fleet in Galicia represent less than 50% of the total catch (Alonso-Fernández, Otero & Bañón, 2021).

This study aimed to determine the drivers of variation in spatial behaviour of *S. canicula* through fine-scale positioning using acoustic telemetry. The temporal variation and the effect of biotic (body size and sex) and abiotic factors (sea bottom temperature) on the movement patterns of *S. canicula* represented by three behavioural traits – residency, activity space and activity – were investigated. The excursions and paths taken to enter and exit the study area were also analysed to get a first insight into possible patterns of connectivity with nearby waters. In addition to contributing to the understanding of the ecology of this heavily fished shark, this study provides important insights for the implementation of spatial and temporal restrictions aimed at reducing the mortality and bycatch of this shark species.

2 | MATERIAL AND METHODS

2.1 | Study site

This study was conducted at the Cíes Archipelago, located at the mouth of the Ría de Vigo (Galicia, NW Spain), between June 2020 and January 2022. The three islands and several islets that comprise the Cíes Archipelago are in the MPA called Parque Nacional Marítimo Terrestre das Illas Atlánticas de Galicia (PNMTIAG), which covers an area of 31 km² (Figure 1a,b). Within the PNMTIAG, there are gear regulations applied to commercial fishing (use of trawling nets is forbidden) and a ban on recreational fishing (Xunta de Galicia, Conselleira de Medio Ambiente, Territorio y Vivienda, 27/12/2018).
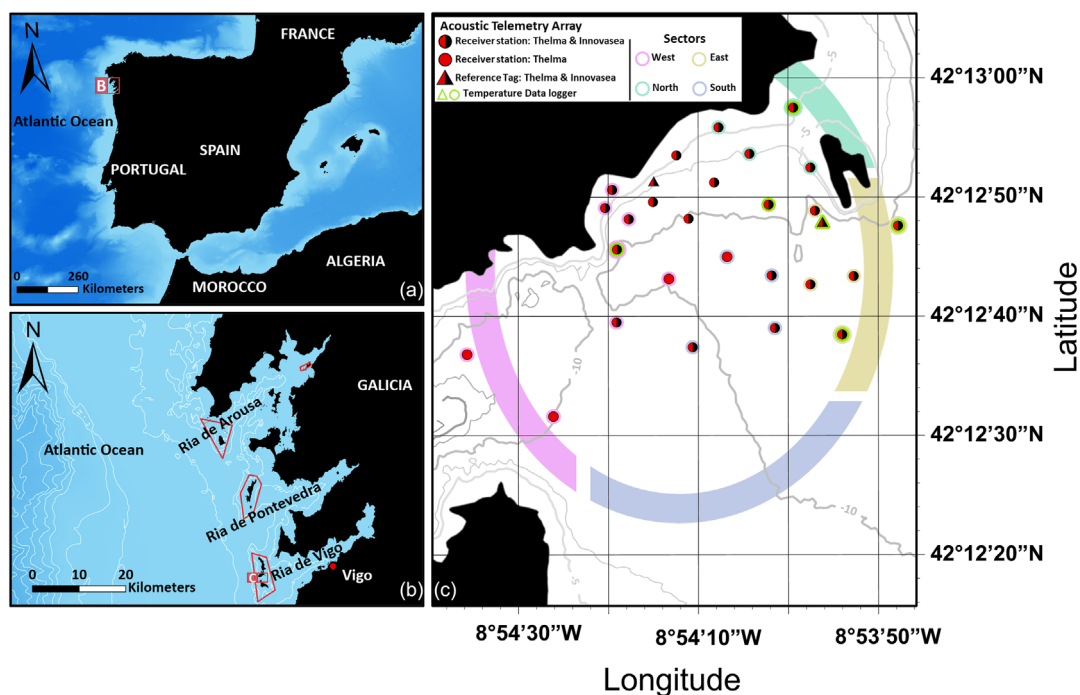
FIGURE 1 Spatial overview of the study area within the Iberian Peninsula (a) and the Cíes Archipelago (b). Detailed view showing the location of 26 out of the 28 acoustic stations and their distribution into four sectors used to identify exits and entries from/to the study area (c). The five innermost stations were not attributed to any sector. Red polygons in (b): limits of the Parque Nacional Marítimo Terrestre das Illas Atlánticas de Galicia (PNMTIAG). (Two temperature data loggers are located 1 m from each other and therefore overlap in (b). Two stations 26 and 28 are located at the extremity of both Ila de Faro and Ila de San Martiño and therefore are not visible in (c)).

The study area comprises shallow waters with depths ranging from 0 to 40 m (Figure 1c). Located in a channel between the two major islands and an islet, the sea bed of the study area is mainly composed of rocky reefs and sandy bottoms. The tidal regime is mesotidal, with a maximum tidal range of around 4 m (Souto et al., 2003).

2.2 | Acoustic telemetry array

To investigate the spatio-temporal patterns of the behaviour of *S. canicula*, a fixed array of 28 acoustic stations was deployed in the study area (Figure 1c). Fifty-two omni-directional receivers (24 Innovasea VR2W and 28 Thelma Biotel TBR700L) were distributed among acoustic stations with one receiver of each type at each station, except at four stations where only Thelma Biotel receivers were deployed. All receivers were tied to the upper end of auger anchors (140 cm high) and screwed 60 cm into the sandy substrate at depths ranging from 3.3 to 13.1 m (Villegas-Ríos et al., 2013; Figure S1a). To provide effective coverage and enough overlap between receiver ranges, the distance between stations was established at 150 m, following range test results (Figure S2). Two Innovasea (V16) and four Thelma Biotel (two 2LP13 and two 2LP9) reference transmitters were deployed in the array (Figure 1c) to assess the error associated with fish positions and evaluate possible environmental effects on detection patterns (Payne et al., 2010).

2.3 | Environmental variables

2.3.1 | Sea bottom temperature

Starting on 5 June 2019, the sea bottom temperature was recorded every 30 min using seven data loggers (©Star: ODDI DSTcenti-T) covering different depths and areas of the study array (Figure 1c). Data loggers were attached to the auger anchors just below the receivers and cleaned regularly to avoid recording failure owing to biofouling. Mean weekly, daily and hourly sea bottom temperatures were calculated by averaging the records of the seven data loggers.

2.3.2 | Sea level

Sea level recorded every 5 min was obtained from the tide gauge of Vigo 2 located at 42°14′24′′ N; 8°43′48′′ W (Prontuario_instalaciones, 2022). Mean hourly sea levels were then computed for later analysis.

2.4 | Fish tagging

Twenty-eight *S. canicula* (19 females and nine males) were captured using two different methods. Eighteen were caught by a small commercial fishing boat inside or near the array, using a bottom long-line (locally known as 'palangrillo') in June, August and October

2020 (Table S1). The remaining 10 individuals were captured by hand through scuba-diving from June to September 2020 and in November 2021 (Table S1). Individuals caught while diving were slowly brought to the surface in a hand net following an ascending rate slower than 3 m min^{-1}. Once on board, all individuals were sexed and measured to the nearest centimetre from the tip of the snout to the end of the caudal fin. Fifteen *S. canicula* were tagged externally by attaching the acoustic transmitter to the first dorsal fin (Figure S1c,d). Thirteen *S. canicula* were tagged internally (Figure S1e). The whole procedure of internal tagging lasted less than 5 min per individual. Eleven individuals were tagged with Innovasea V13P transmitters (expected lifetime of 855 days and a signal transmission delay of 80–160 s), 11 with Innovasea V9AP (lifetime, 453 days; delay, 80–160 s) and six with Thelma Biotel D-LP9L (lifetime, 900 days; delay, 90–150 s; Table S1). In order to avoid recapturing individuals in subsequent samplings and allow fishers and divers to report their potential recaptures, individuals were externally tagged with T-bar tags (©Floy Tag).

To determine the effects of currents, waves and the impact of scavengers on the movement of dead fish, one dead *S. canicula* was internally equipped with an acoustic transmitter (Innovasea V13P) and released inside the study area (Table S1). This allowed us to identify a 'dead' pattern which could be then used to detect if and when a tagged fish had died inside the array (Villegas-Ríos et al., 2020; Alonso-Fernández, Mucientes & Villegas-Ríos, 2022).

The present study complies with the experimental animal project authorization of the regional government (Xunta de Galicia) starting on 14 November 2019. It follows the Experimental Animal Project Authorization: ES360570202001/19/FUN01/BIOL AN.08/AAF01.

2.5 | Data processing and filtering

Detections were downloaded from the receivers in September 2021 and January 2022. Single detections from the same individual occurring alone at a specific receiver within a 24 h period were considered false and therefore removed from the data (Meyer, Holland & Papastamatiou, 2007). Centres of activity were then calculated following Simpfendorfer, Heupel & Hueter (2002) and plotted to investigate the fate of each individual during the study period (Villegas-Ríos et al., 2020; Alonso-Fernández, Mucientes & Villegas-Ríos, 2022). Detections post-mortality date were removed from the dataset for any individual considered dead during the study. Raw detections were pre-processed by Innovasea and Thelma Biotel to determine VPS and Pinpoint high spatial resolution positions, respectively (hereafter 'fish positions'; Figure S3). VPS positions were filtered using Innovasea's horizontal position error. Horizontal position error is a relative, unitless measure of how calculations are prone to errors (Smith, 2013). This study involved three separate data processing sessions at Innovasea. Horizontal position error values are not comparable between different processing sessions (Orrell & Hussey, 2022). Hence, each batch of positions had to be filtered separately. A similar data filtration process was used for the Pinpoint position using Horizontal Precision of Dilution or HDOP (Misra &

Enge, 2012). In this study, only one data processing session was carried out at Thelma Biotel; hence, filtration based on the HDOP value was done once.

2.6 | Estimation of behavioural traits

2.6.1 | Residency

As a means of quantifying residence within the study area, the residency index (*RI*) was calculated for each individual based on filtered detections (Papastamatiou et al., 2010; Espinoza, Farrugia & Lowe, 2011):

$$RI = \frac{DD}{TD}$$

where *DD* is the number of days an individual was detected and *TD* is the number of days between the tagging date and the end of the study. *RI* ranges from 0, indicating no residency, to 1, suggesting absolute residency in the study area.

2.6.2 | Activity space

To investigate the activity space of *S. canicula*, fish positions were used to calculate the 95% kernel utilization distribution (KUD) for each individual. Kernel utilization distributions were calculated weekly and for the whole study period using the entire dataset as well as separately for daytime and night-time. In order to avoid potential bias in the computation of activity space, KUDs were not calculated for weeks with fewer than 4 days of detections (regardless of whether the days were consecutive or not; Leeb et al., 2021).

2.6.3 | Activity

Trajectories were calculated for each individual based on consecutive positions. Individual trajectories were cut into sub-trajectories to exclude cases where two consecutive fish positions were separated by more than 12 h, assuming that in that case, the individual had exited the array. Sub-trajectories composed of fewer than four positions were excluded. Finally, each sub-trajectory was interpolated every 80 s, resulting in regular sub-trajectories for speed calculation. A time period of 80 s was chosen as it matches the minimum possible delay of the transmitters (see above). As such, splitting the time series into 80 s intervals would allow interpolation without losing any of the original positions. Speed (in metres per hour) was calculated as a proxy for activity as (Zamora & Moreno-Amich, 2002):

$$speed = \frac{dist}{dt} \times 3600$$

where *dist* is the distance travelled between each pair of consecutive positions in the interpolated sub-trajectories and dt equals 80 s.

2.6.4 | Excursions

To investigate the existence of preferred paths to enter and exit the study area and therefore explore connectivity patterns with surrounding waters, the array was divided into four sectors (Figure 1c). Each sector included several acoustic stations (east, five stations; west, eight stations; north, four stations; and south, four stations). Excursions outside the study area were defined as a period of absence longer than 24 h. For each excursion (i) the sector with the last detection prior to the fish exiting the array, (ii) the sector with the first detection of the fish returning to the array and (iii) the total duration of the absence were identified. The sectors defined were 'north', which would suggest a movement towards the northern side of the Cíes archipelago, 'south', which would suggest a movement towards the southernmost island, 'east', which would suggest a movement towards the inner part of the Ria de Vigo and 'west', which connects with the channel between the two main islands and ultimately with the continental shelf. Duration of the trip was classified as 'short-term' if it lasted less than 7 days, 'mid-term' if it lasted between 7 and 30 days, and 'long-term' if the fish spent more than 30 days outside the study area. Finally, individual consistency in exit and entry locations was examined for each fish by counting the number of different sectors used to exit and re-enter the study area.

2.7 | Data analysis

Three models were produced for this study, one for each behavioural trait except for visitation patterns, which were explored in a qualitative way (Figure S4). Generalized additive mixed effects models were used to account for non-linearity in the relationships between the response and the explanatory variables as well as integrate non-independence in behavioural measures of the same individual.

2.7.1 | Residency

The probability of being present in the study area on any particular day (1 = present, 0 = absent; binomial distribution) was investigated with the following model structure:

$$P_{it} = \alpha + \beta_1 Sex_i + \beta_2 Total\,Length_i + \beta_3 Capture\,Method_i + s(DOY) + s(Temp_t) + a_i + \varepsilon_{it} \quad (1)$$

where P_{it} is the probability of detection of an individual i on a day t in the study area. Parametric explanatory variables included *Sex* and *Total Length* with their respective linear coefficients β_n. *Capture method* (categorical variable with two levels – 'diving' vs. 'fishing') was also included in the models to account for that individuals were

captured using two different methods. Non-parametric smoothing functions s were fitted with four knots to model the non-linear effect of $Temp_t$ (sea bottom temperature on a day t) on P_{it}. DOY (day of the year) was fitted as a non-parametric smoothing function s with four knots and a cyclic cubic spline.

2.7.2 | Activity space

Activity Space (*AS*) was fitted using a Gaussian family distribution with the following model structure:

$$AS_{it} = \alpha + \beta_1 Sex_i + \beta_2 Total\,Length_i + \beta_3 Capture\,Method_i + \beta_4 Time\,of\,the\,Day + \beta_5 Temp_t + s(WOY) + a_i + \varepsilon_{it} \quad (2)$$

where AS_{it} represents the activity space within the study array of an individual i in week t. The results of the explanatory analysis revealed a linear effect of sea bottom temperature $Temp_t$ on *AS*. Therefore, it was entered into the model as a parametric term together with *Total Length* and *Capture method*, with linear coefficients β_n. To investigate diel variation in *AS*, a categorical variable *Time of the Day* containing two levels ('Day' and 'Night') was added to the model. WOY (week of the year) was fitted as a non-parametric smoothing function s with four knots and a cyclic cubic spline.

2.7.3 | Activity

Mean speed per hour was fitted using a Gamma family distribution (with a log link) using the following model:

$$Speed_{it} = \alpha + \beta_1 sex_i + \beta_2 Total\,Length_i + \beta_3 Capture\,Method_i + s(DOY) + s(HOD) + s(Temp_t) + a_i + \varepsilon_{it} \quad (3)$$

where activity is calculated based on the *Speed* of an individual i in an hour t. Parametric explanatory variables included *Sex*, *Total Length* as well as *Capture method* with their respective linear coefficient β_n. DOY (day of the year), HOD (hour of the day) and $Temp_t$ (sea bottom temperature at an hour t) were fitted as a non-parametric smoothing function s with 5, 5 and 4 knots respectively and a cyclic cubic spline for DOY and HOD.

In all models, random effects (a_i) were considered to be normally distributed with a mean of 0 and a variance of σ_a^2. Because observations were made in sequential order throughout time, an autoregressive term of order 1 (corAR1) was included in all models to prevent non-independence between consecutive observations (Dormann, 2007). The inclusion of both sea bottom temperature and DOY (or WOY) was supported by the lack of a strong correlation between both variables (Pearson correlation coefficient = 0.19).

Data treatment and analysis were carried out in R version 4.0.3. Spatial data were handled using the 'sp' package (Pebesma & Bivand, 2005). Day and night times, based on sunrise and sunset at

42°12′47.6634″ N; −8°54′3.9522″ W, were calculated using the 'suncalc' package (Thieurmel & Elmarhraoui, 2019). Both 'adehabitatHR' and 'adehabitatLT' packages were respectively used in R to calculate the KUDs and trajectories for each individual (Calenge, 2006). All models were fitted using the gamm function of the 'mgcv' package (Wood, Goude & Shaw, 2015; Wood et al., 2017; Li & Wood, 2020). For each of the three behavioural traits, a full model including all the explanatory variables was first tested, then the final model structure was selected through backward model selection, based on the lowest Akaike information criterion (AIC) using the AIC function from the package 'stats'. The most parsimonious model was chosen in where ΔAIC < 2 between two models (Burnham & Anderson, 2002).

3 | RESULTS

Between the 26th of June 2020 and the 17th of January 2022, 2.1 million detections (1.9 million after filtration) were recorded in the acoustic telemetry array. The number of detections varied considerably among individuals ranging from just 190 to 658,452. The average tracking time in the array was 393 days (range 91–570). Raw detections resulted in 220,343 estimated positions being reduced to a total of 173,124 after filtration (78.6% of raw detections).

3.1 | Residency

Of the 28 tagged *S. canicula*, 25 were detected in the array during the study period (Table S2). Two individuals (DESTAC-SCA-20-10 and DESTAC-SCA-20-23) were never detected inside the array and one individual (DESTAC-SCA-20-17) was classified as dead in the 24 h following the tagging procedure and was therefore removed from the analysis. *Scyliorhinus canicula* displayed great variation in residency patterns featuring a mean *RI* of 0.27 (range 0.002–0.998; Table S2). Six *S. canicula* (24%) were detected during more than half of the study period (*RI* > 0.5), with the remaining individuals ($n = 19$) either leaving the array soon after being tagged or being absent for the major part of the study (*RI* < 0.5; Figure 2 and Table S2). Eight recapture events occurred during the study period (Figure S5). Three individuals (DESTAC-SCA-20-01, DESTAC-SCA-20-11 and DESTAC-SCA-20-12) were seen multiple times alive inside the array during the study period. Individual DESTAC-SCA-20-22's fate was associated with fishing mortality on 5 March 2021 within Cíes Archipelago (106 days after being released). One individual (DESTAC-SCA-20-15) was fished ∼5 km north-east of the study area (46 days after being released).

The probability of the presence of *S. canicula* in the study area differed significantly between the sexes (but with low statistical support; Table 1). Females displayed on average a higher probability of presence compared with males (Figure 3a). A slight seasonal variation of the probability of presence in the study area was
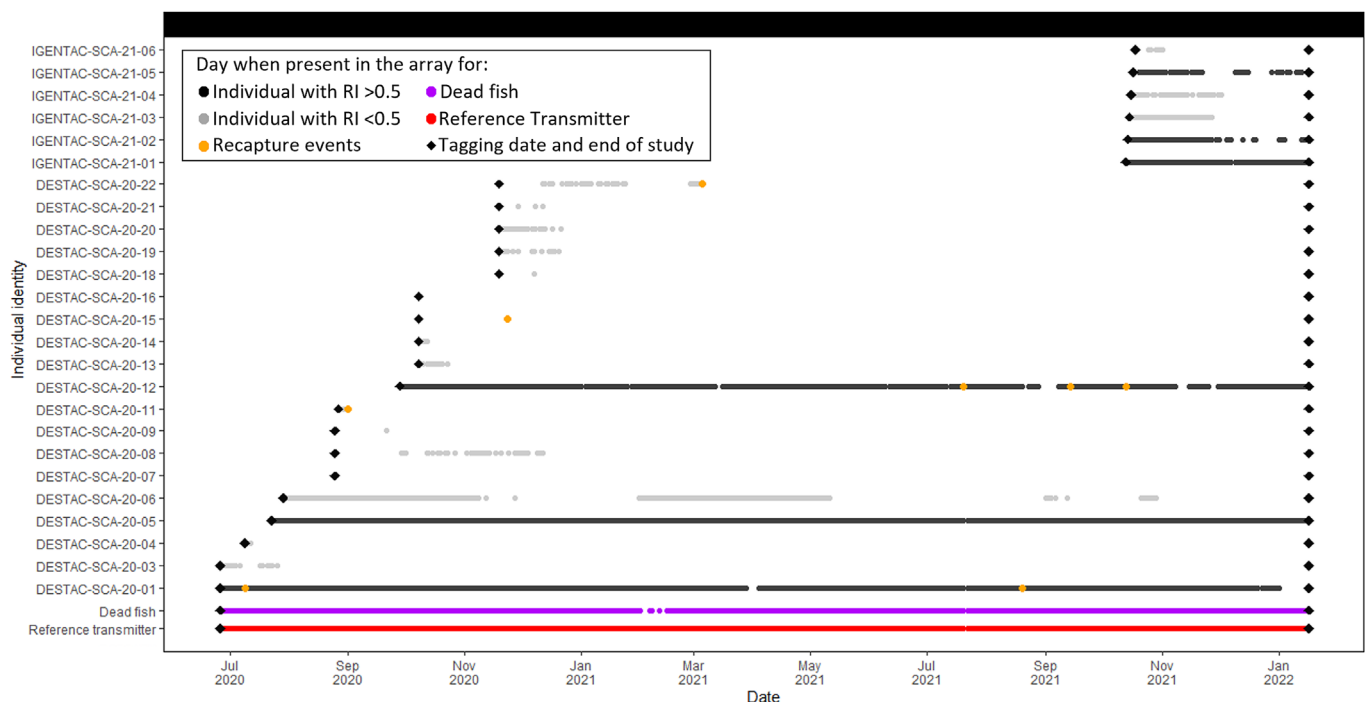

FIGURE 2 Abacus plot showing the daily presence of *Scyliorhinus canicula* in the study area. Days when an individual was present are coloured in black for fish with a residence index (*RI*) > 0.5 and grey for fish with *RI* < 0.5. The two lozenges at the start and end of each individual time series denote tagging date and the end of the study, respectively. Daily presence is also shown for the reference tag (in red) and the dead fish (in purple). Orange dots represent recapture events during diving and tagging missions.

TABLE 1 Summary of the optimal model investigating the different behavioural metrics of *Scyliorhinus canicula* estimated in this study: (i) probability of presence, (ii) activity space and (iii) activity[a].

Parametric coefficients	Estimates	Std error	*t*-Value	Pr(>|*t*|)
(i) Probability of presence				
Intercept	2.085	0.534	3.905	<0.001***
Sex (male)	−1.777	0.889	−1.998	0.046 *
Smooth terms	**Edf**	**Ref.df**	**F**	**P-Value**
s (Temp)	2.206	2.248	10.66	<0.001 ***
s (DOY)	1.724	2.206	6.11	<0.001 ***
R-sq.(adj) = 0.105				
(ii) Activity space				
Intercept	0.208	0.083	2.499	0.013 *
Sex (male)	0.041	0.012	3.344	<0.001 ***
Time of the day (night)	0.025	0.003	9.218	<0.001 ***
Total length	−0.004	0.002	−2.404	0.017 *
Capture method (longline)	0.014	0.005	2.959	0.003 **
Temp	0.004	0.001	3.026	0.003 **
R-sq.(adj) = 0.184				
(iii) Activity				
Intercept	3.989	0.169	23.55	<0.001 ***
Smooth terms	**Edf**	**Ref.df**	**F**	**P-Value**
s (Temp)	2.958	2.958	143.4	<0.001 ***
s (HOD)	2.993	3	2545.6	<0.001 ***
s (DOY)	2.987	3	503.7	<0.001 ***
R-sq.(adj) = 0.182				

[a]Std error, Standard error; edf, effective degrees of freedom; Ref.df, reference degrees of freedom; R-sq.(adj), adjusted coefficient of determination; temp, sea bottom temperature; DOY, day of the year; HOD, hour of the day. Significance codes: *** 0; ** 0.001; * 0.01.

observed (Table 1), with the probability of presence of *S. canicula* decreasing between winter (day 53; highest probability of presence) and summer (day 240; lowest probability of presence; Figure 3b). The probability of presence increased with increasing sea bottom temperatures up to 16.6°C; afterwards it remained fairly stable (Table 1 and Figure 3c).

3.2 | Activity space

The activity space (95% KUD) of *Scyliorhinus canicula* ranged from 0.05 to 0.18 km² (mean = 0.13 ± 0.04 km²; Table S2). Inspection of raw data suggested diel variation of activity space with an average activity space of 0.09 ± 0.02 km² (range 0.05–0.14 km²) during daytime and 0.13 ± 0.04 km² (range 0.05–0.19 km²) at night (Table S2, Figure S6). The model results revealed a larger activity space during the night compared to the day (Table 1; Figure 4a). The predicted activity space of *S. canicula* decreased significantly with increasing body size. The smallest individual in this dataset (51 cm) was predicted to move over a 0.029 km² larger area than the largest individual (59 cm; Figure 4b). The activity space of males was on average 0.041 km² larger than that of females (Figure 4c). Lastly,

S. canicula activity space increased significantly with increasing sea bottom temperature, with a 0.021 km² increase as the temperature rose from 12 to 19°C (the temperature range in the study area; Figure 4e and Table 1).

3.3 | Activity

The mean speed per hour (our proxy of activity) of *Scyliorhinus canicula* ranged from 0 to 2,194 m.h⁻¹ (mean = 79 ± 41 m.h⁻¹; Table S2). The plot of raw speeds of *S. canicula* in the study array suggested increased activity over a larger area at night compared with daytime (Figure S7). The model results showed a diel pattern of activity with a drastic reduction in speed from midnight to midday (Figure 5a). *Scyliorhinus canicula* increased their activity in autumn with a maximum mean speed around day 304 (end of October) compared with the minimum speed observed on day 176 (end of June; Figure 5b and Table 1). The relationship between activity and sea bottom temperature showed a peak of activity at temperatures around 17°C, with a decrease in activity at either lower or higher temperatures (Figure 5c). Neither sex nor total length nor capture method had an effect on the activity patterns of *S. canicula*.
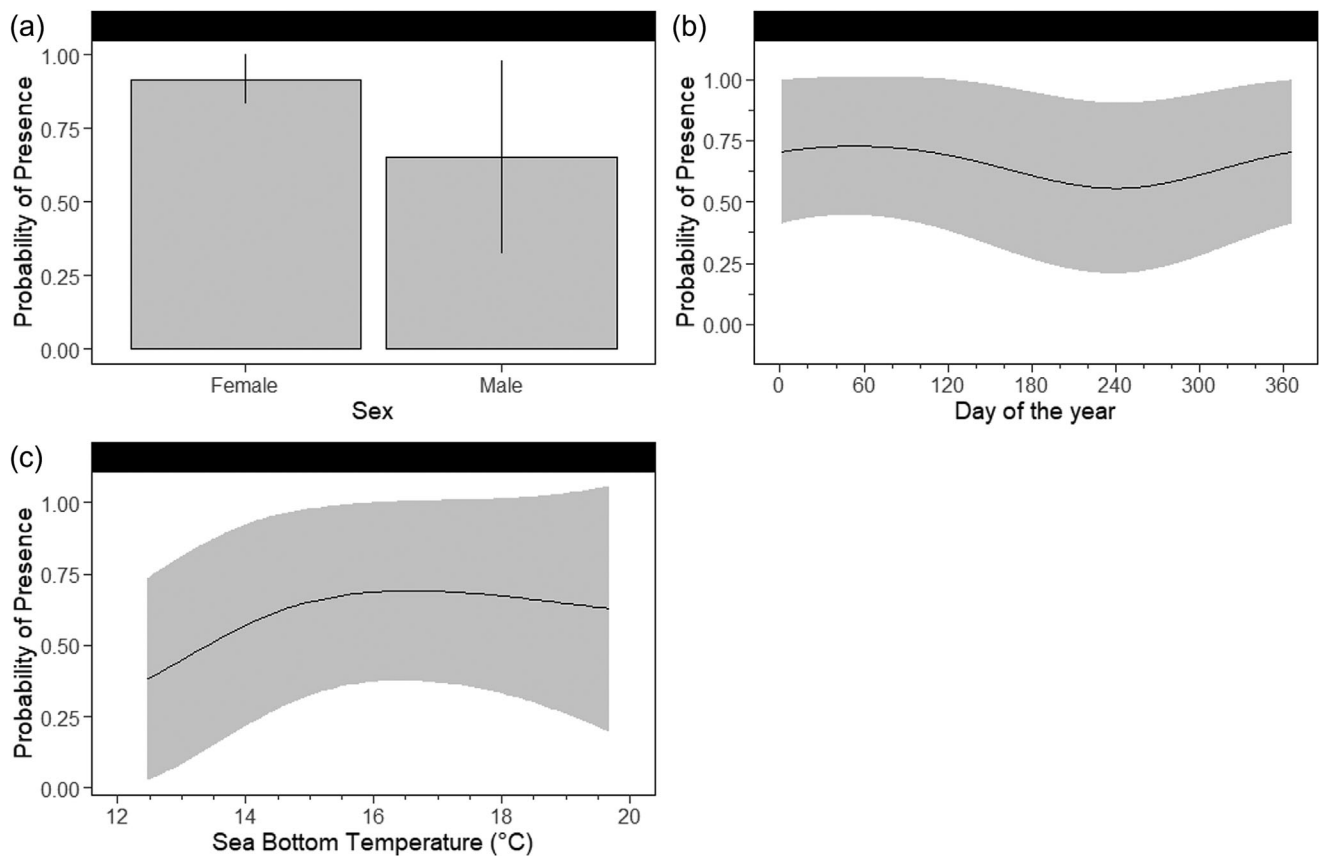
FIGURE 3 Predicted probability of presence of *Scyliorhinus canicula* in the study area as a function of sex (a), day of the year (b) and sea bottom temperature (c). Black bars (a) and grey shaded areas (b, c) represent the 95% confidence interval. Values used for predictions: sex = male; sea bottom temperature = 15°C; day of the year = 150.

3.4 | Excursions

There were 122 excursions over the study period. Of those, five were long-term (>30 days), 15 mid-term (7–30 days) and 102 short-term (<7 days). The mean number of excursions per individual was 4.88, with a range between 0 and 25 (Table S2). In the 570 days of this study, individuals exited and re-entered the study area 102 times in the direction of the Ria de Vigo (east; Figure 6). The sector of the study array connecting to the north was the least used out of the four. High consistency was observed in the sector used to exit and re-enter the study area by *S. canicula* during excursions, with 84% (86 out of 102) of the short-term excursions, 87% (13 out of 15) of the mid-term excursions and 80% (four out of five) of the long-term excursions having the same exit and re-entry sector.

4 | DISCUSSION

The analysis of acoustic telemetry data from 25 *S. canicula* individuals revealed substantial variation in their spatial behaviour over different time scales with significant influence of biotic and abiotic factors. Residency in the array was in general low (average *RI* = 0.27), with the probability of presence in the study area mostly determined by sex (i.e. higher for females). The pattern of excursions suggested strong connectivity with inshore waters, i.e. the Ria de Vigo. These results showed a major increase in activity at night and in autumn (as opposed to summer), with warmer waters related to higher levels of activity and larger activity spaces. Finally, activity space decreased with larger body sizes. This study is of high relevance to understanding the vulnerability patterns of *S. canicula* and to effectively designing spatial protection measures for the species.

4.1 | Seasonal patterns

The presence of *S. canicula* in the study area peaked in winter and decreased towards summer. While 23% of the individuals stayed in the study area for at least half of the study period, the majority (77%) left the array for most of the study. Although the scale of movements and the fate of sharks leaving the study area remain unknown, one recapture from fishers 5 km north-east of the study area (inside the Ria de Vigo) attests to the presence *of S. canicula* in the surrounding waters. The fact that the majority of the studied individuals left the study area for some period combined with the 122 excursions recorded during the 570 days of tracking attest that the home range of *S. canicula* exceeds the limits of the study area. Additionally, the
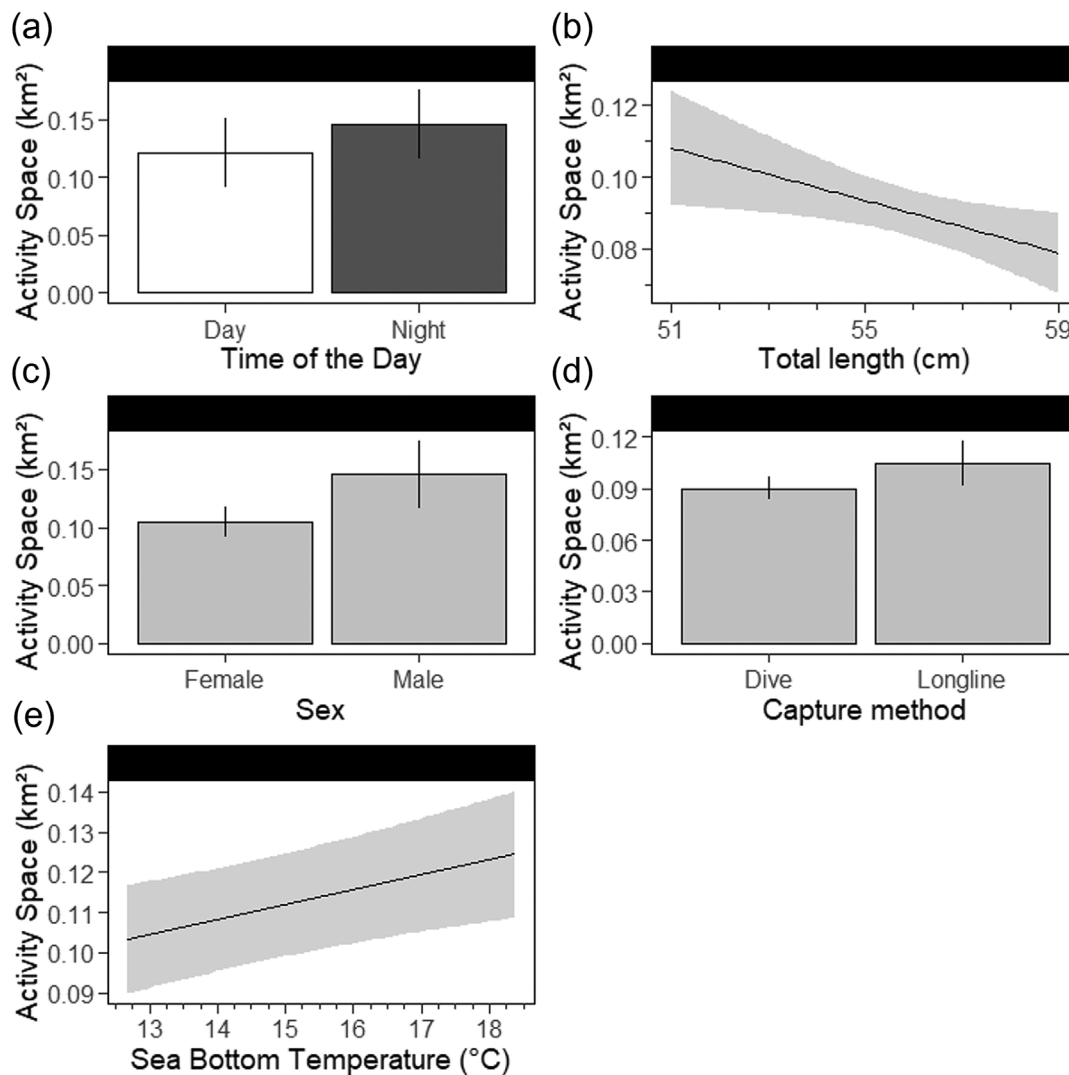
FIGURE 4 Predicted activity space of *Scyliorhinus canicula* within the study area depending on the time of the day (a), total length (b), sex (c), capture method (d) and sea bottom temperature (e). Black error bar (a, c, d) and grey shaded areas (b, e) represent 95% confidence interval. Values used for predictions: sea bottom temperature = 13°C; sex = female; total length = 52 cm; capture method = longline; time of the day = night.

recaptures outside the limits of the national park suggest that the home range of *S. canicula* extends beyond the national park (PNMTIAG). These findings are in line with previous results from a mark–recapture study (Rodríguez-Cabello et al., 2004), where movements of *S. canicula* were estimated to reach a maximum of 286 km with an average of 30 km. However, as in this study, evidence of three individuals remaining in the study area after 1 year suggests that at least part of the population can display a more sedentary pattern (Rodríguez-Cabello et al., 2004). The activity of *S. canicula* was higher in autumn (when the days are shorter), suggesting that the study area may be a preferred foraging ground for this species at that time of the year. Generally regarded as generalist feeders and benthic scavengers, *S. canicula* feeds on a wide spectrum of fish prey and aquatic invertebrates (Šantić, Rada & Pallaoro, 2012). Previous studies have noted that the dietary preference of *S. canicula* mirrors the general abundance and accessibility of prey present in the area (Eales, 1949; Lyle, 1983). While the stomach contents of *S. canicula* in

the area have not been analysed, epibenthic decapods reported to be significant food items for *S. canicula* are known to emerge from their refuges during night-time (Wieczorek et al., 2018), which could coincide with the increase in activity observed in autumn when nights are longer.

4.2 | Diel patterns

Scyliorhinus canicula were much more active and moved over a larger area at night compared with daytime. Clear and consistent patterns of diel activity and space use have already been reported for several shark species (Andrews et al., 2009; Kadar et al., 2019). Similar to *Raja undulata* (a skate species inhabiting the same study area; Leeb et al., 2021), *S. canicula* remained extremely inactive at midday, which could be associated with resting phases during daylight. *Scyliorhinus canicula* are able to filter the water by lowering and raising the floor of
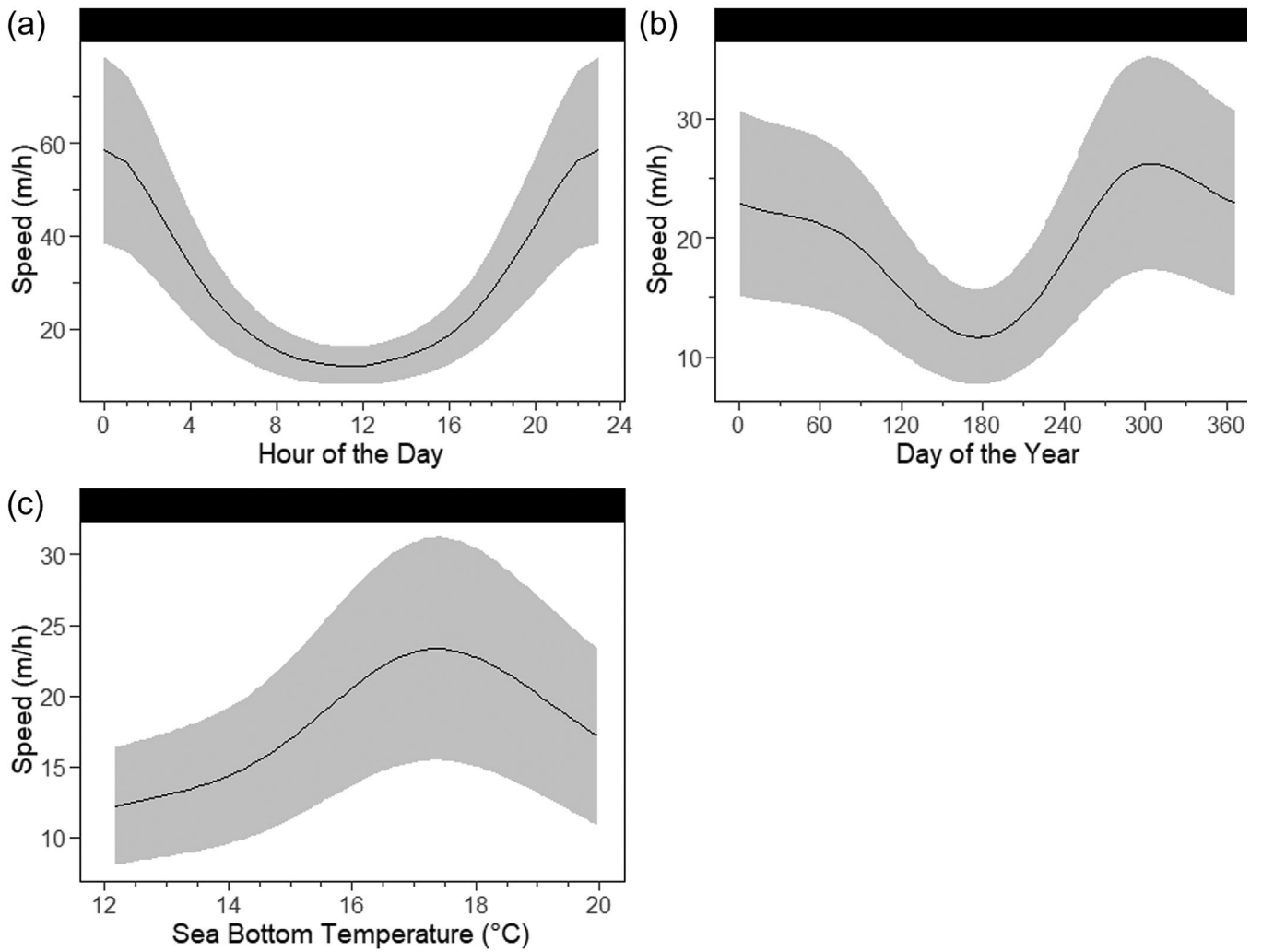
FIGURE 5 Predicted speed of *Scyliorhinus canicula* in the study area as a function of (a) hour of day, (b) day of the year and (c) sea bottom temperature. Grey areas represent 95% confidence interval. Predictions were made using the following fixed values: sea bottom temperature = 12°C; day of the year = 160; hour = 12.
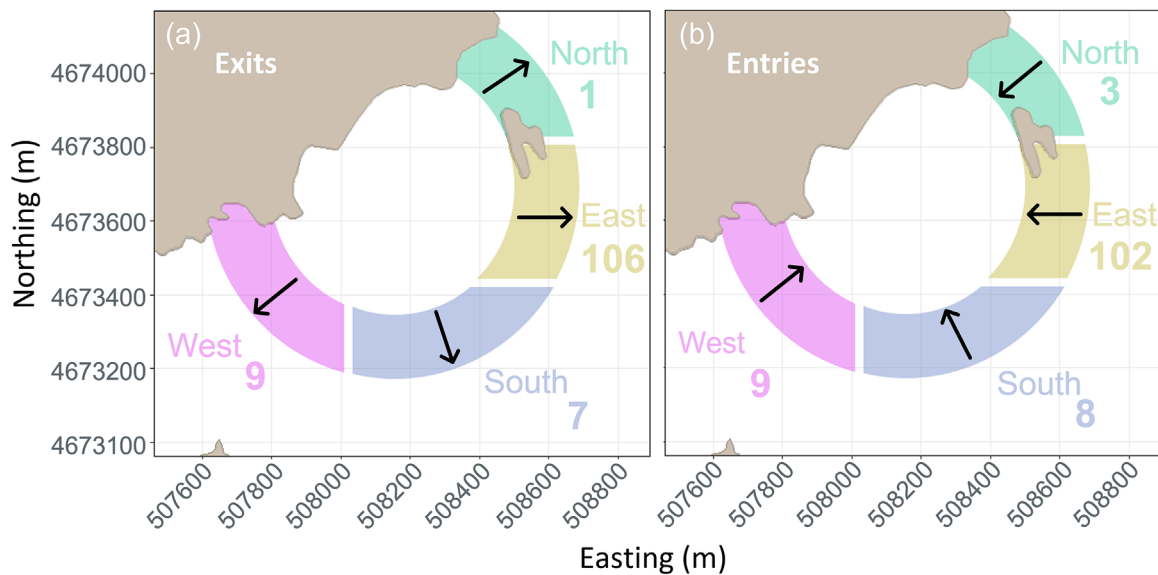

FIGURE 6 Map showing the number of times that each sector was used to exit (a) or enter (b) the study area taking into account all the excursions performed by *Scyliorhinus canicula* during the study period.

the buccal cavity. By ventilating the gills in such manner, buccal pumping *S. canicula* can remain stationary for extended periods of time (Kelly et al., 2020), thus decreasing activity and activity space. Alternation between high activity during night-time associated with foraging behaviour and the resting phase during daytime is believed to facilitate digestion (Sims, 2006). It should be noted that fast movements were likely to be underrepresented in this study owing to the design limitations of the acoustic array. Because of their high energy requirement, fast movements tend to occur at the smallest temporal scale possible for the species (Humphries, Simpson & Sims, 2017), sometimes shorter than the transmission delay of the acoustic transmitter (80–160 s). Moreover, detections of fast movements for an extended period of time were also limited by the size of the array (i.e. *S. canicula* would exit the array prior to speed estimation). It is therefore likely that *S. canicula* moves at higher speeds than estimated in this study.

4.3 | Biotic parameters

Biotic drivers had, in general, a smaller influence on *S. canicula* behaviour than temporal patterns (except for activity space). Sex and body size had a significant effect on certain traits of *S. canicula*. Activity space was larger for males than for females. Furthermore, females stayed on average longer in the study area, with three females having a *RI* over 0.90 while the maximum *RI* for males was 0.08. These findings could be consistent with reports of sexual harassment in *S. canicula* (Sims, Nash & Morritt, 2001; Jacoby, Busawon & Sims, 2010; Wearmouth et al., 2012) and the need to avoid mating situations during egg-laying and gestation periods by females (Sims, 2003; Sims, 2006) by hiding in small crevasses (Jacoby, Croft & Sims, 2011), thus resulting in lower space used. Although female aggregations over rocky substrates have never been reported from the study area, egg cases of *S. canicula* have been observed in the receiver array (Figure S1f; Alonso-Fernández & Mucientes personal communication). While sexual spatial segregation was not analysed in this study, the difference in residency in the study area between males and females could also suggest some kind of sexual segregation that may occur at a larger spatial scale. Several shark species, including *S. canicula*, have been described as sex-segregated by geographic location (Sims, Nash & Morritt, 2001; Werry & Clua, 2013; Drymon et al., 2020).

The results of this study revealed that smaller individuals moved over larger areas. Body size has been shown to be important in the distribution of *S. canicula*, with juveniles (characterized by a body size smaller than 20 cm) distributed in deeper and colder water compared with mature individuals based on landings data (Rodríguez-Cabello et al., 2004). The range of body sizes in this study was just 12 cm (between a 51 cm long female and a 63 cm long male), probably preventing significant effects of body size on most of the variables analysed being identified (note that the maximum length recorded for the species is 100 cm; Wilson & Burton, 2001). However, juveniles or large individuals have barely been observed during sampling,

suggesting that mainly mid-size individuals make use of the study area. Male presence in the study area was significantly smaller than female, thus yielding a smaller amount of data on their activity space, activity and depth pattern. This lack of data for male *S. canicula* prevented testing of interactive effects between sex and the other variables on the different behavioural traits, which might certainly exist.

4.4 | Abiotic parameters

Movement and behaviour of elasmobranchs have been shown to be influenced by temperature (Bernal et al., 2012). Simulation of energy budgets for *S. canicula* under different realistic thermal-choice scenarios suggested that the adoption of a 'hunt warm/rest cool' strategy could reduce daily energy costs (Sims et al., 2006). These results proved to be consistent with these simulations, as *S. canicula* activity space was significantly larger with increasing temperature, thus associating possible foraging behaviour covering larger areas with warmer waters. However, activity of *S. canicula* peaked at 17°C while dramatically declining at warmer or colder temperatures.

4.5 | Implications for conservation

Scyliorhinus canicula is one of the most fished elasmobranchs in coastal waters of the Iberian Peninsula (Rodríguez-Cabello et al., 2005; Alves et al., 2020). Although it is typically discarded (Alonso-Fernández, Otero & Bañón, 2021), fishing impacts on this species may propagate into the whole ecosystem owing to the central role of this species in the food web (Wieczorek et al., 2018). This study provides baseline knowledge to help understand key aspects of the behaviour of *S. canicula*, with relevance for its conservation and management.

The first conservation implication regards the range of movements of *S. canicula*, which exceeds the size of the telemetry array and probably the limits of the Cíes Archipelago. Although the MPA was not originally designated for the protection of this or any other specific species, this study suggests that it still offers some protection to a certain part of the population (e.g. females) during extended periods of time. It is timely to understand the spatial connectivity of individuals to other areas and habitats in order to identify critical locations for protection. Future studies should aim to characterize the biotic (e.g. mating, feeding) and abiotic (e.g. bottom habitats, oceanographic conditions) features that favour the presence of *S. canicula* in the study area and especially those that made females display a more sedentary behaviour. Observation of *S. canicula* egg cases inside the array might attest to the potential use of the area as a nursery ground. This knowledge is crucial to identify and protect other important habitats for the species, or to create networks of small MPAs. More broadly, determining differences in behaviour between the sexes such as those observed in this study can have important management and conservation implications. Such variations

might affect the spatio-temporal distribution of *S. canicula* and thus their potential exposure to fisheries exploitation (Rodríguez-Cabello, Sánchez & Olaso, 2007). Secondly, the studied population was mainly connected to inshore waters as compared with offshore, open ocean waters. This is very important for MPA design, as it suggests that individuals of the size range of those investigated here may benefit from the protection of inshore habitats. Future research should focus on quantifying the whole range of movements of the species and expanding the telemetry array towards the inner part of the Ria seems a reasonable next step. The third conservation implication is related to the activity patterns of the species, especially their higher activity at night. Given that catchability is often positively correlated with activity (Arreguin-Sanchez, 1996; Villegas-Ríos et al., 2013), this suggests that *S. canicula* have a greater chance of being caught at night. Temporal restrictions at night may therefore reduce the bycatch rates of this species. Such restrictions could be implemented by setting soak times for long lines and gillnets that minimize night-time hours. Finally, night deployments involving the use of deterrent devices on fishing gear such as 'SharkGuard' could significantly decrease the bycatch of this species (Doherty et al., 2022).

CONFLICT OF INTEREST STATEMENT

The authors report there are no competing interests to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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