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Drivers of behaviour and movement patterns of the endangered undulate ray, Raja undulata

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'No data can be taken out of this work without prior approval of the thesis promoter'.

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Executive Summary

Understanding the spatial ecology of a species is essential to assess its vulnerability to environmental and anthropogenic stressors and to evaluate the efficiency of potential management measurements. The undulate ray, R. undulata as a late maturing, slow growing, low fecundity endangered elasmobranch species is particularly vulnerable to exploitation. Yet, to date the application of speciesspecific management tools has proven to be challenging, simply due to insufficient information on its biology and ecology. Only few studies have addressed the effectiveness of spatial protection measures for skates and even less tried to identify the environmental drivers for their distribution. The distribution of *R. undulata* has been shown to differ based on sex and body size and might be driven by biological and seasonal cycles. In order to identify the environmental and biological drivers for the movement and behaviour of R. undulata, we used a VPS (Vemco Positioning System) acoustic telemetry array covering an area of 800 000 m² within an MPA in the Galician coast (NW Spain), where aggregations of *R. undulata* have been previously observed. Movements of 44 individuals (21 females, 23 males) and environmental conditions (temperature and upwelling) were monitored from June to December 2019. Generalised Additive Mixed Models were used to identify the drivers for presence, space use and activity patterns in our study area. R. undulata showed a relatively high site-fidelity (residence index 0.65 ± 0.22) and small home range areas differing in shape and size between day $(188 483 \pm 69 8439 \text{ m}^2)$ and night $(263 524 \pm 78 420 \text{ m}^2)$. Movement and behaviour were mainly driven by diel and seasonal cycles, with environmental factors being less important drivers of behaviour. We found no effect of body size. While the presence in the study area and home range size decreased from summer to autumn, activity increased towards mid-September and differed between sexes. Low activity levels during the day were associated with resting behaviour, buried in sand, and activity peaks during the night are likely to correspond to foraging behaviour. Spatial management measures that encompass aggregations of individuals in combination with temporal closures for commercial fisheries when individuals are more active might be suitable for this species. However, long-term studies are needed to assess the reoccurrence of aggregations and the potential role of reproductive behaviour as an underlying biological driver.

Abstract

Spatial ecology and behaviour of a species is essential to assess its vulnerability to environmental and anthropogenic stressors and consequently develop efficiency management strategies. Elasmobranchs, as k-strategy species are particularly vulnerable to exploitation, especially in coastal areas. Species-specific conservation management has proven to be challenging, due to insufficient information on their biology and ecology. In this study we used a VPS acoustic telemetry array to identify biological and environmental drivers for presence, space use and activity of the endangered undulate ray, *Raja undulata*, within an MPA in the southern Galician coast (NW Spain). Movement and behaviour were mainly driven by diel and seasonal patterns, activity levels differed between sexes and temperature and upwelling conditions were less important drivers for behaviour. No effect of body size was observed. While the presence in the study area and home range size decreased from summer to autumn, activity increased towards mid-September and followed a clear diel cycle with nocturnal activity peaks. We hypothesised that foraging and reproduction are likely to be the main underlying biological drivers. Our work thus represents an important contribution to the understanding of the ecology of this endangered, yet commercially important skate in Europe and provides important insights for management strategies.

Keywords: acoustic telemetry, VPS, spatial ecology, R. undulata, environmental driver

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Introduction

The importance of space and behaviour for ecology of aquatic animals (Wolf & Weissing 2012; Tilman & Kareiva 1998; Nathan et al. 2008) and the efficient management of marine resources is broadly recognised (Cardinale et al. 2011; Gandra et al. 2018; Kaplan et al. 2010). In the context of a rapidly and drastically changing marine environment (Bindoff et al. 2019), however, it is crucial to identify the environmental and biological drivers that determine spatial and behavioural patterns (Schlaff et al. 2014) to evaluate not only how animals use space but also to assess their vulnerability to environmental and anthropogenic stressors.

Marine protected areas (MPAs) are a popular solution to manage fisheries and protect vulnerable species (Gandra et al. 2018). They aim to buffer two of the main threats for marine populations: overexploitation (Halpern et al. 2007) and habitat loss (Dulvy et al. 2003). The efficiency of an MPA, however, highly depends on the degree of protection and the enforcement of regulations (Álvarez-Fernández et al. 2020) and, even more fundamentally, on the spatial ecology and behaviour of a species (Gandra et al. 2018). The capacity of an MPA to encompass movements of local populations across different temporal and spatial scales and to protect essential habitats, such as breeding or nursery grounds (Abecasis et al. 2015) determine the suitability of an MPA for a particular species. It is thus essential to identify the drivers of these movements and to predict the spatial behaviour in order to evaluate the performance of an MPA and provide guidelines for future management planning (Gandra et al. 2018; Crossin et al. 2017).

Elasmobranchs are late maturing, slow growing, low fecundity species which make them particularly vulnerable to exploitation, especially in coastal ecosystems, where they are exposed to a broad range of anthropogenic pressures (Dulvy et al. 2014). Yet, species-specific conservation management has proven to be challenging, simply due to insufficient information on their biology and ecology (Elliott et al. 2020). Traditionally, the movements of skates has been assumed to be limited, especially in comparison to sharks, but it has been shown that some of them indeed move over long distances and even display complex movement patterns, such as diel vertical migrations through the water column (Wearmouth & Sims 2009; Siskey et al. 2019). However, only few studies have addressed species-specific spatial protection effectiveness for skates (Neat et al. 2015; Wiegand et al. 2011; Sousa et al. 2019; Simpson et al. 2020) and even less tried to identify the environmental drivers for their distribution (Elliott et al. 2020; Figueiredo et al. 2020).

The undulate ray *Raja undulata* Lacepède, 1802 is a coastal, elasmobranch species classified as endangered by the IUCN Red List (Ellis et al. 2015) and occurs patchily distributed from southern Ireland and England to Senegal (Ebert & Stehmann 2013). In Galicia, NW Spain, *R. undulata* is the most common commercial Rajidae species captured by small scale fishery fleets and its stocks show a decreasing trend (Alonso-Fernández et al. 2019). Its preference for shallow, sandy habitats (Figueiredo et al. 2020) may imply increased vulnerability, particularly during juvenile stages, compared to other skate species with a preference for deeper waters, e.g. *Raja clavata* and *Raja montagui* (Elliott et al. 2020). Despite their high vulnerability, spatial protection measurements for this species have not been assessed yet. While Sousa et al. (2018) investigated the suitability of an MPA as measurement of spatial protection for soft-bottom fish and found a positive response of some species, the effectiveness for *R. undulata* could not be assessed due to its low abundance. More targeted species-specific studies at sites of higher abundances are needed to assess the vulnerability of the species.

Furthermore, most of the studies investigating the spatial ecology and movements of skates (Simpson et al. 2020), including *R. undulata* (Ellis et al. 2011), use capture-mark-recapture methods. These do not allow to study movement patterns at high spatial and temporal resolution and uninterruptedly

over long temporal scales, which are crucial to assess the effectiveness of an MPA. Acoustic telemetry, however, enables the continuous monitoring of the movement of the species. To our knowledge, only one other study used acoustic telemetry for *R. undulata* to estimate survival rates of fisheries discharges (Morfin et al. 2019), another important aspect for the conservation and protection of this species.

Here we aim to provide insights into the behaviour and movement patterns of *R. undulata* within an MPA across different temporal scales and to identify their biological and environmental drivers. We expect that both have an effect on the presence, space use and activity as the distribution of *R. undulata* has been shown to differ based on sex and body size and might be driven by biological and seasonal cycles (Elliott et al. 2020; Serra-Pereira et al. 2015; Ellis et al. 2012). By investigating the effect of sex and body size as well as temperature and upwelling intensity on the behaviour and movement patterns of *R. undulata*, we hope to be able to provide valuable information for efficient spatial management strategies.

Material & Methods

Study system

This study was conducted at the Cíes Archipelago (Galicia, NW Spain; Figure 1) between April and December 2019. The Cíes Archipelago is part of the National Park *Parque Nacional Marítimo Terrestre das Illas Atlánticas de Galicia* (PNMTIAG) and comprises an area of 31 000 000 m² where commercial fishing is allowed with some gear regulations, while recreational fishing is forbidden (Conselleira de Medio Ambiente, Territorio y Vivienda 12/27/2018). It is located in the Southern part of the Galician coast, which is characterised by a series of estuarine inlets, the Rías Baixas. Located at the northernmost limit of the Eastern North Atlantic Upwelling System (Fraga 1981), favourable upwelling conditions that bring cold nutrient-rich waters into the rias prevail during spring and summer (Torres 2003; Gomez-Gesteira et al. 2006). For our study, we selected a shallow coastal area (max depth = 16 m) between the two main islands of the archipelago (Figure 1).



Figure 1. Map of study site. Location of Galicia (A) and the Cíes Archipelago (B), showing our receiver array (C) with acoustic receiver locations (red), tagging location (purple), reference tag positions (blue) and temperature data logger (green)

Acoustic Telemetry

Range Test

On 16th April 2019, a preliminary range test was carried out at the study site using Vemco range test tags V13 and V16, with a fixed delay of 7 sec. Fourteen receivers were deployed close to the bottom in a straight line at 25, 50, 75, 100, 125, 150, 175, 200, 250, 300, 350, 400, 500 and 600 m from the test tags. Each tag type was deployed subsequently and tested for a period of 1 hour. Number of detections decreased considerably (<50%) at distances >200 m for V13 and >250 m for V16 (Figure S1).

Receiver Array

Based on the range test results, a Vemco VPS system that included 20 VR2W acoustic receivers and 20 synchronization tags was deployed in the study area (AMIRIX Systems Inc. 2013). Distance between

neighbouring receivers was ~150 m to assure good coverage and overlapping receiver detection ranges within the study area. Receivers were attached to the upper end of a metallic auger anchor (140 cm high) and screwed ~60 cm into the substrate (Villegas-Ríos et al. 2013). For receiver station 3 and 4, where the substrate was too hard to screw the anchor into the substrate, the receivers were attached to a concrete block with a rope and a floater (Link S1). Receivers were placed at depths between 4 and 13 m and the array covered an area of ~800 000 m², with a higher density closer to the location where fish were tagged and released as well as closer to the shoreline, in order to assure sufficient detection of the transmission among rocky areas.

Two variables were used to monitor the environmental conditions in the array. Upwelling Index (UI) for the Rías Baixas was computed over 6 hour intervals for 2019 based on data collected by the Spanish Institute of Oceanography (http://www.indicedeafloramiento.ieo.es/index_UI_en.html). Positive values of UI correspond to upwelling events and negative values to downwelling (Gonzalez-Nuevo et al. 2014). Sea temperature was monitored using a ©Star:ODDI DST CTD Data Logger deployed at a receiver station close to our tagging location to record temperature every 20 mins starting from 5th June 2019 until the end of the study.

Tagging

A total of 44 individuals (21 females, 23 males) of *R. undulata* were tagged in the study area, 30 in May, 2 in June and 12 in October 2019 (Table S1). All individuals were tagged close to an area, where recreational divers had previously reported high densities of *R. undulata* (José Irisarri, Gonzalo Mucientes, pers. comm.). The skates were captured by scuba divers at 11-12 m depth and slowly brought to the surface (~ 3 m/min) inside a net. Disc length of the individuals was measured to the nearest centimetre and used as the body size indicator in the analyses, as some individuals had an incomplete tail. Sex was visually determined. After measurements were taken, the acoustic tags were surgically implanted in their peritoneal cavity. 10 individuals were tagged with Vemco V16-4x-A69-1602 transmitters, with a random signal transmission delay of 40-80s, 10 individuals with Vemco V13-1x-A69-1602 transmitters and 24 individuals with Vemco V13P-1x-A69-9006 transmitters both with a random signal transmission delay of 80-160s. Two reference tags (V13 and V16) were deployed inside the receiver array as recommended by Payne et al. (2010) in order to assess possible environmental effects on the detection patterns.

Individuals were then externally tagged with T-bar tags to avoid capturing the same skate in successive tagging trips and to enable fishers to report their recaptures. Skates were allowed to recover in a net floating attached to the boat and later released at the capture location using a custom-made cage that accompanied them to the bottom (Link S1). GPS position, depth, date and hour of release as well as time on board, i.e. time out of the water, were recorded for each tagged fish. The entire tagging procedure took 5 ± 1 min.

The present study followed animal welfare national regulations (Real decreto 53/2013 del 1 de febrero de 2013, published in B.O.E. nº 34, on 8 February 2013) with the correspondent authorization of experimental animal project (Expediente N°: ES360570202001/19/FUN01/BIOL AN.08/AAF01).

Data Processing

A total of 3 161 294 detections were downloaded on 3rd December 2019 and processed by Vemco in order to obtain VPS positions for each fish. One individual (TAC-RUN-19-12) that was found dead by divers in an abandoned fishing net was removed from the analyses due to uncertainty of the death date.

Data filtering

Data were filtered to remove potential spurious detections, defined as any single transmitter code occurring alone at a specific receiver within a 24 h period (n=84; 0.003%) (Meyer et al. 2007). The VPS position data was filtered according to the Horizontal Position Error (HPE) value provided by Vemco. Vemco provides this relative, unitless estimate of how sensitive a calculated position is to errors in its inputs. For the reference tags, Vemco also provides a HPE_m, which indicates the position error in meters. As suggested by (Smith 2013) HPE and HPE_m were compared by binning groups of calculated positions based on ranges of HPE. In order to retain enough data with a possibly small error, only VPS data with HPE \leq 50 were used for the analysis. This corresponds to the upper limit of the 99th bin of the HPE values calculated from the reference tags. This limit was chosen based on the cumulative mean HPE_m over the bins (Figure S2). The HPE_m of all reference tag positions with HPE \leq 50 is 1.5 ± 3.0 m and can be interpreted as a rough estimate for the position error in our study system. Thus, carefully inferred also for the calculated fish positions. From 356 886 initial positions, 340 564 positions (95.4%) were retained and used for further analysis.

Trajectory calculation and interpolation of positions

The VPS positions were used to calculate trajectories between positions. Each trajectory was characterized by the following metrics: distance between successive relocations (dist), time between relocations (dt) as well as increments in x and y direction (dx and dy). From these trajectories, speed (v) was calculated as:

$$v = \frac{dist}{dt}$$

In order to assure that all the movements within the study area are represented in our database we interpolated some positions and trajectories. This was done to account for technical restrictions, e.g. loss of signal in rocky areas or when individuals are buried in sand. We assumed that when the skates are buried in the sand, their transmissions do not reach the receivers as in other acoustic telemetry studies (Alós et al. 2012; Grothues et al. 2012; Gandra et al. 2018). In order to distinguish between events when we do not have detections because they are not present in our study area and events when we do not have detections because they are present but buried, we followed a decision tree (Figure 2) and performed several filtering and interpolation steps that are based on the following assumptions:

1) We assume linear movement between two detections.

2) If the time interval between two positions corresponds to 1 transmission delay, we assume that the skates are moving within our study area.

3) If the time interval between two positions is smaller than 2 maximum transmission delays, we assume that the missing transmission is due to technical restrictions, i.e. when skates move between rocks.

4) If the time interval between two positions is bigger than 2 maximum transmission delays and smaller than 12 hours and the estimated distance is smaller than 10 m, we assume that the missing transmissions are due to the skates being buried in the sand.

We filtered the data and interpolated the missing positions and trajectories in between the abovementioned time intervals. Since, we aimed to model only the activity of individuals within our study area, with these filtering steps we also excluded all the trajectories between positions that we assumed correspond to movements leaving and returning to the study area. Speed was calculated for all new trajectories, as well as distance travelled, time between relocations and a new start and end point of the trajectories. In order to also include the events when skates are buried in the sand in the home range (HR) estimation, the start and end positions of the interpolated trajectories were extracted and merged with the filtered VPS positions. All duplicate positions were removed.



Figure 2. Decision Tree for interpolation of missed detections. Filtering criteria, associated biological behaviour and technical restrictions lead to data treatment steps.

Estimation of behavioural metrics

The total HR over the study period and the weekly home range of each individual was estimated as the bivariate normal fixed kernel utilization distributions (KUDs) based on 95% of the positions for any particular week. We also computed day and night weekly and total home ranges using only daytime and nighttime positions during a particular week, the whole study period respectively. The residence index (RI) for each fish, which varied between 0 (no residency) and 1 (absolute residency), was defined (March et al. 2010; Afonso et al. 2008) as:

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

Where DD is the number of detection days and TD the number of tracking days for each fish. Speed was calculated as an indicator for activity (Zamora & Moreno-Amich 2002).

Data analysis

Behavioural metrics were estimated from each fish several times per day. This implies potential correlation among behavioural metrics within each fish. Thus, to include both fixed and random effects, account for the lack of independence and allow for non-linear effects of the explanatory variables, the data were analysed using Generalised additive mixed models, GAMMs (Wood 2017a).

Presence

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

$$P_{i,t} = \alpha + \beta_1 Sex_{i,t} + \beta_2 DL_{i,t} + \beta_3 UI_{i,t} + \beta_4 T_{i,t} + f(DOY_{i,t}) + a + \varepsilon_{i,t}$$
(1)

Where P is the probability of presence in the study area of an individual fish *i* on a day *t*.

Exploratory analysis revealed that the daily means of DL (disc length), UI (Upwelling Index) and sea temperature (T) did not present non-linear effects. Thus, they were modelled as parametric terms with β_n representing the linear coefficients. α is an intercept and f is a nonparametric smoothing function, fitted by 5 knots in order to avoid overfitting and describing the nonlinear effect of DOY (day of the year). a represents the random effect allowing for variation within the same fish.

Space use

To model the drivers of space use, the weekly home range size was used as a response variable in a GAMM (Gaussian distribution). Only weekly HR based on more than 4 different days (not necessarily consecutive) were included in the analysis to exclude bias that could arise from HR calculations based on weeks with a low number of detection days. Additionally, one individual with only one weekly HR value was excluded from the dataset for the model. In order to meet the model assumptions of normality and homoscedasticity of the residuals, HR area was log transformed. HR was fitted using the following model structure:

$$logHR_{i,t} = \alpha + \beta_1 Sex_{i,t} + \beta_2 DL_{i,t} + \beta_3 UI_{i,t} + \beta_4 T_{i,t} + \beta_5 Daytime_{i,t} + f(WOY_{i,t}) + a + \varepsilon_{i,t} \quad (2)$$

Where logHR is the log transformed HR area of an individual fish *i* in a week *t*. Exploratory analysis revealed that the weekly mean of DL (disc length), UI (Upwelling Index) and sea temperature (T) did not present non-linear effects. Thus, they were modelled as parametric terms, with θ_n as linear coefficients. α is an intercept and *f* is a nonparametric smoothing function, fitted by 5 knots in order

to avoid overfitting and describing the effect of WOY (week of the year). *a* represents the random effect allowing for variation within the same fish.

Activity

Speed was used as response variable to model the drivers of activity in a GAMM (Gaussian distribution). Speed was log transformed to meet the model assumptions (normality and homoscedasticity). As this transformation does not allow zeros or negative values, we first replaced 0 m/s in our data set by 1/2 of the minimum speed observed (489 out of 638 420 observations (0.08 %) were replaced by $5.26 \cdot 10^{-6}$ m/s) and then log transformed the new speed values. Finally, speed was fitted using the following model structure:

$$logSpeed_{i,t} = \alpha + \beta_1 Sex_{i,t} + \beta_2 DL_{i,t} + \beta_3 UI_{i,t} + \beta_4 T_{i,t} + f_1 (HOD_{i,t})$$

+ $f_2 (DOY_{i,t}) + a + \varepsilon_{i,t}$ (3)

Where logSpeed is the log transformed speed of a fish *i* at a given time *t*. Exploratory analysis revealed that DL (disc length), UI (Upwelling Index) and sea temperature (T) did not present non-linear effects. Thus, they were modelled as parametric terms with β_n representing the linear coefficients of parametric terms. Note that since sea temperature was measured every 20 min and UI computed every 6 hours, we assigned each speed observation the nearest temperature and UI values. α is an intercept and f_n are nonparametric smoothing functions, fitted by 5 knots in order to avoid overfitting and describing the effect of HOD (hour of the day in UTC) and DOY (day of the year). The smoothing functions were fitted by a penalized cyclic cubic regression spline and a cubic regression spline for HOD and DOY, respectively. *a* represents the random effect allowing for variation within the same fish.

In all the models above, all numerical variables were scaled and centred before included in the models. Random effects were assumed to be normally distributed with mean 0 and variances σ^2_a . Observations were made sequentially over time; thus, errors might not be independent. Therefore, a correlation structure was added to the formulation following an auto-regressive model of order 1 allowing for within time bin autocorrelation between the residuals as follows:

$$\varepsilon_{i,t} = \varphi_1 \varepsilon_{i,t-1} + n_{i,t}$$

A backward stepwise model selection procedure was performed for all the models. First a full model including all the explanatory variables was created and run. Then stepwise the least significant variable eliminated, until all predictors have a significant effect (p < 0.05) (Jacolien van Rij 2016).

All data processing and analysis were conducted in R (R Core Team 2020). Spatial data was treated with the sp package (Edzer J. Pebesma & Roger S. Bivand 2005). Sunrise and sunset times for our location were obtained with the suncalc package (Thieurmel & Elmarhraoui 2019) and KUDs and trajectories were calculated using the adehabitatHR and adehabitatLT package respectively (Calenge 2006). Finally, all models were computed using the bam() function of the mgcv R package (Li & Wood 2020; Wood et al. 2015; Wood et al. 2017b) designed to analyse big datasets with >10 000 observations.

Results

Between 31^{st} May and 3^{rd} December 2019, 3 161 294 detections were recorded from 44 unique individuals. The number of detections ranged between 2 842 and 323 817 (mean = 71 846 ± 67 208) detections per individual (Table S2). These detections resulted in 356 886 estimated positions, ranging between 292 and 36 636 (mean 8 111 ± 7 803) positions per fish. After the filtering and interpolation steps, the number of positions ranged between 665 and 89 799 (mean 19 040 ± 18 162) per individual, which were used for further analysis (Figure S3).

Two individuals were reported to be caught by fishing vessels in February and March 2020 (7.5 km SE of the study site, Northern tip of Cíes Islands respectively; Figure S4) and another individual was recaptured in October 2019 during a tagging campaign at our study site. One individual was found dead during the study period and excluded from all further analysis.

Disc length of tagged individuals ranged from 26 to 48 cm (mean = 41 ± 5 cm). The individuals were detected between 12 and 179 (mean 99 ± 53) days and their residence index varied from 0.23 to 1.00 (mean 0.65 ± 0.22). The mean speed per individual ranged from 0.006 to 0.112 m/s (mean 0.027 ± 0.024 m/s) and the maximum speed registered was 5.797 m/s. The HR area ranged between 99 450 and 373 825 m² (mean 237 778 ± 76 646 m²) and differed in shape and size between day and night (Figure 3, Figure S5). The HR area is generally bigger during the night (263 524 ± 78 420 m²) than during the day (188 483 ± 69 8439 m²). During the day, almost all individuals had the centre of their HR close to our tagging location where skate aggregations have been reported.



Figure 3. Plots of total, day and night HR areas for two individuals TAC-RUN-19-24 (female) and TAC-RUN-19-28 (male). Individuals were selected to represent the difference in HR size and shape between day and night. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the positions.

A) response variable Probability of presence												
Parametric coefficients	Estimate	Std. Error	z value	Pr(> z)								
Intercept	1.67929	0.28957	5.799	6.66e-09								
Upwelling Index	-0.11569	0.03773	-3.066	0.00217								
Approximate significance of smooth terms	edf	Ref.df	Chi.sq	p-value								
Day of the year	3.307	3.74	275.8	<2e-16								
Random effect for individual fish	37.819	42.00	262.8	<2e-16								
R-sq. (adj) = 0.551 Deviance explained = 45.2% ρ = 0.653												
B) response variable <i>HR area</i>												
Parametric coefficients	Estimate	Std. Error	t value	Pr(> t)								
Intercept	11.54141	0.03463	333.27	<2e-16								
Daytime (night)	0.39591	0.02310	17.14	<2e-16								
Approximate significance of smooth terms	edf Ref.df		F	p-value								
Week of the year	1.141	1.261	6.369	0.00668								
Random effect for individual fish	26.876	36.000	4.533	< 2e-16								
R-sq. (adj) = 0.437 [Deviance explain	ed = 46.1% ρ = 0	.101									
C) response variable <i>Speed</i>												
Parametric coefficients	Estimate	Std. Error	t value	Pr(> t)								
Intercept	-5.649704	0.162211	-34.829	<2e-16								
Sex (male)	0.521238	0.221814	2.350	0.0188								
Upwelling Index	0.014574	0.006539	2.229	0.0258								
Temperature	0.031082	0.006809	4.565	5e-06								
Approximate significance of smooth terms	edf	Ref.df	F	p-value								
Hour of the day	2.997	3.000	34140.7	<2e-16								
Day of the year	3.939	3.998	254.0	<2e-16								
Random effect for individual fish	40.361	41.000	193.7	<2e-16								
R-sq. (adj) = 0.343 [Deviance explain	ed = 34.3% ρ = 0	.860									
Std Error standard arror odf offestive degrees of	freedom Defdf	reference degrees a	ffraadam Daa	(adi) adjusted								

Table 1. Summary table of the fitted optimal models for A) presence, B) space use and C) activity

Std. Error – standard error, edf – effective degrees of freedom, Ref.df – reference degrees of freedom, R-sq.(adj) – adjusted coefficient of determination, ρ – error term for temporal autocorrelation

Normalized residuals of body size models did not show any departures from normality or further heterogeneity issues and random effects were reasonably normally distributed for all models (Figure S6-S8).



Figure 4. **Predicted probability of presence** as a function of Day of the year (A) and Upwelling Index (B). Values used for predictions: (A) Upwelling Index = -10.4333; (B) DOY = 180. Grey shade areas represent the 95% confidence interval.

The optimal model for the drivers of presence of *R. undulata* in the study area included individual identity as random effect and Day of the year and Upwelling Index as significant explanatory variables (**Table 1 A**). The presence of *R. undulata* in the study area largely varied over time (**Figure 4**). The highest probability of presence (P=0.99) was observed at the beginning of the study period and stayed high (P>0.75) until the beginning of October. Then, it dropped to very low values by the beginning of December (P=0.10). We also found a very low, but significant effect of the Upwelling Index on the probability of presence, with higher probability when the UI is lower.

The optimal model for space use included individual identity as random effect and only two other significant explanatory variables: daytime and week of the year (**Table 1 B**, **Figure 5**). Day time was the main driver for a difference in HR size. During the night the HR size was 1.3 times bigger (~160 000 m²) than during the day (~110 000 m²). The HR area decreases steadily, almost linearly, with the week of the year, being 1.2 times bigger in the beginning of the study period (~170 000 m²) compared to the end (~140 000 m²).



Figure 5. Predicted Home range size as a function of Week of the year (A) and Daytime (B). Values used for predictions: (A) Daytime = night; (B) WOY = 23. Grey shade areas represent the 95% confidence interval.



Figure 6. Predicted activity indicated as Speed (m/s) as a function of Hour of the Day (A) with nocturnal periods indicated in blue, Day of the year (B), Sex (C), Upwelling Index (D), Sea temperature (E). Values used for predictions: (A) DOY = 280, Sex = male, UI = 489.2763, T = 14.3202°C; (B) HOY = 21, Sex = male, UI = 489.2763, T = 14.3202°C; (C) HOY = 21, DOY = 280, UI = 489.2763, T = 14.3202°C; (D) HOY = 21, DOY = 280, Sex = male, UI = 489.2763. Grey shade areas (A, B, D, E) and black bars (C) represent the 95% confidence interval.

The optimal model for the drivers of activity include individual identity as random effect and Hour of the day, Day of the year, Sex, UI and Temperature as fixed effects (**Table 1 C**). Hour of the day was the main driver for differences in activity (**Figure 6**), with individuals showing a cyclic pattern and moving around 7 times faster around midnight (~0.022 m/s) than during midday (~0.003 m/s). Additionally, individuals had lower activity in summer (~0.010 m/s), which is increasing towards autumn, where from around day 260 (mid-September) individuals moved twice as fast compared to the beginning of the study period (~0.020 m/s). The activity then stayed relatively stable until the end of the study period. Activity levels differed between sex of individuals: male individuals being ~60% more active (~0.018 m/s) than female individuals (~0.011 m/s). Both environmental variables, UI and sea temperature had a small, yet significant, positive effect on activity. Activity was 1.15 higher at strong upwelling events (~0.02 m/s) compared to downwelling events (~0.017 m/s). Also, the effect of temperature was in a similar size range, with activity being 1.15 times higher at higher temperatures (17°C) compared to lower temperatures (12.5°C).

Discussion

Using acoustic tracking over 6 months, we have been able to identify the main drivers of behaviour and movements patterns of *R. undulata* in a coastal area in NW Spain. We found that movement and behaviour of *R. undulata* were mainly driven by diel cycles and seasonal patterns, with oceanographic factors being less important drivers of behaviour. While the presence in the study area and home range size decreased from summer to autumn, activity peaked in mid-September and differed between sexes. Our work represents an important contribution to the understanding of the ecology of this endangered, yet commercially important skate in Europe.

As we inserted the acoustic transmitters in the abdominal cavity of the skates, we probably prevented transmissions from being detected by our receiver array while the skates were buried in the sand (Alós et al. 2012; Gandra et al. 2018; Grothues et al. 2012). In order to compensate for these potentially missed detections, we interpolated positions using a decision tree based on time and distance between relocations. The interpolation makes our results more comparable to behavioural studies of species exhibiting longer periods of immobile behaviour, that however can be continuously tracked and detected. Despite our efforts to include all important movement patterns in our activity model, we might not have been able to detect very fast movements due to the way we determined speed. Firstly, fast movements are highly energy demanding (Humphries et al. 2017) and might thus occur at a temporal scale smaller than the transmission delay of the acoustic tags (40-160 sec). Secondly, even if individuals move at high speed for a longer time, the size of our study area (~800 m diameter) limits the possibility of their detection, as signal transmission would have to happen right at the moment when individuals are at the edges of the study area in order to register high speeds. In fact, only 22 relocations happened with a speed bigger than 2 m/s and the highest recorded speed was 5.797 m/s. This suggests that *R. undulata* is capable of swimming at higher speeds, which might be related to specific behavioural patterns and finally affecting their vulnerability. These movements could not be included in our analysis.

Seasonal patterns

We observed that the presence of R. undulata in our coastal telemetry array decreased towards winter, similar to Elliott et al. (2020). R. clavata and R. radiata have shown similar behaviour in the North Sea, where they moved to deeper waters during winter (Skjæraasen & and Bergstad 2000; Hunter et al. 2005) and used shallower waters as nursery grounds (Hunter et al. 2005). In northern Portugal, R. undulata develop eggs between December and May (Serra-Pereira et al. 2015), which are laid shortly after (Moura et al. 2007; Serra-Pereira et al. 2015). Furthermore, an asynchrony between the occurrence period of reproductively active females (December to May) and males (whole year, with peaks between July and January) has been reported (Serra-Pereira et al. 2015). Female R. undulata, as other skate species, are able to store sperm in their oviducal gland (Serra-Pereira et al. 2015). Thus, it is possible that mating occurs not only during the period when females are reproductively active (December to May), but the whole year around, including shortly after egg laying in the early summer months. Yet, associating the observed aggregations of *R. undulata* with reproductive behaviour needs to be done with caution, as even though considering the observed local differences between size at maturity (Serra-Pereira et al. 2015; Coelho & Erzini 2006; Moura et al. 2007) most of the female skates in our study are smaller than reported sizes at maturity (86.2 ± 2.6 cm total length in the North of Portugal; Serra-Pereira et al. 2015). The size of males individuals in our study, however, suggests that more than half of the individuals have reached size at maturity (76.6 \pm 2.4 cm total length; Serra-Pereira et al. 2015). The differences in activity levels between sexes might thus be linked to different maturity stages, where male behavioural patterns might be driven by mating, but also the observed dietary differences between sexes and different life stages (Moura et al. 2008). These might be reflected in different foraging strategies and thus movement and behaviour patterns.

Decreasing probability of presence and HR size towards the end of the year suggest that the importance of our study area for *R. undulata* is decreasing in the second half of our study period. Activity levels shifted from lower speeds in late spring to higher speeds in autumn, which might indicate a behavioural shift from summer to autumn. This could be explained by a change in the biological cycle as well as by a variation in prey availability. Moura et al. (2008) found dietary differences between seasons for *R. undulata* in Portuguese waters, where adult individuals feed mainly on brachyuran crabs, particularly *Polybius henslowii*, which is also highly abundant in the Galician coast (Signa et al. 2008). Their abundance is strongly correlated with chlorophyll *a* concentration and thus local productivity (Signa et al. 2008). Favourable upwelling conditions inducing high productivity occur mainly during spring and summer (Torres 2003; Gomez-Gesteira et al. 2006). A difference in prey abundance might reflect a change of feeding behaviour in *R. undulata*, which could explain the change in movement and behaviour patterns.

Diel cycle

Foraging and predator-prey interaction might also be the main reason for the high nocturnal activity, with a peak at midnight, and increased space use during the night. Although elasmobranchs are assumed to show higher activities during the night, only few studies have investigated nocturnal activity, especially for skates (Hammerschlag et al. 2016). These studies found increased activity levels during crepuscular periods (Hammerschlag et al. 2016). Although dietary aspects and feeding habits have been studied for *R. undulata* (Moura et al. 2008) and other skate species analysing their stomach contents (Schmitt et al. 2015; Barbini et al. 2010), little is known about their diel foraging patterns (Wearmouth & Sims 2009). The daily activity pattern is furthermore characterised by strikingly low levels of activity during some hours around midday. Being buried in the sand during the day when the light conditions and visibility are good, might be a strategy for predator avoidance (Heithaus & Vaudo 2012) while resting in order to restore energy (Houston & McNamara 2014). Resting during these daylight hours also explains the smaller HR size during the day and that its small, circular centre. This suggests that individuals rest in the same place each day as otherwise several circular centres would be visible.

Environmental drivers

We found little evidence to support a behavioural response of undulate ray to environmental drivers at the scale we conducted the study. Similar to Elliott et al. (2020), who found a negative relationship between chlorophyll a concentration and *R. undulata* presence, we found a negative effect of upwelling on the presence of *R. undulata* in the study area. It might seem counterintuitive that skates are less present during strong upwelling events, which indicate favourable conditions for primary production and consequently food availability (Pérez et al. 2000). Yet, it is important to consider that the Upwelling Index corresponds to a larger area (Rias Baixas) and skates might be feeding outside of our study area. Interpreting the UI as an indicator for food availability, however, needs to be done with caution, as there is a time shift of several days between upwelling events and biomass production (Nogueira et al. 1997), which has not been taken into account in our analysis. Thus, the UI could also reflect the meteorological and hydrological factors that underlie the primary production dynamics (Pérez et al. 2000) and as such drive *R. undulata* presence and movement.

Although temperature has been shown to play an important role in elasmobranch movement and behaviour (Bernal et al. 2012), few studies have identified temperature-driven movement patterns for skates. Even if it has been shown that temperature increases metabolic rates for some skate species in laboratory experiments (Schwieterman et al. 2019), no temperature-mediated movements could be identified in the wild (Humphries et al. 2016) and some skates have been shown to occupy a wide temperature range (Farrugia et al. 2016). In our study, we did not find an effect of temperature on the presence and space use of *R. undulata* and the positive effect on activity levels is rather small, possibly driven by hydrodynamic processes. As we did not find an effect of temperature on presence, it is unlikely that the effect of temperature is connected to variation through the seasons. Furthermore, higher activity at higher temperatures contradicts a correlation with diurnal cycles, where we found higher activity during the night. However, it is also possible that the temperature that we measured at one location on the bottom in our study site is not the temperature that the skates are actually experiencing. In our study we did not take into account potential vertical movements along the water column where temperature might be more variable, as it has been observed for other skates (Humphries et al. 2017; Wearmouth & Sims 2009).

Finally, we did not find an effect of body size on the behaviour and movement of *R. undulata*. Body size has been shown to be an important factor in the distribution of *R. undulata* (Ellis et al. 2012), with juveniles being found in shallower waters closer to the coast (Elliott et al. 2020; Serra-Pereira et al. 2015). Furthermore ontogenetic dietary shifts have also been observed in *R. undulata* (Moura et al. 2008) which could potentially impact foraging-related movement patterns. That we did not find an effect of body size in our study, might be explained by the fact that only rather large individuals were tagged and that our telemetry array covered a relatively small and shallow area. Further studies including smaller individuals and maturity statutes and might give further insight into differences in movement related to life stages of the species.

Implications for management and conservation

The identified drivers of the movement patterns and behaviour *R. undulata* and the underlying biological cycles are valuable indications for efficient management and conservation measures (Crossin et al. 2017). R. undulata has been shown to spend long periods of time in our study area occupying rather small HR (300 000 m²), which indicates that a relatively small MPA could potentially be an efficient conservation measurement (Kramer & Chapman 1999), especially if the study area can be confirmed as a breeding ground for the species (Abecasis et al. 2015). However, this needs to be confirmed by long-term studies in order to investigate if the observed high presence of individuals in late spring and summer is a recurring process. Furthermore temporal closures for fisheries that take into account activity levels and space use could be an effective management measurement (Dunn et al. 2011). As such, during periods when individuals are present in the study area, commercial fishing could be restricted during the night, when with activity peaks also the probability of encountering static fishing gear increases (Rudstam et al. 1984) and recreational fisheries such as spearfishing during the day, when aggregations of *R. undulata* are easily encountered and targeted (pers. obs.). During our study period males have shown higher activity levels compared to females, which might increase their catchability and result in a change in the demographic composition of the population as has been shown for *Raja clavata* in the Adriatic Sea (Krstulovićsifner et al. 2009).

Conclusion

Seasonal patterns and diel cycles could be identified to be the main drivers for movement and behaviour of *R. undulata* in a coastal area in the NW of Spain. Environmental drivers have been shown to have a smaller impact on movement and behaviour but could become potentially more important in the context of a rapidly changing marine environment. Based on the identified drivers, we were able to build further hypotheses about the underlying biological traits. Yet, further studies are needed to assess the hydrodynamic conditions and productivity, i.e. food availability, in the study area and to relate movement with important behavioural patterns, such as foraging and mating. Furthermore, the possible importance of our study site as mating and nursery ground needs to be investigated in order to fully understand the vulnerability of the aggregations found at this site and consequently also assess the efficiency of the MPA in place. Our findings indicate that the MPA might be an efficient conservation tool at least during late spring and summer months, but a more extended monitoring system is necessary to evaluate the efficiency of the whole MPA. Considering the high site-fidelity during summer, their migratory behaviour in autumn and the possible underlying biological cycles, a combination of spatial and temporal management measurements has been identified to be a promising strategy for the conservation and protection of the endangered skate *R. undulata*.

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Supplementary Material

S1. Range test and tagging



Figure S1. Range test of Transmitter V13 (A) and V16 (B). Variation of Percentage of the of detected transmissions (Detection %) with distance of receivers from the test transmitter tags.

Link S1. Video illustrating receiver deployment and tagging procedure of TAC Project (Telemetria Acustica de comportamiento) of the IIM-CSIC (in Spanish)

https://www.youtube.com/watch?v=-XloYXQ_faQ

Table S1. Overview table of tagged individuals including biometric parameters (sex, total length, disc length) and tagging information (date, time, time on board, location, depth, transmitter type)

ID	Sex	Total Length [cm]	Disc Length [cm]	Date	Time	Time on board [min]	Lat	Lon	Depth [m]	Transmitter Type
TAC-RUN-19-01	male	84	41	24/05/2019	18:45	0:11	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-02	male	88	47	24/05/2019	19:07	0:08	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-03 ¹	male	89	44	24/05/2019	19:23	0:09	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-04	male	77	41	24/05/2019	19:36	0:05	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-05	male	70	36	24/05/2019	19:49	0:05	42.21169	-8.89925	12	V13-1x
TAC-RUN-19-06	male	59	31	24/05/2019	20:01	0:06	42.21169	-8.89925	12	V13-1x
TAC-RUN-19-07	female	68	37	24/05/2019	20:11	0:07	42.21169	-8.89925	12	V13-1x
TAC-RUN-19-08	female	82	47	24/05/2019	20:48	0:05	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-09	male	67	41	24/05/2019	20:54	0:05	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-10	male	83	46	24/05/2019	21:03	0:04	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-11	male	82	47	24/05/2019	21:08	0:05	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-12 ²	female	86	46	24/05/2019	21:14	0:06	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-13	male	80	43	24/05/2019	21:23	0:06	42.21169	-8.89925	12	V16-4x
TAC-RUN-19-14	female	80	44	31/05/2019	9:53	0:06	42.21169	-8.89962	11	V13-1x
TAC-RUN-19-15	male	70	38	31/05/2019	10:04	0:05	42.21169	-8.89962	11	V13-1x

¹ 10/03/2020 fished on the Northern tip of the Cíes Islands, Tag recovered at the Lonxa de Cangas

² 04/09/2019 found dead by divers in a ghost fishing net

ID	Sex	Total Length [cm]	Disc Length [cm]	Date	Time	Time on board [min]	Lat	Lon	Depth [m]	Transmitter Type	
TAC-RUN-19-16	male	80	45	31/05/2019	10:12	0:05	42.21169	-8.89962	11	V13-1x	
TAC-RUN-19-17	male	69	39	31/05/2019	10:21	0:03	42.21169	-8.89962	11	V13-1x	
TAC-RUN-19-18	male	60	35	31/05/2019	10:27	0:04	42.21169	-8.89962	11	V13-1x	
TAC-RUN-19-19	female	78	44	31/05/2019	10:33	0:05	42.21169	-8.89962	11	V13-1x	
TAC-RUN-19-20	female	82	47	31/05/2019	10:40	0:05	42.21169	-8.89962	11	V13-1x	
TAC-RUN-19-21	male	84	46	31/05/2019	10:49	0:04	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-22	female	65	38	31/05/2019	10:54	0:04	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-23	male	69	40	31/05/2019	10:59	0:04	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-24	female	79	45	31/05/2019	11:53	0:04	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-25 ³	male	73	38	31/05/2019	11:59	0:03	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-26 ⁴	female	80	43	31/05/2019	12:04	0:04	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-27	female	78	42	31/05/2019	12:11	0:04	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-28	male	89	48	31/05/2019	12:17	0:05	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-29	female	63	38	31/05/2019	12:24	0:04	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-30	female	65	36	31/05/2019	12:30	0:05	42.21169	-8.89962	11	V13P-1x	
TAC-RUN-19-31	female	75	41	10/06/2019	12:39	0:05	42.21153	-8.90005	12	V13P-1x	
TAC-RUN-19-32	female	57	31	10/06/2019	12:47	0:05	42.21153	-8.90005	12	V13P-1x	

³ 11/10/2019 found alive in Rayalandia during tagging campaign

⁴ 26/02/2020 fished close to Monte Ferro (ca. 7.5 km SE of study site), Tag recovered at the Lonxa de Cangas

ID	Sex	Total Length [cm]	Disc Length [cm]	Date	Time	Time on board [min]	Lat	Lon	Depth [m]	Transmitter Type
TAC-RUN-19-33	female	69	38	11/10/2019	11:04	0:07	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-34	male	86	45	11/10/2019	11:19	0:08	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-35	female	71	41	11/10/2019	11:30	0:06	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-36	male	73	38	11/10/2019	11:38	0:05	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-37	female	75	41	11/10/2019	11:45	0:08	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-38	male	90	48	11/10/2019	11:55	0:09	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-39	female	65	35	11/10/2019	12:06	0:05	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-40	female	48	26	11/10/2019	12:13	0:05	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-41	male	81	45	11/10/2019	13:46	0:07	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-42	female	70	39	11/10/2019	13:55	0:05	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-43	female	84	46	11/10/2019	14:02	0:05	42.21139	-8.89923	12	V13P-1x
TAC-RUN-19-44	male	81	44	11/10/2019	14:09	0:05	42.21139	-8.89923	12	V13P-1x

S2. Data processing



Figure S2. Mean Error [m] and Mean HPE vs. % of retained data. Cumulative mean error (HPE_{m;} blue) and cumulative mean HPE (black) were calculated over 100 bins. In the 100th bin the mean error (m) is drastically increasing. In order to be conservative, the upper limit of the 99th bin was chosen as filter criteria for HPE.

Figure S3. Distribution of VPS positions used for analysis. The graph shows the distribution of untreated (red) and interpolated (blue) positions per hours of the day.

S3. Behavioural metrics, recaptures and HR plots

Table S2. Summary table of behavioural metrics for all individuals. ID - individual fish ID, DL - disc length (cm), #D - number of detections, #VPS - number of VPS positions before filtering and interpolation steps, #VPS total - number of VPS positions used for analysis, <math>DD - detected days, TD - total tracked days, RI - residence index, HR total - total HR area (m^2), $HR day - HR area (<math>m^2$) during the day, HR night - HR area (m^2) during the night, v min - minimum speed observed (m/s), v max - maximum speed observed (m/s), v mean - mean speed observed (m/s)

ID	Sex	DL	Release Date	#D	#VPS	#VPS total	DD	TD	RI	HR total	HR day	HR night	v min	v max	v mean
TAC-RUN-19-01	male	41	24/05/2019	39652	3538	4882	115	193	0.60	346462.5	331387.5	327250	5.85e-04	1.409	0.112
TAC-RUN-19-02	male	47	24/05/2019	158955	18250	39831	108	193	0.56	344912.5	239037.5	410200	0	2.055	0.038
TAC-RUN-19-03	male	44	24/05/2019	83190	9580	23825	104	193	0.54	228400	128687.5	368262.5	0	1.026	0.027
TAC-RUN-19-04	male	41	24/05/2019	130513	13263	23306	152	193	0.79	298400	252400	321562.5	0	4.105	0.058
TAC-RUN-19-05	male	36	24/05/2019	94279	11071	28385	125	193	0.65	198300	183937.5	222962.5	0	0.560	0.014
TAC-RUN-19-06	male	31	24/05/2019	141161	16449	33960	155	193	0.80	326325	268000	336000	0	0.736	0.021
TAC-RUN-19-07	female	37	24/05/2019	34117	4270	10710	54	193	0.28	202475	167237.5	296225	0	0.565	0.015
TAC-RUN-19-08	female	47	24/05/2019	105588	11286	19748	147	193	0.76	338850	276675	347762.5	0	5.797	0.056
TAC-RUN-19-09	male	41	24/05/2019	323817	36636	89799	173	193	0.90	261050	196775	362000	0	5.095	0.030
TAC-RUN-19-10	male	46	24/05/2019	41716	3856	5970	75	193	0.39	346687.5	308137.5	323387.5	0	1.438	0.065
TAC-RUN-19-11	male	47	24/05/2019	93316	7339	12073	143	193	0.74	353612.5	268687.5	393687.5	1.56e-04	1.363	0.059
TAC-RUN-19-12 ⁵	female	46	24/05/2019	214759	25407	52722	95	193	-	-	-	-	-	-	-
TAC-RUN-19-13	male	43	24/05/2019	57484	4687	7281	118	193	0.61	373825	227775	426075	0	1.359	0.063
TAC-RUN-19-14	female	44	31/05/2019	114361	13382	27882	134	186	0.72	213325	195925	215937.5	0	0.969	0.026
TAC-RUN-19-15	male	38	31/05/2019	230220	26665	54161	165	186	0.89	320725	280387.5	332037.5	0	3.326	0.021
TAC-RUN-19-16	male	45	31/05/2019	51103	5535	10352	137	186	0.74	284187.5	240950	301862.5	0	0.552	0.042
TAC-RUN-19-17	male	39	31/05/2019	128873	14910	31709	176	186	0.95	261787.5	166150	304025	0	2.064	0.024
TAC-RUN-19-18	male	35	31/05/2019	62535	7218	16580	55	186	0.30	228562.5	179000	259087.5	0	0.446	0.015
TAC-RUN-19-19	female	44	31/05/2019	20892	2104	3810	78	186	0.42	247037.5	221212.5	229325	1.74e-04	0.430	0.023
TAC-RUN-19-20	female	47	31/05/2019	116116	13164	22881	150	186	0.81	317225	289700	332462.5	0	0.701	0.038
TAC-RUN-19-21	male	46	31/05/2019	12176	1060	2431	125	186	0.67	311937.5	209387.5	347487.5	1.04e-04	0.328	0.019
TAC-RUN-19-22	female	38	31/05/2019	35455	3611	16601	106	186	0.57	212800	172725	243237.5	0	0.852	0.007

⁵ Excluded from analysis for behavioural metrics and models

ID	Sex	DL	Release Date	#D	#VPS	#VPS total	DD	TD	RI	HR total	HR day	HR night	v min	v max	v mean
TAC-RUN-19-23	male	40	31/05/2019	76902	9989	27400	168	186	0.90	99450	89262.5	104050	0	0.434	0.014
TAC-RUN-19-24	female	45	31/05/2019	68778	7861	30239	147	186	0.79	214100	204837.5	221900	0	0.753	0.009
TAC-RUN-19-25	male	38	31/05/2019	89048	10964	48656	179	186	0.96	139237.5	93262.5	216312.5	0	0.580	0.006
TAC-RUN-19-26	female	43	31/05/2019	133795	16818	54467	168	186	0.90	147300	134200	152762.5	0	0.584	0.011
TAC-RUN-19-27	female	42	31/05/2019	17922	1829	3889	87	186	0.47	366037.5	258500	334537.5	3.04e-05	0.293	0.016
TAC-RUN-19-28	male	48	31/05/2019	19702	2251	11211	71	186	0.38	146212.5	64862.5	315687.5	0	0.369	0.006
TAC-RUN-19-29	female	38	31/05/2019	18760	2059	3726	51	186	0.27	256612.5	248675	215600	3.05e-04	0.424	0.023
TAC-RUN-19-30	female	36	31/05/2019	56083	5681	13184	148	186	0.80	307687.5	296312.5	278362.5	6.06e-05	0.836	0.017
TAC-RUN-19-31	female	41	10/06/2019	85482	10470	31891	149	176	0.85	177750	148050	201625	0	0.731	0.013
TAC-RUN-19-32	female	31	10/06/2019	63092	7238	25440	112	176	0.64	188250	133500	194612.5	0	3.093	0.011
TAC-RUN-19-33	female	38	11/10/2019	15917	1832	5577	25	53	0.47	159337.5	126300	171987.5	0	0.439	0.013
TAC-RUN-19-34	male	45	11/10/2019	4964	464	665	14	53	0.26	280812.5	197575	253387.5	1.12e-04	0.325	0.103
TAC-RUN-19-35	female	41	11/10/2019	3448	396	1325	12	53	0.23	139750	88825	166275	1.34e-04	0.247	0.011
TAC-RUN-19-36	male	38	11/10/2019	57228	7471	21590	52	53	0.98	129687.5	102200	150575	0	0.492	0.012
TAC-RUN-19-37	female	41	11/10/2019	21176	2103	7601	38	53	0.72	166200	128937.5	203700	0	0.284	0.009
TAC-RUN-19-38	male	48	11/10/2019	2842	292	1269	21	53	0.40	181750	143737.5	244850	1.61e-04	0.339	0.014
TAC-RUN-19-39	female	35	11/10/2019	21196	2553	8120	31	53	0.58	153737.5	129837.5	160437.5	0	0.250	0.011
TAC-RUN-19-40	female	26	11/10/2019	42936	5237	16153	48	53	0.91	220675	207862.5	229425	0	0.512	0.009
TAC-RUN-19-41	male	45	11/10/2019	34031	4118	10045	53	53	1.00	163775	87575	207750	0	0.470	0.023
TAC-RUN-19-42	female	39	11/10/2019	6013	344	825	41	53	0.77	205500	132900	224375	1.28e-04	0.396	0.018
TAC-RUN-19-43	female	46	11/10/2019	25299	2921	7739	26	53	0.49	170500	158112.5	167125	0	0.618	0.019
TAC-RUN-19-44	male	44	11/10/2019	6318	714	1530	30	53	0.57	193200	125287.5	215350	0	0.676	0.025

Figure S4. Map of recaptured individuals. Positions of their recaptures by fishing vessels in relation to our study area. One individual was recaptured in February 2020 at the Northern tip of the Cíes Islands (ca. 4 km N from our study site) and a second one in March 2020 at Monte Ferro (ca. 7.5 km SE of study site). Red markers are recapture locations, yellow highlighted area is our study area.

Figure S5a. Total, day and night HR areas for all individuals. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the position

Figure S5b. Total, day and night HR areas for all individuals. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the position

Figure S5c. Total, day and night HR areas for all individuals. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the position

Figure S5d. Total, day and night HR areas for all individuals. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the position

Figure S5e. **Total, day and night HR areas for all individuals**. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the position

Figure S5f. Total, day and night HR areas for all individuals. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the position

Figure S5g. Total, day and night HR areas for all individuals. Red dots represent the acoustic telemetry receiver locations and the shaded area the HR (KUD95 = kernel utilization distribution based on 95% of the positions); %KUD = kernel utilization distribution based on x% of the position

S4. Model validation

Figure S6. Model validation plots for the optimal presence model. QQplot of model residuals (A); Residuals vs. *fitted values (B); Histogram of residuals (C); Observed vs. fitted values (D)*

Figure S7. Model validation plots for the optimal space use model. QQplot of model residuals (A); Residuals vs. *fitted values (B); Histogram of residuals (C); Observed vs. fitted values (D)*

Figure S8. Model validation plots for the optimal activity model. QQplot of model residuals (A); Residuals vs. *fitted values (B); Histogram of residuals (C); Observed vs. fitted values (D)*