Drivers of the spatial behaviour of the threatened thornback skate (Raja clavata)

Kenn Papadopoulo1,2,* , David Villegas-Ríos1, Gonzalo Mucientes1, Alina Hillinger1,2 and Alexandre Alonso-Fernández1

1 Instituto de Investigaciones Marinas (IIM-CSIC), Eduardo Cabello 6, 36208 Vigo, Spain
2 International Master in Marine Biology (IMBRSea), Ghent University, Gent, Belgium

Received 21 April 2023 / Accepted 13 June 2023

Handling Editor: AE David Kaplan

Abstract – Fish movements are fundamental to their ecology and survival. Understanding the causes and consequences of the spatial behaviour of fish is of high relevance as it provides critical knowledge for conservation purposes. Skate (Rajidae) populations face an unprecedented global decline due to overfishing. In this study, we used acoustic telemetry to track the movements of nine individuals of the near threatened thornback skate (Raja clavata) around the Cíes Islands, a small marine protected area in the northwest of the Iberian Peninsula. Our results demonstrate the significant impacts of biotic and abiotic drivers on the spatial behaviour of R. clavata. Overall residency inside the study array was low (0.073), differed between sexes (higher for females) and over the course of the year (peaking in summer). The analysis of the direction of the excursions performed by R. clavata individuals revealed high consistency in the exit and entry areas and a strong connectivity with inshore waters connecting with the Ría de Vigo, as compared with offshore waters connecting with the open ocean. Finally, the activity space of R. clavata also varied over the time of the year with a peak in summer. This study provides an important baseline information for understanding the spatial behaviour of R. clavata that can serve as a starting point for planning future conservation actions or studies.

Keywords: Acoustic telemetry / behaviour / marine protected area / Raja clavata / skates / spatial ecology

1 Introduction

Animal movement is fundamental to life and shapes many ecological and evolutionary processes (Nathan et al., 2008; Cooke et al., 2022). For instance, spatial behaviour affects population dynamics, connectivity, exposure to threats and the ability to cope with environmental changes (Morales et al., 2010). At the same time, the movement of organisms is influenced by a myriad of biotic and abiotic factors at multiple temporal and spatial scales (Lédée 2015; Cooke et al., 2022). Understanding the causes and consequences of movement is therefore of high interest in ecological and evolutionary research (Shaw, 2020).

From a practical standpoint, a comprehensive understanding of the spatial ecology of marine organisms is essential to assess and inform marine conservation policies and management plans (Crossin et al., 2017; Hays et al., 2019). Combining information on the movement ecology of highly migratory species with the spatial distribution of fishing efforts has revealed a high and concerning overlap between fish abundance and fishing pressure (Queiroz et al., 2019). A growing number of marine protected areas (MPAs) are now being designed and evaluated based on the extent of species home ranges and habitat selection (MacKeracher et al., 2018; Gilmour et al., 2022). Spatial ecology studies have revealed essential habitats for marine animals such as foraging grounds (Warwick-Evans et al., 2018) or spawning and nursing areas (Hays et al., 2019). Finally, innovative research using movement monitoring succeeded in estimating key demographic parameters such as mortality rates for neonates and juveniles (Heupel and Simpfendorfer, 2002) as well as survival rates from fisheries discard (Morfin et al., 2019; Alonso-Fernández et al., 2022).

Over one-third of species of the class Chondrichthyes are threatened by the loss and degradation of habitat, climate change, pollution and overfishing (Dulvy et al., 2021). Skate (Rajidae) populations have been experiencing a severe decline worldwide as a result of habitat loss and overexploitation (McPhie and Campana, 2009, Simpson et al., 2020, 2021).
Dulvy et al., 2021). Most skate species have low population growth due to their slow development rates and late sexual maturity (Licandeo et al., 2006; Pardo et al., 2016). Consequently, the majority of skate species are unable to withstand high levels of fishing pressure (McPhie and Campana, 2009; Dulvy et al., 2014) and are considered among the most vulnerable groups of fish (Dulvy et al., 2000). Current population declines of skates have resulted in the inclusion of many Rajidae species on the IUCN (International Union for the Conservation of Nature) Red List. As of today, 158 species of Rajidae are present on the IUCN Red List with 36% of species (ray and skates) classified as threatened (n=220 of 611 species) (Dulvy et al., 2021; IUCN, 2022).

Despite a few studies focused on skate ecology (Neat et al., 2014; Sousa et al., 2019; Simpson et al., 2020), many aspects of their life cycle still remains unknown. In fact, 13.3% of all skate species present on the IUCN Red List are still considered “data deficient” (IUCN, 2022) and the populations of skates in Europe are considered data-limited stocks without analytical stock assessments (ICES, 2022). Filling these ecological knowledge gaps is a pressing need if we want to counteract the global diversity loss (Joppa et al., 2016).

Technological advancements have made it possible to track marine animals in conditions that would otherwise be impossible to achieve, thus fostering the rapid development of the field of movement ecology (Lennox et al., 2017; Lowerre-Barbieri et al., 2019). In systems ranging from lakes and rivers to the open ocean, acoustic telemetry is the most used method to track submerged aquatic organisms (Hussey et al., 2015). The use of underwater acoustic telemetry allows for an in-depth understanding of fish movement ecology, such as home range (Leeb et al., 2021), activity (Bohaboy et al., 2022) as well as diel and seasonal differences in movement patterns during the year (Williams-Grove and Szedlmayer, 2016). This represents a particularly suitable technique to meet the actions of the “Sustainable Development Goal 14” of the United Nations (Alós et al., 2022). In a context of ever-growing anthropogenic disturbances such as habitat degradation, migration barriers and climate change, furthering our understanding of the drivers of animal behaviour is of the utmost importance to increase the effectiveness of conservation efforts (Hays et al., 2019; Lowerre-Barbieri et al., 2019).

The thornback skate, Raja clavata (Linnaeus 1758), is amongst the most common and widespread skates in the northeast Atlantic and Mediterranean Sea (Ellis, 2016). This bottom-dwelling and coastal species can be found from the South of the Arctic Circle (Iceland, Norway) to the east Atlantic coast of south Africa (Steinhann, 1995). Like most skates, the thornback skate spends the majority of its time in areas as deep as 300 m (Whitehead et al., 1986; Last et al., 2016; Trenkel et al., 2022). Characterised as an opportunistic, mobile and active predator, thornback skates feed on a wide variety of prey (mainly invertebrates and some fish), thus granting it a wide foraging area (Ellis et al., 1996; Farias et al., 2006). As with all Rajidae species, female thornback skates spawn egg capsules which they bury or attach to the substrate (Maia et al., 2015).

Classified globally as “Near Threatened” by the IUCN Red List (Ellis, 2016), the thornback skate is among the most frequently captured skates by commercial fisheries in northwest Europe (Santos et al., 2021). In 2019, the global catch of thornback skate reached 6,874 tonnes, most of them being captured as bycatch of trawls and gillnets (FAO, 2021). The thornback skate is a common species in European multispecies and multi-gear fisheries, including the small-scale fishing sector (Bañon Diaz et al., 2008; Figueiredo et al., 2020); in partially protected areas (Di Lorenzo et al., 2022). Thornback skates rarely escape trawl nets because of their large size and thorns; this, coupled with the slow growth rate and low fertility of skates, makes overfishing a great threat to their populations (Ellis, 2016). It is important to note that, the conservation status of R. clavata appears to show signs of improvement in recent years, with increased biomass and indications of low exploitation levels in the northeast Atlantic (ICES, 2022). However, variations and uncertainties in different assessments, emphasize the need for continued monitoring and management measures to ensure the long-term sustainability of the species. Although the general latitudinal and bathymetric distribution of the species is understood, there have been virtually no studies assessing the fine-scale behaviour of the species in which may however be relevant for understanding the applicability of conservation measures such as marine protected areas. In this study, we filled this knowledge gap by using fine-scale positioning based on acoustic telemetry to track the spatial ecology of thornback skates in the Cies Islands, a small MPA in the northwest of the Iberian Peninsula. Our objectives were to (1) identify the residence patterns in the study area; (2) assess the timing, duration and direction of the excursions out of the study area; (3) quantify the temporal variation in space use. This study allows inferences about thornback skates in the Cies archipelago that were previously not possible.

2 Methods

2.1 Study array

This study was carried out in the Cies islands, at the mouth of the Ría de Vigo (Galicia, northwest Spain), between October 2020 and June 2022. The Cies islands are part of a partially protected area called the Parque Nacional Marítimo-Terrestre das Illas Atlánticas de Galicia (PNMTIAG). This archipelago is made up of several islands and islets that together cover an area of 31 km² (Figs. 1a–c). Inside the PNMTIAG recreational fishing is prohibited and different uses are regulated (Xunta de Galicia, Consellería de Medio Ambiente, Territorio y Vivienda, 27/12/2018). Waters surrounding the Cies islands are subject to upwelling events, rendering them particularly productive and therefore valued as important fishing grounds by the small-scale local fishers (Aristegui et al., 2004; Broullón et al., 2023).

An array of 22 ©Innovasea (formerly Vemco) VR2W acoustic omni-directional receivers was deployed in the study area. Receivers were mounted at the top of auger anchors (140 cm high and screwed 60 cm deep into the sandy substrate), at depths ranging from 3.3 to 13.1 m (Villegas-Ríos et al., 2013) (Fig. S1). Two ©Innovasea reference transmitters (V13 and V16) were placed at fixed positions within the receiver array to assess potential environmental effects on the detection patterns and the error associated to...
skate positions (Payne et al., 2010). Following range tests (Leeb et al., 2021), the distance between stations was set at ~150 m to ensure adequate coverage and overlap between receiver’s detection ranges. Assuming an average detection range of ≈150 m (corresponding to 50% of the proportion of the detections received during the range test (Leeb et al., 2021)) the area covered by the array would be 0.58 km².

2.2 Skate tagging

All thornback skates ($n = 14$) were caught by a small commercial boat using “palangrillo” (Galician local name for small bottom long-lines) baited with pilchard or squid near or within the acoustic array. The fishing gear used in the study comprised sets of four and six pieces containing approximately 160 hooks per piece. Longline sets covered an average distance...
of 2.26 ± 0.88 km and the soak time of the experimental fishing trips varied between 26 min and 4 h and 15 min. Eleven thornback skates were externally tagged (anchored with monofilament) in the pectoral fin (Fig. S1) with ©Innovasea V13P-1x (lifetime: 855 days; signal transmission delay: 80–160 s) and three with ©Innovasea V9AP-2x (lifetime: 453 days; delay: 80–160 s) transmitters equipped with pressure sensors. Fish were tagged on two dates: 08th of October and 19th of November 2020. Each tagged skate was sexed and the disc length (DL) measured to the nearest cm; individuals were subsequently returned to the sea as quickly as possible (<5 min). External T-bar tags (©Floy Tag) were attached to the pectoral fin of the individuals to prevent possible repeated tagging in subsequent samplings and to enable divers to report their recaptures (Fig. S1).

A dead thornback skate was equipped with an acoustic transmitter (©Innovasea V13P) and released inside the telemetry array to determine the effects of currents, waves, or scavengers on the movement of a dead individual. As a result, we were able to identify a “dead” pattern, which could be used to assess whether a tagged skate had died inside the array (Villegas-Ríos et al., 2020; Alonso-Fernández et al., 2022) (Fig. S2). This is important to make sure that the behavioural variables are only estimated when the fish are alive (Villegas-Ríos et al., 2020).

This study complied with animal welfare regulations of the regional government (Xunta de Galicia) starting on the 14th of November 2019. It follows the Experimental Animal Project Authorization: ES360570202001/19/FUN01/BIOL AN.08/AAF01.

2.3 Data treatment and analysis

Detection data were offloaded from acoustic receivers every 6 months starting in September 2020 until June 2022. The data was stripped from single detections occurring within 24 hours at receivers as they were considered false detections (Meyer et al., 2007). The fate and “fate date” for each tagged skate were assigned by examining plots of position and depth over the study time based on Centres of Activity (COAs) (Villegas-Ríos et al., 2020; Alonso-Fernández et al., 2022) (Fig. S3). Behavioural analyses only included skates that were alive and within the acoustic array for at least three days post-release to exclude individuals which died after release. Moreover, any detections post the assigned fate date were filtered from the analysis (Fig. S3).

2.4 Residency

The residence index (RI) for each skate was computed as follows:

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

where DD corresponds to the number of days an individual was detected and TD to the total number of days between the tagging date and the end of the study. RI range of values goes from 0 (never detected in the array) to 1 (continuous residency in the array) (Papastamatiou et al., 2010; Espinoza et al., 2011).

2.5 Characterizing excursions

To determine possible preferred routes used for entering and exiting the study area, we divided the array into four sectors (Fig. 1d). Excursions out of the study area were identified as instances when an individual was absent for more than 24 h. For all excursions, we retained: (i) the sector where the last detection of the skate leaving the array was recorded, (ii) the sector which recorded the first detection of the skate returning into the array and (iii) the duration of the excursion. We defined four sectors mirroring the four cardinal points: ‘north’ — suggesting a movement towards the northern side of the archipelago; ‘east’ — suggesting a movement towards the inner part of the Ría de Vigo; ‘south’ — which suggests that the skate was heading towards the southernmost island; and ‘west’ — which is linked with the channel that separates the two main islands and ultimately leads to the continental shelf. Excursions were classified based on their duration as: (1) ‘short-term’ — when the time spent outside the study area was less than seven days; (2) ‘medium-term’ — when it was comprised between seven days and one month; and (3) ‘long-term’ — when it was longer than one month. Lastly, the degree of consistency with which fish used different sectors to exit and re-enter the study area was examined by calculating the number of excursions that had the same exit and entry sector.

2.6 Activity space

Activity space was defined as the 95% Kernel Utilization Distribution (KUDs) of each skate (i.e. a central area or volume within which an animal is 95% likely to be found) (Powell, 2000). KUDs were computed on a weekly basis using “adehabitatHR” packages in R (Calenge, 2006). We did not estimate KUDs for weeks with positions in less than four days (consecutive or non-consecutive) to eliminate bias from activity space computation based on weeks with few detection days (Leeb et al., 2021).

2.7 Environmental variables

Oceanographic conditions within and near the acoustic telemetry arrays were monitored throughout the study period. Sea levels were acquired from the tide gauge “Vigo 2” located at 42°14’24"N; 8°43’48"W (Prontuario instalaciones, 2022). Sea bottom temperature (“Temp”) was recorded every half hour using a combination of data loggers (©Star: ODDI DSTcenti-T) and Thelma acoustic receivers only used as temperature loggers and covering different depths and areas of the study array (Fig. 1d).

2.8 Statistical analysis

Along with observed environmental conditions, the day of the year (DOY: 1-366) was included in the models to explain seasonal effects. Similarly, week of the year (WOY: 1-53) was added to describe the yearly cycles in skate behaviour. 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 in R (Thieumel and Elmarhraoui, 2022).
We used Generalized Additive Mixed-effects Models (GAMMs) implemented in the R package “mgcv” to assess the relationship between independent variables and skate probability of presence as well as activity space (Wood et al., 2014, 2017; Li and Wood, 2019). In all models, individuals were handled as a random effect (via random intercept), an autoregressive term of order one (corAR1) was used since observations were made throughout time in a sequential manner (Dormann, 2007). The addition of the autoregressive term when describing weekly integrated activity space was based on a previous study demonstrating that employing weekly replicates of behavior yielded less biased repeatability estimates (Villegas-Ríos et al., 2017). Common fixed effects in the model included sex (male, female) and disc length (cm). Maximum likelihood criteria were used to fit GAMMs and a backward (decreasing number of variables) selection method was used to construct them. Non-parametric smoothing functions \( s \) were fitted with four knots to model the non-linear effect of sea bottom temperature on a day \( t \) ('Temp\(_t\)) on the residency. Day of the year ('DOY') and week of the year ('WOY') were fitted as non-parametric smoothing functions \( s \) with four knots and cyclic cubic splines.

3 Results

A total of 381,884 detections (29,344 post filtration) were retrieved from the receiver array at the end of the study period, on the 14th of June 2022. After filtering out the detections of two dead individuals that remained dead inside the array during most of the study (DESTAC-SPP-20-03 and DESTAC-SPP-20-04), we retained 29,344 detections for analysis. The number of tracking days varied greatly among skates ranging from just 3 to 160 days (Tabs. S1 and S2).

3.1 Residency

Of the 14 tagged individuals (mean disc length = 34.79 cm, range: 22–49 cm), only nine were present in the array for three or more days after the tagging date and thus included in the analyses (Tab. S1). Amongst those nine skates, two individuals were classified as dead during the study period (Fig. 2). The residence index was low, ranging from 0.005 to 0.260 (mean RI = 0.073) (Tab. S2).

The probability of presence of *R. clavata* in the study area was influenced by both biotic and abiotic factors. *R. clavata* residency in the array followed a bell curve (Fig. 3a), reaching its maximum in summer (DOY = 159). Females had a higher probability of presence in the study area compared to males (Tab. 1; Fig. 3b). Finally, there was some support (Tab. 1) for a higher probability of presence at temperatures around 15 \(^\circ\)C with a small decrease towards higher and lower temperatures (Fig. 3c).

3.2 Excursions

Over the course of the study, we identified 70 excursions. Among them, six were long-term (average duration = 175 ± 54 days), 12 were medium term (average duration = 15 ± 7 days) and 52 were short-term (average duration = 3 ± 2 days). The
number of excursions per individual ranged from 0 to 26, with a mean of 7.8 excursions per individual (Tab. S2). In the 615 days of the study, individuals exited and re-entered the study area 55 times in the direction of the Ría de Vigo (East). Interestingly, from the four sectors composing the array, the sector connecting to the West (continental shelf) was never used. High consistency was observed in the sector used to exit and re-enter the study area by *R. clavata* during excursions, with 82% (43 out of 52) of the short term excursions and 66% (8 out of 12) of the medium term excursions having the same exit and re-entry sector. Long-term excursions had less consistency with only 50% (3 out of 6) having the same exit and re-entry sector.

### 3.3 Activity space

*R. clavata* activity space in the study area ranged from 0.12 to 0.50 km² (mean AS = 0.27 ± 0.13 km²) (Tab. S2, Fig. S4). Observation of raw data based on COAs indicated a sexual
variation in activity space with females displaying a higher occupied space (0.33 ± 0.11 km$^2$) than males (0.21 ± 0.08 km$^2$) (Tab. S2). While some individuals may have utilized the entire depth range of the study array, it appeared that R. clavata had a preference for the deeper waters within the array (Fig. S4). The activity space of R. clavata had no significant diel variation, with daytime activity space (0.25 ± 0.11 km$^2$) mirroring the activity space at night (0.26 ± 0.13 km$^2$). Finally, results of the GAMM (Tab. 1) confirmed seasonal variation of the activity space of R. clavata, reaching its maximum in summer (0.25 ± 0.03 km$^2$ at WOY = 29) (Fig. 5). It is important to note that, having very few individuals present in the array in summer, this estimate is likely influenced by this small sample size.

4 Discussion

The analysis of data retrieved from nine acoustically tagged R. clavata showed significant variations in their spatial behaviour at different timescales, influenced by both biotic and abiotic factors. On average, the probability of presence in the study area for R. clavata was very low (mean RI = 0.073). The likelihood of presence was mostly affected by sex, with females being more likely to be present than males. The excursion patterns indicated a strong connection to inshore waters, specifically the Ría de Vigo. Our results showed a major increase in activity space in summer. This study provides an important baseline for understanding and linking the ecology of the vulnerable thornback skate with possible conservation actions.

The first key result of our study is that R. clavata spent very little time inside the study area. Most of the individuals left after five days or less and were not detected again. This alone suggests that small MPAs of just a few square kilometres are probably not enough to protect this species over long periods of time. It is important to point out the pronounced difference in residency between Scyliorhinus canicula RI (0.27) and R. clavata RI (0.073) in the same study area (Papadopoulo et al., 2023). An alternative explanation for the limited use of the study area by R. clavata may indicate a higher level of residence in a nearby area or to sporadic dispersal movements. For the few individuals that were detected for more than 30 days ($n = 4$), a seasonal pattern of presence was observed, with a higher presence in summer. In fact, two individuals were detected in two consecutive spring-summer seasons after being absent in winter. Although based on a small number of individuals, this may suggest a seasonal use of the study area for at least part of the population, matching the behaviour observed in another skate species in the same study area (Leeb et al., 2021). The reason why individuals of these species spend more time in the study area in spring and summer remains unknown, but it might be related to their life cycle (Chevolot, 2006). Prior studies have indicated that skates may exhibit seasonal movements, with individuals moving from deeper waters during winter, to shallower waters during spring and summer, where they are believed to mate and spawn (Walker et al., 1997; Hunter et al., 2005a). Although no egg cases of R. clavata have been reported inside the array, these seasonal patterns in skate movement could account for their migration in and out of the study area.

The second main result is the observation that space use varied seasonally. R. clavata had the highest activity space inside the array in summer and the smallest in spring. Seasonal variation in the home range of R. clavata has been observed in different studies, however, they focused on the variation in its vertical range (Hunter et al., 2005a, 2005b; Cabral, 2014). In these studies, the breeding cycle appeared to be the main driver of variation in R. clavata vertical range, thus affecting its home range (Hunter et al., 2005a, 2005b). Within the study area, another species of skate (Raja undulata) displayed a seasonal

![Fig. 4. Overview of all sectors, showing the number of exits (a) and entry (b) routes taken during the study period by Raja clavata.](image-url)
variation in activity space, although with a peak in spring and a steady decrease towards winter (Leeb et al., 2021). The main drivers of this variation were also associated with breeding cycles with R. undulata using sheltered, shallow habitats as nursery grounds. The ultimate drivers of variation of activity space in R. clavata could be related to biological needs and cycles (e.g. feeding or mating) (Hunter et al., 2005b) but compelling evidence is not available. It is worth mentioning that this study did not investigate any evidence of sex/size-related segregation patterns that could account for the observed variation in space use. Therefore, any association between seasonal variation in space use and the reproductive cycle of R. clavata should be approached with caution.

The third key result is about the patterns of excursions from and to the study area. The telemetry data revealed the many instances (70) during when R. clavata individuals travelled outside the array to later return. These observations combined with the overall low residency index suggest that R. clavata true home range extends far beyond the limit of the study area and is in agreement with previous studies conducted on two different elasmobranchs species at this site (Leeb et al., 2021; Papadopoulo et al., 2023). A previous mark-recapture study found that most adult R. clavata were recaptured within 37 km of the release site (Chevolot et al., 2006). Interestingly, R. clavata demonstrated high consistency in the sector taken to exit and re-enter the array with the majority of excursions heading to the Ría de Vigo. This result mirrors the excursion patterns of S. canicula at the same site (Papadopoulo et al., 2023) and suggests importance of the inshore waters of the Ría de Vigo for coastal elasmobranchs. Notably, although R. clavata appears to follow a specific route for entering and exiting the array, it is important to acknowledge that our approach points to the most probable direction taken after leaving the array, but it does not provide confirmation of the final destination of the excursions.

Our findings establish a significant relationship between sea bottom temperature, sex, day of the year and the probability of presence, thus contributing significantly to our understanding of animal movements and the ecological drivers of their behaviour. However, the amount of variance explained by all those factors was low (adjusted $R^2 = 0.132$). This suggests that other unaccounted biotic factors such as life cycle and abiotic factors such as habitat type, salinity or tides are also likely drivers of the presence of animals in the study area, as it has been observed in other studies (Collins et al., 2008; Heupel and Simpfendorfer, 2014; Elston et al., 2022).

Despite being limited in sample size, temporal and spatial scope, this study has provided a preliminary insight into the spatial ecology of the thornback skate in Galicia. In order to effectively manage mobile elasmobranchs, it is crucial to gather information on the factors that influence their use of space and length of stay in a certain area. In this study, we have identified two distinct patterns of movement exhibited by the thornback skate. (1) A peak of presence in the study area in summer, when their space use is at its maximum. Similar to R. clavata, R. undulata displayed a peak in its probability of presence during the summer, while its highest activity space occurred in late spring (Leeb et al., 2021). In contrast, S. canicula had the lowest probability of presence in summer and did not exhibit significant variations in its activity space throughout the year (Papadopoulo et al., 2023). (2) Mirroring S. canicula, R. clavata preferred sector for exiting and reentering the array was the sector pointing towards the Ría de Vigo. These findings highlight distinct patterns of presence and activity space among three elasmobranch species in the same area, emphasizing the importance of considering species-
specific behaviours and environmental factors in understanding their distribution and ecology. This knowledge can be useful to implement conservation strategies to better protect the thornback skate.

Further research is needed to explore the migratory patterns of thornback skates once they leave the array in the direction of the Ria de Vigo. It is important to understand their foraging habits and reproductive cycle in order to identify other areas and environmental conditions that are crucial for the completion of their life cycle. Continued research into the behavioural ecology of thornback skates is therefore necessary to allow the implementation of effective management plans around this commercially important and near threatened species of skate.

**Declaration of interest statement**

The authors report there are no competing interests to declare.

**Funding**

This work was supported by European Union's Erasmus program, Fundación Biodiversidad, DESTAC and CONECTEE.

**Acknowledgements.** K. Papadopoulo was supported by the European Union’s Erasmus+ programme. This study was funded by the projects DESTAC and CONECTEE with the collaboration of the Fundación Biodiversidad, from the Ministerio para la Transición Ecológica y el Reto Demográfico (Spanish Government), through the Pleamar program, cofounded by the FEMP and the research program of Red Parques Nacionales. The acoustic telemetry array was supported by the ATLAZUL project (0755 ATLAZUL 6_E) co-funded by the European Regional Development Fund (ERDF) through the Interreg V-A Spain-Portugal Program (POCTEP) 2014-2020. DVR has received funding from the Ramón y Cajal programme from the Spanish Ministry of Science and Innovation (RYC2021-032594-I).

**Supplementary Material**

**Table S1.** Information of all Raja clavata tagged (including the dead individual used as control) displaying their biometric parameters and tagging information. Individuals were excluded from the analysis if they had less than three detection days.

**Table S2.** Behavioural metrics of the nine individuals of Raja clavata considered in the analysis. Individual fish ID, FD: number of filtered detections, DD: detected days, TD: total tracked days, RI: residence index, AS Tot: total activity space (km²), AS day: activity space (km²) during the day, AS night: activity space (km²) during the night, Excursion: number of times an individual left and returned to the study area, : not enough data to estimate parameters.

**Figure S1.** Panel displaying: (a) Innovasea omnidirectional acoustic receiver attached to an auger anchor, screwed in the seabed (b) acoustic transmitter V13P-1x externally attached with double zip tie fixation system, (c) Raja clavata on measuring ruler marked with both T-bar tags (©Floy Tag) (left) and acoustic transmitter (right).

**Figure S2.** Time series of latitudinal and longitudinal position as well as distance travelled between consecutive centres of activity (see definition in the main text) and depth records of a discarded control dead individual of Raja clavata. The depth variation in the control individual corresponds to the tidal range.

**Figure S3.** Workflow displaying the steps taken to obtain the different parameters of Raja clavata considered in this study.

**Figure S4.** Total, day and night activity space areas for all Raja clavata based on centre of activities. Red dots symbolise ©Innovasea acoustic telemetry receiver locations and the shaded area of the activity space (KUD = kernel utilization distribution).

**Figure S5.** Total, day and night activity space areas for all Raja clavata based on centre of activities. Red dots symbolise ©Innovasea acoustic telemetry receiver locations and the shaded area of the activity space (KUD = kernel utilization distribution).

The Supplementary Material is available at https://www.alr.fr/10.1051/alr/2023017/olm.

**References**


