Seasonal movement dynamics of the commercially important thornback ray (*Raja clavata*) in a coastal marine protected area

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ARTICLE INFO

ABSTRACT

Elasmobranchs are a group of slow growing species whose populations are in decline mostly due to their susceptibility to overfishing. A common approach to protect marine species is to establish marine protected areas (MPAs). Data on the spatial ecology of species is key information for MPA implementation and management. However, this information is usually lacking, particularly for elasmobranchs. In this study, thornback rays were tagged with acoustic transmitters to track their movement patterns in a marine protected area in Portugal. Individuals were detected for up to 1323 days, and transient and resident behaviours were observed. Residents exhibited a seasonal pattern of presence, peaking during late winter and spring. Weekly occurrence range size reached its maximum from mid-summer to mid-autumn. Diel changes in movement, mainly as increases in activity, were detected during night and twilight. These findings highlight the seasonal and daily dynamics of thornback rays and how these can influence their protection in an MPA. The area where the LSMP is established appears to be dominated by males, indicating that most of the protection provided to this species is towards this sex. These results provide valuable insights for the conservation and adaptive management of this commercially relevant species.

1. Introduction

Global fishing activity has grown prominently over the last decades, driven by an increasing demand for food security and economic stability (FAO, 2020). To meet this rising need, this industry has expanded in reach, catches have increased in volume, and more people have been employed, in turn increasing pressure on marine ecosystems (FAO, 2020). Elasmobranchs (sharks, skates and rays) are largely caught as bycatch, and their captures reflect the same pattern of increased exploitation (Dulvy et al., 2021). In turn, the increase in fishing pressure has generated declines in many marine populations (McCauley et al., 2015). Most elasmobranchs are ill-equipped to withstand this pressure because of their K-selected life history strategies (Hoenig and Gruber, 1990; Musick, 1999), exhibiting extreme longevity, slow growth rates, late maturity ages and low fecundity. As a result, over a third of these species are currently threatened with extinction due to overfishing (Dulvy et al., 2021) despite various conventional management approaches that have failed to arrest their decline (Davidson et al., 2016). To this end, new approaches such as marine spatial planning have been used to help in this task.

Marine protected areas (MPAs) are a common method used to address the effects of overfishing by providing spatial protection to species and habitats (Gell and Roberts, 2003). MPAs are defined as "clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley, 2008) and can be multidimensional in their influence, benefiting areas like fisheries, human well-being, economics, knowledge development, and conservation and management (Ban et al., 2019; Lester et al., 2009). Elasmobranchs can respond positively to MPAs (Le Port et al., 2012; Speed et al., 2018), yet the effect is generally variable and often moderate (Dwyer et al., 2020; MacKeracher et al., 2019). This generally occurs because many MPAs are not specifically designed with elasmobranchs as their target and thus often fail to properly encompass their movements (Dwyer et al., 2020; MacKeracher et al., 2019).

Understanding species movement patterns is directly linked to protection success (Kramer and Chapman, 1999), and therefore a key factor

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to be assessed in the context of MPAs (MacKeracher et al., 2019). A well-suited method for this task is passive acoustic telemetry. Compared to traditional tagging methods like tag-recapture, by using acoustic telemetry the long-term movements of multiple tagged individuals can be monitored and more accurate data can be collected in a mostly automated way (Hussey et al., 2015). Acoustic telemetry has improved knowledge on space use patterns of skates, for example by providing more precise home range estimates and detecting previously unnoticed seasonal migrations and ontogenetic changes in movement (Siskey et al., 2019). This method is also very cost-effective in the long term, as an established array of acoustic receivers is of low maintenance compared to the amount of data it can provide (Heupel et al., 2006). Acoustic telemetry has been used extensively to study the movements of elasmobranchs in the context of MPAs (Elston et al., 2023; Espinoza et al., 2015; Knip et al., 2012; Lavender et al., 2021).

The thornback ray is a batoid species that reaches a maximum total length (TL) of 130 cm (Last et al., 2016) and inhabits shelves and slopes at depths between 5 and 1020 m, from Iceland, along the coast of Europe to South Africa and Madagascar, including the Mediterranean (Last et al., 2016). This species is among the most fished elasmobranchs (Carbonara et al., 2020; Figueiredo et al., 2020; Walker and Hislop, 1998); however, their catch data is likely underestimated because of a lack of historical species-specific identification in mixed-species stocks, mislabeling, unreported extraction, and discard at sea (Alves et al., 2020; Dulvy et al., 2000; Figueiredo et al., 2020). Mortality rates in the fisheries where they are captured as bycatch can be as high or higher than the targeted species (Piet et al., 2009). For example, in the North Sea, up to 71% of the standing biomass of thornback rays was estimated to be captured each year by the bottom trawl and otter trawl fisheries (Piet et al., 2009). As a result, their populations have declined in areas such as the North Sea (Walker and Hislop, 1998), the Irish and Celtic seas (Dulvy et al., 2000) and the Adriatic Sea (Krstulović Šifner et al., 2009), and are currently classified as Near Threatened by the IUCN Red List (IUCN, 2016). However, efforts to restore their stocks have been carried out in recent years, resulting in increases in biomass in areas such as the North Sea and English Channel (ICES, 2024), while signs of recovery have also been noted in the western Mediterranean (Marongiu et al., 2017; Ramírez-Amaro et al., 2020).

This species is particularly important to artisanal or small-scale fisheries of some countries, like Portugal (Figueiredo et al., 2020). Mean annual landings are estimated at around 270 tons, and an additional 1123 tons are landed as *Raja* spp. (Alves et al., 2020), but similar issues to those found elsewhere, such as multi-species fisheries, unreported catches, undocumented trips, misidentifications, make the estimation of landings of this species and other Rajiformes in Portugal a difficult task (Figueiredo et al., 2020). Nonetheless, management efforts have made it mandatory to land this species separately (i.e., as *Raja clavata*) since 2009 (EC, 2009), and established seasonal ban of their targeted capture was established during the months of May and June as well as a minimum landing size of 52 cm (Serra-Pereira et al., 2018). These actions have resulted in a stable proportion of thornback rays in the landings of some fisheries during the last decade, such as bottom trawler landings (ICES, 2022).

The Professor Luiz Saldanha Marine Park (LSMP) is a coastal MPA found off the Setúbal peninsula, Portugal. In 2010, an acoustic telemetry array was deployed in the LSMP to study the spatial ecology and protection of commercially important species of bony fishes and cuttlefish (Abecasis et al., 2014b), and four batoids (Cabral, 2014; Kraft et al., 2023b, 2024; Sousa et al., 2019). However, the study on thornback rays was based on three individuals and under two months of monitoring, thus a longer study with more individuals is warranted to answer these questions more robustly (Cabral, 2014). In this study, thornback rays were acoustically tagged and long-term movement data was collected to study their movement patterns in the LSMP and to assess the contribution of coastal MPAs to the protection of this species. To obtain a better understanding of their spatial ecology, the residency, occurrence areas, activity, and depth use of thornback rays were estimated. This information is relevant to the adaptive management of the LSMP and similar MPAs in other areas of their distribution.

2. Materials and methods

2.1. Study area

After its designation in 1998, the LSMP's first zoning actions took place in 2005 and became fully implemented (with all protection levels established) by 2009 (Portuguese legislation, Council of Ministers Resolution 141/2005). Its 53 km^2 are divided into three protection levels, a total protection area of 4.30 km^2 to which access and any kind of fishing are prohibited except when authorized for research and educational purposes; four partial protection areas of a total 21 km^2 where only octopus traps and jigging are allowed beyond 200 m from the coastline; and three partial protection areas or buffer areas of a total 28 km^2 where only local licensed fishing boats under 7 m are allowed to operate (Fig. 1). The LSMP covers 38 km of the south-western shore of the Setúbal peninsula. To the east is the Sado estuary in which a natural reserve is in place, the Reserva Natural do Estuário do Sado. Further north is the Tejo estuary, inside which the Reserva Natural do Estuário do Tejo is placed. The latter two natural reserves are RAMSAR sites (wetland sites designated of international importance under the Ramsar Convention) due to their importance for many aquatic birds and as a nursery area for several fish and invertebrate species.

2.2. Data collection and tracking

Thornback rays were captured using trammel nets (2019 and 2021) and longlines (2021 and 2022). The monofilament trammel nets were 500 m in length and 1.6 m in height, with 100 mm inner panels of stretched mesh and outer panels of 600 mm. The longlines had between 100 and 150 hooks that were baited with 2–5 cm chunks of frozen European pilchard (*Sardina pilchardus*). The fishing gears were deployed at depths between 5 and 40 m, mostly inside the full protection area, and also in the partial protection area. Deployments and retrievals were done in the morning at approximately the same time resulting in a soaking time of around 24 h. Captured individuals were brought on board and placed into a container filled with seawater that was changed after every individual. First, hooks were removed from the individuals caught by longline if possible and a hydrophone was used to detect previously tagged individuals. A measuring tape was used to obtain total length (TL), disc width, and clasper length for males. Sizes were compared to regional lengths at first maturity ($TL_{50} = 67.60$ cm for males and 78.40 cm for females, Serra-Pereira et al., 2011), to determine if the individuals were over the total length size at 50% maturity. These individuals were classified as "mature" for reference purposes, as reproductive organs were not directly inspected. To implant the acoustic transmitters, a 2 cm incision was made in the peritoneal cavity using a scalpel and then closed it using absorbable suture. Three types of Innovasea 69 kHz acoustic tags were used: V9, V13, and V9P (with pressure sensor). Respective expected battery lifetimes were 651, 1317 and 404 days according to the manufacturer. The appropriate tag size was selected based on previously deployed tag types, tag type availability, and animal size, as to not exceed the 2% tag-to-body weight rule of thumb (Winter, 1996). Additionally, each individual was fitted with a Petersen disc tag (www.floytags.com) with a unique ID number and contact information. Capture, handling, and tagging were done under permits of the Portuguese Institute for Nature Conservation and Forests (permits n°145/2019/CAPT; 13/2020/CAPT; 70/2021/CAPT; 38/2022/CAPT) and the Veterinary General Directorate (permit n° 2018-08-29 015,730). Tagging procedures were also approved by the Animal Welfare Committee of the Centro de Ciências do Mar (CCMAR - ORBEA).

Individuals were tracked using an array of 37 Innovasea VR2W
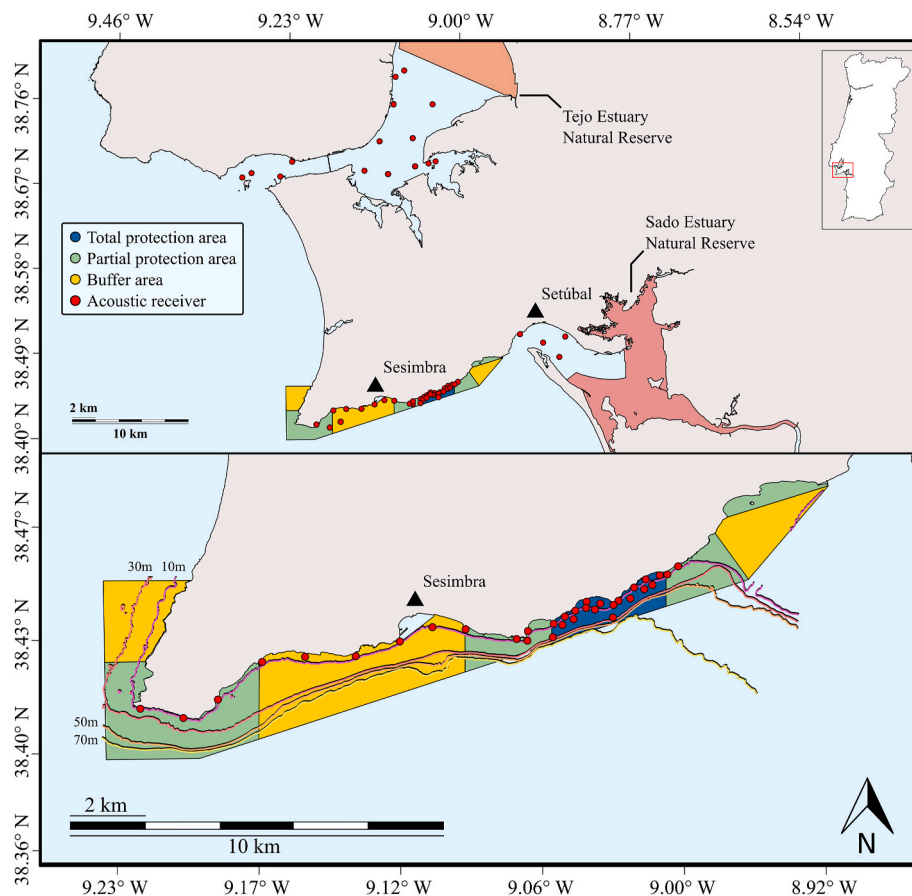
Fig. 1. Map of the study area. Top panel: general overview of the Professor Luiz Saldanha Marine Park (LSMP) and the Setúbal peninsula, with the Tejo estuary and its natural reserve (orange) to the north and the Sado estuary and its natural reserve (red) to the East. Bottom panel: LSMP and its three different protection levels. Only the aquatic portions of the Natural Reserves are shown. The bathymetry lines are colour coded.

acoustic receivers. The array was at its densest in the full protection area (19 receivers, Fig. 1). Most receivers were active throughout the study period, but some were only present for a shorter period of at least 6 months (3 receivers in the buffer area, 1 in the partial protection area and 2 in the Sado estuary), either because they were lost to rough weather conditions, or removed by fishing gear or because the structure they were attached to (e.g., a buoy) was removed from the water. Receivers were serviced once to twice a year.

2.3. Data analysis

The first 24 h of data of each individual were deleted to eliminate possible behavioural anomalies that may have been produced by the tagging process (except for residency estimation to account for their presence on the day of capture). Detection efficacy was assumed to be constant based on previous evaluations that showed no major influence from environmental variables, diel patterns and/or background noises (Abecasis et al., 2014a; Sousa et al., 2019). Detections were classified into diel phases using the R package suncalc (Thieurmel and Elmarh-raoui, 2019), setting "daytime" as the time between sunrise and sunset (appearance and disappearance of the sun over the horizon), "twilight" as morning and evening twilight, and "night" as the period between evening twilight and morning twilight.

2.3.1. Detection patterns and residency

Detection patterns were visually inspected and the fate of individuals was assessed following Villegas-Ríos et al., (2020) to identify events like emigration from the study site, post-release mortality or tag loss, and fishing mortality. A residency index (I_R) was estimated as the total number of days detected by at least one receiver (D_d) divided by the duration of the monitoring period (D_t, time between release and last data download or tag expiration): $I_R = D_d/D_t$. Tag lifetime was used instead of D_t if the latter was shorter than the total monitoring period (Abecasis et al., 2013). The presence of thornback rays in the LSMP throughout the year was evaluated using a Generalized Additive Mixed Model (GAMM) in the R package mgcv (Wood, 2011). For this, the detections were transformed to daily presence (1) or absence (0) per individual. Four models were tested using day of the year (in all models) and individual size as covariates, and individual as random effect: the first model only with day of the year, the second model with day of the year and size, the third model with day of the year and individual effect, and the fourth full model with all factors (supplementary material). Sex was not included because of the uneven sex ratio. Day of the year was modelled using a cyclic cubic spline. The best model was selected using the Akaike Information Criterion (AIC) in the R package AICcmodavg (Mazerolle, 2023). The lowest scoring model was selected, and if two or more models had similar scores (AIC <2), the simplest one was preferred. To properly investigate the long-term detection patterns in such a time frame, only individuals with detection intervals (i.e., number of days between first and last detection) of at least a year (n = 23, D_i = 350–1323 days) were used in the presence/absence GAMM to reduce the possible biases introduced by transient or fished individuals. For example, transient individuals will increase the probability of presence before leaving, and conversely, an unaccounted transient individual that leaves or an individual that is fished will artificially lower the estimated probability of presence.

2.3.2. Occurrence areas

Centers of activity (COAs) were estimated as a weighted mean position every 30 min (Simpfendorfer et al., 2002) before calculating space use areas. The dynamic Brownian bridge movement model (dBBMM) (Kranstauber et al., 2012) was implemented in the R-package move (Kranstauber et al., 2021). This is a probability distribution-based occurrence estimator that calculates the area used during the study period by reconstructing its movement path and an associated uncertainty around it. Consecutive location points are connected to create segments around which the probability of occurrence is estimated based on the distance and time difference between the pair of points, obtaining the utilisation distribution (UD). This model was chosen over other classic home range estimators because it accounts for the natural autocorrelation of movement data and because the acoustic array did not cover the entire home range of the tracked individuals (Fleming et al., 2015). A location error of 200 m was used, while window size (w = 31) and margin size (m = 11) were set to default values. Segments longer than 24 h were removed before estimating UDs to avoid unrealistic large uncertainty areas.

Weekly and total occurrence areas at the 50% and 95% levels (contours) were estimated. Weekly occurrence areas were used to evaluate changes throughout the year, implementing a GAMM in the R package mgcv (Wood, 2011). Week of the year was modelled using a cyclic cubic spline and individual was set as random effect. Four models were tested for each contour level (supplementary material): the first one only with week of the year as covariate; the second model with week of the year and size; the third model with week of the year and individual effect; and the fourth model with all variables (week of the year, size, and individual effect). All models used REML as the smoothing parameter estimation method, and a log-linked Gamma distribution was fitted as the distribution function because the response variable was positive, continuous, and right skewed. The best fitting model was chosen based on the lowest AIC value. If two or more models had similar scores (AIC <2), the simplest one was preferred.

2.3.3. Depth

Local daily tide values were obtained using the R-package PTtidaltools (Martins, 2021) to remove the effect of tides on the pressure readings by subtracting tide height from the raw depth values. The final depth values correspond to depth compared to the local lowest historical tide, which were used to calculate average depth every 10 min. Depth was evaluated in three ways: 1) throughout the year (per day of the year), 2) throughout the day (per diel phase), and 3) as vertical movements into the water column. Importantly, these depth assessments are constrained to the detection range of the array and may not reflect the true depth range occupied by the thornback rays in this area.

1) The variation of depth (response variable) throughout the year was evaluated using a GAMM as implemented in the R package mgcv (Wood, 2011). Four models were tested with day of the year (in all models) and individual size as covariates, while individual was set as random effect. The first model only contained day of the year, the second model had day of the year and size, the third model had day of the year and individual effect, and the fourth model had all factors. Sex was left out because all individuals with depth data were males. Day of the year was modelled using a cyclic cubic spline, and a log-linked Gamma as the distribution function because the response variable was positive, continuous, and right skewed. After setting up the models, the best one was selected using the AIC by selecting the lowest scoring model. If two or more models had similar scores, the simplest one was preferred (AIC <2).

2) Depth changes throughout the day were evaluated using linear mixed-effects models in the R package nlme (Pinheiro and Bates, 2023). Diel phases (daytime, night, twilight) were assigned using the R package suncalc (Thieurmel and Elmarhraoui, 2019). Diel phase was preferred over hour of the day for this analysis because with

changing sunlight hours throughout the year certain hours of the day can correspond to different diel phases, adding noise to the results; the models included depth as an autocorrelated variable, and individual and day of the year as random effects.

3) Finally, to investigate vertical movements, average depth and position every 10 min were calculated and seafloor depth at each COA was obtained using a bathymetry raster of the study area. Tag depth was then compared to seafloor depth.

2.3.4. Activity

Mean activity was estimated as minimum distance covered per time unit (hereon, step length) between successive COAs in a straight line using the R package adehabitatLT (Calenge, 2006). Estimations were done as a global mean and per diel phase. Step lengths of 30 min were retained and discarded those of longer duration (i.e., 60 min or more) as these had detection gaps (no detections for 30 min or more) and were therefore more likely to also include movements outside of the marine park.

3. Results

3.1. Tagging and detection data

Thirty-five thornback rays were tagged with a sex ratio skewed towards males (29 vs. 6, two-tailed binomial test, p < 0.01). For individuals Rc 01 to 11 only disc width was measured, so their total length was estimated based on the size conversion factors of Serra-Pereira et al., (2010). Average disc width was 49.26 cm and ranged between 33.50 and 61.00 cm disc width, and average total length (TL) was 72.79 cm and ranged between 45.00 and 86.18 cm (Table 1). Male disc width averaged 49.41 cm (range 33.50–58.00 cm) and total length averaged 73.57 cm (range 47.18–93.00 cm), while the disc width of females averaged 48.00 cm (range 38.00–61.00 cm), while total length averaged 69.01 cm (range 45–93.00 cm). Comparing our sizes to regional lengths at first maturity (TL_{50} = 67.60 cm for males and 78.40 cm for females, Serra-Pereira et al., 2011), three of six females (50%) and 21 of 29 males (72%) were over the total length size at 50% maturity (Table 1). These individuals were classified as "mature" for reference purposes, as there was no direct visual inspection of the reproductive organs. Individuals Rc 22 and 23 were classified as deceased based on their detection patterns and subsequently removed; of the 33 remaining individuals, 14 dispersed at some point during the study and 19 were detected throughout the entire study period or expected battery lifetime. Of the eight individuals that were released with the hook still in, five survived, two dispersed, and one died (Rc 23). An average of 785 ± 375 days of monitoring and a detection interval of 477 ± 408 days were obtained per individual (Table 1).

3.2. Detection patterns and residency

Different residency patterns were noted among individuals (Fig. 2). Some individuals were steadily detected (e.g., Rc 07, Rc 13), while others had detection intervals of similar length but presented large detection gaps in-between (e.g., Rc 02, Rc 33). Some individuals were infrequently detected over long periods (e.g., Rc 03, Rc 32), while others permanently left the array shortly after tagging (e.g., Rc 08, Rc 09, Rc 19).

Average residency was I_R = 0.38 (range I_R = 0.00–0.99) and markedly contrasted between sexes, with a much higher average for males than females (I_R = 0.46 vs. 0.05) (Table 1). Two general detection patterns were seen among females. Three were detected sporadically over long detection intervals (Rc 11, 12 and 14, respective D_i = 674, 242, 507) and had residency indexes between I_R = 0.07–0.14, while the other three (Rc 17, 19 and 26) were detected only in their tagging day and had a residency index of I_R = 0.00. The female with the highest residency index (Rc 11) was detected in 188 different days over a

Table 1

Summary data of the tagged individuals (asterisks by the name indicate individuals with V9P pressure tags), including biological data on sex (M = males, F = females) and maturity based on length (in cm); residency indices (D_d = days detected, D_i = detection interval, D_t = monitoring time (all in number of days), I_R = residency index; dynamic Brownian bridge movement model (dBBMM) occurrence areas at the 50% and 95% (in km²); and individual fish fate following Villegas-Ríos et al., (2020). Asterisks in total length indicate measurements obtained using disc width and the size conversion factors of Serra-Pereira et al. (2010). Asterisks in tag duration indicate tags that completed their expected lifetime during the study.

R. clavata n°	Sex	Maturity	Disc width (cm)	Total length (cm)	Tagging date	Tag duration	Exp. Date/last data download	D_d	D_i	D_t	I_R	dBBMM (km²) 95%	dBBMM (km²) 50%	Fish fate
01	M	Mature	52.00	77.27*	30/03/2019	1317*	06/11/2022	183	215	1317	0.14	1.93	0.32	Dispersed
02	M	Immature	46.00	65.81*	30/03/2019	1317*	06/11/2022	937	1323	1317	0.71	2.14	0.24	Survived
03	M	Immature	33.50	47.18*	02/04/2019	651*	12/01/2021	9	429	651	0.01	0.00	0.00	Survived
04	M	Immature	46.80	67.95*	03/04/2019	1317*	10/11/2022	1177	1225	1317	0.89	1.39	0.19	Survived
05	M	Immature	46.50	66.52*	03/04/2019	1317*	10/11/2022	471	1263	1317	0.36	1.48	0.16	Survived
06	M	Mature	48.00	68.67*	20/10/2019	1317	18/05/2023	986	1306	1306	0.75	0.96	0.21	Survived
07	M	Immature	45.00	64.38*	21/10/2019	1317	18/05/2023	1159	1306	1305	0.89	1.94	0.38	Survived
08	M	Mature	58.00	86.18*	21/10/2019	1317	18/05/2023	1	1	1305	0.00	–	–	Dispersed
09	M	Mature	56.00	83.21*	21/10/2019	1317	18/05/2023	2	4	1305	0.00	0.59	0.13	Dispersed
10	M	Immature	47.00	67.24*	22/10/2019	651*	03/08/2021	636	657	651	0.98	2.14	0.26	Survived
11	F	Mature	61.00	85.08*	22/10/2019	1317	18/05/2023	188	674	1304	0.14	1.54	0.24	Dispersed
12	F	Immature	38.00	56.00	06/04/2021	651*	17/01/2023	48	242	651	0.07	2.93	0.50	Dispersed
13	M	Mature	47.00	73.00	06/04/2021	1317	18/05/2023	762	773	773	0.99	1.19	0.20	Survived
14	F	Mature	54.00	81.00	06/04/2021	1317	18/05/2023	63	507	773	0.08	1.08	0.18	Dispersed
15	M	Mature	51.00	77.00	06/04/2021	1317	18/05/2023	228	773	773	0.29	4.29	0.42	Survived
16	M	Mature	51.00	78.00	06/04/2021	1317	18/05/2023	36	50	773	0.05	1.17	0.23	Dispersed
17	F	Immature	38.00	54.00	06/04/2021	651*	17/01/2023	1	1	651	0.00	–	–	Dispersed
18	M	Mature	50.00	75.00	07/04/2021	1317	18/05/2023	81	490	772	0.10	4.07	0.72	Dispersed
19	F	Immature	37.00	45.00	09/04/2021	651*	20/01/2023	1	1	651	0.00	–	–	Dispersed
20	M	Immature	42.00	57.00	20/05/2021	1317	18/05/2023	350	350	729	0.48	1.46	0.28	Dispersed (hook in)
21	M	Mature	58.00	83.00	20/05/2021	1317	18/05/2023	622	728	729	0.85	2.80	0.38	Survived
22	M	Mature	52.00	80.00	20/05/2021	404*	28/06/2022	–	–	–	–	–	–	Deceased
23	M	Mature	57.00	71.00	20/05/2021	651*	02/03/2023	–	–	–	–	–	–	Deceased (hook in)
24*	M	Mature	53.00	69.00	13/10/2021	404*	21/11/2022	401	409	404	0.99	2.27	0.22	Survived
25*	M	Immature	44.00	64.00	14/10/2021	404*	22/11/2022	158	322	404	0.39	1.91	0.21	Survived (hook in)
26	F	Mature	60.00	93.00	15/10/2021	1317	24/05/2025	1	1	1317	0.00	–	–	Dispersed (hook in)
27*	M	Mature	49.00	71.00	03/05/2022	404	18/05/2023	228	373	381	0.60	3.79	0.65	Survived
28*	M	Mature	54.00	86.00	03/05/2022	404	18/05/2023	318	379	381	0.83	4.22	0.59	Survived
29	M	Mature	48.00	82.00	04/05/2022	651	18/05/2023	103	378	380	0.27	2.94	0.32	Survived (hook in)
30*	M	Mature	50.00	80.00	04/05/2022	404	18/05/2023	164	369	380	0.43	1.61	0.32	Survived
31*	M	Mature	47.00	80.00	04/05/2022	404	18/05/2023	206	372	380	0.54	3.07	0.42	Survived (hook in)
32	M	Mature	54.00	78.00	04/05/2022	651	18/05/2023	79	331	380	0.21	2.91	0.53	Survived (hook in)
33	M	Mature	53.00	78.00	04/05/2022	651	18/05/2023	86	313	380	0.23	3.31	0.65	Survived (hook in)

Table 1 (*continued*)

R. clavata n°	Sex	Maturity	Disc width (cm)	Total length (cm)	Tagging date	Tag duration	Exp. Date/last data download	D_d	D_i	D_t	I_R	dBBMM (km²) 95%	50%	Fish fate
34	M	Mature	48.00	80.00	04/05/2022	651	18/05/2023	128	148	380	0.34	2.33	0.33	Dispersed
35	M	Mature	46.00	77.00	04/05/2022	651	18/05/2023	8	16	380	0.02	1.69	0.32	Dispersed
Total	35	24 mat, 11 imm.	49.26	72.79		933		298	477	785	0.38	2.18	0.33	
Males	29	21 mat, 8 imm.	49.41	73.57		913		353	530	762	0.46	2.21	0.33	
Females	6	3 mat, 3 imm.	48.00	69.01		984		50	238	891	0.05	1.85	0.31	
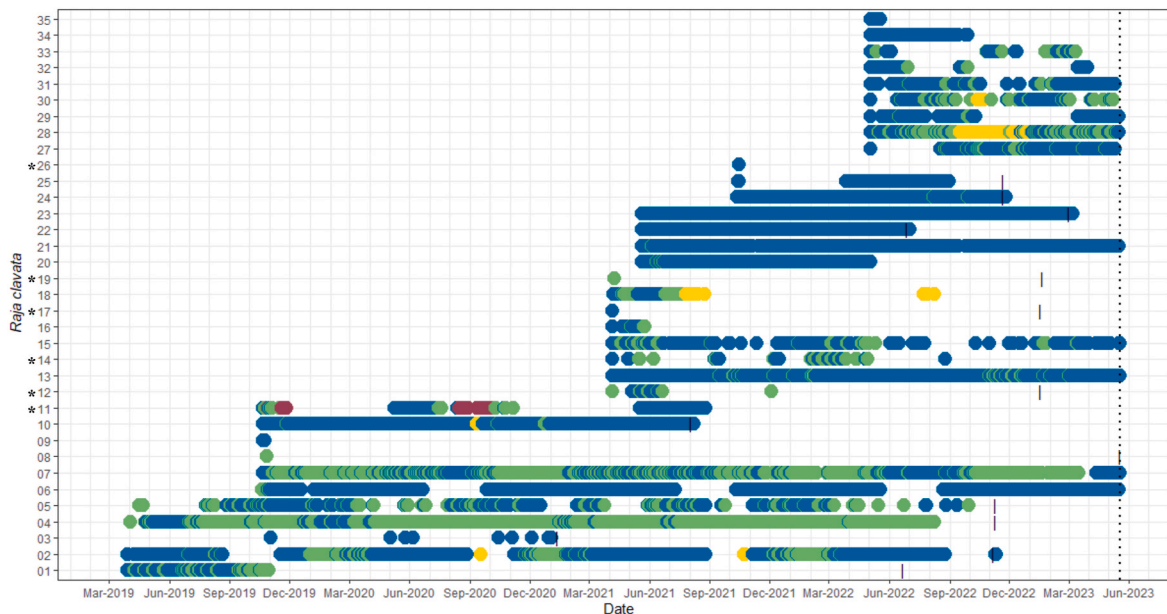
Fig. 2. Abacus plot of thornback ray detections, colour-coded by area: total protection area (blue), partial protection area (green), buffer area (yellow) and Sado estuary (red). Vertical solid dashes indicate expected battery expiration dates, and the dotted vertical line marks the end of the study period. Asterisks by individual names indicate females.

monitoring period of 1317 days.

Average residency between tagging years (2019 and 2021) did not vary significantly ($I_{R, 2019} = 0.44$, $I_{R, 2021} = 0.33$: ANOVA, F = 0.29, p 0.75). Disc width was not correlated with residency (r(31) = 0.03, p = 0.87).

Five males were detected in the buffer area in front of the port of Sesimbra. Four were detected in this area between days of the year 200 and 300 (mid-July to late October). These detections occurred in consecutive years in the cases of Rc 02 and Rc 18. The start of the detection window of Rc 28 in the buffer area overlapped with the window of the other individuals, but extended to December and the first days of January. One mature female (Rc 11) was seasonally detected in Sado in two consecutive years, between late October and late November in 2019 and mid-August to early October in 2020 (supplementary material). No individuals were detected in the Tejo estuary.

The best GAMM model for describing the presence of thornback rays in the LSMP included the effects of day of the year and individual factors (AIC 14769.61). The probability of presence of thornback rays varied throughout the year, as there was a significant effect of day of the year (GAMM: edf = 7.26, Chi.sq = 30,794), and as well as of individual variability (GAMM: edf = 21.89, Chi.sq = 4470), both with p < 2e-16. The deviance explained by the model was 38%. Probability of presence varied between approximately 0.29–0.71. Its highest value was observed during late winter and throughout spring, after which it

decreased during summer to its lowest at the beginning of autumn. Then it started increasing again throughout autumn and winter, with a period
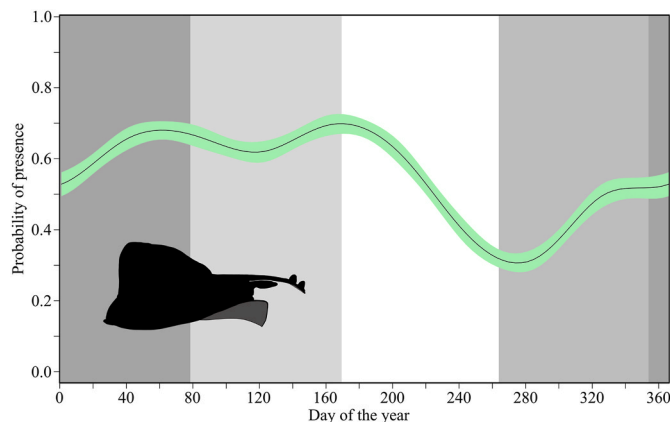

Fig. 3. Predicted probability of presence of thornback rays in the LSMP throughout the year. Included were individuals with around a year or more of data (n = 23). The area in green represents the 95% confidence interval. Grey shading represents seasons of the year (from left to right: winter, spring, summer, autumn, winter).

of stability at around 0.50 from late autumn to early winter (Fig. 3).

3.3. Occurrence area

Total and weekly occurrence areas were calculated for 29 of the 33 available individuals, as four individuals were excluded due to insufficient detections (Rc 08, 17, 19 and 26, and Rc 03 for the calculation of occurrence area per diel phase). The total occurrence areas averaged 0.33 km^2 (range 0.00–0.72 km^2) at the 50% level and 2.18 km^2 (range 0.00–4.29 km^2) at the 95% level. The contours of all areas were located inside the partial and full protection areas, except for an isolated segment of the 95% contour of Rc 18, which fell in the buffer area. Rc 28 was also frequently detected in the buffer area, but none of its occurrence areas included this protection level (Fig. 2). Per diel phase, the respective average 50% and 95% total occurrence areas were 0.30 and 1.82 km^2 for daytime, 0.43 and 2.00 km^2 for night-time and 0.28 and 1.68 km^2 for twilight.

Total occurrence area did not significantly correlate with disc width at the 50% (r(27) = 0.22, p = 0.26) or 95% levels (r(27) = 0.24, p = 0.23). To evaluate sex-based differences, a two-tailed Welch's *t*-test of uneven variances was used because of the uneven sex ratio (n = 26 vs. 3). No statistically significant differences were obtained for either 50% (Welch's *t*-test; t = 0.26, p = 0.81) or 95% area estimations (Welch's *t*-test; t = 0.61, p = 0.60).

The weekly occurrence area GAMM that best fit the data did not include size and included individual as random effect (AIC = −1895.06 for 50% and AIC = 3810.53 for the 95% level, supplementary material). In this model, week of the year significantly influenced the occurrence areas (50%: GAMM: edf = 3.49, F = 3.57, p = 1.41e-05 and 95%: GAMM: edf = 4.544, F = 3.89, p = 6.76e-07). Individual effect was also significant for both contour levels with p < 2e-16 (GAMM results for 50%: edf = 22.20, F = 12.39; for 95%: edf = 20.17, F = 7.17). The deviance explained was 20.5% for the 50% weekly occurrence area and 14.8% for the 50% areas. Weekly occurrence area decreased from the beginning of the year to its lowest in spring, between mid-April and May. After this point, areas increased and reached their highest point in late summer and early autumn, to then start decreasing again towards the end of the year (Fig. 4).
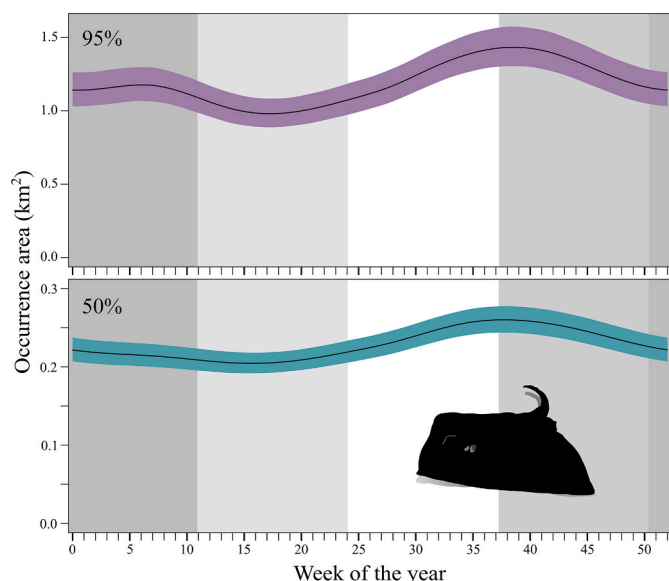

Fig. 4. Occurrence area of thornback rays in the LSMP throughout the year. Predicted probability of the change in weekly occurrence area at the 50% (green) and 95% level (purple). Coloured area indicates the confidence intervals, and the shaded background indicates the seasons of the year (in order from left to right: winter, spring, summer, autumn, winter).

3.4. Depth

Six of the seven V9P tags yielded between 158 and 401 days of depth data. Depths ranged between 0.50 and 74.90 m, close to the tag's depth sensor limit of ~76 m. Of all depth readings, only 129 were shallower than 5 m; these were obtained from five of the six individuals: Ra 24 (8.50% of readings), Ra 25 (1.60%), Ra 27 (3.20%), Ra 28 (28.80%) and Ra 31 (60.80%). All individuals but Rc 25 were detected deeper than 60 m (max. depth of Rc 25 = 38 m).

Per diel phase, all individuals were deeper during daytime than twilight and the night. All individuals except Rc 25 were found at their shallowest during the night (Table 2). The linear mixed-effects model indicated a significant effect of diel phase on depth. With daytime as reference level (estimate = 19.26), the coefficients for twilight and night were respectively −1.00 and −0.94, predicting that they occur shallower in these diel phases and particularly at night. Post-hoc tests showed statistically significant differences between daylight and both twilight (difference = 1.00, p < 0.01) and night (difference = 0.94, p < 0.01), and not between night and twilight (difference = −0.60, p = 0.21).

The best scoring GAMM included day of the year and individual as random effect (AIC = −12279.71, supplementary material). Day of the year had a significant effect on depth (GAMM edf: 6.29, F = 52.48, p < 2e-16) and so did individual effect (GAMM edf: 4.89, F = 46.10, p < 2e-16). Deviance explained was 38%. The GAMM predicted an increase in depth from day of the year 1 until around day 250 (early September), the deepest point in the year. Depth did not decrease uniformly: it declined steadily until day 120 (end of April-beginning of May) and then slightly increased until around day 180 (end of June), to then abruptly decrease until about day 250. Depth then increased rapidly until the end of the year. The shallowest depths were attained from late December to early February (Fig. 5).

3.5. Activity

Two individuals were removed for having an insufficient number of steps (Rc 03, 5 steps; Rc 09, 28 steps). Overall, Rc 32 presented the highest step length average (127.22 m), and Rc 06 the lowest (27.16 m) (Fig. 6). Per diel phase, the depth of all individuals combined was on average highest during the night (86.22 m) followed closely by twilight (82.47 m) and lastly by daytime (60.81 m). Conversely, most individuals recorded their highest average during the night (n = 15), followed by twilight (n = 9), and day (n = 3), while most recorded their lowest averages during the day (n = 22), followed by night (n = 3) and twilight (n = 2).

4. Discussion

Understanding the effects overexploitation has on fish populations is a necessary step to address its ecological, economic, and social consequences (FAO, 2020). Thirty-five thornback rays were tracked to improve the understanding of their movement patterns and to obtain results on their long-term residency, diel changes in occurrence area and activity, and (although limited) depth use. To our knowledge, this is the first long-term study to track this species in southern Europe, as most are from the English Channel. This provides movement data for a region with different environmental conditions, hydrology, and fishing pressure, which is valuable to inform local management decisions in the LSMP and other similar coastal MPAs.

4.1. Space use

4.1.1. Seasonal space use

In general, thornback rays were mostly detected in the full and partial protection areas. Few individuals (n = 6, 18% of tagged individuals) were detected in either the buffer areas or the Sado estuary,

Table 2

Minimum, maximum, and median depth of each thornback ray with an Innovasea V9P tag, per diel phase and overall.

| Raja clavata	Daytime			Twilight			Night			Total		
	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median
24	8.55	73.80	15.10	3.71	69.70	14.80	2.33	73.90	13.80	2.33	73.90	14.60
25	11.20	37.70	16.80	7.00	29.80	16.40	4.74	29.20	16.40	4.74	37.70	16.60
27	7.24	74.90	20.30	4.72	74.80	17.40	4.26	73.20	15.20	4.26	74.90	17.10
28	9.45	45.40	24.30	2.31	52.60	17.90	0.53	61.70	15.70	0.53	61.70	20.00
30	6.34	56.30	19.40	7.70	56.70	17.70	5.32	69.20	16.90	5.32	69.20	18.10
31	4.55	74.40	15.10	4.45	34.20	13.70	1.09	53.90	13.30	1.09	74.40	14.00
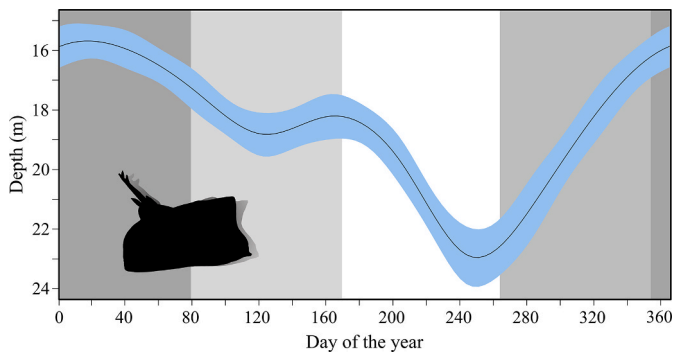
Fig. 5. Depth variation of thornback rays in the LSMP throughout the year. Result of the General Additive Mixed Model assessing how depth varies throughout the year. Confidence interval shown in blue. Grey shading represents seasons of the year (from left to right: winter, spring, summer, autumn, winter).

which could be at least partially attributed to the lower receiver coverage. The detections obtained from the five individuals in the buffer area indicate that there might be recurrence in these movements, as two individuals were detected there at similar times of the year (i.e., after the 200th day of the year) in two consecutive years, and three additional individuals were detected once but at a similar time of the year. The female that was detected in Sado also presented a similar pattern over two consecutive years. However, to more robustly assess this, receiver coverage would need to be increased in the buffer areas and Sado.

Although the results of the resident individuals suggest that the presence of thornback rays in the LSMP fluctuates with the seasons of the year, they were still in the LSMP throughout the year and presence never decreased to 0, for example as noted for *Dasyatis pastinaca* (Kraft et al., 2023b). This, and the general variability observed in detection patterns (i.e., transient and resident individuals) is a characteristic of populations that present partial migration, which has been reported in elasmobranchs as well, but has been seldomly investigated (Chapman et al., 2012, 2015).

This seasonal pattern resembles findings from other areas of the North Atlantic, although the function is unclear. For example, thornback rays in the Bay of Douarnenez (France) move into shallower waters in early spring to mate (Rousset, 1990). A similar increase in presence was seen between March and August in the Thames estuary (United Kingdom), to then return to deeper waters during autumn and winter (Hunter et al., 2006), although in the western English Channel they appear to remain inshore year-round (Humphries et al., 2016). A
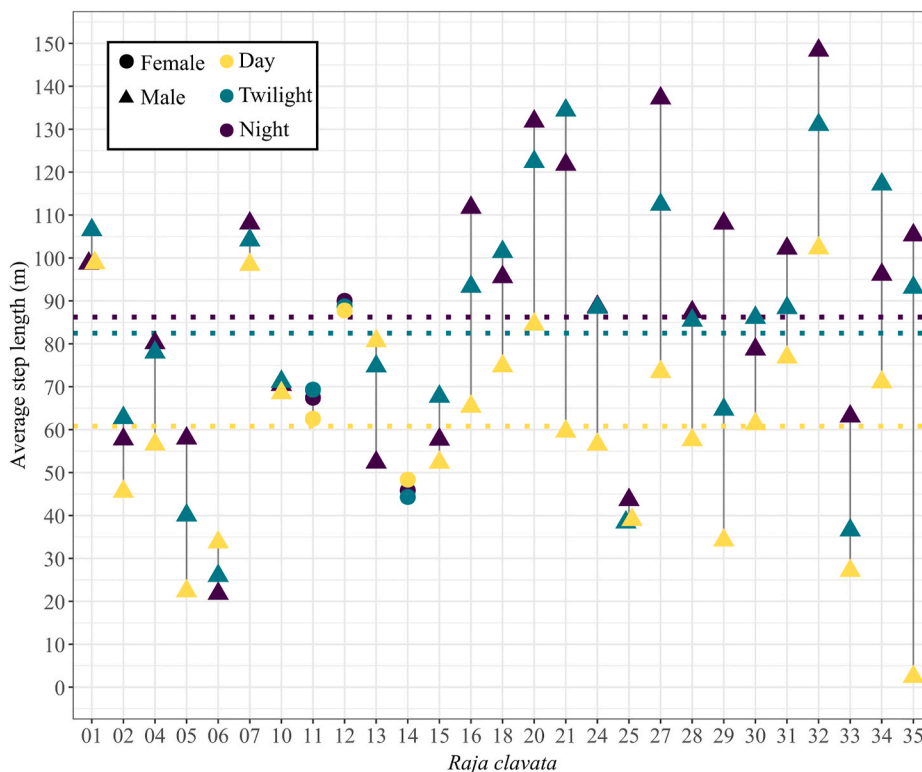
Fig. 6. Average step length per thornback ray per diel phase. Averages represent the distance covered per 30 min per diel phase per individual. Dotted lines indicate the average distance per diel phase: day (60.81 m), night (86.22 m), and twilight (82.47 m).

seasonal presence was also described off the northwest Iberian Peninsula in Spain, with a high point in summer (Papadopoulo et al., 2023).

4.1.2. Diel space use

Before discussing these results, an important difference between the present study and other studies that have investigated depth distribution in this species, e.g., (Humphries et al., 2016; Hunter et al., 2006), needs to be highlighted. In the present study, the estimation of depth was limited to the detection range of the array and tag depth (pressure) sensor limit of ~76 m. Other studies have used data storage tags (DSTs) (Humphries et al., 2016; Hunter et al., 2006), which are not constrained to an acoustic array and provide a more fitting alternative to study the depth preferences of these species. Consequently, our approach restricted our survey to the shallow end of the depth distribution of thornback rays, which can reach up to 1000 m in many areas (Last et al., 2016). Therefore, although thornback rays can restrict their occurrence to shallow waters (e.g., Humphries et al., 2016), the underestimation of depth preferences cannot be ruled out in this study, limiting our interpretations to their movements within the array.

The diel changes in activity and depth displayed by the thornback rays are shared with several elasmobranchs (Hammerschlag et al., 2016). Diel vertical migrations or nocturnal ascent has been described for thornback rays and other skates in the genus *Raja* (Humphries et al., 2017; Poos et al., 2023; Speed et al., 2010; Wearmouth and Sims, 2009). This can function as a strategy to forage, as well as a predator avoidance strategy seen in central place foragers like many batoids, with which shallow productive feeding grounds are traded for deeper and safer areas (Humphries et al., 2017).

However, the diel changes in activity and in occurrence area in our study did not completely correlate; despite the increase in activity during all dark periods, occurrence area was greater in daytime than twilight. Although many elasmobranchs become more mobile during the night and twilight, reflected as increased activity and area of use (Hammerschlag et al., 2016; Humphries et al., 2017), the consistency of this as a general pattern in elasmobranchs is still to be demonstrated (Hammerschlag et al., 2016). A possible explanation for this result could be the coverage of the acoustic array. If it is not accurately covering the occurrence area of these individuals, the estimation of how changes across diel phases could be affected (i.e., the array is capable of assessing changes in activity, but not occurrence area).

4.1.3. Sexual segregation

Combining the 195 males and 123 females captured in this and in a previous study in this area (Martínez-Ramírez et al., 2021) results in a total male-biased sex ratio of 1.6:1. Although this is more balanced than our study (29:6, or 4.8:1), it still deviates from an expected 1:1 ratio (binominal test, p < 0.01). The sampling in these studies was conducted in different seasons (mainly spring and autumn), which lowers the likelihood of a seasonal bias. Additionally, our results showed that females were not only less abundant but also spent over nine times less time within the protected area than males ($I_R = 0.05$ vs. 0.46).

These factors suggest that thornback rays may be sexually segregated, with the frequency of females increasing with depth. Depth-related sexual segregation has been reported for thornback rays before. For example, between Ericeira (West coast of Portugal, app. 100 km north of the LSMP) and Nazaré (app. 39° 36′ N, 9° 04′ W) females were more abundant closer to shore and males became more dominant deeper than 100 m (Serra-Pereira et al., 2014). Females also had an overall higher presence in the Azores (1:1.61) (Santos et al., 2021). In other areas, females have reported to be more abundant in the northwest Iberian Peninsula (Papadopoulo et al., 2023), in the Thames, England (Hunter et al., 2005), the Western English Channel (Simpson et al., 2021), and other areas of Ireland and the British Isles well (Day, 1880). In other areas like the Bay of Douarnenez, France (Rousset, 1990) and the Gulf of Gabès, central Mediterranean (Kadri et al., 2014), males were more common and females increased in abundance in deeper waters.

This kind of population distribution in skates can arise from several factors, for example from physiological differences between sexes that result in distinct diet and habitat requirements, or from females seeking to avoid male harassment (Simpson et al., 2021). In connection with the previous comments on the depth limitations in this study, this could be further investigated by tagging females with data logging tags like pop-up satellite archival tags (PSATs) or DSTs to evaluate their depth preferences.

4.2. Conservation and management

A better understanding of the movement patterns of a species can directly benefit spatial protection efforts like MPAs by using this data to inform management and conservation decisions (Knip et al., 2012). Information on the spatial ecology of a species is important for this process, as it provides an idea of how the spatial characteristics of an MPA (e.g., size and position) influence protection and mitigate risk exposure (Abecasis et al., 2014b; Papadopoulo et al., 2023; Villegas-Ríos et al., 2021).

The LSMP's reserve effect on soft bottom fish species was assessed by two studies using fishing surveys (Martínez-Ramírez et al., 2021; Sousa et al., 2018). While both found a statistically significant increase in thornback ray biomass over time, only one detected a significant increase in abundance, size, and a positive reserve effect (Sousa et al., 2018). Although reserve effect might be a long process for species of slow life history traits and large sizes like most elasmobranchs (Martínez-Ramírez et al., 2021; Sousa et al., 2018), spatial closures have been regarded as an effective management strategy for thornback rays, especially during their reproductive season (Hunter et al., 2006; Wiegand et al., 2011). Other protection measures have also been instituted. A seasonal closure is established during May and June, contributing to the protection of this species by prohibiting the capture of skates in mainland Portugal (Portaria no 315/2011 and Portaria no 47/2016). A minimum landing size of 52 cm in total length was also introduced (Serra-Pereira et al., 2018). Considering the higher number of thornback ray males and their higher residency, males may be better protected than females in the LSMP. This is important to consider for the management of the marine park, as sexual segregation can result in uneven protection (Mucientes et al., 2009). The protection of large females is prioritized in the management of many elasmobranch fisheries because of their reproductive potential and the dependence populations have on them to recover (Dell'Apa et al., 2014; Wearmouth and Sims, 2008). It is important to acknowledge these intra-specific differences to obtain a more realistic estimation of the protection MPAs provide.

The LSMP's full protection area and the two adjacent partial protection areas provide a combined 11.09 km^2 of continuous protection to thornback rays and other elasmobranchs, as these species are not affected by the activities allowed in these protection levels. This combined surface is almost 3 times the largest total 95% occurrence area estimate, and almost 6 times the total average. However, the LSMP can be as narrow as 450 m in this protected segment, which increases their chances of reaching or crossing the border. Because risk increases with greater proximity to the border when inside the protected area, the position of the occurrence areas of thornback rays in relation to the MPA's border is relevant as well (Villegas-Ríos et al., 2021).

In this sense, offshore movements could pose as a greater risk source compared to movements along the coast, exposing them to factors like edge effect (Ohayon et al., 2021) and fishing the line (Kellner et al., 2007). Similarly, the observed diel changes in movement, of greater activity during night and twilight, could also indicate an increase in the chances of nearing or crossing an MPA's border and of encountering passive fishing gear, which are usually set for 24 h (Hammerschlag et al., 2016; Uusiheikkila et al., 2008).

Risk exposure can also change inside the marine park if it has different protection levels (Abecasis et al., 2014b). Ventures of thornback rays into the buffer area also expose them to fishing, as activities

that could catch them are permitted in this protection level. The restricted time period in which individuals were detected there may suggest that this source of risk is seasonal, although this remains to be better assessed. The effectiveness of measures like temporal gear restrictions, despite increasing MPA's efficacy (Simpson et al., 2020), also remain to be evaluated. This is required to properly estimate the number of individuals that move into this area and gauge the effect such restrictions could have on other goals of the LSMP, which could be addressed in future studies.

Throughout the year, thornback rays seemed to be best protected during late winter and spring, as the simultaneous higher presence, smaller occurrence areas, and shallow depth suggest a restriction of their movements to around the coastal area of the LSMP. After spring, and especially after mid-summer, occurrence areas expanded and the presence of thornback rays decreased in the MPA, suggesting they gradually start making use of larger areas as summer progresses, which likely drives them out of the protected area. An example of this is the detection of a mature female in the Sado estuary in two consecutive years. To investigate the longer-distance movements, use of nearby areas, and true depth preferences of this species (i.e., not constrained to the detection range of the array and the acoustic tag's depth limit), additional tagging technologies such as PSATs and DSTs could be employed. This could contribute to the evaluation of the impact of and placement of additional protection areas to support the protection of this species.

Contributions

DA and SK conceptualized and designed the study. SK, ACW and DA captured and tagged the individuals of this study and acquired the data. SK, ACW and DA maintained the receiver network. SK conducted the analyses, prepared the figures for publication, and drafted the article. SK, ACW and DA interpreted the data. SK, ACW and DA revised it critically for important intellectual content. All authors approved the final article.

Funding

CRediT authorship contribution statement

S. Kraft: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **A.C. Winkler:** Writing – review & editing, Investigation, Data curation. **D. Abecasis:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation.

Declaration of Generative AI and AI-assisted technologies in the writing process

No Generative AI and AI-assisted technologies were used to write this manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2024.107210.

References

Abecasis, D., Afonso, P., Erzini, K., 2014a. Can small MPAs protect local populations of a coastal flatfish, *Solea senegalensis*? Fish. Manag. Ecol. 21, 175–185. https://doi.org/10.1111/fme.12061.

Abecasis, D., Afonso, P., Erzini, K., 2014b. Combining multispecies home range and distribution models aids assessment of MPA effectiveness. Mar. Ecol. Prog. Ser. 513, 155–169. https://doi.org/10.3354/meps10987.

Abecasis, D., Bentes, L., Lino, P.G., Santos, M.N., Erzini, K., 2013. Residency, movements and habitat use of adult white seabream (*Diplodus sargus*) between natural and artificial reefs. Estuar. Coast Shelf Sci. 118, 80–85. https://doi.org/10.1016/j.ecss.2012.12.014.

Alves, L.M.F., Correia, J.P.S., Lemos, M.F.L., Novais, S.C., Cabral, H., 2020. Assessment of trends in the Portuguese elasmobranch commercial landings over three decades (1986–2017). Fish. Res. 230, 105648 https://doi.org/10.1016/j.fishres.2020.105648.

Ban, N.C., Gurney, G.G., Marshall, N.A., Whitney, C.K., Mills, M., Gelcich, S., Bennett, N. J., Meehan, M.C., Butler, C., Ban, S., Tran, T.C., Cox, M.E., Breslow, S.J., 2019. Well-being outcomes of marine protected areas. Nat. Sustain. 2, 524–532. https://doi.org/10.1038/s41893-019-0306-2.

Cabral, S., 2014. *Raja* Spp. Spatial Dynamics in the Arrábida Marine Park (M. Sc. Thesis). Universidade do Algarve.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017.

Carbonara, P., Bellodi, A., Palmisano, M., Mulas, A., Porcu, C., Zupa, W., Donnaloia, M., Carlucci, R., Sion, L., Follesa, M.C., 2020. Growth and age Validation of the thornback ray (*Raja clavata* linnaeus, 1758) in the south Adriatic Sea (central mediterranean). Front. Mar. Sci. 7, 586094 https://doi.org/10.3389/fmars.2020.586094.

Chapman, B.B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P.A., Hansson, L.-A., Brönmark, C., 2012. Partial migration in fishes: definitions, methodologies and taxonomic distribution. J. Fish. Biol. 81, 479–499. https://doi.org/10.1111/j.1095-8649.2012.03349.x.

Chapman, D.D., Feldheim, K.A., Papastamatiou, Y.P., Hueter, R.E., 2015. There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. Ann. Rev. Mar. Sci 7, 547–570. https://doi.org/10.1146/annurev-marine-010814-015730.

Davidson, L.N.K., Krawchuk, M.A., Dulvy, N.K., 2016. Why have global shark and ray landings declined: improved management or overfishing? Fish Fish. 17, 438–458. https://doi.org/10.1111/faf.12119.

Day, Francis, 1880. The Fishes of Great Britain and Ireland. Williams and Norgate, London, pp. 1880–1884.

Dell'Apa, A., Cudney-Burch, J., Kimmel, D.G., Rulifson, R.A., 2014. Sexual segregation of spiny dogfish in fishery-dependent surveys in cape cod, Massachusetts: potential management benefits. Trans. Am. Fish. Soc. 143, 833–844. https://doi.org/10.1080/00028487.2013.869257.

Dudley, N. (Ed.), 2008. Guidelines for Applying Protected Area Management Categories. IUCN, Gland, Switzerland.

Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G., Reynolds, J., 2000. Fishery stability, local extinctions, and shifts in community structure in skates. Conserv. Biol. 14, 283–293.

Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., Herman, K.B., Sherman, C.S., VanderWright, W.J., Lawson, J.M., Walls, R.H.L., Carlson, J.K., Charvet, P., Bineesh, K.K., Fernando, D., Ralph, G.M., Matsushiba, J.H., Hilton-Taylor, C., Fordham, S.V., Simpfendorfer, C.A., 2021. Overfishing drives over one-third of all

sharks and rays toward a global extinction crisis. Curr. Biol. 31, 4773–4787.e8. https://doi.org/10.1016/j.cub.2021.08.062.

Dwyer, R.G., Krueck, N.C., Udyawer, V., Heupel, M.R., Chapman, D., Pratt, H.L., Garla, R., Simpfendorfer, C.A., 2020. Individual and population benefits of marine reserves for reef sharks. Curr. Biol. 30, 480–489.e5. https://doi.org/10.1016/j.cub.2019.12.005.

EC, 2009. Council Regulation (EC) No 43/2009 of 16 January 2009 fixing for 2009 the fishing opportunities and associated conditions for certain fish stocks and groups of fish stocks, applicable in Community waters and, for Community vessels. In: Waters where Catch Limitations Are Required.

Elston, C., Cowley, P.D., Murray, T.S., Parkinson, M.C., 2023. Novel insights into coastal site affinity and habitat connectivity of a benthic stingray with implications for management. Biodivers. Conserv. https://doi.org/10.1007/s10531-022-02494-7.

Espinoza, M., Lédée, E.J.I., Simpfendorfer, C.A., Tobin, A.J., Heupel, M.R., 2015. Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management. Ecol. Appl. 25, 2101–2118. https://doi.org/10.1890/14-2293.1.

FAO, 2020. The State of World Fisheries and Aquaculture 2020: Sustainability in Action, the State of World Fisheries and Aquaculture (SOFIA). FAO, Rome, Italy.

Figueiredo, I., Maia, C., Lagarto, N., Serra-Pereira, B., 2020. Bycatch estimation of Rajiformes in multispecies and multigear fisheries. Fish. Res. 232, 105727 https://doi.org/10.1016/j.fishres.2020.105727.

Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., Calabrese, J.M., 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96, 1182–1188. https://doi.org/10.1890/14-2010.1.

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol. Evol. 18, 448–455. https://doi.org/10.1016/S0169-5347(03)00189-7.

Hammerschlag, N., Skubel, R.A., Calich, H., Nelson, E.R., Shiffman, D.S., Wester, J., Macdonald, C.C., Cain, S., Jennings, L., Enchelmaier, A., Gallagher, A.J., 2016. Nocturnal and crepuscular behavior in elasmobranchs: a review of movement, habitat use, foraging, and reproduction in the dark. Bull. Mar. Sci. 93, 355–374. https://doi.org/10.5343/bms.2016.1046.

Heupel, M.R., Semmens, J.M., Hobday, A.J., 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar. Freshwater Res. 57, 1. https://doi.org/10.1071/MF05091.

Hoenig, J.M., Gruber, S.H., 1990. Life history patterns in the elasmobranchs: implications for fisheries management. In: Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries., NOAA Tech. Rep. NMFS 90. U.S. Department of Commerce, Washington, D.C., pp. 1–16

Humphries, N., Simpson, S., Sims, D., 2017. Diel vertical migration and central place foraging in benthic predators. Mar. Ecol. Prog. Ser. 582, 163–180. https://doi.org/10.3354/meps12324.

Humphries, N., Simpson, S., Wearmouth, V., Sims, D., 2016. Two's company, three's a crowd: fine-scale habitat partitioning by depth among sympatric species of marine mesopredator. Mar. Ecol. Prog. Ser. 561, 173–187. https://doi.org/10.3354/meps11937.

Hunter, E., Berry, F., Buckley, A.A., Stewart, C., Metcalfe, J.D., 2006. Seasonal migration of thornback rays and implications for closure management: ray migration and closure management. J. Appl. Ecol. 43, 710–720. https://doi.org/10.1111/j.1365-2664.2006.01194.x.

Hunter, E., Buckley, A.A., Stewart, C., Metcalfe, J.D., 2005. Migratory behaviour of the thornback ray, Raja clavata, in the southern North Sea. J. Mar. Biol. Assoc. U. K. 85, 1095–1105. https://doi.org/10.1017/S0025315405012142.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Mills Flemming, J.E., Whoriskey, F.G., 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348, 1255642. https://doi.org/10.1126/science.1255642, 1255642.

ICES, 2024. Thornback ray (Raja clavata) in subarea 4 and in divisions 3.a and 7.d (North Sea, skagerrak, kattegat, and eastern English channel) [object Object]. https://doi.org/10.17895/ICES.ADVICE.21856875.

ICES, 2022. Thornback ray (Raja clavata) in division 9.a (atlantic iberian waters) [object Object]. https://doi.org/10.17895/ICES.ADVICE.19754434.V1.

IUCN, 2016. Raja clavata: Ellis, J.: The IUCN Red List of Threatened Species 2016: e. T39399A103110667. International Union for Conservation of Nature. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T39399A103110667.en.

Kadri, H., Marouani, S., Saïdi, B., Bradai, M.N., Bouaïn, A., Morize, E., 2014. Age, growth, sexual maturity and reproduction of the thornback ray, Raja clavata (L.), of the Gulf of Gabès (south-central Mediterranean Sea). Mar. Biol. Res. 10, 416–425. https://doi.org/10.1080/17451000.2013.797584.

Kellner, J.B., Tetreault, I., Gaines, S.D., Nisbet, R.M., 2007. Fishing the line near marine reserves in single and multispecies fisheries. Ecol. Appl. 17, 1039–1054. https://doi.org/10.1890/05-1845.

Knip, D.M., Heupel, M.R., Simpfendorfer, C.A., 2012. Evaluating marine protected areas for the conservation of tropical coastal sharks. Biol. Conserv. 148, 200–209. https://doi.org/10.1016/j.biocon.2012.01.008.

Kraft, S., Winkler, A.C., Abecasis, D., 2023b. Small coastal marine protected areas offer recurring, seasonal protection to the common stingray (Dasyatis pastinaca). Ocean Coast Manag. 246, 106891 https://doi.org/10.1016/j.ocecoaman.2023.106891.

Kraft, S., Winkler, A.C., Abecasis, D., 2024. Horizontal and vertical movements of the critically endangered Rostroraja alba in a coastal marine protected area. Aquat. Conserv.: Marine and Freshwater Ecosystems 34 (6), e4204. https://doi.org/10.1002/aqc.4204.

Kramer, D.L., Chapman, M.R., 1999. Implications of fish home range size and relocation for marine reserve function. Environ. Biol. Fish. 55, 65–79. https://doi.org/10.1023/A:1007481206399.

Kranstauber, B., Kays, R., LaPoint, S.D., Wikelski, M., Safi, K., 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement: the dynamic Brownian bridge movement model. J. Anim. Ecol. 81(4), 738–746. https://doi.org/10.1111/j.1365-2656.2012.01955.x.

Kranstauber, B., Smolla, M., Scharf, A.K., 2021. move: visualizing and analyzing animal track data. Rpackage version 4.0.6. http://cran.r-project.org/package=move.

Krstulović Šifner, S., Vrgoč, N., Dadić, V., Isajlović, I., Peharda, M., Piccinetti, C., 2009. Long-term changes in distribution and demographic composition of thornback ray, Raja clavata, in the northern and central Adriatic Sea. J. Appl. Ichthyol. 25, 40–46. https://doi.org/10.1111/j.1439-0426.2008.01204.x.

Last, P.R., Séret, B., Stehmann, M.F.W., Weigmann, S., 2016. Skates, family rajidae. In: Last, Peter Robert, White, W.T., de Carvalho, M.R., Séret, Bernard, Stehmann, M., Naylor, G.J.P., Marshall, L. (Eds.), Rays of the World. CSIRO Publishing, Clayton South VIC, pp. 204–363.

Lavender, E., Aleynik, D., Dodd, J., Illian, J., James, M., Wright, P.J., Smout, S., Thorburn, J., 2021. Movement patterns of a critically endangered elasmobranch (Dipturus intermedius) in a marine protected area. Aquat. Conserv.: Marine and Freshwater Ecosystems aqc 3753. https://doi.org/10.1002/aqc.3753.

Le Port, A., Lavery, S., Montgomery, J.C., 2012. Conservation of coastal stingrays: seasonal abundance and population structure of the short-tailed stingray Dasyatis brevicaudata at a Marine Protected Area. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 69, 1427–1435. https://doi.org/10.1093/icesjms/fss120.

Lester, S., Halpern, B., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B., Gaines, S., Airamé, S., Warner, R., 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser. 384, 33–46. https://doi.org/10.3354/meps08029.

MacKeracher, T., Diedrich, A., Simpfendorfer, C.A., 2019. Sharks, rays and marine protected areas: a critical evaluation of current perspectives. Fish Fish. 20, 255–267. https://doi.org/10.1111/faf.12337.

Marongiu, M.F., Porcu, C., Bellodi, A., Cannas, R., Cau, A., Cuccu, D., Mulas, A., Follesa, M.C., 2017. Temporal dynamics of demersal chondrichthyan species in the central western Mediterranean Sea: the case study in Sardinia Island. Fish. Res. 193, 81–94. https://doi.org/10.1016/j.fishres.2017.04.001.

Martínez-Ramírez, L., Priester, C.R., Sousa, I., Erzini, K., Abecasis, D., 2021. Reserve effect of a small North-East Atlantic marine protected area (Arrábida, Portugal) on soft-sediment fish species. Aquat. Conserv. Mar. Freshw. Ecosyst. 31, 1584–1595. https://doi.org/10.1002/aqc.3577.

Martins, M., 2021. PTtidaltools - R package to retrieve and manipulate data from the Portuguese National Hydrographic Institute. https://doi.org/10.5281/ZENODO.4562490.

Mazerolle, M.J., 2023. AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c). R Package Version 2.3.2.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. Science 347, 1255641. https://doi.org/10.1126/science.1255641.

Mucientes, G.R., Queiroz, N., Sousa, L.L., Tarroso, P., Sims, D.W., 2009. Sexual segregation of pelagic sharks and the potential threat from fisheries. Biol. Lett. 5, 156–159. https://doi.org/10.1098/rsbl.2008.0761.

Musick, J.A., 1999. Life in the slow lane: ecology and conservation of long-lived marine animals. In: Musick, J.A. (Ed.), Ecology and Conservation of Long-Lived Marine Animals. American Fisheries Society. https://doi.org/10.47886/9781888569155.

Ohayon, S., Granot, I., Belmaker, J., 2021. A meta-analysis reveals edge effects within marine protected areas. Nature Ecology & Evolution 5, 1301–1308. https://doi.org/10.1038/s41559-021-01502-3.

Papadopoulo, K., Villegas-Ríos, D., Mucientes, G., Hillinger, A., Alonso-Fernández, A., 2023. Drivers of the spatial behaviour of the threatened thornback skate (Raja clavata). Aquat. Living Resour. 36, 21. https://doi.org/10.1051/alr/2023017.

Piet, G.J., Van Hal, R., Greenstreet, S.P.R., 2009. Modelling the direct impact of bottom trawling on the North Sea fish community to derive estimates of fishing mortality for non-target fish species. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 66, 1985–1998. https://doi.org/10.1093/icesjms/fsp162.

Pinheiro, J., Bates, D., 2023. Nlme: linear and nonlinear mixed effects models. R package version 3, 1–164. https://CRAN.R-project.org/package=nlme.

Poos, J.J., Staeudle, T., Greenway, E., Batsleer, J., 2023. Spatial Distribution, Migration, and Population Structure of North Sea Rays. Wageningen University, & Research, Wageningen. https://doi.org/10.18174/632935.

Ramírez-Amaro, S., Ordines, F., Esteban, A., García, C., Guijarro, B., Salmerón, F., Terrasa, B., Massutí, E., 2020. The diversity of recent trends for chondrichthyans in the Mediterranean reflects fishing exploitation and a potential evolutionary pressure towards early maturation. Sci. Rep. 10, 547. https://doi.org/10.1038/s41598-019-56818-9.

Rousset, J., 1990. Population structure of thornback rays Raja clavata and their movements in the Bay of Douarnenez. J. Mar. Biol. Assoc. U. K. 70, 261–268. https://doi.org/10.1017/S0025315400035384.

Santos, R., Medeiros-Leal, W., Novoa-Pabon, A., Crespo, O., Pinho, M., 2021. Biological knowledge of thornback ray (Raja clavata) from the Azores: improving scientific information for the effectiveness of species-specific management measures. Biology 10, 676. https://doi.org/10.3390/biology10070676.

Serra-Pereira, B., Erzini, K., Maia, C., Figueiredo, I., 2014. Identification of potential essential fish habitats for skates based on Fishers' knowledge. Environ. Manag. 53, 985–998. https://doi.org/10.1007/s00267-014-0257-3.

Serra-Pereira, B., Farias, I., Moura, T., Gordo, L.S., Santos, M., Figueiredo, I., 2010. Morphometric ratios of six commercially landed species of skate from the Portuguese

continental shelf, and their utility for identification. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 67, 1596–1603. https://doi.org/10.1093/icesjms/fsq056.

Serra-Pereira, B., Figueiredo, I., Gordo, L.S., 2011. Maturation, fecundity, and spawning strategy of the thornback ray, *Raja clavata*: do reproductive characteristics vary regionally? Mar. Biol. 158, 2187–2197. https://doi.org/10.1007/s00227-011-1723-6.

Serra-Pereira, B., Maia, C., Lagarto, N., Figueiredo, I., 2018. A investigação realizada no IPMA de suporte ao aconselhamento científico para a gestão de espécies de raias, No. 21.

Simpfendorfer, C.A., Heupel, M.R., Hueter, R.E., 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can. J. Fish. Aquat. Sci. 59, 23–32. https://doi.org/10.1139/f01-191.

Simpson, S., Humphries, N., Sims, D., 2021. Habitat selection, fine-scale spatial partitioning and sexual segregation in Rajidae, determined using passive acoustic telemetry. Mar. Ecol. Prog. Ser. 666, 115–134. https://doi.org/10.3354/meps13701.

Simpson, S.J., Humphries, N.E., Sims, D.W., 2020. The spatial ecology of Rajidae from mark-recapture tagging and its implications for assessing fishery interactions and efficacy of Marine Protected Areas. Fish. Res. 228, 105569 https://doi.org/10.1016/j.fishres.2020.105569.

Siskey, M.R., Shipley, O.N., Frisk, M.G., 2019. Skating on thin ice: identifying the need for species-specific data and defined migration ecology of Rajidae spp. Fish Fish. 20, 286–302. https://doi.org/10.1111/faf.12340.

Sousa, I., Baeyaert, J., Gonçalves, J.M.S., Erzini, K., 2019. Preliminary insights into the spatial ecology and movement patterns of a regionally critically endangered skate (*Rostroraja alba*) associated with a marine protected area. Mar. Freshw. Behav. Physiol. 52, 283–299. https://doi.org/10.1080/10236244.2019.1705805.

Sousa, I., Gonçalves, J.M.S., Claudet, J., Coelho, R., Gonçalves, E.J., Erzini, K., 2018. Soft-bottom fishes and spatial protection: findings from a temperate marine protected area. PeerJ 6, e4653. https://doi.org/10.7717/peerj.4653.

Speed, C., Field, I., Meekan, M., Bradshaw, C., 2010. Complexities of coastal shark movements and their implications for management. Mar. Ecol. Prog. Ser. 408, 275–293. https://doi.org/10.3354/meps08581.

Speed, C.W., Cappo, M., Meekan, M.G., 2018. Evidence for rapid recovery of shark populations within a coral reef marine protected area. Biol. Conserv. 220, 308–319. https://doi.org/10.1016/j.biocon.2018.01.010.

Thieurmel, B., Elmarhraoui, A., 2019. R Package "Suncalc": Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase, vol. 10.

Uusiheikkila, S., Wolter, C., Klefoth, T., Arlinghaus, R., 2008. A behavioral perspective on fishing-induced evolution. Trends Ecol. Evol. 23, 419–421. https://doi.org/10.1016/j.tree.2008.04.006.

Villegas-Ríos, D., Claudet, J., Freitas, C., Moland, E., Thorbjørnsen, S.H., Alonso-Fernández, A., Olsen, E.M., 2021. Time at risk: individual spatial behaviour drives effectiveness of marine protected areas and fitness. Biol. Conserv. 263, 109333 https://doi.org/10.1016/j.biocon.2021.109333.

Villegas-Ríos, D., Freitas, C., Moland, E., Thorbjørnsen, S.H., Olsen, E.M., 2020. Inferring individual fate from aquatic acoustic telemetry data. Methods Ecol. Evol. 11, 1186–1198. https://doi.org/10.1111/2041-210X.13446.

Walker, P., Hislop, J.R.G., 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 55, 392–402. https://doi.org/10.1006/jmsc.1997.0325.

Wearmouth, V.J., Sims, D.W., 2009. Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. J. Exp. Mar. Biol. Ecol. 380, 77–87. https://doi.org/10.1016/j.jembe.2009.07.035.

Wearmouth, V.J., Sims, D.W., 2008. Chapter 2 sexual segregation in marine fish, reptiles, birds and mammals. In: Advances in Marine Biology. Elsevier, pp. 107–170. https://doi.org/10.1016/S0065-2881(08)00002-3.

Wiegand, J., Hunter, E., Dulvy, N.K., 2011. Are spatial closures better than size limits for halting the decline of the North Sea thornback ray. Raja clavata? Marine and Freshwater Research 62, 722. https://doi.org/10.1071/MF10141.

Winter, J.D., 1996. Advances in underwater biotelemetry. In: Fisheries Techniques, second ed. American Fisheries Society, Bethesda, Maryland, pp. 555–590.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. Roy. Stat. Soc. 73, 3–36.