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Contribution to the Theme Section 'Marine functional connectivity'

Movement ecology determines isotopic niche width in the undulate skate *Raja undulata*

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ABSTRACT: Functional connectivity patterns of threatened species provide critical information for effective management and conservation spatial planning. In this study, we used a non-lethal novel combination of acoustic telemetry and stable isotope analysis (SIA) on the Near Threatened elasmobranch *Raja undulata* to evaluate shifts in resource/space use in response to differences in residency patterns within a marine protected area (MPA) in NW Spain. By using acoustic telemetry, we classified individuals of a local population of *R. undulata* as high- or low-residence fish based on estimates of residence index (% of days present within the studied MPA). Individuals with a high residence index (≥50%) showed a narrower isotopic niche width than low-residence fish, as they were exposed to a limited variety of habitats and food resources. Conversely, low-residence fish (mainly females) showed wider isotopic niche widths, indicative of greater diversity of resources from different environments. Therefore, we hypothesize that low-residence individuals play an important role connecting different habitats and even populations, particularly through dispersion patterns of females along the coast. This study provides valuable insights into the movement and resource ecology of *R. undulata* and their role in the functional connectivity of the coastal ecosystem, with direct applicability to inform management of the studied MPA.

KEY WORDS: Stable isotope analysis · Acoustic telemetry · Isotopic niche width · Movement patterns · Resource use · Functional connectivity · *Raja undulata* · Marine protected area

1. INTRODUCTION

Marine species play an important role in connecting ecosystems as they move between different habitats for spawning, foraging and searching for shelter, or as a result of ontogenetic habitat shifts (Olds et al. 2016, Porter et al. https://doi.org/10.20944/preprints202101.0340.v1). Interconnected habitats, i.e. seascapes (Pittman et al. 2021), link metapopulations via the exchange of matter, nutrients and energy (Engelhard et al. 2017). The movement patterns and behavioural response of marine organisms to seascape structure is known to directly affect ecosystem functioning (Porter et al. 2021), playing a major role in marine connectivity (Weeks 2017). Such connectivity provides the resilience of metapopulations towards potential disturbances such as environmental change or overfishing (Engelhard et al. 2017, Albouy et al. 2019, Gao et al. 2023), but can also exacerbate associated impacts such as the dispersal of pollutants or invasive species and ultimately jeopardize ecosystem stability and health (Albouy et al. 2019).

There are many ways to measure marine connectivity, including use of larval dispersal model or genomic tools; analysis of otoliths or chemical markers like stable isotopes; and tracking of tagged organisms (i.e.

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acoustic telemetry or mark–recapture) (Calò et al. 2013). Connectivity plays a pivotal role in species persistence and therefore needs to be accounted for to efficiently implement spatial conservation actions, such as marine protected areas (MPAs) (Assis et al. 2021). However, despite the recognized importance of connectivity in marine spatial planning, its integration into real-world plans has been limited due to challenges in quantifying ecological connectivity by practitioners and decision-makers (Beger et al. 2022).

The most direct methodology to assess animal movement and behaviour in the aquatic environment is through acoustic telemetry or satellite technology (Hussey et al. 2015). Acoustic telemetry has been shown to be valuable in inferring the individual fate of marine organisms in the wild (Klinard & Matley 2020, Villegas-Ríos et al. 2020). As a result, this technique is used to estimate the survival rate of elasmobranchs discarded in fisheries, such as *Raja undulata* (Morfin et al. 2019, Alonso-Fernández et al. 2022). Acoustic telemetry is also used to enhance MPA design, as has been done in the islands of D'Arros and St Joseph in the Amirantes, Seychelles (Lea et al. 2016). Considering these and many other examples of the use of acoustic telemetry in the aquatic environment, this method has been proven to provide relevant data that can be used to inform conservation and fisheries management (Crossin et al. 2017, Hays et al. 2019, Alós et al. 2022) However, despite its high precision in following animal movements, acoustic telemetry relies on the detection of the sonic pulses emitted by animal-borne transmitters within a pre-established array of hydrophones at specific locations. This limits the spatial extent of movement studies to the detection limits of the established array. Consequently, additional sources of information, such as stable isotope analysis (SIA), can complement acoustic telemetry data to study the spatial ecology of marine organisms.

Connectivity can be assessed at a larger geographical scale through SIA (Madigan et al. 2021, Brownscombe et al. 2022). This approach provides relevant insights about trophic ecology, movement patterns and habitat/resource use (Peterson & Fry 1987, Post 2002, Martínez del Rio et al. 2009, Shipley & Matich 2020). SIA relies on the differential use of the heavier vs. lighter stable isotopes (or fractionation, noted as δ) of certain elements (most frequently carbon and nitrogen) during metabolism (Dubois et al. 2007). Combining both $\delta^{13}C$ and $\delta^{15}N$ into a 2-dimensional geometry space, i.e. isotopic niche, helps to understand animal behaviour and ecosystem functioning (Newsome et al. 2007) and to identify niche shifts/overlaps throughout a species' life history (Swanson et al. 2015, Gallagher et al. 2017, Reddin et al. 2018).

Therefore, SIA enables the assessment of resource ecology patterns at multiple scales (both spatial and temporal) ranging from individuals to ecosystems (Martínez del Rio et al. 2009), playing a pivotal role in identifying trans-oceanic movements (Madigan et al. 2021) and connectivity patterns in transitional ecosystems (i.e. estuarine environments) (Shipley et al. 2021). Lastly, through increasing our knowledge of ecological connectivity and functioning (Meyer et al. 2010, Hussey et al. 2015), SIA allows us to investigate the reliance on different energy sources (Brownscombe et al. 2022) and it can provide insights into migratory patterns (Trueman et al. 2012), site fidelity (Green et al. 2012), foraging grounds (Ogilvy et al. 2022) and guiding/evaluating conservation initiatives (Haywood et al. 2019, Blanco et al. 2021). This approach requires the establishment of an isotopic baseline (i.e. reference information regarding the isotopes present in the environment in which organisms dwell) to identify feeding patterns and trophic interactions within a specific geographic context (Post 2002). For example, Hussey et al. (2012) described an increasing trend of carbon isotopic values in species spending larger periods in inshore habitats. Additionally, species isotopic composition can also reflect physiological changes associated with growth, nutritional status and/or reproductive stage, which may therefore limit the understanding of the data provided (Gorokhova 2018, Lübcker et al. 2020, Whiteman et al. 2021, Shipley et al. 2022).

The combination of acoustic telemetry and SIA was found to be a powerful tool to elucidate seascape connectivity and to combine species spatial movements and resource ecology information (Hussey et al. 2012, Papastamatiou et al. 2015, TinHan et al. 2018, Shipley et al. 2021, Brownscombe et al. 2022). For instance, the combination of the 2 methods has resulted in the identification of the coexistence of 2 ecotypes of Atlantic cod *Gadus morhua* with differences in their functional role in marine ecosystems in Norwegian fjords (Kristensen et al. 2021). Similarly, the 2 approaches have also been used to shed light on the relationship between individual variation in movement of wild burbot *Lota lota* and their reliance on littoral and pelagic prey specialization (Harrison et al. 2017).

There is a significant lack of basic knowledge regarding the biology and ecology of vulnerable species, such as elasmobranchs, which face escalating threats (Ellis et al. 2017). Increasing our understanding of their spatial patterns and resource use is crucial for conserving and effectively managing these ecologically significant species. This study focuses on the undulate skate *Raja undulata* Lacepède, 1802, which is listed as Near Threatened on the Red List of the International Union for Conservation of Nature (IUCN) (Ellis et al. 2015). Recent research utilizing acoustic telemetry (Leeb et al. 2021) identified a local aggregation of a population of *R. undulata* within a partial MPA off NW Spain (Galicia), the Parque Nacional Marítimo-Terrestre Illas Atlánticas de Galicia (PNMTIAG). In Galicia, this species is of particular commercial relevance for small-scale fisheries (Bañón et al. 2008). Although a decreasing trend in the relative abundance of *R. undulata* over the past 2 decades has been reported in Galicia (Alonso-Fernández et al. 2019, 2021), fundamental knowledge for effective management of this species (i.e. reproductive period and specific habitat, aggregation areas, connectivity between populations) is still lacking.

Through the combination of isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) and acoustic telemetry data, this work aims to provide information about the spatial and resource ecology of *R. undulata* and to provide insights into the role of this species in functional connectivity between the local MPA (PNMTIAG) and surrounding fishing grounds, with emphasis on conservation and management goals.

2. MATERIALS AND METHODS

2.1. Case study: species and location

Raja undulata are patchily distributed from southern Ireland and England to the Gulf of Guinea, including the Mediterranean Sea, typically inhabiting soft sandy seabeds in coastal shallow waters (<40 m deep), estuaries, lagoons and bays (Ellis et al. 2012, Elliott et al. 2020, Figueiredo et al. 2020). This species is found in depths over 100 m, but become less abundant with increasing depth (Serra-Pereira et al. 2015). *R. undulata* display aggregation behaviours, being seasonally abundant in specific locations, as reported in coastal areas around the English Channel and Bay of Biscay (Elliott et al. 2020), along the Portuguese continental coast (Coelho & Erzini 2006, Serra-Pereira et al. 2015, Figueiredo et al. 2020) and in the Rías of NW Spain (Leeb et al. 2021). A trend of coastal areas being used as nursery grounds during springtime has been observed (Elliott et al. 2020). *R. undulata* primarily prey on benthic and semi-pelagic species, with an increasing preference for brachyuran crabs as they grow. They mainly feed on the decapod *Polybius henslowii* (Moura et al. 2008).

This study was conducted in the Cíes archipelago, which is part of the PNMTIAG (Fig. 1). The Cíes archipelago is situated at the mouth of the Ría de Vigo, a highly productive ría sensu lato (Cotton 1956). The area is characterized by periodical coastal upwelling (spring and summer) and downwelling (autumn and winter) events (Álvarez-Salgado et al. 2000). The sampling array is located at the eastern side of the Cíes archipelago, which is dominated by a variety of substrates, such as rocky reefs, sandy patches, gravel and kelp forests (Fernández et al. 2020). Commercial fishing is allowed within the PNMTIAG, whereas recreational fishing is banned (Xunta de Galicia, Conselleira de Medio Ambiente, Territorio y Vivienda, 27/12/ 2018).

2.2. Acoustic telemetry array

To study the movement patterns of *R. undulata*, we deployed an acoustic array in the Cíes archipelago close to a shallow (<20 m depth) tidal channel mainly composed of sandy bottoms and patchy rocky reef (Fig. 1). The telemetry array is composed of 28 acoustic stations: 24 stations with both Innovasea (VR2W) and Thelma Biotel receivers (TBR-700L) and 4 stations only consisting of Thelma Biotel receivers. Receivers were installed ~150 m from one another to provide effective overlapping between receiver ranges, based on a previous detection range test (see details in Papadopoulo et al. 2023). There were no significant differences between the 2 types of receivers in terms of detection range and probability of detection.

2.3. Tagging and biological sampling

A total of 98 individuals were captured, tagged and sampled between June 2019 and June 2021 within the telemetry array. Undulate rays were caught by hand during scuba-diving at 11 to 12 m depth, bringing them slowly to the surface to avoid barotrauma (approximately 3 m min^{-1}). Once on the boat, each individual was anaesthetised, sexed and measured (to the nearest cm). Disc length (DL) was used as body size indicator, as some individuals presented incomplete tails. All individuals were tagged internally with acoustic transmitters (1 with an Innovasea V16 transmitter, expected lifetime of 1825 d and a signal transmission delay of 40–80 s; 67 with Innovasea V13P/V13AP transmitters, expected lifetime of 730–855 d and a signal transmission delay of 80–160 s;

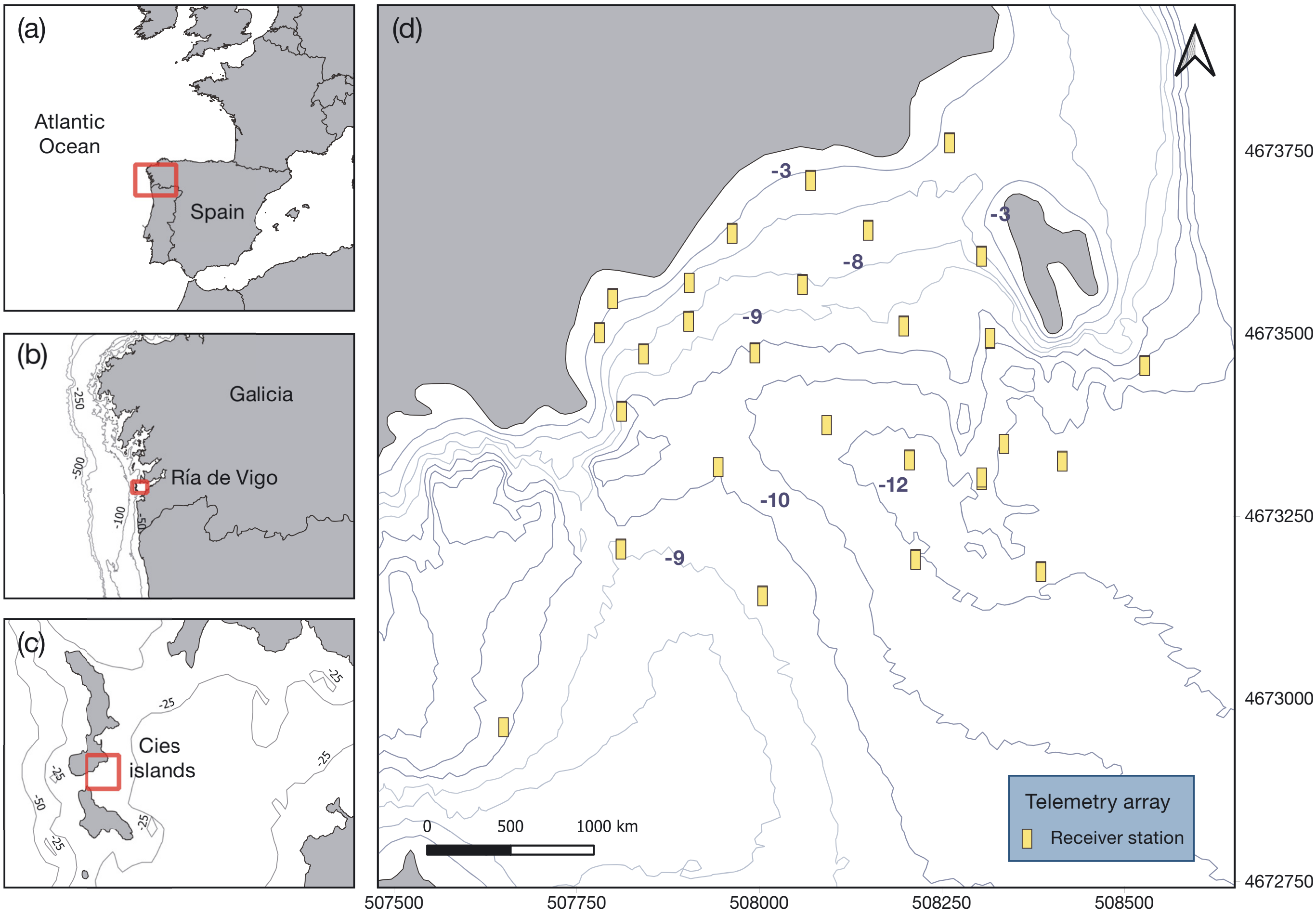

Fig. 1. Acoustic telemetry array located in (a) Galicia, Spain, (b) at the mouth of Ría de Vigo, (c,d) in the Cíes Archipelago

6 with Innovasea V9AP transmitters, expected lifetime 453 d and a signal transmission delay of 80–160 s; 1 with a Thelma Biotel D-LP9L, expected lifetime 900 d and a signal transmission delay of 90–150 s; 23 with Thelma Biotel D-LP13L transmitters, expected lifetime 1653 d and a signal transmission delay of 90–150 s) and externally with plastic T-bar tags (©Floy Tag). Acoustic tags were implanted in the peritoneal cavity via surgery. We decided on the size of the transmitter to be used to tag individuals based on the size of the fish to optimise the battery life: the bigger, the better. T-bar tags were implanted to avoid resampling and as a way to be informed in case of potential recaptures by fishermen. Tagged individuals were sampled for SIA of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Dorsal fin clips were collected and frozen at −80°C until processed (Rangel et al. 2019). These non-lethal methods reduce significant impacts on the animals' welfare. Individuals were retained until their condition and reflexes returned to normal (good respiratory rate and active response to external stimulus) and then released at the capture location.

All procedures were performed according to national animal welfare regulations (Real Decreto 53/2013 del 1 de febrero de 2013, published in B.O.E. n 34, on 8 February 2013). The present study complied with the corresponding experimental animal project authorization resolution of the regional government (Xunta de Galicia) starting on 14 November 2019. It followed Experimental Animal Project Authorization ES360570202001/19/FUN01/ BIOLAN.08/AAF01.

2.4. Stable isotope analysis

Elasmobranch fins have a slow turnover rate (Matich et al. 2010) and are composed of several tissues, including cartilage, skin, muscle, blood and connective tissue (Hussey et al. 2011). Prior to analysis, all samples were defrosted, triple rinsed with distilled water, dried and ground into a fine powder. Samples were then freeze-dried and stored in a vacuum dryer to prevent damage from moisture.

Homogeneous dried powder of each sample was weighted (0.3 ± 0.05 mg) into a cadmium tin cup and combusted for δ^{13}C and δ^{15}N stable isotope compositions. Isotopic analyses were conducted at the Laboratorio de Isótopos Estables of the Estación Biológica de Doñana (LIE-EBD), using a Delta-V advantage isotope ratio mass spectrometer combined with an element analyzer (Thermo-Scientific Flash HT Plus) through a CONFLO IV interface (Thermo Fisher Scientific). LIE-EBD used 4 reference standards for SIA of carbon and nitrogen: IAEA-600 (−27.77 ± 0.04 [SD] ‰ for δ^{13}C, +1.0 ± 0.2‰ for δ^{15}N); LIE-P-22 (−26.98 ± 0.13‰ for δ^{13}C, +5.94 ± 0.08‰ for δ^{15}N); LIE-BB (−18.6 ± 0.08‰ for δ^{13}C, +9.97 ± 0.07‰ for δ^{15}N); and LIE-PA (−15.69 ± 0.08‰ for δ^{13}C, +16.47 ± 0.09‰ for δ^{15}N). To compensate for measurement drift over time, 3 samples of these references were analysed after every 9 samples. In addition, 2 internal standards were included in the analysis. The standard error for carbon and nitrogen analysis was 0.15‰.

Stable isotope signatures were measured as the ratios in delta (δ) values expressed in parts per thousand (‰), based on the ratio between sample and a recognized standard, using the following equation:

$$\delta(‰) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}} - 1}\right) \times 1000 \qquad (1)$$

where R is the ratio of heavy to light isotope (^{13}C:^{12}C and ^{15}N:^{14}N), R_{sample} is the ratio of *R. undulata* samples, and R_{standard} is the ratio of the reference standard used (Pee Dee belemnite carbonate for δ^{13}C and atmospheric nitrogen for δ^{15}N) (Peterson & Fry 1987).

2.5. Behavioural metrics

Up to 3 yr of detection data were used to estimate the presence and absence of the tagged skates in the study area to study their residence patterns within the study area. We estimated the residency index (RI) for each individual by calculating the number of days detected (DD), and the total of days that each skate had been monitored, from the first day the skate was tagged to the last data download (TD), following the formula (Afonso et al. 2008, March et al. 2010):

$$\text{RI} = \left(\frac{DD}{TD}\right) \qquad (2)$$

RI values were quantified from 0, representing total absence, to 1, representing a daily presence within the telemetry array. Based on the RI of *R. undulata*, individuals were classified as high-residence (HR; RI ≥ 0.5) and low-residence (LR; RI < 0.5) individuals.

2.6. Statistical analysis

Generalised least squares (GLS) were used to study the relationship of the isotopic composition (δ^{13}C and δ^{15}N) with main biological drivers (DL, sex) and residence patterns (HR and LR). We used GLS models to deal with the lack of homogeneity of variances among behavioural types, using the 'nlme' package in R (Zuur et al. 2009, Pinheiro et al. 2022). In order to simplify the model structure, the 2 nominal explanatory variables (sex and residency type) were categorised into a unique explanatory variable named 'category'(*Cat*) with 4 levels: HR males, HR females, LR males and LR females.

We studied the sources of variation in isotopic composition using the following model structure:

$$Y_{ij} = \alpha + \beta_1\text{Cat}_j + \beta_2\text{DL}_{ij} + \beta_3(\text{Cat}_j \times \text{DL}_{ij}) + \varepsilon_{ij} \qquad (3)$$

where the response variable Y_{ij} is the isotopic composition, δ^{13}C or δ^{15}N, of fish i that belongs to category (*Cat*) j. The covariate disc length, *DL*, was assumed to account for ontogenetic changes in the isotopic composition (resources and prey type, δ^{13}C; trophic position, δ^{15}N) of individual fish. The potential interaction between *DL* and *Cat* was also included in the model structure to study potential changes in the size effect in the different strata of *Cat*. GLS allows adding a variance structure with different spread per stratum, *Cat*, as follows:

$$\varepsilon_{ij} \sim N(0,\sigma_j^2) \qquad j = 1,\ldots,4 \qquad (4)$$

We followed a backward model selection procedure to choose the optimal model based on Akaike's information criterion (AIC). We first compared different variance structures using the restricted maximum likelihood (REML) method and then model structure using the maximum likelihood (ML) method (Zuur et al. 2009). An optimal model was run with REML to estimate coefficients. Model validation was based on visual inspection of residuals.

The Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011) was used to make statistical comparisons of niche width using Bayesian methods among the different residence groups (HR and LR) and sex, using *Cat* as the grouping variable. To test the hypothesis that undulate rays with HR patterns occupy different isotopic niches compared to LR individuals that disperse to other areas, calculation of convex-hull areas of each group and estimation of Bayesian standard ellipse area (SEA_B) were applied. Convex-hull area provides a biplot of $\delta^{13}C$ and $\delta^{15}N$ values of every individual, which contains the area of the smallest convex polygon and allows us to estimate the total area (TA) occupied (Layman et al. 2007, Jackson et al. 2011). SEA_B is displayed in units per mil squared (‰^{2}). In order to avoid any bias with the smaller sample size (HR females), corrected standard ellipse areas (SEA_C) were calculated (Jackson et al. 2011).

3. RESULTS

The RI of tagged individuals ranged from 0.013 to 0.871, with an average RI of 0.374 ± 0.248 (mean ± SD). The average RI was 0.344 ± 0.346 (range 0.027–0.871) for females and 0.392 ± 0.249 (range 0.013–0.815) for males. Residence patterns of a total of 98 undulate rays were classified based on their RI in the study area. We classified 34 individuals as HR (9 females and 25 males) and 64 individuals as LR (28 females and 36 males) (Table 1; Table S1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m731p147_supp.pdf). Seven individuals were recaptured by commercial fisheries close to the study area (<10 km), except 1 female that was captured ~60 km away from the tagging location (Fig. S2).

The average isotopic signature of carbon and nitrogen were similar among groups, but there were differences (albeit not significant) in stable isotope variation (Table 1). LR females featured the widest range in their isotopic composition, for both carbon (−12.87 to −15.36‰) and nitrogen (13.76 to 10.02‰), followed by LR males (−13.18 to −15.26‰ in $\delta^{13}C$, 12.83 to 11.02‰ in $\delta^{15}N$). On the other hand, $\delta^{13}C$ and $\delta^{15}N$ values of HR females (−13.94 to −15.25‰, 12.65 to 11.69‰, respectively) and males (−13.79 to −15.34‰ and 13.58 to 11.36‰, respectively) had similar isotope range values and were narrower than LR individuals (see Fig. 3). The mean C:N ratio was estimated as an indicator of fin quality (2.77 ± 0.26) as was the C:N range (3.02 to 1.04). The optimal models for $\delta^{13}C$ and $\delta^{15}N$ included different variances for each category level (Table S2). LR females presented the highest variances in both the carbon and nitrogen stable isotopes models (Table S2). In the case of $\delta^{13}C$, only DL resulted in strong evidence for an effect (Table 2, Fig. 2; Table S2). Carbon stable isotope values increased with increasing body size of skates ($p < 0.0001$, $R^2 = 0.06$; Fig. 2). On the other hand, in the case of $\delta^{15}N$, none of the explanatory variables was significant (Table 2).

Table 1. Summary of tagged *Raja undulata*. HR: high residence; LR: low residence; DL: disc length; RI: residence index. Carbon and nitrogen isotopic values ($\delta^{13}C$ and $\delta^{15}N$) are also shown. Values are mean ± SD. Individual values are provided in Table S1 in the Supplement

Residence pattern	Sex	n	DL (cm)	RI	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
HR	F	9	36.7 ± 7.8	0.69 ± 0.12	−14.60 ± 0.36	12.00 ± 0.29
	M	25	39.2 ± 6.1	0.66 ± 0.07	−14.51 ± 0.36	12.10 ± 0.46
LR	F	28	42.1 ± 6.3	0.23 ± 0.15	−14.34 ± 0.57	11.94 ± 0.77
	M	36	41.9 ± 5.6	0.21 ± 0.13	−14.41 ± 0.48	12.02 ± 0.44

Table 2. Summary of the fitted optimal generalised least squares models for carbon and nitrogen isotopes; DL: disc length

Response	Coefficient	Estimate	SE	*t*	p
$\delta^{13}C$	Intercept	−15.829684	0.2487919	−63.62621	<0.0001
	DL	0.033886	0.00614792	5.51172	<0.0001
$\delta^{15}N$	Intercept	12.02281	0.04599457	261.3964	<0.0001

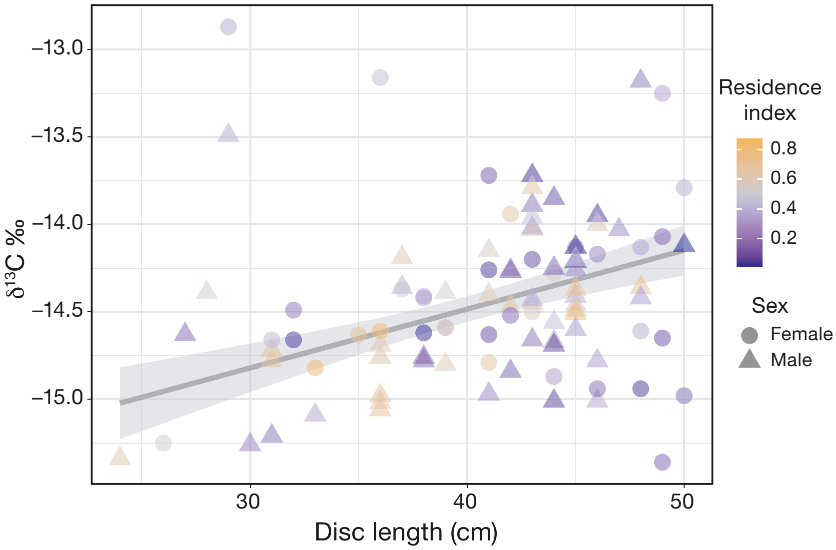

Fig. 2. Model prediction for the effect of disc length on carbon isotopic values for *Raja undulata*. Colours indicate residence index values; sex of individuals is represented by 2 different shapes; $p < 0.0001$, $R^2 = 0.06$

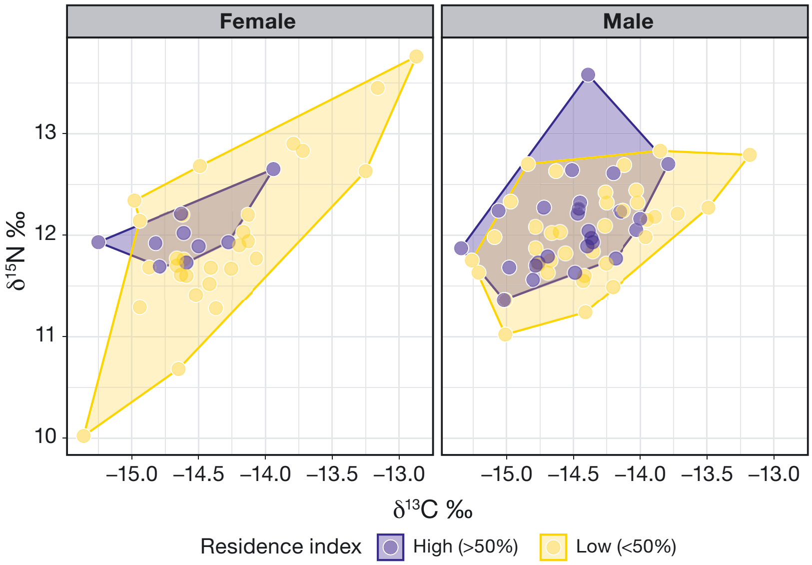

Fig. 3. Biplot of δ^{13}C and δ^{15}N from fin tissue of *Raja undulata*. Individuals (each circle) with high residence are presented in blue and those with low residence in yellow. Shaded areas represent the convex hull areas for high- and low-residence groups

The convex hull areas for δ^{13}C–δ^{15}N represent the isotopic niche width expressed as the TA of each group (Fig. 3). The isotopic niche space of LR females (3.12 TA) was larger than that of LR males (2.13 TA), HR males (1.78 TA) and HR females (0.78 TA) (Fig. 3). The isotopic niche width was significantly higher in LR skates than HR skates (Fig. 4). Moreover, there were significant differences in the isotopic niche width between LR females and males. Isotopic niches represented by the SEA_B showed that HR females exhibited the smallest SEA_B (mode: 0.29‰^{2}, 95% credible interval: 0.15–0.62‰^{2}), followed by HR males (mode: 0.50‰^{2}, 95% credible interval: 0.34–0.75‰^{2}), LR males (mode: 0.60‰^{2}, 95% credible interval: 0.43–0.84‰^{2}) and LR females with the largest SEA_B (mode: 0.90‰^{2}, 95% credible interval: 0.65–1.36‰^{2}, Fig. 4), which was further supported by SEA_C values (0.30 for HR females, 0.50 for HR males, 0.60 LR for males and 0.90 for LR females). SEA_C values are very close to the modes, indicating an appropriate sample size for all estimations (Fig. 4; Jackson et al. 2011).

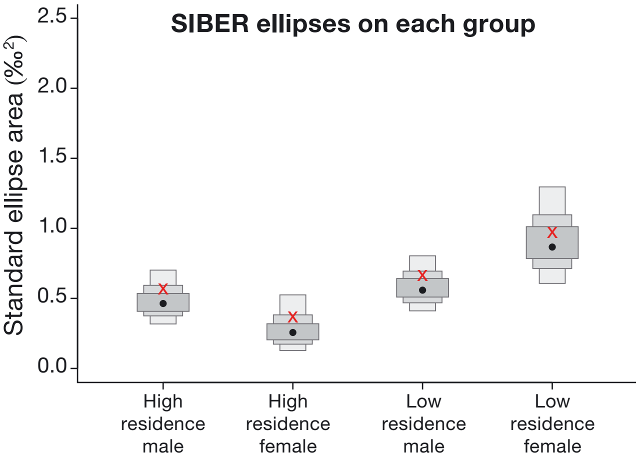

Fig. 4. Bayesian standard ellipse area (SEA_B) distribution of the different groups of *Raja undulata*. Black dots indicate mode values; red crosses represent the corrected SEA (SEA_C) values. The shaded boxes represent credible intervals (50%, 75% and 95%, from dark to light grey)

The proportion of the non-overlapping area of 2 ellipses varied among the different groups of skates studied in the SEA analysis. For HR and LR females, the non-overlapping proportion was 0.24 (95% confidence interval, CI95%: 0.12–0.45) and 0.57 (CI95%: 0.34–0.72) for males. This proportion was 0.37 (CI95%: 0.11–0.57) between LR males and females, and 0.50 (CI95%: 0.34–0.68) between HR males and females. Finally, LR females and HR males showed a proportion of non-overlapping area of 0.38 (CI95%: 0.18–0.56) and 0.41 (CI95%: 0.24–0.58), respectively.

4. DISCUSSION

By combining up to 3 yr of acoustic telemetry data with stable isotope (C and N) composition of a threatened species, *Raja undulata*, we provide insights into its movement patterns and individual biological features, including space use and resource ecology. Our results highlight the importance of LR individuals in the functional connectivity between locations and their role in the transfer of matter and energy as they move outside the aggregation area, inside of which our telemetry acoustic array is placed.

The studied population of *R. undulata* exhibits a summer aggregation at a specific location within a marine protected area, the PNMTIAG (Leeb et al. 2021, Hillinger 2022). The overall RI of tagged *R. undulata* varied among individuals, with ~35% of the population presenting high residency (≥0.5 RI) and ~65% low residency (<0.5 RI), in agreement with previously published data (Leeb et al. 2021). HR individuals stay within the study area most of the time, whereas LR skates generally disperse from the aggregation site during autumn and winter (Leeb et al. 2021). Although describing the primary drivers of this aggregation is beyond the scope of this work as they remain elusive (Leeb et al. 2021), it is evident that the sampled location constitutes an essential habitat for this local population of *R. undulata*. Nevertheless, other species of the class Elasmobranchii are known to disperse due to environmental conditions such as dissolved oxygen (a critical factor, Espinoza et al. 2011) and oceanographic currents. Additionally, species of the family Rajidae aggregate due to factors such as reproduction and feeding (Siskey et al. 2019). Although the breeding season in Galicia remains unknown, this aggregation could be associated with a potential reproductive gathering, as discussed by Leeb et al. (2021). In northern Portugal, *R. undulata* develops eggs between December and May (Serra-Pereira et al. 2015), which are laid shortly after (Moura et al. 2007, Serra-Pereira et al. 2015). Seasonal inshore–offshore migrations, transitioning from spawning habitats to adult habitats, are known to occur among other species of Rajidae (i.e. *Dipturus chilensis* and *D. trachyderma*) (reviewed by Siskey et al. 2019). They likely also occur in *R. undulata*, which are capable of storing sperm and undertake migrations to other areas for offspring production (Serra-Pereira et al. 2015). Furthermore, studies on the flapper skate *D. intermedius* indicate significant variability in migratory strategies within populations, including residents, seasonal residents and migratory individuals, demonstrating a high degree of conspecific behaviour (Siskey et al. 2019).

The individual variation in residence patterns of *R. undulata* within the PNMTIAG could have profound implications for conservation strategies. While the presence of HR individuals may indicate a match between species requirements and habitat suitability, LR individuals may play a significant role in seascape connectivity (Alves et al. 2019). Differences in stable isotope composition and isotopic niche between HR and LR skates helped us to form an understanding of the space use by this population and its role in functional connectivity. The isotopic composition of an organism reflects its space and resource use over time as a function of the sampled tissue and its turnover rate. By analysing fin-clip samples of *R. undulata*, we gathered habitat and resource use information over the previous year (Matich et al. 2010), which, along with telemetry data, provides us insights into the movement patterns before and after tagging. As expected, the isotopic composition of LR individuals revealed significantly larger isotopic niches, as they move outside the array area more often. Therefore, LR are exposed to a wider range of resources (linked to spatial isotopic differences caused by environmental conditions and/or habitat types) (Bearhop et al. 2004, Hobson et al. 2010). Conversely, HR individuals (delimited to a smaller geographical area and, consequently, to limited resources) had smaller isotopic niches, as they are exposed to similar resources and environmental conditions year-round. However, stable isotope niches are also subject to other sources of variability, namely changes in the base of food webs associated with distinct geographical areas (isotopic baseline), prey availability, diet switching, differences in prey trophic levels, individual physiological condition and individual diet–tissue fractionation (Bearhop et al. 2004, Dubois et al. 2007, Hobson et al. 2010, Shipley et al. 2022). Variations in isotopic niche width can be caused by any combination of one or several of these factors. Despite the factors influencing isotopic variability, the combination of acoustic telemetry and SIA provides relevant information for conservation and fisheries management. For instance, the finding of differences in δ^{13}C and δ^{15}N signatures allowed researchers to identify different isotopic niches of 2 coexisting ecotypes of Atlantic cod in the coastal Skagerrak, highlighting the importance of applying management actions that ensure the persistence of both functionally divergent ecotypes (Kristensen et al. 2021).

The present work also established a sexual dimorphism in the isotopic niche width, where LR females showed greater isotopic niche width than LR males, while HR males and females showed a similar isotopic niche width. This suggests that LR females are exposed to a larger diversity of resources and prey species from different trophic levels and/or are exposed to different environments (i.e. distinct isotopic baselines). In a study conducted in Portugal, significant differences in diet were detected between males and females of *R. undulata* (Moura et al. 2008), which in this study could only be applied to LR individuals. LR females could be undergoing distinct stages of gestation, since δ^{15}N tends to decrease as gestation progresses (Whiteman et al. 2021, Shipley et al. 2022), which could also explain the observed variability in nitrogen values in LR females. Nevertheless, the furthest recapture reported from the aggregation area was of a female (unpublished data), which might represent evidence of higher dispersal rates of females than males (Fig. S2). Such sexual dimorphism in the isotopic niche width also suggests different space use patterns between LR males and females. Such differences could be explained by seasonal sexual segregation, as the abundance of female

R. undulata is greater than that of males in offshore and inshore waters throughout the year (Elliott et al. 2020). Other elasmobranchs, such as the round stingray *Urobatis halleri,* showed similar seasonal and sexual segregation patterns in response to their reproductive cycle and the search for suitable habitats for their offspring (Jirik & Lowe 2012).

Similarly, the δ^{13}C range of LR males (−13.18 to −15.26‰) in the present study indicates similar food sources as in HR individuals (−13.94 to −15.25‰ in females and −13.79 to −15.34‰ in males), suggesting that they might stay closer to the study array or move to areas with similar resources. Conversely, differences in the δ^{15}N range between HR and LR males might be related to the isotopic baseline of their prey (13.58 to 11.36‰ and 12.83 to 11.02‰, respectively). Moreover, the variability in carbon and nitrogen isotopic signatures associated with residency patterns and sex were mainly driven by LR females and, to a lesser extent LR males, which supports the abovementioned results.

Differences in δ^{13}C values, but not δ^{15}N, in response to body size suggest ontogenetic habitat and/or prey (of similar trophic level) shifts in *R. undulata.* Ontogenetic habitat shifts have already been described in *R. undulata* (Elliott et al. 2020), in batoids and in other elasmobranchs (Elston et al. 2020, 2021, DeGroot et al. 2021) based on their changing use of carbon resources as they develop from juveniles to adults, as is mirrored by small differences in δ^{13}C between them as juveniles which then increase as individuals expand their home range as they grow (Elston et al. 2020, 2021). Accordingly, and in line with the previously suggested pattern of migration in LR females related to the suitability of habitats for their offspring, smaller skates may inhabit different areas as adults with distinct baseline habitats. On the flip side, ontogenetic shifts in dietary patterns have also previously been documented in undulate skates (Moura et al. 2008). Nevertheless, it is important to exercise caution when interpreting these results due to the predominant presence of adult individuals in the sampled population within the study area. Therefore, in order to enhance the precision of our evaluation regarding the assessment of ontogenetic change, it becomes imperative to procure samples of varying size categories.

In addition, we have identified study limitations that need to be considered when interpreting the discussed results in terms of study array size, which ideally should be extended to other areas to provide more accurate information on migratory patterns; lack of baseline isoscapes, which is essential to depict animal foraging movements, isotopic niche shifts, use of specific resources, trophic ecology level and reliance on specific areas (Hobson et al. 2010); and individual physiological factors, including nutritional and reproductive status and growth stage. For instance, Brownscombe et al. (2022) integrated isoscape and telemetry data to identify *Trachinotus falcatus* spatial (habitat connectivity) and trophic (resource use) ecology and further suggested conservation and fisheries management to ensure both habitat representation and species persistence. Thus, future steps to extend the scope of the present study must include mapping the stable isotope baseline (i.e. isoscape) to estimate the foraging movements driving functional connectivity patterns between sub-populations from inside the MPA and surrounding habitats. Based on current results, the use of stable isotopes is a promising tool to differentiate between resident and non-resident populations in the context of an MPA. This has important implications for the design of MPAs, as their effectiveness depends on the space use and movement patterns of the populations under protection (Villegas-Ríos et al. 2021).

This study is an example of the valuable combination of acoustic telemetry data and SIA to provide insights into the spatial and resource ecology of *R. undulata* with implications in conservation and management. By adding our results (longer time series and stable isotope data) to the only previously published data from a 1 yr residency study (Leeb et al. 2021), we were able to confirm the existence of 2 different residency patterns within this population; i.e. HR and LR individuals. HR individuals were present in the study area during more days throughout the year. By incorporating SIA data, we can now obtain a better understanding of the dynamics, both inside and outside the aggregation site, as residency patterns (from acoustic telemetry data) aligned with isotopic niche use (from SIA data). Thus, individuals (both males and females) that spend most of their time within the study area (HR individuals) have similar isotopic niche widths, as they are exposed to the same resources and conditions. In contrast, LR individuals (particularly females) seem to be exposed to different stable isotope sources and therefore have wider isotopic niche widths, which might be related to migratory behaviours. Considering the reproductive ecology of *R. undulata* (Serra-Pereira et al. 2015) and their migratory behaviour (Leeb et al. 2021, this study), this species is likely interacting with surrounding populations and thus connecting habitats, both structurally (as they move for reproduction) and functionally (as they feed while migrating). SIA revealed sexual dimorphism among LR individuals, and also suggests an ontogenetic shift, confirming observed trends in the undulate skate (Elliott et al. 2020).

The differences in trophic ecology and habitat use of LR and HR individuals could potentially have diverse yet significant impacts on the interconnections between food webs and specific habitats within or outside the MPA (Quevedo et al. 2009). These interconnections establish links between populations within the MPA and patches located outside the reserve, thus influencing the spillover effect observed in our study area (Olds et al. 2016). Furthermore, it is worth noting that spatial connectivity resulting from seasonal dynamics can significantly impact the structural composition of benthic communities through trophic cascades, particularly as consumers of benthic semi-pelagic species (Moura et al. 2008, Olds et al. 2016). This valuable information enables us to focus our study more effectively and develop improved management strategies for this population. Identifying whether and how the studied MPA is effective in preserving *R. undulata* metapopulations will enable the strategic design of management plans accounting for aspects of individual behaviour (Villegas-Ríos et al. 2021). Overall, the results presented in the present work indicate that the site under study is an important hotspot for a specific proportion of the local population of this species. The study shows different levels of protection exerted by the MPA and vulnerability to fishing due to various behavioral and trophic ecology patterns. These findings have significant implications for estimating the overall effectiveness of MPAs in safeguarding all segments of the local population.

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