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Stable isotopes reveal intrapopulation heterogeneity of porbeagle shark (*Lamna nasus*)

Sandrine Serre [a],[*], Armelle Jung [b],[c], Yves Cherel [d], Caroline Gamblin [e], Cédric Hennache [b],[f], François Le Loc'h [a], Anne Lorrain [a], Anne Priac [a], Gauthier Schaal [a], Éric Stephan [b]

[a] *Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280 Plouzané, France*
[b] *Association Pour l'Etude et la Conservation des Sélaciens (APECS), 13 rue J-F Tartu, 29200 Brest, France*
[c] *Des requins et des hommes, Bibliothèque la Pérouse, Technopole Brest Iroise, 15 rue Dumont d'Urville, 29280 Plouzané, France*
[d] *Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 du CNRS-La Rochelle Université, 79360 Villiers-en-Bois, France*
[e] *CNPMEM, 134 avenue de Malakoff, 75116 Paris, France*
[f] *CAPENA, Site d'Oléron, Prise de Terdoux, 17480 Le Château d'Oléron, France*

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ABSTRACT

Porbeagle (*Lamna nasus*) is an ubiquist, highly mobile and long-living shark species with spatial and temporal sex and size segregation observed in catches. Porbeagle sharks were targeted by commercial fisheries in the European waters until the closure of the fishery in 2010. Most of the French fleet catches were located in Bay of Biscay, Celtic Sea and the English Channel. The aim of the study was to find out occurrences of spatial segregation within the shark population in the Northeast Atlantic Ocean based on the stable isotope method. Carbon and nitrogen stable isotopes (δ^{13}C, δ^{15}N) were measured in muscle of porbeagle sharks fished in the Bay of Biscay and the Celtic Sea between April and September 2008, and April and June 2009. Neither influence of sex nor ontogenic isotopic shift was detected in the sampled sharks, but muscle δ^{13}C and δ^{15}N values increased significantly from offshore towards coastal area, which reflected inter-areas variability. Realized isotopic niches were similar amongst offshore areas whilst in St Georges' Channel muscle isotopic composition exhibited higher inter-individual variability. This underpins the lack of information on life history of porbeagle sharks and underlines the need of more information on the species movements to support population management in European waters.

1. Introduction

The porbeagle shark *Lamna nasus* (Bonnaterre 1788) is a widely distributed and long-lived shark species which occurs mostly in epipelagic waters from coastal areas to the open ocean (Campana and Joyce, 2004; Francis et al., 2008). During decades, it has been targeted by fisheries in the North Atlantic Ocean (Gauld, 1989; ICES, 2009), leading to a drastic decrease of populations (Campana et al., 2002). The species is listed as Vulnerable since 2006 in the IUCN Red List (Stevens *et al.*, 2006). Fisheries targeting porbeagle shark are closed in the European waters since 2010 (Council Regulation (EU), 2010), after the joint ICCAT-ICES porbeagle assessment in 2009 (ICCAT, 2010; ICES, 2009). Porbeagle sharks are considered opportunists, feeding on teleosts and cephalopods from epibenthic to pelagic communities (Belleggia et al., 2021; Ellis and Shackley, 1995; Gauld, 1989; Joyce et al., 2002; Stevens, 1973). They undergo large seasonal movements across coastal and

oceanic areas (Biais et al., 2017; Pade et al., 2009; Saunders et al., 2011), which are likely associated with spatial and temporal sex and size segregation. Indeed, from catches data over the North Atlantic Ocean, fishing area is the most important factor for size, while fishing period is the most important factor for sex distribution (Campana et al., 2010; Campana and Joyce, 2004; Jensen et al., 2002; Jung, 2008; Mejuto et al., 2020). Thus, considering the wide distribution range of the species and its foraging movement patterns over different areas, feeding sources of porbeagle sharks may vary according to space and time, and between individuals.

Tracking feeding sources of free-ranging animals has been developed for decades using stable isotopes ratios occurring naturally, such as carbon (^{13}C/^{12}C, expressed as δ^{13}C) and nitrogen (^{15}N/^{14}N, expressed as δ^{15}N) (Trueman et al., 2019). Isotopes ratios are incorporating the food webs through primary producers and propagate along the food chain through metabolic processes (Boecklen et al., 2011; Ramos and

González-Solís, 2012). δ^{13}C values varies little along the food web, and, for piscivorous feeders such as porbeagle sharks, those values mainly reflect feeding sources in relation with primary production origin (Canseco et al., 2022). In the marine environment, δ^{13}C values provide information on contribution of inshore-offshore gradient or pelagic-benthic gradient to feeding sources (Cherel and Hobson, 2007; Ramos and González-Solís, 2012). By contrast, δ^{15}N values varies along the food chain with a stepwise enrichment in heavier stable isotope (^{15}N), consequently δ^{15}N values reflect trophic position of the consumer in the food web (McCutchan et al., 2003; Post, 2002). Nonetheless, in mobile species, isotopic composition is a dynamic process relying on turnover of tissues and reflects time integrated dietary inputs from multiple food webs (Fry and Arnold, 1982), providing clues on movements across environments and wandering behaviors (Trueman et al., 2019). Turnover of white muscle in elasmobranchs has been estimated to over a year for the low growth species, *Squalus acanthias* (Logan and Lutcavage, 2010); hence, it is expected to be similar in low growth porbeagle shark. Consequently, muscle stable isotope composition of porbeagle shark does not depict the recent feeding strategy but reflects the long-term integrated assimilation of food (MacNeil et al., 2005). Consequently, muscle values would be averaged across seasonal movements of porbeagle sharks in a population depicting similar life histories across scales. Stable isotopic compositions can be described in a bi-dimensional space (δ^{13}C, δ^{15}N), so called realized isotopic niche (Layman et al., 2007; Post, 2002), thus providing a quantitative approach used to quantify intra-specific variability.

L. nasus is known to perform seasonal movements from summer grounds on the continental shelf and shelf break to wintering offshore areas (Biais et al., 2017; Campana et al., 2010; Skomal et al., 2021). The aim of our study was to compare muscle isotopic composition in porbeagle sharks caught in offshore fishing grounds where seasonal movements have been studied (Biais et al., 2017) with porbeagle sharks from inshore fishing grounds. Hence, similar realized trophic niches were expected in relation with similar seasonal movements averaging muscle isotopic composition across the Northeast Atlantic Ocean.

2. Material and method

2.1. Sample collection

Individuals of porbeagle sharks were caught by French commercial longliners targeting this species, from April to September 2008 (n = 58) and April to June 2009 (n = 93) (Table SI, Supporting Information). The fishing grounds were located along the continental shelf in the Bay of Biscay (South and North Bay of Biscay), around Belle-Ile and in the Celtic Sea (South Ireland and St Georges' Channel) (Fig. 1). The South Ireland, and North and South Bay of Biscay are offshore areas, whilst St Georges' Channel and Belle-Ile are coastal areas. The porbeagle sharks were identified on board with a label attached to the caudal fin and stored in ice until they were landed at Les Sables d'Olonne (France). At the fish market, landed porbeagles were measured (fork length, in cm) and sexed (Table 1). Dorsal white muscle was sampled on individuals and stored in ethanol 70%. Sampled porbeagle sharks were all mature and immature males and mainly immature females based on the estimated length-at-maturity of 166 cm (males) and 208 cm (females) (Jensen et al., 2002; Natanson et al., 2002), with only three individuals caught at size close to 70–90 cm, the estimated size range at birth (Francis et al., 2008; Francis and Stevens, 2000). Overview on sampling size distribution can be found in Supplementary materials (Fig. SI) and further information about the fisheries and sampling can be found in Hennache and Jung (2010, in French).

2.2. Stable isotope analysis

At the laboratory, muscle samples were dried at 50 °C for 48 h to remove ethanol. They were then crushed into fine powder. As lipids are
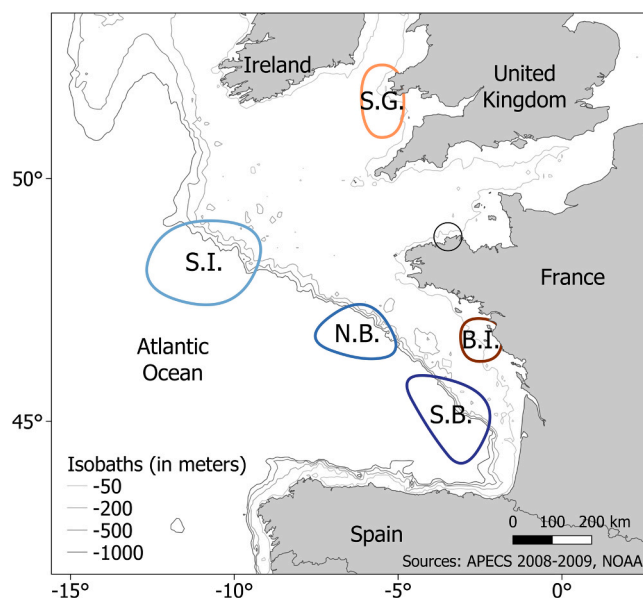

Fig. 1. Sampling areas. Sampling areas of porbeagle sharks. S.G.: St Georges' Channel, S.I.: South Ireland, N.B.: North Bay of Biscay, S.B.: South Bay of Biscay, B.I.: Belle-Ile.

Table 1
Sampling information. Size and muscle δ^{13}C and δ^{15}N values of porbeagle sharks from the five sampling areas with South Ireland, North and South Bay of Biscay as offshore areas and St Georges' Channel and Belle-Ile as coastal areas.

Area	Fork length (cm)n samples			Muscle δ^{13}C (‰)	Muscle δ^{15}N (‰)
	Females	Males	All	mean ± SD	mean ± SD
South Ireland	145 ± 46 n = 7	163 ± 26 n = 15	158 ± 34 n = 22	-17.4 ± 0.5	13.4 ± 0.8
North Bay of Biscay	189 ± 37 n = 20	176 ± 31 n = 10	185 ± 35 n = 30	-17.5 ± 0.4	13.4 ± 0.7
South Bay of Biscay	181 ± 20 n = 11	169 ± 32 n = 15	174 ± 28 n = 26	-17.4 ± 0.5	13.0 ± 0.6
St Georges' Channel	154 ± 28 n = 38	149 ± 14 n = 31	152 ± 23 n = 69	-16.9 ± 0.8	14.4 ± 0.5
Belle-Ile	146 n = 1	143 ± 5 n = 3	144 ± 4 n = 4	-17.2 ± 0.3	14.7 ± 0.1
Total	166 ± 35 n = 77	159 ± 25 n = 74	163 ± 31 n = 151	-17.2 ± 0.7	13.8 ± 0.9

depleted in ^{13}C (DeNiro and Epstein, 1978), they were extracted using cyclohexane before analysis and samples were dried out during 12 h at 50 °C. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyzer (Flash EA1112 Thermo Scientific, Italy) at the Littoral, Environment and Societies (LIENSs) Joint Research Unit stable isotope facility at the La Rochelle University, France. Results were expressed in standard δ notation based on international standards, Vienna Pee Dee Belemnite for δ^{13}C and atmospheric nitrogen for δ^{15}N, following the formula $\delta X = \left[\left(R_{sample}/R_{standard} \right) - 1 \right] \times 10^3$, where X is ^{13}C or ^{15}N and R is the ratio ^{13}C/^{12}C or ^{15}N/^{14}N.

Replicate measurements of five random samples indicate measurement errors < 0.20‰ for both δ^{13}C and δ^{15}N values.

While several studies unveiled possible confounding effect of lipids and urea on elasmobranch muscle (Carlisle et al., 2017; Hussey et al., 2012; Kim and Koch, 2012), this study was conducted in 2008 and 2009 and did not address effects of urea. However, a correction was performed on $\delta^{15}N$ values based on methodological study (unpublished data) using the following equation: $\delta^{15}N_{corrected} = 0.77 \times \delta^{15}N_{cyclohexane} + 3.4$, where $\delta^{15}N_{corrected}$ is the $\delta^{15}N$ value when sample underwent lipid and urea extraction as recommended by Li et al. (2016) and $\delta^{15}N_{cyclohexane}$ is $\delta^{15}N$ value when sample underwent cyclohexane treatment.

2.3. Statistical analysis

Due to the low number a samples in Belle-Ile area (n = 4, Table 1), those samples were excluded from the following quantitative analysis.

Independence of categorical variables sex and area was tested using Chi^2 test. Normality of quantitative variables (length, $\delta^{13}C$, $\delta^{15}N$) was tested with Shapiro-Wilk tests and variance homogeneity with Bartlett's tests. Normality and homoscedasticity were assessed for individual length distribution solely. Therefore, Two-Way ANOVAs were performed to test effect of sex and area on individual length. Correlations between individual length and $\delta^{13}C$ and $\delta^{15}N$ values were performed using a Spearman's rank correlation. All results from tests were judged significant when $p < 0.05$. Values are means ± SD.

Since multivariate normality assumption was not met for stable isotope ratios, a Bayesian posterior distribution of muscle $\delta^{13}C$ and $\delta^{15}N$ values was estimated for each area using a vague prior following a Normal Inverted Wishart distribution (R package *nicheROVER*, (Swanson et al., 2015)). Using Bayesian framework provided estimates of niche areas, known as corrected standard ellipse areas (Jackson et al., 2011), that are insensitive to sample size. Overlap metric of niches and associated Credible Intervals (CI) were calculated from wider niche areas provided by 100,000 draws from inferred posterior distributions. Values are means ($CI_{95\%}$).

Statistical analyses were conducted using R 4.2 (Core Team, 2023).

3. Results

Muscle $\delta^{13}C$ and $\delta^{15}N$ values were measured on 151 porbeagle sharks (Table 1). Spatial sampling was unbalanced with 69 individuals analyzed from St Georges' Channel and only four from Belle-Ile. Males and females numbered 74 and 77, respectively. Nevertheless, area had a significant effect on length (Two-way ANOVA $p << 0.01$), unlike sex compositions and combined variables (Two-way ANOVA $p = 0.34$ and 0.36, respectively). No significant correlation was found between isotopic values ($\delta^{13}C$ and $\delta^{15}N$) and individual length (Spearman's rank test, $\rho < 0.01$ and $\rho = -0.12$, respectively, both $p > 0.05$). No significant effect of sex on $\delta^{13}C$ and $\delta^{15}N$ values were detected (Kruskal-Wallis test, $p = 0.2$ and 0.3, respectively).

Overall, muscle $\delta^{13}C$ values ranged from -18.5 to $-13.8‰$, and $\delta^{15}N$ from 11.3 to 15.7‰ (Table 1). Muscle $\delta^{13}C$ value in the coastal area of St Georges' Channel ($-16.9 \pm 0.8‰$) was significantly higher than in the offshore areas: South Ireland ($-17.4 \pm 0.5‰$, Mann-Whitney $p < 0.01$), North Bay of Biscay ($-17.5 \pm 0.4‰$, Mann-Whitney $p << 0.01$) and South Bay of Biscay ($-17.4 \pm 0.5‰$, Mann-Whitney $p << 0.01$). Biplot of stable isotopes ratios and their marginal distribution (Fig. 2) indicated variations in muscle $\delta^{15}N$ values distribution amongst sites whilst muscle $\delta^{13}C$ values distribution exhibits less variation. Most of the muscle $\delta^{13}C$ and $\delta^{15}N$ values were packed in the normal distribution range delineated by ellipses. However, five immature females ranging from 126 to 170 cm and one immature male of 157 cm, all sampled in the coastal area of St Georges' Channel, were visibly outside ellipses due to higher $\delta^{13}C$ values ranging from -15.5 to $-13.8‰$.

Offshore isotopic niches depicted strong overlap between areas. Hence, South Ireland's isotopic niche strongly overlapped North and South Bay of Biscay's niches, 96% with $CI_{95\%} = [86,100]\%$ and 92% with $CI_{95\%} = [77,99]\%$, respectively (Fig. 3). In contrast, coastal
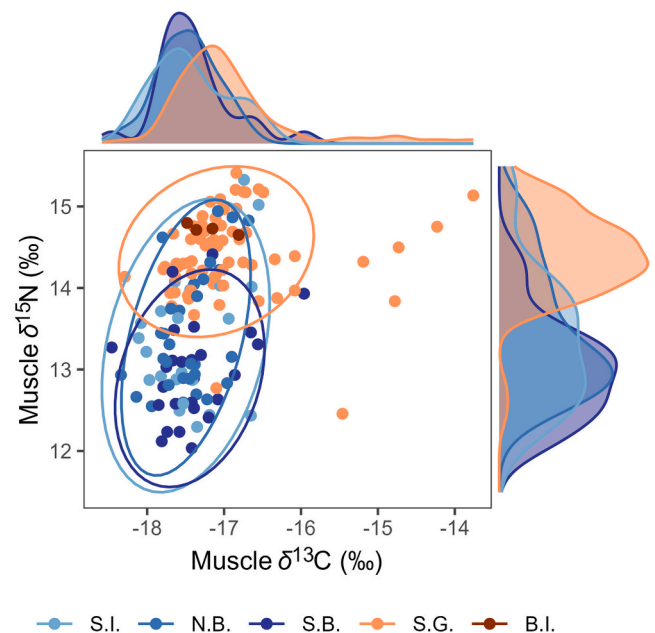

Fig. 2. Muscle $\delta^{13}C$ and $\delta^{15}N$ biplot. Muscle $\delta^{13}C$ and $\delta^{15}N$ values, 95%-ellipses and marginal distribution within each sampling area. S.G.: St Georges' Channel, S.I.: South Ireland, N.B.: North Bay of Biscay, S.B.: South Bay of Biscay, B.I.: Belle-Ile. Belle-Ile samples are only plotted in the biplot without ellipse due to low sample size (n = 4). Shades of blue are offshore areas while shades of orange are inshore areas.

isotopic niche of St Georges' Channel exhibited lower overlap with other isotopic niches of South Ireland (58%, $CI_{95\%} = [39,77]\%$), North Bay of Biscay (63%, $CI_{95\%} = [45,81]\%$) and South Bay of Biscay (37%, $CI_{95\%} = [19,59]\%$). These overlaps are likely driven by differences in $\delta^{15}N$ values (Fig. 2). Offshore Bay of Biscay areas were overlapping in the same magnitude of values: South Bay of Biscay isotopic niche encompassed 81% of North Bay of Biscay isotopic niche with $CI_{95\%} = [68,97]\%$ and North Bay of Biscay encompassed also 85% of South Bay of Biscay with $CI_{95\%} = [63,94]\%$.

4. Discussion

4.1. Sampling and method

Porbeagles were sampled from spring to autumn during the species' fishing season of the French longline fleet. Therefore, our study provides information restricted to the fishing season and fishing area based on fishers' empirical knowledge of optimal fishing grounds. Hence, it did not cover the whole year and did not represent the entire distribution range of the porbeagle shark population in the Northeast Atlantic. Indeed, this population is considered as homogeneous across the NE Atlantic Ocean, with limited exchanges with NW Atlantic Ocean population (González et al., 2021; Testerman, 2014). Another limitation is that only four porbeagle sharks have been sampled in Belle-Ile coastal area; they can be considered as preliminary observations that merit further investigation.

Muscle samples were stored in ethanol 70%, which can potentially affect stable isotope values (Burgess and Bennett, 2017; Kim and Koch, 2012; Olin et al., 2014). Nevertheless, several studies on a variety of biological models, including elasmobranchs used the same sample conservation protocol mostly for logistical reasons (Argüelles et al., 2012; Chan et al., 2022; Lelièvre et al., 2018), and without any significant alteration of the isotopic composition of tissues (Hobson et al., 1997; Kelly et al., 2006; Kim et al., 2012b). Moreover, all our samples underwent the same treatment, which make unlikely the introduction of any comparative bias into the results.
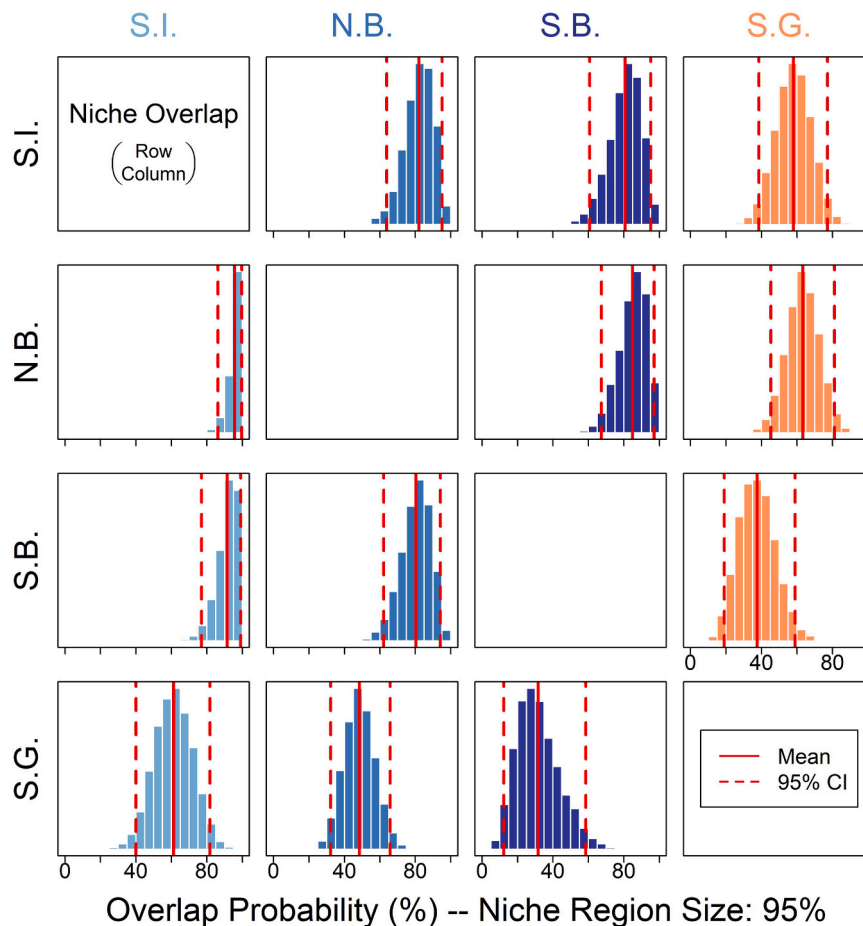
Fig. 3. Niche overlap between sampled areas. Niche overlap between offshore areas (blue shades) and inshore area (orange) based on Bayesian posterior probabilities. The overlap reflected the percentage of estimated isotopic niche from areas in row encompassed in the estimated isotopic niche from areas in column.

4.2. No influence of sex and size

Muscle isotopic values of porbeagle shark reflect dietary inputs integrated over a period probably exceeding a year, considering its large size when compared to species on which estimates are available (Kim et al., 2012a; Logan and Lutcavage, 2010). Consequently, the stable isotope composition of this tissue is unlikely to be strongly affected by seasonal diet variations, even though the isotopic values of prey consumed over the last months should dominate the shark values (Ballutaud et al., 2022). The porbeagle shark is considered as a generalist pelagic/demersal feeder, whose diet is generally dominated (up to 90%) by teleosts, with cephalopods as a secondary prey throughout its distribution range (Belleggia et al., 2021; Ellis and Shackley, 1995; Joyce et al., 2002). Around the coasts of Great Britain, its diet is dominated by mackerels (*Scomber* spp.), clupeids, epibenthic teleosts and cephalopods (Ellis and Shackley, 1995; Gauld, 1989). The diet of porbeagle shark has been reported to be consistent among sexes in the NW Atlantic, with seasonal variability associated to foraging in shallower waters in autumn (Joyce et al., 2002). Accordingly, no isotopic difference was detected among sexes in any of the five sampling areas in the NE Atlantic, which suggest that whenever they are present in sympatry, there is no sex-related resource partitioning in porbeagle sharks. Temporary trophic specialization associated with sex segregation, a feature of porbeagle shark ecology (Campana et al., 2010; Jensen et al., 2002), yet cannot be totally ruled out, even though the time-integrating nature of stable isotopes in muscle makes it unlikely on the analyzed population. The foraging behavior of porbeagle is expected to vary with growth in relation with jaw gape size, as observed in other pelagic species, such as blue shark *Prionace glauca* (Estupiñán-Montaño et al., 2019) or the

related white shark *Carcharodon carcharias* (Cortés, 1999). However, no isotopic shift related to likely ontogenic dietary shift was found in porbeagle sharks in our study, which is in line with results obtained in the Southwest Atlantic Ocean (Belleggia et al., 2021). This is probably related to embryonic development of jaws and teeth in *L. nasus* with free-swimming young exhibiting jaws and dentition with similar variations as large mature porbeagle sharks (Bemis et al., 2015; Francis and Stevens, 2000; Shimada, 2002). Consequently, immature and mature porbeagle have no morphological limitation to exhibit similar diets. Nonetheless, due to our unbalanced sampling of sizes for both males and females, more information is needed on small individuals of both sexes and on mature females to confirm the absence of ontogenic dietary shift in porbeagle sharks in the NE Atlantic.

4.3. Spatial isotopic overlap

The main difference of porbeagle shark isotopic niches amongst areas was related to the distance to the shore, with more positive muscle $\delta^{13}C$ and $\delta^{15}N$ values in coastal (St Georges' Channel and Belle-Ile) than offshore individuals. Thus, porbeagle sharks spent enough time (months) in these different areas to exhibit significant differences in their muscle isotopic composition. Higher $\delta^{13}C$ values in coastal than offshore sharks were likely related to the well-known inshore/benthic-offshore/pelagic gradient in $\delta^{13}C$ particulate organic matter that propagate all along the food web (Cherel and Hobson, 2007; France, 1995; McMahon et al., 2013). Indeed, high $\delta^{13}C$ values are generally associated to coastal habitats driven by benthic food webs, whilst offshore areas are more likely plankton-based food webs with lower $\delta^{13}C$ values (Chouvelon et al., 2012; France, 1995; Nerot et al., 2012).

The porbeagle sharks $\delta^{15}N$ values were consistent with a relatively high trophic level in line with their diet on small and medium teleosts and cephalopods (Layman et al., 2015; Post, 2002). However, Bay of Biscay is a spatio-temporally dynamic environment that affects the $\delta^{15}N$ baseline (Chouvelon et al., 2012; Nerot et al., 2012; Post, 2002) and therefore, $\delta^{15}N$ values should be interpreted with caution. Spatial models of variation in isotopic baselines, namely isoscapes, do not have yet sufficient spatial resolution to support *a posteriori* baseline estimates for our study (Magozzi et al., 2017; McMahon et al., 2013). Nevertheless, baseline $\delta^{15}N$ values generally decrease from coastal to offshore areas and this difference also propagates along the food web (Chouvelon et al., 2012), in line with the variations of $\delta^{15}N$ values observed in our study. This support hypothesis of spatial intra-population differences with long-term diets likely reflecting long-term associations to offshore or coastal areas.

Porbeagle sharks are considered as opportunist feeders (Belleggia et al., 2021; Ellis and Shackley, 1995), therefore the range of $\delta^{13}C$ and $\delta^{15}N$ values across individuals feeding in similar areas in the similar proportion of prey should be relatively narrow according to Matthews and Mazumder (2004). In addition, Bird et al. (2018) suggest that shelf sharks such as *L. nasus* are generalist consumers feeding on distinct food webs but largely dependent on foraging within shelf areas with some individuals being more specialists than others. Indeed, in our study, the ranges of $\delta^{13}C$ values in *L. nasus* are relatively narrow in the offshore areas ($2.0 \pm 0.5‰$) with little inter-individual variations amongst areas supporting the hypothesis of similar diet across space and time. However, porbeagle sharks caught in St Georges' Channel exhibit greater $\delta^{13}C$ range ($4.5‰$) in association with higher inter-individual variability. This inter-individual variability might be related to greater differences in their feeding habits within the area (Bird et al., 2018) or different past migration patterns (Abrantes and Barnett, 2011). Indeed, heterogeneity in stable isotope compositions within an area could also be related to staging arrival or to different previous individuals' life histories (Abrantes and Barnett, 2011). As shown by tracking studies (Biais et al., 2017; Pade et al., 2009; Saunders et al., 2011), *L. nasus* does not permanently reside in a given area and realizes seasonal migration out of the sampled areas for winter but returns to sampled shelf break next spring/summer. However, the migration of coastal porbeagle sharks from the St Georges' Channel remains unknown, as well as patterns of movement between strictly coastal and offshore areas in the Northeast Atlantic for porbeagle shark population. Seemingly, some immature porbeagle sharks from this area were exhibiting isotopic compositions diverging from the isotopic composition of their mature and immature counterparts. Consequently, further analyses on different time-integrating tissues such as blood, liver and muscle (Logan and Lutcavage, 2010; MacNeil et al., 2005) should help elucidate the heterogeneity observed, in association with tracking studies focusing on porbeagle sharks frequenting coastal areas.

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CRediT authorship contribution statement

Sandrine Serre: Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Armelle Jung:** Conceptualization, Methodology, Experimental design, Investigation, Writing – review & editing, Funding acquisition. **Yves Cherel:** Resources, Methodology, Experimental design, Writing – review & editing. **Caroline Gamblin:** Resources, Writing – review & editing, Project administration, Funding acquisition. **Cédric Hennache:** Investigation, Writing – review & editing, Project administration. **François Le Loc′h:** Supervision, Resources, Writing – review & editing. **Anne Lorrain:** Supervision, Resources, Methodology, Experimental design, Data analysis, Writing – review & editing. **Anne Priac:** Data analysis, Investigation, Writing – review & editing. **Gauthier Schaal:** Supervision, Resources, Writing – review & editing. **Éric Stephan:** Supervision, Resources, Writing – review & editing.

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.

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2023.103340.

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