



Trophic ecology and coastal niche partitioning of two sympatric shark species in the Azores (mid-Atlantic)

C. Robert Priester^{1,*}, Jan Dierking², Thomas Hansen³, David Abecasis⁴,
Jorge M. Fontes¹, Pedro Afonso¹

¹Institute of Marine Sciences–OKEANOS, University of the Azores, 9901-862 Horta, Portugal

²Marine Ecology, GEOMAR Helmholtz Centre for Ocean Research Kiel, 24105 Kiel, Germany

³Central lab for Chemical Analysis (ZLCA), GEOMAR Helmholtz Centre for Ocean Research Kiel, 24105 Kiel, Germany

⁴CCMAR–Centre of Marine Sciences, University of Algarve, 8005-139 Faro, Portugal

ABSTRACT: The exploitation of marine resources has caused drastic declines of many large predatory fishes. Amongst these, sharks are of major conservation concern due to their high vulnerability to overfishing and their ecological role as top predators. The 2 protected and endangered shark species tope *Galeorhinus galeus* and smooth hammerhead *Sphyrna zygaena* use overlapping coastal areas around the globe as essential fish habitats, but data to assess their trophic ecology and niche partitioning are scarce. We provide the first comparative assessment of the trophic ecology, ontogenetic shifts, and niche partitioning of the co-occurring tope and juvenile smooth hammerhead around the Azores Islands, mid-north Atlantic, based on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ (CNS) stable isotope analysis of muscle tissue of the sharks and their putative prey species. Overall, isotopic niches of both species indicated a reliance on similar resources throughout the sampled sizes (tope: 35–190; smooth hammerhead 54–159 cm total length), with significant ontogenetic shifts. Topes displayed a gradual shift to higher trophic levels and a more generalist diet with increasing size (increasing $\delta^{15}\text{N}$ values and isotopic niche volumes, respectively), whereas smooth hammerhead diet shifted towards prey with lower $\delta^{34}\text{S}$ at a constant trophic level and a more specialized diet than tope of comparable body size (decreasing $\delta^{34}\text{S}$ and constant $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively). Our results indicate contrasting ontogenetic shifts in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ along with pronounced differences between niche overlap of life stages pointing to intra- and interspecific niche partitioning of habitat and prey.

KEY WORDS: *Sphyrna zygaena* · *Galeorhinus galeus* · Carbon · Nitrogen · Sulfur · Stable isotope analysis · Isotopic niche · Essential fish habitats · Shark nursery

1. INTRODUCTION

In recent decades, overfishing and climate change have caused significant declines of large predatory shark species (Dulvy et al. 2021, Pacoureau et al. 2021), which are particularly vulnerable due to life-history characteristics such as low fecundity, late maturity,

high longevity, and wide-ranging migratory patterns (Frisk et al. 2005, Dulvy et al. 2014, Gallagher et al. 2014). Sharks play a key ecological role in ecosystems through the balancing and controlling of populations at lower trophic levels (Heithaus et al. 2012). Their loss can therefore provoke top-down cascading effects that often reverberate through entire food webs

*Corresponding author: email: robert.priester@posteo.de

(Ferretti et al. 2010, Heithaus et al. 2012). The protection of critical habitats for shark spawning, breeding, feeding or growth to maturity, also often termed 'essential fish habitats' (EFHs), can help to slow these declines (Knip et al. 2012, Martín et al. 2020). The integration of EFHs into ecosystem-based management has thus been emphasised as a key factor for attaining sustainable fisheries management and legislation (Hueter et al. 2005, Speed et al. 2010). Incorporating EFHs into such conservation efforts requires empirical data about their location and role in the species' life cycle. Nevertheless, assessments of most shark populations remain data deficient with regards to their ecology and habitat use (Castro et al. 1999, IUCN 2018), thus preventing the identification of EFHs and hampering conservation efforts (Dulvy et al. 2017, Heupel et al. 2018).

The Azores are an oceanic archipelago situated in the mid-north Atlantic within the confluence of productive temperate waters and the subtropical Azores current (Amorim et al. 2017, Caldeira & Reis 2017). These islands have been identified as a marine megafauna hotspot (Afonso et al. 2020) and are a high conservation priority. They harbour a wide diversity of sharks in high abundance (Das & Afonso 2017) and provide EFHs for some of these species, including nursery areas (Vandeperre et al. 2014, Afonso et al. 2022). These shark nurseries are typically characterised by regular and high abundances of juveniles and mature females (Heupel et al. 2007) and are often used communally by several shark species (Simpfendorfer & Milward 1993, Heupel et al. 2019). Understanding shark ecology, including trophic interactions during the time spent within EFHs, would help to fill critical knowledge gaps in the Azores archipelago and thus support the establishment of effective marine protected areas (MPAs) (Afonso et al. 2020, Torres et al. 2014).

Shark species of high conservation concern in the North Atlantic and the Azores include the tope *Galeorhinus galeus* (Linnaeus, 1758) (IUCN status Critically Endangered, Walker et al. 2020; Convention on the Conservation of Migratory Species of Wild Animals [CMS] listed Appendix II) and the smooth hammerhead *Sphyrna zygaena* (Linnaeus, 1758) (IUCN status Vulnerable, Rigby et al. 2019; Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES] listed Appendix II; CMS listed Appendix II). The tope is a cosmopolitan predator typically found in temperate waters (Cox & Francis 1997, Ebert & Stehmann 2013), with juveniles occurring mostly in shallow waters and adults in shelf and oceanic waters (Thorburn et al.

2019, Schaber et al. 2022), capable of occasional long-distance oceanic migrations (Holden & Horrod 1979, Colloca et al. 2019, Thorburn et al. 2019). The smooth hammerhead is a cosmopolitan predator of tropical to warm-temperate waters (Compagno 1984, Santos & Coelho 2018), with juveniles using coastal waters and the highly migratory adults inhabiting the open ocean (Compagno 1998). Little is known about this species compared to the closely related scalloped hammerhead *S. lewini* (Camhi et al. 2009). Both shark species have been found to occupy similar or overlapping habitats along various coasts of the world (Smith & Benson 2001, Watson 2013, Gonzalez-Pestana et al. 2021). In the Azores, the year-round presence in coastal waters and aggregations of young-of-the-year (YOY; animals less than 1 yr old) and immature juveniles of these 2 species suggest the presence of pupping grounds and coastal nurseries in shallow waters (Afonso et al. 2022, D. Das et al. unpubl. data). However, our understanding of their coastal habitat preferences and resource use throughout their ontogeny (i.e. growth and development) remains scarce (Das & Afonso 2017, Afonso et al. 2020, GAMPA 2020, Santos et al. 2020), impeding their conservation in the North Atlantic.

Bulk stable isotope analysis is a powerful tool to assess animal trophic ecology, diet, and habitat use (Hobson 1999, Boecklen et al. 2011), including valuable ecological information on the 2 study species (Table 1). The ratio of heavy to light stable isotopes in tissues is commonly used to infer time-integrated diet-related proxies based on the concept 'you are what you eat' (Peterson & Fry 1987). Stable isotope analysis of carbon (C) and nitrogen (N) has been most frequently used to assess shark trophic ecology with complementary properties that facilitate ecological interpretations: $\delta^{13}\text{C}$ (the ratio between ^{13}C and ^{12}C isotopes) undergoes little fractionation when assimilated into consumer tissue and thus reflects the signatures of primary producers at the base of food webs (DeNiro & Epstein 1978, Fry & Sherr 1989). Hence, contrasting $\delta^{13}\text{C}$ values of different primary producers can be used to draw inferences on the trophic ecology of consumers. Pronounced $\delta^{13}\text{C}$ gradients lie between coastal and offshore primary producers (Peterson & Fry 1987, Perry et al. 1999) and demersal and pelagic producers (France 1995). By contrast, $\delta^{15}\text{N}$ (the ratio between ^{15}N and ^{14}N) increases with each trophic transfer and thus is often used to infer trophic positions (DeNiro & Epstein 1981, Hobson 1993). Sulphur (S) stable isotope analysis can be a powerful tracer to differentiate between pelagic versus demersal and offshore versus coastal primary

Table 1. Summary of peer-reviewed stable isotope analysis articles of the study species tope (GG) and smooth hammerhead (SZ). TP: trophic position. Isotope and TP values given as: mean, mean \pm SD or (minimum–maximum)

Source	Species	Location	Isotopes	Tissues	N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	TP	Context
Alfaro-Cordova et al. (2018)	GG, SZ	Peru	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	11	GG: -14.7 ± 0.6	15.0 ± 1.1	GG: 4.4 ± 0.3	Interspecific trophic interactions, niche overlapping with 2 other species
					45	SZ: -15.7 ± 0.5	15.7 ± 1.9	SZ: 4.5 ± 0.4	
Besnard et al. (2023)	SZ	Mexico	$\Delta^{199}\text{Hg}$, $\Delta^{200}\text{Hg}$, $\Delta^{201}\text{Hg}$	Muscle	102				Ontogenetic diet shift to offshore mesopelagic prey and associated timing
Botto et al. (2011)	GG	Argentina and Uruguay	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	1	-16.2	19.5		Trophic structure of an estuarine ecosystem
Davenport & Bax (2002)	GG, SZ	Australia	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	13	GG: -17.0 ± 0.6	GG: 13.3 ± 0.5		Trophic structure of larger ecosystem
					1	SZ: -16.8	SZ: 14.2		
Domi et al. (2005)	GG	Celtic Sea	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	6	-15.5 ± 0.5	16.7 ± 0.9		Feeding ecology of 5 commercial shark species
					6	-16.1 ± 0.6	14.2 ± 1.04		
Li et al. (2018)	SZ	Central Eastern Pacific	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	20	-15.9 ± 0.2	16.1 ± 1.3	4.7 ± 0.8	Trophic niche and position
Loor-Andrade et al. (2015)	SZ	Peru	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	64	-16.1 ± 0.4	14.8 ± 0.8		Trophic niche overlap with scalloped hammerhead
					20	-13.4 ± 0.7	12.4 ± 1.8		
Miller et al. (2010)	GG	California, USA	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	1	-16.5	15.4	3.8	Trophic structure of larger ecosystem
Ochoa Diaz (2009)	SZ	Mexico	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	38	(-14.9 to -15.8)	(17.64 – 19.86)	(3.7 – 4.1)	Trophic spectrum of SZ
Pantoja-Echevarría et al. (2022)	SZ	Mexico	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	4	-17.9 ± 0.5	18.4 ± 0.9		Trophic niche overlap of 3 sympatric sharks
Segura-Cobena et al. (2021)	SZ	Peru	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	43	-16.0 ± 0.7	15.8 ± 0.4		Trophic niche overlap between nurseries
					44	-17.9 ± 1.3	14.2 ± 0.5		
Torres et al. (2014)	GG	Azores	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Muscle	124	(-18.6 to -17.2)	(12.3 – 14.8)	(4.0 – 4.4)	Trophic and feeding ecology
Valdez et al. preprint https://doi.org/10.21203/rs.3.rs-1631337/v1	SZ	Japan	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Dental collagen	12	-14.4 ± 0.6	12.2 ± 0.8		Trophic niche width of several shark species

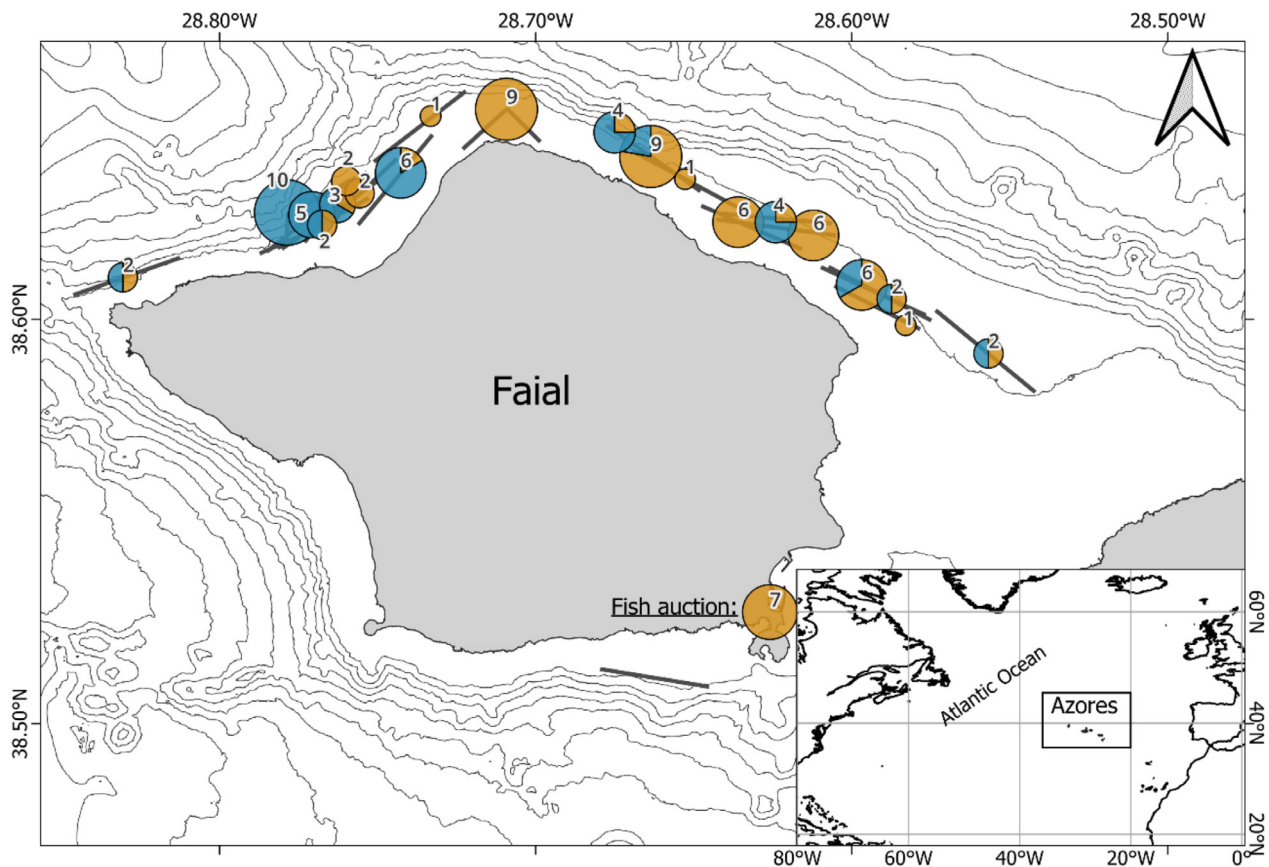


Fig. 1. Sample locations, with black bars showing deployed longlines. Pie charts represent the proportion of smooth hammerhead (blue) and tope samples (brown); numbers: number of respective shark samples. Grey contours: 100 m depth intervals

production, and it can add power when $\delta^{13}\text{C}$ values alone are inconclusive (Connolly et al. 2004, Szpak & Buckley 2020). Three-element (CNS) stable isotope data can thus be analysed in a multidimensional space (see Swanson et al. 2015, Rossman et al. 2016) for a more accurate estimation and subsequent comparison of isotopic niche characteristics (Shipley & Matich 2020).

In this study, we investigated the trophic ecology and resource use of tope and immature smooth hammerhead around the Azores Islands. We analysed CNS stable isotope data of the 2 shark species and putative prey species and then used 3D Bayesian ellipse niche analysis to characterise and compare the trophic niches, ontogenetic shifts, and inter- and intra-specific isotopic niche partitioning. This study constitutes the first comparative study of the trophic ecology of these 2 commonly co-occurring shark species of high conservation concern and provides a much-needed baseline for the scarcely studied smooth hammerhead in the Atlantic.

2. MATERIALS AND METHODS

2.1. Shark sampling

Live sharks were sampled non-lethally between 2013 and 2019 during tagging campaigns on the north shore of Faial Island, Azores, Portugal (Fig. 1). Additional samples were collected opportunistically from dead specimens captured on the island shelf and sold at the local fish auction. All sampling was conducted according to Portuguese laws for the use of vertebrates in research and the guidelines for the use of fishes in research of the American Fisheries Society. The handling and sampling protocols were approved by the Azorean Directorate of Sea Affairs of the Azores Autonomous Region (permits DRAM/SRRN ref. 24/2010). Sharks were caught with modified bottom-anchored longlines set on the island shelf (Fig. 1) at depths between 160 and 40 m. Longlines had an average length of 2 nautical miles with approximately 100 circle hooks (size 9/0, baited with squid) every

30–40 m. To reduce the impact on the particularly sensitive smooth hammerhead, soak times were limited to a maximum of 3 h (mean: 1 h 50 min) between setting start and continuous hauling. All sharks were landed on deck using a scoop net, de-hooked using a hook remover and retained in a large onboard rehabilitation tank (ca. 5000 l) filled with continuously replenished oxygen-saturated saltwater. Once the sharks had recovered from capture stress (showing unimpeded reflexes; see Davis 2010), they were put into tonic immobility (state of cessation of movements except rhythmic breathing and vision when the sharks' ventral side is facing up; Henningsen 1994) and placed on a wet surgery mat with their eyes covered and a constant seawater flow over the gills. Here, they were measured (unstretched total length [TL], fork length, pre-caudal length, sex, maturity stage, and hook position) and tagged for a concurrent study (for more details see Afonso et al. 2022). Muscle samples were excised from the dorsal side of the body close to the dorsal fin using a 6 mm biopsy punch or a scalpel. All open wounds were washed with seawater and treated with povidone-iodine (Harms 2005). After sampling and tagging (never exceeding a handling time of 5 min), sharks were taken out of tonic immobility and kept in the rehabilitation tank until they showed unimpeded natural reflexes. Then they were released back into the sea within the longline set area. Samples for stable isotope analysis were stored in 2 ml Eppendorf vials and kept on ice until returning to the laboratory, where they were frozen at -20°C until being freeze-dried. Tope sampled at the local fish auction were measured as described above, and muscle was excised using a clean scalpel. Even though the exact capture locations were not disclosed, it was confirmed that they were caught on the Faial Island shelf.

2.2. Food web samples

Samples of representative prey taxa of the Azorean marine food webs were analysed to assess the overlap of sharks with 3 different food webs: coastal, demersal, and epipelagic. Samples were taken from by-catch obtained during the shark longline tagging campaign, the catch of recreational coastal fishermen on the island of Faial in 2019 and 2020, and a benthic longline set from the island shelf of Faial as part of the annual multi-specific fisheries research cruise ARQDAÇO2020 in 2020 (for details see Pinho et al. 2020). Muscle tissue was sampled from all teleosts, and mantle tissue was sampled from cephalopods. Species were classified as coastal, demersal, or epi-

pelagic, and trophic positions based on local literature (GAMPA 2020 and references therein) and Fish-Base (Froese & Pauly 2010).

2.3. Stable isotope analysis

Samples were pre-processed in the laboratory in the Azores and analysed in the Central Lab for Chemical Analysis (ZLCA) at the GEOMAR Helmholtz-Centre for Ocean Research Kiel, Germany. Pre-processing followed Kim & Koch (2012) by extracting urea from muscle samples by washing and sonicating with 10 ml of de-ionized water for 3 consecutive cycles. No lipid extraction was conducted since acidification during chemical lipid extraction processes has been shown to alter the S isotope ratios (Connolly & Schlacher 2013). Freeze-dried samples were sent to GEOMAR, where they were ground to a fine powder for homogenization. A mass of $50 \pm 10 \mu\text{g}$ of tissue was weighed using a micro-scale (MC 5 Micro Balance; Sartorius) and placed into tin cups ($3.2 \times 4.0 \text{ mm}$, Hekatech). Vanadium oxide (V_2O_5) was added ($400 \pm 100 \mu\text{g}$) into the tin cups as a catalyst to ensure complete oxidation of S. These were then folded, compressed to small cubes, and stored in 96-well plates for mass spectrometry analysis. Samples were analysed by a high-sensitivity elemental analyser (HSEA) connected to an isotope ratio mass spectrometer (DeltaPlus Advantage, Thermo Fisher Scientific) as described by Hansen et al. (2009). The measured isotope ratios are expressed as δ values in per mil deviation (‰) from the standard reference material Vienna Pee-Dee Belemnite (VPDB), atmospheric nitrogen, and Vienna Canyon Diablo Troilite (VCDT):

$$\delta X (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$$

where X stands for ^{13}C , ^{15}N , or ^{34}S and R represents the respective ratios ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, $^{34}\text{S}/^{32}\text{S}$). System calibration was implemented by the combustion of International Atomic Energy Agency (N1-, N2-, NO3-) and National Institute of Standards and Technology (NBS-22 and NBS-600) compounds. All $\delta^{34}\text{S}$ values were calculated against primary standards IAEA-S1, IAEA-S2, NBS123 and NBS127 and laboratory standards (LS) CdS and hay powder. Analyses of the LS hay powder during all measurements within the range of 20–100 mg C, 2.5–8.0 mg N, and 0.3–0.9 mg S, with an overall precision of $\pm 0.2\text{‰}$ (mean SD) for $\delta^{13}\text{C}$, $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$, and $\pm 0.4\text{‰}$ for $\delta^{34}\text{S}$. Calculations of the stable isotope values were performed by the ISODAT (Thermo Fisher) software. Carbon ratios were mathematically lipid-corrected following Carlisle et al. (2017)

using the linear model of Logan et al. (2008) with class-specific parameters (see Text A1 in the Appendix).

2.4. Data analysis

2.4.1. Ecologically meaningful life stage classification

Ecologically meaningful size classes were first defined for both shark species, based on published size at maturity and growth curves (Table 2). All individuals were assigned a class, ranging from YOY, juvenile, subadult, to adult; YOY included all smaller sharks up to the corresponding TL of 1 yr of age, as per growth curves established by McMillan et al. (2021) and Rosa et al. (2017). The juvenile size class, when sharks are assumed to bear a pure signature of juvenile habitat and diet, included individuals > 1 yr of age up to the onset of maturity (minimum size at maturity: 108 and 210 cm for tope and smooth hammerhead respectively; Table 2). The subadult size class included the size spectrum from minimum to maximum size at first maturity. All individuals larger than the maximum size at first maturity were considered adults. No smooth hammerhead larger than the minimum size at maturity were captured. Thus, all smooth hammerheads were considered immature (in the case of males, verified *in situ*) and hence limited to YOY and juveniles. We distinguished YOY from juvenile sharks, as new-born shark muscle proteins are expected to be influenced by maternal isotopic signatures for up to 1 yr (Olin et al. 2011).

2.4.2. Statistical analysis

Isotope distributions of shark and food web items were displayed as biplots to assess positioning in isotope space. Two outliers (one tope and one pelagic food web sample) were excluded from the analysis due to biologically unrealistic $\delta^{13}\text{C}$ values (> 50‰, tope) and very high lipid content (C:N ratio > 10, pelagic sample).

The distribution of consumer and prey values in isotope space was inspected to assess the assumptions and applicability of stable isotope diet mixing models (Phillips et al. 2014). Differences between coastal, demersal, and pelagic prey means were assessed with Kruskal-Wallis tests and post hoc Dunn tests. Then, prey isotope values were corrected using mean diet–tissue discrimination factors (DTDFs) and their respective standard deviations from Post (2002) and McCutchan et al. (2003) and were plotted using the MixSIAR package (Stock et al. 2018). Only one shark sample fell within the mixing polygons on all 3 axes (see Fig. 2). Shark mean values were approximately 2.2‰ more enriched in $\delta^{13}\text{C}$, 2‰ more enriched in $\delta^{15}\text{N}$, and approximately 0.5‰ more depleted in $\delta^{34}\text{S}$ compared to the original prey sample mean. Due to the violation of various assumptions underlying mixing models (i.e. consumer values mostly lying outside of mixing polygons, insignificant differences between some prey groups; see Phillips et al. 2014) and several confounding uncertainties concerning DTDFs and baseline shifts between sampling years, these models were not developed further.

Differences between means of each isotope per life stage were examined using Kruskal-Wallis and Mann-Whitney *U*-tests for non-normally distributed groups with unequal variances (assessed using Shapiro-Wilk, quantile-quantile plot, and Levene's tests respectively) and the Student's *t*-test for differences in *C* between the smooth hammerhead life stages (the only group with normal distribution and homogenous variances). The effect of sex and year on isotope values was assessed for each species and isotope using permutational multivariate analysis of variance (PERMANOVA). Each isotope was analysed as a function of TL in interaction with sex and, in a separate model, TL as interaction with year, using 999 permutations and the Bray-Curtis dissimilarity index (R package 'vegan'; Oksanen et al. 2013). The isotopic niches of our study species were compared using Bayesian standard ellipses given their statistical robustness to compare the distribution, variability, and propagated uncertainties of stable isotope data in isotope space. We

Table 2. Life stage definition, sizes in total length (TL), and corresponding references for tope and smooth hammerhead. NA: not available

	Tope	Smooth hammerhead
Young-of-the-year	≤ 71 cm TL (supplementary data in McMillan et al. 2021)	≤ 80.2 cm TL using von Bertalanffy growth function with fixed birth size (Rosa et al. 2017)
Juvenile	71–107 cm TL	> 80.2 cm TL
Subadult	108–125 cm TL (Lucifora et al. 2004)	NA (length at maturity: 210–265 cm TL; Froese & Pauly 2010)
Adult	> 125 cm TL	NA

calculated 3D Bayesian ellipse volumes (SEV_B) and their respective overlaps using the R functions of Skinner et al. (2019), who adapted SIBER standard ellipse area calculations of Jackson et al. (2011) for 3D data sets. For all SEV_B calculations, we used 3 chains of 100 000 iterations with a burn-in of 10 000, thinning of 25, and the default uninformative priors. All data analysis was performed in R (R Core Team 2013) using significance levels of $\alpha = 0.05$.

3. RESULTS

Tope ($n = 54$; 28 females, 26 males; 35–190 cm TL) covered an isotopic space ranging from -17.8 to

-13.9‰ in $\delta^{13}\text{C}$, 10.4 to 16.2‰ in $\delta^{15}\text{N}$, and 16.2 to 19.9‰ in $\delta^{34}\text{S}$. By comparison, smooth hammerhead ($n = 36$; 22 females, 14 males; 54–159 cm TL) covered a space ranging from -17.4 to -14.0‰ in $\delta^{13}\text{C}$, 10.3 to 13.4‰ in $\delta^{15}\text{N}$, and 13.8 to 21.1‰ in $\delta^{34}\text{S}$ (Table 3). Overall isotope means of the 2 shark species indicated differences in C and N space (Mann-Whitney U -test $\delta^{13}\text{C}$: $U = 700$, $p < 0.05$, $\delta^{15}\text{N}$: $U = 621$, $p < 0.01$) but showed a high overlap of the 3D standard ellipse volumes (SEV_B overlap $\geq 44\%$; Fig. 2). The prey species analysed covered an overall isotopic space ranging from -20.3 to -13.5‰ in $\delta^{13}\text{C}$, 6.5 to 18.2‰ in $\delta^{15}\text{N}$, and 16.9 to 20.4‰ in $\delta^{34}\text{S}$ (Fig. 2, Table 4). Coastal, demersal, and pelagic prey differed significantly in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ but not $\delta^{34}\text{S}$. Coastal prey had

Table 3. Summary of the number of samples (N), sex ratio (females:males, F:M), mean and range of total length (TL), and mean \pm SD lipid-corrected $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ stable isotope analysis results of tope and smooth hammerhead shark life stages. YOY: young-of-the-year

Species	N (F:M)	TL (cm) Mean (min.–max.)	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		$\delta^{34}\text{S}$ (‰)	
			Mean	SD	Mean	SD	Mean	SD
Tope	54 (28:26)	112 (35–190)	-16.7	± 0.7	12.1	± 1.4	18.1	± 0.8
YOY	5 (4:1)	60 (35–70)	-16.7	± 0.6	11.0	± 0.7	17.7	± 0.7
Juvenile	21 (5:16)	84 (71–96)	-17.1	± 0.4	11.5	± 0.7	18.3	± 0.7
Subadult	10 (3:7)	116 (108–125)	-16.9	± 0.7	11.7	± 1.0	17.9	± 0.9
Adult	18 (16:2)	155 (129–190)	-16.1	± 0.8	13.3	± 1.6	18.2	± 0.9
Smooth hammerhead	36 (22:14)	93 (54–159)	-16.4	± 0.7	12.5	± 0.8	18.2	± 1.2
YOY	17 (12:5)	70 (54–80)	-16.2	± 0.6	12.7	± 0.8	18.7	± 1.0
Juvenile	19 (10:9)	113 (81–159)	-16.6	± 0.8	12.3	± 0.7	17.8	± 1.3

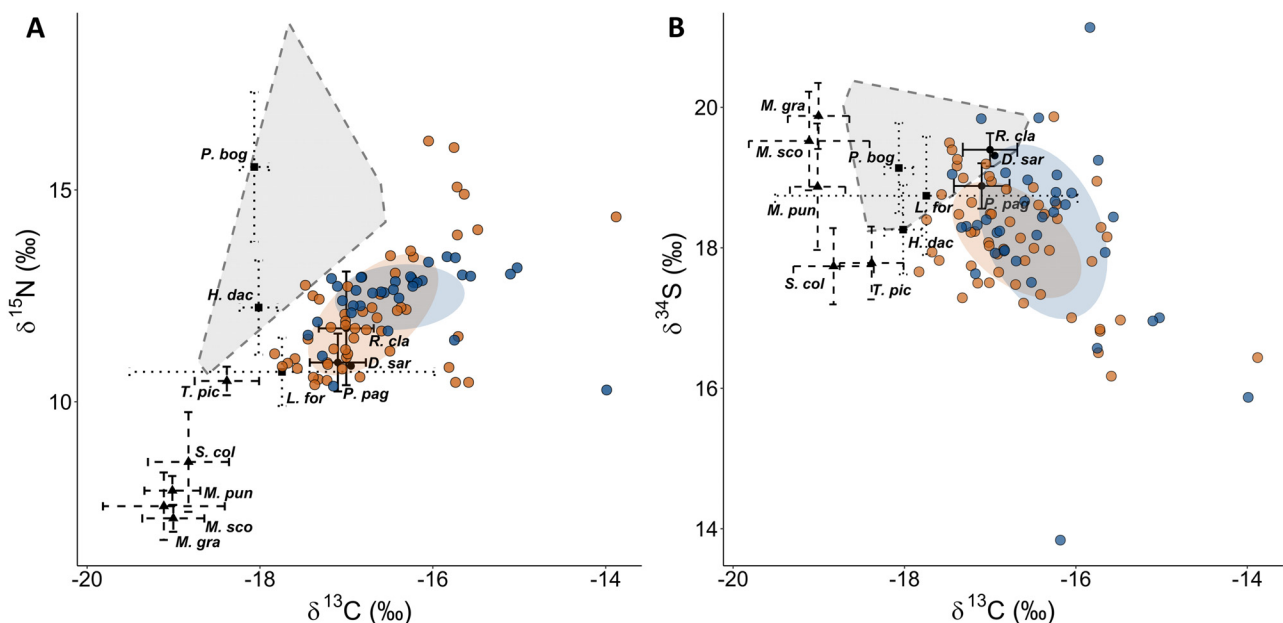


Fig. 2. Bulk muscle stable isotope values of (A) $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ and (B) $\delta^{13}\text{C}$ versus $\delta^{34}\text{S}$ for tope and smooth hammerhead sharks (blue) with shaded standard ellipse areas. Prey species uncorrected results are shown as mean points and standard deviation error bars (solid: coastal; dotted: demersal; dashed: pelagic) with the mixing polygon of enrichment corrected prey samples depicted as grey area. See Table 4 for species names

Table 4. Framework prey samples from the Azorean food webs with sample size, trophic position (TP), and stable isotope analysis results (mean ± SD)

	N	TP	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		$\delta^{34}\text{S}$ (‰)	
			Mean	SD	Mean	SD	Mean	SD
Demersal food web	21		-18.0	±0.2	13.5	±2.1	18.6	±0.8
Actinopterygii								
<i>Helicolenus dactylopterus</i>	8	3.5	-18.0	±0.2	12.2	±1.1	18.3	±0.6
<i>Pagellus bogaraveo</i>	5	4.2	-18.1	±0.2	15.5	±1.8	19.1	±0.6
Cephalopoda								
<i>Loligo forbesii</i>	8	4.2	-17.8	±1.8	10.7	±0.8	18.7	±0.8
Coastal food web	6		-17.0	±0.3	11.2	±0.9	19.1	±0.4
Actinopterygii								
<i>Diplodus sargus</i>	1	3.4	-17.0		10.9		19.3	
<i>Pagrus pagrus</i>	3	3.9	-17.1	±0.3	10.9	±0.7	18.9	±0.3
Chondrichthyes								
<i>Raja clavata</i>	2	3.8	-17.0	±0.3	11.7	±1.3	19.4	±0.2
Epipelagic food web	32		-18.9	0.5	8.1	1.5	18.9	1.2
Actinopterygii								
<i>Macroramphosus gracilis</i>	6	3.4	-19.0	±0.4	7.3	±0.3	19.9	±0.5
<i>Macroramphosus scolopax</i>	5	3.5	-19.1	±0.7	7.5	±0.8	19.5	±0.7
<i>Myctophum punctatum</i>	6	3.4	-19.0	±0.3	7.9	±0.4	18.9	±0.9
<i>Scomber colias</i>	6	3.9	-18.8	±0.5	8.6	±1.2	17.7	±0.5
<i>Trachurus picturatus</i>	6	3.3	-18.4	±0.4	10.5	±0.3	17.8	±0.5

the most elevated mean $\delta^{13}\text{C}$ values and pelagic prey had the lowest.

The analysis of isotope values in the context of shark size and life stages revealed clear trends and significant differences in both species. Tope showed an increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ but not in $\delta^{34}\text{S}$ values between life stages (Kruskal-Wallis test $\delta^{13}\text{C}$: $H_3 = 16.2$, $p < 0.01$; $\delta^{15}\text{N}$: $H_3 = 17.8$, $p < 0.001$), with significant differences in $\delta^{13}\text{C}$ between adults and juveniles, and adults and subadults, while in $\delta^{15}\text{N}$ we detected differences between adults and YOY, and between adults and juveniles (post hoc Dunn tests, $p < 0.5$; Fig. 3A,B,D, E). Values of $\delta^{15}\text{N}$ were particularly elevated in the largest individuals, all of which were adult females. By contrast, smooth hammerhead showed less pronounced stable iso-

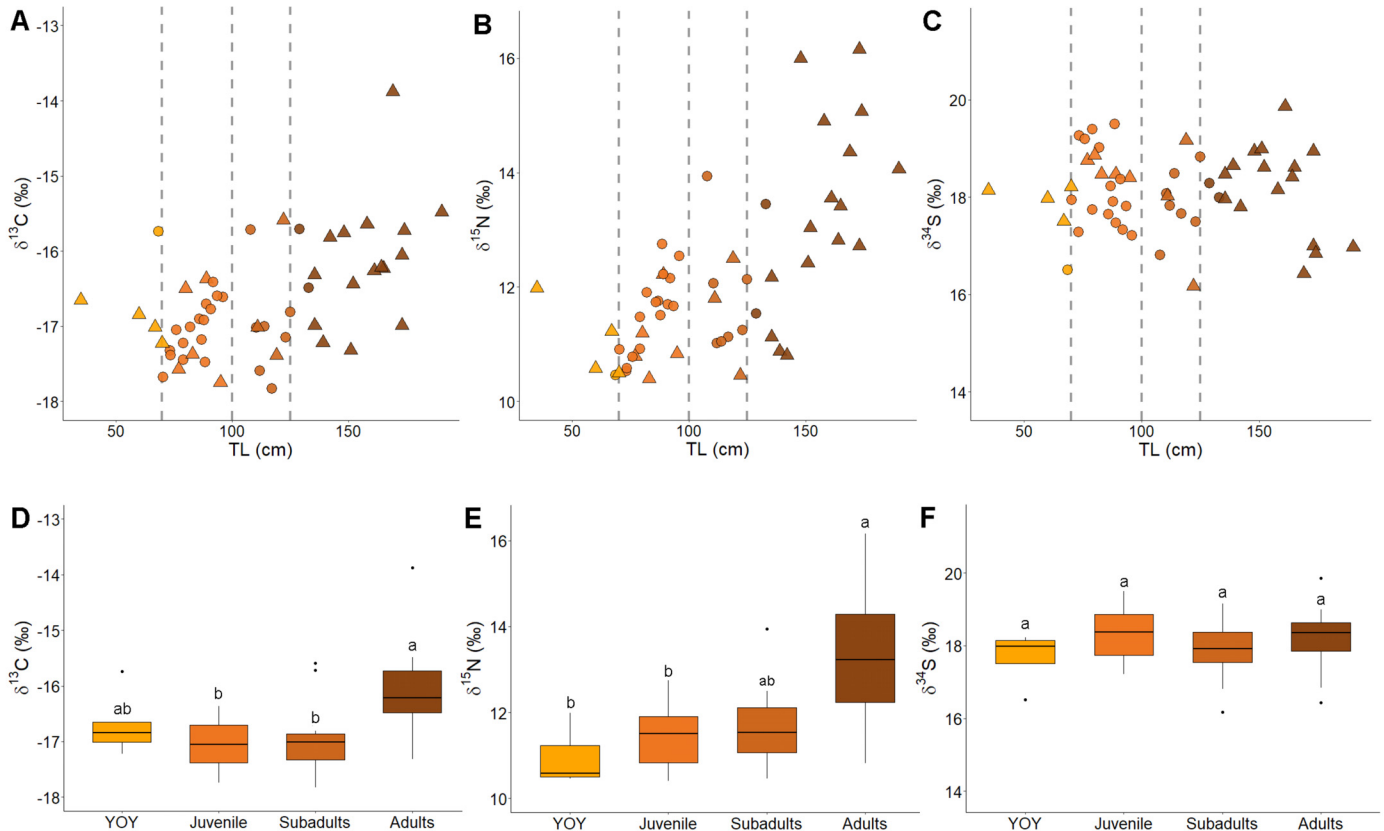


Fig. 3. Tope $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values by (A–C) size and (D–F) life stage. (A–C) Circles represent males and triangles represent females, with colours corresponding to different life stages. Dashed vertical lines: life stage intervals; (D–F) Bar: median; box: 25th–75th percentile; whiskers: max./min. $1.5 \times$ IQR above/below box; dots: outliers. YOY: young-of-the-year

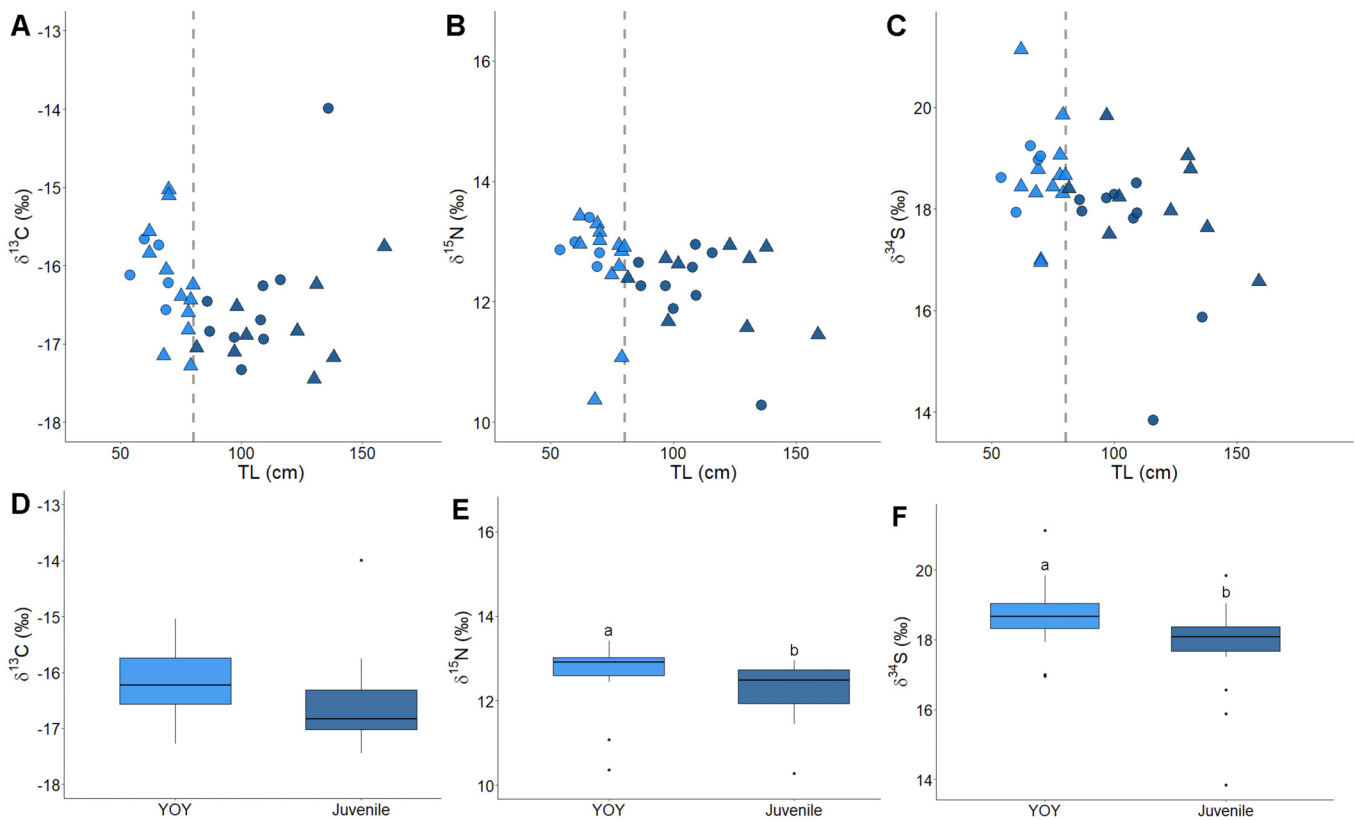


Fig. 4. As in Fig. 3, but for smooth hammerhead

tope differences among sizes and life stages than tope, with small decreases in $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ with size (Mann-Whitney U -test $\delta^{15}\text{N}$: $U = 234$, $p < 0.01$; $\delta^{34}\text{S}$: $U = 229$, $p < 0.05$; Fig. 4). The sexes of both species showed no difference in CNS isotopes PERMANOVA models (Table 5), nor was there a significant difference of patterns between years (Table 5).

To assess the isotopic niche characteristics of the 2 species and across the life stages, SEV_B and respective overlap probabilities were calculated. Overall SEV_B of both species had a similar volume with a high overlap ($\geq 44\%$) but ellipse volumes and their respective overlap differed substantially among different life stages (Figs. 5 & 6). In tope, juveniles had the smallest and adults had the largest SEV_B . Smooth hammerhead YOY had a smaller SEV_B (3.8) than juvenile smooth hammerhead (5.9). The overlap probabilities of isotopic niche volumes between the different life stages, both intra and inter-specific, varied between 1 and 49% for SEV_B . Immature tope (YOY, juveniles, and subadults) had higher overlap between each other (12–42% SEV_B overlap) than with all smooth hammerhead (1–27% SEV_B overlap). Overall, the niche overlap was particu-

larly low between younger (YOY and juveniles) and adult tope (2–7%), and young tope with the 2 immature smooth hammerhead life stages. Immature tope (YOY, juveniles, and subadults) had low overlap with smooth hammerhead YOY (1–5%) but an increasing overlap with hammerhead juveniles as size increased (4–27%). Adult tope had the broadest niche, overlapping more with smooth hammerhead, particularly YOY (41%), than with immature conspecifics (1–5%).

4. DISCUSSION

The present study provides the first comparative, life stage-resolved study of the trophic ecology of 2 shark species of high conservation concern, tope and smooth hammerhead, with a specific focus on the Azores Islands (North Atlantic). The CNS isotope analysis of shark muscle provided multi-dimensional isotopic niche metrics and the first data of $\delta^{34}\text{S}$ for these species, in turn enabling insights into the resource use in coastal habitats of the Azores, where both species occur in aggregations.

Table 5. PERMANOVA results in which each isotope was analysed as a function of total length (TL) in interaction with year and, in a separate model, TL as interaction with sex, using 999 permutations and the Bray-Curtis dissimilarity index. Significant p-values ($p < 0.05$) are highlighted in **bold**

Response	Effect	MS ($\times 10^{-4}$)	Pseudo- <i>F</i>	p	Effect	MS ($\times 10^{-4}$)	Pseudo- <i>F</i>	p
Tope								
C	TL	74.4	20.54	< 0.001	TL	74.4	18.61	< 0.001
	Year	11.5	3.17	0.09	Sex	1.7	0.42	0.52
	TL:Year	10.3	2.85	0.10	TL:Sex	1.3	0.34	0.58
N	TL	739.3	42.57	< 0.001	TL	739.3	42.22	< 0.001
	Year	0.2	0.01	0.96	Sex	2.2	0.12	0.73
	TL:Year	15.4	0.89	0.34	TL:Sex	6.2	0.36	0.55
S	TL	1.5	0.29	0.58	TL	1.5	0.28	0.61
	Year	11.7	2.27	0.14	Sex	3.7	0.69	0.40
	TL:Year	3.7	0.72	0.43	TL:Sex	0.1	0.02	0.91
Smooth hammerhead								
C	TL	1.8	0.35	0.58	TL	1.8	0.33	0.59
	Year	13.6	2.66	0.11	Sex	2.3	0.43	0.52
	TL:Year	7.5	1.47	0.20	TL:Sex	9.3	1.71	0.20
N	TL	45.8	4.73	< 0.05	TL	45.8	5.03	< 0.05
	Year	0.7	0.08	0.80	Sex	0.1	0.02	0.91
	TL:Year	1.6	0.17	0.59	TL:Sex	20.4	2.24	0.13
S	TL	77.0	7.68	< 0.01	TL	77.0	8.36	< 0.01
	Year	27.2	2.71	0.14	Sex	24.8	2.69	0.11
	TL:Year	3.5	0.35	0.46	TL:Sex	31.4	3.41	0.07

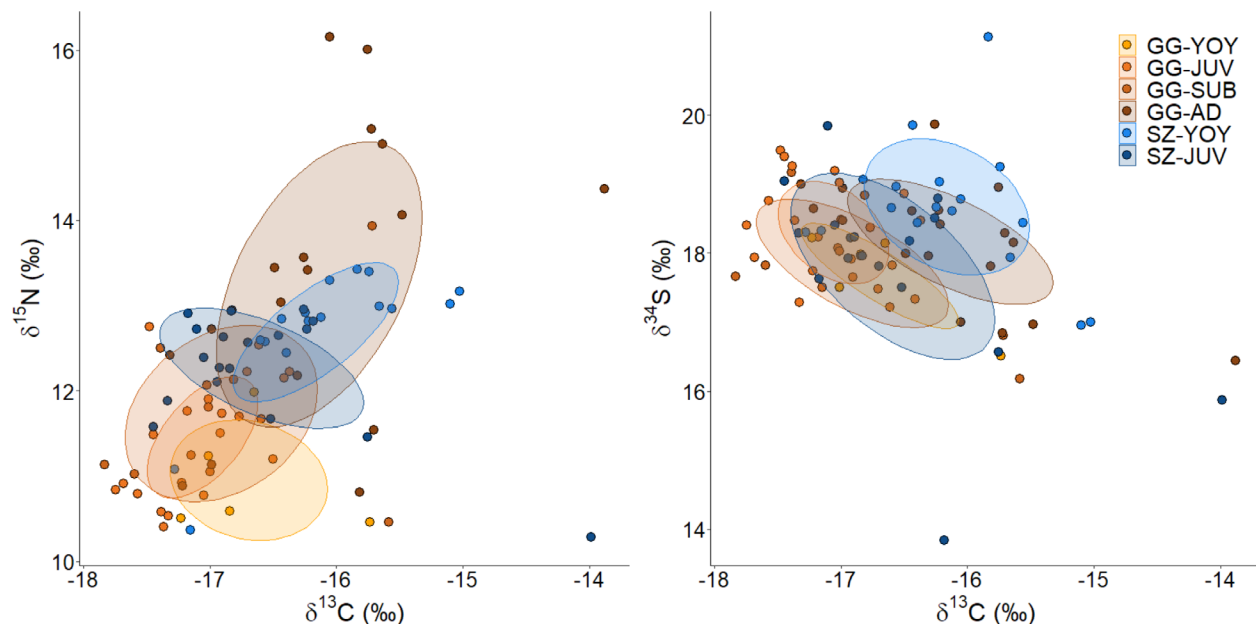


Fig. 5. Biplots of stable isotope values and Bayesian standard ellipse areas of the different life stages of tope (GG) and smooth hammerhead (SZ). YOY: young-of-the-year; JUV: juveniles; SUB: subadults; AD: adults

4.1. Trophic ecology of tope *Galeorhinus galeus*

The stable isotope analysis of tope representing all life stages of this species, from YOY to mature adults, suggests the relevance of similar (most pro-

bably coastal–benthic) resources overall but also significant ontogenetic trophic shifts with increasing size. Overall, the gradual increase of isotopic niche volumes and $\delta^{15}\text{N}$ values with size indicated a shift from a specialized to a more generalist diet with

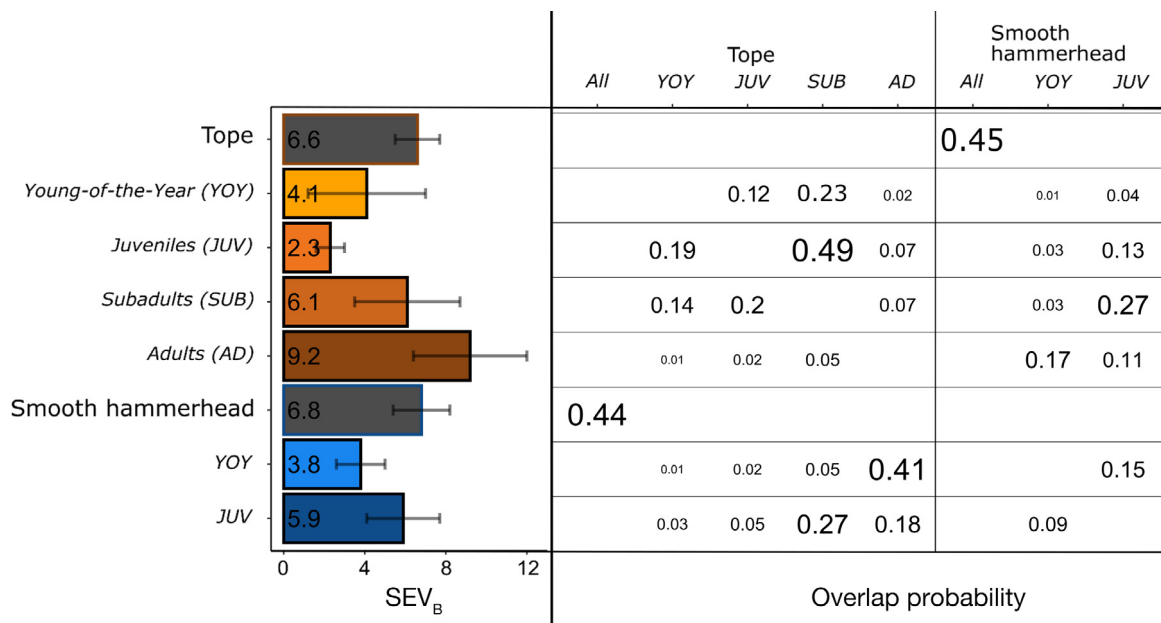


Fig. 6. Tope and smooth hammerhead life stage Bayesian mean \pm SD standard ellipse volumes (SEV_B) and the Bayesian SEV_B overlap probabilities of each row group with respective column groups. Number size: proportional to probability

increasing size. This finding is in line with ontogenetic dietary shifts reported from other locations (Domi et al. 2005, Lucifora et al. 2006, Poiesz et al. 2021). Here, the transition might reflect the more specialised diet and narrower prey diversity accessible to juveniles in coastal nurseries, followed by larger inter-individual differences as subadults start dispersing more, using different habitats and switching to a more generalist feeding mode (Lucifora et al. 2006). Closer to the time of birth, however, the broader isotopic niche of YOY compared to juveniles could be attributed to 2 processes: (1) the maternal isotopic influences integrated in neonate tissues, reflecting the contrasting ecological niche of adult females (Olin et al. 2011), and (2) a still inexperienced foraging mode, with limitations in gape size and speed of neonates limiting the access to larger and more mobile higher trophic level prey (Stevens & West 1997), as supported by the low $\delta^{15}N$ values of YOY. At the same time, the low isotopic niche differentiation, with comparable CNS distributions and the high isotopic niche overlaps among the 3 immature tope life stages (YOY, juvenile and sub-adult), indicated a similar resource use before reaching adulthood. The recurrent and aggregated local catches (Menezes et al. 2006) and oceanic movements restricted to mature individuals (Thorburn et al. 2019, Schaber et al. 2022) suggest that young tope rely on the islands' shelf habitats and local resources for an extended amount of time.

At the onset of maturity, we identified a pronounced ontogenetic shift along with the consistent absence of male tope above 150 cm TL on coastal longlines. We thus propose that in the Azores, tope undergo an ontogenetic diet and habitat shift around this size, probably concomitant with sexual segregation (as found in Argentinian populations; Lucifora et al. 2006). The elevated $\delta^{13}C$, typically associated with a more coastal or demersal diet (Table A2), together with the increasing $\delta^{15}N$, indicate that mature females do not rely on a pelagic diet but rather the consumption of diverse, potentially deeper, high trophic level prey, as observed in other studies (Davenport & Bax 2002, Domi et al. 2005, Botto et al. 2011). It is likely that females had been relying on this prey for at least several months before being captured, given the prolonged turnover time of elasmobranch muscle isotopes (> 1 yr; Logan & Lutcavage 2010, Kim et al. 2012).

Our results contradict the 2 previous studies of tope diet composition in the Azores (Morato et al. 2003, Torres et al. 2014), which found large proportions of different small pelagic species. However, both studies are limited by inherent biases: Morato et al. (2003)'s stomach content analysis samples were taken in a sampling period of unusually high abundances of *Capros aper* (P. Afonso pers. comm.), identified as the most important prey item (index of relative importance: 93.2%). Torres et al. (2014) compared the CN stable isotope values of prey samples

from a different ecosystem from Colaço et al. (2013) to tope samples taken 3–4 yr later. While the mixing models converged, these results should be considered with care as there was no way to account for potential baseline differences and no inclusion of coastal or benthic prey sources. By contrast, our results agree with those from other parts of the world (see Table 1), indicating that immature and adult female tope have a more mixed diet, possibly composed of both coastal and demersal prey (Lucifora et al. 2006, Gonzalez-Pestana et al. 2021, Biton-Porsmoguer 2022), also around oceanic islands.

4.2. Trophic ecology of juvenile smooth hammerhead *Sphyrna zygaena*

After the recent identification of a smooth hammerhead nursery area on the north coast of Faial Island (Afonso et al. 2022), this study reveals the first insights into their trophic ecology and provides baseline isotope data for YOY and juveniles. Smooth hammerhead YOY isotopes are, like tope YOY, probably influenced by maternal isotopic signatures. The identified enriched $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values of YOY fit the isotope signatures expected for adult females occupying oceanic habitats and feeding on a high trophic level diet (Ebert & Stehmann 2013). By contrast, juveniles presented the lowest $\delta^{34}\text{S}$ values of the entire study, typically associated with coastal or demersal foraging (Peterson & Fry 1987, Connolly et al. 2004). In the Azores, however, the organic matter and freshwater runoff that normally causes the coastal signature with low $\delta^{34}\text{S}$ values (Fry & Chumchal 2011) is low (DROTRH 2006), potentially resulting in $\delta^{34}\text{S}$ signatures principally reflecting the benthic versus pelagic foraging component (similar to the findings of Szpak & Buckley 2020). The telemetry data of Afonso et al. (2022) and a recent mercury stable isotope study of Besnard et al. (2023) offer further hints supporting demersal foraging: tagging information of the same specimens and size range analysed here (Afonso et al. 2022) found most of them to perform night-time migrations towards further offshore but also significantly deeper waters over the shelf while sustaining high activity levels that are usually associated with foraging (Speed et al. 2010). In the Pacific, Besnard et al. (2023) identified a coinciding shift to deeper prey resources, interpreted as increased mesopelagic predation. The low $\delta^{34}\text{S}$ signatures across juveniles of < 160 cm TL in our study could be caused by a diet shift to deeper prey; however, contrary to the interpretation of

Besnard et al. (2023), we speculate that it could be related to predation on non-planktonic, primary-production-based food chains, possibly demersal prey (Table A2). Our overall results for smooth hammerhead (minor decreases in $\delta^{15}\text{N}$, increase of isotopic niche) are in line with stable isotope analysis studies of comparable size classes from Pacific populations (Ochoa Díaz 2009, Loor-Andrade et al. 2015). The persistently low $\delta^{34}\text{S}$ of large juveniles with a high degree of residency (Afonso et al. 2022) adds to the growing body of evidence suggesting an ontogenetic shift to offshore habitat with a pelagic diet for animals larger than 160 cm TL.

4.3. Niche partitioning of tope and smooth hammerhead

Even though tope and smooth hammerhead use overlapping habitats in several coastal regions of the globe (Smith & Benson 2001, Watson 2013, Gonzalez-Pestana et al. 2021), only one study has briefly compared the general isotopic niches of tope and smooth hammerhead in the Pacific (Alfaro-Cordova et al. 2018). The authors found some evidence of potentially overlapping isotopic niches, yet the unbalanced sample size, sampling locations, and lack of information on movement ecology impeded further inferences. In the Azores, we found a considerable isotopic niche overlap of the 2 study species. Around the islands, the catch of both species on the same long-lines along with common sightings of both sharks on coastal baited remote underwater videos (BRUVs) (D. Das et al. unpubl. data) further underline the overlapping habitat use of tope and smooth hammerhead. A closer look at the isotopic patterns by size provides first insights into potential niche partitioning mechanisms, with ontogenetic isotope shifts and size-dependent interspecific isotopic niche overlap.

The similar isotopic niche space occupied by immature tope (YOY to subadults) and significant differences from both the adult conspecifics and smooth hammerhead indicated that young tope occupy a different ecological niche. While the $\delta^{13}\text{C}$ differences alone could be explained by the occupation of a different habitat, the ca. 1.5‰ differences in $\delta^{15}\text{N}$ were probably associated with a lower trophic level diet than adult tope and smooth hammerhead. Small tope were most commonly found by 60 m deep BRUVs in a local study, while smooth hammerhead appeared almost exclusively above 60 m (D. Das et al. unpubl. data). Telemetry data from the Azores and abroad support the predominant use of surface waters of ju-

venile smooth hammerhead (Francis 2016, Santos & Coelho 2018, Afonso et al. 2022), while tope have mostly been tracked to remain close to the seafloor (Rogers et al. 2017, Thorburn et al. 2019). We thus interpret the isotopic signatures to reflect partitioning of habitat on a vertical, and to a lesser degree, horizontal scale, associated diet, and trophic level. Such size-dependent spatial segregation and niche partitioning as indicated here has been found in other shark EFHs (Guttridge et al. 2012). By using a different habitat than other larger sharks, young sharks not only decrease the risk of predation but may also reduce potential inter- and intra-specific interactions and thus increase the potential for feeding opportunities (Heithaus 2007). For YOY and juvenile smooth hammerhead, on the other hand, our study provides little evidence of such partitioning, with a large isotopic niche overlap with adult tope hinting at the occupation of a similar habitat and/or diet. D. Das et al. (unpubl. data) found evidence of this co-occurrence using experimental pelagic longlines, with adult tope females being caught more frequently alongside juvenile smooth hammerhead. While it is unlikely that these life stages of the 2 species are competing for the same trophic resources given their differences in size, the spatial overlap of large tope may represent increased predation risk for the smaller smooth hammerhead. Predation among sharks is common (Wetherbee et al. 2012), and tope have been found to feed on other chondrichthyans including small sharks (Lucifora et al. 2006). Stomach content analyses or faecal DNA metabarcoding of adult tope could provide valuable insights to clarify this potential predation on the local smooth hammerhead.

4.4. Prey samples and predator–prey mismatch

The overall isotopic gradients of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the selected prey were consistent with the patterns established in the wider literature: in particular, pelagic fishes displayed enriched $\delta^{13}\text{C}$ values compared to coastal and demersal species. Furthermore, high trophic level species (e.g. *Pagellus bogoraveo*) exhibited more elevated $\delta^{15}\text{N}$ than species with lower established trophic positions (e.g. *Macroramphosus gracilis*). However, this first analysis of $\delta^{34}\text{S}$ in the Azores did not reveal any patterns between the different ecosystems based on the represented prey species. This is surprising, as S has been shown to commonly discriminate different primary producers to a higher degree than C and N (Connolly et al. 2004). Another unexpected result was the observed prey–predator

mismatch after correcting prey samples with literature DTDF values. Both findings could be caused by several non-exclusive confounding effects offering lessons for future studies: (1) missing prey sources, (2) incorrect DTDFs, (3) isotopic baseline shifts between sampling dates, and (4) different isotopic gradients between local ecosystems.

As to point (1), the limited information about the diet of both sharks locally increases the possibility that the opportunistically collected prey did not capture the necessary isotopic spectrum to properly assess the isotopic contribution of the different sources. Given the isotopic mismatch, the missing prey are likely obligate coastal or demersal species such as benthic cephalopods, malacostraca, or deeper demersal species such as *Capros aper*. Concerning point (2), the variety of factors influencing stable isotope DTDFs, including taxonomy, dietary quality, temperature, and growth rate (Trueman et al. 2005, Barnes et al. 2007, Caut et al. 2009), continues to confound the interpretation of predator–prey isotopic overlap and resulting mixing models (Stephens et al. 2022), with the few controlled laboratory experiments of sharks providing conflicting experimental results (Hussey et al. 2012). Even less information is available for S DTDFs, forcing studies like ours to draw on non-elasmobranch values. This reiterates the need for further DTDF elasmobranch research, in particular for $\delta^{34}\text{S}$. Regarding point (3), while the shark stable isotope values did not indicate any differences between years, the slow isotopic turnover of elasmobranchs may smooth out temporal baseline changes such as upwelling events and seasonal primary producer composition changes. The significantly shorter stable isotope turnover times of S (Vander Zanden et al. 2015) in the prey samples could constitute snapshots of the differing primary producer composition throughout the sampling period in local ecosystems, potentially causing a mismatch between putative prey and consumer stable isotope ranges. Finally, regarding point (4), oceanic islands such as the Azores typically differ from continental areas in species assemblage, oceanographic conditions, and meteorology, all impacting the ecological drivers behind the extent of classically found isotopic gradients (Peterson & Fry 1987). As discussed above, $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values in particular might be impacted by the low freshwater and organic matter discharge, reflecting the underlying primary production sources in a different way than typically assumed (Szpak & Buckley 2020). Here, a broader study of local isoscapes and the underlying isotopic gradients would provide valuable information for the interpretation of future studies.

Despite these uncertainties, our data provide evidence of ontogenetic shifts and inter- and intra-species differences in the trophic ecology of these 2 shark species in the Azores, with implications for future conservation efforts.

4.5. Relevance for shark conservation and EFH designation

Identifying areas that support essential life stages is critical for the conservation of imperilled species (Bonfil 1997). The coastal habitat use of tope and juvenile smooth hammerhead around the Azores has received considerable recent attention (Afonso et al. 2014, Das & Afonso 2017, Santos et al. 2020), including the delineation of a smooth hammerhead nursery along the north shore of Faial (Afonso et al. 2022). Our study provides insights into the inter- and intraspecific partitioning of the resources of these 2 species around the Azores. The results of this study suggest that both species share a similar trophic niche but partition the resources on finer ontogenetic scales, both between conspecifics and between species. The overlap of large tope and YOY smooth hammerhead furthermore hints at potential predation pressure on young smooth hammerhead by these larger high trophic level tope sharks. As a next step, we call for the delineation of priority areas around the islands and the determination of principal prey species to allow more refined future conservation approaches.

Acknowledgements. We acknowledge funds provided by the Portuguese Science & Technology Foundation (FCT) through individual contracts and grants to P.A. (IF/01640/2015), J.M.F. (M3.1.a/F/062/201), D.A. DL57/2016/CP1361/CT0036, and C.R.P. (2022.11640.BD), through the research project Island-Shark (PTDC/BIA-BMA/32204/2017), UIDB/04326/2020, UIDP/04326/2020, LA/P/0101/2020, and through the Strategic Program to Okeanos R&D Centre; by the Oceanário de Lisboa and the Shark Conservation Fund through the Island-Shark project; and by the EC through the Meeso (H2020-LC-BG-03-2018–817669) and Mission Atlantic (H2020-LC-BG-08-2018) research projects. We thank the entire IslandShark team and the crews of RVs 'Arquipelago' and 'Carolina' for the support and sample collection, Merlin Weichler for helping with the weighing of samples, and Mara Schmiing for statistical advice.

LITERATURE CITED

- Afonso P, Vandeperre F, Fontes J, Porteiro F (2014) Conservation of pelagic elasmobranchs in the Azores. In: Carreira G, Cardigos F, Porteiro FM (eds) *Arquipelago: life and marine sciences*, Suppl 8. The sea of the Azores: scientific forum for decision support. University of the Azores, Ponta Delgada, p 25–30
- Afonso P, Fontes J, Giacomello E, Magalhães MC and others (2020) The Azores: a mid-Atlantic hotspot for marine megafauna research and conservation. *Front Mar Sci* 6:826
- Afonso P, Gandra M, Graça G, Macena B, Vandeperre F, Fontes J (2022) The multi-annual residency of juvenile smooth hammerhead shark in an oceanic island nursery. *Front Mar Sci* 9:957
- Alfaro-Cordova E, Solar AD, Gonzalez-Pestana A, Acuña-Perales N and others (2018) Isotopic niches of four commercially important pelagic elasmobranch species captured by the small-scale driftnet fishery of northern Peru. *Lat Am J Aquat Res* 46:482–488
- Amorim P, Perán AD, Pham CK, Juliano M, Cardigos F, Tempera F, Morato T (2017) Overview of the ocean climatology and its variability in the Azores region of the North Atlantic including environmental characteristics at the seabed. *Front Mar Sci* 4:56
- Barnes C, Sweeting CJ, Jennings S, Barry JT, Polunin NV (2007) Effect of temperature and ration size on carbon and nitrogen stable isotope trophic fractionation. *Funct Ecol* 21:356–362
- Besnard L, Lucca BM, Shipley ON, Le Croizier G and others (2023) Mercury isotope clocks predict coastal residency and migration timing of hammerhead sharks. *J Appl Ecol* 60:803–813
- Biton-Porsmoquer S (2022) Diet strategies of starry smoothhound *Mustelus asterias* and tope shark *Galeorhinus galeus* (Carcharhiniformes: Triakidae) in the eastern English Channel: implication for conservation. *Cah Biol Mar* 63:129–137
- Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. *Annu Rev Ecol Evol Syst* 42:411–440
- Bonfil R (1997) Marine protected areas as a shark fisheries management tool. In: Seret B, Sire JY (eds) *Proc 5th Indo-Pacific Fish Conference*, 3–8 November 1997, Nouméa. Société Française d'Ichtyologie, Paris, p 217–230
- Botto F, Gaitán E, Mianzan H, Acha M, Giberto D, Schiariti A, Iribarne O (2011) Origin of resources and trophic pathways in a large SW Atlantic estuary: an evaluation using stable isotopes. *Estuar Coast Shelf Sci* 92:70–77
- Caldeira R, Reis JC (2017) The Azores confluence zone. *Front Mar Sci* 4:37
- Camhi MD, Valenti S, Fordham S, Fowler S, Gibson C (eds) (2009) *The conservation status of pelagic sharks and rays: report of the IUCN Shark Specialist Group Pelagic Shark Red List workshop*. IUCN Species Survival Commission Shark Specialist Group, Newbury
- Carlisle AB, Litvin SY, Madigan DJ, Lyons K, Bigman JS, Ibarra M, Bizzarro JJ (2017) Interactive effects of urea and lipid content confound stable isotope analysis in elasmobranch fishes. *Can J Fish Aquat Sci* 74:419–428
- Castro JI, Woodley CM, Brudek RL (1999) A preliminary evaluation of the status of shark species. *FAO, Rome*
- Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J Appl Ecol* 46:443–453
- Colaço A, Giacomello E, Porteiro F, Menezes G (2013) Trophodynamic studies on the Condor seamount (Azores, Portugal, North Atlantic). *Deep Sea Res II* 98: 178–189
- Colloca F, Scannella D, Geraci ML, Falsone F, Batista G, Vitale S, Di Lorenzo M (2019) British sharks in Sicily: records of long distance migration of tope shark (*Galeorhi-*

- nus galeus*) from North-eastern Atlantic to Mediterranean Sea. *Mediterr Mar Sci* 20:309–313
- Compagno LJ (1984) *Sharks of the world: an annotated and illustrated catalogue of shark species known to date*. FAO, Rome
- Compagno L (1998) *Sphyrnidae. Hammerhead and bonnethead sharks*. FAO identification guide for fishery purposes. The living marine resources of the western central Pacific. FAO, Rome, p 1361–1366
- ✦ Connolly RM, Schlacher TA (2013) Sample acidification significantly alters stable isotope ratios of sulfur in aquatic plants and animals. *Mar Ecol Prog Ser* 493:1–8
- ✦ Connolly RM, Guest MA, Melville AJ, Oakes JM (2004) Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia* 138:161–167
- Cox GJ, Francis M (1997) *Sharks and rays of New Zealand*. Canterbury University Press, Christchurch
- ✦ Das D, Afonso P (2017) Review of the diversity, ecology, and conservation of elasmobranchs in the Azores region, mid-north Atlantic. *Front Mar Sci* 4:354
- ✦ Davenport SR, Bax NJ (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. *Can J Fish Aquat Sci* 59:514–530
- ✦ Davis MW (2010) Fish stress and mortality can be predicted using reflex impairment. *Fish Fish* 11:1–11
- ✦ DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- ✦ DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- ✦ Domi N, Bouquegneau JM, Das K (2005) Feeding ecology of five commercial shark species of the Celtic Sea through stable isotope and trace metal analysis. *Mar Environ Res* 60:551–569
- DROTRH (2006) *Relatório síntese de caracterização da Região Hidrográfica, Arquipélago dos Açores, Portugal*. DROTRH, Ponta Delgada
- ✦ Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. *eLife* 3:e00590
- ✦ Dulvy NK, Simpfendorfer CA, Davidson LNK, Fordham SV, Bräutigam A, Sant G, Welch DJ (2017) Challenges and priorities in shark and ray conservation. *Curr Biol* 27:R565–R572
- Dulvy NK, Pacoureau N, Rigby CL, Pollom RA and others (2021) Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology* 31:4773–4787.e8
- Ebert DA, Stehmann MF (2013) *Sharks, batoids and chimaeras of the North Atlantic*. FAO, Rome
- ✦ Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecol Lett* 13:1055–1071
- ✦ France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar Ecol Prog Ser* 124:307–312
- ✦ Francis MP (2016) Distribution, habitat and movement of juvenile smooth hammerhead sharks (*Sphyrna zygaena*) in northern New Zealand. *NZ J Mar Freshw Res* 50:506–525
- ✦ Frisk MG, Miller TJ, Dulvy NK (2005) Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. *J Northwest Atl Fish Sci* 35:27–45
- ✦ Froese R, Pauly D (eds) (2010) *FishBase*. www.fishbase.org
- ✦ Fry B, Chumchal MM (2011) Sulfur stable isotope indicators of residency in estuarine fish. *Limnol Oceanogr* 56:1563–1576
- Fry B, Sherr EB (1989) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. In: Rundel PW, Ehleringer JR, Nagy KA (eds) *Stable isotopes in ecological research*. Ecological Studies, Vol 68. Springer, New York, NY, p 196–229
- ✦ Gallagher AJ, Hammerschlag N, Shiffman DS, Giery ST (2014) Evolved for extinction: the cost and conservation implications of specialization in hammerhead sharks. *Bioscience* 64:619–624
- GAMPA (2020) *Coastal fisheries resources of the Azores: an X-ray*. Tech Rep 1.1 of the MoniCO program. IMAR/Okeanos, University of the Azores, Ponta Delgada
- ✦ Gonzalez-Pestana A, Mangel JC, Alfaro-Córdova E, Acuña-Perales N and others (2021) Diet, trophic interactions and possible ecological role of commercial sharks and batoids in northern Peruvian waters. *J Fish Biol* 98:768–783
- ✦ Guttridge TL, Gruber SH, Franks BR, Kessel ST and others (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Mar Ecol Prog Ser* 445:279–291
- ✦ Hansen T, Burmeister A, Sommer U (2009) Simultaneous $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ measurements of low-biomass samples using a technically advanced high sensitivity elemental analyzer connected to an isotope ratio mass spectrometer. *Rapid Commun Mass Spectrom* 23:3387–3393
- ✦ Harms CA (2005) Surgery in fish research: common procedures and postoperative care. *Lab Anim (NY)* 34:28–34
- Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. *Am Fish Soc Symp* 50:3–13
- ✦ Heithaus MR, Wirsing A, Dill L (2012) The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. *Mar Freshw Res* 63:1039–1050
- ✦ Henningsen AD (1994) Tonic immobility in 12 elasmobranchs: use as an aid in captive husbandry. *Zoo Biol* 13:325–332
- ✦ Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. *Mar Ecol Prog Ser* 337:287–297
- ✦ Heupel MR, Kanno S, Martins AP, Simpfendorfer CA (2018) Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. *Mar Freshw Res* 70:897–907
- ✦ Heupel MR, Munroe SE, Lédée EJ, Chin A, Simpfendorfer CA (2019) Interspecific interactions, movement patterns and habitat use in a diverse coastal shark assemblage. *Mar Biol* 166:1–17
- ✦ Hobson KA (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Mar Ecol Prog Ser* 95:7–18
- ✦ Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314–326
- ✦ Holden M, Horrod R (1979) The migrations of tope, *Galeorhinus galeus* (L), in the eastern North Atlantic as determined by tagging. *ICES J Mar Sci* 38:314–317
- ✦ Hueter R, Heupel M, Heist E, Keeney D (2005) Evidence of philopatry in sharks and implications for the management of shark fisheries. *J Northwest Atl Fish Sci* 35:239–247
- ✦ Hussey NE, MacNeil MA, Olin JA, McMeans BC, Kinney MJ, Chapman DD, Fisk AT (2012) Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. *J Fish Biol* 80:1449–1484

- IUCN (2018) The IUCN Red List of Threatened Species. www.iucnredlist.org/
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. *J Anim Ecol* 80:595–602
- Kim SL, Koch PL (2012) Methods to collect, preserve, and prepare elasmobranch tissues for stable isotope analysis. *Environ Biol Fishes* 95:53–63
- Kim SL, del Rio CM, Casper D, Koch PL (2012) Isotopic incorporation rates for shark tissues from a long-term captive feeding study. *J Exp Biol* 215:2495–2500
- Knip DM, Heupel MR, Simpfendorfer CA (2012) Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biol Conserv* 148:200–209
- Li YK, Gao X, Wang LY, Fang L (2018) Trophic niche partitioning of pelagic sharks in Central Eastern Pacific inferred from stable isotope analysis. *Ying Yong Sheng Tai Xue Bao* 29:309–313 (in Chinese with English Abstract)
- Logan JM, Lutcavage ME (2010) Stable isotope dynamics in elasmobranch fishes. *Hydrobiologia* 644:231–244
- Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J Anim Ecol* 77:838–846
- Loor-Andrade P, Galván-Magaña F, Elorriaga-Verplancken FR, Polo-Silva C, Delgado-Huertás A (2015) Population and individual foraging patterns of two hammerhead sharks using carbon and nitrogen stable isotopes. *Rapid Commun Mass Spectrom* 29:821–829
- Lucifora LO, Menni RC, Escalante AH (2004) Reproductive biology of the school shark, *Galeorhinus galeus*, off Argentina: support for a single south western Atlantic population with synchronized migratory movements. *Environ Biol Fishes* 71:199–209
- Lucifora LO, García VB, Menni RC, Escalante AH (2006) Food habits, selectivity, and foraging modes of the school shark *Galeorhinus galeus*. *Mar Ecol Prog Ser* 315:259–270
- Martín G, Espinoza M, Heupel M, Simpfendorfer CA (2020) Estimating marine protected area network benefits for reef sharks. *J Appl Ecol* 57:1969–1980
- McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390
- McMillan MN, Semmens JM, Huveneers C, Sims DW, Stehfest KM, Gillanders BM (2021) Grow or go? Energetic constraints on shark pup dispersal from pupping areas. *Conserv Physiol* 9:coab017
- Menezes GM, Sigler MF, Silva HM, Pinho MR (2006) Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). *Mar Ecol Prog Ser* 324:241–260
- Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. *Mar Ecol Prog Ser* 420:15–26
- Morato T, Solà E, Grós MP, Menezes G (2003) Diets of thornback ray (*Raja clavata*) and tope shark (*Galeorhinus galeus*) in the bottom longline fishery of the Azores, northeastern Atlantic. *Fish Bull* 101:590–602
- Ochoa Díaz MR (2009) Espectro trófico del tiburón martillo *Sphyrna zygaena* (Linnaeus, 1758) en Baja California Sur: aplicación de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$. Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz
- Oksanen J, Blanchet FG, Kindt R, Legendre P and others (2013) vegan: community ecology package, version 2: 1-295. <https://cran.r-project.org/web/packages/vegan/index.html>
- Olin JA, Hussey NE, Fritts M, Heupel MR, Simpfendorfer CA, Poulakis GR, Fisk AT (2011) Maternal meddling in neonatal sharks: implications for interpreting stable isotopes in young animals. *Rapid Commun Mass Spectrom* 25:1008–1016
- Pacoureau N, Rigby CL, Kyne PM, Sherley RB and others (2021) Half a century of global decline in oceanic sharks and rays. *Nature* 589:567–571
- Pantoja-Echevarría LM, Tamburín E, Elorriaga-Verplancken FR, Marmolejo-Rodríguez AJ and others (2022) How to stay together? Habitat use by three sympatric sharks in the western coast of Baja California Sur, Mexico. *Environ Sci Pollut Res Int* 29:61685–61697
- Perry RI, Thompson PA, Mackas DL, Harrison PJ, Yelland DR (1999) Stable carbon isotopes as pelagic food web tracers in adjacent shelf and slope regions off British Columbia, Canada. *Can J Fish Aquat Sci* 56:2477–2486
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Phillips DL, Inger R, Bearhop S, Jackson AL and others (2014) Best practices for use of stable isotope mixing models in food-web studies. *Can J Zool* 92:823–835
- Pinho M, Medeiros-Leal W, Sigler M, Santos R, Novoa-Pabon A, Menezes G, Silva H (2020) Azorean demersal longline survey abundance estimates: procedures and variability. *Reg Stud Mar Sci* 39:101443
- Poiesz SS, Van Elderen T, Witte JI, Van Der Veer HW (2021) Historical trophic ecology of some divergent shark and skate species in the Dutch coastal North Sea zone. *Mar Biol* 168:1–15
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rigby CL, Barreto R, Carlson J, Fernando D and others (2019) *Sphyrna zygaena*. The IUCN Red List of Threatened Species 2019:e.T39388A2921825, <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39388A2921825.en>
- Rogers P, Knuckey I, Hudson R, Lowther A, Guida L (2017) Post-release survival, movement, and habitat use of school shark *Galeorhinus galeus* in the Great Australian Bight, southern Australia. *Fish Res* 187:188–198
- Rosa D, Coelho R, Fernandez-Carvalho J, Santos MN (2017) Age and growth of the smooth hammerhead, *Sphyrna zygaena*, in the Atlantic Ocean: comparison with other hammerhead species. *Mar Biol Res* 13:300–313
- Rossmann S, Ostrom PH, Gordon F, Zipkin EF (2016) Beyond carbon and nitrogen: guidelines for estimating three-dimensional isotopic niche space. *Ecol Evol* 6:2405–2413
- Santos CC, Coelho R (2018) Migrations and habitat use of the smooth hammerhead shark (*Sphyrna zygaena*) in the Atlantic Ocean. *PLOS ONE* 13:e0198664
- Santos R, Novoa-Pabon A, Silva H, Pinho M (2020) Elasmobranch species richness, fisheries, abundance and size composition in the Azores archipelago (NE Atlantic). *Mar Biol Res* 16:103–116
- Schaber M, Gastauer S, Cisewski B, Hielscher N and others (2022) Extensive oceanic mesopelagic habitat use of a migratory continental shark species. *Sci Rep* 12:2047
- Segura-Cobena E, Alfaro-Shigueto J, Mangel J, Urzua A,

- Górski K (2021) Stable isotope and fatty acid analyses reveal significant differences in trophic niches of smooth hammerhead *Sphyrna zygaena* (Carcharhiniformes) among three nursery areas in northern Humboldt Current System. PeerJ 9:e11283
- ✦ Shipley ON, Matich P (2020) Studying animal niches using bulk stable isotope ratios: an updated synthesis. Oecologia 193:27–51
- ✦ Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ Biol Fishes 37:337–345
- ✦ Skinner C, Mill AC, Newman SP, Newton J, Cobain MR, Polunin NV (2019) Novel tri-isotope ellipsoid approach reveals dietary variation in sympatric predators. Ecol Evol 9:13267–13277
- Smith PJ, Benson PG (2001) Biochemical identification of shark fins and fillets from the coastal fisheries in New Zealand. Fish Bull 99:351–355
- ✦ Speed CW, Field IC, Meekan MG, Bradshaw CJ (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408:275–293
- ✦ Stephens RB, Ouimette AP, Hobbie EA, Rowe RJ (2022) Reevaluating trophic discrimination factors ($\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$) for diet reconstruction. Ecol Monogr 92:e1525
- Stevens JD, West GJ (1997) Investigation of school and gummy shark nursery areas in southeastern Australia. CSIRO Marine Research, Hobart
- ✦ Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096
- ✦ Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist JD (2015) A new probabilistic method for quantifying n -dimensional ecological niches and niche overlap. Ecology 96:318–324
- ✦ Szapak P, Buckley M (2020) Sulfur isotopes ($\delta^{34}\text{S}$) in Arctic marine mammals: indicators of benthic vs. pelagic foraging. Mar Ecol Prog Ser 653:205–216
- ✦ Thorburn J, Neat F, Burrett I, Henry LA, Bailey DM, Jones CS, Noble LR (2019) Ontogenetic variation in movements and depth use, and evidence of partial migration in a benthopelagic elasmobranch. Front Ecol Evol 7:353
- ✦ Torres P, da Cunha RT, Maia R, dos Santos Rodrigues A (2014) Trophic ecology and bioindicator potential of the North Atlantic tope shark. Sci Total Environ 481:574–581
- ✦ Trueman CN, McGill RA, Guyard PH (2005) The effect of growth rate on tissue–diet isotopic spacing in rapidly growing animals. An experimental study with Atlantic salmon (*Salmo salar*). Rapid Commun Mass Spectrom 19:3239–3247
- ✦ Vandepierre F, Aires-Da-Silva A, Fontes J, Santos M, Serrão Santos R, Afonso P (2014) Movements of blue sharks (*Prionace glauca*) across their life history. PLOS ONE 9:e103538
- ✦ Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLOS ONE 10:e0116182
- ✦ Walker TI, Rigby C, Pacoureaux N, Ellis J, Kulka DW, Chiaramonte GE, Herman K (2020) *Galeorhinus galeus*. The IUCN Red List of Threatened Species 2020:e.T39352A2907336, <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T39352A2907336.en>
- Watson RGA (2013) Baited remote underwater survey of chondrichthyans in False Bay, South Africa. MSc thesis, University of Cape Town
- Wetherbee BM, Cortés E, Bizzarro JJ (2012) Food consumption and feeding habits. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, p 225–246

Appendix.

Text A1. Linear model of Logan et al. (2008) used for the lipid correction of C ratios:

$$\Delta\delta^{13}\text{C} = \beta_0 + \beta_1 \ln(\text{C:N}_U)$$

where $\Delta\delta^{13}\text{C}$ is the difference between the carbon isotope ratio of urea-extracted tissue and urea and lipid-extracted tissue ($\delta^{13}\text{C}_U - \delta^{13}\text{C}_{LU}$), β_0 and β_1 are the parameters used for the different samples (given in Table A1) and C:N_U is the uncorrected elemental ratio between carbon and nitrogen of urea-extracted tissue.

Table A1. Model parameters used for the lipid-correction of $\delta^{13}\text{C}$ values of muscle samples

Species	β_0 parameter	β_1 parameter	Source
Shark samples	-7.7 ± 0.8	6.7 ± 0.7	Carlisle et al. (2017)
Fish and cephalopod samples	-4.8 ± 0.1	4.4 ± 0.1	Logan et al. (2008)

Table A2. Established aquatic isotopic gradients of $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ with relevant references

Gradients	References	Determined primary production isotopic gradients
Coastal–Pelagic	$\delta^{13}\text{C}$: Peterson & Fry (1987), Perry et al. (1999) $\delta^{34}\text{S}$: Peterson & Fry (1987)	Coastal > offshore pelagic Coastal < offshore pelagic
Demersal– Pelagic	$\delta^{13}\text{C}$: Peterson & Fry (1987), France (1995) $\delta^{34}\text{S}$: Peterson & Fry (1987), Szpak & Buckley (2020)	Demersal > pelagic Demersal < pelagic

*Editorial responsibility: Robert M. Suryan,
Juneau, Alaska, USA
Reviewed by: M. C. Livernois and 2 anonymous referees*

*Submitted: December 7, 2022
Accepted: November 9, 2023
Proofs received from author(s): January 8, 2024*