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Resource partitioning in hammerhead shark species out-migrating from coastal ecosystems in the Gulf of California

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Abstract :

Juveniles of large hammerhead shark species occupy coastal nurseries before migrating offshore to reproduce. In the central Gulf of California, artisanal elasmobranch fisheries have reported catches of juvenile scalloped Sphyrna lewini and smooth S. zygaena hammerhead sharks, but their local foraging habits are yet to be fully understood. In this study, the trophic niches of both hammerhead species as well as of sympatric Pacific sharpnose sharks Rhizoprionodon longurio were investigated using stable isotope values (δ13C, δ34S and δ15N) and fatty acid compositions in whole blood and muscle tissues. Despite interspecific similarities among trophic niches, smooth hammerheads were characterized by lower δ13C, higher δ34S and greater proportion of docosahexaenoic acid (DHA) in both tissues, suggesting they were already partly relying on offshore pelagic resources. For scalloped hammerheads, muscle reflected coastal dietary resources, while offshore trophic markers were detected in blood integrating prey signal over shorter time periods, indicating their more recent initiation of ontogenetic migration. Multidimensional niche calculation revealed low overlap between hammerhead shark trophic niches, implying that potential fine-scale differences in habitat use could reduce competition between these morphologically and ecologically similar species. In the meantime, the isotopic niches of juvenile scalloped and smooth hammerheads were smaller than that of Pacific sharpnose sharks, suggesting they could be more specialized consumers. Overall, the identification of foraging grounds for juvenile hammerhead sharks calls for a future characterization of their residency time in coastal ecosystems to further understand their interactions with fishing pressure in the Gulf of California.

Keywords : Sphyrna spp., Trophic niche, Carbon isotopes, Nitrogen isotopes, Sulfur isotopes, Fatty acids, Sympatric sharks, Ontogenetic habitat shif, Artisanal fisheries

1. Introduction

Nearshore areas are among the most productive ecosystems, providing major goods and services to human populations (Costanza et al. 1997, Barbier et al. 2011). They include a diversity of habitats whose environmental features vary over time and space and are generally used by marine biota for feeding and/or reproduction (Gray 1997). In many fish, juvenile and adult habitats are often separated to avoid intraspecific competition, and coastal ecosystems are frequently used as nursery grounds. Nurseries are mainly characterized by the high abundance of neonate, young-of-the-year and juvenile individuals in a sheltered and productive area, which ultimately results in higher rates of recruitment into adult populations (Beck et al. 2001). Because of their absence of maternal care and low productivity (i.e., slow growth, late maturity, limited number of pups), large-bodied sharks commonly use coastal ecosystems as nurseries to maintain juvenile populations with low mortality rates (Heupel et al. 2007, 2018, Knip et al. 2010).

Among large hammerhead shark species, scalloped hammerhead sharks (*Sphyrna lewini*) and smooth hammerhead sharks (*Sphyrna zygaena*) are known to use coastal nurseries (Duncan & Holland 2006, Diemer et al. 2011, Francis 2016, Estupiñán-Montaño et al. 2021). Both species share common life history traits, as early juveniles inhabit nursery areas before migrating toward offshore pelagic waters, where individuals regroup and eventually reproduce (Gallagher & Klimley 2018, Besnard et al. 2023). The Gulf of California is characterized by high fishing pressure on coastal habitats, which results in depleted hammerhead shark populations (Pérez-Jiménez 2014). This includes juvenile scalloped and

47 smooth hammerhead sharks, which are frequently reported in the catches of artisanal
48 fisheries (Torres-Rojas et al. 2015, Saldaña-Ruiz et al. 2017). While movements of late juveniles
49 in the pelagic habitat have been characterized (e.g., Besnard et al. 2021, Jorgensen et al. 2009,
50 Klimley et al. 1993), the dietary dependency of early life stages to coastal and offshore
51 resources, especially during their ontogenetic habitat shift in the central region of the Gulf of
52 California, is not fully understood, albeit essential for their conservation (Kinney &
53 Simpfendorfer 2009, Besnard et al. 2023).

54 Trophic biomarkers, such as stable isotopes (SI; here $\delta^{13}C$, $\delta^{34}S$ and $\delta^{15}N$) and fatty acids (FAs),
55 provide a powerful approach to describe consumer trophic niches and can easily be carried
56 out on samples collected from fisheries catches (Belicka et al. 2012~~b~~, Sardenne et al. 2016). In
57 marine ecosystems, baseline $\delta^{13}C$ values are reflected in predator tissues due to minimal
58 trophic enrichment, and depict shark foraging habitats by discriminating coastal (e.g.,
59 seagrasses, macrophytes) from phytoplanktonic offshore primary producers~~,~~ due to different
60 inorganic carbon sources and photosynthesis pathways (Miller et al. 2010, Bird et al. 2018).
61 Meanwhile, $\delta^{15}N$ values are classically used as a proxy for trophic position owing to ^{15}N-
62 stepwise enrichment throughout the food webs (Hussey et al. 2014). Compared to $\delta^{13}C$ and
63 $\delta^{15}N$, $\delta^{34}S$ exhibits wider variations and has a higher discrimination potential across coastal
64 primary producers (Peterson et al. 1985, Connolly et al. 2004, Seubert et al. 2019). $\delta^{34}S$ has
65 been used to describe organic matter pathways to marine consumers and is characterized by
66 no or small isotopic fractionations between prey and predators (McCutchan et al. 2003). In
67 the water column, sulfur is found under the form of ^{34}S-enriched sulfate but accumulates as
68 ^{34}S-depleted sulfide in anaerobic sediment (Fry et al. 1982, Connolly et al. 2004, Croisetière et
69 al. 2009). Therefore, $\delta^{34}S$ has the potential to identify coastal shark foraging strategies along
70 a benthic to pelagic gradient (Plumlee & Wells 2016, Curnick et al. 2019, Raoult et al. 2019).

Finally, FAs, the main components of lipids, can also be used to infer food sources (Dalsgaard et al. 2003, Parrish 2013, Meyer et al. 2019). In trophic ecology, FAs of reserve lipids (i.e., neutral lipids) are often preferred to membrane lipids (i.e., polar lipids), as they are transferred with limited modifications from prey to predators (Robin et al. 2003). Polyunsaturated FAs (PUFAs), such as docosahexaenoic acid (DHA, 22:6n-3), eicosapentaenoic acid (EPA, 20:5n-3), and arachidonic acid (ARA, 20:4n-6) are essential for the development of fish early life stages, as they support somatic growth, cognitive functions and behavioral competences (Závorka et al. 2023). PUFAs are dietary acquired by consumers as primary producers are the only species able to *de novo* synthesize them (Parrish 2013), providing information on their trophic resources (Sargent et al. 1995, Belicka et al. 2012). Combined, SI and FA offer the opportunity to describe trophic niches on multiple dimensions and efficiently address resource partitioning (Sardenne et al. 2016, Every et al. 2017).

This study describes the trophic niches of juvenile scalloped and smooth hammerhead sharks to assess their use of coastal habitats and potential overlap in dietary resources. As young hammerhead sharks exhibit multiple trophic shifts, from maternal provisioning to active foraging in nursery grounds and then to offshore ecosystems (Jorgensen et al. 2009, Lyons et al. 2020, Besnard et al. 2021, Besnard et al. 2023), a multi-tissue approach providing different temporal windows into shark diet was used by analyzing muscle and whole blood. Indeed, sharks acquire dietary signals within a different timeframe between the metabolically active blood, which integrates prey biochemical composition at shorter time scale (i.e., days/weeks), and less metabolically active tissues, such as muscle (i.e., months) (Malpica-Cruz et al. 2012, Beckmann et al. 2014, Bierwagen et al. 2019). In addition to scalloped and smooth hammerhead sharks, we also considered a third co-occurring species, the Pacific sharpnose shark (*Rhizoprionodon longurio*). The Pacific sharpnose shark is a small-bodied species (< 160

cm total length) living on the continental shelf of the Gulf of California, where it is traditionally caught along with hammerhead sharks (Márquez-Farías et al. 2005, Saldaña-Ruiz et al. 2017). Species of the genus *Rhizoprionodon* are generally described as productive (i.e., fast growing with important fecundity) and consequently are considered not to rely on nursery areas (Knip et al. 2010, Heupel et al. 2018). They can perform broad movements within coastal ecosystems (Carlson et al. 2008, Munroe et al. 2014, Heupel et al. 2019), adapting their diet to regional variation in prey availability (Drymon et al. 2012). In the Gulf of California, the diet of Pacific sharpnose sharks is mainly composed of coastal demersal prey, with lower consumption of pelagic cephalopods and fishes, the proportions of which change opportunistically depending on the local distribution of prey (Alatorre-Ramirez et al. 2013, Gayford & Whitehead 2023, Hernández-Aparicio et al. 2023). Therefore, Pacific sharpnose shark SI and FA compositions were used as a proxy of the continental shelf foraging signal to better estimate the hammerhead shark dietary dependency on coastal or offshore resources. Given the similarity of their foraging habitats, overlapping trophic niches were expected between early life stages of scalloped and smooth hammerhead sharks, as well as Pacific sharpnose sharks. Distinct variations between muscle and blood SI and FA compositions, indicative of recent dietary changes, may reflect a recent transition between coastal and offshore waters for some hammerhead sharks, thereby reducing trophic competition within the more spatially constrained coastal habitat.

2. Materials & Methods

2.1. Sample collection

Sharks analyzed in this study originated from the artisanal fishing camp of Santa Rosalía (27°20’26”N; 112°15’54”W), located in the western coast of the Gulf of California, in March,

November and December 2019. Three species were studied: the scalloped hammerhead shark, *Sphyrna lewini* (*n* = 20), the smooth hammerhead shark, *Sphyrna zygaena* (*n* = 19), and the Pacific sharpnose shark, *Rhizoprionodon longurio* (*n* = 20). All sharks were sexed and measured for total length (TL). Scalloped and smooth hammerhead sharks ranged from 76 to 143 cm (TL) and from 94 to 138 cm (TL), corresponding only to juveniles between 1 and 3 years old (Anislado-Tolentino et al. 2008, Torres-Huerta et al. 2008) and between 2 and 5 years old (Morán-Villatoro et al. 2018, Nava Nava & Márquez-Farías 2014), respectively. Pacific sharpnose sharks were caught between 92 and 125 cm (TL), corresponding to a size close to or later than sexual maturity (Corro-Espinosa et al. 2011).

Tissue sampling took place as soon as the sharks were landed on shore. Whole blood and muscle were sampled for each specimen. Between 1 and 3 mL of blood was drawn via caudal venipuncture using a 10 mL single-use syringe and approximately 1 g of muscle was sampled from the shark dorsal region. Both tissues were transferred into different glass vials (previously heated at 450°C) containing 6 mL of $CHCl_3$/MeOH (2:1, v/v) solvent mixture to initiate lipid extraction (Folch et al. 1957). Samples were held on ice during the transport to the laboratory (CIBNOR – Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur). There, vials containing tissues in solvent mixture were vortexed for 5 minutes. For muscle samples, mechanical crushing using a Dounce homogenizer was performed in order to enhance lipid extraction. Then, for all samples, solvent mixture (i.e., the lipid extract) and residual tissues were separated into different glass vials. Vials containing lipid extracts were immediately flushed with N_2 and stored at -80°C while blood and muscle samples were stored at -20°C until further treatments.

2.2. Stable isotope analysis

As lipids and urea are known to alter $\delta^{13}C$ and $\delta^{15}N$ values respectively (Post et al. 2007, Li et al. 2016, Shipley & Matich 2020), all samples were urea-extracted prior to SI analysis in addition to the previously described lipid extraction procedure. Measurement of $\delta^{34}S$ values were also performed on lipid- and urea-extracted samples as previously described for shark blood and muscle samples (e.g., Plumlee & Wells 2016, Seubert et al. 2019). Urea was extracted by immersing each sample into 6 mL of distilled water. The mixture was subsequently vortexed for 1 minute, left at room temperature for 24 hours and centrifuged for 5 minutes before water removal. This process was repeated three times. All samples were then freeze-dried and homogenized prior to analysis.

SI ratios (δ notation) are expressed relatively to international standards: Vienna Pee Dee Belemnite for $\delta^{13}C$, Vienna Canyon Diablo Troilite for $\delta^{34}S$ and atmospheric air for $\delta^{15}N$. $\delta^{13}C$ and $\delta^{15}N$ values were measured using a Thermo Scientific Flash EA 2000 elemental analyzer coupled to a Delta V Plus mass spectrometer at the Pole Spectrométrie Océan (IUEM, Plouzané, France). For these analyses, approximately 0.5 mg of dry muscle or blood powder were weighted into tin cups. $\delta^{34}S$ values were determined separately using a vario Pyrocube elemental analyzer (EA) with “Purge and Trap” technology connected online in continuous flow mode to an IsoPrime100 mass spectrometer (Elementar UK Ltd Cheadle, UK) equipped with a diluter system at the Plateforme d’Écologie Isotopique of the Laboratoire d’Écologie des Hydrosystèmes Naturels et Anthropisés (LEHNA), hosted by the Université Claude Bernard Lyon1 (UCBL) and part of the RéGEF national network (Fourel et al. 2014). For this analysis, between 1.0 and 1.5 mg of dry muscle or blood powder were weighted into tin cups. All isotopic values are expressed in per mil (‰) with R the $^{13}C/^{12}C$, the $^{34}S/^{32}S$ or the $^{15}N/^{14}N$ ratios and X the corresponding ^{13}C, ^{34}S or ^{15}N:

164 $$\delta X\ (‰) = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000$$

165 International standards were analyzed throughout the sample run and validated correct
166 isotopic measurements: IAEA-600 Caffeine, IAEA-CH-6 Sucrose, IAEA-N-1 and IAEA-N-2
167 Ammonium Sulfate for $\delta^{13}C/\delta^{15}N$ and Poly(1,4-Phenylene Ether-Sulfone) B2203 for $\delta^{34}S$.
168 Analytical uncertainties were calculated using an Acetanilide in-lab certified substance for
169 $\delta^{13}C/\delta^{15}N$ values and were ± 0.17‰ for $\delta^{13}C$ and ± 0.11‰ for $\delta^{15}N$. For sulfur isotope
170 measurements, typical analytical precision (2σ) is lower than 0.3‰. All samples presented a
171 C:N ratio below 3.5, validating a good lipid and urea removal as pure protein sample is
172 expected to be around 3.0 (Post et al. 2007, Hussey et al. 2012).

173 ## 2.3. Fatty acid composition

174 FA analysis was performed at the Lipidocean facility (LEMAR, Plouzané, France). Lipid extracts
175 of both blood and muscle were shaken for 20 minutes at room temperature and centrifuged
176 at 3000 rpm (~738 *g*) for 15 minutes. An aliquot of 250 µL of each muscle extract and of 500
177 µL of each whole blood extract was transferred to new glass vials and evaporated to dryness
178 under N_2 flux. Dry extracts were recovered by three consecutive re-suspension in 500 µL of
179 $CHCl_3$/MeOH (98:2, v/v) and deposited at the top of a silica gel micro-column (40 mm × 4 mm,
180 silica gel 60A, previously heated at 450°C, 63-200 µm rehydrated with 6% H_2O; 70-230 mesh).
181 Neutral lipids (i.e., reserve lipids) were eluted using 10 mL of $CHCl_3$/MeOH (98:2, v/v) and
182 collected in glass vials (Le Grand et al. 2014). 2.3 µg of C23:0 (i.e., tricosanoic acid), an internal
183 standard, was added to each glass vial. Following elution, neutral lipid fractions were
184 evaporated to dryness using an EZ-2 centrifugal evaporator (Genevac). Neutral lipid fractions

were subsequently recovered by three consecutive re-suspension in 500 µL of $CHCl_3$/MeOH (2:1, v/v), transferred to 7 mL glass vials and evaporated to dryness under N_2 flux.

Blood neutral lipids underwent a basic saponification directly followed by an acidic transmethylation, while muscle samples underwent acidic transmethylation alone. Basic saponification consisted in the addition of 1 mL of KOH/MeOH (0.5M); the solution was flushed under N_2, vortexed and incubated at 80°C for 30 minutes. After cooling at room temperature, acidic transmethylation was achieved by adding directly 1600 µL of H_2SO_4/MeOH (3.4%, v/v) and heating at 100°C for 10 minutes. Then, 800 µL of hexane was added to recover fatty acid methyl esters (FAME) and this organic phase was washed three times with 1.5 mL of hexane-saturated distilled water. The organic phase was then purified on a Dionex P680 HPLC system equipped with an ASI-100 auto-sampler, detected with a DAD-detector at 205 nm to isolate FAME from sterols, squalene and fatty alcohols (Marty et al. 1999). Two columns (250 mm x 4 mm I.D., 5 µm) aligned in series were used: a Lichrospher Si 60 (Merck) and a Lichrospher 100 Diol (Merck). The mobile phase was composed of a mixture of two solvents, A) hexane and B) hexane/isopropanol (90:10, v/v), at 1 $mL.min^{-1}$ following a gradient from: 100% of solvent A between 0-2 min, 85% of solvent A between 2-10 min; 50% of solvent A between 10-16 min and 100% of solvent A between 16-35 min. FAME were collected from 12 to 18 minutes with an Isco Foxy Jr. fraction collector in 7 mL glass vials, evaporated to dryness under N_2 flux and finally recovered by resuspension into 800 µL of hexane.

FAME analysis was performed using a CP 8400 (Varian) gas chromatograph coupled to a flame ionization detector (GC-FID). Oven was programmed in temperature (from 0°C to 150°C at 50°C min^{-1}, then to 170°C at 3.5°C min^{-1}, to 185°C at 1.5°C min^{-1}, to 225°C at 2.4°C min^{-1}, and

finally to 250°C at 5.5°C min^{-1} for 15 min). The GC-FID was equipped with an auto-sampler, two split-less injectors regulated at 220°C and two flame-ionization detectors (280°C) using hydrogen as vector gas.

FAME were separated simultaneously on two different capillary columns, a polar (DBWAX -30 m × 0.25 mm i.d., 0.25-µm thickness, Agilent) and an apolar (DB5 -30 m × 0.25 mm i.d., 0.25-µm thickness, Agilent). FAME were identified by comparison of their retention time with those of commercial standards (Supelco 37 Component FAME Mix, the PUFA No.1 and No.3, and the Bacterial Acid Methyl Ester Mix from Sigma) and in-house standard mixtures from marine bivalves, fish, micro- and macroalgae. Peak integration was realized with the software Galaxy Chromatography Data System (v. 1.9, Varian). Individual FA contents are expressed as the mass percentage (%) of the total FA content.

2.4. Data analysis

All analyses were performed using R (R Core Team 2023). Species isotopic niches were described using Layman metrics based on convex hull areas drawn inside the $\delta^{13}C/\delta^{15}N$ or $\delta^{34}S/\delta^{15}N$ δ-space (Layman et al. 2007), which included isotopic ranges ($\delta^{13}C$ rg, $\delta^{34}S$ rg and $\delta^{15}N$ rg) as the distance between the highest and lowest $\delta^{13}C$, $\delta^{34}S$ or $\delta^{15}N$ values, respectively, the total area (TA) as the surface of the convex hull area and the mean distance to the centroid (CD) as the mean distance of each individual to the $\delta^{13}C/\delta^{15}N$ or $\delta^{34}S/\delta^{15}N$ centroid. Core regions of the isotopic niches were described based on 40% kernel density surfaces using the rKIN package (Eckrich et al. 2020). Areas of overlap between isotopic niches were assessed based on ellipse representations encompassing 95% of the data using the SIBER package (Jackson et al. 2011). Overlaps were expressed as a proportion of the non-overlapping area

between two ellipses in the $\delta^{13}C/\delta^{15}N$ or $\delta^{34}S/\delta^{15}N$ δ-space and were separately calculated for muscle and blood values.

FAs accounting for less than 1.5% of the total FA contents were removed from the analysis. In blood, 14 FAs were selected: 14:0, 16:0, 18:0, 16:1n-7, 18:1n-7, 18:1n-9, 20:1n-9, 24:1n-9, 20:4n-6 (ARA), 20:5n-3 (EPA), 22:4n-6, 22:5n-3, 22:5n-6 and 22:6n-3 (DHA). In muscle, 3 more FAs were considered: 16:1n-9, 18:2n-6 and 16:0 dimethylacetal (16:0DMA). A non-parametric permutational multivariate analysis of variance (PERMANOVA) was used to test if FA composition differed between species based on Bray-Curtis matrix of dissimilarities using 1000 random permutations among species. To avoid giving excessive weight to rare FAs, Euclidean distances were calculated (Legendre & Gallagher 2001) and the most discriminant FAs (here selected as accounting for more than 90% of the dissimilarities between species) were identified through a test of similarity percentages (SIMPER). Finally, principal component analyses (PCA) were separately performed for both tissues to further investigate the variation in FA compositions among shark species.

After checking for normality (Shapiro-Wilk test) and variance homogeneity (Bartlett's test), interspecific differences were assessed trough one-way ANOVAs followed by post-hoc Tukey's HSD tests for muscle $\delta^{13}C$ values, and Kruskal-Wallis tests followed by Dunn's post-hoc tests with Bonferroni's adjustment for FA composition, $\delta^{34}S$, $\delta^{15}N$ and blood $\delta^{13}C$ values ($\alpha = 0.05$ for all statistical tests). Intraspecific differences in isotopic values and FA proportions between tissues, sampling seasons and sexes were tested using Student's *t*-tests or a non-parametric analogue, the Wilcoxon signed-rank test (detailed in Supplementary Information). For each species, ontogenetic variations in isotopic values and FA proportions were assessed through ordinary least squares linear regressions.

Finally, overlaps between species trophic niches were estimated considering both SI and FA compositions using the nicheROVER package (Swanson et al. 2015). The package functions allow to delineate niche regions in a multivariate space and to estimate the overlap between them as the probability for an individual from one species to be found in the niche region of a second species. Here, each species trophic niche was set as a 95% probability region using $\delta^{13}C$, $\delta^{34}S$, $\delta^{15}N$ and the coordinates of the first three most explaining dimensions of the PCA performed on FA composition (explaining 59.3% and 66.5% of the total variance in muscle and blood, respectively) to give similar weight to SI and FA analyses in the calculation of overlapping areas. To account for uncertainty, 1000 Monte Carlo draws of niche region projections were used for overlap estimation in a Bayesian framework. This analysis was run separately for muscle and blood tissues to compare overlap estimations between them.

3. Results

3.1. Nitrogen, carbon and sulfur stable isotopes

Significant differences in $\delta^{15}N$ values were observed between species in both tissues ($\chi^2_{2,58}$ = 7.9, $p < 0.05$ for muscle and $\chi^2_{2,58}$ = 18.4, $p < 0.001$ for blood values) (Table 1). Muscle of smooth hammerhead sharks were ^{15}N-depleted compared to scalloped hammerhead sharks (Dunn's test, $p < 0.05$), while Pacific sharpnose sharks displayed intermediate values and did not significantly differ from other species. In blood, the Pacific sharpnose shark had the highest $\delta^{15}N$ values compared to both hammerhead sharks (Dunn's tests, $p < 0.001$). Interspecific differences in muscle and blood $\delta^{13}C$ values were also detected ($F_{2,58}$ = 15.6, $p <$ 0.001 and $\chi^2_{2,58}$ = 23.4, $p < 0.001$, respectively). In both tissues, smooth hammerhead sharks showed the lowest $\delta^{13}C$ values (in muscle Tukey's HSD tests, $p < 0.001$ and $p < 0.05$ for scalloped hammerhead and Pacific sharpnose sharks, respectively; in blood Dunn's tests, $p <$

0.001 for both species). Considering muscle values, scalloped hammerhead sharks had significantly higher $\delta^{13}C$ than Pacific sharpnose sharks (Tukey's HSD test, $p < 0.05$). Finally, $\delta^{34}S$ values also displayed significant interspecific differences ($\chi^2_{2,58} = 33.5$, $p < 0.001$ for muscle and $\chi^2_{2,58} = 14.0$, $p < 0.001$ for blood values). The scalloped hammerhead shark had systematically smaller $\delta^{34}S$ values compared to the other species (in muscle Dunn's tests, $p < 0.001$ and $p < 0.05$ for smooth hammerhead and Pacific sharpnose sharks, respectively; in blood Dunn's tests, $p < 0.01$ for both species) and muscle of smooth hammerhead sharks had higher $\delta^{34}S$ values than Pacific sharpnose sharks (Dunn's test, $p < 0.01$).

For hammerhead shark species, isotopic values measured in both tissues did not differ between sexes, except for scalloped hammerhead shark blood $\delta^{15}N$ values ($t_{18} = -2.28$, $p < 0.05$). For the Pacific sharpnose shark, significant differences were found in $\delta^{13}C$ ($t_{18} = -2.52$, $p < 0.05$ for blood and $t_{17} = -2.14$, $p < 0.05$ for muscle) and muscle $\delta^{15}N$ ($W = 89$, $p < 0.01$) values between females and males. Because the Pacific sharpnose shark was not the main focus of this study and considered as an outgroup for comparison with hammerhead species, such differences were not explored and both sexes were combined. There were no intraspecific differences in isotopic values between sampling seasons, with the exception of scalloped hammerhead shark muscle $\delta^{13}C$ values ($t_{18} = -2.34$, $p < 0.05$) and Pacific sharpnose shark muscle $\delta^{13}C$ and $\delta^{15}N$ values ($t_{14} = 2.30$, $p < 0.05$ and $W = 3$, $p < 0.001$, respectively). Scalloped hammerhead shark $\delta^{13}C$ values significantly decreased with total length, while they increased for the Pacific sharpnose shark, in both muscle and blood (Figure 1A and 1B). In all three species, there was no significant ontogenetic variation in $\delta^{34}S$, excepted for the increasing values in the blood of Pacific sharpnose sharks (Figure 1C and 1D). Finally, $\delta^{15}N$ significantly increased with total length in both muscle and blood of smooth hammerhead sharks and decreased in the muscle of Pacific sharpnose sharks (Figure 1E and 1F).

For muscle values, scalloped hammerhead shark isotopic niche width was similar to the one of Pacific sharpnose sharks only in the $\delta^{13}C/\delta^{15}N$ δ-space (Figure 2A and 2B, Table 2). For blood and muscle $\delta^{34}S/\delta^{15}N$ δ-space, the isotopic niche of Pacific sharpnose sharks was larger than both hammerhead sharks (Figure 2C and 2D, Table 2). Smooth hammerhead sharks systematically occupied a narrower isotopic niche, the only exception in muscle occurred inside the $\delta^{34}S/\delta^{15}N$ δ-space where the scalloped hammerhead shark had equivalent TA but narrower $\delta^{34}S$ rg and CD, as well as in the blood $\delta^{13}C/\delta^{15}N$ δ-space where the scalloped hammerhead shark had narrower $\delta^{15}N$ rg and TA. Isotopic niche width of smooth hammerhead sharks appeared similar in both tissues and δ-spaces. Core isotopic regions (i.e., 40% kernel density surface) were systematically larger for Pacific sharpnose sharks and narrower for smooth hammerhead sharks with scalloped hammerhead sharks exhibiting intermediate values (Figure 2, Table 2).

Shark isotopic niches overlapped. This was first apparent from the convex hull areas of Pacific sharpnose sharks almost entirely encompassing the ones of both hammerhead shark species, but was particularly striking analyzing 95% ellipse areas (Figure 2). Considering muscle tissue, the Pacific sharpnose shark isotopic ellipse area overlapped at 54% with the one of the scalloped hammerhead shark and at 41% with the one of the smooth hammerhead shark in the $\delta^{13}C/\delta^{15}N$ δ-space, while respectively overlapping at 39% and 50% in the $\delta^{34}S/\delta^{15}N$ δ-space. Such estimates decreased in blood (i.e., 35% and 31% in the $\delta^{13}C/\delta^{15}N$ δ-space and 24% and 19% in the $\delta^{34}S/\delta^{15}N$ δ-space, respectively), rather as a consequence of the larger size of the Pacific sharpnose shark isotopic niche (covering nearly entirely hammerhead shark isotopic niches) more than of a clear separation between isotopic niches. Between both hammerhead species, estimates of overlapping regions between isotopic ellipse areas

increased from muscle to blood estimates in both the $\delta^{13}C/\delta^{15}N$ δ-space (i.e., from 29 to 34%) and the $\delta^{34}S/\delta^{15}N$ δ-space (i.e., from 18 to 38%).

3.2. Fatty acid composition

FAs proportions varied between sexes in Pacific sharpnose sharks but not in hammerhead sharks, except for muscle 16:1n-7, 18:1n-9, 20:1n-9 and 22:4n-6, as well as blood 14:0 and 16:1n-7 in smooth hammerhead sharks. Pacific sharpnose shark FA content varied between sampling seasons, while only muscle 16:0, 24:1n-9 and 18:2n-6, as well as blood 24:1n-9 and 22-5n-3 seasonally differed in scalloped hammerhead sharks (detailed in Supplementary Information). The percentage of FAs in both tissues significantly differed between species (PERMANOVA, $F_2 = 7.26$, $p < 0.001$ for muscle, $F_2 = 4.69$, $p < 0.01$ for blood), mainly due to the contribution of 13 FAs for muscle and 10 FAs for blood (SIMPER). However, intraspecific variability in FA composition (mostly expressed on the PCA first axis, explaining 26.5% and 32.8% of the variance for muscle and blood, respectively) was systematically higher than interspecific variability (mostly expressed on the PCA second axis, explaining 18.6% and 21.4% of the variance for muscle and blood, respectively) (Figure 3A and 3C).

Interspecific differences in FA compositions were observed for polyunsaturated FAs (Figure 3B and 3D). Smooth hammerhead sharks were characterized by higher proportions of DHA compared to scalloped hammerhead sharks ($\chi^2_{2,53} = 15.3$, $p < 0.001$, Dunn's test, $p < 0.001$ in muscle and $\chi^2_{2,45} = 7.3$, $p < 0.05$, Dunn's test, $p < 0.05$ in blood) and higher percentages of ARA compared to Pacific sharpnose sharks ($\chi^2_{2,53} = 26.0$, $p < 0.001$, Dunn's test, $p < 0.001$ in muscle and $\chi^2_{2,45} = 10.0$, $p < 0.01$, Dunn's test, $p < 0.01$ in blood). EPA contents were significantly different among species only in muscle ($\chi^2_{2,53} = 8.7$, $p < 0.05$) with higher proportion in the smooth hammerhead shark compared to the Pacific sharpnose shark (Dunn's test, $p < 0.001$).

Other interspecific differences included higher relative amount of muscle 22:4n-6 ($\chi^2_{2,53}$ = 25.3, $p < 0.001$, Dunn's tests, $p < 0.001$) and blood 22:5n-3 ($\chi^2_{2,45}$ = 10.2, $p < 0.01$, Dunn's tests, $p < 0.01$) in Pacific sharpnose sharks along with higher percentage of muscle 16:0DMA and lower proportion of blood 16:1n-7 in smooth hammerhead sharks compared to the other species ($\chi^2_{2,53}$ = 11.2, $p < 0.01$, Dunn's tests, $p < 0.05$ and $\chi^2_{2,45}$ = 14.0, $p < 0.001$, Dunn's tests, $p < 0.01$, respectively). Some FA proportions varied with total length and main ontogenetic differences were found in the muscle of scalloped hammerhead sharks (detailed in Supplementary Information), with an increase in 22:4n-6 (R^2 = 0.69, F = 35, $p < 0.001$) and 24:1n-9 (R^2 = 0.40, F = 10, $p < 0.01$), and a decrease in 18:1n-9 (R^2 = 0.50, F = 16, $p < 0.01$).

3.3. Overlap between trophic niches

Considering SI values ($\delta^{13}C$, $\delta^{34}S$, $\delta^{15}N$) and FA compositions (PCA first three explaining dimensions), the mean probability to find Pacific sharpnose sharks within the niche of hammerhead sharks were similar for both species and across tissues (i.e., 77% and 72%, for scalloped hammerhead sharks and 72% and 70% for smooth hammerhead sharks in muscle and blood, respectively) (Figure 4A and 4B). The probability of scalloped hammerhead sharks to be found within the niche of Pacific sharpnose sharks remained equivalent in both tissues (i.e., 30% and 25% in muscle and blood, respectively) (Figure 4A). However, it was not the case for smooth hammerhead sharks which displayed decreasing probabilities of sharing the niche of Pacific sharpnose sharks from muscle (27%) to blood (9%) estimates (Figure 4B). Finally, the probability of encountering scalloped hammerhead sharks inside the niche of smooth hammerhead sharks increased from 12% in the muscle to 44% in blood, while the probability for smooth hammerheads to share the niche of scalloped hammerheads were similar in both tissues (18% in muscle and 15% in blood) (Figure 4C).

4. Discussion

4.1. Similarities in trophic niches

SI and FAs revealed similarities in foraging traits among species. Mean interspecific variations in $\delta^{13}C$ and $\delta^{15}N$ values did not exceed 1‰, implying that sharks relied on prey deriving their carbon from a homogeneous pool of primary producers and feeding at equivalent trophic levels (Hussey et al. 2014, Bird et al. 2018). The range of $\delta^{15}N$ and $\delta^{13}C$ suggested that sharks were tertiary consumers, foraging mainly over the continental shelf and influenced by both nearshore and offshore production, in accordance with published data of marine biota in the Gulf of California (i.e., fishes and squids with $\delta^{15}N$ higher than 20‰ and $\delta^{13}C$ ranging from -15 to -12‰ in Aurioles-Gamboa et al., 2013). Considering $\delta^{34}S$ large fluctuation in marine ecosystems (Fry et al. 1982, Connolly et al. 2004, Croisetière et al. 2009), interspecific differences in mean $\delta^{34}S$ values were small in both tissues supporting the overall similarity in the three species foraging habitat. Muscle and blood $\delta^{34}S$ range of values were typical of sharks feeding on a mix of demersal and pelagic prey (Plumlee & Wells 2016, Raoult et al. 2019). The highest $\delta^{34}S$ variations found in Pacific sharpnose sharks, especially in blood, were in accordance with their described diet in the region focusing on both compartments (Alatorre-Ramirez et al. 2013, Hernández-Aparicio et al. 2023). Isotopic similarity across species therefore resulted in important overlapping isotopic niches between hammerheads and the Pacific sharpnose shark regardless of the used metrics (i.e., 95% ellipse areas, convex hulls or 40% kernel densities).

FAs reported in the tissues of hammerhead sharks agreed with the composition of both species in previous studies (Davidson et al. 2014, Segura-Cobeña et al. 2021, Xu et al. 2022) and with the similarities in dietary niches described by isotopic values. Indeed, intraspecific

dissimilarities exceed interspecific variations, a pattern observed among sympatric species with phylogenetic and ecological proximity, including trophic redundancy, as described for tuna species (Sardenne et al. 2016), reef sharks (Bierwagen et al. 2019) and coastal/euryhaline sharks (Every et al. 2017). Moreover, similarity in the FA composition of co-occurring scalloped and smooth hammerhead sharks was also described when they shared similar diet (Davidson et al. 2014). When both SI and FAs were considered for the estimation of trophic niches, important mean probabilities of encountering Pacific sharpnose sharks inside the trophic niche of both hammerhead species were therefore detected (i.e., > 70% in both tissues). However, inter-tissues differences in trophic biomarkers between scalloped and smooth hammerhead sharks suggested a possible role of contrasted foraging habitat dynamics in supporting resource partitioning.

4.2. Ontogenetic habitat shifts in hammerhead sharks

While a potential effect of maternal provisioning could be observed for scalloped hammerhead sharks, it seems not to be the case for smooth hammerhead sharks. Muscle FA content of scalloped hammerhead sharks displayed more pronounced ontogenetic variations than in blood or compared to smooth hammerhead sharks (detailed in Supplementary Information). Shark maternal provisioning has been previously linked to high level of ARA, DHA and monounsaturated n-9 FAs at early life stages (Belicka et al. 2012, Pethybridge et al. 2011, Rangel et al. 2021). In scalloped hammerhead sharks, significant ontogenetic variations were mainly observed through the increase in the proportion of 22:4n-6 and 24:1n-9 and the decrease in the proportion of 18:1n-9. Maternal provisioning could therefore provide sustainable levels of essential DHA, ARA and EPA for the development of neonates, while other PUFAs, such as 22:4n-6, would be obtained through the development of foraging skills

during ontogeny (Pethybridge et al. 2011, Rangel et al. 2021). In the meantime, the high proportions of monounsaturated FAs, mainly 18:1n-9 here which decrease ontogenetically, may arise from their use as energy sources by early life stages of the scalloped hammerhead shark (Belicka et al. 2012, Lyons et al. 2020, Pethybridge et al. 2011). Hypothetically, the increase in muscle and blood 24:1n-9 (i.e., nervonic acid) of scalloped hammerhead sharks might be linked to the development of nervous tissues and brain functions (Liu et al. 2021) facilitated by the maternal provisioning of 18:1n-9 as a precursor (Song et al. 2022). Future examination of the genes and/or enzymes involved in these FA biosynthesis pathways could clarify the underlying physiological mechanisms and their ties to maternal inputs. Without adult specimens, the effect of maternal provisioning on scalloped hammerhead shark isotopic values was equivocal but difficult to refute given the length classes sampled (Vaudo et al. 2010, Niella et al. 2021). In slow growing placentatrophic sharks, maternal effect is observed when adult and early juvenile foraging habitats are isotopically distinct (Belicka et al. 2012, Niella et al. 2021). However, it is not the case in scalloped hammerhead sharks for which both adults and early juveniles share similar coastal feeding grounds and isotopic values (Cerutti-Pereyra et al. 2022). Irrespective of maternal provisioning, early juveniles actively foraging would display coastal signals and observed ontogenetic changes in isotopic values were most likely tied to dietary and habitat shifts.

The trophic niche of juvenile smooth hammerhead sharks suggested they have already initiated their transition between coastal nurseries and offshore ecosystems. Indeed, smooth hammerhead sharks displayed the lowest $\delta^{13}C$ and highest muscle $\delta^{34}S$ values indicating a stronger reliance on prey from ^{13}C-depleted and ^{34}S-enriched phytoplankton-based food web (Fry & Sherr 1984, Plumlee & Wells 2016, Bird et al. 2018, Curnick et al. 2019). They also had the highest proportions of DHA in both muscle and blood, which is recognized as revealing the

contribution of pelagic dinoflagellates (Dalsgaard et al. 2003, Parrish et al. 2015, Gladyshev et al. 2018) and that concentrated in the tissues of juvenile smooth hammerhead sharks feeding on offshore prey (Segura-Cobeña et al. 2021, Xu et al. 2022). In the northeastern Pacific region, the transition from a coastal- to a mesopelagic-dominant diet was established around 2 years old for the smooth hammerhead shark (Besnard et al. 2023). Given isotopic muscle turnover rates (i.e., months to years) (e.g., Logan & Lutcavage 2010), the fact that smooth hammerhead sharks between 2 to 5 years old have already initiated their ontogenetic diet shift (i.e., still overlapping with nearshore species but with clear markers of a pelagic diet) is in direct accordance with a habitat shift occurring between 2 and 3 years old in the Gulf of California.

The scalloped hammerhead shark isotopic niche was not consistent when analyzed in muscle or whole blood, likely reflecting a more recent transition to offshore foraging grounds compared to the smooth hammerhead shark. In the muscle, the species had the highest $\delta^{13}C$ values suggesting it more extensively relied on coastal prey (Fry & Sherr 1984, Bird et al. 2018). It also displayed the lowest muscle $\delta^{34}S$ values, possibly reflecting the occurrence of coastal benthic invertebrate in the diet of young juveniles, like it has been observed for bonnethead sharks (*Sphyrna tiburo*) in the Gulf of Mexico (Plumlee & Wells 2016). Indeed, foraging on benthic prey is a common behavior of juvenile scalloped hammerhead sharks during their coastal phase as previously observed in Hawaii (Bush 2003), southern Mexican Pacific (Flores-Martínez et al. 2017) and southeastern Gulf of California (Torres-Rojas et al. 2014). Rather than a dissimilarity in trophic positions between species, higher muscle $\delta^{15}N$ found in scalloped hammerhead sharks than in smooth hammerhead sharks could result from higher $\delta^{15}N$ baseline in coastal environments compared to offshore habitats (e.g., Kurle & McWhorter 2017, Shipley et al. 2021). Such coastal foraging signal could potentially originate from nursery grounds. Still, scalloped hammerhead shark isotopic niche width was similar to

463 the one of Pacific sharpnose sharks in the muscle $\delta^{13}C/\delta^{15}N$ δ-space indicating that some
464 specimens may have already fed on offshore prey. This is reinforced by the observed
465 ontogenetic decrease in muscle $\delta^{13}C$ values, highlighting the initiation of foraging in the
466 pelagic realm by larger juveniles. Surprisingly, this was not observed in the muscle $\delta^{34}S/\delta^{15}N$
467 δ-space, suggesting that, while dietary intraspecific differences might have resulted in
468 different carbon organic pools, muscle sulfur origin remained analogous among scalloped
469 hammerhead sharks.

470 The scalloped hammerhead shark trophic niche was closer to the pelagic one of the smooth
471 hammerhead shark in blood than in muscle, as shown by the increasing probability of
472 encountering scalloped hammerhead sharks inside the trophic niche of smooth hammerhead
473 sharks from 12% in muscle to 44% in blood (a pattern also observed isotopically in the
474 $\delta^{13}C/\delta^{15}N$ and $\delta^{34}S/\delta^{15}N$ δ-spaces). Smooth hammerhead sharks occurred at larger size with
475 markers of pelagic diet identified in both muscle and blood, while they were only detectable
476 in blood for smaller scalloped hammerhead sharks. Blood has a shorter turnover and therefore
477 reflects more recent dietary sources compared to muscle (Malpica-Cruz et al. 2012, Beckmann
478 et al. 2014). The ontogenetic diet shift was therefore more recent for scalloped hammerhead
479 sharks, likely occurring in the size range of this study, from 76 to 143 cm (TL). Such more recent
480 specialization on offshore prey was reflected in the comparable probabilities of encountering
481 the species inside the trophic niche of Pacific sharpnose sharks regardless of the tissue
482 considered (i.e., displaying a mixed signature between coastal and pelagic prey). This agrees
483 with the recorded movement of a female scalloped hammerhead shark, captured at 95 cm
484 and recaptured at 123 cm (TL) in the Bay of La Paz (with horizontal migration up to this study
485 sampled site), characterized by an increasing exploration of pelagic grounds likely link to
486 foraging purposes (Hoyos-Padilla et al. 2014).

Whether such interspecific difference in reliance on pelagic subsidies is an artifact of sampling (i.e., smooth hammerhead sharks sampled at larger size than scalloped hammerhead sharks) or a real asynchrony in migration timing remains to be clarified. Even though at a more advanced stage of their transition, smooth hammerhead sharks did not yet reach steady-state with offshore habitats and specialization on pelagic prey was still occurring. This was indicated by the decreasing probabilities of encountering the species inside the niche of Pacific sharpnose sharks between muscle and blood estimates and by the similar probabilities of encountering it inside the niche of scalloped hammerhead sharks in both tissues. Moreover, specialization on higher trophic level prey in pelagic ecosystems likely resulted in the observed significant ontogenetic increase in smooth hammerhead shark $\delta^{15}N$ values (Hussey et al. 2014). Juvenile sharks co-existing in a shared ecosystem generally partition foraging habitats and resources (Kinney et al. 2011, Legare et al. 2015, Shaw et al. 2016, Heupel et al. 2019). While such partitioning has been observed between morphologically distinct hammerhead sharks (Bethea et al. 2011, Galindo et al. 2021), it has not been demonstrated for early life stages of scalloped and smooth hammerhead sharks sharing similar body size, opportunistic feeding behavior and ontogenetic habitat shift (Bush & Holland 2002, Bethea et al. 2011, Gallagher & Klimley 2018, Estupiñán-Montaño et al. 2019). The described fine-scale differences in ontogenetic migration timing to offshore habitats between both hammerhead species could allow for the optimization of resource partitioning, favoring the fitness of sensible early life stages.

4.3. Trophic plasticity

While Pacific sharpnose sharks could display significant movements across continental shelves (Carlson et al. 2008, Gayford & Whitehead 2023, Munroe et al. 2014, Heupel et al. 2019),

feeding on benthic and pelagic prey (Alatorre-Ramirez et al. 2013, Hernández-Aparicio et al. 2023), their isotopic niche was still expected narrower (or similar) than the ones of juvenile hammerhead sharks foraging in inshore and pelagic ecosystems with more important horizontally and vertically offshore migrations (Gallagher & Klimley 2018). Isotopically, this was only observed in the muscle $\delta^{13}C/\delta^{15}N$ δ-space for scalloped hammerhead sharks, due to above explained intraspecific dietary variations between pelagic and coastal trophic signals. However, hammerhead sharks displaying markers of a pelagic diet (i.e., smooth hammerhead sharks in both tissues and scalloped hammerhead sharks in the blood) systematically occupied narrower isotopic niches than Pacific sharpnose sharks. In the eastern Pacific, late juveniles target mesopelagic cephalopods in both scalloped (Galván-Magaña et al. 2013, Torres-Rojas et al. 2015, Estupiñán-Montaño et al. 2019) and smooth hammerhead sharks (Besnard et al. 2021, Galván-Magaña et al. 2013, Gonzalez-Pestana et al. 2017). Such low prey diversity and potential trophic redundancy in hammerhead sharks foraging in offshore environments might explained the observed narrow isotopic niches. Considering their known generalist foraging behavior, the three mesopredator species could exert distinct predation modes. While the larger isotopic niches displayed by adult Pacific sharpnose sharks could be the result from individuals specialized on different sources (i.e., benthic or pelagic), redundancy in foraging on the most available prey could explain the narrower isotopic niches of both juvenile hammerhead sharks transiting between ecosystems (Heupel et al. 2014). Interestingly, potential migrations across coastal ecosystems in the Gulf of California have been hypothesized in Pacific sharpnose sharks (Gayford & Whitehead 2023). In the absence of clear ontogenetic change in stomach contents (Alatorre-Ramirez et al. 2013, Osuna-Peralta et al. 2014), foraging on different prey or on contrasted isotopic baselines along such putative migrations could potentially explain ontogenetic changes in isotopic values and wider isotopic

534 niches (Drymon et al. 2012). Overall, such intraspecific trophic variability could have resulted
535 in the observed trophic marker variations between sexes and sampling seasons.

536 Considering their entire juvenile stage, the large isotopic niches of scalloped and smooth
537 hammerhead sharks might therefore mask a higher degree of specialization at different stages
538 of their ontogenetic migration as previously noted in young bull sharks (*Carcharhinus leucas*)
539 transiting from a freshwater to a marine diet (e.g., Belicka et al. 2012). In coastal nurseries,
540 hammerhead young-of-the-year foraging activity, even if opportunistic, is restricted to a small
541 core area (Duncan & Holland 2006, Rosende-Pereiro & Corgos 2018) leading to narrow trophic
542 niches (Bush & Holland 2002, Bethea et al. 2011, Estupiñán-Montaño et al. 2019). This study
543 further indicates narrow isotopic niches also when juveniles are switching to a pelagic diet, a
544 specialization supported by the absence of significant differences in blood isotopic values
545 between sampling seasons implying a homogeneous diet throughout the year (Malpica-Cruz
546 et al. 2012, Seubert et al. 2019). While ontogenetic habitat shift allows for the diminution of
547 predation risk and intraspecific competition, it could result in hammerhead sharks narrow
548 trophic niches before reaching adult habitats, potentially limiting their capacities of
549 adaptation against anthropogenic or environmental disturbances and implying mortality
550 events (Bush & Holland 2002, Duncan & Holland 2006). In the Gulf of California, this remains
551 to be validated by additional investigations as isotopic niches cannot be seen as a direct
552 depiction of trophic niches due to similar isotopic signatures across prey items (especially in
553 the pelagic realm) or changes in metabolism with growth (Hussey et al. 2012, Aurioles-
554 Gamboa et al. 2013, Shipley & Matich 2020).

555 # 5. Conclusion

This study presents first information on the dietary resources and habitat use of smooth hammerhead sharks and fills a gap on the trophic ecology of scalloped hammerhead sharks in the central western Gulf of California. Once leaving nursery grounds, both hammerhead shark species seem to initiate their movement toward offshore habitats after a prolonged period during which they still rely on coastal dietary resources. Such dependency of juveniles on coastal ecosystems, main location of shark fishing in the Gulf of California (e.g., Saldaña-Ruiz et al. 2017), could be one of the reasons of the decline of hammerhead shark populations in this region (Pérez-Jiménez 2014). This calls for a better characterization of scalloped and smooth hammerhead shark coastal residency (Besnard et al., 2023), including seasonal sampling effort, the rigorous identification of nurseries (Heupel et al. 2018, Rodriguez-Arana Favela et al. 2022) and the implementation of tracking studies (Queiroz et al. 2019). Ultimately, areas extensively used by juveniles that overlap with high fishing pressure should be considered as conservation priorities under the form of spatial closure of fisheries or marine protected areas.

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Tables and Figures

Table 1–Number of individuals (*n*), mean and range values of total length (TL) for scalloped hammerhead, smooth hammerhead and Pacific sharpnose sharks. C, S and N isotope values for muscle and blood are presented and expressed in mean values (± standard deviation). Upper case letters indicate significant differences between species.

Species	*n*	TL (cm)	Muscle			Blood		
			$\delta^{13}C$ (‰)	$\delta^{34}S$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{34}S$ (‰)	$\delta^{15}N$ (‰)
Scalloped hammerhead	20	97 (76-143)	-14.6 (± 0.4)^{A}	17.5 (± 0.4)^{C}	22.2 (± 0.4)^{A}	-14.6 (± 0.4)^{A}	20.5 (± 0.9)^{B}	21.0 (± 0.4)^{B}
Smooth hammerhead	19	126 (94-138)	-15.3 (± 0.3)^{C}	18.9 (± 0.6)^{A}	21.8 (± 0.5)^{B}	-15.2 (± 0.3)^{B}	21.7 (± 0.8)^{A}	20.6 (± 0.4)^{B}
Pacific sharpnose	20	105 (92-125)	-14.9 (± 0.4)^{B}	18.1 (± 0.8)^{B}	22.0 (± 0.5)^{AB}	-14.5 (± 0.6)^{A}	22.0 (± 2.3)^{A}	21.4 (± 0.6)^{A}

Table 2–Isotopic metrics based on the convex hull areas (i.e., Layman metric) or 40% kernel density regions of each species isotopic niches drawn inside the $\delta^{13}C/\delta^{15}N$ or $\delta^{34}S/\delta^{15}N$ δ-

space. Isotopic ranges, total area (TA), mean distance to the centroid (CD) and 40% kernel density surface (KD) are presented. All values are in ‰ except for TA and KD in ‰².

Species	Tissue	Isotopic ranges			$\delta^{13}C/\delta^{15}N$ δ-space			$\delta^{34}S/\delta^{15}N$ δ-space		
		$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	TA	CD	KD	TA	CD	KD
Scalloped hammerhead	Muscle	1.47	1.66	1.56	1.57	0.54	0.70	2.30	0.51	0.62
	Blood	1.29	1.37	3.58	0.89	0.48	0.53	3.17	0.82	1.47
Smooth hammerhead	Muscle	0.83	1.50	2.87	0.78	0.45	0.40	2.30	0.56	0.42
	Blood	1.11	1.54	3.15	0.93	0.39	0.33	2.56	0.70	0.90
Pacific sharpnose	Muscle	1.48	1.58	3.28	1.64	0.62	0.88	2.99	0.56	1.30
	Blood	2.04	2.56	9.07	2.58	0.73	1.27	12.24	1.94	6.12

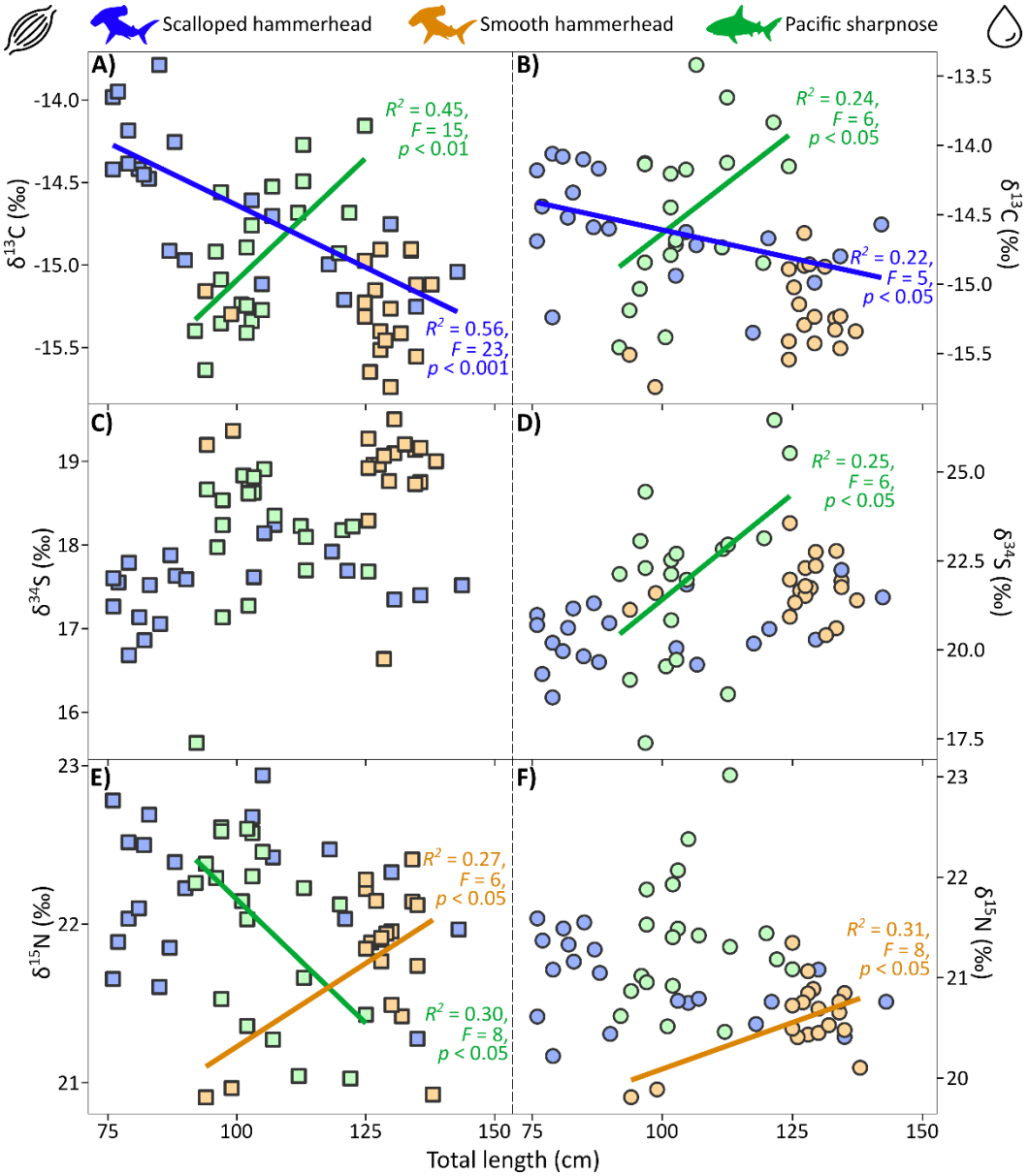


Figure 1–Relationship between stable isotope values (i.e., $\delta^{13}C$, $\delta^{34}S$, $\delta^{15}N$) and total length of scalloped hammerhead, smooth hammerhead and Pacific sharpnose sharks for muscle (A, C and E) and blood (B, D and F). Linear regressions were performed separately for each species and are shown with their associated R^2, F and p-values when significant.

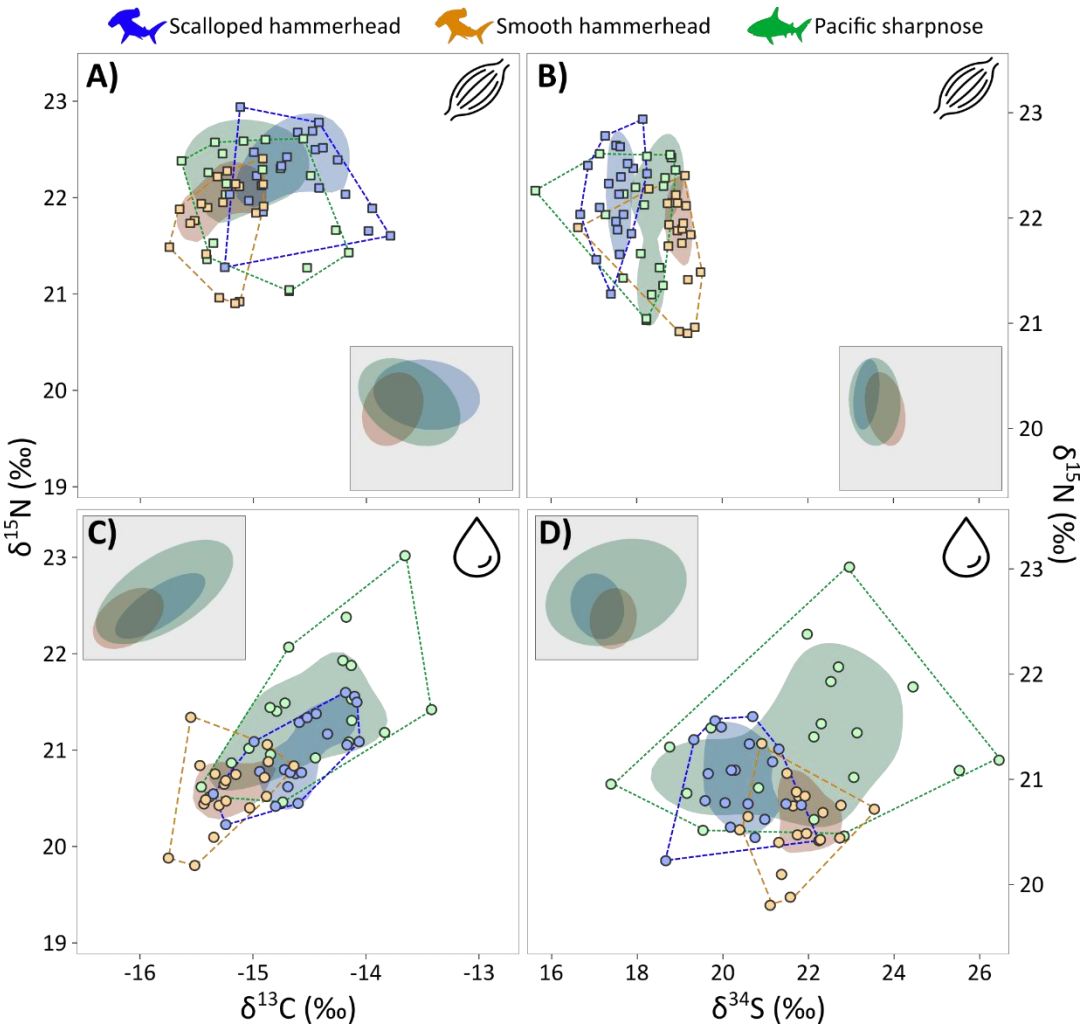
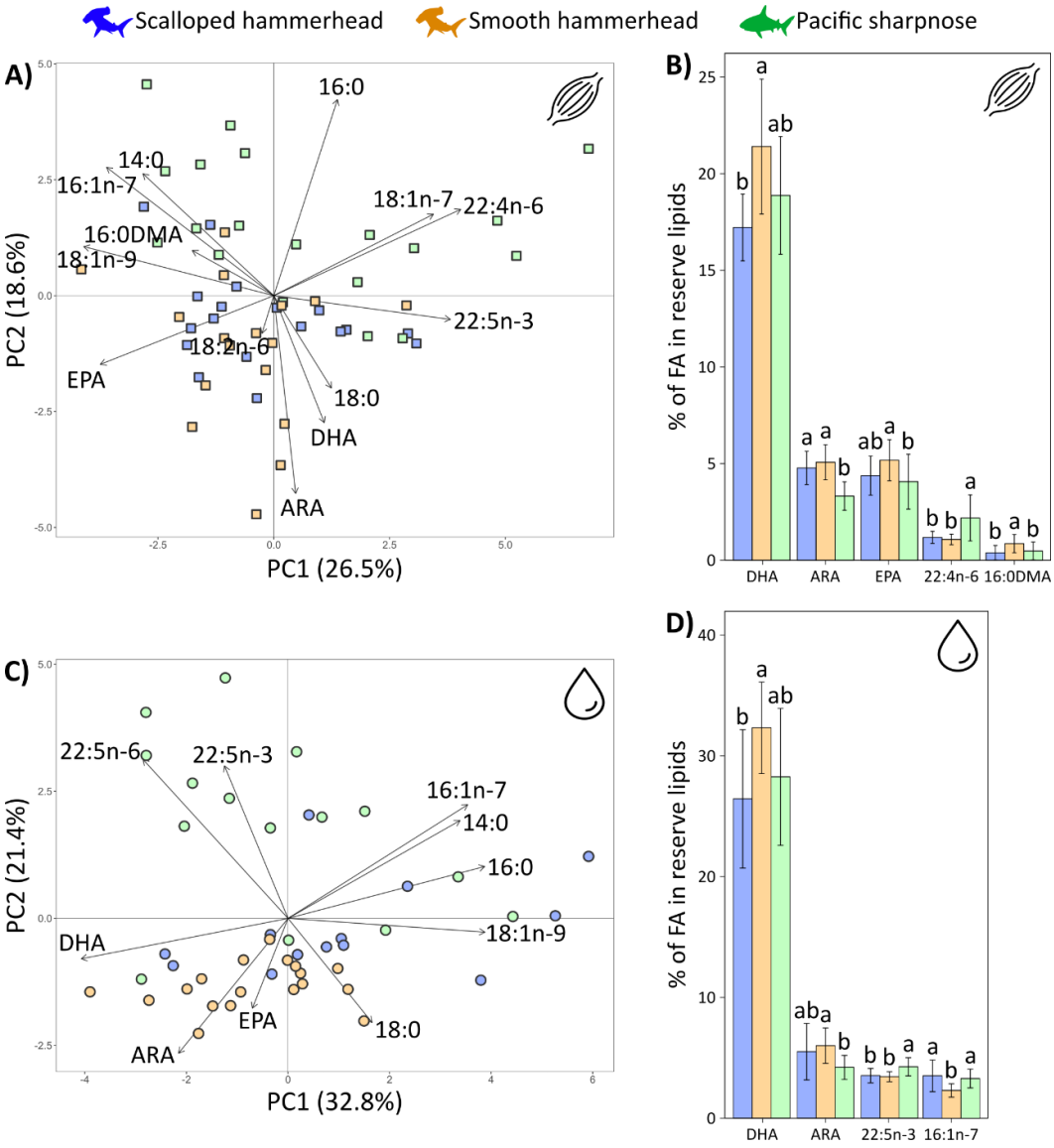
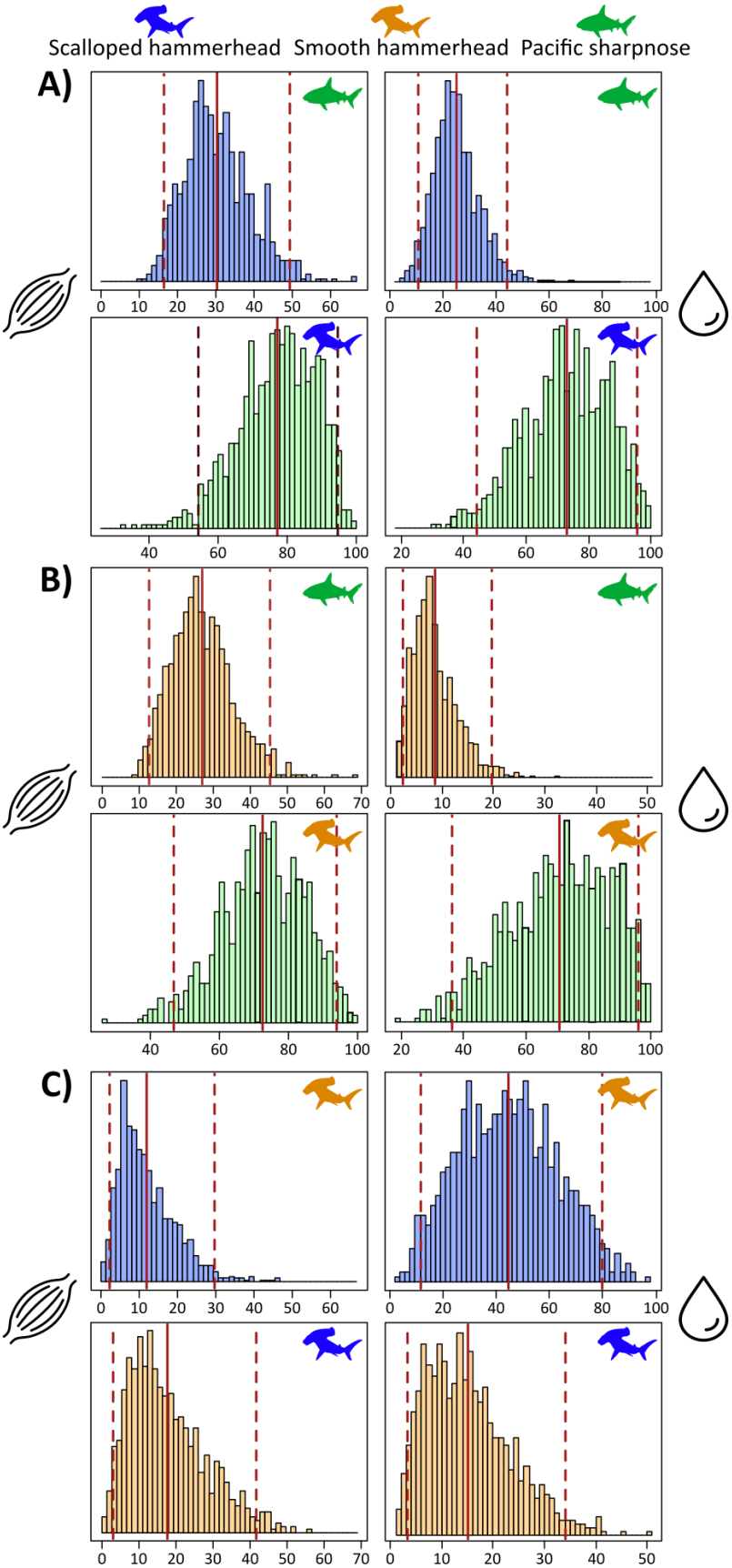


Figure 2–Isotopic niches of scalloped hammerhead, smooth hammerhead and Pacific sharpnose sharks in muscle $\delta^{13}C/\delta^{15}N$ δ-space (A) and $\delta^{34}S/\delta^{15}N$ δ-space (B), and in blood $\delta^{13}C/\delta^{15}N$ δ-space (C) and $\delta^{34}S/\delta^{15}N$ δ-space (D). For each species, 40% kernel density surface and convex hull area are represented along with ellipse encompassing 95% of the isotopic values in each grey panel.



927

928 Figure 3–Scatter plots of principal component analyses using neutral lipid fatty acid
929 proportions (%) of sharks among species separately performed for muscle (A) and blood (C).
930 Fatty acids that account for > 90% of the contribution of dissimilarity between species in the
931 similarity of percentages analyses (SIMPER) are represented. Among them, fatty acids that
932 displayed significant interspecific variations were shown in histograms (mean ± standard
933 deviation) and significant differences were indicated by lower case letters (B and D).


Scalloped hammerhead
Smooth hammerhead
Pacific sharpnose
A)
B)
C)
Overlap Probability (%) - Niche Region Size: 95%

934

Figure 4–Posterior distributions of the probabilistic niche overlap metrics of six variables ($\delta^{13}C$, $\delta^{34}S$, $\delta^{15}N$, and the first three dimensions of the PCA using FA compositions of the three species) separately performed for muscle (left column) and blood (right column). Means are presented in full lines and 95% credible intervals in dashed lines. Overlaps are estimated as the probability of one shark (i.e., color of the histogram) being found within the niche of another shark (i.e., shark icon). Panels show the overlap probability distributions between the scalloped hammerhead shark and the Pacific sharpnose shark niches (A), between the smooth hammerhead shark and the Pacific sharpnose shark niches (B) and between the scalloped and smooth hammerhead shark niches (C). For example, the first top left panel represents the probability distribution of the scalloped hammerhead shark being found in the niche of the Pacific sharpnose shark using muscle values.