Deep–Sea Research I 229 (2026) 104681

Contents lists available at ScienceDirect

Deep-Sea Research Part I

journal homepage: www.elsevier.com/locate/dsri

Inter- and intra-specific trophic niche partitioning, and cryptic speciation in three deep-sea predators in the Indian Ocean

Baptiste Le Bourg [a,*], Jeremy J. Kiszka [b], Jérôme Spitz [c,d], Toby S. Daly-Engel [e], Paco Bustamante [f,g]

[a] Muséum National d'Histoire Naturelle, Station Marine de Concarneau, Quai de la Croix, Concarneau, 29900, France
[b] Institute of Environment, Department of Biological Sciences, Florida International University, 3000 NE 151th Street, North Miami, FL, 33181, USA
[c] Observatoire Pelagis, UAR 3462, La Rochelle Université-CNRS, 5 allée de l'Océan, 17000, La Rochelle, France
[d] Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 La Rochelle Université-CNRS, 5 allée de l'Océan, 17000, La Rochelle, France
[e] Department of Ocean Engineering and Marine Sciences, Florida Institute of Technology, Melbourne, FL, 32901, USA
[f] LIttoral ENvironnement et Sociétés (LIENSs), UMR 7266 CNRS-La Rochelle Université, 2 rue Olympe de Gouges, 17000, La Rochelle, France
[g] Institut Universitaire de France (IUF), 1 rue Descartes, 75005, Paris, France

ARTICLE INFO

Keywords:
$\delta^{13}C$
$\delta^{15}N$
Indian ocean
Mercury
Sharks
Stomach contents
Trophic ecology

ABSTRACT

Assessing the trophic interactions of marine predators is critical for understanding community structure and functioning but is rarely examined in deep-sea environments. Here, we investigated the trophic niches and interactions in three species of mesopelagic sharks in the southwestern Indian Ocean. For this, we used multiple dietary indicators including stomach contents, stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes, and total mercury (THg). Because of the strong morphological convergence among deep-sea sharks, we also sequenced mitochondrial DNA to genetically identify all specimens. We found evidence of three distinct species, the smallfin gulper shark (*Centrophorus moluccensis*) and two undescribed dogfish sharks (genus *Squalus*). Trophic niches between the three species overlapped substantially based on stomach contents (Pianka's index 0.87-0.98), and $\delta^{13}C$ and $\delta^{15}N$ isotope values in the liver (38.7-59.9% overlap), though isotopic niches inferred from muscle revealed some dietary segregation (12.1-25.9% overlap). Trophic niches overlapped between sexes on a short- (Pianka's index 0.78-0.99) and medium-term basis (20.1-57.2% overlap in liver), but not long-term (14.9-19.5% overlap in muscle). THg, $\delta^{13}C$, and $\delta^{15}N$ in both tissues showed significant ontogenetic shifts, suggesting dietary segregation by age. Overall, the combination of multiple dietary tracers revealed complex patterns in trophic niche dynamics within a deep-sea predator community, specifically that niche partitioning mechanisms can operate at both inter-specific and intra-specific scales.

1. Introduction

Understanding spatial and temporal dynamics of ecological niche partitioning is a central question in ecology (Grinnell, 1924; Pianka, 1974), and many efforts have been produced in the recent years to address this question, particularly within marine predator communities (e.g., Olson et al., 2016; Matich et al., 2017a,b; Belleggia et al., 2019; Murillo-Cisneros et al., 2019; Petalas et al., 2021; Marsaly et al., 2023). Taxonomically and/or morphologically similar species co-occurring within the same ecosystems or habitats may rely on similar food sources and would compete for food if/when resources are limited (Kiszka et al., 2011; Stewart et al., 2017; Dehnhard et al., 2020; Planque et al., 2021; Estupiñán-Montaño et al., 2024). The degree to which species partition resources within communities is driven by inter-specific competition, itself driven by resource availability, the abundance of the competing species (Pool et al., 2017; Kaymak et al., 2023; Fernández-Corredor et al., 2025) and the capacity of predators to modify their diet during variable oceanic conditions that may impact the abundance of their prey (Fernández-Aguirre et al., 2022; Martinez-Ayala et al., 2025). Thus, resource partitioning becomes critical when food sources are limiting to avoid competitive interactions, as they may lead some consumer species to decline (Pianka, 1974; Schoener, 1974; Bøhn et al., 2008; Juncos et al., 2015). Intra-specific variations of the diet of marine predators may also occur, and may lead to intra-specific trophic niche

---

* Corresponding author.
E-mail address: lebourg.bapt@gmail.com (B. Le Bourg).

https://doi.org/10.1016/j.dsr.2026.104681
Received 17 June 2025; Received in revised form 14 February 2026; Accepted 19 March 2026
Available online 20 March 2026

partitioning in addition to the inter-specific one. These variations may occur between individuals (Vander Zanden et al., 2010; Matich et al., 2011, 2019; Trystram et al., 2017), sexes (Hussey et al., 2011; Kernaleguen et al., 2015; Barría et al., 2018b) or through ontogeny (Hussey et al., 2011; Carlisle et al., 2015; Kiszka et al., 2014), and may be driven by spatial sexual segregation (e.g., Sims, 2005; Mucientes et al., 2009; Braccini and Taylor, 2016), sexual dimorphism (Finotto et al., 2023) or the development of foraging skills (Martin et al., 2009; Newman et al., 2012).

Sharks (Selachii) occur from coastal to open ocean ecosystems, and from epi- to bathypelagic habitats (Kiszka and Heithaus, 2014). Most species are generalist mesopredators feeding on a range of prey, including teleosts, cephalopods, and crustaceans (e.g., Wetherbee et al., 2012; Martin and Mallefet, 2023). Limited knowledge is available on the trophic ecology of deep-sea sharks and on their ecological importance in these ecosystems (Martin and Mallefet, 2023). Furthermore, it is known that the diversity of sharks is underestimated, both due to difficulty in conducting comprehensive marine surveys and the high degree of morphological convergence among sharks, especially in deep-sea habitats. The advent of molecular tools for species identifications has led to the discovery of several cryptic species, which are spatially and morphologically indistinguishable but genetically distinct from more common taxa (Straube et al., 2011; Veríssimo et al., 2014). This has led to a rise in the rate of novel species descriptions, including within the gulper sharks (genus *Centrophorus*; e.g. White et al., 2008; Bellodi et al., 2022) and dogfish sharks (genus *Squalus*; e.g. Veríssimo et al., 2017; Daly-Engel et al., 2018; Pfleger et al., 2018; Ziadi-Künzli et al., 2020; Ferrari et al., 2021) in the twilight zone (Randhawa et al., 2015). Nevertheless, taxonomic uncertainties continue to hamper the study of the ecology of deep-sea sharks, as mistakenly pooling these species may induce false inferences of their trophic niche.

Various methods have been used to investigate the trophic interactions of marine predators. Stomach content analysis is a well-known method that provides both qualitative (ingested prey type or species) and quantitative (relative importance of prey species in the diet) data on the feeding ecology of marine predators (Hyslop, 1980; Amundsen and Sánchez-Hernández, 2019). Although such methods provide detailed information on ingested prey (i.e., high taxonomic identification of prey, individual prey body size and mass estimates), prey found and identified in stomachs reflects the diet of consumers over a relatively short period of time before capture (one to several days for sharks, Wetherbee et al., 2012). In addition, the proportion of empty stomachs can be high for deep-sea sharks because of their slow metabolism and the scarcity of resources leading to more infrequent feeding in the deep sea, and because regurgitation often occurs during capture (Stevens, 1973; Bowman, 1986; Martin and Mallefet, 2023). Bulk carbon (^{13}C:^{12}C; $\delta^{13}C$) and nitrogen isotopic compositions (^{15}N:^{14}N; $\delta^{15}N$) in predator tissues result from the proportional mixing of stable isotope contents from the various food items assimilated and from the enrichment in heavy isotopes at each trophic levels, which results from the multiple chemical and physical processes linked to animal metabolism (DeNiro and Epstein, 1978, 1981; Vander Zanden and Rasmussen, 2001; Mill et al., 2007). Stable isotope values may provide longer-term dietary tracers, depending on the turnover rate of the tissue considered (Thomas and Crowther, 2015). Tissues with short turnover may provide information from previous weeks or months, allowing to assess seasonal variations in the trophic niche, while tissues with long turnover may provide integrated information for the whole year, thus providing a more general view of the predator's trophic niche (MacNeil et al., 2006; Logan and Lutcavage, 2010; Malpica-Cruz et al., 2012; MacNeil et al., 2005; Malpica-Cruz et al., 2013; Niella et al., 2021). $\delta^{13}C$ values are generally used to determine the origin of primary sources of carbon in food webs or foraging habitats because of the differences of stable isotope composition between the different types of primary producers and of the low ^{13}C enrichment in organisms relative to their diet (DeNiro and Epstein, 1978; France, 1995; Hobson, 1999; Michener and Kaufman, 2007). $\delta^{15}N$ values are generally used to estimate the trophic position of consumers, as organisms are generally more enriched in ^{15}N relative to their diet (DeNiro and Epstein, 1981; Michener and Kaufman, 2007). In addition, mercury (Hg), a non-essential metal released by natural and anthropogenic sources, can be used to identify the foraging habitats and relative trophic level of organisms (Kiszka et al., 2015; Sardenne et al., 2017; Murillo-Cisneros et al., 2018). Indeed, Hg concentrations can be correlated to foraging habitat, with higher Hg concentrations indicating foraging in mesopelagic or deeper waters (Choy et al., 2009; Madigan et al., 2018; Le Bourg et al., 2019), where increased methylation rates of inorganic Hg produce methylmercury (MeHg), which induce higher Hg bioavailability (Blum et al., 2013). Hg also biomagnifies with the trophic level of organisms, resulting in higher Hg concentrations in higher trophic level predators (Atwell et al., 1998; Lavoie et al., 2010; Murillo-Cisneros et al., 2018, 2019; Le Bourg et al., 2019).

Here, we investigated the trophic interactions among three deep-sea shark species from the oligotrophic southwestern Indian Ocean (an oceanic region stretching from South Africa to the Mascarene Islands), sampled near the island of La Réunion, and including two cryptic dogfishes identified with molecular tools for the first time. Their trophic ecology was assessed with a combination of short- (stomach contents, stable isotopes of carbon and nitrogen and Hg in liver tissues) and long-term dietary indicators (stable isotopes of carbon and nitrogen and Hg in muscle tissues), allowing us to assess the temporal variability of their trophic interactions. These indicators were also used to compare the trophic niches between species and sexes to assess inter- and intra-specific trophic niche partitioning. Stable isotopes of carbon and nitrogen and Hg were also measured to assess ontogenetic changes in diet that indicate intra-specific trophic niche partitioning between adults and juveniles. We hypothesize that trophic niche partitioning between species would be significant because oligotrophic marine ecosystems are resource limited and therefore should require species to use distinct food sources. We further hypothesize that we will see some degree of trophic partitioning between males and females due to differences in life history and physiological requirements, or spatial sexual segregation.

2. Materials and methods

2.1. Sampling

Sharks were caught using longlines off the island La Réunion, in the southwestern Indian Ocean (*ca* 21° 05′ S; 55° 14’ E), in November 2011. Species, sex and fork length (i.e., length from the snout tip to the caudal fork) were recorded. Dissections were conducted to collect stomachs, white muscle (dorsal region), and liver samples, which were frozen at −20 °C until further processing. For genetic analyses confirming species identification, additional small (<1 cm^3) samples of fin or muscle tissue were collected and stored in 2 mL vials of >70% ethanol. In the laboratory, muscle and liver samples were freeze-dried and grounded into a homogenous powder with a porcelain mortar and a pestle to allow stable isotope and Hg analyses. The tools were cleaned and decontaminated with 90° ethanol before grinding each sample.

2.2. DNA sequence analyses

We were able to identify the smallfin gulper shark (*Centrophorus moluccensis*) by visual examination, as this species is thought to be the only one that occurs in this region. There are thought to be multiple dogfish species, though, so for these we amplified approximately 765 base pairs of the NADH dehydrogenase 2 gene (ND2) using the universal primers tMetShkND2_F (5′- CCC CAA CCA TGT TGG TTA AA-3′) and tAlaShkND2_R (5′- AAA GCA TCT GGG TTG CAT TC- 3′) from O'Brien et al. (2013). We extracted DNA from muscle tissue stored in ethanol using a Dneasy Blood & Tissue Kit from Qiagen (Germantown, MD) and primers obtained from Integrated DNA Technologies, Inc. (Coralville, Indiana). PCR reactions consisted of 7 μL BioMix Red from Bioline

(London, UK) at the recommended concentration, 1 μL (3 μg) template DNA, and 1 μL (1.0 μM) of each primer (10 μL total PCR volume). PCR amplification on a T100 Thermal Cycler (Bio-Rad; Hercules, California) consisted of an initial denaturation at 95 °C for 4 min followed by 36 cycles of 1 min at 95 °C, followed by 30 s at 58 °C, and 30 s at 72 °C with a final extension at 72 °C for 20 min. PCR products were cleaned with the ExoFAP protocol (Thermo Fisher Scientific) and sequenced on an Applied Biosystems 3730XL DNA Analyzer at the University of Arizona Genetics Core. DNA sequences were trimmed in Geneious v9.1.4 (Kearse et al., 2012) and aligned using Mafft (Katoh et al., 2002). The mutational model was calculated using jModeltest (Posada, 2008). MrBayes v3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was used to construct a Bayesian inference phylogenetic tree with a burn-in phase of 10,000 steps and posterior clade probabilities. Genetic distance expressed as percent sequence divergence was calculated in MrBayes (Huelsenbeck and Ronquist, 2001). Representatives from each clade were compared to all other publicly available DNA sequences in the database GenBank (Benson et al., 2012) using the nucleotide BLAST search tool from the National Center for Biotechnology Information (NCBI).

2.3. Stomach content analysis

Stomach content analysis describes the diet in terms of prey occurrence and relative abundance, following a standard procedure for marine top predators (Pierce and Boyle, 1991; Spitz et al., 2011, 2013). The diagnostic prey items, whose shape allows the species to be identified and individuals to be estimated, were recovered from stomach contents. These prey remains were then stored dry for teleosts bones and otoliths or in 70% ethanol for cephalopod beaks, crustacean remains and any remains with flesh attached. The diagnostic prey items were identified to the lowest taxonomic level using published guides (Clarke, 1986; Smith and Heemstra, 1986; Rivaton and Bourret, 1999) and our reference collection of specimens caught around La Réunion. The total number of ingested prey individuals was estimated as the highest number, given by either the number of paired structures (e.g., otoliths, operculum, hyomandibular, dentary and premaxillary for teleosts, upper and lower beaks for cephalopods, and eyes for crustaceans) or unpaired structures (e.g., parasphenoid for teleosts, gladii for cephalopods, and carapace and telson for crustaceans). Prey were also grouped into their respective broad habitat (epipelagic, mesopelagic, benthodemersal), although the habitat of five unidentified prey could not be determined. The occurrence of a prey species was defined as the number of stomachs in which this species was observed. The relative abundance was defined as the number of individuals of that species found throughout the sample. These two indices were only calculated for non-empty stomachs, and were expressed as percentage frequencies: respectively, percentage of occurrence (%O) and percentage by number (%N), which were calculated as:

$$\%O_i = \frac{n_i}{N} \times 100 \tag{1}$$

where n_i is the number of stomachs where prey i was found, and N is the total number of stomachs.

$$\%N_i = \frac{x_i}{X} \times 100 \tag{2}$$

where x_i is the number of prey i found, and X is the total number of prey. The lack of relationships between the hard parts and the body size and mass of the prey species found in this study meant that we were unable to provide an index based on ingested biomass. Consequently, the weight percentage (%W) and the index of relative importance (IRI, Pinkas et al., 1971) and its transformation in percentage (%IRI, Cortés, 1997) could not be computed.

2.4. Stable isotope analysis

Lipids are highly depleted in ^{13}C relative to other tissue components (DeNiro and Epstein, 1977), while trimethyl-amine oxide (TMAO) can affect δ^{15}N values (Hussey et al., 2012). Consequently, lipids and TMAO were removed from samples by three successive extractions (1 h shaking in cyclohexane at room temperature and subsequent centrifugation) prior to stable isotope analysis as described by Chouvelon et al. (2011). This standardized data among individuals and across species within the food web (Hussey et al., 2012). After drying, lipid-free sub-samples (0.35 to 0.45 mg ± 0.01 mg) were weighed in tin cups for stable isotope analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (IR-MS, Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyzer (Flash EA1112 Thermo Scientific, Italy). Reference gas were calibrated against International Reference Materials (IAEA-N1, IAEA-N2 and IAEA-N3 for nitrogen; NBS-21, USGS-24 and IAEA-C6 for carbon). Results are expressed in the δ notation, relative to isotopic ratios in standards, according to the equation:

$$\delta X_{sample} = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1000 \tag{3}$$

where X is the heavy isotope (^{13}C or ^{15}N) and R are the isotope ratios (^{13}C:^{12}C or ^{15}N:^{14}N) for the sample (R_{sample}) and the standard ($R_{standard}$). Standards were carbonated rostrum of Vienna PeeDee Belemnite for δ^{13}C and nitrogen isotopic ratios in the air for δ^{15}N. Replicate measurements of a laboratory standard (acetanilide) indicated that analytical errors were <0.10 ‰ for δ^{13}C and δ^{15}N. Percent C and N elemental composition of tissues were obtained using the elemental analyzer and used to calculate the sample C:N ratio, indicating good lipid removal efficiency when C:N < 4.

2.5. Mercury analysis

Measurements of total Hg (hereafter Hg) were performed using a solid sample atomic absorption spectrometer AMA-254 (Advanced Mercury Analyser-254 from Altec©). At least two aliquots of 5 to 15 mg of homogenized dry tissue subsamples for each individual were analysed. The analytical quality (i.e. accuracy and reproducibility) of the Hg measurements by the AMA-254 was assessed by the analyses of blanks and TORT-2 Certified Reference Material (CRM, Lobster Hepatopancreas Reference Material from the National Research Council of Canada) at the beginning and at the end of the analytical cycle, and by running it every 10 samples. Results of quality controls showed a satisfactory precision with a relative standard deviation of 6.0%. The recovery of the CRM was 93% of the assigned concentration (n = 14). The detection limit of the AMA was 0.1 ng. All Hg concentrations in tissues reported below are expressed in μg.g^{-1} dry weight (dw).

2.6. Data analysis

2.6.1. Stomach contents

Some descriptive indexes were calculated to estimate and compare the characteristics of dietary niches based on stomach content analyses. The specific richness (R) is the number of species found in the diet of a given predator. The biodiversity of prey was calculated by the Shannon-Wiener index (H') which considers both the specific richness and the number of specimens for each species and for each sex within each species.

$$H' = -\sum p_i \log_2 p_i \tag{4}$$

where p_i is the percentage by number of the prey i found in the diet.

The equitability (E) gives the balance between the percentage by number of each prey. It varies from 0 to 1; 1 indicating that each prey

Table 1
Prey found in stomach contents of deep-sea shark species from La Reunion Island (%O, percentage of occurrence; %N, percentage by number).

		Shark species	*Centrophorus moluccensis* (n = 11)		*Squalus* sp. 1 (n = 39)		*Squalus* sp. 2 (n = 10)	
			%O	%N	%O	%N	%O	%N
EPIPELAGIC PREY			18.2	7.1			10.0	3.4
TELEOSTS	**Scombridae**	Unid. mackerels					10.0	3.4
CEPHALOPODS	**Ommastrephidae**	Unid. flying squids	18.2	7.1				
MESOPELAGIC PREY			**72.7**	**89.3**	**86.4**	**87.2**	**80.0**	**82.8**
TELEOSTS	**Alepocephalidae**	Unid. slickheads			2.6	0.8		
	Myctophidae	*Bolinichthys* spp.	27.3	10.7	5.1	1.5		
		Ceratoscopelus warmingii	63.6	35.7	56.4	58.3	80.0	79.3
		Dasyscopelus selenops			12.8	4.5		
		Diaphus sp. A	18.2	7.1	10.3	3.0	10.0	3.4
		Diaphus sp. B	18.2	7.1	10.3	3.8		
		Diaphus sp. C	9.1	3.6	5.1	2.3		
		Diaphus sp. D	18.2	7.1				
		Diaphus sp. E	9.1	7.1				
		Lampanyctus sp.	9.1	3.6				
		Unid. lanternfish			12.8	4.5		
	Bregmacerotidae	*Bregmaceros* sp.			2.6	0.8		
	Gempylidae	Unid. snake mackerels			2.6	0.8		
	Sternoptychidae	*Argyropelecus* spp.			12.8	4.5		
CEPHALOPODS	**Cranchiidae**	Unid. glass squids			2.6	0.8		
	Histioteuthidae	*Histioteuthis* type A	9.1	3.6				
		Histioteuthis type B	9.1	3.6				
	Onycoteuthidae	Unid. hooked squids			2.6	0.8		
BENTHODERMERSAL PREY			**9.1**	**3.6**	**12.8**	**5.3**	**10.0**	**6.9**
TELEOSTS	**Acropomatidae**	Splitfin perches sp. A					10.0	3.4
		Splitfin perches sp. B	9.1	3.6				
	Caproidae	Unid. boarfish					10.0	3.4
	Chlorophtalmidae	Unid. greeneyes			2.6	0.8		
	Diodontidae	Unid. porcupinefish			2.6	0.8		
	Macrouridae	Unid. grenadiers			2.6	0.8		
	Monacanthidae	Unid. leatherjackets			2.6	0.8		
	Moridae	Unid. morid cod			2.6	0.8		
	Sternoptychidae	*Argyripnus* sp.			2.6	0.8		
CEPHALOPODS	**Sepiolidae**	Unid. bobtail squids			2.6	0.8		
PREY WITH UNKNOWN HABITAT					**25.6**	**8.3**	**20.0**	**6.9**
CHONDRICHTHYANS	***Incertae sedis***	Unid. small shark			2.6	0.8		
TELEOSTS	**Anguilliform**	Unid. eels			2.6	0.8		
	Incertae sedis	Teleost species A			2.6	0.8		
CEPHALOPODS	***Incertae sedis***	Unid. cephalopods					10.0	3.4
CRUSTACEANS	***Incertae sedis***	Unid. shrimps			17.9	6.1	10.0	3.4

has the same percentage by number.

$$E = \frac{H'}{\log_2 R} \tag{5}$$

Dietary overlaps by number (O) among the three deep-sea shark species, and among sex within each species, were calculated using the Pianka index (Pianka, 1974), which varies from 0 (no overlap) to 1 (complete overlap):

$$O = \frac{\sum P_{IA} P_{IB}}{\sqrt{\sum P_{IA}^2 \sum P_{IA}^2}} \tag{6}$$

where p_{iA} is the percentage by number of prey i found in the diet of shark A and p_{iB} is the percentage by number of prey i found in the diet of shark B. Pianka index values greater than 0.5 are considered to reveal a high overlap.

The package vegan in R was used to build a dissimilarity matrix, based on the Bray-Curtis index computed with proportions of each prey in each stomach, and to perform permutational analyses of variance (PERMANOVA) to test whether there were variations in stomach content depending on fork length, species and sex. Marginal probability values were computed, meaning that the effect of each variable is controlled after the effect of all other variables is accounted for. The PERMANOVAs were first performed for first order interactions, and then for the variables alone if none of the interactions had a significant effect. The second order interaction was not tested because of the low number of individuals in several groups ($n < 10$). Species accumulation curves were also generated for the three species.

2.6.2. Stable isotopes and mercury

Seven liver samples still had C:N ratios higher than 4 after lipid extraction (5 female *Centrophorus moluccensis*, 1 female and 1 male *Squalus* sp. 1). Data from these individuals were discarded from the analyses. Because liver has a faster turnover than the muscle, stable isotope values and Hg concentrations measured in muscle and liver provide long (from *ca* 2 months to *ca* 2 years of isotopic half-life in sharks, depending on the stable isotopes, the growth stage and the model considered, Logan and Lutcavage, 2010; Malpica-Cruz et al., 2012) and short-term (from *ca* 2 weeks to *ca* 1 month half-life for δ^{15}N values in ocellate river stingrays *Potamotrygon motoro*, MacNeil et al., 2006) information on the trophic ecology, respectively. Consequently, type III analyses of covariance (ANCOVAs) were performed in R 4.4.1 (R Core Team, 2024) for each tissue to assess the influence of the species and sex (as factors) and of the fork length (as covariate), as well as the first order interactions between these variables, on δ^{13}C and δ^{15}N values and Hg concentrations. The second order interaction was discarded because of the low number of individuals in several groups ($n < 10$). For these models, no transformations were necessary for δ^{13}C muscle and liver values and for δ^{15}N muscle values. Hg concentrations were $\log_{10}$-transformed to obtain a normal distribution of residuals. Raw δ^{15}N values from the liver were used as no transformation appeared to be suitable to obtain a normal distribution for residuals. Scheffe post-hoc analyses were conducted in case of significant influence of the species. Similarly, Pearson correlation tests were computed in case of significant

Table 2
Prey found in stomach contents of each sex in each species of deep-sea sharks from La Reunion Island (%O, percentage of occurrence; %N, percentage by number).

		Shark species	*Centrophorus moluccensis* (n = 11)				*Squalus* sp. 1 (n = 39)				*Squalus* sp. 2 (n = 10)			
		Sex	Females (n = 7)		Males (n = 4)		Females (n = 14)		Males (n = 25)		Females (n = 7)		Males (n = 3)	
			%O	%N	%O	%N	%O	%N	%O	%N	%O	%N	%O	%N
EPIPELAGIC PREY			**28.6**	**10.5**							**14.3**	**4.8**		
TELEOSTS	**Scombridae**	Unid. mackerels									14.3	4.8		
CEPHALOPODS	**Ommastrephidae**	Unid. flying squids	28.6	10.5										
MESOPELAGIC PREY			**71.4**	**89.5**	**75.0**	**88.9**	**85.7**	**91.2**	**88.0**	**82.7**	**71.4**	**76.2**	**100.0**	**100.0**
TELEOSTS	**Alepocephalidae**	Unid. slickheads							4.0	1.3				
	Myctophidae	*Bolinichthys* spp.	28.6	10.5	25.0	11.1	7.1	1.8	4.0	1.3				
		Ceratoscopelus warmingii	57.1	36.8	75.0	33.3	64.3	71.9	52.0	48.0	71.4	71.4	100.0	100.0
		Dasyscopelus selenops					14.3	3.5	12.0	5.3				
		Diaphus sp. A	14.3	5.3	25.0	11.1			16.0	5.3	14.3	4.8		
		Diaphus sp. B	14.3	5.3	25.0	11.1	7.1	1.8	12.0	5.3				
		Diaphus sp. C			25.0	11.1	14.3	5.3						
		Diaphus sp. D	28.6	10.5										
		Diaphus sp. E	14.3	10.5										
		Lampanyctus sp.			25.0	11.1								
		Unid. lanternfish					7.1	1.8	16.0	6.7				
	Bregmacerotidae	*Bregmaceros* sp.					7.1	1.8						
	Gempylidae	Unid. snake mackerels							4.0	1.3				
	Sternoptychidae	*Argyropelecus* spp.					14.3	3.5	12.0	5.3				
CEPHALOPODS	**Cranchiidae**	Unid. glass squids							4.0	1.3				
	Histioteuthidae	*Histioteuthis* type A	14.3	5.3										
		Histioteuthis type B	14.3	5.3										
	Onycoteuthidae	Unid. hooked squids							4.0	1.3				
BENTHODERMERSAL PREY					**25.0**	**11.1**			**20.0**	**9.3**	**14.3**	**9.5**		
TELEOSTS	**Acropomatidae**	Splitfin perches sp. A									14.3	4.8		
		Splitfin perches sp. B			25.0	11.1								
	Caproidae	Unid. boarfish									14.3	4.8		
	Chlorophtalmidae	Unid. greeneyes							4.0	1.3				
	Diodontidae	Unid. porcupinefish							4.0	1.3				
	Macrouridae	Unid. grenadiers							4.0	1.3				
	Monacanthidae	Unid. leatherjackets							4.0	1.3				
	Moridae	Unid. morid cod							4.0	1.3				
	Sternoptychidae	*Argyripnus* sp.												
CEPHALOPODS	**Sepiolidae**	Unid. bobtail squids							4.0	1.3				
PREY WITH UNKNOWN HABITAT							**5.0**	**8.8**	**20.0**	**8.0**	**14.3**	**9.5**		
CHONDRICHTHYANS	***Incertae sedis***	Unid. small shark					7.1	1.8						
TELEOSTS	**Anguilliform**	Unid. eels					7.1	1.8						
	Incertae sedis	Teleost species A							4.0	1.3				
CEPHALOPODS	***Incertae sedis***	Unid. cephalopods									14.3	4.8		
CRUSTACEANS	***Incertae sedis***	Unid. shrimps					21.4	5.3	16.0	6.7	14.3	4.8		

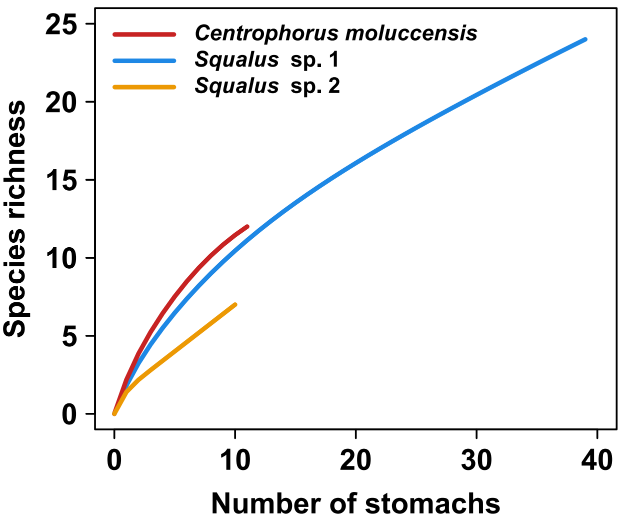

Fig. 1. Species accumulation curves showing the total number of species observed in a given number of stomachs for each deep-sea shark species sampled near La Réunion.

influence of the fork length or of its interactions with the factors.

Standard ellipses, which were developed to assess the isotopic and thus the trophic diversity within groups of organisms, are a bivariate representation of the standard deviation of both stable isotope values and thus are a proxy of the trophic niche (Jackson et al., 2011). Their area is an estimation of the trophic niche size of an organism group while the percentage of overlap between two ellipses provides indications about trophic overlap between two or more groups. A high overlap indicates similar foraging habitats and possible high resource overlap. For each species and each tissue, sample-size corrected (SEA_C) and Bayesian (based on 10^5 successive iterations; SEA_B) estimates of areas of the standard ellipses (SEA) generated with $\delta^{13}C$ and $\delta^{15}N$ values were computed with the SIBER package (Jackson et al., 2011). This procedure was also repeated by separating sexes in each species. Pairwise comparisons of SEA_B were done by calculating the percentage of the estimated SEA that differed between two ellipses. This percentage is the posterior probability (p) that a given ellipse has larger or smaller SEA than the other one. If this percentage exceeded 95% or was lower than 5%, the probability that two ellipses have different SEA is higher than 95 % and, then, the differences between the compared SEA were considered as meaningful (Jackson, 2023). The orderPvalue function in the agricolae package in R (de Mendiburu, 2020) was used to order the posterior probabilities p according to the SEA_B modes, which required that p values higher than 50 % had to be transformed into (1 – p) values (Le Bourg et al., 2021). SEA_B for which probability of difference was less than 95 % were attributed an identical symbol. Otherwise they get different symbols. For example, if SEA_B of the species A, B, C get the symbol a, b, c, respectively, they all differ from each other, with a probability higher than 95%. Species A, B, C getting the symbols a, a, b, respectively, means that species A and B have similar SEA_B while the SEA_B from species C differs from those of species A and B. Finally, species A, B, C getting the symbol a, ab, b, respectively, suggests that SEA_B of B is not different from SEA_B of A and SEA_B of C.

The percentages of ellipse overlap (%Ov) between two species and between sexes within species were calculated for each tissue. %Ov between two groups of sharks were expressed as the ratio between the area of overlap and the cumulative ellipse area:

$$\%Ov = \frac{Ov}{SEA_{CA} + SEA_{CB} - Ov} \tag{7}$$

where Ov is the overlapping area of the two ellipses, SEA_{CA} is the sample-size corrected ellipse area for shark A and SEA_{CB} is the sample-size corrected ellipse area for shark B.

3. Results

3.1. Genetic identification

The molecular evolutionary model for the *Squalus* ND2 gene was estimated by jModeltest to be HKY (Aikake Information Criteria), and the Bayesian analysis returned an unrooted topology that identified two distinct clades among our samples with 100% posterior support. Within clade genetic distance ranged from 0 to 0.14%, while genetic distance between the two ranged from 5.20 to 5.92% sequence divergence, which exceeds the species-level differentiation identified between other closely-related species pairs in the genus *Squalus* (Ward et al., 2005; Daly-Engel et al., 2018; Pfleger et al., 2018). The nucleotide BLAST search returned no identical or near-identical sequences to either group in Genbank; the nearest neighbors to both were separated by over 1% sequence divergence. Though the dogfish from Reunion are colloquially called *Squalus megalops*, representative sequences from our two groups clustered most closely with sequences from the Atlantic Ocean identified

Table 3

Results of analyses of covariance (ANCOVA) assessing the impact of fork length, species, sex and their interactions on $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations in a) the muscle and b) the liver of deep-sea sharks sampled near La Réunion. Bold results are significant at the P = 0.05 level.

a) Muscle

		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		$\log_{10}$[Hg] ($\mu g.g^{-1}$ dw)	
	df	F	P	F	P	F	P
Fork length	1,75	**19.411**	**< 0.001**	**50.936**	**< 0.001**	**78.085**	**< 0.001**
Species	2,75	**4.420**	**0.015**	2.547	0.085	**3.686**	**0.030**
Sex	1,75	1.921	0.170	3.458	0.067	0.891	0.348
Species:Sex	2,75	1.202	0.306	**5.007**	**0.009**	2.899	0.061
Fork length:Species	2,75	**6.702**	**0.002**	2.462	0.092	1.284	0.283
Fork length:Sex	1,75	2.144	0.147	**6.538**	**0.013**	2.281	0.135

b) Liver

		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		$\log_{10}$[Hg] ($\mu g.g^{-1}$ dw)	
	df	F	P	F	P	F	P
Fork length	1,68	**13.983**	**< 0.001**	1.296	0.259	**31.731**	**< 0.001**
Species	2,68	1.749	0.182	0.712	0.494	0.673	0.513
Sex	1,68	0.212	0.646	0.037	0.848	0.874	0.353
Species:Sex	2,68	2.036	0.138	0.090	0.914	1.196	0.309
Fork length:Species	2,68	0.851	0.432	0.694	0.503	0.917	0.405
Fork length:Sex	1,68	0.017	0.896	0.159	0.691	0.561	0.456

Table 4
Mean ± SD (and range) of lengths, $\delta^{13}C$ and $\delta^{15}N$ values, and Hg concentrations for each species, sex and tissue of deep-sea sharks sampled near La Réunion.

a) Muscle

Sex	n	Fork length (cm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	[Hg] (μg.g^{-1} dw)
Centrophorus moluccensis					
Females	10	63.0 ± 18.8 (29.0, 77.5)	−16.6 ± 0.3 (−17.2, −16.0)	12.0 ± 0.4 (11.3, 12.6)	3.97 ± 2.33 (0.19, 6.55)
Males	6	48.5 ± 10.5 (31.5, 61.5)	−16.8 ± 0.4 (−17.4, −16.4)	12.2 ± 0.6 (11.2, 12.7)	2.33 ± 1.56 (0.32, 4.05)
***Squalus* sp. 1**					
Females	23	55.1 ± 11.4 (35.0, 69.5)	−16.8 ± 0.2 (−17.1, −16.6)	12.5 ± 0.3 (11.7, 13.0)	7.79 ± 3.74 (1.43, 14.80)
Males	34	46.1 ± 10.5 (26.0, 64.0)	−17.0 ± 0.1 (−17.3, −16.8)	12.1 ± 0.6 (10.4, 13.3)	5.21 ± 3.74 (0.24, 15.35)
***Squalus* sp. 2**					
Females	8	47.4 ± 13.8 (31.0, 64.0)	−16.9 ± 0.2 (−17.2, −16.8)	12.0 ± 0.6 (11.1, 12.7)	4.62 ± 3.58 (0.70, 8.65)
Males	4	48.3 ± 12.0 (36.0, 59.0)	−16.8 ± 0.2 (−17.0, −16.6)	12.4 ± 0.5 (11.8, 13.0)	8.02 ± 4.35 (2.26, 12.30)

b) Liver

Sex	n	Fork length (cm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	[Hg] (μg.g^{-1} dw)
Centrophorus moluccensis					
Females	5	51.2 ± 21.1 (29.0, 73.5)	−17.1 ± 0.6 (−18.0, −16.4)	12.7 ± 1.0 (11.5, 14.1)	1.64 ± 2.04 (0.03, 4.48)
Males	6	48.5 ± 10.5 (31.5, 61.5)	−17.3 ± 0.6 (−18.3, −16.6)	13.0 ± 1.1 (11.6, 14.7)	0.56 ± 0.64 (0.04, 1.41)
***Squalus* sp. 1**					
Females	22	55.2 ± 11.7 (35.0, 69.5)	−17.0 ± 0.3 (−17.6, −16.6)	12.7 ± 0.9 (11.6, 14.9)	1.11 ± 1.41 (0.05, 5.37)
Males	33	46.1 ± 10.6 (26.0, 64.0)	−17.1 ± 0.4 (−18.0, −16.2)	13.0 ± 1.2 (10.2, 15.4)	0.63 ± 0.93 (0.02, 3.84)
***Squalus* sp. 2**					
Females	8	47.4 ± 13.8 (31.0, 64.0)	−17.1 ± 0.5 (−18.0, −16.4)	12.6 ± 0.7 (11.6, 14.0)	0.25 ± 0.34 (0.02, 1.06)
Males	4	48.3 ± 12.0 (36.0, 59.0)	−16.6 ± 0.6 (−17.1, −16.1)	12.6 ± 0.5 (12.0, 13.3)	0.75 ± 0.73 (0.07, 1.68)

as *Squalus blainville* (Accession # KY909812.1), with 100% query cover and 98.56% sequence similarity, and *Squalus clarkae* (Accession # PV651710.1), with 100% query cover and 98.83% sequence similarity, respectively. We denote these two groups as *Squalus* sp. 1 and 2 for the remainder of the manuscript (Accession numbers PX960991-PX961056). The results of the genetic sequence analysis showed that our sample set included 10 female and 6 male *C. moluccensis*, 23 female and 34 male *Squalus* sp. 1, and 8 female and 4 male *Squalus* sp. 2.

3.2. Stomach contents

Centrophorus moluccensis- Identifiable material was retrieved from 11 individuals (7 females and 4 males). A total of 28 prey items were found, accounting for a species richness R of 12 (9 teleosts and 3 squid species). Myctophidae (lantern fish) dominated the diet composition with more than 82% of the total number of prey items (Table 1). Warming's lantern fish (*Ceratoscopelus warmingii*, %N = 35.7%) and *Diaphus* spp. (combined %N = 32.1%) were the most important prey by number, followed by *Bolinichthys* spp. (%N = 10.7%). Cephalopods had a relative abundance of around 15%. Calculated Shannon-Wiener (H') and equitability (E) indexes were 2.92 and 0.82, respectively. H' indexes were 2.79 and 2.64 for females and males, respectively. Although females had a richer diet (R = 9) than males (R = 7), both sexes had similarly equitable diets (E = 0.88 for females and E = 0.94 for males). There is a slight degree of trophic segregation between females and males, as suggested by Pianka's index (O = 0.78), with 21.1% of prey consumed by females being cephalopods, including epipelagic ones (%N = 10.5), while males fed exclusively on teleosts (Table 2).

Squalus sp. 1- Identifiable material was retrieved from 39 stomachs (14 females and 25 males). A total of 132 prey items were found, belonging to a wide range of species (R = 24), including one small shark, teleosts, cephalopods and crustaceans (Table 1). *C. warmingii* was the most important prey (%N = 58.3%), other prey species accounted for a low part of the diet composition (%N < 5%) except shrimps which reached 6.1% in terms of relative abundance. Calculated H' and E indexes were 2.65 and 0.58, respectively. H' indexes were 1.74 and 3.01 for females and males, respectively. Males had a richer (R = 20) and more equitable diet (E = 0.71) than females (R = 11, E = 0.50), as only males occasionally consumed cephalopods (%N = 3.9) and benthodemersal prey (%O = 20.0, %N = 8.0, Table 2). Nevertheless, the computed Pianka's index (O = 0.97) suggested high dietary overlap between sexes.

Squalus sp. 2- Identifiable material was retrieved from 10 individuals (7 females and 3 males). A total of 29 prey items were found from only 7 different prey species (Table 1). *C. warmingii* largely dominated the diet with close to 80% of the relative abundance. Other prey species accounted for a low part of the diet composition (%N < 5%) but belonged to a wide range of habitats. Calculated H' and E indexes were 1.27 and 0.45, respectively. All the prey species were found in females, for which H' and E were 1.60 and 0.57, respectively. These indexes could not be calculated for males as only one species (*C. warmingii*) was retrieved from their stomach (Table 2). Despite the richer and more equitable diet recorded in females, the computed Pianka's index (O = 0.99) suggested high dietary overlap between sexes.

Overall, the three species fed mostly on mesopelagic prey (%N from 82.3 to 89.3). Occasional consumption of benthodemersal prey was also observed, mostly in *Squalus* sp. 1 thanks to the higher number of full stomachs. Epipelagic prey, like two cephalopods in *C. moluccensis* and a mackerel in *Squalus* sp. 2, were also observed. Nevertheless, *C. warmingii* dominated the diet of the three species even if its relative abundance varied among species (from 35% for *C. moluccensis* to 80% for *Squalus* sp. 2). The first order interactions did not have any impact on stomach contents according to the PERMANOVAs. The fork length alone had an impact ($F_{1,59} = 2.448$; $P = 0.023$), but not the species ($F_{1,59} = 1.527$; $P = 0.085$) and the sex ($F_{1,59} = 0.781$; $P = 0.608$). Consequently, dietary niches inferred from stomach content analysis overlapped between species and sex, as shown by high Pianka's index values. The highest Pianka's index value is between the two species of *Squalus* (O = 0.98). *C. moluccensis* exhibited a slight degree of segregation from *Squalus* sp. 1 (O = 0.88) and *Squalus* sp. 2 (O = 0.87). Nevertheless, some differences could be identified among the diet of these three predators. The dietary niche of *C. moluccensis* appeared to be the most diversified and highly equilibrated, as shown by high Shannon-Wiener index and equitability values. On the opposite, the dietary niche of *Squalus* sp. 2 might really be centred on one prey, *C. warmingii*. In terms of prey type differences, crustaceans were exclusively found in the diet of *Squalus* spp., mainly in *Squalus* sp. 1, whereas cephalopods constituted a significant part of the diet only for the *C. moluccensis*. Finally, if we except *C. warmingii*, which is common to the three species, the composition of the teleost communities was relatively different between the diet of *C. moluccensis* and *Squalus* sp. 2. Nevertheless, species accumulation curves did not reach

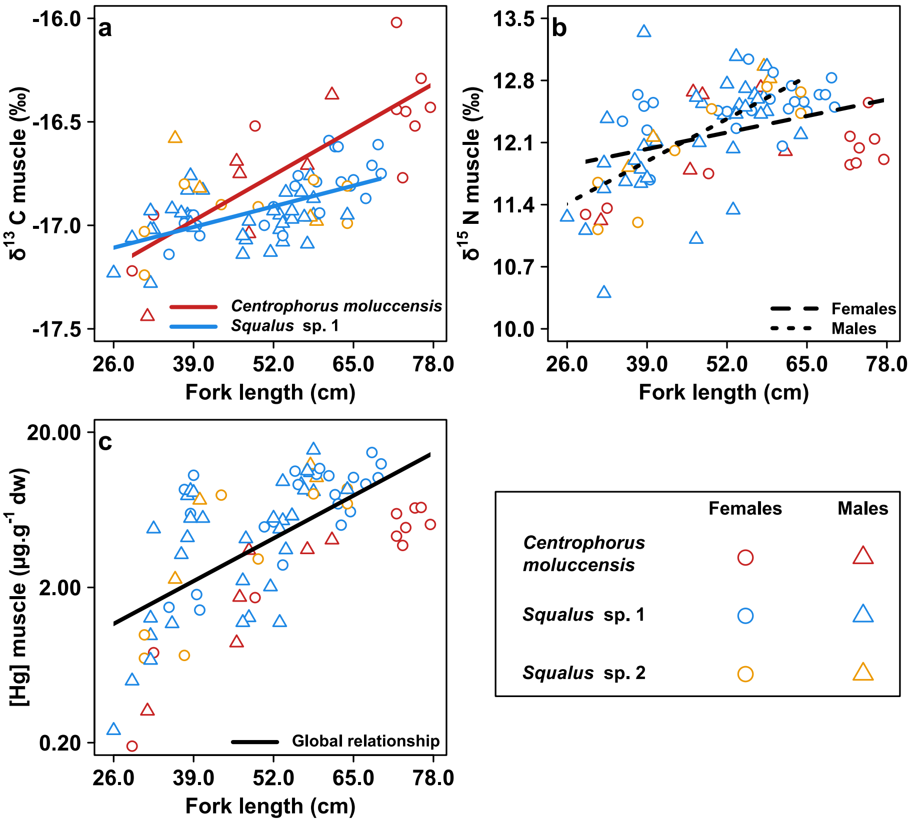

Fig. 2. Relationships between fork length and δ^{13}C (a), δ^{15}N (b) values, and Hg concentrations ($\log_{10}$ scale, c) measured in the muscle in deep-sea sharks sampled near La Réunion. The linear relationships are shown by species (a), sex (b) and globally (c) according to the ANCOVA results shown in Table 3.

an asymptote for the three species (Fig. 1).

3.3. Stable isotopes and mercury

The results of the linear models (Table 3a) show that δ^{13}C values in the muscle increased with fork length (r = 0.643, $P < 0.001$, slope = 0.011). δ^{13}C values differed between species, with *C. moluccensis* (−16.7 ± 0.4 ‰) having higher and more variable values than *Squalus* sp. 1 (−16.9 ± 0.1 ‰) and *Squalus* sp. 2 (−16.9 ± 0.2 ‰, Table 4a). The significant interaction between fork length and species showed that the increase of δ^{13}C values with fork length was steeper in *C. moluccensis* (r = 0.807, $P < 0.001$, slope = 0.017) than in *Squalus* sp. 1 (r = 0.602, $P < 0.001$, slope = 0.008), but did not occur in *Squalus* sp. 2 (r = 0.098, P = 0.762, Fig. 2a). Smaller sharks of the three species had similar δ^{13}C values. There was a significant influence of the interaction between species and sex on δ^{15}N values, with males having higher δ^{15}N values than females in *C. moluccensis* and *Squalus* sp. 2, but lower values in *Squalus* sp. 1 (Table 4a). δ^{15}N values increased with fork length (r = 0.502, $P < 0.001$, slope = 0.021, Table 3a), this relationship being stronger and steeper in males (r = 0.615, $P < 0.001$, slope = 0.037) than in females (r = 0.439, P = 0.004, slope = 0.014, Fig. 2b). The larger size of females than of males (55.5 ± 14.6 cm for females, 46.6 ± 10.4 cm for males, t = 3.206, P = 0.002) may explain this pattern. Log_{10}-transformed Hg concentrations in muscle increased with the fork length (r = 0.639, $P < 0.001$, slope = 0.021, Table 4a; Fig. 2c). Hg concentrations also differed between species, with *C. moluccensis* having lower Hg concentrations (3.35 ± 2.18 μg g^{-1} dw) than *Squalus* sp. 1 (6.25 ± 3.92 μg g^{-1} dw) while *Squalus* sp. 2 had intermediate concentrations (5.75 ± 4.02 μg g^{-1} dw).

The ANCOVA results for liver (Table 3b) indicated that δ^{13}C values were only correlated with fork length (r = 0.482, $P < 0.001$, slope = 0.017, Fig. 3a), but did not differ between species and sexes (Table 4b). δ^{15}N in liver was not influenced by fork length (Fig. 3b) and was not significantly different between species and sexes (Table 4b). Lastly, Hg concentrations in the liver increased with the fork length (r = 0.651, $P < 0.001$, slope = 0.033, Fig. 3c) but did not differ between species and sexes (Table 4b).

3.4. Isotopic niches

Isotopic niches were consistently larger in liver than in muscle, whether sexes are combined (Figs. 4 and 5) or separated (Figs. 6 and 7) for each species. In muscle, *C. moluccensis* had a larger niche than *Squalus* sp. 1 while *Squalus* sp. 2 had a niche of intermediate size (Fig. 4). The niche of *C. moluccensis* poorly overlapped with those of *Squalus* sp. 1 (12.1%) and sp. 2 (25.9%) while strong overlap occurred between *Squalus* sp. 1 and *Squalus* sp. 2 (65.4%, Fig. 4a). In the liver, *C. moluccensis* had a larger niche than *Squalus* sp. 1 and *Squalus* sp. 2 (Fig. 5). Stronger overlap of the isotopic niche of *C. moluccensis* with those of *Squalus* sp. 1 (59.9%) and sp. 2 (38.7%) occurred in the liver than in the muscle. Strong overlap also occurred between *Squalus* sp. 1 and *Squalus* sp. 2 in the liver (52.4% and Fig. 5a). Within each species, the percentage of isotopic niche overlap between sexes never exceeded 20% in muscle (14.9% in *C. moluccensis*, 19.5% in *Squalus* sp. 1 and 15.2% in *Squalus* sp. 2, Fig. 6a). It was stronger in the liver (57.2% in *C. moluccensis*, 45.4% in *Squalus* sp. 1) except between male and female *Squalus* sp. 2 for which it reached 20.1% (Fig. 7a).

4. Discussion

Previous studies on deep-sea shark communities reported variable level of trophic niche overlap depending on species communities, but also trophic niche partitioning between sexes and life stages in several species (e.g., Churchill et al., 2015; Valls et al., 2017; Barría et al.,

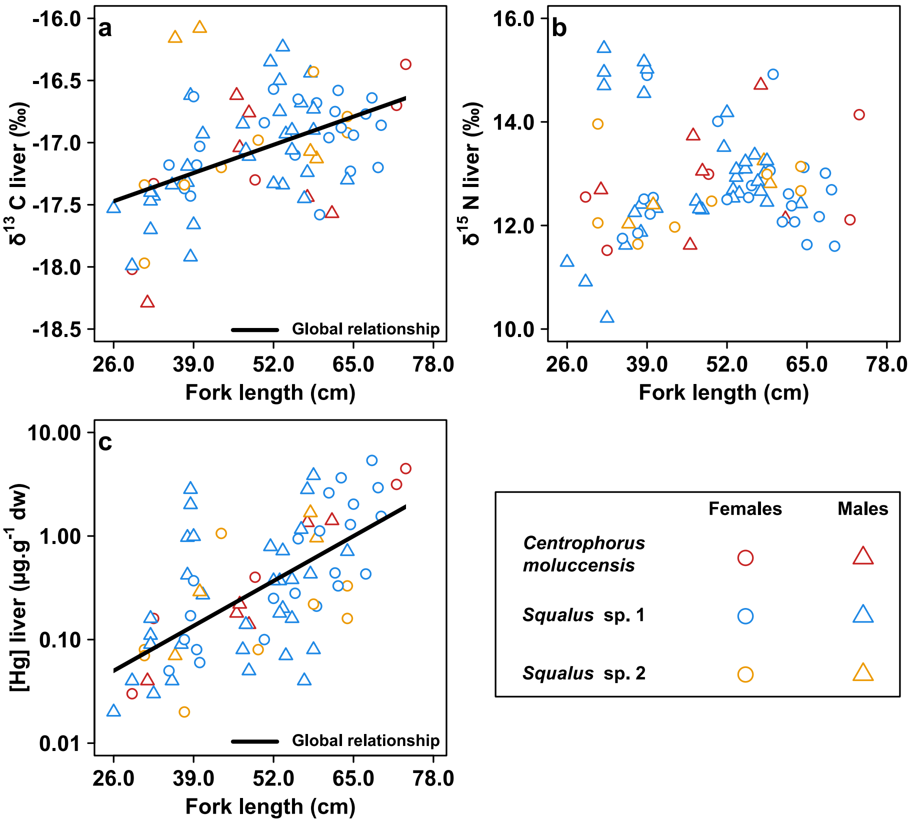

Fig. 3. Relationships between fork length and δ^{13}C (a), δ^{15}N (b) values, and Hg concentrations ($\log_{10}$ scale, c) measured in the liver in deep-sea sharks sampled near La Réunion. The linear relationships are shown globally (a, c) or not (b) according to the ANCOVA results shown in Table 3.

2018a; Munroe et al., 2020). This partitioning can be related to resource availability in the considered community (Churchill et al., 2015; Valls et al., 2017). Here, we combined several dietary indicators to assess the trophic ecology and interactions of three deep-sea sharks from the oligotrophic southwestern Indian Ocean, including two cryptic species that have not yet been described using genetics. Although the sample size was low for several species and sexes, especially for stomach contents, the results highlight contrasting levels of trophic overlap between species depending on the dietary indicator (and therefore time scales). Furthermore, our results demonstrate that intra-specific trophic niche partitioning occurs at multiple levels, both between sexes, and across ontogeny. Such results highlight the necessity to take sex and ontogeny into account when investigating the trophic interactions between multiple species within a community.

4.1. *Identification of Squalus sp. 1 and Squalus sp. 2*

The use of molecular tools highlighted the occurrence of two species of *Squalus* spp. in our samples. *Squalus* is a diverse genus with more than 30 species described. In the southwestern Indian Ocean, described dogfish species have included *Squalus acanthias*, *Squalus blainvillei*, *Squalus megalops* and *Squalus mitsukurii*. However, further investigations resulted in *Squalus megalops* being redescribed as *Squalus acutipinnis* (Viana and de Carvalho, 2016). Furthermore, other species have been described in the region since the redescription of *S. acutipinnis* (Viana et al., 2018; Fricke et al., 2023). *S. acutipinnis* has notably been observed in Mauritius, close to La Réunion (Viana and de Carvalho, 2016), while *Squalus longispinis* has been specifically described in La Réunion (Fricke et al., 2023). However, the description of these species did not include genetic identifications but relied on morphology alone, and morphological differences between sympatric species with strong convergence in body form may be difficult to distinguish for non-specialists. In the case of *S. acutipinnis* and *S. longispinis*, both species are mostly distinguished by their dermal denticles (Fricke et al., 2023). In this context, the use of molecular tools prevented *Squalus* sp. 1 and *Squalus* sp. 2 to be considered wrongly as the same species. Further studies combining morphological and molecular tools should be conducted to assess the full diversity of the *Squalus* genus in the southwestern Indian Ocean.

4.2. *Trophic niche partitioning between species*

Stomach contents provide short-term information on the diet of sharks because of quick gastric evacuation (one to several days, Wetherbee et al., 2012). Carbon and nitrogen stable isotope values, and Hg concentrations in the liver provide medium-term information because of the short tissue turnover in the liver (from two weeks to one month of isotopic half-life for δ^{15}N values, MacNeil et al., 2006). Stomach contents, stable isotope values and Hg concentrations in the liver overlapped among the three shark species.

Species accumulation curves for stomach contents did not reach an asymptote for each shark species, suggesting that sample size was limited and thus the whole diversity of prey consumed by sharks was not observed. Nevertheless, stomach contents still show that sharks feed predominantly on myctophids, with *C. warmingii* being the main prey species found of all the three shark species, and with the genus *Diaphus* being the second most consumed prey for *C. moluccensis*. Myctophids are an important component of mesopelagic teleost communities in most mesopelagic ecosystems (Vipin et al., 2012; Klevjer et al., 2020) and *C. warmingii* and *Diaphus* spp. are the most abundant myctophids in the southwestern Indian Ocean (Cherel et al., 2020). The predominance of *C. warmingii* in the diet of the three species is a likely driver of the high trophic niche overlap indexes computed with stomach contents. Nevertheless, minor differences of short-term trophic ecology between shark species were also apparent with *C. moluccensis* having a more

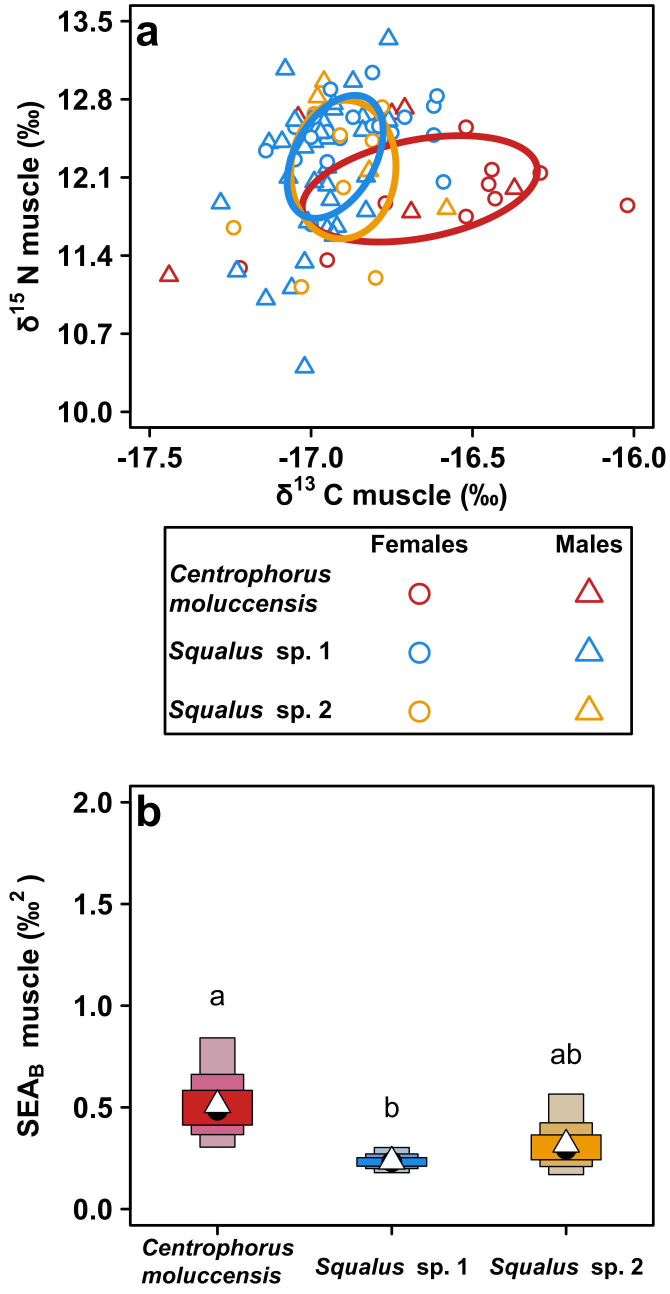

Fig. 4. Sample-size corrected standard ellipses generated with δ^{13}C and δ^{15}N values measured in the muscle of each species of deep-sea sharks sampled near La Réunion (a) and subsequent sample-size corrected (SEA$_C$, white triangles) and Bayesian estimation (SEA$_B$, shaded boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of standard ellipse area (SEA, b). Letters over density boxes are groups of ellipses with similar SEA$_B$.

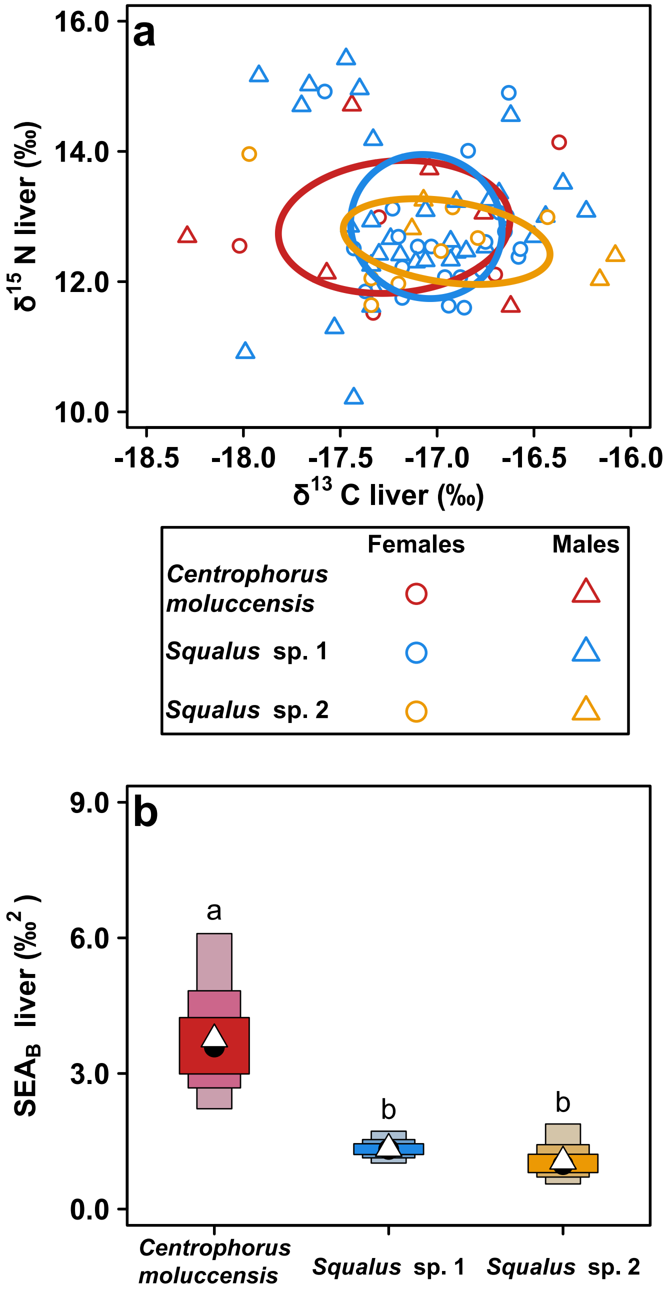

Fig. 5. Sample-size corrected standard ellipses generated with δ^{13}C and δ^{15}N values measured in the liver of each species of deep-sea sharks sampled near La Réunion (a) and subsequent sample-size corrected (SEA$_C$, white triangles) and Bayesian estimation (SEA$_B$, shaded boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of standard ellipse area (SEA, b). Letters over density boxes are groups of ellipses with similar SEA$_B$.

diverse diet than the two *Squalus* species according to the higher equitability value computed from its stomach contents.

Similarly to liver, δ^{15}N values in muscle tissues did not differ between species, suggesting that the three species generally have similar trophic positions. By contrast, δ^{13}C values in muscle tissue for *C. moluccensis* were higher and more variable than those of both *Squalus* species, and isotopic niche overlap (65.4%) occurred only between *Squalus* species, suggesting differences of foraging habitats between *C. moluccensis* and *Squalus* spp. Similarly, higher Hg concentrations in the muscle of *C. moluccensis* than in *Squalus* sp. 1 may result from habitat differences instead of trophic level as these species had similar δ^{15}N values (Le Bourg et al., 2019). Considering the longer isotopic turnover in muscle (from *ca* 2 months to *ca* 2 years of isotopic half-life in sharks, Logan and Lutcavage, 2010; Malpica-Cruz et al., 2012), the trophic niche overlap inferred from stomach contents and stable isotope values in liver may have occurred over short periods of time and the δ^{13}C values and Hg concentrations in muscle may indicate that *C. moluccensis* consume more island-associated prey than *Squalus* spp. This is supported by the high diversity and proportion of *Diaphus* spp. in stomach contents of *C. moluccensis*. Indeed, the distribution of *Diaphus* spp. is restricted to mesopelagic-boundary zones, where mesopelagic waters meet the upper insular slope (Reid et al., 1991; Cherel et al., 2020). The higher

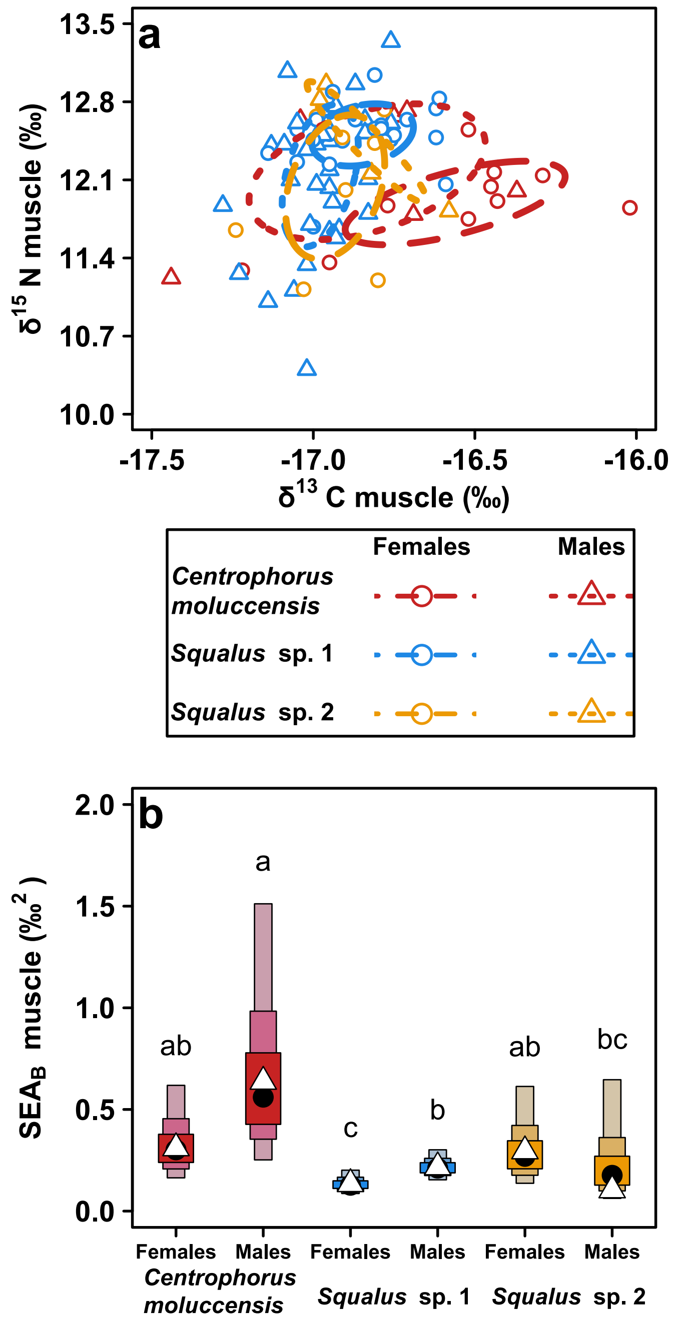

Fig. 6. Sample-size corrected standard ellipses generated with δ^{13}C and δ^{15}N values measured in the muscle of each sex in each species of deep-sea sharks sampled near La Réunion (a) and subsequent sample-size corrected (SEA$_C$, white triangles) and Bayesian estimation (SEA$_B$, shaded boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of standard ellipse area (SEA, b). Letters over density boxes are groups of ellipses with similar SEA$_B$.

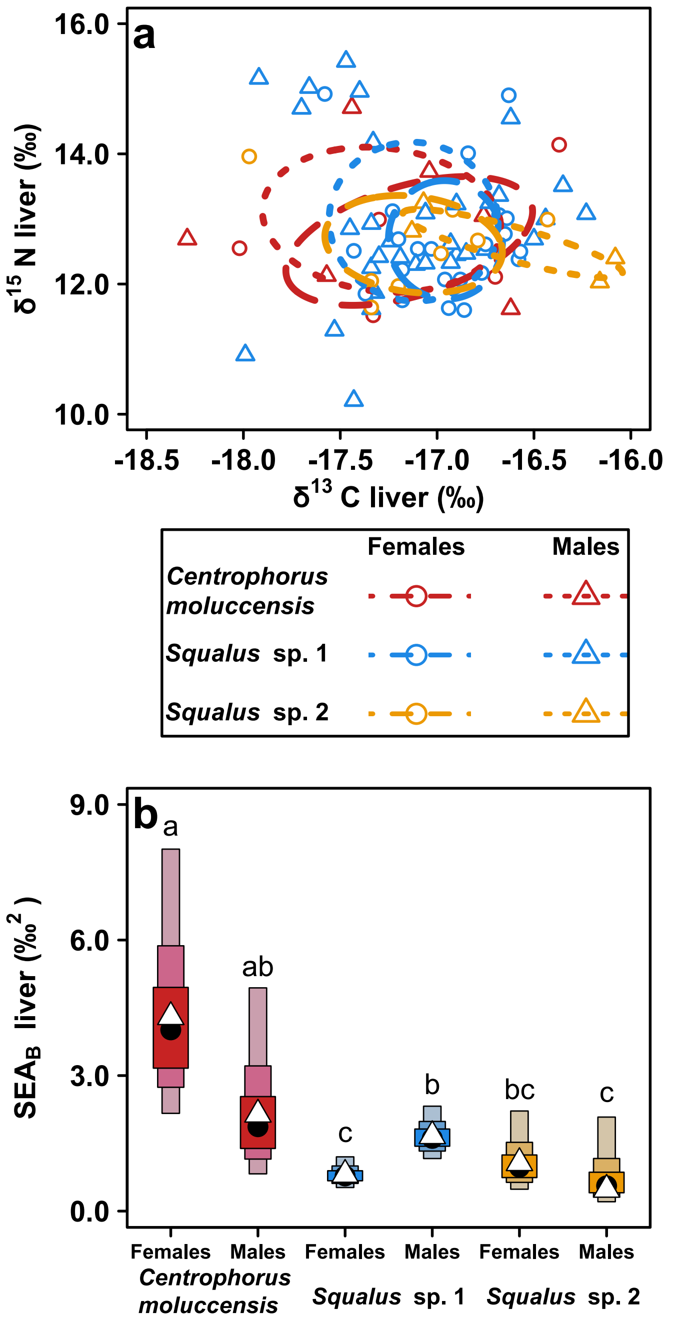

Fig. 7. Sample-size corrected standard ellipses generated with δ^{13}C and δ^{15}N values measured in the liver of each sex in each species of deep-sea sharks sampled near La Réunion (a) and subsequent sample-size corrected (SEA$_C$, white triangles) and Bayesian estimation (SEA$_B$, shaded boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of standard ellipse area (SEA, b). Letters over density boxes are groups of ellipses with similar SEA$_B$.

variability of δ^{13}C values in *C. moluccensis* may also suggest the exploitation of a wider range of habitats, as suggested by the lower occurrence of mesopelagic prey in the stomach contents of this species compared to *Squalus* spp. In contrast, the cryptic *Squalus* spp. likely share the same trophic niche restricted in more oceanic habitats than *C. moluccensis*, as shown by their lower and less variable δ^{13}C values in muscle tissue, their isotopic niche overlap and their higher proportions of oceanic *C. warmingii* (Reid et al., 1991; Cherel et al., 2020) in their stomachs. Prey availability is a critical driver of the size of trophic niches and of the extent to which species overlap in their diets (Gladics et al., 2014; Pool et al., 2017; Kaymak et al., 2023). Since *C. warmingii* is one of the most abundant mesopelagic myctophids in the southwestern Indian Ocean (Cherel et al., 2020), it may be possible that its availability for predators may not be limiting. This may allow both *Squalus* species (and *C. moluccensis* to a lesser extent) to continuously forage on the same prey without competitive interaction in the long term, explaining their narrow isotopic niches and their overlap in the muscle. However, the occasional presence of other prey in the stomachs and the consistently larger isotopic niches in the liver than in the muscle, may indicate higher inter-individual variation for the consumption and assimilation of secondary prey in addition to *C. warmingii*.

4.3. Sex differences

Sample size was limited for both stomach contents and stable isotope values for each sex in *C. moluccensis* and *Squalus* sp. 2. Consequently, caution may be necessary when interpreting the results for sexes. Nevertheless, for each species, isotopic niche overlap between sexes was consistently observed with stomach contents and stable isotopes in the liver but it was limited with stable isotopes in muscle.

Although trophic overlap inferred from stomach contents was high, stomach contents of *Squalus* sp. 1 may provide some hints of trophic segregation, as males included more often cephalopods and benthodemersal prey in their diet. Female *C. moluccensis* also tend to consume a higher proportion of cephalopods while males fed exclusively on teleosts, but more caution is necessary regarding the interpretation of this result considering the low sample size.

Similar stable isotope values and isotopic niche overlap in liver indicate similarities in the diets of both sexes in *Squalus* spp. (not in *C. moluccensis*), which is consistent with results from stomach contents. The differences in overlap results between stable isotope values in muscle and stable isotope values in liver and stomach contents could indicate temporal variation of the trophic niche overlap between sexes. Trophic overlap occurred over short periods of time and females and males may usually partition their trophic niches.

In muscle, the significant influence of the interaction between species and sex on δ^{15}N values and the lack of influence of sex on δ^{13}C values suggests sexual trophic segregation through trophic levels in the long term. Such segregation through the trophic level was observed in several shark species, with males consuming higher-trophic level prey (Hussey et al., 2011; Barría et al., 2018b). However, this result and its interpretation is contradicted by the lack of differences of Hg concentrations between sexes. Considering how Hg may have been more an indicator of foraging habitat when assessing its inter-specific variations, similar δ^{13}C values and Hg concentrations between sexes may suggest exploitation of the same foraging habitats by both sexes. Spatial niche segregation between sexes is known to occur and has been documented in several shark species (e.g., Sims, 2005; Mucientes et al., 2009; Braccini and Taylor, 2016), including within the genus *Squalus* (Graham, 2005; Jones et al., 2013; Haugen et al., 2017; Yano et al., 2017) and *Centrophorus*, including *C. moluccensis* (Graham and Daley, 2011). Yet, our results do not highlight spatial sexual segregation between shark species. An explanation to the apparent lack of sexual segregation of foraging habitat observed with stable isotopes and Hg despite sexual segregation potentially occurring could be the foraging in the same habitat at different times in the day by both sexes (Dell'Apa et al., 2014).

4.4. Ontogenetic dietary shifts

δ^{13}C and δ^{15}N values and Hg concentrations increased with body length in muscle tissues. A similar shift occurred in liver tissues, except for δ^{15}N. Ontogenetic changes of foraging habitat often occur in predatory shark species (Grubbs, 2010), and the positive relationships between δ^{13}C values and body size may be indicative of these changes, with increasing δ^{13}C values with body size indicating a shift from offshore-pelagic to coastal-benthic feeding grounds (e.g., Borrell et al., 2011; Carlisle et al., 2015; Marsh et al., 2017; Park et al., 2018). Higher δ^{13}C values in larger sharks in our data may indicate that they forage closer to island-associated habitats as they grow, where the investigated species preferentially occur (Compagno, 1984). A steeper increase of muscle δ^{13}C values with body length occurred in *C. moluccensis* than in *Squalus* sp. 1, and no increase occurred in *Squalus* sp. 2. The δ^{13}C values of the smallest sharks were also quite similar between the species. This may indicate that, while adult *C. moluccensis* feed more in the mesopelagic-boundaries zones near islands, as previously discussed, the juveniles may preferentially forage in more oceanic environments, where they may coexist with *Squalus* spp. Higher δ^{15}N values in muscle of larger sharks can indicate an increasing relative trophic position with body length, probably thanks to the larger mouth gape size of larger sharks. Increasing Hg concentrations with length in both tissues can indicate an increasing relative trophic position too, or a change in habitat. However, bioaccumulation of Hg with age can also explain this result, especially in the muscle, considering its slower turnover than the liver. This result is consistent with previous observations in teleosts (e.g., Chouvelon et al., 2014; Marsh et al., 2017) and elasmobranchs (e.g., Hussey et al., 2011; Raoult et al., 2015 Nielsen et al., 2019).

Sharks were not separated by maturity stages as gonad maturity was not assessed and no information on reproductive biology is available for the 2 *Squalus* species, that were not identified previously. Consequently, trophic overlap between juveniles and adults was not assessed with stomach contents. However, the significant impact of fork length on stomach contents further suggests ontogenetic variations of the diet.

4.5. Conclusions

The combination of dietary tracers allowed to investigate the trophic ecology of sharks from the mesopelagic southwestern Indian Ocean at both qualitative and quantitative scales and over short and long periods of time. Interspecific trophic niche partitioning was observed when using long-term dietary indicators (isotopic niches in muscle). However, interspecific trophic niche overlap was also observed when using short-term dietary indicators (stomach contents and isotopic niches in liver). Intra-specific mechanisms of trophic niche partitioning were also highlighted, as shown by differences of diet between sexes and ontogenetic shifts. Trophic niche partitioning between mesopelagic sharks in the southwestern Indian Ocean is then not only occurring between species but also within species and is temporally variable. The combination of inter- and intra-specific mechanisms of trophic segregation may reduce risks of competition between deep-sea sharks in the oligotrophic southwestern Indian Ocean, while the temporal plasticity may indicate periods of trophic overlaps when resources may be abundant. Overall, the results of this work suggest that the co-existence between predators is mediated the dynamics of their trophic niches at different scales.

CRediT authorship contribution statement

Baptiste Le Bourg: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Jeremy J. Kiszka:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Jérôme Spitz:** Writing – review & editing, Investigation, Data curation. **Toby S. Daly-Engel:** Writing – review & editing, Investigation. **Paco Bustamante:** Writing – review & editing, Project administration, Methodology, Funding acquisition.

Declaration of competing interest

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

Acknowledgements

We would like to thank IFREMER in La Réunion for providing shark samples. We are also grateful to G. Guillou and P. Richard (LIENSs) for running the stable isotope analyses and to Carine Churlaud and Maud Brault-Fravrou for their support during Hg analyses. We thank the anonymous reviewers for their helpful comments. This study was supported financially by LIENSs, the CPER (Contrat de Plan État-Région) and the FEDER (Fonds Européen de Développement Régional) through the funding of the IR-MS and AMA-254 of LIENSs laboratory. This is contribution #2103 from the Institute of Environment at Florida International University.

Data availability

Data will be made available on request.

References

Amundsen, P.A., Sánchez-Hernández, J., 2019. Feeding studies take guts–critical review and recommendations of methods for stomach contents analysis in fish. J. Fish. Biol. 95, 1364–1373. https://doi.org/10.1111/jfb.14151.

Atwell, L., Hobson, K.A., Welch, H.E., 1998. Biomagnification and bioaccumulation of mercury in an arctic marine food web: insights from stable nitrogen isotope analysis. Can. J. Fish. Aquat. Sci. 55, 1114–1121. https://doi.org/10.1139/f98-00.

Barría, C., Navarro, J., Coll, M., 2018a. Feeding habits of four sympatric sharks in two deep-water fishery areas of the western Mediterranean Sea. Deep Sea Res. Oceanogr. Res. Pap. 142, 34–43. https://doi.org/10.1016/j.dsr.2018.09.010.

Barría, C., Navarro, J., Coll, M., 2018b. Trophic habits of an abundant shark in the northwestern Mediterranean Sea using an isotopic non-lethal approach. Estuar. Coast Shelf Sci. 207, 383–390. https://doi.org/10.1016/j.ecss.2017.08.021.

Belleggia, M., Battagliotti, C., Cortés, F., Colonello, J.H., 2019. Feeding together: a global diet analysis of twenty-three species of chondrichthyes on a feeding ground area. Hydrobiologia 842, 77–99. https://doi.org/10.1007/s10750-019-04027-w.

Bellodi, A., Benvenuto, A., Melis, R., Mulas, A., Barone, M., Barría, C., Cariani, A., Carugati, L., Chatzispyrou, A., Desrochers, M., Ferrari, A., Guallart, J., Hemida, F., Mancusi, C., Mazzoldi, C., Ramírez-Amaro, S., Rey, J., Scannella, D., Serena, F., Tinti, F., Vella, A., Follesa, M.C., Cannas, R., 2022. Call me by my name: unravelling the taxonomy of the gulper shark genus *Centrophorus* in the Mediterranean Sea through an integrated taxonomic approach. Zool. J. Linn. Soc. 195, 815–840. https://doi.org/10.1093/zoolinnean/zlab110.

Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Sayers, E.W., 2012. GenBank. Nucleic Acids Res. 41, D36–D42. https://doi.org/10.1093/nar/gks1195.

Blum, J.D., Popp, B.N., Drazen, J.C., Choy, C.A., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918.

Bøhn, T., Amundsen, P.A., Sparrow, A., 2008. Competitive exclusion after invasion? Biol. Invasions 10, 359–368. https://doi.org/10.1007/s10530-007-9135-8.

Borrell, A., Cardona, L., Kumarran, R.P., Aguilar, A., 2011. Trophic ecology of elasmobranchs caught off Gujarat, India, as inferred from stable isotopes. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 68, 547–554. https://doi.org/10.1093/icesjms/fsq170.

Bowman, R.E., 1986. Effect of regurgitation on stomach content data of marine fishes. Environ. Biol. Fish. 16, 171–181. https://doi.org/10.1007/BF00005169.

Braccini, M., Taylor, S., 2016. The spatial segregation patterns of sharks from Western Australia. R. Soc. Open Sci. 3, 160306. https://doi.org/10.1098/rsos.160306.

Carlisle, A.B., Goldman, K.J., Litvin, S.Y., Madigan, D.J., Bigman, J.S., Swithenbank, A. M., Kline, Jr TC., Block, B.A., 2015. Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. Proc. Biol. Sci. 282, 20141446. https://doi.org/10.1098/rspb.2014.1446.

Cherel, Y., Romanov, E.V., Annasawmy, P., Thibault, D., Ménard, F., 2020. Micronektonic fish species over three seamounts in the southwestern Indian Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr. 176, 104777. https://doi.org/10.1016/j.dsr2.2020.104777.

Chouvelon, T., Spitz, J., Cherel, Y., Caurant, F., Sirmel, R., Mèndez-Fernandez, P., Bustamante, P., 2011. Interspecific and ontogenic-related differences in δ^{13}C and δ^{15}N values and Hg and Cd concentrations of cephalopods. Mar. Ecol. Prog. Ser. 433, 107–120. https://doi.org/10.3354/meps09159.

Chouvelon, T., Caurant, F., Cherel, Y., Simon-Bouhet, B., Spitz, J., Bustamante, P., 2014. Species-and size-related patterns in stable isotopes and mercury concentrations in fish help refine marine ecosystem indicators and provide evidence for distinct management units for hake in the Northeast Atlantic. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 71, 1073–1087. https://doi.org/10.1093/icesjms/fst199.

Choy, C.A., Popp, B.N., Kaneko, J.J., Drazen, J.C., 2009. The influence of depth on mercury levels in pelagic fishes and their prey. Proc. Natl. Acad. Sci. 106, 13865–13869. https://doi.org/10.1073/pnas.0900711106.

Churchill, D.A., Heithaus, M.R., Vaudo, J.J., Grubbs, R.D., Gastrich, K., Castro, J.I., 2015. Trophic interactions of common elasmobranchs in deep-sea communities of the Gulf of Mexico revealed through stable isotope and stomach content analysis. Deep Sea Res. Part II Top. Stud. Oceanogr. 115, 92–102. https://doi.org/10.1016/j.dsr2.2014.10.011.

Clarke, M.R., 1986. A Handbook for the Identification of Cephalopod Beaks. Clarendon Press, Oxford.

Compagno, L.J.V., 1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1 – hexanchiformes to Lamniformes. Fao Fish. Synop. 4, 1–249.

Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can. J. Fish. Aquat. Sci. 54, 726–738. https://doi.org/10.1139/f96-316.

Daly-Engel, T.S., Koch, A., Anderson, J.M., Cotton, C.F., 2018. Description of a new deep-water dogfish shark from Hawaii, with comments on the *Squalus mitsukurii* species complex in the West Pacific. ZooKeys 798, 135–157. https://doi.org/10.3897/zookeys.798.28375.

de Mendiburu, F., 2020. Package 'agricolae'. R Package Version 1.3–2. https://cran.r-project.org/web/packages/agricolae/agricolae.pdf.

Dehnhard, N., Achurch, H., Clarke, J., Michel, L.N., Southwell, C., Sumner, M.D., Eens, M., Emmerson, L., 2020. High inter-and intraspecific niche overlap among three sympatrically breeding, closely related seabird species: generalist foraging as an adaptation to a highly variable environment? J. Anim. Ecol. 89, 104–119. https://doi.org/10.1111/1365-2656.13078.

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

DeNiro, M.J., Epstein, S., 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197, 261–263. https://doi.org/10.1126/science.327543.

DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochem. Cosmochim. Acta 42, 495–506. https://doi.org/10.1016/0016-7037(78)90199-0.

DeNiro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochem. Cosmochim. Acta 45, 341–351. https://doi.org/10.1016/0016-7037(81)90244-1.

Estupiñán-Montaño, C., Polo-Silva, C.J., Elorriaga-Verplancken, F.R., Sánchez-González, A., Zetina-Rejón, M.J., Delgado-Huertas, A., Rojas-Cundumí, J., Galván-Magaña, F., 2024. Marine community trophic structure of Malpelo Island, Colombia from stable isotopes approach. J. Mar. Syst. 244, 103973. https://doi.org/10.1016/j.jmarsys.2024.103973.

Fernández-Aguirre, E., Galván-Magaña, F., Sánchez-González, A., González-Armas, R., Abitia-Cárdenas, L.A., Elorriaga-Verplancken, F.R., Villalejo-Fuerte, M.T., Tripp-Valdéz, A., Barajas-Calderón, A.V., Delgado-Huertas, A., Torres-García, R.Q., 2022. Changes in the feeding habits of the bat ray *Myliobatis californica* (Gill 1865) during climatic anomalies off the west coast of the Baja California Peninsula, Mexico. Reg. Stud. Mar. Sci. 53, 102462.

Fernández-Corredor, E., Navarro, J., Fuster-Alonso, A., Giménez, J., García-Barcelona, S., Rueda, L., Macías, D., Coll, M., Ramírez, F., 2025. Pelagic productivity and abundance of competitors modulate trophic niche segregation between large predators. Proc. Biol. Sci. 292, 20251809. https://doi.org/10.1098/rspb.2025.1809.

Ferrari, A., Di Crescenzo, S., Cariani, A., Crobe, V., Benvenuto, A., Piattoni, F., Mancusi, C., Bonnici, L., Bonello, J.J., Schembri, P.J., Serena, F., Massi, D., Titone, A., Tinti, F., 2021. Puzzling over spurdogs: molecular taxonomy assessment of the *Squalus* species in the Strait of Sicily. European Zool. J. 88, 181–190. https://doi.org/10.1080/24750263.2020.1849436.

Finotto, L., Berto, D., Rampazzo, F., Raicevich, S., Bonanomi, S., Mazzoldi, C., 2023. Trophic partitioning among three mesopredatory shark species inhabiting the Northwestern Adriatic Sea. Diversity 15, 1163. https://doi.org/10.3390/d15121163.

France, R.L., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar. Ecol. Prog. Ser. 124, 307–312. https://doi.org/10.3354/meps124307.

Fricke, R., Durville, P., Potin, G., Mulochau, T., 2023. *Squalus longispinis*, a new species of spurdog (Elasmobranchii: squalidae) from La Réunion, southwestern Indian Ocean. TAXA 2, ad23203.

Gladics, A.J., Suryan, R.M., Brodeur, R.D., Segui, L.M., Filliger, L.Z., 2014. Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current. Mar. Biol. 161, 837–851. https://doi.org/10.1007/s00227-013-2384-4.

Graham, K.J., 2005. Distribution, population structure and biological aspects of *Squalus* spp. (Chondrichthyes: squaliformes) from New South Wales and adjacent Australian waters. Mar. Freshw. Res. 56, 405–416. https://doi.org/10.1071/MF04275.

Graham, K.J., Daley, R.K., 2011. Distribution, reproduction and population structure of three gulper sharks (*Centrophorus*, Centrophoridae) in south-east Australian waters. Mar. Freshw. Res. 62, 583–595. https://doi.org/10.1071/MF10158.

Grinnell, J., 1924. Geography and evolution. Ecology 5, 225–229. https://doi.org/10.2307/1929447.

Grubbs, R.D., 2010. Ontogenetic shifts in movement and habitat use. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Sharks and their Relatives II: Biodiversity, Adaptive Physiology, and Conservation. CRC Press, Boca Raton, USA, pp. 319–350.

Haugen, J.B., Curtis, T.H., Fernandes, P.G., Sosebee, K.A., Rago, P.J., 2017. Sexual segregation of spiny dogfish (*Squalus acanthias*) off the northeastern United States: implications for a male-directed fishery. Fish. Res. 193, 121–128. https://doi.org/10.1016/j.fishres.2017.04.007.

Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120, 314–326. https://doi.org/10.1007/s004420050865.

Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755. https://doi.org/10.1093/bioinformatics/17.8.754.

Hussey, N.E., Dudley, S.F.J., McCarthy, I.D., Cliff, G., Fisk, A.T., 2011. Stable isotope profiles of large marine predators: viable indicators of trophic position, diet, and movement in sharks? Can. J. Fish. Aquat. Sci. 68, 2029–2045. https://doi.org/10.1139/f2011-115.

Hussey, N.E., MacNeil, M.A., Olin, J.A., McMeans, B.C., Kinney, M.J., Chapman, D.D., Fisk, A.T., 2012. Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. J. Fish. Biol. 80, 1449–1484. https://doi.org/10.1111/j.1095-8649.2012.03251.x.

Hyslop, E.J., 1980. Stomach content analysis—a review of methods and their application. J. Fish. Biol. 17, 411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x.

Jackson, A.L., 2023. Comparing Populations. Retrieved from. https://cran.r-project.org/web/packages/SIBER/vignettes/siber-comparing-populations.html.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER - stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Jones, L.M., Driggers, I.I.I.W.B., Hoffmayer, E.R., Hannan, K.M., Mathers, A.N., 2013. Reproductive biology of the Cuban dogfish in the Northern Gulf of Mexico. Mar. Coast. Fish. 5, 152–158. https://doi.org/10.1080/19425120.2013.768572.

Juncos, R., Milano, D., Macchi, P.J., Vigliano, P.H., 2015. Niche segregation facilitates coexistence between native and introduced fishes in a deep Patagonian lake. Hydrobiologia 747, 53–67. https://doi.org/10.1007/s10750-014-2122-z.

Katoh, K., Misawa, K., Kuma, K.I., Miyata, T., 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res. 30, 3059–3066. https://doi.org/10.1093/nar/gkf436.

Kaymak, N., Emre, N., Yalim, F.B., Toslak, C., Emre, Y., Akin, Ş., 2023. Seasonal variation in trophic niches and niche overlap between native and introduced cyprinid fishes. Spectrosc. Lett. 56, 227–237. https://doi.org/10.1080/00387010.2023.2202229.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A., 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199.

Kernaleguen, L., Cherel, Y., Knox, T.C., Baylis, A.M., Arnould, J.P., 2015. Sexual niche segregation and gender-specific individual specialisation in a highly dimorphic marine mammal. PLoS One 10, e0133018. https://doi.org/10.1371/journal.pone.0133018.

Kiszka, J.J., Heithaus, M.R., 2014. The state of knowledge on sharks for conservation and management. In: Techera, E.J., Klein, N. (Eds.), Sharks: Conservation, Governance and Management. Earthscan, New York, USA, pp. 69–88.

Kiszka, J., Simon-Bouhet, B., Martinez, L., Pusineri, C., Richard, P., Ridoux, V., 2011. Ecological niche segregation within a community of sympatric dolphins around a tropical island. Mar. Ecol. Prog. Ser. 433, 273–288. https://doi.org/10.3354/meps09165.

Kiszka, J.J., Charlot, K., Hussey, N.E., Heithaus, M.R., Simon-Bouhet, B., Humber, F., Caurant, F., Bustamante, P., 2014. Trophic ecology of common elasmobranchs exploited by artisanal shark fisheries off south-western Madagascar. Aquat. Biol. 23, 29–38. https://doi.org/10.3354/ab00602.

Kiszka, J.J., Aubail, A., Hussey, N.E., Heithaus, M.R., Caurant, F., Bustamante, P., 2015. Plasticity of trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by stable isotope and mercury analyses. Deep Sea Res. Oceanogr. Res. Pap. 96, 49–58. https://doi.org/10.1016/j.dsr.2014.11.006.

Klevjer, T., Melle, W., Knutsen, T., Strand, E., Korneliussen, R., Dupont, N., Salvanes, A. G.V., Wiebe, P.H., 2020. Micronekton biomass distribution, improved estimates across four north Atlantic basins. Deep Sea Res. Part II Top. Stud. Oceanogr. 180, 104691. https://doi.org/10.1016/j.dsr2.2019.104691.

Lavoie, R.A., Hebert, C.E., Rail, J.F., Braume, B.M., Yumvihoze, E., Hill, L.G., Lean, D.R. S., 2010. Trophic structure and mercury distribution in a Gulf of st. Lawrence (Canada) food web using stable isotope analysis. Sci. Total Environ. 408, 5522–5539. https://doi.org/10.1016/j.scitotenv.2010.07.053.

Le Bourg, B., Kiszka, J.J., Bustamante, P., Heithaus, M.R., Jaquemet, S., Humber, F., 2019. Effect of body length, trophic position and habitat use on mercury concentrations of sharks from contrasted ecosystems in the southwestern Indian Ocean. Environ. Res. 169, 387–395. https://doi.org/10.1016/j.envres.2018.11.024.

Le Bourg, B., Kuklinski, P., Balazy, P., Lepoint, G., Michel, L.N., 2021. Interactive effects of body size and environmental gradient on the trophic ecology of sea stars in an Antarctic fjord. Mar. Ecol. Prog. Ser. 674, 189–202. https://doi.org/10.3354/meps13821.

Logan, J.M., Lutcavage, M.E., 2010. Stable isotope dynamics in elasmobranch fishes. Hydrobiologia 644, 231–244. https://doi.org/10.1007/s10750-010-0120-3.

MacNeil, M.A., Skomal, G.B., Fisk, A.T., 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. Mar. Ecol. Prog. Ser. 302, 199–206. https://doi.org/10.3354/meps302199.

MacNeil, M.A., Drouillard, K.G., Fisk, A.T., 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Can. J. Fish. Aquat. Sci. 63, 345–353. https://doi.org/10.1139/f05-219.

Madigan, D.J., Li, M., Yin, R., Baumann, H., Snodgrass, O.E., Dewar, H., Krabenhoft, D. P., Baumann, Z., Fisher, N.S., Balcom, P., Sunderland, E.M., 2018. Mercury stable isotopes reveal influence of foraging depth on mercury concentrations and growth in Pacific bluefin tuna. Environ. Sci. Technol. 52, 6256–6264. https://doi.org/10.1021/acs.est.7b06429.

Malpica-Cruz, L., Herzka, S.Z., Sosa-Nishizaki, O., Lazo, J.P., 2012. Tissue-specific isotope trophic discrimination factors and turnover rates in a marine elasmobranch: empirical and modeling results. Can. J. Fish. Aquat. Sci. 69, 551–564. https://doi.org/10.1139/f2011-172.

Malpica-Cruz, L., Herzka, S.Z., Sosa-Nishizaki, O., Escobedo-Olvera, M.A., 2013. Tissue-specific stable isotope ratios of shortfin mako (*Isurus oxyrinchus*) and white (*Carcharodon carcharias*) sharks as indicators of size-based differences in foraging habitat and trophic level. Fish. Oceanogr. 22, 429–445. https://doi.org/10.1111/fog.12034.

Marsaly, B., Daugherty, D., Shipley, O.N., Gelpi, C., Boyd, N., Davis, J., Fisher, M., Matich, P., 2023. Contrasting ecological roles and flexible trophic interactions of two estuarine apex predators in the western Gulf of Mexico. Mar. Ecol. Prog. Ser. 709, 55–76. https://doi.org/10.3354/meps14281.

Marsh, J.M., Mueter, F.J., Iken, K., Danielson, S., 2017. Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes. Deep Sea Res. Part II Top. Stud. Oceanogr. 135, 78–94. https://doi.org/10.1016/j.dsr2.2016.07.010.

Martin, U., Mallefet, J., 2023. The diet of deep-water sharks. Deep Sea Res. Oceanogr. Res. Pap. 192, 103898. https://doi.org/10.1016/j.dsr.2022.103898.

Martin, R.A., Rossmo, D.K., Hammerschlag, N., 2009. Hunting patterns and geographic profiling of white shark predation. J. Zool. 279, 111–118. https://doi.org/10.1111/j.1469-7998.2009.00586.x.

Martinez-Ayala, J.C., Tripp-Valdez, A., Galván-Magaña, F., González, A.S., Klimley, A.P., 2025. The trophic response of *Mustelus lunulatus* to the oceanic process, the Blob, in Bahía Tortugas, Baja California Sur, Mexico. Environ. Biol. Fish. 108, 1677–1686. https://doi.org/10.1007/s10641-025-01709-4.

Matich, P., Heithaus, M.R., Layman, C.A., 2011. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J. Anim. Ecol. 80, 294–305. https://doi.org/10.1111/j.1365-2656.2010.01753.x.

Matich, P., Ault, J.S., Boucek, R.E., Bryan, D.R., Gastrich, K.R., Harvey, C.L., Heithaus, M. R., Kiszka, J.J., Paz, V., Rehage, J.S., Rosenblatt, A.E., 2017a. Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. Limnol. Oceanogr. 62, 934–953. https://doi.org/10.1002/lno.10477.

Matich, P., Kiszka, J.J., Mourier, J., Planes, S., Heithaus, M.R., 2017b. Species co-occurrence affects the trophic interactions of two juvenile reef shark species in tropical lagoon nurseries in Moorea (French Polynesia). Mar. Environ. Res. 127, 84–91. https://doi.org/10.1016/j.marenvres.2017.03.010.

Matich, P., Kiszka, J.J., Heithaus, M.R., Le Bourg, B., Mourier, J., 2019. Inter-individual differences in ontogenetic trophic shifts among three marine predators. Oecologia 189, 621–636. https://doi.org/10.1007/s00442-019-04357-5.

Michener, R.H., Kaufman, L., 2007. Stable isotopes ratios as tracers in marine food webs: an update. In: Michener, R., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing, Malden, USA, pp. 238–282. https://doi.org/10.1002/9780470691854.ch9.

Mill, A.C., Pinnegar, J.K., Polunin, N.V.C., 2007. Explaining isotope trophic-step fractionation: why herbivorous fish are different. Funct. Ecol. 21, 1137–1145. https://doi.org/10.1111/j.1365-2435.2007.01330.x.

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

Munroe, S.E., Rigby, C.L., Hussey, N.E., 2020. Evidence for inter-and intraspecific trophic niche separation among deepwater elasmobranchs on the southern Great Barrier Reef, Australia. Mar. Ecol. Prog. Ser. 636, 107–121. https://doi.org/10.3354/meps13221.

Murillo-Cisneros, D.A., O'Hara, T.M., Castellini, J.M., Sánchez-González, A., Elorriaga-Verplancken, F.R., Marmolejo-Rodríguez, A.J., Marín-Enríquez, E., Galván-Magaña, F., 2018. Mercury concentrations in three ray species from the Pacific Coast of Baja California Sur, Mexico: variations by tissue type, sex and length. Mar. Pollut. Bull. 126, 77–85. https://doi.org/10.1016/j.marpolbul.2017.10.060.

Murillo-Cisneros, D.A., O'Hara, T.M., Elorriaga-Verplancken, F.R., Sánchez-González, A., Marín-Enríquez, E., Marmolejo-Rodríguez, A.J., Galván-Magaña, F., 2019. Trophic structure and biomagnification of total mercury in ray species within a benthic food web. Arch. Environ. Contam. Toxicol. 77, 321–329. https://doi.org/10.1007/s00244-019-00632-x.

Newman, S.P., Handy, R.D., Gruber, S.H., 2012. Ontogenetic diet shifts and prey selection in nursery bound lemon sharks, *Negaprion brevirostris*, indicate a flexible foraging tactic. Environ. Biol. Fish. 95, 115–126. https://doi.org/10.1007/s10641-011-9828-9.

Niella, Y., Raoult, V., Gaston, T., Peddemors, V.M., Harcourt, R., Smoothey, A.F., 2021. Overcoming multi-year impacts of maternal isotope signatures using multi-tracers and fast turnover tissues in juvenile sharks. Chemosphere 269, 129393. https://doi.org/10.1016/j.chemosphere.2020.129393.

Nielsen, J., Christiansen, J.S., Grønkjær, P., Bushnell, P., Steffensen, J.F., Kiilerich, H.O., Præbel, K., Hedeholm, R., 2019. Greenland shark (*Somniosus microcephalus*) stomach contents and stable isotope values reveal an ontogenetic dietary shift. Front. Mar. Sci. 6, 125. https://doi.org/10.3389/fmars.2019.00125.

Olson, R.J., Young, J.W., Ménard, F., Potier, M., Allain, V., Goni, N., Logan, J.M., Galván-Magaña, F., 2016. Bioenergetics, trophic ecology, and niche separation of tunas. In: Curry, B.E., Fuiman, L.A., Young, C.M., Gooday, A.J., Shumway (Eds.), Advances in Marine Biology, vol. 74. Academic Press, London, United Kingdom, pp. 199–344. https://doi.org/10.1016/bs.amb.2016.06.002.

O'Brien, S.M., Gallucci, V.F., Hauser, L., 2013. Effects of species biology on the historical demography of sharks and their implications for likely consequences of contemporary climate change. Conserv. Genet. 14, 125–144. https://doi.org/10.1007/s10592-012-0437-8.

Park, H.J., Park, T.H., Lee, C.I., Kang, C.K., 2018. Ontogenetic shifts in diet and trophic position of walleye pollock, *Theragra chalcogramma*, in the western East Sea (Japan Sea) revealed by stable isotope and stomach content analyses. Fish. Res. 204, 297–304. https://doi.org/10.1016/j.fishres.2018.03.006.

Petalas, C., Lazarus, T., Lavoie, R.A., Elliott, K.H., Guigueno, M.F., 2021. Foraging niche partitioning in sympatric seabird populations. Sci. Rep. 11, 2493. https://doi.org/10.1038/s41598-021-81583-z.

Pfleger, M.O., Grubbs, R.D., Cotton, C.F., Daly-Engel, T.S., 2018. *Squalus clarkae* sp. Nov., a new dogfish shark from the Northwest Atlantic and Gulf of Mexico, with comments on the *Squalus mitsukurii* species complex. Zootaxa 4444, 101–119. https://doi.org/10.11646/zootaxa.4444.2.1.

Pianka, E.R., 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. 71, 2141–2145. https://doi.org/10.1073/pnas.71.5.2141.

Pierce, G.J., Boyle, P.R., 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanogr. Mar. Biol. Annu. Rev. 29, 409–486.

Pinkas, L.M., Oliphant, S., Iverson, I.L.K., 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. Fish. Bull. 152, 1–105.

Planque, Y., Spitz, J., Authier, M., Guillou, G., Vincent, C., Caurant, F., 2021. Trophic niche overlap between sympatric harbour seals (*Phoca vitulina*) and grey seals

(*Halichoerus grypus*) at the southern limit of their European range (Eastern English Channel). Ecol. Evol. 11, 10004–10025. https://doi.org/10.1002/ece3.7739.

Pool, T., Holtgrieve, G., Elliott, V., McCann, K., McMeans, B., Rooney, N., Smits, A., Phanara, T., Cooperman, M., Clark, S., Phen, C., Chhuoy, S., 2017. Seasonal increases in fish trophic niche plasticity within a flood-pulse river ecosystem (Tonle Sap Lake, Cambodia). Ecosphere 8, e01881. https://doi.org/10.1002/ecs2.1881.

Posada, D., 2008. jModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25, 1253–1256. https://doi.org/10.1093/molbev/msn083.

R Core Team, 2024. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Randhawa, H.S., Poulin, R., Krkošek, M., 2015. Increasing rate of species discovery in sharks coincides with sharp population declines: implications for biodiversity. Ecography 38, 96–107. https://doi.org/10.1111/ecog.00793.

Raoult, V., Gaston, T.F., Williamson, J.E., 2015. Not all sawsharks are equal: species of co-existing sawsharks show plasticity in trophic consumption both within and between species. Can. J. Fish. Aquat. Sci. 72, 1769–1775. https://doi.org/10.1139/cjfas-2015-0307.

Reid, S.B., Hirota, J., Young, R.E., Hallacher, L.E., 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. Mar. Biol. 109, 427–440. https://doi.org/10.1007/BF01313508.

Rivaton, J., Bourret, P., 1999. Les otolithes des poissons de l'Indo-Pacifique. Documents Scientifiques Et Techniques II 2. IRD, Nouméa, New Caledonia.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180.

Sardenne, F., Hollanda, S., Lawrence, S., Albert-Arrisol, R., Degroote, M., Bodin, N., 2017. Trophic structures in tropical marine ecosystems: a comparative investigation using three different ecological tracers. Ecol. Indic. 81, 315–324. https://doi.org/10.1016/j.ecolind.2017.06.001.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27–39. https://doi.org/10.1126/science.185.4145.27.

Sims, D.W., 2005. Differences in habitat selection and reproductive strategies of male and female sharks. In: Ruckstuhl, K.E., Neuhaus, P. (Eds.), Sexual Segregation in Vertebrates. Campbridge University Press, Cambridge, UK, pp. 127–147. https://doi.org/10.1017/CBO9780511525629.009.

Smith, M.M., Heemstra, P.C., 1986. Smiths' Sea Fishes. Springer-Verlag, Berlin, Germany.

Spitz, J., Cherel, Y., Bertin, S., Kiszka, J., Dewez, A., Ridoux, V., 2011. Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. Deep Sea Res. Oceanogr. Res. Pap. 58, 273–282. https://doi.org/10.1016/j.dsr.2010.12.009.

Spitz, J., Chouvelon, T., Cardinaud, M., Kostecki, C., Lorance, P., 2013. Prey preferences of adult sea bass *Dicentrarchus labrax* in the northeastern Atlantic: implications for bycatch of common dolphin *Delphinus delphis*. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 70, 452–461. https://doi.org/10.1093/icesjms/fss200.

Stevens, J.D., 1973. Stomach contents of the blue shark (*Prionace glauca* L.) off south-west England. J. Mar. Biol. Assoc. U. K. 53, 357–361. https://doi.org/10.1017/S0025315400022323.

Stewart, J.D., Rohner, C.A., Araujo, G., Avila, J., Fernando, D., Forsberg, K., Ponzo, A., Rambahiniarison, J.M., Kurle, C.M., Semmens, B.X., 2017. Trophic overlap in mobulid rays: insights from stable isotope analysis. Mar. Ecol. Prog. Ser. 580, 131–151. https://doi.org/10.3354/meps12304.

Straube, N., Kriwet, J., Schliewen, U.K., 2011. Cryptic diversity and species assignment of large lantern sharks of the *Etmopterus spinax* clade from the Southern Hemisphere (Squaliformes, Etmopteridae). Zool. Scr. 40, 61–75. https://doi.org/10.1111/j.1463-6409.2010.00455.x.

Thomas, S.M., Crowther, T.W., 2015. Predicting rates of isotopic turnover across the animal kingdom: a synthesis of existing data. J. Anim. Ecol. 84, 861–870. https://doi.org/10.1111/1365-2656.12326.

Trystram, C., Rogers, K.M., Soria, M., Jaquemet, S., 2017. Feeding patterns of two sympatric shark predators in coastal ecosystems of an oceanic island. Can. J. Fish. Aquat. Sci. 74, 216–227. https://doi.org/10.1139/cjfas-2016-0105.

Valls, M., Rueda, L., Quetglas, A., 2017. Feeding strategies and resource partitioning among elasmobranchs and cephalopods in Mediterranean deep-sea ecosystems. Deep Sea Res. Oceanogr. Res. Pap. 128, 28–41. https://doi.org/10.1016/j.dsr.2017.09.002.

Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. 46, 2061–2066. https://doi.org/10.4319/lo.2001.46.8.2061.

Vander Zanden, H.B., Bjorndal, K.A., Reich, K.J., Bolten, A.B., 2010. Individual specialists in a generalist population: results from a long-term stable isotope series. Biol. Lett. 6, 711–714. https://doi.org/10.1098/rsbl.2010.0124.

Veríssimo, A., Cotton, C.F., Buch, R.H., Guallart, J., Burgess, G.H., 2014. Species diversity of the deep-water gulper sharks (Squaliformes: centrophoridae: *centrophorus*) in North Atlantic waters-current status and taxonomic issues. Zool. J. Linn. Soc. 172, 803–830. https://doi.org/10.1111/zoj.12194.

Veríssimo, A., Zaera-Perez, D., Leslie, R., Iglésias, S.P., Séret, B., Grigoriou, P., Sterioti, A., Gubili, C., Barría, C., Duffy, C., Hernández, S., Batjakas, I.E., Griffiths, A. M., 2017. Molecular diversity and distribution of eastern Atlantic and Mediterranean dogfishes *Squalus* highlight taxonomic issues in the genus. Zool. Scr. 46, 414–428. https://doi.org/10.1111/zsc.12224.

Viana, S.T.F., de Carvalho, M.R., 2016. Redescription of *Squalus acutipinnis* Regan, 1908, a valid species of spiny dogfish from Southern Africa (Chondrichthyes: squaliformes: squalidae). Copeia 104, 539–553. https://doi.org/10.1643/CI-14-217.

Viana, S.T.F.L., Lisher, M.W., de Carvalho, M.R., 2018. Two new species of short-snouted dogfish sharks of the genus *Squalus* Linnaeus, 1758, from southern Africa (Chondrichthyes: squaliformes: squalidae). Mar. Biodivers. 48, 1787–1814. https://doi.org/10.1007/s12526-017-0673-8.

Vipin, P.M., Ravi, R., Fernandez, T.J., Pradeep, K., Boopendranath, M.R., Remesan, M.P., 2012. Distribution of myctophid resources in the Indian Ocean. Rev. Fish Biol. Fish. 22, 423–436. https://doi.org/10.1007/s11160-011-9244-4.

Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R., Hebert, P.D.N., 2005. DNA barcoding Australia's fish species. Phil. Trans. Biol. Sci. 360, 1847–1857. https://doi.org/10.1098/rstb.2005.1716.

Wetherbee, B.M., Cortés, E., Bizzarro, J.J., 2012. Food consumption and feeding habits. In: Cortés, E., Brooks, E.N., Gedamke, T., Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Biology of Sharks and their Relatives. CRC Press, Boca Raton, USA, pp. 239–264.

White, W.T., Ebert, D.A., Compagno, L.J., 2008. Description of two new species of gulper sharks, genus *Centrophorus* (Chondrichthyes: squaliformes: centrophoridae) from Australia. Descriptions of New Australian Chondrichthyans. CSIRO Mar. Atmospher. Res. Paper 22, 1–21.

Yano, T., Hattori, T., Tamukai, T., Ohshimo, S., 2017. Body-length frequency and spatial segregation of the North Pacific spiny dogfish *Squalus suckleyi* in Tsugaru Strait, northern Japan. Fish. Sci. 83, 917–928. https://doi.org/10.1007/s12562-017-1127-8.

Ziadi-Künzli, F., Soliman, T., Imai, H., Sakurai, M., Maeda, K., Tachihara, K., 2020. Re-evaluation of deep-sea dogfishes (genus *Squalus*) in Japan using phylogenetic inference. Deep Sea Res. Oceanogr. Res. Pap. 160, 103261. https://doi.org/10.1016/j.dsr.2020.103261.