Resource use by *Sphyrna mokarran* and *S. lewini* (Chondrichthyes) neonates and juveniles in the western Arabian Gulf: a stable isotope analysis

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ABSTRACT: The great hammerhead shark *Sphyrna mokarran* and the scalloped hammerhead shark *S. lewini* are marine top predators with global distributions. However, limited information is available on the trophic ecology of hammerhead sharks in the Indian Ocean. In this study, we measured stable nitrogen and carbon isotopes in the muscle tissues of neonates and juveniles of *S. mokarran* and *S. lewini* from the waters of the western Arabian Gulf. In general, values of $\delta^{15}N$ were lower in *S. mokarran* (10.8—18.7‰) than in *S. lewini* (12.2—18.7‰), indicating a reliance on food sources with low nitrogen values. Isotopic niche similarities were observed between female and male *S. mokarran*. We further observed considerable ontogenetic changes in the $\delta^{15}N$ values of both *S. mokarran* and *S. lewini* neonates (a reduction from 19 to 12‰), reflecting the maternal effect. The effects of total length and sex on the nitrogen and stable isotope values were nonsignificant in *S. mokarran* juveniles. The western Arabian Gulf likely serves as a key feeding ground for both the neonates and the juveniles of *S. mokarran*. By contrast, *S. lewini* appears to have a low level of reliance on this region.

KEY WORDS: Hammerhead shark · *Sphyrna* · Arabian Gulf · Trophic ecology · $\delta^{15}N$ · $\delta^{13}C$

1. INTRODUCTION

The great hammerhead shark *Sphyrna mokarran* (Rüppell, 1837) is the largest species of hammerhead shark, with a maximum total length of 6 m (Compagno 1984, Ebert et al. 2013) and a maximum reported lifespan of 45 yr (Piercy et al. 2010, Tovar-Ávila & Gallegos-Camacho 2014). This species is found in tropical and temperate waters worldwide, and it inhabits coastal areas along the continental shelf (Compagno

1984). *S. mokarran* exhibits nomadic and migratory behaviours; it engages in large-scale, long-distance migrations and exhibits seasonal residency, site fidelity, and extensive international movements (Compagno 1984, Hammerschlag et al. 2011, Guttridge et al. 2017, Gallagher & Klimley 2018). As apex predators, large *S. mokarran* primarily consume other sharks and rays (Raoult et al. 2019). In the Arabian Gulf (also known as the Persian Gulf), *S. mokarran* neonates predominantly feed on teleosts (e.g. flathead fishes of

the family Platycephalidae), shifting to feeding on eagle rays (family: Myliobatidae) as they mature (Hsu et al. 2022a).

The scalloped hammerhead shark *Sphyrna lewini* (Griffith & Smith, 1834) is another large hammerhead species, with a maximum total length of >4 m (Froese & Pauly 2023) and a maximum reported lifespan of 15 yr (Liu & Chen 1999). This species is found in tropical and warm temperate waters worldwide (Compagno 1984, Ebert et al. 2013). It exhibits complex spatial usage patterns associated with both coastal and oceanic habitats (Estupiñán-Montaño et al. 2021). *S. lewini* is highly mobile and has diverse migratory patterns (Compagno 1984). Female *S. lewini* utilise various habitats throughout their life, whereas male sharks alternate between coastal and pelagic migratory patterns, either remaining near-shore throughout their life or migrating offshore before returning to coastal habitats (Coiraton et al. 2020). As a tertiary consumer, *S. lewini* exhibits considerable trophic plasticity and feeds on various prey items, including bony fishes, crustaceans, and cephalopods (Torres-Rojas et al. 2010, Rojas et al. 2014).

Both *S. mokarran* and *S. lewini* have experienced population declines (Noriega et al. 2011, Pérez-Jiménez 2014, Ayres et al. 2024). Because they are targeted or bycatch species, *S. mokarran* and *S. lewini* face major threats from fisheries exploitation (Bezerra et al. 2016, Guzman et al. 2020). Given their longevity and slow growth rates (Liu & Chen 1999, Harry et al. 2011, Drew et al. 2015, Hsu et al. 2021), both species have been classified as Critically Endangered on the International Union for Conservation of Nature Red List of Threatened Species (Rigby et al. 2019a,b). Although *S. lewini* has been extensively studied, considerable gaps remain in the knowledge regarding hammerhead sharks, particularly regarding the trophic ecology of *S. mokarran* (Gallagher & Klimley 2018).

Stable isotopes can serve as effective ecological tracers for investigating diet, trophic position, and movement as well as broader questions regarding community dynamics and feeding strategies among aquatic organisms (Hussey et al. 2012, Shipley & Matich 2020). The most common elements used in studies on diet and trophic structure are carbon and nitrogen, which are typically expressed as the ratios $\delta^{15}N$ ($^{15}N/^{14}N$) and $\delta^{13}C$ ($^{13}C/^{12}C$), respectively. These ratios provide insights into the dietary niche and habitat history of consumers (Shiffman et al. 2012). Stable isotope data can also help with constructing an isotopic niche, that is, a multivariate space defined by isotopic values, to elucidate ecological shifts (Newsome

et al. 2007). Furthermore, isotopes in neonates can reflect the maternal diet and foraging locations because neonates rely on maternal energy stores, such as the yolk and placenta (Hussey et al. 2010, Olin et al. 2011).

To date, stable isotope analysis has predominantly been used to investigate *S. lewini* (Arnés-Urgellés et al. 2021, Cerutti-Pereyra et al. 2022). Few studies have focused on *S. mokarran*, and each of the studies that have done so analysed fewer than 30 individuals (Rumbold et al. 2014, Raoult et al. 2019, Peterson et al. 2020, Lubitz et al. 2023). Furthermore, the Indian Ocean has been much less studied (Ducatez 2019), resulting in a lack of isotope data for *S. mokarran* in this area. In this study, we measured stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) in the muscle tissues of neonate and juvenile *S. mokarran* and *S. lewini* from the western Arabian Gulf, which is part of the Indian Ocean. Because the sample size was only sufficient for *S. mokarran* (n = 73), we tested the following hypotheses. (1) No between-sex differences in isotopic niche are present in *S. mokarran* juveniles. (2) *S. mokarran* juveniles do not exhibit any ontogenetic changes in isotopic niche as they mature.

2. MATERIALS AND METHODS

2.1. Sample collection

Between April 2016 and November 2020, we collected 73 *Sphyrna mokarran* samples (5 neonates; 39 female and 29 male juveniles) and 10 *S. lewini* samples (7 neonates; 1 female and 2 male juveniles) from the Jubail fish market, Eastern Province, Saudi Arabia (27° 00' 08.6" N, 49° 40' 18.7" E). Neonates were identified by open umbilical scars, and all specimens were immature juveniles (Hsu et al. 2021, 2022b). The specimens were caught by commercial fishing vessels operating in Saudi Arabian waters of the Arabian Gulf by using gillnets, longlines, trolls, and handlines, with gillnets being the predominant gear (Hsu et al. 2022b). Precaudal length, fork length, and total length were measured to the nearest 0.1 cm. Total somatic weight was measured to the nearest 0.01 kg.

2.2. Stable isotope measurement

We referenced Bond & Hobson (2012) for the terminology of stable isotope ratios. Approximately 10 g of muscle samples were extracted from the dorsal ante-

rior part of the shark body to measure the values of $\delta^{13}C$ and $\delta^{15}N$. The samples were dried at 70°C, ground to a fine powder, and transported to the Laboratorio de Biogeoquímica de Isótopos Estables, Instituto Andaluz de Ciencias de la Tierra (CSIC-UGR, Granada, Spain) for analysis. The transportation of samples was facilitated by CITES Export Permits issued by the Kingdom of Saudi Arabia (permit numbers: 19-SA-0010008-PD—19-SA-0010015-PD) and Spain (permit numbers: ES-MA-00001-19P and ES-MA-00002-19P).

The samples were exposed to chloride vapours overnight to eliminate inorganic carbon. Organic matter was then analysed for its isotopic composition by using a Carlo Erba NC1500 elemental analyser connected to a Delta Plus XP mass spectrometer (EA-IRMS; Thermo-Finnigan). Commercial CO_2 and N_2 were used as internal standards for the carbon and nitrogen isotopic analyses, respectively. Internal standards for $\delta^{13}C$ were set at −30.63 and −11.65‰ (Vienna Peedee belemnite), and those for $\delta^{15}N$ were set at −1.02 and +16.01‰ (air). Reference gases and in-house standards (with different C:N ratios and isotopic composition) were calibrated against international reference materials for carbon (USGS-24 and IAEA-C6) and nitrogen (IAEA-N1, IAEA-N2, and IAEA-N3). The precision, calculated after adjustment for the daily drift of the mass spectrometer and systematic incorporation of standards in analytical batches, was higher than ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.

The isotopic composition is reported in terms of δ‰, which were calculated as follows:

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

where $R = {}^{13}C/{}^{12}C$ for $\delta^{13}C$ and ${}^{15}N/{}^{14}N$ for $\delta^{15}N$.

Although urea and lipid treatments are often recommended for isotope analysis (Li et al. 2016, Carlisle et al. 2017, Bennett-Williams et al. 2022), neither was performed for the muscle samples in the current study, which followed the precedent set by Lubitz et al. (2023). Only 3 samples had a C:N ratio of >3.5, indicating that lipid extraction was unnecessary (Post et al. 2007). Urea treatment has been demonstrated to increase $\delta^{15}N$ in the muscle tissue of elasmobranchs (Carlisle et al. 2017, Crook et al. 2019, Bennett-Williams et al. 2022). Hence, we used the equation ($\delta^{15}N_{\text{treated}} = 0.984 \times \delta^{15}N_{\text{untreated}} + 2.063$; $R^2 = 0.89$) to convert the untreated-sample values to treated-sample values, which are reported alongside the untreated-sample values to facilitate comparison with other studies on *S. mokarran* (Peterson et al. 2020, Lubitz et al. 2023). For $\delta^{13}C$, we present the untreated

Table 1. Sample size (N) and mean ± SD and range of total length (L_T), total somatic weight (W_T), $\delta^{15}N$ (subscript $_U$ indicates values from samples without urea treatment and $_{TR}$ indicates estimated values for urea-treated samples based on the formula proposed by Li et al. 2016) and $\delta^{13}C$ value (‰) and C:N ratio of *Sphyrna mokarran* and *S. lewini* by sex (neonate, female, and male) from Saudi Arabian waters in the western Arabian Gulf

	N	L_T (cm)		W_T (kg)		$\delta^{15}N_U$		$\delta^{15}N_{TR}$		$\delta^{13}C$		C:N	
		Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range
S. mokarran													
Neonate	5	81.5±9.8	74.0–98.0	1.94±0.51	1.38–2.71	13.3±2.6	10.8–17.6	15.2±2.6	12.7–19.4	−14.3±0.8	−15.6 to −13.7	3.13±0.12	3.01–3.33
Female	39	144.9±32.9	104.0–236.0	15.35±13.69	4.65–65.00	11.8±1.2	9.9–18.2	13.7±1.2	11.8–20.0	−14.6±1.1	−16.3 to −11.1	3.18±0.27	2.87–4.56
Male	29	143.8±32.4	103.0–211.0	14.64±10.94	4.50–48.00	11.6±0.6	10.6–12.7	13.5±0.6	12.5–14.6	−14.3±1.2	−16.4 to −11.6	3.11±0.21	2.81–3.92
S. lewini													
Neonate	7	54.2±2.9	50.6–60.0	0.61±0.12	0.49–0.82	15.7±2.0	12.5–18.7	17.5±2.0	14.4–20.5	−15.1±1.0	−16.2 to −13.6	3.29±0.27	2.84–3.71
Female	1	88.8		3.81		11.8		13.7		−14.47		3.09	
Male	2	131.8±66.1	85.0–178.5	14.86±17.18	2.71–27.00	13.1±1.3	12.2–14.0	14.9±1.3	14.1–15.8	−14.5±0.2	−14.7 to −14.4	3.21±0.02	3.20–3.23

sample values because a study reported that lipid/ urea treatment led to minimal variations in $\delta^{13}C$ (approximately 0‰) in the muscle tissue of elasmobranchs (Bennett-Williams et al. 2022).

2.3. Statistical analysis

Only *S. mokarran* had a sufficient sample size, and therefore, only this species was included in the statistical analysis. The 95% confidence interval region on the $\delta^{15}N$ and $\delta^{13}C$ biplot was determined using the 'cov.mve' function in the R package 'MASS' (Venables & Ripley 2002). Between-group isotopic niche partitioning was indicated by nonoverlapping 95% confidence interval regions. For juveniles, a log-linear model with a Gaussian likelihood function was used to measure the effects of sex and total length on $\delta^{15}N$ and $\delta^{13}C$, which were log-transformed to approximate Gaussian distribution values. Between-sex overlap in 95% confidence intervals was calculated using the 'overlap' function in the R package 'niche-ROVER' (Lysy et al. 2023) with 5000 iterations. All computations were performed using R (version 4.2.1; R Core Team 2022).

3. RESULTS

The total lengths of the *Sphyrna mokarran* neonates ranged from 74.0 to 98.0 cm, whereas those of the *S. mokarran* juveniles ranged from 103.0 to 236.0 cm (Table 1). The total lengths of the *S. lewini* neonates ranged from 50.6 to 60.0 cm, whereas those of the *S. lewini* juveniles ranged from 85.0 to 178.5 cm (Table 1). The *S. mokarran* samples predominantly comprised juveniles (93%; n = 68/73), whereas the *S. lewini* samples predominantly comprised neonates (70%; n = 7/10). For both species, the $\delta^{15}N$ values were higher in neonates than in juveniles, whereas the $\delta^{13}C$ values were similar between neonates and juveniles. Furthermore, the $\delta^{15}N$ values were lower in *S. mokarran* juveniles (11.8 ± 1.0‰, ±SE) than in *S. lewini* juveniles (12.7 ± 1.6‰). However, the $\delta^{13}C$ values were

similar between *S. mokarran* (−14.5 ± 1.1‰) and *S. lewini* (−14.5 ± 0.1‰). The small sample size of *S. lewini* juveniles precluded a statistical comparison of $\delta^{15}N$ and $\delta^{13}C$ between the species. The C:N ratios were generally lower than 3.5 (Table 1).

The 95% confidence interval region for female *S. mokarran* juveniles (Fig. 1a) substantially overlapped with that for male juveniles; approximately 62.5% of all female juveniles overlapped with male juveniles, and 95.3% of all male juveniles overlapped with female juveniles, indicating similar isotopic niches between the sexes. However, a few individuals exhibited extreme values; 1 female juvenile and 1 neonate of *S. mokarran* exhibited very high $\delta^{15}N$ values (>18‰ for untreated muscle tissues). Furthermore, 1 female and 1 male *S. mokarran* juvenile exhibited very high $\delta^{13}C$ values (more than −12‰; Fig. 1a).
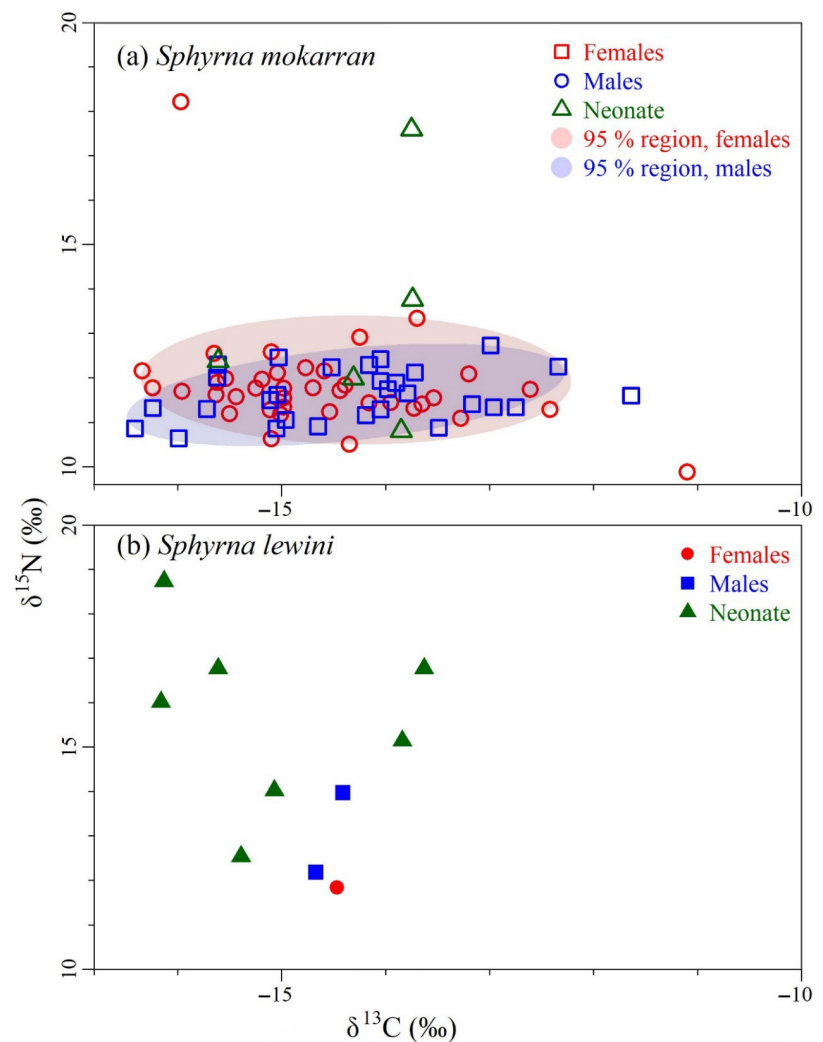

Fig. 1. Biplot of $\delta^{15}N$ and $\delta^{13}C$ in untreated muscle tissues of (a) *Sphyrna mokarran* and (b) *S. lewini*. All examined specimens were neonates or juveniles. No lipid or urea treatment was performed

$S.$ *lewini* neonates generally exhibited high $\delta^{15}N$ values (Fig. 1b).

Both species exhibited prominent ontogenetic changes in the $\delta^{15}N$ value (Fig. 2a). The $\delta^{15}N$ value decreased from 14 to 11‰ as the total length increased from 70 to 100 cm. As individuals became juveniles, the $\delta^{15}N$ value stabilised at approximately 11−12‰; the $\delta^{15}N$ values of the female juveniles mixed with those of the male juveniles. The *S. lewini* neonates also experienced a decrease in $\delta^{15}N$ values as they grew from 50 to 60 cm in total length, with $\delta^{15}N$ values of *S. lewini* juveniles indistinguishable from those of the *S. mokarran* juveniles (Fig. 2b). The log-linear model revealed no significant effect of total length or sex on the $\delta^{15}N$ values of the *S. mokarran* juveniles (log-linear model, p = 0.053 and 0.410, respectively; Table 2).

No between-species, between-sex, or between-developmental-stage pattern was observed in the $\delta^{13}C$ values (Fig. 2b). The effects of total length and sex on the $\delta^{13}C$ values of *S. mokarran* juveniles were nonsignificant (p = 0.103 and 0.286, respectively; Table 2).

4. DISCUSSION

In this study, we elucidated the trophic ecology of 2 large hammerhead shark species, *Sphyrna mokarran* and *S. lewini*, by measuring $\delta^{15}N$ and $\delta^{13}C$ in their muscle tissues. This study improves the understanding of *S. mokarran*, offering insights into the effects of sex, total length, and developmental stage on resource utilisation by this species.

Sex exerted no significant effect on the $\delta^{15}N$ and $\delta^{15}C$ values of the *S. mokarran* juveniles: no between-sex difference was noted in feeding patterns or habitat use. This finding differs from the sexual segregation observed by Klimley (1987) in *S. lewini* but is consistent with the finding of Lubitz et al. (2023), who observed no significant between-sex difference in *S. lewini* from eastern Australian waters. Female *S. lewini* move offshore at smaller sizes than
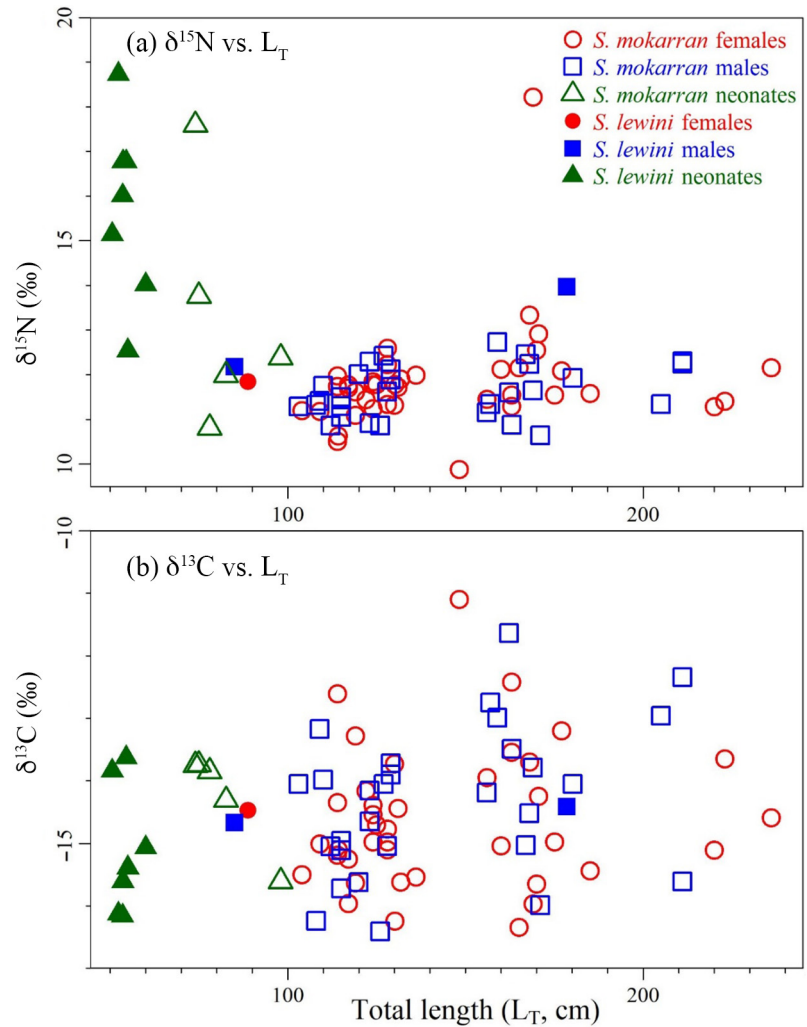

Fig. 2. Effects of total length (L_T) on (a) $\delta^{15}N$ and (b) $\delta^{13}C$ of juvenile and neonate hammerhead sharks

Table 2. Estimates, standard errors (SE), and corresponding p-values for the logarithm of $\delta^{15}N$ and $\delta^{13}C$ values of *Sphyrna mokarran* juveniles as the response variable and the total length and sex (female as the reference level). Neonates were removed from modelling to avoid the interference from the maternal effect

Response variable	Covariate	Estimate	SE	p
$\delta^{15}N$	Total length	5.47×10^{-4}	2.77×10^{-4}	0.053
	Sex	-1.49×10^{-2}	1.80×10^{-2}	0.410
$\delta^{13}C$	Total length	1.25×10^{-3}	7.56×10^{-4}	0.103
	Sex	5.30×10^{-2}	4.92×10^{-2}	0.286

do their male counterparts, forming schools composed primarily of intermediate-sized females (Klimley 1987). Sexual segregation can be also observed on the basis of isotopic profiles: male *S. lewini* from the eastern tropical Pacific Ocean exhibit reduced hab-

itat use and less varied movement patterns compared with females (Estupiñán-Montaño et al. 2021). That study suggested that sexual segregation is not a universal trait in *Sphyrna* spp. and varies depending on species, developmental stage, and geographic region.

In our study, the $\delta^{15}N$ values for untreated muscle tissues of *S. mokarran* juveniles from the Arabian Gulf ranged from 11.6 to 11.8‰ (Table 1), which closely align with the mean value for untreated muscle tissues of *S. mokarran* juveniles from eastern Australia (11.4‰) (Lubitz et al. 2023). This consistency suggests similar feeding patterns between *S. mokarran* populations in the Arabian Gulf and eastern Australia, despite limited gene flow and movement between these regions (Brunjes et al. 2024). Dietary analysis indicated that *S. mokarran* juveniles in the western Arabian Gulf predominantly consume bony fish and shift to consuming eagle rays as they mature (Hsu et al. 2022a). *S. mokarran* juveniles mostly consume the bartail flathead *Platycephalus indicus* (Linnaeus, 1758); in addition, they consume cephalopods, crustaceans, and bivalve molluscs (Hsu et al. 2022a).

A prominent maternal effect was observed in the $\delta^{15}N$ values of both *S. mokarran* and *S. lewini* neonates. This effect results from a shift from yolk to placental feeding before neonates develop effective foraging skills (Hussey et al. 2010) and is widely observed across *Sphyrna* spp. (Olin et al. 2018). Although muscle tissue exhibits a slower isotopic turnover than do liver tissue and blood (Logan & Lutcavage 2010, Niella et al. 2021), considerable changes occur in both $\delta^{15}N$ and $\delta^{13}C$ at 30 d after a shift to isotope-depleted diets (Logan & Lutcavage 2010). The total length at which the maternal effect was observed was approximately 70—100 cm, which corresponded to 40—137 d, in *S. mokarran* (Hsu et al. 2021), and 60 cm, which corresponded to approximately 50 d, in *S. lewini* (Chen et al. 1990). These durations are sufficient to reflect a shift in energy sources for neonates (Hussey et al. 2010, Olin et al. 2018).

This study has 2 major implications for the conservation of threatened hammerhead shark species. First, nearshore shallow waters, where hammerhead sharks face the highest risk of extinction (Dulvy et al. 2021), are key habitats of shark prey serving as carbon sources. Our findings of elevated $\delta^{13}C$ values in some *S. mokarran* individuals indicate the use of these nearshore shallow waters as feeding grounds (Roemer et al. 2016). Second, the $\delta^{13}C$ values indicated that *S. mokarran* exhibits a higher degree of dependence on the shallow waters of the western Arabian Gulf (maximum depth: approximately 50 m), using it as a feeding ground for both neonates and juveniles, than does *S. lewini*. This finding is supported by the fact that *S. mokarran* individuals were sighted 10 times more often than *S. lewini* individuals were (111 vs. 11 times, respectively) during 135 visits to the main fishing landing site in the western Arabian Gulf over a 4 yr period (Hsu et al. 2022b).

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