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# Unravelling the trophic ecology of poorly studied and threatened elasmobranchs inhabiting the Persian Gulf and Gulf of Oman

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### Abstract

Elasmobranch population declines due to human impacts have been documented at a global scale, having impacts on the functioning and structure of marine ecosystems. This situation leads to an international focus on the conservation of their populations and a key step in the management and conservation of elasmobranch populations is to understand their trophic ecology. Here, by using stable isotopes analysis, we investigated the trophic relationships, trophic niche breadth, and trophic redundancy among 21 batoids and 12 sharks inhabiting the Persian Gulf and Gulf of Oman, two productive areas of the Arabian Sea considered global elasmobranch hotspots. Isotopic results revealed differences in the trophic niche and trophic position among the elasmobranch sampled at species and at family level. For example, the batoids of the family Torpedinidae and the sharks of the family Triakidae occupied higher trophic positions and the family Glaucostegidae showed a lower trophic niche width, whereas the batoids of the family Myliobatidae or Gymnuridae, in overall, showed lower higher trophic niche width, reflecting the trophic habits described for most of the sampled species. We also provided some insights into the ecology of poorly known species, especially relevant for those that are endangered at a global or regional scale. In conclusion, we provide new information about the trophic ecology among batoids and sharks inhabiting the Persian Gulf and Gulf of Oman. This information is highly useful to study the consequences of future changes on their feeding preferences due to natural or human-related factors.

Keywords Elasmobranchs  $\cdot$  Food-web  $\cdot$  Marine predators  $\cdot$  Marine ecosystems  $\cdot$  Conservation biology  $\cdot$  Rays  $\cdot$  Stable isotopes  $\cdot$  Sharks  $\cdot$  Skates  $\cdot$  Trophic ecology

# Introduction

Elasmobranchs (sharks and batoids) are important top and mesopredators in marine ecosystems, being considered keystone species because of their ecological role in marine food webs (Baum and Worm 2009; Cortes 1999; Wetherbee and Cortés 2004). However, population declines of these species have been documented worldwide due to several human impacts such as fisheries or habitat degradation,

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☑ Joan Navarro joan@icm.csic.es having impacts on the functioning and structure of marine ecosystems (Baum 2003; Dulvy et al. 2014, 2008; Ferretti et al. 2010; Stevens 2000). For example, the decrease of large-sized sharks decreases the mortality of their main prey, contributing to variations in the abundance of other less competitive mesopredators (Ferretti et al. 2010) or affecting the numbers of primary consumers (Ruppert et al. 2013). This global situation leads to an international focus on the conservation of their populations, given the importance they have at the ecosystem level (Dulvy et al. 2014; Ferretti et al. 2010; Moore and Grubbs 2019; Myers et al. 2007; Worm et al. 2013).

A key step in the management and conservation of elasmobranch populations is to understand their trophic niche and trophic interactions (Barría et al. 2015; Navia et al. 2017; Papastamatiou et al. 2006; Vidal et al. 2023). This information is required to predict the potential consequences of natural or human-related changes in the availability of particular prey for a particular elasmobranch species (Bascompte et al.

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2005; Coll et al. 2013; Dulvy et al. 2014; Simpfendorfer et al. 2001). For example, knowing the ecological interactions among ecologically similar elasmobranchs is fundamental for understanding how these species could coexist in the same ecosystem (Albo-Puigserver et al. 2015; Navia et al. 2017). Furthermore, understanding the trophic interactions amongst elasmobranch species could also allow for the pairwise comparison of species as ecologically similar or distinct (Matich et al. 2011). Based on the principle of competitive exclusion, predators occupying equivalent ecological niches are expected to be segregated (Pianka 2000). However, related species do occasionally coexist in the same ecosystems if there is no limitation on prey availability (e.g. Albo-Puigserver et al. 2015; Navia et al. 2017). Trophic niche partitioning by prey or habitat has been indicated as the central mechanism explaining the presence of sharks and batoids in the same ecosystem (Albo-Puigserver et al. 2015; Heithaus et al. 2013; Papastamatiou et al. 2006; Platell et al. 1998). Similarly, the degree of trophic specialization (*i.e.* trophic niche width) at the species level could affect the capability of this species to cope with changes in the main consumed prey, being the specialist potentially more vulnerable to anthropogenic pressures (Barbini et al. 2020; Coll et al. 2013; Gallagher et al. 2015; Isaac and Cowlishaw 2004).

The Gulf of Oman and the Persian Gulf, two adjacent productive areas of the northern part of the Arabian Sea, are considered global hotspots of marine elasmobranch diversity (Jabado et al. 2015a, b; Valinassab et al. 2006). The Arabian Sea hosts around 153 species (Jabado et al. 2015a, b) including some worldwide iconic species of the order Rhinopristiformes (sawfishes, guitarfishes, wedgefishes, and banjo rays) or endemic species such the oceallate eagle ray (Aetomylaeus milvus), the smoothtooth blacktip shark (*Carcharhinus leiodon*) or the Arabian carpetshark (Chiloscyllium arabicum) (Hsu et al. 2022; Jabado 2018; Jabado et al. 2017). Despite the high conservation value of these marine areas, many elasmobranchs inhabiting the Arabian Sea seem to be declining associated with a high fishing pressure focused on obtaining meat and fins (Hsu et al. 2022; Jabado and Spaet 2017). This intense fishing pressure in combination with other threats associated with marine pollution or habitat alterations has resulted in the population declines of most of these predators in this area (Jabado et al. 2017). From a conservation point of view, 63% of the elasmobranchs present in this area are classified as threatened species by the IUCN (International Union for the Conservation of Nature) (Hsu et al. 2022; Jabado et al. 2017). However, the research conducted on these marine predators in the Persian Gulf and the Gulf of Oman, and in general along the Arabian Sea, is very scarce (Jabado et al. 2017; Jabado et al. 2015a, b; Randall 1995; Rastgoo et al.

2018). Therefore, there is a necessity to increase the biological and ecological information of these predators inhabiting this basin, including a better understanding of their trophic habits, trophic interactions, and levels of trophic redundancy among them.

The assessment of the trophic ecology of elasmobranchs is complex, because these marine predators include diverse ecological guilds with considerable variation in diet and trophic positions both within and between species (Barría et al. 2015; Cortes 1999; Hussey et al. 2010; Kiszka et al. 2014; Raoult et al. 2015; Rastgoo et al. 2018). Also, the high frequency of empty stomachs observed in most elasmobranchs (Ehemann et al. 2019) entails a great limitation when analyzing the diet of these species by using traditional stomach content analyses (SCA) (Hyslop 1980). Moreover, SCA requires a relatively high number of individuals to quantify the diet, which could be a logistic constraint for threatened or rare species (Cortes 1999; Hyslop 1980; Navarro et al. 2014). As alternative or complementary to SCA, the analysis of the stable isotopic of carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) values, and the utilization of different isotopic metrics have been used to investigate the trophic ecology of elasmobranchs (Bird et al. 2018; Shiffman et al. 2012). Both  $\delta^{13}$ C and  $\delta^{15}$ N together provide quantitative information into the trophic niche of a particular consumer, reflecting what it assimilates from its diet and the habitat in which it forages (Bearhop et al. 2004; Newsome et al. 2007). These biomarkers are useful for investigating niche partitioning and trophic relationships between sympatric species (Gaspar et al. 2022; Giménez et al. 2018), and have been used in elasmobranchs too (Albo-Puigserver et al. 2015; Barría et al. 2015; Kiszka et al. 2014; Shiffman et al. 2019). Therefore, stable isotope approaches may provide, therefore, the necessary information to quantify the trophic niche overlap/ segregation between sympatric species and identify those drivers of trophic segregation within species.

In the present study, our main aims were to assess the trophic relationships, trophic niche breadth, and trophic redundancy among 21 batoids and 12 sharks inhabiting the Iranian waters of the Persian Gulf and Gulf of Oman. All these 33 elasmobranchs are poorly studied and commonly caught in artisanal fisheries operating in the Arabian Sea and based on the regional assessments of the IUCN, 9 of the sampled species are considered Endangered, 9 Vulnerable, 12 Near Threatened, and 1 Data Deficient (Table 1). We hypothesized that a certain niche partitioning must be occurring within this great number of species and within the basin in order to coexist. Our results will provide novel insights into the trophic relationships between different elasmobranch species and it will contribute to a better understanding of the ecological role of these elasmobranchs.

**Table 1** Sample size (n), mean  $\pm$  SD of  $\delta^{15}$ N and  $\delta^{13}$ C values, and mean of Bayesian Standard Ellipse Areas (SEA<sub>B</sub>; mean, minimum and maximums) and Bayesian trophic level (TL) for 33 elasmobranch

species (grouped by Order and Family) sampled in the Persian Gulf and Gulf of Oman (north of Arabian Sea) during 2016–2017

	п	IUCN	δ <sup>15</sup> N (‰)	δ <sup>13</sup> C (‰)	$\frac{\text{SEA}_{\text{B}} \text{ (min, max)}}{(\%^2)}$	Similar SIA to	Main prey	References
Myliobatiformes								
Family Aetobatidae <sub>b.c</sub>					3.85 (3.18-4.70)			
Aetobatus flagellum	10	EN	$12.51 \pm 0.66_{A,B,C}$	$-13.58 \pm 2.87$	1.32 (0.97–1.54)			
Aetobatus ocellatus	3	VU	9.06±0.61	$-12.45 \pm 0.82$			Gastropods, Bivalves	(Randall 1995)
Family Dasyatidae <sub>c,d</sub>					10.64 (9.71– 11.70)			
Brevitrygon walga	10	NT	$13.26 \pm 0.63_{B,C,D}$	$-15.53 \pm 1.61$	3.32 (2.49–3.88)		Crustaceans	(Rastgoo et al. 2018)
Himantura leoparda	6	VU	$13.99 \pm 1.47_{\rm D,E}$	$-12.62 \pm 2.81$	2.37 (1.52-2.82)	H. uarnak	Fish, Crustaceans	Present study
Himantura uarnak	2	VU	$13.19 \pm 2.23$	$-11.50 \pm 0.15$			Fish, Crustaceans	(Randall 1995)
Maculabatis ger- rardi	4	EN	$13.67 \pm 1.70$	$-15.51 \pm 2.05$		M. randalli	Crustaceans	Present study
Maculabatis ran- dalli	18	LC	$12.68 \pm 0.92_{B,C}$	$-16.81 \pm 3.16$	6.75 (5.52–7.62)		Crustaceans	(Rastgoo et al. 2018)
Pastinachus sephen	10	NT	$11.54 \pm 0.89_{A,G}$	$-15.71 \pm 2.88$	7.56 (5.69–8.78)		Bivalves, Poly- chaetes	(Rastgoo et al. 2018)
Pateobatis fai	3	NT	$11.19 \pm 0.21$	$-11.96 \pm 0.51$				
Urogymnus asper- rimus	1	VU	11.81	- 12.41			Polychaeta, Crustaceans	(Randall 1995)
Family Gymnuridae <sub>d,e</sub>					10.49 (8.88– 12.63)			
Gymnura poecilura	19	NT	$13.54 \pm 1.31_{C,D}$	$-15.96 \pm 3.55$	10.49 (8.88– 12.63)		Fish	(Rastgoo et al. 2018)
Family Mobulidae <sub>a</sub>					1.49 (1.16–2.04)			
Mobula kuhlii	7	NT	$9.54 \pm 0.66_{ m H}$	$-13.44 \pm 1.55$	1.49 (1.16–2.04)			
Family Myliobatidae <sub>b,c,d</sub>					4.98 (3.09–5.93)			
Aetomylaeus milvus	10	EN	$12.27 \pm 2.44_{A,B,G}$	$-15.36 \pm 3.97$	8.19 (5.80–9.76)	A. nichofii	Crustaceans	Present study
Aetomylaeus nichofii	10	VU	$12.16 \pm 1.73_{A,B,G}$	$-13.45 \pm 0.80$	4.24 (3.18–4.96)		Crustaceans	(Carassou et al. 2017)
Family Rhinopteridae <sub>b</sub>					10.31 (8.23– 11.79)			
Rhinoptera javanica	14	EN	$11.29 \pm 2.01_{\rm G}$	$-14.92 \pm 1.72$	10.31 (8.23– 11.79)			
TORPEDIFORMES								
Family Narcinidae								
Narcine atzi	3	NT	$14.66 \pm 1.31$	$-16.73 \pm 1.67$				
Family Narkidae <sub>c,d</sub>					0.65 (0.42-0.77)			
Narke dipterygia	5	NT	$12.77 \pm 0.19_{B,C}$	$-15.16 \pm 1.06$	0.65 (0.42-0.77)			
Family Torpedinidaeg					3.13 (2.44–3.63)			
Torpedo sinuspersici	12	DD	$15.48 \pm 0.66_{\rm F}$	$-14.89 \pm 1.42$	3.13 (2.44–3.63)		Fish	(Rastgoo et al. 2018)
Rhinopristiformes								
Family Glaucoste- gidae								
Glaucostegus granulatus	3	EN	$11.22 \pm 2.15$	$-12.02 \pm 1.20$				
Family Rhinidae <sub>e,f</sub>					3.09 (2.37-3.61)			
Rhinobatos annan- dalei	10	NT	$14.28 \pm 0.56_{D,E}$	$-15.44 \pm 1.59$	3.09 (2.37–3.61)		Crustaceans	(Rastgoo et al. 2018)
Family Rhinobatidae								
Rhynchobatus laevis	4	EN	$12.24 \pm 1.59$	$-12.04 \pm 0.77$			Crustaceans, Molluscs	(Randall 1995)

#### Table 1 (continued)

	n	IUCN	δ <sup>15</sup> N (‰)	δ <sup>13</sup> C (‰)	$\frac{\text{SEA}_{B} \text{ (min, max)}}{(\% o^{2})}$	Similar SIA to	Main prey	References
Carcharhiniformes								
Family Carcharhinidae <sub>d,e</sub>					4.20 (3.89–4.56)			
Carcharhinus brevi- pinna	1	VU	14.07	- 19.64			Fish	(Randall 1995)
Carcharhinus dus- sumieri	10	EN	$13.43 \pm 1.53_{C,D}$	$-14.79 \pm 3.51$	5.16 (3.83-6.03)		Fish	(Raeisi et al. 2015)
Carcharhinus leucas	2	EN	$12.95 \pm 1.06$	$-20.67 \pm 0.10$			Fish	(Randall 1995)
Carcharhinus macloti	31	NT	$13.42 \pm 0.50_{C,D}$	$-15.36 \pm 2.19$	3.23 (2.80-3.59)	Carcharhinus spp.	Fish	Present study
Carcharhinus sorrah	3	VU	$13.65 \pm 0.75$	$-14.64 \pm 1.49$			Fish	(Randall 1995)
Rhizoprionodon acutus	19	NT	$13.86 \pm 0.49_{D}$	$-15.60 \pm 1.84$	2.42 (2.00–2.75)		Fish	(R. W. Jabado et al. 2015a, b)
Rhizoprionodon oligolinx	13	NT	$13.83 \pm 0.69_{D}$	$-15-09 \pm 1.87$	2.91 (2.25–3.38)		Fish	(Purushottama et al. 2017)
Family Hemigaleidae								
Chaenogaleus macrostoma	3	VU	$13.52 \pm 0.87$	$-12.81 \pm 0.31$				
Family Sphyrnidae								
Sphyrna lewini	3	EN	$12.97 \pm 1.63$	$-14.04 \pm 2.00$			Fish	(Randall 1995)
Family Triakidae <sub>f.g</sub>					2.56 (1.93-2.99)			
Iago omanensis	10	LC	$14.97 \pm 0.62_{E,F}$	$-15.97 \pm 1.21_{A,C}$	2.56 (1.93–2.99)		Fish	(Rastgoo et al. 2019)
Orectolobiformes								
Family Hemiscyliidae <sub>d.e</sub>					4.88 (4.04–5.54)			
Chiloscyllium arabicum	18	NT	$13.24 \pm 0.65_{B,C,D}$	$-15.32 \pm 2.49_{A,C}$	4.88 (4.04–5.54)		Molluscs, Bivalves	(Randall 1995)
Family Stegostoma- tidae								
Stegostoma fascia- tum	2	VU	$12.27 \pm 0.95$	$-12.20 \pm 0.04$			Molluscs	(Randall 1995)

IUCN conservation status in the Arabian Sea is indicated for each species. (*DD* data deficient, *LC* least concern, *NT* near threatened, *VU* vulnerable, *EN* endangered; Jabado et al. 2017). The main prey present in the diet of each species based on published studies conducted in the Arabian Sea are also indicated. The diet assigned to the species without previous published information about their diet in the Arabia Sea are also indicated. The diet assigned to the species without previous published information about their diet in the Arabic Sea based on the similarity of stable isotopic values (SIA) with other similar species of the same Family is also indicated. Letters (A–H) with the same subscript indicate no significant difference in the  $\delta^{15}N$  (‰) values between species based on Tukey HSD tests. For statistical comparisons, only species or families with more than five individuals sampled are considered

# Methodology

### **Fieldwork procedures**

We conducted this study in the Iranian waters of the Persian Gulf and Gulf of Oman. In total, 278 specimens of 33 elasmobranch species were opportunistically collected from the bycatch generated by fisheries in 2017. All individuals were collected from fishing vessels of two fishing ports: Bandar Abbas—latitude =  $27.17^{\circ}$ ,

longitude =  $56.26^{\circ}$ , and Qeshm–latitude =  $26.98^{\circ}$ , longitude =  $56.26^{\circ}$ ). Because both fishing ports were very close, we assumed that all the individuals were collected in a similar marine area, reducing the potential effect of spatial variability on the stable isotopic values (Kjeldgaard et al. 2021; Post 2002). After collection, each individual was identified at the species level, and the sex, body length (in the case of sharks), and disk width (in the case of batoids) were recorded ( $\pm 1$  cm). From each collected individual, a sample of muscle was collected and frozen at  $- 20^{\circ}$ C. The sampling included 21 batoids from 3 orders and 12 families and 12 sharks from 2 orders and 6 families (Table 1).

### Stable isotopic analysis

Prior to the stable isotope determination, urea content from the muscle samples was removed to prevent potential bias in the estimation of the stable isotopic values (see Kim and Koch 2012; Shiffman et al. 2012). To extract urea, all muscle samples were placed in 2 ml vials with 1.5 mL of deionized water in a sonication machine for 15 min to remove the supernatant of urea. After this process, samples were dried, powdered, and between 0.28 and 0.33 mg was packed into tin capsules. All stable isotope determinations were conducted at the Stable Isotopes Facilities (LIE) of the Estación Biológica de Doñana CSIC (http://www.ebd.csic.es/lie/index.html). Samples were combusted at 1020 °C using a continuous flow isotope ratio mass spectrometry system (Thermo Fisher Scientific, Bremen, German) by means of a Flash HT Plus elemental analyzer interfaced with a Delta V Advantage mass spectrometer. Replicate assays of standards routinely inserted within the sampling sequence indicated analytical measurement errors of + 0.1% and + 0.2% for  $\delta^{13}$ C and  $\delta^{15}$ N, respectively. The standards used were: EBD-23 (cow horn, internal standard), LIE-BB (whale baleen, internal standard) and LIE-PA (feathers of Razorbill, internal standard). These laboratory standards were previously calibrated with international standards supplied by the International Atomic Energy Agency (IAEA, Vienna). Stable isotope ratios were expressed in the standard  $\delta$ -notation (%) relative to Vienna Pee Dee Belemnite VPDB for  $\delta^{13}$ C values and atmospheric N<sub>2</sub> (Air) for  $\delta^{15}$ N values. Based on laboratory standards, the precision (± standard deviation) was + 0.1 and + 0.2 for  $\delta^{13}$ C and  $\delta^{15}$ N, respectively. As the ratio between the percentage of carbon and the percentage of nitrogen was lower than 3.3 % for all samples, no lipid correction on the  $\delta^{13}$ C values was applied (Logan et al. 2008; Post et al. 2007).

### Isotopic metrics and statistical analyses

Standard Ellipses Area (SEA<sub>c</sub>, *i.e.* area containing the 40% of the isotopic data) and Bayesian Standard Ellipse Areas (SEA<sub>B</sub>) were computed with the SIBER package (Jackson et al. 2011) in the open-source program R v.3.5.2 (http://cran.r-project. org/) to estimate the niche width and niche overlap between species (Jackson et al. 2011). The Bayesian framework takes into account the uncertainty in the data and incorporates the error arising from the sampling process, propagating it through to the derived metric (Jackson et al. 2011). Furthermore, the estimation via Bayesian inference allows robust comparison

between species with uneven sample sizes (Jackson et al. 2011). SEA<sub>B</sub> areas were computed using 10,000 posterior draws. A total of 10,000 posterior draws were generated using a sampling–importance–resampling (SIR) algorithm (Jackson et al. 2011) to calculate SEA<sub>B</sub>.

 $\delta^{13}$ C and  $\delta^{15}$ N values were compared between species and families by using ANOVA and post hoc Tukey tests, only with species and families of more than five sampled individuals. We also explored the relationships between isotopic values and body size (total length and disk width; a proxy of ontogenetic effect) by linear regressions. Due to the reduce number of individual samples for most of the species, we only evaluate the relationships between body size and stable isotopes for the species that have more than ten individuals.

# Identification of the potential diet of species with no published data

We revised the published information of the diet based on SCA of all collected elasmobranchs. For the species with no published diet data, we assigned its potential diet based on the knowing diet of isotopic-similar species within the same taxonomic family. That is, we assumed that if two species of sharks or batoids showed similar stable isotope values within the same family, their diet might be similar.

### Results

# Stable isotopic differences between species and taxonomic orders

 $\delta^{15}$ N values differed among families (ANOVA tests, F<sub>11, 260</sub>=20.91, *p* < 0.001; Fig. 1). In particular, Mobulidae and Torpedinidae showed the lowest and highest  $\delta^{15}$ N values, respectively (Fig. 3) and post hoc tests grouped the different families in seven groups (Fig. 1). Regarding  $\delta^{13}$ C values, we did not find differences among orders (F<sub>11, 260</sub>=1.48, *p*=0.14; Table 1, Fig. 1).

At inter-specific level, we found significant differences in  $\delta^{15}$ N (F<sub>32, 278</sub> = 15.41, p < 0.0001) and  $\delta^{13}$ C values (F<sub>32, 278</sub> = 1.08, p = 0.02) (Table 1, Figs. 1 and 2). Eight groups were defined according to the similar  $\delta^{15}$ N values, with the lowest and highest values shown in *M. kuhlii* and *T. sinuspersici*, respectively (Table 1, Figs. 1 and 2). In the case of  $\delta^{13}$ C values, only two groups were defined according to post hoc tests, with the lowest and highest values showed in *M. randalli* and *H. leoparda*, respectively (Table 1, Fig. 1).

Regarding the relationship between isotopic values and body length, we found that only the sharks *C. arabicum* and *I. omanensis* showed significant relationship between  $\delta^{15}$ N and their total body length (p < 0.05; Fig. 3). For the other species with more than ten sampled individuals we did not find significant relationships between  $\delta^{15}$ N and body length (all cases p > 0.05).

### Standard ellipse areas

Regarding the isotopic niche, we found that *C. macrostoma* (mean [5% Credible Interval-95% Credible Interval], 0.87 [0.45–1.02]) presents the smallest isotopic niche, while *S. lewini* (14.79 [7.60–17.07]) is the largest within the shark species. For rays, the smallest isotopic niche is found in *P. fai* (0.30 [0.15–0.35]) and the largest in *M. gerrardi* (14.39 [8.58–17.04]) (Tables 1 and S1). By family, we found differences in the isotopic niche, with Narkidae (0.57 [0.43–0.79]), Hemigaleidae (0.68 [0.47–1.04]) or Mobulidae (1.49 [1.14–1.99]) with the lower niches, and Gymnuridae (10.49 [8.81–12.61]), Dasyatidae (10.64 [9.71–11.70]) or Sphyrnidae (11.05 [7.56–17.07]) with the higher niches (Fig. 2; Table 1).

Regarding the isotopic niche overlap, we found that the families of each order overlapped to a certain degree between them, in special for the families of the order Myliobatiformes (Table 2). The higher overlap was found between Myliobatidae and Aetobatidae (0.29 [9.71–11.70]). The lowest overlap between families was found within the orders Rhinopristiformes and Carcharhiniformes (Table 2). Nevertheless, when analyzed each species individually, some of them were segregated from the rest of the species of the same family, such as *H. leoparda* and *M. gerrardi* for Dasyatidae, or *A. milvus and A. ocellatus* for Aetobatidae (Fig. 2; Table S1). Others, such *R. oligolinx* and *R. acutus* for Carcharhinidae showed high overlap (Fig. 2; Table S1).

Niche breath was dispersed in both axes ( $\delta^{13}$ C and  $\delta^{15}$ N) such as in *M. gerrardi* or *G. poecilura* but some exceptions were present in this elasmobranch community where the dispersion is more pronounced in one of the isotopic axes. For example specially for  $\delta^{13}$ C, *M. randalli*, *P. sephen*, *C. dussumieri*, *C. macloti* and *C. arabicum* present a larger dispersion indicating greater variability in the assimilation of prey living in dissimilar habitats. On the other hand, for  $\delta^{15}$ N, *A. milvus*, *A. nichofii*, *H. leoparda*, *R. laevis*, *G. granulatus* and *C. macrostoma* present a larger dispersion suggesting the assimilation of prey of diverse trophic levels (see Fig. 2).

# Assignation of the potential diet based on SIA similarity

We found 11 species without any published data on their diet (Table 1). After comparing the stable isotope values of these 11 species with other sharks and batoids with published diet data, we assigned a potential diet for these species. In particular, we assigned a diet composed mainly by crustaceans for *A. milvus* and *M. gerrardi*, by fish for *C. macloti*, and by fish and crustaceans for *H. leoparda* (Table 1) (Fig. 2).

# Discussion

In this study, we present new ecological data regarding the trophic interactions and isotopic niches of 33 species of uncommon and threatened elasmobranchs inhabiting a data-poor region of the Persian Gulf and Gulf of Oman. In comparison with the accurate information provided with stomach content or DNA barcoding methodologies (Davis and Pineda-Munoz 2016), stable isotope values only allow to estimate the isotopic niche (as a proxy of the trophic niche) and trophic relationships among species (Layman et al. 2012). Nonetheless, as stable isotope values in muscle reflect the diet of elasmobranchs during the 9–10 months before sampling (Shiffman et al. 2012), this approach informs us about the trophic habits in the long-term (Navarro et al. 2014).

Stable isotope results revealed differences in the trophic niche among the elasmobranch sampled at two levels: at family level and at the species level within each family. Regarding the differences between families, we found differences in their isotopic position (indicated by mean  $\delta^{15}$ N values) and their isotopic niche width. For example, the batoids of the family Torpedinidae and the sharks of the order Carcharhinidae and Triakidae occupied higher trophic position and the sharks of the family Narkidae showed the lower trophic niche width, whereas the batoids of the family Mobulidae showed lower trophic position but a high trophic niche width. These differences reflected the inter-specific differences in the stable isotope values and the trophic habits described by the species of each family.

In marine environments, the consumers that include prey occupying high trophic levels in the ecosystem were expected to have high  $\delta^{15}$ N values (Bird et al. 2018; Shiffman et al. 2012). This is the case of the elasmobranchs of the family Carcharhinidae or the Torpedinidae, with a diet composed mainly by fish, with some of them preying also on other shark species (Jabado et al. 2015a, b; Raeisi et al. 2015; Randall 1995; Rastgoo et al. 2019, 2018). In contrast, other species that prey on lower trophic levels, such the Myliobatiformes *M. kulhii* or *A. ocellatus* with a diet composed by gastropods and bivalves (Randall 1995). In the case of *M. kulhii*, although its diet has not been well-studied (Barbato et al. 2019), dietary research on similar mobulids has described the group as mostly planktivorous, feeding on various zooplankton and small fish (Couturier et al. 2012).

In the case of the trophic diversity at family level, we found that two families of the Order Myliobatiformes,



**Fig.1** A Mean and standard error of  $\delta^{15}$ N and  $\delta^{13}$ C values of 33 elasmobranch species sampled in the Persian Gulf and Gulf of Oman during 2017. Standard ellipse area (SEA<sub>C</sub>) of each family grouped by Orders (**B**–**E**)

exhibit a great isotopic diversity, indicating that the different species included in this group, exploit a wider range of resources. For example, some of these batoids such *A. flagellum*, *A. milvus*, or *A, nichofii* mainly prey on crustaceans, others such *U. asperrimus* and *R. javanica* prey on polychaetes and bivalves and others such *G. poecilura*, *H. leoparda* or *H. uarnak* prey of fish (Carassou et al. 2017; Randall 1995; Rastgoo et al. 2018). In contrast, the different species

**Table 2** Median, 5% and 95% Credible Interval of the overlap between the Bayesian Standard Ellipse Areas (SEA<sub>B</sub>) of each elasmobranch family within each order from the Persian Gulf and Gulf of Oman (north of Arabian Sea) during 2016–2017

Myliobatiformes						
	Aetobatidae	Dasyatidae	Gymnuridae	Mobulidae	Myliobatidae	Rhinopteridae
Aetobatidae		0.08 [0.02-0.19]	0.04 [0-0.18]	0.06 [0-0.19]	0.29 [0.03-0.049]	0.03 [0-0.16]
Dasyatidae	0.1		0.37 [0.19-0.57]	0	0.18 [0.13-0.25]	0.27 [0.13-0.39]
Gymnuridae	0.04	0.4		0	0.16 [0.07-0.23]	0.13 [0.02-0.28]
Mobulidae	0.04	0	0		0.04 [0-0.15]	0.04 [0-0.12]
Myliobatidae	0.33	0.19	0.17	0.03		0.04 [0-0.14]
Rhinopteridae	0	0.28	0.14	0.03	0.03	
Rhinopristiformes						
	Glaucostegidae	Rhinidae	Rhinobatidae			
Glaucostegidae		0.18 [0.01-0.040]	0 [0-0.02]			
Rhinidae	0.24		0.01 [0-0.04]			
Rhinobatidae	0	0				
Torpediformes						
	Narcinidae	Narkidae	Torpedinidae			
Narcinidae		0 [0-0.01]	0.09 [0-0.28]			
Narkidae	0		0			
Torpedinidae	0.16	0				
Carcharhiniformes						
	Carcharhinidae	Hemigaleidae	Sphyrnidae	Triakidae		
Carcharhinidae		0.01 [0-0.07]	0.14 [0.04-0.28]	0.03 [0-0.22]		
Hemigaleidae	0		0.04 [0-0.12]	0		
Sphyrnidae	0.15	0		0.02 [0-0.10]		
Triakidae	0	0	0.01			

included in the families order Carcharhinidae and Hemiscyliidae showed diet mainly composed by fish and bivalves, respectively (Randall 1995).

Unexpectedly, only two sharks, *C. arabicum* and *I. omanensis*, presented positive and significant relationships between  $\delta^{15}$ N and their total body length. This probably was due to the small range of body lengths sampled for the rest of the species due to the opportunistic nature of the sampling. For this reason, a reassessment of these relationships with the other elasmobranch species should be carried out if smaller and larger individuals will be obtained. In any case, these relationships could be reflecting an ontogenetic change in the trophic level of the prey consumed by these two sharks. In particular, the increase of  $\delta^{15}$ N values in larger individuals could be indicating the consumption of large-size prey and/or an increase in the quantity of fish or other prey such sea snakes or cephalopods (Liu et al. 2020; Rastgoo et al. 2019; Waller and Baranes 1994).

We have provided some insights into the ecology of poorly known species. This is especially important for those that are classified endangered by the IUCN at global or regional scale. The comparison of their stable isotope values to other more studied species provides us with some but limited information, as isotopic similarity not always means trophic similarity as different prey can have similar isotopic values. On the other hand, when presenting dissimilar isotopic values, we are more certain that there are feeding on different prey. Nevertheless, higher taxonomical precision is needed for a proper conservation strategy for those endangered elasmobranch species. We encourage performing stomach content analysis or DNA metabarcoding using bycatch individuals to gain more precise information on their diet.

In conclusion, in the present study, we provide information relating to the trophic preferences, trophic interactions, and levels of trophic redundancy among batoids and sharks inhabiting the Persian Gulf and Gulf of Oman, highly useful to future predictions on the consequences



**Fig. 2** Standard ellipse areas (SEAc) of each species by elasmobranch family sampled in the Persian Gulf and Gulf of Oman during 2016–2017. Only species with more than two individuals sampled are represented



**Fig.3** Relationships between the body length (anal length, cm) and  $\delta^{15}$ N of *Iago omanensis* and *Chiloscyllium arabicum* sampled in the Persian Gulf and Gulf of Oman

of changes in their abundance due to natural or humanrelated factors.

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**Data availability** The datasets analyzed during the current study are available from the corresponding author on reasonable request.

### Declarations

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethical approval** No ethical approvals were required as no animals were handled during this work. All field activities were carried out in compliance with national laws.

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# References

- Albo-Puigserver M, Navarro J, Coll M, Aguzzi J, Cardona L, Sáez-Liante R (2015) Feeding ecology and trophic position of three sympatric demersal chondrichthyans in the northwestern Mediterranean. Mar Ecol Prog Ser 524:255–268. https://doi.org/10. 3354/meps11188
- Barbato M, Kovacs T, Coleman MA, Broadhurst MK, de Bruyn M (2019) Metabarcoding for stomach-content analyses of Pygmy devil ray (*Mobula kuhlii cf. eregoodootenkee*): Comparing tissue and ethanol preservative-derived DNA. Ecol Evol 9:2678–2687. https://doi.org/10.1002/ece3.4934
- Barbini SA, Lucifora LO, Sabadin DE, Figueroa DE (2020) Ecological specialization is associated with high conservation concern in skates (Chondrichthyes, Rajiformes). Anim Conserv 29:222–228. https://doi.org/10.1111/acv.12531
- Barría C, Coll M, Navarro J (2015) Unravelling the ecological role and trophic relationships of uncommon and threatened elasmobranchs in the western Mediterranean Sea. Mar Ecol Prog Ser 539:225–240. https://doi.org/10.3354/meps11494
- Bascompte J, Melián CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. Proc Natl Acad Sci USA 102:5443–5447. https://doi.org/10.1073/pnas.0501562102
- Baum JK (2003) Collapse and conservation of shark populations in the Northwest Atlantic. Science 299:389–392. https://doi.org/10. 1126/science.1079777
- Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78:699–714. https:// doi.org/10.1111/j.1365-2656.2009.01531.x
- Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012. https://doi.org/10. 1111/j.0021-8790.2004.00861.x
- Bird CS, Veríssimo A, Magozzi S, Abrantes KG, Aguilar A, Al-Reasi H, Barnett A, Bethea DM, Biais G, Borrell A, Bouchoucha M, Boyle M, Brooks EJ, Brunnschweiler J, Bustamante P, Carlisle A, Catarino D, Caut S, Cherel Y, Chouvelon T, Churchill D, Ciancio J, Claes J, Colaço A, Courtney DL, Cresson P, Daly R, de Necker L, Endo T, Figueiredo I, Frisch AJ, Hansen JH, Heithaus M, Hussey NE, Iitembu J, Juanes F, Kinney MJ, Kiszka JJ, Klarian SA, Kopp D, Leaf R, Li Y, Lorrain A, Madigan DJ, Maljković A, Malpica-Cruz L, Matich P, Meekan MG, Ménard F, Menezes GM, Munroe SEM, Newman MC, Papastamatiou YP, Pethybridge H, Plumlee JD, Polo-Silva C, Quaeck-Davies K, Raoult V, Reum J, Torres-Rojas YE, Shiffman DS, Shipley ON, Speed CW, Staudinger MD, Teffer AK, Tilley A, Valls M, Vaudo JJ, Wai T-C, Wells RJD, Wyatt ASJ, Yool A, Trueman CN (2018) A global perspective on the trophic geography of sharks. Nat Ecol Evol 2:299-305. https://doi.org/10.1038/s41559-017-0432-z
- Carassou L, Al-Kindi AS, Dobretsov S (2017) Preliminary assessment of the trophic structure of demersal fish community in the Sea of Oman. Reg Stud Mar Sci 16:145–151. https://doi.org/10.1016/j. rsma.2017.08.008
- Coll M, Navarro J, Palomera I (2013) Ecological role, fishing impact, and management options for the recovery of a Mediterranean endemic skate by means of food web models. Biol Conserv 157:108–120. https://doi.org/10.1016/j.biocon.2012.06.029

- Cortes E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717. https://doi.org/10.1006/jmsc. 1999.0489
- Couturier LIE, Marshall AD, Jaine FRA, Kashiwagi T, Pierce SJ, Townsend KA, Weeks SJ, Bennett MB, Richardson AJ (2012) Biology, ecology and conservation of the Mobulidae. J Fish Biol 80:1075–1119. https://doi.org/10.1111/j.1095-8649.2012.03264.x
- Davis M, Pineda-Munoz S (2016) The temporal scale of diet and dietary proxies. Ecol Evol 6:1883–1897. https://doi.org/10.1002/ ece3.2054
- Dulvy NK, Baum JK, Clarke S, Compagno LJV, Cortés E, Domingo A, Fordham S, Fowler S, Francis MP, Gibson C, Martínez J, Musick JA, Soldo A, Stevens JD, Valenti S (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquat Conserv 18:459–482. https://doi.org/10. 1002/aqc.975
- Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LNK, Fordham SV, Francis MP, Pollock CM, Simpfendorfer CA, Burgess GH, Carpenter KE, Compagno LJV, Ebert DA, Gibson C, Heupel MR, Livingstone SR, Sanciangco JC, Stevens JD, Valenti S, White WT (2014) Extinction risk and conservation of the world's sharks and rays. Elife 3:e00590–e00590. https://doi.org/10.7554/eLife.00590
- Ehemann NR, Abitia-Cardenas LA, Navia AF, Mejía-Falla PA, Cruz-Escalona VH (2019) Zeros as a result in diet studies, is this really bad? *Rhinoptera steindachneri* as a case study. J Marine Biol Assoc UK 99:1661–1666. https://doi.org/10.1017/S002531541 9000511
- Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–1071. https://doi.org/10.1111/j.1461-0248. 2010.01489.x
- Gallagher AJ, Hammerschlag N, Cooke SJ, Costa DP, Irschick DJ (2015) Evolutionary theory as a tool for predicting extinction risk. Trends Ecol Evol 30:61–65. https://doi.org/10.1016/j.tree. 2014.12.001
- Gaspar C, Giménez J, Andonegi E, Astarloa A, Chouvelon T, Franco J, Goñi N, Corrales X, Spitz J, Bustamante P, Louzao M (2022) Trophic ecology of northern gannets *Morus bassanus* highlights the extent of isotopic niche overlap with other apex predators within the Bay of Biscay. Mar Biol 169:105. https://doi.org/10. 1007/s00227-022-04079-y
- Giménez J, Cañadas A, Ramírez F, Afán I, García-Tiscar S, Fernández-Maldonado C, Castillo JJ, de Stephanis R (2018) Living apart together: Niche partitioning among Alboran Sea cetaceans. Ecol Indic 95:32–40. https://doi.org/10.1016/j.ecolind.2018.07.020
- Heithaus M, Vaudo J, Kreicker S, Layman C, Krützen M, Burkholder D, Gastrich K, Bessey C, Sarabia R, Cameron K, Wirsing A, Thomson J, Dunphy-Daly M (2013) Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. Mar Ecol Prog Ser 481:225–237. https://doi.org/10.3354/meps10235
- Hsu HH, Yacoubi L, Lin Y-J, Le Loc'h F, Katsanevakis S, Giovos I, Qurban MA, Nazeer Z, Panickan P, Maneja RH, Prihartato PK, Loughland RA, Rabaoui LJ, (2022) Elasmobranchs of the western Arabian Gulf: Diversity, status, and implications for conservation. Reg Stud Mar Sci 56:102637. https://doi.org/10.1016/j.rsma.2022. 102637
- Hussey NE, Brush J, McCarthy ID, Fisk AT (2010)  $\delta^{15}$ N and  $\delta^{13}$ C diet-tissue discrimination factors for large sharks under semi-controlled conditions. Comp Biochem Physiol A Mol Integr Physiol 155:445–453. https://doi.org/10.1016/j.cbpa.2009.09.023
- Hyslop EJ (1980) Stomach contents 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

- Isaac NJB, Cowlishaw G (2004) How species respond to multiple extinction threats. Proc R Soc Lond B Biol Sci 271:1135–1141. https://doi.org/10.1098/rspb.2004.2724
- Jabado RW (2018) The fate of the most threatened order of elasmobranchs: shark-like batoids (Rhinopristiformes) in the Arabian Sea and adjacent waters. Fish Res 204:448–457. https://doi.org/10. 1016/j.fishres.2018.03.022
- Jabado RW, Spaet JLY (2017) Elasmobranch fisheries in the arabian seas region: characteristics, trade and management. Fish Fish 18:1096–1118. https://doi.org/10.1111/faf.12227
- Jabado RW, Al Ghais SM, Hamza W, Henderson AC, Al Mesafri AA (2015a) Diet of two commercially important shark species in the United Arab Emirates: milk shark, *Rhizoprionodon acutus* (Rüppell, 1837), and slit-eye shark, *Loxodon macrorhinus* (Müller & Henle, 1839). J Appl Ichthyol 31:870–875. https://doi.org/10. 1111/jai.12156
- Jabado RW, Al Ghais SM, Hamza W, Shivji MS, Henderson AC (2015b) Shark diversity in the Arabian/Persian Gulf higher than previously thought: insights based on species composition of shark landings in the United Arab Emirates. Mar Biodivers 45:719–731. https://doi.org/10.1007/s12526-014-0275-7
- Jabado RW, Kyne PM, Pollom RA, Ebert DA, Simpfendorfer CA, Ralph GM, Dulvy NK (2017) The conservation status of sharks, rays, and chimaeras in the arabian sea and adjacent waters. Environment agency—Abu Dhabi, UAE and IUCN Species Survival Commission Shark Specialist group. Vancouver, Canada, p 236
- Jackson A, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER-stable isotope bayesian ellipses in R. J Anim Ecol 80:595–602. https://doi. org/10.1111/j.1365-2656.2011.01806.x
- Kim SL, Koch PL (2012) Methods to collect, preserve, and prepare elasmobranch tissues for stable isotope analysis. Environ Biol Fishes 95:53–63. https://doi.org/10.1007/s10641-011-9860-9
- Kiszka J, Charlot K, Hussey N, Heithaus M, Simon-Bouhet B, Humber F, Caurant F, Bustamante P (2014) Trophic ecology of common elasmobranchs exploited by artisanal shark fisheries off southwestern Madagascar. Aquat Biol 23:29–38. https://doi.org/10. 3354/ab00602
- Kjeldgaard MK, Hewlett JA, Eubanks MD (2021) Widespread variation in stable isotope trophic position estimates: patterns, causes, and potential consequences. Ecol Monogr 91:e01451. https://doi.org/ 10.1002/ecm.1451
- Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA, Post DM, Bearhop S (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol Rev 87:545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x
- Liu K-M, Lin Y-H, Chang S-K, Joung S-J, Su K-Y (2020) Examining an ontogenetic shift in the diet of the whitespotted bamboo shark *Chiloscyllium plagiosum* in northern Taiwanese waters. Reg Stud Mar Sci 35:101234. https://doi.org/10.1016/j.rsma.2020.101234
- Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. J Anim Ecol 77:838–846. https://doi.org/10.1111/j. 1365-2656.2008.01394.x
- Matich P, Heithaus MR, Layman CA (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
- Moore ABM, Grubbs RD (2019) Shark and ray conservation research: absent where the need is greatest. Aquat Conserv 29:2017–2017. https://doi.org/10.1002/aqc.3192
- Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a

coastal ocean. Science 315:1846–1850. https://doi.org/10.1126/ science.1138657

- Navarro J, López L, Coll M, Barría C, Sáez-Liante R (2014) Shortand long-term importance of small sharks in the diet of the rare deep-sea shark *Dalatias licha*. Mar Biol 161:1697–1707. https:// doi.org/10.1007/s00227-014-2454-2
- Navia AF, Mejía-Falla PA, López-García J, Giraldo A, Cruz-Escalona VH (2017) How many trophic roles can elasmobranchs play in a marine tropical network? Mar Freshw Res 68:1342–1353. https:// doi.org/10.1071/MF16161
- Newsome SD, Martinez del Rio C, Bearhop S, Donald DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436. https:// doi.org/10.1890/060150.01
- Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Mar Ecol Prog Ser 320:239–251. https://doi.org/10. 3354/meps320239
- Pianka ER (2000) Evolutionary ecology. Addison Wesley, San Francisco, USA
- Platell M, Potter I, Clarke K (1998) Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. Mar Biol 131:719–734
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718. https:// doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189. https://doi.org/10.1007/ s00442-006-0630-x
- Purushottama GB, Ramasubramanian V, Dash G, Akhilesh KV, Ramkumar S, Kizhakudan SJ, Singh VV, Zacharia PU (2017) Reproductive biology and diet of the grey sharpnose shark *Rhizoprionodon oligolinx* Springer, 1964 (Chondrichthyes: Carcharhinidae) from the north-eastern Arabian Sea. Indian J Fish 64:9–20. https:// doi.org/10.21077/ijf.2017.64.4.63379-02
- Raeisi H, Kamrani E, Patimar R, Sourinejad I (2015) Determination of White cheek shark *Carcharhinus dussumieri* (Müller & Henle, 1839) feeding habitat in Hormozgan waters, Persian Gulf. J Appl Ichthyol Res 3:19–34
- Randall JE (1995) Coastal fishes of Oman. University of Hawaii Press, Honolulu, Hawaii, USA
- Raoult V, Gaston TF, Williamson JE (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
- Rastgoo AR, Navarro J, Valinassab T (2018) Comparative diets of sympatric batoid elasmobranchs in the Gulf of Oman. Aquat Biol 27:35–41. https://doi.org/10.3354/ab00694
- Rastgoo AR, Etemadi-Deylami E, Mirzaei MR (2019) Feeding habits of Bigeye Houndshark, *Iago omanensis* (Elasmobranchii;

Triakidae; a typical deep water shrk from the Gulf of Oman. Int J Aquat Biol 7:374–382. https://doi.org/10.22034/ijab.v7i6.668

- Ruppert JLW, Travers MJ, Smith LL, Fortin M-J, Meekan MG (2013) Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. PLoS ONE 8:e74648. https://doi.org/10.1371/journal.pone.0074648
- Shiffman DS, Gallagher AJ, Boyle MD, Hammerschlag-Peyer CM, Hammerschlag N (2012) Stable isotope analysis as a tool for elasmobranch conservation research: a primer for non-specialists. Mar Freshw Res 63:635. https://doi.org/10.1071/MF11235
- Shiffman DS, Kaufman L, Heithaus M, Hammerschlag N (2019) Intraspecific differences in relative isotopic niche area and overlap of co-occurring sharks. Aquat Ecol 53:233–250. https://doi.org/ 10.1007/s10452-019-09685-5
- Simpfendorfer C, Goodreid A, McAuley R (2001) Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environ Biol Fishes 61:37–46. https://doi.org/10.1023/A:1011021710183
- Stevens J (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494. https://doi.org/10.1006/jmsc.2000. 0724
- Valinassab T, Daryanabard R, Dehghani R, Pierce GJ (2006) Abundance of demersal fish resources in the Persian Gulf and Oman Sea. J Mar Biol Assoc UK 86:1455–1462. https://doi.org/10.1017/ S0025315406014512
- Vidal A, Cardador L, García-Barcelona S, Macias D, Druon JN, Coll M, Navarro J (2023) The relative importance of biological and environmental factors on the trophodynamics of a pelagic marine predator, the blue shark (*Prionace glauca*). Mar Env Res 183:105808. https://doi.org/10.1016/j.marenvres.2022.105808
- Waller GNH, Baranes A (1994) Food of *Iago omanensis*, a deep water shark from the northern Red Sea. J Fish Biol 45:37–45. https:// doi.org/10.1111/j.1095-8649.1994.tb01284.x
- Wetherbee B, Cortés E (2004) Food consumption and feeding habits. In: Carrier J, Musick J, Heithaus M (eds) Biology of sharks and their relatives. CRC Press, Florida USA
- Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber SH (2013) Global catches, exploitation rates, and rebuilding options for sharks. Mar Policy 40:194–204. https://doi.org/10.1016/j.marpol.2012.12.034

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