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Stomach Content Analysis for Juvenile Great Hammerhead Sharks *Sphyrna mokarran* (Rüppell, 1837) from the Arabian Gulf

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Abstract: The stomach contents of 30 male and 43 female (age < 3 years; 74–236 cm total length) juvenile great hammerhead sharks (*Sphyrna mokarran* (Rüppell, 1837)) obtained from commercial fisheries operating in Saudi Arabian waters of the Arabian Gulf were analyzed for the first time. After exclusion of parasites and abiotics, a total of 31 prey items, including the remains of cephalopods, fish, crustaceans, and bivalve mollusks, were identified in the stomachs of 59 great hammerheads. Based on the index of relative importance, teleosts were their main prey, and *Platycephalus indicus* (Linnaeus, 1758) was the most important prey at the species level. Significant age-related dietary differences were noted (F = 1.57, $p = 0.026$), indicating that the prey of the hammerheads aged 0–3 years shifted from Platycephalidae to Myliobatidae. Levin's niche overlap index was low (0.05–0.21), indicating that <3-year-old juvenile great hammerheads are specialized predators. The estimated trophic level was 4.40–5.01 (mean $\pm$ SD, 4.66 $\pm$ 0.45), indicating that the great hammerhead is a tertiary consumer.

Keywords: elasmobranch; feeding habit; top predator; trophic level

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1. Introduction

The great hammerhead *Sphyrna mokarran* (Rüppell, 1837), which is the largest hammerhead species belonging to the family Sphyrnidae, can grow over 6.1 m in length and inhabits circumtropical coastal reefs, lagoons, continental shelves, and deep waters throughout the world [1–6]. Because the great hammerhead is caught by various fisheries operating from the coastal to pelagic zones, its populations have drastically declined in the past three decades [1,5,7–9]. This species has thus been addressed in Appendix II of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (2012), listed in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (2014), and registered as Critically Endangered on the International Union for Conservation of Nature Red List of Threatened Species (2019) [10–12].

This species has been suspected to have declined by at least 50% over the past 75 years in the Arabian Sea region, and this decline is expected to worsen further [9]. Life history parameters are crucial for assessing the population status and helping to establish relevant management policies; however, only limited biological information is available for this critically endangered species in the northwestern Indian Ocean, particularly the Arabian Gulf.

Age- and growth-related parameters such as growth function have been estimated for the northwestern Atlantic, Pacific, Arabian Gulf and Australian great hammerhead populations [7,13–16]. Their asymptotic lengths were estimated to be 264.2 (males) and

307.8 (females) cm fork length in the northwestern Atlantic, and 402.7 (sexes combined) cm stretched total length in eastern Australian waters, respectively [7,15]. Moreover, the reproduction process of this species was studied using samples from the northern and eastern Australian and eastern South African waters [2,15,17]. Size at maturity of Australian populations was estimated to be 210–225 cm total length (TL), and 217–237 cm precaudal length for the South African population [2,15,17]. Litter size was found to be 3–42 individuals with 2-year reproductive cycle, and a size-at-birth of 50–70 cm TL [1,12,15,17]. More recently, the "Sustaining Project-Shark Study" was conducted to assess great hammerheads in the Saudi Arabian waters of the Arabian Gulf between April 2016 and January 2020; only juveniles (aged < 3 years) occurred in this region, and their early growth and reproduction processes were assessed [13]. In particular, the great hammerheads in the Arabian Gulf had larger size at birth and size at maturity than elsewhere, and the growth rates from after birth to the age of 2.9 years were estimated as 83.3 and 22.7 cm year^{-1}, respectively [13]. Studies on the great hammerheads' diet have reported that these sharks feed on a variety of prey, favoring stingrays and other batoids, groupers, and ariid catfishes [1]. A study found that elasmobranchs were the most commonly found items in the stomachs of eight great hammerheads [18]. Teleosts and elasmobranchs were the main items found in the stomachs of 347 great hammerheads sampled from northern Australia [17]. Great hammerheads preying on stingrays have been observed in the Bahama waters [19]. In addition, through stable isotope analysis, eastern Australian great hammerheads were found to prey on members of the coastal, pelagic, and benthic food webs [20].

Feeding studies will help better define their ecological role in marine communities of the Arabian Gulf [21]. Therefore, the aims of the present study were to investigate diet compositions and to estimate trophic levels for the great hammerheads in the Arabian Gulf based on stomach content analysis. The results of this study provide knowledge on the first feeding habits of great hammerheads in their early life stages sampled from the Saudi Arabian waters of the Arabian Gulf.

2. Materials and Methods

2.1. Study Site and Sampling

Most of the analyzed stomachs derived from specimens (69 sharks) used in our previous paper dealing with maturity and growth of the species, collected between April 2016 and November 2019 [13]. Four further specimens were sampled in January 2020. The sharks (30 males, TL: 75–211 cm; 43 females, TL: 74–236 cm) were caught by several types of gear (trawls, drift and set gill nets, drift and set longlines, trolls, and handlines) and landed at Qatif fishing port and Jubail landing auction fish market (Figure 1). Sexual maturity stage was assigned by macroscopic inspection of claspers and uteruses. Age was estimated by readings of a thin section of vertebra. A more detailed description of the methods is reported in [13].

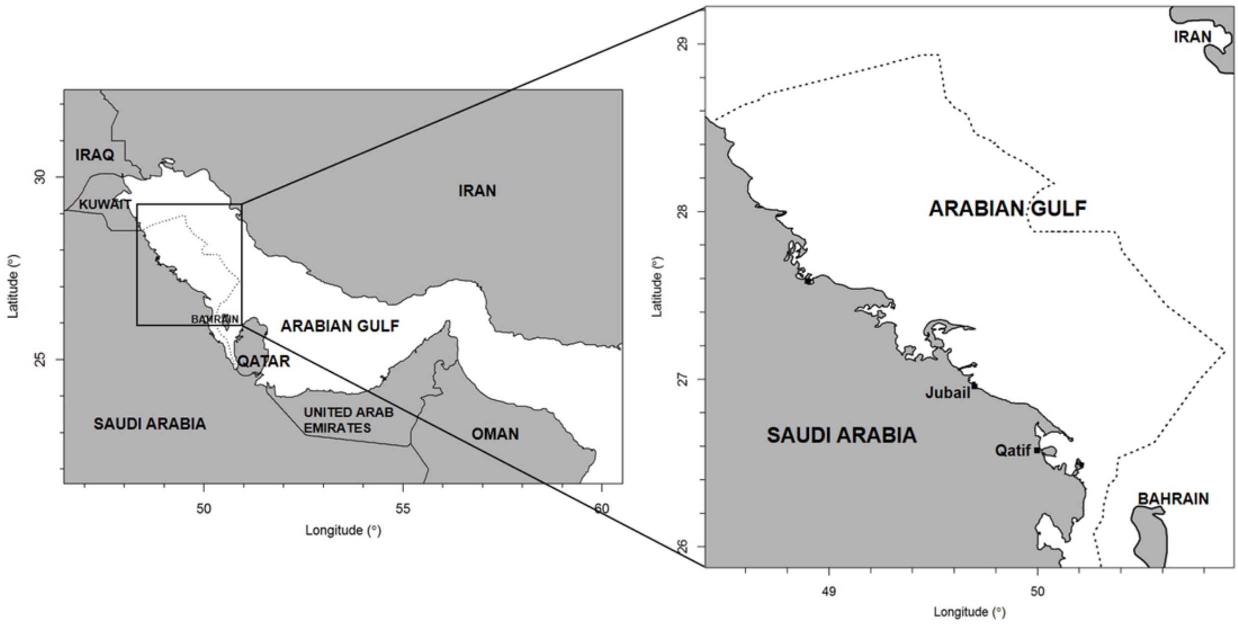

Figure 1. Study area showing the sampling sites of great hammerheads caught in the Saudi Arabian waters of the Arabian Gulf. The dotted lines show the exclusive economic zone boundary of Saudi Arabia.

2.2. Stomach Fullness

Four stomach fullness ranks were considered: Empty, small, big, and full stomach. Empty referred to no or only liquid contents in the stomach; small referred to contents of <50% of the stomach volume; big referred to contents of 50–100% of the stomach volume; and full referred to a full stomach of contents, with even the shape of the contents visible on the stomach. The vacuity index was calculated as the percentage of the number of empty stomachs with respect to the total number of stomachs [22].

Comparisons between sexes, fishing gear (nets vs. hook and line), and stomach fullness ranks (empty and small vs. big and full) were distinguished using the chi-squared test [17].

2.3. Stomach Content Analysis

The stomachs of the samples were weighed, and the contents were recovered through dissection in the laboratory. All of the stomach contents were segregated, identified to the lowest possible taxon, counted, and weighed. To avoid overestimating the occurrence of a particular item, the number of individuals of each content type was determined as the minimum number that these fragments could have originated from [22].

To assess the importance of each prey to the diet, the index of relative importance (IRI) was calculated using the following formula: IRI = (%N + %W) × (%O), where %O is the percentage of prey taxa occurrence in each stomach and %N and %W are the individual numbers of each content type and the total weight as a percentage of each prey taxon, respectively. The IRI values were standardized to percentages (%IRI) according to the protocol mentioned in a previous study [23]. The trophic niche breadth was estimated using Levin's index (Bi):

$$B_i = (\Sigma\, P_{ij}{}^2)^{-1}$$

where P_{ij} is the fraction of N represented by each prey j in the diet [23]. The B_i values were standardized using B_A, which ranged from 0 to 1:

$$B_A = (B_i - 1) \times (N - 1)^{-1}$$

where N is the number of prey categories [24]. Lower B_A values indicate more specialized diets. A species is classified as specialist feeder when $B_A < 0.40$, as intermediate feeder when the B_A value is between 0.40 and 0.60, or as generalist feeder when $B_A > 0.60$ [25].

To assess the trophic overlap in diet between sexes and age groups, the Morisita–Horn index (C_λ) [26] was calculated as follows:

$$C_\lambda = \frac{2\sum_{i=1}^{n}(P_{xi} \times P_{yi})}{\sum_{i=1}^{n} P_{xi}^2 + \sum_{i=1}^{n} P_{yi}^2}$$

where P_{xi} is the proportion of prey i of the total prey hunt by predator x; P_{yi} is the proportion of prey i of the total prey hunt by predator y; and n is the total number of prey species. The Morisita–Horn index ranges from 0 to 1, with values closer to 1 indicating higher similarities in the prey consumed [24]. A nonparametric permutational multivariate analysis of variance (PERMANOVA) was used to test the shifts in diet across years, seasons, sexes, and age groups [23]. This method allows the analysis of multivariate data, with *p* values obtained using 999 permutations by applying the R package (R Development Core Team; www.r-project.org (accessed on 22 June 2022)). The seasons were defined as follows: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February) [27]. The samples were grouped into three classes based on age, from 0^+ to 2^+ years [13].

2.4. Trophic Level

The standardized trophic level was calculated using the trophic index (TrL) [21]:

$$\mathrm{TrL} = 1 + \left(\sum_{j=1}^{n} P_j \times \mathrm{TrL}_j\right)$$

where P_j is the proportion of each prey category j in the predator's diet based on the number of analyzed stomachs [21]. The trophic levels of the prey were obtained using FishBase for fishes [28]; SeaLifeBase for cephalopods and *Penaeus semisulcatus* De Haan, 1844 [29]; and the sources stated in previous studies for *Marsupenaeus japonicus* (Spence Bate, 1888) [30] and for bivalve mollusks [21].

3. Results

3.1. Gear and Stomach Fullness

The sex ratio (male:female) did not differ significantly from 1 (X^2 = 1.11, p = 0.29) for the 73 great hammerhead sharks. One (1.4%) shark was caught using a trawl, 47 (64.4%) using gill nets, 22 (30.1%) using longlines, and 3 (4.1%) using other hook and line gears; thus, 65.8% sharks were caught using net gear, which is significantly higher than the 34.2% caught using the other hook and line gear (X^2 = 7.25, p = 0.007).

Of the 73 great hammerhead stomachs, five from male sharks and nine from female sharks were empty. The vacuity index was 16.7% for the males and 20.9% for the females (overall: 19.2%). The sex ratio in terms of stomach fullness ranks did not differ significantly from 1 (X^2 = 0.98, p = 0.807). In addition to the 14 (19.2%) empty stomachs, 35 (47.9%) small stomachs, 17 (23.3%) big stomachs, and seven (9.6%) full stomachs were noted. The percentage of stomachs with empty or small status was 67.1%, significantly higher than those with big or full status (X^2 = 8.56, p = 0.003).

3.2. Stomach Content Analysis

The stomach contents were identified and categorized into nine groups: cephalopods, elasmobranchs, teleosts, crustaceans, bivalve mollusks, plants (seagrass), insects (cockroaches), parasites (Nematode and Cestoda), and abiotics (hooks and lines). Excluding parasites and abiotics, a total of 31 prey items were identified, including remains of cephalopods, fish, crustaceans, and bivalve mollusk (Table 1).

Table 1. Stomach contents of juvenile great hammerheads caught from Saudi Arabian waters of the Arabian Gulf between April 2016 and January 2020.

Content Items	%N	%W	%O	IRI	%IRI
Cephalopods	**2.60**	**1.48**	**5.08**	**22.25**	**0.18**
Octopus cyaneus Gray, 1849	0.65	0.23	1.82	1.59	0.06
Fam. Sepiidae	1.30	1.24	1.82	4.62	0.18
Cephalopod remains	0.65	0.02	1.82	1.21	0.05
Elasmobranchs	**5.19**	**21.92**	**11.86**	**345.07**	**2.84**
Maculabatis randalli (Last, Manjaji-Matsumoto & Moore, 2012)	0.65	11.02	1.82	21.22	0.84
Fam. Dasyatidae	0.65	4.82	1.82	9.95	0.39
Fam. Myliobatidae	3.25	5.93	7.27	66.74	2.64
Ord. Myliobatiformes	0.65	0.14	1.82	1.44	0.06
Teleosts	**54.55**	**73.32**	**83.05**	**13,948.84**	**93.81**
Saurida tumbil (Bloch, 1795)	1.30	5.77	3.64	25.70	1.02
Saurida spp.	1.95	4.81	3.64	24.56	0.97
Grammoplites suppositus (Troschel, 1840)	1.95	4.63	3.64	23.93	0.95
Platycephalus indicus (Linnaeus, 1758)	4.55	14.81	10.91	211.15	8.34
Epinephelus coioides (Hamilton, 1822)	0.65	7.26	1.82	14.37	0.57
Epinephelus spp.	1.30	9.23	1.82	19.15	0.76
Sillago sihama (Forsskål, 1775)	1.30	0.26	1.82	2.83	0.11
Megalaspis cordyla (Linnaeus, 1758)	0.65	1.51	1.82	3.92	0.15
Lutjanus ehrenbergii (Peters, 1869)	0.65	2.47	1.82	5.68	0.22
Gerres spp.	0.65	0.24	1.82	1.61	0.06
Acanthopagrus bifasciatus (Forsskål, 1775)	1.30	1.21	3.64	9.12	0.36
Lethrinus nebulosus (Forsskål, 1775)	0.65	0.42	1.82	1.94	0.08
Nemipterus japonicus (Bloch, 1791)	0.65	1.22	1.82	3.41	0.13
Otolithes ruber (Bloch & Schneider, 1801)	1.30	0.38	1.82	3.05	0.12
Siganus canaliculatus (Park, 1797)	0.65	4.71	1.82	9.75	0.39
Pseudorhombus spp.	1.30	0.66	1.82	3.56	0.14
Fam. Platycephalidae	3.90	4.14	10.91	87.69	3.46
Fam. Serranidae	0.65	1.98	1.82	4.78	0.19
Fam. Scombridae	0.65	0.57	1.82	2.22	0.09
Fish remains	28.57	7.04	49.09	1748.29	69.06
Crustaceans	**5.84**	**3.10**	**11.86**	**113.80**	**0.94**
Marsupenaeus japonicus (Spence Bate, 1888)	0.65	1.13	1.82	3.24	0.13
Penaeus semisulcatus De Haan, 1844	1.30	0.57	1.82	3.39	0.13
Fam. Penaeidae	3.25	1.39	7.27	33.75	1.33
Crustacean remains	0.65	0.01	1.82	1.19	0.05
Bivalves	**0.65**	**<0.01**	**1.69**	**1.18**	**0.01**
Bivalve remains	0.65	<0.01	1.82	1.18	0.05
Plants	**6.49**	**0.01**	**1.69**	**23.64**	**0.10**
Sargassum angustifolium C.Agardh 1820	0.65	<0.01	1.82	1.18	0.05
Halodule uninervis (Forssk.) Boiss.	5.84	0.01	1.82	10.64	0.42
Insects	**0.65**	**<0.01**	**1.69**	**1.19**	**0.01**
Fam. Blattidae	0.65	<0.01	1.82	1.19	0.05
Parasites	**23.38**	**0.03**	**10.17**	**255.35**	**2.10**
Phylum Nematoda	20.78	0.02	7.27	151.27	5.98
Class Cestoda	2.60	0.01	3.64	9.48	0.37
Abiotic substances	**0.65**	**0.14**	**1.69**	**1.44**	**0.01**
Hook and line	0.65	0.14	1.82	1.44	0.06

%N: percent number; %W: percent weight; %O: percent frequency of occurrence; IRI: index of relative importance; %IRI: percent index of relative importance.

Their diet mainly comprised teleosts, as evidenced by the highest occurrence (83.1%), number (54.6%), and weight (73.3%), with a %IRI of 93.81%. Elasmobranchs (2.84%) were the second most significant component of the juvenile great hammerheads' diet. The %IRI indicated that *Platycephalus indicus* (Linnaeus, 1758) (8.34%) was the most important prey found in the juvenile great hammerheads' stomachs (Table 1).

Males and females did not exhibit significant dietary differences across years (F = 0.79, p = 0.74) or seasons (F = 1.00, p = 0.45) due to small sample size. However, significant dietary differences were observed across age groups (F = 1.57, p = 0.026), indicating that the main prey items of the sharks in the 0^{+} and 2^{+} years-of-age groups shifted from Platycephalidae (particularly *P. indicus*) to Myliobatidae (particularly *Maculabatis randalli* [Last, Manjaji-Matsumoto & Moore, 2012]) and from teleosts to elasmobranchs (Table 2), respectively. In addition, the diets of the males and females across age groups were also slightly different (F = 1.36, p = 0.062). The males aged 1^{+} year preferred to prey on teleosts and favored *P. indicus* but changed to *Epinephelus* spp. fishes when they reached 2^{+} years of age; the females also liked to prey on teleosts after birth, but preferred batoids rather than teleosts in their second and third years of life (Table 2).

Table 2. Stomach content spectrum by sex and age group based on %IRI.

Content Items	Male %IRI (n = 27)				Female %IRI (n = 32)				Sex-Combined %IRI (n = 59)			
	0^{+} yr	1^{+} yr	2^{+} yr	All	0^{+} yr	1^{+} yr	2^{+} yr	All	0^{+} yr	1^{+} yr	2^{+} yr	All
Cephalopods	**0.18**	**0.42**	**6.83**	**0.58**	**0**	**0**	**0**	**0**	**0.04**	**0.07**	**3.88**	**0.18**
Octopus cyaneus	0.59	0	0	0.26	0	0	0	0	0.16	0	0	0.06
Fam. Sepiidae	0	0	14.83	0.73	0	0	0	0	0	0	9.97	0.18
Cephalopod remains	0	1.25	0	0.20	0	0	0	0	0	0.29	0	0.05
Elasmobranchs	**0**	**6.04**	**0**	**0.56**	**0**	**14.70**	**85.71**	**5.65**	**0**	**9.40**	**22.17**	**2.84**
Maculabatis randalli	0	0	0	0	0	0	57.98	2.99	0	0	24.51	0.84
Fam. Dasyatidae	0	7.67	0	1.47	0	0	0	0	0	2.82	0	0.39
Fam. Myliobatidae	0	0	0	0	0	33.5	17.02	9.07	0	12.56	4.0	2.64
Ord. Myliobatiformes	0	1.42	0	0.24	0	0	0	0	0	0.35	0	0.06
Teleosts	**98.93**	**87.33**	**88.61**	**96.61**	**93.17**	**76.77**	**14.29**	**90.42**	**97.02**	**83.79**	**70.97**	**93.81**
Saurida tumbil	0	0	0	0	0	6.05	25.0	3.57	0	2.14	8.0	1.02
Saurida spp.	1.76	0	0	0.62	0	6.03	0	1.12	0.15	2.24	0	0.97
Grammoplites suppositus	0	0	0	0	8.46	0	0	3.27	2.61	0	0	0.95
Platycephalus indicus	0	45.50	0	8.60	17.0	0	0	6.58	5.24	16.07	0	8.34
Epinephelus coioides	0	10.91	0	2.12	0	0	0	0	0	4.09	0	0.57
Epinephelus spp.	0	0	46.8	2.84	0	0	0	0	0	0	24.97	0.76
Sillago sihama	0	0	0	0	0	1.42	0	0.36	0	0.69	0	0.11
Megalaspis cordyla	1.68	0	0	0.60	0	0	0	0	0.43	0	0	0.15
Lutjanus ehrenbergii	0	4.53	0	0.85	0	0	0	0	0	1.58	0	0.22
Gerres spp.	0	1.55	0	0.26	0	0	0	0	0	0.40	0	0.06
Acanthopagrus bifasciatus	0	0	6.19	0.28	0	1.96	0	0.38	0	0.77	4.41	0.36
Lethrinus nebulosus	0	0	0	0	0	1.17	0	0.26	0	0.50	0	0.08
Nemipterus japonicus	1.44	0	0	0.52	0	0	0	0	0.37	0	0	0.13
Otolithes ruber	0	0	0	0	1.04	0	0	0.39	0.30	0	0	0.12
Siganus canaliculatus	4.40	0	0	1.44	0	0	0	0	1.10	0	0	0.39
Pseudorhombus spp.	1.35	0	0	0.57	0	0	0	0	0.36	0	0	0.14
Fam. Platycephalidae	2.54	2.24	0	2.84	9.13	0	0	3.51	6.34	0.68	0	3.46
Fam. Serranidae	0	0	0	0	0	3.60	0	0.66	0	1.32	0	0.19
Fam. Scombridae	0.88	0	0	0.35	0	0	0	0	0.23	0	0	0.09
Fish remains	82.56	6.24	22.28	66.09	57.07	26.80	0	59.48	78.56	27.15	16.48	69.06
Crustaceans	**0.27**	**0.47**	**0**	**0.19**	**6.45**	**0**	**0**	**1.78**	**2.47**	**0.09**	**0**	**0.94**
Marsupenaeus japonicus	0	0	0	0	1.14	0	0	0.44	0.35	0	0	0.13
Penaeus semisulcatus	0	0	0	0	1.16	0	0	0.44	0.34	0	0	0.13
Fam. Penaeidae	0.85	1.42	0	1.15	3.32	0	0	1.25	2.13	0.35	0	1.33
Crustacean remains	0	0	0	0	0.40	0	0	0.15	0.11	0	0	0.05
Bivalves	**0**	**0**	**0**	**0**	**0**	**0.22**	**0**	**0.03**	**0**	**0.07**	**0**	**0.01**
Bivalve remains	0	0	0	0	0	0.51	0	0.15	0	0.28	0	0.05
Plants	**0**	**0**	**0**	**0**	**0**	**2.25**	**0**	**0.63**	**0**	**0.71**	**0**	**0.10**
Sargassum angustifolium	0	0	0	0	0	0.51	0	0.15	0	0.28	0	0.05
Halodule uninervis	0	0	0	0	0	4.61	0	1.33	0	2.52	0	0.42
Insects	**0**	**0**	**0**	**0**	**0**	**0.23**	**0**	**0.03**	**0**	**0.07**	**0**	**0.01**
Fam. Blattidae	0	0	0	0	0	0.52	0	0.15		0.28		0.05
Parasites	**0.62**	**5.47**	**4.56**	**2.06**	**0.24**	**5.84**	**0**	**1.42**	**0.43**	**5.79**	**2.98**	**2.10**
Phylum Nematoda	1.98	17.26	0	7.56	0	13.32	0	3.83	0.56	22.63	0	5.98
Class Cestoda	0	0	9.90	0.40	0.79	0	0	0.30	0.22	0	7.66	0.37
Abiotic substances	**0**	**0**	**0**	**0**	**0.14**	**0**	**0**	**0.04**	**0.04**	**0**	**0**	**0.01**
Hook and line	0	0	0	0	0.49	0	0	0.18	0.14	0	0	0.06

3.3. Niche Breadth and Trophic Overlap

Excluding abiotics and parasites from the stomach content items, the values of the standardized Levin's niche breadth index B_A were <0.40 (0.05–0.21) for all age groups of the male, female, and combined sexes, indicating that juvenile great hammerheads aged < 3 years are specialized predators (Table 3).

Table 3. The Morisita–Horn index (**C_λ**) for trophic overlap, trophic level (TrL), and niche breadth (**B_A**) estimated in juvenile great hammerheads sampled from Saudi Arabian waters of the Arabian Gulf for different sexes and age groups (0^+ to 2^+ years).

Sex and Age Class	Male			Female			All Male	All Female	Sex Combined			TrL	B_A	
	0^+	1^+	2^+	0^+	1^+	2^+			0^+	1^+	2^+		Lower Taxa (Order to species)	Group Class
M 0^+, n = 16	-	-	-	-	-	-	-	-	-	-	-	4.76	0.05	0.03
M 1^+, n = 8	0.007	-	-	-	-	-	-	-	-	-	-	4.71	0.21	0.16
M 2^+, n = 3	0	0	-	-	-	-	-	-	-	-	-	4.40	0.08	0.16
F 0^+, n = 20	0.04	0.53	0	-	-	-	-	-	-	-	-	4.56	0.13	0.10
F 1^+ yr, n = 9	0.12	0	0.003	0	-	-	-	-	-	-	-	4.61	0.10	0.23
F, 2+ yr, n = 3	0	0	0	0	0.08	-	-	-	-	-	-	5.01	0.06	0.13
All male, n = 27	-	-	-	-	-	-	-	-	-	-	-	4.70	0.12	0.07
All female, n = 32	-	-	-	-	-	-	0.23	-	-	-	-	4.62	0.16	0.20
All 0^+, n = 36	-	-	-	-	-	-	-	-	-	-	-	4.65	0.10	0.07
All 1^+, n = 17	-	-	-	-	-	-	-	-	0.34	-	-	4.65	0.16	0.22
All 2^+, n = 6	-	-	-	-	-	-	-	-	0	0.04	-	4.70	0.15	0.21

M: male; F: female.

The Morisita–Horn index indicated that different age groups of the male and female consumed different preys; only males aged 0^+ years and females aged 1^+ year (C_λ = 0.53) exhibited a high trophic overlap (Table 3).

3.4. Trophic Level

The overall mean trophic level was 4.66 ± 0.45. The mean trophic level for the males was 4.70, whereas that for the females was 4.62. When estimated according to age group, the mean trophic level ranged from 4.76 to 4.40 for males, and from 4.56 to 5.01 for females, indicating that great hammerheads are tertiary consumers (Table 3) [21].

4. Discussion

Although *S. mokarran* is distributed globally, owing to difficulty in sampling, only a few studies are available on the feeding habits of great hammerheads. This species is not abundant in the Arabian Gulf, and only 2.7% elasmobranch landings have been reported from the Saudi Arabian Gulf [31]. This study examined the specimens obtained from landings in Saudi Arabia. To the best of our knowledge, this study is the first providing stomach content information for this critically endangered shark species sampled from the northwestern Indian Ocean.

The vacuity index of 19.2% for the *S. mokarran* from the Arabian Gulf was close to a vacuity index of 18.5% for those sampled from eastern South Africa and higher than that for those sampled from northern Australia (12.4%) [2,17]. Compared with other large hammerhead (>2 m TL) species, the vacuity index of *S. mokarran* was close to that of the scalloped hammerhead *Sphyrna lewini* (Griffith & Smith, 1834) found in the southern Gulf of California and northern Australia (19.2%–21.5%); moreover, the vacuity index of *S. mokarran* was higher than that of the winghead shark *Eusphyra blochii* (Cuvier, 1816) found in northern Australia (14.3%) and the smooth hammerhead *Sphyrna zygaena* (Linnaeus, 1758) found in Ecuadorean waters (8.1%); however, the vacuity index of *S. mokarran* was obviously lower than that of the scalloped (67.9–73.2%) and smooth (48.5%) hammerheads found in Taiwan's waters [17,23,32,33]. Most great hammerheads used in this study were caught using gill nets [31], similarly to that reported for the hammerheads (winghead, smooth and scalloped hammerheads) in a previous study [17]; by contrast, the hammerheads obtained from the southern Gulf of California and Taiwan waters were caught using longlines [32–34]. The southern Gulf of California's longline fishery is operated in coastal and inshore shallow waters (<90 m) using traditional fleets; by contrast, the Taiwan longline fishery is operated 20–200 m deep in offshore waters with a much longer main line and hundreds of hooks [32–34]. Therefore, the hammerheads caught from the Taiwan waters were soaked much longer and struggled more than those caught from elsewhere, resulting in a higher vacuity index.

In general, teleosts were the main prey of *E. blochii*, *S. mokarran*, and *S. lewini* found in northern Australia [17] and of *S. mokarran* found in the Arabian Gulf (Table 1). However, the scalloped hammerheads in the Pacific were found to mainly feed on not only teleosts but also cephalopods for their diet [33–35]. For *S. zygaena*, cephalopods were always the dominant prey item [24,34,36]. However, small-sized (<2 m TL) hammerhead shark species preferred shrimps [35].

In addition to teleosts and cephalopods, elasmobranchs were a part of the hammerhead sharks' diets, particularly of *S. mokarran*. Several studies have reported that great hammerheads feed on other elasmobranchs [1,17–19]. Compagno reported that great hammerheads seemed to especially favor stingrays and other batoids [1]. *Hypanus americanus* (Hildebrand & Schroeder, 1928), the southern stingray, is reportedly preyed on by a 3-m-TL great hammerhead in the Bahama waters, the western North Atlantic [19]. An adult female great hammerhead was observed to attack a school of approximately 100 gray reef sharks (*Carcharhinus amblyrhynchos* [Bleeker, 1856]) and prey on one of them in French Polynesian waters [4]. In northern Australia, elasmobranchs were found in 30.6% of 304 *S. mokarran* stomachs [17], higher than the 11.9% rate observed in the present study on the same species sampled from the Arabian Gulf (Table 1). In eastern South Africa, elasmobranchs were found in 83.2% of *S. mokarran* stomachs, batoids being their predominant prey [2]. In eastern Australia, large great hammerheads mainly feed on other sharks and rays, with a preference for benthic species [20]. In the present study, neonatal great hammerheads seemed to be unable to prey on other elasmobranchs; however, this ability increased with age in females, such that at ≥2 years, the females reached the highest trophic level (TrL = 5.0) (Tables 2 and 3). Other large and more pelagic hammerhead sharks, such as the scalloped, smooth hammerheads and the winghead shark, did not feed on elasmobranchs as frequently as *S. mokarran* did. Elasmobranchs were found neither in the scalloped hammerhead from the southern Gulf of California nor in the smooth hammerhead from the Ecuadorean and northeastern Taiwan waters [24,32,34]. Elasmobranchs barely contributed to the dietary composition of the scalloped hammerhead and winghead shark in northern Australia (0.3%–0.8%) and the scalloped hammerhead in the northeastern Taiwan waters (0.8%–1.3%) [17,33,34].

The juvenile great hammerheads were determined to be specialized predators in this study (Table 3). In eastern Australia, through stable isotope analysis, adult great hammerheads were found to be specialists that fed primarily on elasmobranchs [20]. Other large hammerheads, such as *S. lewini* (B_A: 0.32–0.39) and *S. zygaena* (B_A: 0.07–0.23), were mostly determined to be specialized predators [24,33,34], although *S. lewini* from the Mexican Pacific coastal waters was considered an opportunistic predator [37]. Unlike large-sized hammerhead species, small-sized demersal sharks, such as several Scyliorhinidae spp. (e.g., *Galeus melastomus* Rafineque 1810), opportunistic generalist predators that adapt their diet to the available prey in various environments, seem to be better able to resist heavy exploitation [25,38]. Hence, the impact of target and bycatch fishing for large hammerhead species needs more concern.

Ontogenetic shifts in resource use were detected for several large hammerheads, including *S. mokarran*. The diets of the Arabian Gulf *S. mokarran* shifted from teleosts to elasmobranchs within 3 years after birth. Smaller *S. mokarran* may feed more on teleosts; when they grow, they shift to apex predator roles [20]. Smaller *S. zygaena* (<150 cm TL) from Ecuador consumed prey of coastal origin, whereas larger individuals fed in oceanic waters and near the continental shelf [24]. Using both stomach content and stable isotope analyses, resource-use shifts relating to size increase were also detected for *S. lewini* from the Taiwan waters [33,34].

The trophic level estimate for *S. mokarran* was scanty. The mean trophic level of the juvenile great hammerheads in this study was 4.66, slightly higher than the 4.3 reported in another study of *S. mokarran* [21]. This value was close to that of the large hammerhead species, such as the smooth hammerhead in the east (4.7) and northwest Pacific (4.82) [24,34] and the scalloped hammerhead in the east (4.22–4.95) and northwest Pacific (4.89) [34,37]. Conversely, small-sized hammerhead species, such as *Sphyrna corona* Springer, 1940, *Sphyrna media* Springer, 1940, and *Sphyrna tiburo* (Linnaeus, 1758), seemed to occupy lower trophic positions and had a maximum TL of 0.92–1.5 m and a lower trophic level of 3.95–4.26 [35].

Among all Sphyrnidae species, *S. tiburo* had the lowest trophic level (3.2–3.95; always <4) [21,35]. The main reason for this is that seagrass commonly occurs in the diets of *S. tiburo* [39]. Subsequent studies confirmed that *S. tiburo* is an omnivore that can digest and assimilate seagrass nutrients [40]. The great hammerhead is mostly a carnivore; however, two seagrass species were found in one great hammerhead stomach in the present study (Table 1). Seagrass might have been incidentally ingested and may not be a common food of great hammerheads. Not only seagrass but also terrestrial cockroach ingestion was found in another stomach; therefore, it can be inferred that some individuals frequented shallower and more coastal waters as their habitat. In other regions, great hammerheads were also found to use inshore, flat shallow water environments (<1.5 m), and young-of-the-year *S. mokarran* used nearshore, even highly human-impacted marine habitats as its nursery ground [41–44].

Classical stomach content analysis and the more recently introduced stable isotope analysis have their limitations [45]. Using stomach content analysis with stable isotope analysis on various tissues (e.g., muscles, the liver, and the vertebra) provides insights into the trophic niches at different time scales (from days to years); however, to realize the latest feeding behaviors and food composition patterns, stomach content analysis remains important and difficult to replace. Studies are necessary on the biology and ecology of the great hammerhead, as the second largest predatory shark after the tiger shark *Galeocerdo cuvier* (Péron & Lesueur, 1822) in the Arabian Gulf and the largest predatory shark in Saudi Arabian waters [9,13,27,32]. Cooperation among the countries in the Arabian Gulf is required for large-scale investigations and beyond, in order to gain a better understanding of the life history of this critically endangered species and devise appropriate management policies and strategies.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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References

1. Compagno, L.J.V. *Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date*; FAO Fisheries Synopsis; FAO Species Catalogue; Food and Agriculture Organization of the United Nations: Rome, Italy, 1984; Volume 4, pp. 251–655.
2. Cliff, G. Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The Great hammerhead shark *Sphyrna mokarran* (Rüppell). *S. Afr. J. Mar. Sci.* **1995**, *15*, 105–114. [CrossRef]
3. Ebert, D.A.; Fowler, S.; Compagno, L. *Sharks of the World—A Fully Illustrated Guide*; Wild Nature Press: Plymouth, UK, 2013; p. 528.
4. Mourier, J.; Planes, S.; Buray, N. Trophic interactions at the top of the coral reef food chain. *Coral Reefs* **2013**, *32*, 285. [CrossRef]
5. Guttridge, T.L.; Van Zinnicq Bergmann, M.P.M.; Bolte, C.; Howey, L.A.; Finger, J.S.; Kessel, S.T.; Brooks, J.L.; Winram, W.; Bond, M.E.; Jordan, L.K.B.; et al. Philopatry and regional connectivity of the great hammerhead shark, *Sphyrna mokarran* in the U.S. and the Bahamas. *Front. Mar. Sci.* **2017**, *4*, 3. [CrossRef]
6. Gallagher, A.J.; Klimley, A.P. The biology and conservation status of the large hammerhead shark complex: The great, scalloped, and smooth hammerheads. *Rev. Fish Biol. Fish.* **2018**, *28*, 777–794. [CrossRef]
7. Piercy, A.N.; Carlson, J.K.; Passerotti, M.S. Age and growth of the great hammerhead shark, *Sphyrna mokarran*, in the north-western Atlantic Ocean and Gulf of Mexico. *Mar. Freshw. Res.* **2010**, *61*, 992–998. [CrossRef]
8. Gulak, S.J.B.; de Ron Santiago, A.J.; Carlson, J.K. Hooking mortality of scalloped hammerhead *Sphyrna lewini* and great hammerhead *Sphyrna mokarran* sharks caught on bottom longlines. *Afr. J. Mar. Sci.* **2015**, *37*, 267–273. [CrossRef]
9. Jabado, R.W.; Kyne, P.M.; Pollom, R.A.; Ebert, D.A.; Simpfendorfer, C.A.; Ralph, G.M.; Dulvy, N.K. *The Conservation Status of Sharks, Rays, and Chimaeras in the Arabian Sea and Adjacent Waters*; Environment Agency—Abu Dhabi and IUCN Species Survival Commission Shark Specialist Group: Abu Dhabi, United Arab Emirates, 2017; p. 230.
10. Checklist of CITES Species. Available online: http://checklist.cites.org/#/en (accessed on 21 June 2022).
11. Appendices I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS). Available online: https://goo.gl/Ta4agj (accessed on 21 June 2022).
12. Rigby, C.L.; Barreto, R.; Carlson, J.; Fernando, D.; Fordham, S.; Francis, M.P.; Herman, K.; Jabado, R.W.; Liu, K.M.; Marshall, A.; et al. *Sphyrna mokarran*; The IUCN Red List of Threatened Species 2019: e.T39386A2920499; International Union for Conservation of Nature and Natural Resources: Gland, Switzerland, 2019. Available online: https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39386A2920499.en (accessed on 27 November 2022).
13. Hsu, H.H.; Nazeer, Z.M.; Lin, Y.J.; Panickan, P.; Al-Abdulkader, K.; Loughland, R.; Qurban, M.A. Biological aspects of juvenile great hammerhead sharks *Sphyrna mokarran* from the Arabian Gulf. *Mar. Freshw. Res.* **2021**, *72*, 110–117. [CrossRef]
14. Passerotti, M.S.; Carlson, J.K.; Piercy, A.N.; Campana, S.E. Age validation of great hammerhead shark (*Sphyrna mokarran*), determined by bomb radiocarbon analysis. *Fish. Bull.* **2010**, *108*, 346–351.
15. Harry, A.V.; Macbeth, W.G.; Gutteridge, A.N.; Simpfendorfer, C.A. The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia. *J. Fish Biol.* **2011**, *78*, 2026–2051. [CrossRef]
16. Tovar-Ávila, J.; Gallegos-Camacho, R. Oldest estimated age for *Sphyrna mokarran* (Carcharhiniformes: Sphyrnidae) in the Mexican Pacific. *Hidrobiológica* **2014**, *24*, 163–165.
17. Stevens, J.D.; Lyle, J.M. Biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from Northern Australia. *Mar. Freshw. Res.* **1989**, *40*, 129–146. [CrossRef]
18. Bass, A.J.; D'Aubrey, J.D.; Kistnasamy, N. Sharks of the east coast of Southern Africa. III. In *The Families Carcharhinidae (Excluding Mustelus and Carcharhinus) and Sphyrnidae*; Oceanography Research Institute: Durban, South Africa, 1975; Volume 38, pp. 44–45.
19. Strong, W.R., Jr.; Snelson, F.F., Jr.; Gruber, S.H. Hammerhead shark predation on stingrays: An observation of prey handling by *Sphyrna mokarran*. *Copeia* **1990**, *1990*, 836–840. [CrossRef]
20. Raoult, V.; Broadhurst, M.K.; Peddemors, M.; Williamson, M.E.; Gaston, M.F. Resource use of great hammerhead sharks *Sphyrna mokarran* off eastern Australia. *J. Fish Biol.* **2019**, *95*, 1430–1440. [CrossRef]
21. Cortés, E. Standardized diet compositions and trophic levels of sharks. *ICES J. Mar. Sci.* **1999**, *56*, 707–717. [CrossRef]
22. Rastgoo, A.R.; Navarro, J.; Valinassab, T. Comparative diets of sympatric batoid elasmobranchs in the Gulf of Oman. *Aquat. Biol.* **2018**, *27*, 35–41. [CrossRef]
23. Cortés, E. A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* **1997**, *54*, 726–738. [CrossRef]
24. Estupiñán-Montaño, C.; Cedeño-Figueroa, L.; Estupiñán-Ortiz, J.F.; Galván-Magaña, F.; Sandoval-Londoño, A.; Castañeda-Suarez, D.; Polo-Silva, V.J. Feeding habits and trophic level of the smooth hammerhead shark, *Sphyrna zygaena* (Carcharhiniformes: Sphyrnidae), off Ecuador. *J. Mar. Biol. Assoc. U. K.* **2019**, *99*, 673–680. [CrossRef]
25. D'Iglio, C.; Albano, M.; Tiralongo, F.; Famulari, S.; Rinelli, P.; Savoca, S.; Spanò, N.; Capillo, G. Biological and ecological aspects of the blackmouth catshark (*Galeus melastomus* Rafinesque, 1810) in the southern Tyrrhenian Sea. *J. Mar. Sci. Eng.* **2021**, *9*, 967. [CrossRef]
26. Smith, E.P.; Zaret, T.M. Bias in estimating niche overlap. *Ecology* **1982**, *63*, 1248–1253. [CrossRef]
27. Jabado, R.W.; Al-Ghais, S.M.; Hamza, W.; Shivji, M.S.; Henderson, A.C. 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.* **2015**, *45*, 719–731. [CrossRef]

28. Froese, R.; Pauly, D. FishBase. World Wide Web Electronic Publication, Version (12/2019). Available online: www.fishbase.org (accessed on 5 September 2022).
29. Palomares, M.L.D.; Pauly, D. SeaLifeBase. World Wide Web Electronic Publication, Version (07/2020). 2020. Available online: www.sealifebase.org (accessed on 5 September 2022).
30. Guo, K.; Zhao, W.; Wang, S.; Liu, B.; Zhang, P. Food web structure and trophic levels in a saltwater pond sea cucumber and prawn polyculture system. *Acta Oceanol. Sin.* **2016**, *35*, 58–62. [CrossRef]
31. Hsu, H.H.; Yacoubi, L.; Lin, Y.-J.; Le Loc'h, F.; Katsanevakis, S.; Giovos, I.; Qurban, M.A.; Nazeer, Z.; Panickan, P.; Maneja, R.H.; et al. Elasmobranchs of the western Arabian Gulf: Diversity, status, and implications for conservation. *Reg. Stud. Mar. Sci.* **2022**, *56*, 102637. [CrossRef]
32. Torres-Rojas, Y.E.; Hernandez-Herrera, A.; Galván-Magaña, F. Feeding habits of the scalloped hammerhead shark, *Sphyrna lewini*, in Mazatlán waters, southern Gulf of California, Mexico. *Cybium* **2007**, *30*, 85–90.
33. Lai, W. Analyzes of Stomach Contents of Four Large Shark Species in the Waters of Northeastern Taiwan. Master Thesis, National Taiwan Ocean University, Keelung, Taiwan, June 2011. (In Chinese with English Abstract)
34. Yeh, S.Y. Feeding Ecology of Two Hammerhead Shark Species from Northeastern Taiwan Waters. Master Thesis, National Taiwan Ocean University, Keelung, Taiwan, July 2017. (In Chinese with English Abstract)
35. Galindo, E.; Giraldo, A.; Navia, A.F. Feeding habits and trophic interactions of four sympatric hammerhead shark species reveal trophic niche partitioning. *Mar. Ecol. Prog. Ser.* **2021**, *665*, 159–175. [CrossRef]
36. Smale, M.J. Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape coast of South Africa. *S. Afr. J. Mar. Sci.* **1991**, *11*, 31–42. [CrossRef]
37. Torres-Rojas, Y.E.; Páez Osuna, F.; Camalich, J.; Galván-Magaña, F. Diet and trophic level of scalloped hammerhead shark (*Sphyrna lewini*) from the Gulf of California and Gulf of Tehuantepec, Mexico. *Iran. J. Fish. Sci.* **2015**, *14*, 767–785.
38. D'Iglio, C.; Savoca, S.; Rinelli, P.; Spanò, N.; Capillo, G. Diet of the deep-Sea shark *Galeus melastomus* Rafinesque, 1810, in the Mediterranean Sea: What we know and what we should know. *Sustainability* **2021**, *13*, 3962. [CrossRef]
39. Cortés, E.; Manire, C.A.; Hueter, R.E. Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in southwest Florida. *Bull. Mar. Sci.* **1996**, *58*, 353–367.
40. Leigh, S.C.; Papastamatiou, Y.P.; German, D.P. Seagrass digestion by a notorious 'carnivore'. *Proc. R. Soc. B Biol. Sci.* **2018**, *285*, 20181583. [CrossRef]
41. Hueter, R.E.; Tyminski, J.P. Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off peninsular Florida and Texas. *Am. Fish. Soc. Symp.* **2007**, *50*, 193–223.
42. Roemer, R.P.; Gallagher, A.J.; Hammerschlag, N. Shallow water tidal flat use and associated specialized foraging behavior of the great hammerhead shark (*Sphyrna mokarran*). *Mar. Freshw. Behav. Physiol.* **2016**, *49*, 235–249. [CrossRef]
43. Barker, A.M.; Frazier, B.S.; Bethea, D.M.; Gold, J.R.; Portnoy, D.S. Identification of young-of-the-year great hammerhead shark *Sphyrna mokarran* in northern Florida and South Carolina. *J. Fish Biol.* **2017**, *91*, 664–668. [CrossRef]
44. Macdonald, C.; Jerome, J.; Pankow, C.; Perni, N.; Black, K.; Shiffman, D.; Wester, J. First identification of probable nursery habitat for critically endangered great hammerhead *Sphyrna mokarran* on the Atlantic Coast of the United States. *Conserv. Sci. Pract.* **2021**, *3*, e418. [CrossRef]
45. Hammerschlag, N. Quantifying shark predation effects on prey: Dietary data limitations and study approaches. *Endanger. Species Res.* **2019**, *38*, 147–151. [CrossRef]