

# Feeding habits and trophic level of the smooth hammerhead shark, *Sphyrna zygaena* (Carcharhiniformes: Sphyrnidae), off Ecuador

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*As apex predators, sharks are known to play an important role in marine food webs. Detailed information on their diet and trophic level is however needed to make clear inferences about their role in the ecosystem. A total of 335 stomachs of smooth hammerhead sharks, *Sphyrna zygaena*, were obtained from commercial fishing vessels operating in the Ecuadorian Pacific between January and December 2004. A total of 53 prey items were found in the stomachs. According to the Index of Relative Importance (%IRI), cephalopods were the main prey (*Dosidicus gigas*, *Sthenoteuthis oualaniensis*, *Ancistrocheirus lesueurii* and *Lolliguncula [Loliolopsis] diomedea*). *Sphyrna zygaena* was thus confirmed to be a teutophagous species. The estimated trophic level of *S. zygaena* was between 4.6 and 5.1 (mean  $\pm$  SD: 4.7  $\pm$  0.16; males: 4.7; females: 4.8). Levin's index ( $B_A$ ) was low (overall: 0.07; males: 0.08; females: 0.09), indicating a narrow trophic niche. We found that sharks <150 cm in total length consumed prey of coastal origin, whereas sharks  $\geq$ 150 cm foraged in oceanic waters and near the continental shelf. The analyses indicate that *S. zygaena* is a specialized predator consuming mainly squids.*

**Keywords:** Diet, Ecuador, ontogeny, top predator, food web, seasonal variations

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## INTRODUCTION

Some shark species have experienced population declines, mainly due to overfishing, bycatch, pollution and habitat degradation (Dulvy *et al.*, 2008). Recent studies suggest that populations of large sharks have declined by 90% or more in some regions (Myers *et al.*, 2007), making them one of the most threatened group of marine animals worldwide (Heithaus *et al.*, 2010; Lucifora *et al.*, 2011). The implementation of effective strategies for the conservation and management of sharks is often hampered by the lack of information regarding their diet, life history and behaviour (Shiffman *et al.*, 2012). For example, few studies have focused on describing the dietary habits of *Sphyrna zygaena* around the world. Galván-Magaña *et al.* (1989) described the diet of *S. zygaena* in the Gulf of California, Mexico, as being based on pelagic cephalopods (*Histioteuthis heteropsis*,

*Onychoteuthis banksii* and squids of the family Cranchiidae). Off the coast of South Africa, Smale (1991) noted that the diet of juveniles of *S. zygaena* was composed mainly of small fishes, followed by cephalopods (e.g. *Loligo reynaudii*), some elasmobranchs and teleosts (*Merluccius capensis*, *Trachurus capensis* and *Lepidopus caudatus*). The squid *Loligo reynaudii*, found in coastal habitats, was however the most important prey, indicating a preference for neritic cephalopod species.

Also in South Africa, Smale & Cliff (1998) showed that the diet of small *S. zygaena* specimens (<100 cm precaudal length) was dominated in both number and mass by neritic cephalopods (of the families Lolliginidae and Sepiidae), while that of larger specimens (>100 cm precaudal length) included oceanic squids (*Ancistrocheirus lesueurii*, *Ommastrephes bartramii*, *Ornithoteuthis volatilis*, *Sthenoteuthis oualaniensis*, *Todarodes filippovae* and *Todarodes* spp.), which suggests a change in habitat use as sharks mature.

Off the southern coast of Brazil, Bornatowski *et al.* (2007) described *S. zygaena* as ichthyophagous and teutophagous, with a preference for coastal areas at the juvenile stage, when its diet is composed mainly of squids of the genus *Loligo*. Also

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in Brazil, Bornatowski *et al.* (2014a) concluded that juveniles of *S. zygaena* are teutophagous, with a diet based on the inshore squids *Doryteuthis* spp. and *Lolliguncula* (*Lolliguncula*) *brevis*. Galván-Magaña *et al.* (2013) and Rosas-Luis *et al.* (2015) also reported that in the Mexican and Ecuadorian Pacific, respectively, *S. zygaena* preys on various squid species.

Understanding the ecological role of a species within an ecosystem depends on the knowledge of its trophic relationships (Braga *et al.*, 2012). Trophic studies allow us to understand the functional role of organisms within marine communities (e.g. predator–prey relationships), hence providing important information on resource partitioning, competition, energy transfer, and food dynamics (Navia *et al.*, 2010; Bornatowski *et al.*, 2014a). A quantitative understanding of the feeding ecology of shark species enables researchers to describe complex marine food webs (Navia *et al.*, 2010; Bornatowski *et al.*, 2014a) and develop ecosystem models for evaluating the function of each prey species within the ecosystem, and predicting possible changes due to fishing effects (Stevens *et al.*, 2000). Studies of a species' feeding ecology are important not only for knowing the relative frequency of each particular prey in its diet, but also for revealing whether this species (of, e.g. shark or batoid) acts as a link between different levels of the food chain (Bornatowski *et al.*, 2014b).

These complex approaches depend on the availability of data describing the species' basic diet, and are thus affected by the lack of basic knowledge of the diet of some fish species (Bornatowski *et al.*, 2014b). Studies such as this one, in conjunction with other biological studies, will thus ultimately allow more appropriate management and conservation measures to be implemented for elasmobranch species (Galván-Magaña *et al.*, 1989).

*Sphyrna zygaena* is the fourth most commonly caught shark species in Ecuador (Martínez-Ortiz *et al.*, 2007). It is listed as 'Vulnerable' in the International Union for Conservation of Nature (IUCN) Red List (Casper *et al.*, 2005). The aim of this study was (1) to describe the species' dietary spectrum; (2) to estimate its relative trophic level; and (3) to identify ontogenetic shifts in diet between maturity stages.

## MATERIALS AND METHODS

The diet of 335 smooth hammerhead sharks, *Sphyrna zygaena* (Linnaeus, 1758), was determined using stomach content analysis. A total of 156 sharks (72 males and 84 females) were caught between July and December 2003 (rainy season), and 179 more (95 males and 84 females) were caught between January and June 2004 (dry season). The sharks were caught in Ecuadorian waters and landed in the port of Manta (Ecuador). The study area extended from 02°N to 02°S, and from the coast to 84°W. For each shark specimen, total length was measured and sex was determined before extracting the digestive tract. Stomach contents were removed and filtered through a 1.5-mm mesh sieve, stored in plastic bags, and preserved on ice for transportation to the laboratory.

To determine whether the number of stomachs was adequate to describe the diet of *S. zygaena*, cumulative prey curves were constructed using the Shannon method, and samples were randomized 500 times with the 'sample-based rarefaction' routine in EstimateS 9.10 software (Colwell, 2013). The coefficient of variation (CV = 0.05) served as the

basis for determining whether the number of stomachs was sufficient. In addition, a quantitative criterion for assessing sample-size sufficiency was used to determine whether the cumulative prey curves approached an asymptote, by comparing the slope of the line generated from the curve's four last points to a slope of zero through a Student's *t*-test. If the slopes were not significantly different ( $P > 0.05$ ), the prey curve was considered to approach an asymptote (Bizzarro *et al.*, 2007). Sample-size sufficiency could not be tested for individual size classes because of the small number of individuals in each class.

To assess the importance of each prey taxon to the diet of *S. zygaena*, the Index of Relative Importance (IRI; Pinkas *et al.*, 1971) was calculated as follows:  $IRI = (\%N + \%W) (\%FO)$ ; where %N is the number of a given prey type as a percentage of the total number of prey taxa (Hyslop, 1980), %W is the mass of a given prey type as a percentage of the total mass of prey consumed, and %FO is the percentage of frequency of occurrence of each prey type (Hyslop, 1980). IRI values were standardized to percentages according to Cortés (1997).

Diet niche breadth was estimated using Levin's index ( $B_i$ ):  $B_i = (\sum P_{ij}^2)^{-1}$  (Krebs, 1999), where  $P_{ij}$  is the fraction by  $N$  of each food  $j$  in the diet ( $\sum P_j = 1$ ).  $B_i$  values were standardized ( $B_A$ ) so that they ranged from 0 to 1 by using the equation:  $B_A = (B_i - 1) (N - 1)^{-1}$ , where  $N$  is the number of classes (Krebs, 1999). Low  $B_A$  values indicate narrow, specialized diets, whereas high values indicate generalist diets.

Trophic overlap was assessed by calculating the Morisita–Horn index ( $C_\lambda$ ; Smith & Zaret, 1982) to detect possible differences in diet between sexes and size classes:

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

where  $P_{xi}$  is the proportion of the  $i^{th}$  prey with respect to all prey of predator  $x$ ;  $P_{yi}$  is the proportion of the  $i^{th}$  prey with respect to all prey of predator  $y$ , and  $n$  is the total number of prey species. This index ranges from 0 to 1, with values close to zero indicating dietary differences, and values close to one, similarity in the prey consumed.

To test for shifts in diet between years, sexes and maturity stages, a one-way non-parametric permutational multivariate analysis of variance (PERMANOVA) was used (Anderson, 2001). This method allows multivariate data to be analysed based on any distance or dissimilarity measure, with  $P$  values obtained using 500 permutations.

The maturity stage of each shark was recorded using the criteria proposed by Nava & Márquez-Farías (2014), where the size at first maturity is 194 cm total length for males, and 200 cm total length for females. The specimens of *S. zygaena* measuring 90 to 300 cm total length were grouped into three size classes (Size I = 90.0–142.5 cm; Size II = 142.5–195.0 cm; Size III = 195.0–300.0 cm).

The standardized trophic level (TL) of sharks was calculated using the trophic index proposed by Cortés (1999):

$$TL_k = 1 + \left( \sum_{j=1}^n P_j \times TL_j \right)$$

where  $TL_k$  is the trophic level of each prey taxon  $j$  and  $P_j$  is the proportion of each prey category  $j$  in the predator's diet, based

on %N values (Cortés, 1999). The trophic level was estimated for each specimen of *S. zygaena*, and then was averaged. The trophic levels of prey were obtained from Cortés (1999), Hobson & Welch (1992), [www.fishbase.org](http://www.fishbase.org) (Froese & Pauly, 2015) and [www.seararoundus.org](http://www.seararoundus.org) (Pauly & Zeller, 2015).

## RESULTS

### Cumulative prey curves

Of the 335 *Sphyrna zygaena* specimens examined (130 males, 171 females and 34 unsexed individuals), 91.9% ( $N = 308$ ) had food in their stomach, that is, 86.92% of the males ( $N = 113$ ) and 94.15% of the females ( $N = 161$ ). Fifty-three prey items could be identified, together with fish and squid remains.

Based on the constructed cumulative prey curves, sample size was adequate to describe the general diet of *S. zygaena* ( $N_{\min} = 31$ ; Student's  $t$ -test:  $t = -1.73$ ,  $P = 0.18$ ) as well as that of males ( $N_{\min} = 42$ ;  $t = -1.73$ ,  $P = 0.18$ ) and females ( $N_{\min} = 36$ ;  $t = 0.65$ ,  $P = 0.56$ ; Figure 1).

### Diet

The diet of *S. zygaena* was mainly composed of cephalopods and teleosts, cephalopods making up the highest percentage in number, weight and frequency of occurrence. The %IRI indicated that *Dosidicus gigas*, *Sthenoteuthis oualaniensis* and *Ancistrocheirus lesueurii* were the most important prey in the stomach contents (Table 1).

Within years, males and females did not show significant dietary differences, both sexes consuming *Dosidicus gigas* and *Sthenoteuthis oualaniensis* (global  $F = 10.14$ ,  $P = 0.38$  for 2003;  $P = 0.69$  for 2004; Table 3). However, *S. oualaniensis* made a much smaller contribution to the diet of females compared with that of males (Table 2). When comparing the

males and females between years, however, significant dietary differences were found ( $F = 10.14$ ,  $P = 0.02$  for both males and females; Table 3).

The most important prey of sharks of all sizes was *Dosidicus gigas* (for Size-I<sub>2003</sub>, Size-I<sub>2004</sub>, Size-II<sub>2003</sub>, Size-II<sub>2004</sub>, Size-III<sub>2003</sub> and Size-III<sub>2004</sub>) and, to a much lesser extent, *Lolliguncula (Loliolopsis) diomedae* (for Size-I<sub>2004</sub> and Size-II<sub>2004</sub> sharks), *Sthenoteuthis oualaniensis* (for Size-I<sub>2004</sub>, Size-II<sub>2003</sub>, Size-II<sub>2004</sub> and Size-III<sub>2004</sub> sharks), *Ancistrocheirus lesueurii* (for Size-II<sub>2003</sub>, Size-III<sub>2003</sub> and Size-III<sub>2004</sub> sharks) and *Mastigoteuthis* spp. (for Size-III<sub>2003</sub> sharks), suggesting ontogenetic changes in diet, both within and between years (global  $F = 7.88$ ,  $P = 0.02$ ; Figure 2; Table 3).

The trophic analysis by maturity stage showed that both juveniles and adults consume a large proportion of *D. gigas* (IRI = 83.58% and 82.22%, respectively). However, juveniles complement their diet with the squids *S. oualaniensis* and *L. (Loliolopsis) diomedae* (IRI = 6.73% and 4.04%, respectively), while adults complement theirs with the squids *Mastigoteuthis* spp. and *A. lesueurii* (IRI = 6.14% and 5.89%, respectively). Overall, this suggests that sharks at different maturity stages have a similar diet (global  $F = 0.82$ ,  $P = 0.62$ ; Figure 3).

The trophic analysis by season showed that in both the rainy and dry season, sharks consumed *D. gigas* (IRI = 84.6% and 57.8%, respectively), *S. oualaniensis* (IRI = 6.66% and 22.4%, respectively), *A. lesueurii* (IRI = 5.11% and 0.67%, respectively) and *L. (Loliolopsis) diomedae* (IRI = 1.94% and 5.46%, respectively; global  $F = 28.7$ ,  $P = 0.002$ ).

### Niche breadth and trophic overlap

Values of standardized Levin's niche breadth were  $< 0.6$  for males, females and both sexes combined (Table 4), which indicates that *S. zygaena* is a specialized predator.

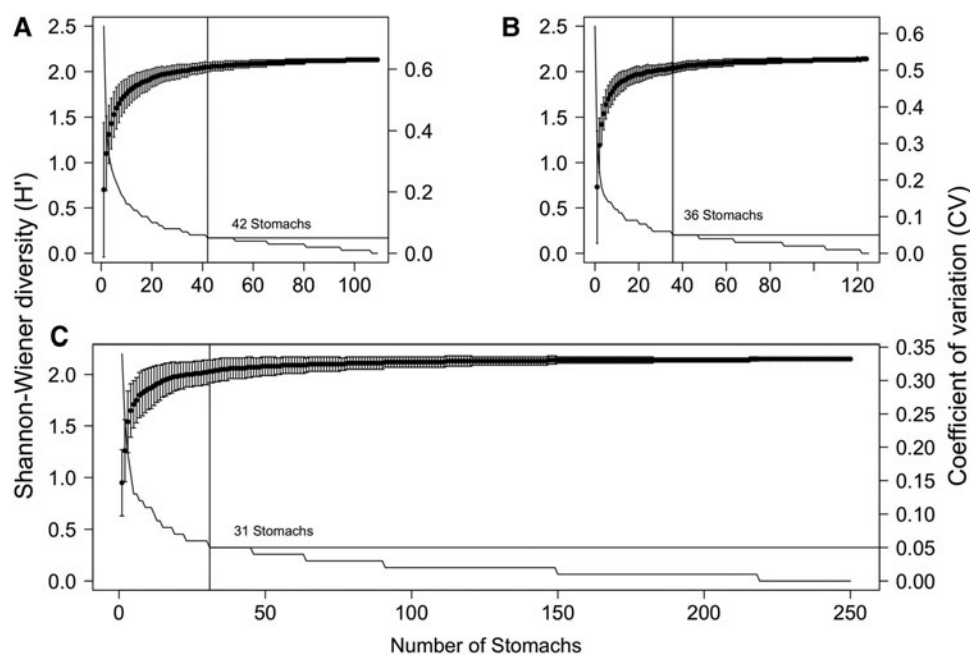


Fig. 1. Prey accumulation curves for *Sphyrna zygaena* caught in Ecuador (A: males, B: females and C: both sexes combined).

**Table 1.** Trophic spectrum of *Sphyrna zygaena* caught in Ecuador and trophic level (TL) of each prey species.

Prey species	%N	%W	%FO	%IRI	TL <sup>a</sup>
<b>Cephalopods</b>	<b>90.18</b>	<b>97.40</b>	–	<b>98.46</b>	
<i>Lolliguncula (Loliolopsis) diomedea</i>	6.10	0.43	8.12	0.67	3.90
<i>Ancistrocheirus lesueurii</i>	7.44	3.41	24.35	3.32	4.13
<i>Abraliopsis</i> spp.	0.07	<0.01	0.65	<0.01	4.13
<i>Argonauta</i> spp.	0.10	<0.01	0.97	<0.01	3.58
<i>Gonatus</i> spp.	0.20	0.03	1.30	<0.01	4.13
<i>Histioteuthis</i> spp.	0.59	0.19	4.22	0.04	4.13
<i>Mastigoteuthis</i> spp.	6.91	0.23	15.91	1.43	4.13
<i>Octopoteuthis</i> spp.	1.73	0.59	9.74	0.28	4.13
<i>Dosidicus gigas</i>	42.86	73.81	53.57	78.49	4.14
<i>Ommastrephes bartramii</i>	0.13	<0.01	0.97	<0.01	4.20
<i>Sthenoteuthis oualaniensis</i>	15.07	16.86	25.65	10.28	4.09
<i>Onychoteuthis banksii</i>	0.52	0.70	1.62	0.02	4.13
<i>Thysanoteuthis rhombus</i>	2.64	0.01	8.77	0.29	4.13
<i>Octopus</i> spp.	0.03	<0.01	0.32	<0.01	3.58
<i>Pholidoteuthis boschmaii</i>	0.26	0.15	1.62	0.01	4.13
<i>Vitreledonella richardii</i>	0.65	<0.01	3.90	0.03	3.58
Squid remains	4.89	0.98	48.70	3.59	–
<b>Teleosts</b>	<b>9.78</b>	<b>2.60</b>	–	<b>1.54</b>	
<i>Synodus</i> spp.	0.07	0.01	0.65	<0.01	4.30
<i>Exocoetus monocirrus</i>	0.26	0.01	2.27	0.01	3.57
<i>Hyporhamphus</i> spp.	0.03	<0.01	0.32	<0.01	3.00
<i>Oxyporhamphus micropterus</i>	0.39	0.02	3.25	0.02	3.20
<i>Opisthonema libertate</i>	0.16	0.02	1.62	<0.01	2.90
<i>Anchoa</i> spp.	0.82	0.08	4.55	0.05	2.70
<i>Merluccius gayi</i>	0.20	0.01	1.95	0.01	4.30
<i>Brotula clarkae</i>	0.03	0.01	0.32	<0.01	4.21
<i>Oligoplites refulgens</i>	0.03	0.01	0.32	<0.01	4.02
<i>Selene peruviana</i>	0.03	<0.01	0.32	<0.01	4.30
<i>Eucinostomus currani</i>	0.03	<0.01	0.32	<0.01	3.30
<i>Caulolatilus affinis</i>	0.07	<0.01	0.65	<0.01	3.24
<i>Aluterus monoceros</i>	0.03	<0.01	0.32	<0.01	3.80
<i>Larimus argenteus</i>	0.55	0.01	1.30	0.01	3.10
<i>Larimus</i> spp.	0.16	<0.01	0.32	<0.01	3.10
<i>Auxis thazard</i>	1.44	0.43	11.69	0.27	4.33
<i>Katsuwonus pelamis</i>	0.42	0.53	3.57	0.04	4.30
<i>Thunnus albacares</i>	0.72	0.70	4.22	0.08	4.30
<i>Thunnus</i> spp.	0.13	0.06	0.97	<0.01	4.30
<i>Scomberomorus sierra</i>	0.07	<0.01	0.32	<0.01	4.50
<i>Sphyaena ensis</i>	0.03	<0.01	0.32	<0.01	4.00
<i>Sphyaena</i> spp.	0.03	<0.01	0.32	<0.01	4.00
<i>Diodon</i> spp.	0.03	<0.01	0.32	<0.01	4.00
<i>Canthidermis maculatus</i>	0.13	0.03	1.30	<0.01	3.47
<i>Cheilopogon atrisignis</i>	0.10	<0.01	0.97	<0.01	3.24
<i>Cheilopogon spilotopterus</i>	0.07	<0.01	0.65	<0.01	3.24
<i>Coryphaena hippurus</i>	0.07	0.11	0.65	<0.01	4.47
<i>Coryphaena</i> spp.	0.10	0.02	0.97	<0.01	4.47
<i>Sarda orientalis</i>	0.03	0.02	0.32	<0.01	4.20
<i>Fistularia</i> spp.	0.07	0.01	0.32	<0.01	3.24
<i>Sarda sarda</i>	0.07	0.07	0.32	<0.01	4.34
<i>Gempylus serpens</i>	0.10	<0.01	0.65	<0.01	4.35
Fam. Carangidae	0.13	0.03	1.30	<0.01	4.05
Fam. Exocoetidae	0.29	0.01	2.60	0.01	3.57
Fam. Ophichthidae	0.07	<0.01	0.65	<0.01	3.64
Fam. Hemirhamphidae	0.03	<0.01	0.32	<0.01	2.82
Fam. Scombridae	0.07	0.12	0.65	<0.01	4.26
Fish remains	2.74	0.24	27.27	1.02	–
<b>Crustaceans</b>	<b>0.03</b>	<b>&lt;0.01</b>	–	<b>&lt;0.01</b>	
Crustacean remains	0.03	<0.01	0.32	<0.01	–

%N, percentage in number; %W, percentage in weight; %FO, percentage in frequency of occurrence; and %IRI, percentage Index of Relative Importance.

<sup>a</sup>Taken from: Froese & Pauly (2015), Cortés (1999), Pauly et al. (1998), Hobson & Welch (1992) and Pauly & Zeller (2015).

**Table 2.** Trophic spectrum by sex and year of *Sphyrna zygaena* caught in Ecuador based on the percentage Index of Relative Importance (%IRI).

Prey species	2003		2004	
	Male	Female	Male	Female
<b>Cephalopods</b>				
<i>Ancistrocheirus lesueurii</i>	0.18	1.78	3.55	5.86
<i>Dosidicus gigas</i>	59.26	77.71	84.61	80.94
<i>Lolliguncula (Loliolopsis) diomedea</i>	3.87	5.65	0.01	0.02
<i>Sthenoteuthis oualaniensis</i>	18.51	0.29	6.79	6.33
<i>Histioteuthis</i> spp.	0.57	0.17	0.01	<0.01
<i>Mastigoteuthis</i> spp.	0.68	0.69	0.89	2.63
<i>Octopoteuthis</i> spp.	0.05	0.13	0.21	0.54
Other squids	10.66	7.35	2.64	2.89
Subtotal	93.78	93.77	98.71	99.21
<b>Teleosts</b>				
<i>Auxis thazard</i>	2.63	1.65	0.15	0.01
<i>Merluccius gayi</i>	0.14	0.01	–	–
<i>Anchoa</i> spp.	0.4	1.97	–	–
<i>Thunnus albacares</i>	0.01	0.01	0.16	0.09
<i>Thunnus</i> spp.	1.00	0.2	–	0.01
Fam. Exocoetidae	0.03	0.09	0.01	–
Other fishes	2.99	2.49	0.96	0.67
Subtotal	7.17	6.42	1.29	0.79

The trophic overlap index showed that similar prey were consumed by males and females ( $C_{\lambda-overall} = 0.98$ , 95% CI = 0.97–0.98;  $C_{\lambda-2003} = 0.98$ , 95% CI = 0.97–0.98; and  $C_{\lambda-2004} = 0.84$ , 95% CI = 0.82–0.87) and by sharks of different size classes (Table 4).

## Relative trophic level

The mean trophic level estimated for both sexes combined was  $4.7 \pm 0.16$  (mean  $\pm$  SD;  $TL_{2003} = 4.8 \pm 0.13$ ;  $TL_{2004} = 4.0 \pm 0.13$ ). The mean trophic level of males was 4.7 ( $TL_{2003} = 4.8$ ;  $TL_{2004} = 4.5$ ), and that of females, 4.8 ( $TL_{2003} = 4.9$ ;  $TL_{2004} = 4.5$ ). When estimated by size class, mean trophic level ranged from 4.6 to 5.1, increasing with size, indicating that the smooth hammerhead shark is a tertiary carnivore (Table 4; Cortés, 1999).

## DISCUSSION

The diet of *Sphyrna zygaena* was dominated by three cephalopod species: *Dosidicus gigas*, *Sthenoteuthis oualaniensis* and *Ancistrocheirus lesueurii*. Other studies worldwide have reported that this shark species consumes a variety of teleosts (e.g. anchovies, saltwater catfish, perch, mackerel, snapper), smaller sharks, guitarfish, rays, shrimps, crabs, as well as squids and other cephalopods (see, among others, Bigelow & Schroeder, 1948; Bass et al., 1975; Compagno, 1984; Stevens, 1984; Bornatowski et al., 2014b).

Our trophic analysis showed similarity in the diets of males and females ( $C_{\lambda} = 0.98$ ): in the same year, both sexes used the same food resources, although in different proportions (*D. gigas*, *S. oualaniensis*, *A. lesueurii* and *Lolliguncula (Loliolopsis) diomedea*). However, males consumed more *S. oualaniensis* and less *A. lesueurii* and *L. (Loliolopsis) diomedea* than females, which suggests that they spend most of their

**Table 3.** Permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distance matrix of prey data from stomach contents of *Sphyrna zygaena* off Ecuador, for sexes (M = males; F = females), size classes and years.

Factor	Sex				Maturity stage								
	2003		2004		2003			2004			2003 × 2004		
	M × F	M × F	M × M	F × F	Size I × Size II	Size I × Size III	Size II × Size III	Size I × Size II	Size I × Size III	Size II × Size III	Size I	Size II	Size III
df	1	1	1	1	1	1	1	1	1	1	1	1	1
F	10.14	10.14	10.14	10.14	7.88	7.88	7.88	7.88	7.88	7.88	7.88	7.88	7.88
P	0.38	0.69	0.02	0.02	0.03	0.04	0.03	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

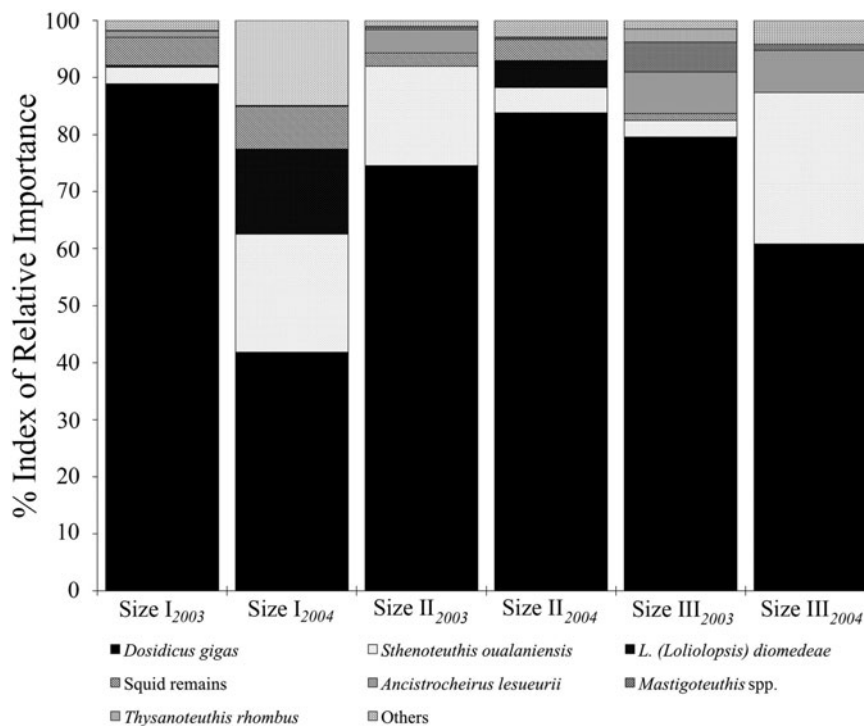
df, Degrees of freedom; F, F-value; P, P-value (0.05).

time feeding in oceanic areas, while females search for food in both coastal and oceanic areas. This may reflect a temporary sex segregation that occurs when females migrate toward the coast to give birth, as was reported for *Sphyrna lewini* (Torres-Rojas *et al.*, 2015). However, for both sexes dietary differences were found between years, and even within the same year. This may be due to temporal variations in prey abundance in the sampling area, because sharks were caught in the same area in both years (30 to 60 nautical miles from the coast).

We also found dietary differences between seasons. These differences may be due to this shark species feeding more on *L. (Loliolopsis) diomedea* during the dry season, and more on the squid *A. lesueurii* during the rainy season.

Other studies have reported similar feeding habits in other hammerhead sharks (e.g. *S. lewini*), with sharks consuming coastal squids (Torres-Rojas *et al.*, 2006; Estupiñán-Montaña *et al.*, 2009) and coastal fishes (Torres-Rojas *et al.*, 2006; Avendaño-Alvarez *et al.*, 2013), females feeding in coastal areas, and males spending more time in the oceanic zone (Estupiñán-Montaña *et al.*, 2009).

In the Mexican Pacific, *S. zygaena* was reported to feed mostly on cephalopods (Galván-Magaña *et al.*, 1989). In a study conducted off Brazil, however, Bornatowski *et al.* (2007, 2014a) categorized *S. zygaena* as ichthyophagous and teutophagous, consuming a high proportion of the squids *Loligo* spp., *Doryteuthis* spp. and *Lolliguncula (Lolliguncula) brevis*. Galván-Magaña *et al.* (2013) and Rosas-Luis *et al.* (2015) also reported that *S. zygaena* preys on various squid species in the Mexican and Ecuadorian Pacific. Our results agree with the studies cited above. Indeed, the diet of *S. zygaena* consisted mainly of cephalopods, teleosts being consumed in smaller proportion and elasmobranchs being absent from the stomach contents. In the Eastern Tropical Pacific, the diets of *S. zygaena* and *S. lewini* were shown to include similar groups of prey, with a predominance of cephalopods (Torres-Rojas *et al.*, 2006; Estupiñán-Montaña *et al.*, 2009; Galván-Magaña *et al.*, 2013; Bornatowski *et al.*, 2014a; Rosas-Luis *et al.*, 2015). The predominance of this prey item may be related to its abundance and broad distribution in this part of the Pacific (Taípe *et al.*, 2001).



**Fig. 2.** Trophic spectrum by size class of *Sphyrna zygaena* caught in Ecuador, based on the percentage Index of Relative Importance (%IRI).

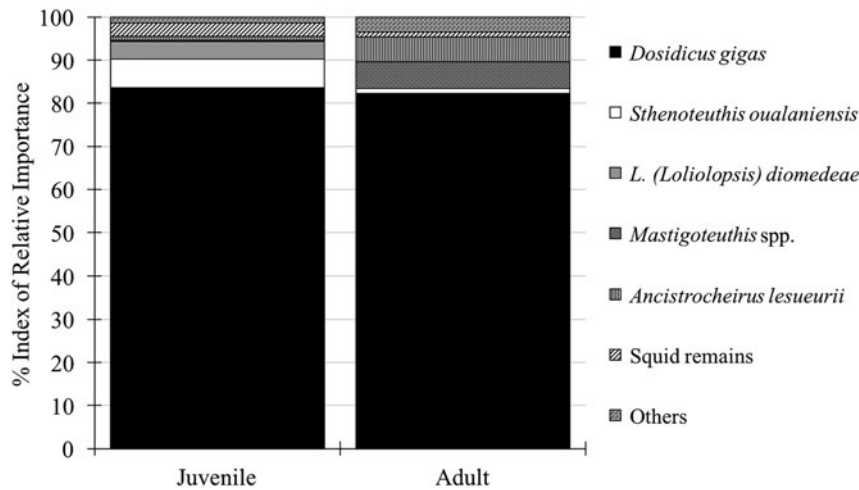


Fig. 3. Trophic spectrum by maturity stage of *Sphyrna zygaena* caught in Ecuador, based on the percentage Index of Relative Importance (%IRI).

Our analysis by size class suggests possible changes in *S. zygaena*'s diet with size: indeed, the presence of the coastal cephalopod *L. (Loliolopsis) diomedea* among the most important prey in the diet of the specimens <140 cm total length suggests that the juveniles feed in coastal areas. This hypothesis agrees with Bornatowski *et al.* (2007, 2014a), who reported coastal cephalopods of the genera *Doryteuthis*, *Loligo* and *Lolliguncula* as *S. zygaena*'s most important prey off the southern coast of Brazil.

*Lolliguncula (Loliolopsis) diomedea* and its genus, as well as the genera *Doryteuthis* and *Loligo*, are demersal squids that inhabit coastal areas or areas near the continental shelf, at a depth of 50 to 200 m (Jereb & Roper, 2010). Their occurrence in the diet of small specimens of *S. zygaena* suggests that they use coastal habitats. In contrast, squids like *D. gigas* and *S. oualaniensis* were the most important prey in the stomach contents of the larger specimens of *S. zygaena* ( $\geq 150$  cm total length), which suggests that they forage in oceanic areas or areas near the continental shelf. This shift in habitat would lead to changes in the shark's diet as individuals mature and grow.

Ontogenetic changes in diet are common among sharks and have been documented through both stomach content analysis (Lowe *et al.*, 1996; Marshall *et al.*, 2008; Newman *et al.*, 2012) and stable isotope analysis (Estrada *et al.*, 2006; Kim *et al.*, 2012; Loor-Andrade *et al.*, 2015). These shifts may be associated with increased body size. As they mature and grow, indeed, smooth hammerhead sharks become less susceptible to predation by other sharks, thus promoting horizontal migration from coastal to oceanic areas, where larger prey are available.

Four squid species dominated the diet of *S. zygaena* in this study: two of the family Ommastrephidae (*D. gigas* and *S. oualaniensis*), one of the family Ancistrocheiridae (*A. lesueurii*), and one of the family Loliginidae (*L. (Loliolopsis) diomedea*). In conjunction with Levin's index ( $B_A < 0.6$ ), this finding suggests that *S. zygaena* is a specialist predator, as was also reported in Brazil by Bornatowski *et al.* (2014a) and in Peru by Gonzalez-Pestana *et al.* (2017), consuming coastal prey during the juvenile stage and oceanic prey during the adult stage. This conclusion is supported by the abundance of *D. gigas* and *S. oualaniensis* and, to a lesser degree, of other squid species (*Histioteuthis* spp., *Mastigoteuthis* spp., *Onychoteuthis banksii* and *Ommastrephes bartramii*) in the shark's diet. This specialization may be related to prey availability, with the smooth hammerhead shark specialized in hunting the prey species that are most abundant in the area in order to maximize consumption and optimize energy use. When prey is scarce, in contrast, *S. zygaena* may be forced to feed on whatever prey is available, which implies a greater expenditure of energy (Wetherbee *et al.*, 1990).

To date, few studies have estimated the trophic level of *S. zygaena*. Cortés (1999) and Bornatowski *et al.* (2014a) concluded that this shark is a tertiary predator (TL = 4.2). Our results agree with these studies, as the mean TL estimated here ranged from 4.45 to 4.91 (mean  $\pm$  SD: 4.73  $\pm$  0.16). As top predators, these sharks would be able to influence lower trophic levels of the food chain through both direct and indirect effects (Stevens *et al.*, 2000; Myers *et al.*, 2007; Heithaus *et al.*, 2008; Navia *et al.*, 2010).

The similarity in the estimated trophic levels of males and females supports the high trophic overlap between sexes and

Table 4. Trophic overlap (based on the Morisita–Horn index,  $C_h$ ), trophic level (TL) and niche breadth ( $B_A$ ) estimated in *Sphyrna zygaena* off Ecuador for different size classes and years.

Size class	Size I <sub>2003</sub> N = 37	Size II <sub>2003</sub> N = 61	Size III <sub>2003</sub> N = 47	Size I <sub>2004</sub> N = 118	Size II <sub>2004</sub> N = 97	Size III <sub>2004</sub> N = 3	TL	$B_A$
Size I <sub>2003</sub>	–	–	–	–	–	–	4.6	0.08
Size II <sub>2003</sub>	0.96	–	–	–	–	–	4.8	0.08
Size III <sub>2003</sub>	0.85	0.86	–	–	–	–	4.9	0.10
Size I <sub>2004</sub>	0.49	0.51	0.34	–	–	–	4.4	0.22
Size II <sub>2004</sub>	0.83	0.79	0.73	0.81	–	–	4.6	0.14
Size III <sub>2004</sub>	0.82	0.92	0.80	0.57	0.73	–	5.1	0.44

absence of sexual segregation found above, and suggests that both sexes feed on prey at similar trophic levels. It was also shown that as smooth hammerhead sharks increase in size, they tend to consume prey at higher trophic levels, suggesting ontogenetic changes in their diet.

This study seeks to remedy the lack of knowledge on the biology and ecology of *S. zygaena* off Ecuador, and is one of the first studies to address this topic in detail. Further research is needed, however, to expand upon this initial study and elucidate the species' feeding patterns and preferences, ontogenetic changes and habitat use.

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## REFERENCES

- Anderson M.J. (2001) Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 626–639.
- Avendaño-Alvarez J.O., Pérez-España H., Salas-Monreal D. and García-Rodríguez E. (2013) Captures and diet of three shark species in the Veracruz reef system. *Open Journal of Marine Science* 3, 66–73.
- Bass A.J., D'Aubrey J.D. and Kistnasamy N. (1975) Sharks of the east coast South Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. *Oceanographic Research Institute Investigational Report* 38, 1–100.
- Bigelow H.B. and Schroeder W. (1948) Fishes of the western North Atlantic. Part I: lancelets, Cyclostomes, Sharks. *Memoir Sears Foundation for Marine Research* 1, 1–576.
- Bizzarro J.J., Robinson H.J., Rinewalt C.S. and Ebert D.A. (2007) Comparative feeding ecology of four sympatric skate species off central California, USA. *Environmental Biology of Fishes* 80, 197–220.
- Bornatowski H., Braga R.R., Abilhoa V. and Corrêa M.F.M. (2014a) Feeding ecology and trophic comparisons of six shark species in a coastal ecosystem off southern Brazil. *Journal of Fish Biology* 85, 246–263.
- Bornatowski H., Costa L., Roberte M.C. and da Pina J.V. (2007) Hábitos alimentares de tubarões-martelo jovens, *Sphyrna zygaena* (Carcharhiniformes: Sphyrnidae), no litoral sul do Brasil. *Biota Neotropica* 7, 213–216.
- Bornatowski H., Navia A.F., Braga R.R., Abilhoa V. and Corrêa M.F.M. (2014b) Ecological importance of sharks and rays in a structural food

web analysis in southern Brazil. *ICES Journal of Marine Science* 71, 1586–1592.

- Braga R.R., Bornatowski H. and Vitule J.R.S. (2012) Feeding ecology of fishes: an overview of worldwide publications. *Reviews in Fish Biology and Fisheries* 22, 915–929.
- Casper B.M., Domingo A., Gaibor N., Heupel M.R., Kotas E., Lamónaca A.F., Pérez-Jimenez J.C., Simpfendorfer C., Smith W.D., Stevens J.D., Soldo A. and Vooren C.M. (2005) *Sphyrna zygaena*. The IUCN red list of threatened species 2005. e.T39388A10193797. Available at <http://dx.doi.org/10.2305/IUCN.UK.2005.RLTS.TT39388A10193797.en>.
- Colwell R.K. (2013) EstimateS: statistical estimation of species richness and shared species from simple (Software and User's Guide), Version 9.10. University of Connecticut, USA- URL. Available at <http://viceroy.eeb.uconn.edu/estimates>.
- Compagno L.J.V. (1984) FAO species catalogue. Sharks of the world. An annotated and illustrated catalogue of shark species known date. Part 1–2. Volume 4. Hexanchiformes to Carcharhiniformes. *FAO Fisheries Synopsis* 125. Rome: FAO.
- Cortés E. (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 726–738.
- Cortés E. (1999) Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* 56, 707–717.
- Dulvy N.K., Baum J.K., Clarke S., Compagno L.J.V., Cortés E., Domingo A., Fordham S., Fowler S., Francis M.P., Gibson C., Martínez J., Musick J.A., Soldo A., Stevens J.D. and Valenti S. (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 459–482.
- Estrada J.A., Rice A.N., Natanson L.J. and Skomal G.B. (2006) Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology* 87, 829–834.
- Estupiñán-Montaño C., Cedeño-Figueroa L.G. and Galván-Magaña F. (2009) Feeding habits of the scalloped hammerhead shark *Sphyrna lewini* (Griffith & Smith, 1834) (Chondrichthyes) in the Ecuadorian Pacific. *Revista de Biología Marina y Oceanografía* 44, 379–386.
- Froese R. and Pauly D. (eds) (2015) *FishBase*. World Wide Web electronic publication. Available at <http://www.fishbase.org>, Version (09/2015).
- Galván-Magaña F., Nienhuis H.J. and Klimley A.P. (1989) Seasonal abundance and feeding habits of sharks of the lower Gulf of California, Mexico. *California Fish and Game* 75, 74–84.
- Galván-Magaña F., Polo-Silva C., Hernández-Aguilar S.B., Sandoval-Londoño A., Ochoa-Díaz R.M., Aguilar-Castro N., Castañeda-Suárez D., Chávez-Costa A., Baigorri-Santacruz Á., Torres-Rojas Y.E. and Abitia-Cárdenas A.L. (2013) Shark predation on cephalopods in the Mexican and Ecuadorian Pacific Ocean. *Deep-Sea Research II* 95, 52–62.
- Gonzalez-Pestana A., Acuña-Perales N., Coasaca-Cespedes J., Cordova-Zavaleta F., Alfaro-Shigueto J., Mangel J.C. and Espinoza P. (2017) Trophic ecology of the smooth hammerhead shark (*Sphyrna zygaena*) off the coast of northern Peru. *Fishery Bulletin* 115, 451–459.
- Heithaus M.R., Frid A., Vaudo J.J., Worm B. and Wirsing A.J. (2010) Unravelling the ecological importance of elasmobranchs. In Carrier J.C., Musick J.A. and Heithaus M.R. (eds) *Biology of sharks and their relatives II*. Boca Raton, FL: CRC Press, pp. 611–637.
- Heithaus M.R., Frid A., Wirsing A.J. and Worm B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23, 202–210.

- Hobson K.A. and Welch H.E.** (1992) Determination of trophic relationships within a high Arctic marine food web using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Marine Ecology Progress Series* 84, 9–18.
- Hyslop E.J.** (1980) Stomach contents analysis – a review of methods and their application. *Journal of Fish Biology* 17, 411–429.
- Jereb P. and Roper C.F.E.** (2010) *Cephalopods of the world. An annotated and illustrated catalogue of cephalopods species known to date. Volume 2. Myopsid and Oegopsid squids. FAO Species Catalogue for Fishery Purposes* 4. Rome: FAO.
- Kim S.L., Tinker M.T., Estes J.A. and Koch P.L.** (2012) Ontogenetic and among-individual variation in foraging strategies of northeast Pacific white sharks based on stable isotope analysis. *PLoS ONE* 7, e45068.
- Krebs C.J.** (1999) *Ecological methodology*. New York, NY: Addison Wesley Longman, p. 620.
- Loor-Andrade P., Galván-Magaña F., Elorriaga-Verplancken F.R., Polo-Silva C. and Delgado-Huertas A.** (2015) Population and individual foraging patterns of two hammerhead sharks using carbon and nitrogen stable isotopes. *Rapid Communications in Mass Spectrometry* 29, 821–829.
- Lowe C.G., Wetherbee B.M., Crow G.L. and Tester A.L.** (1996) Ontogenetic dietary shifts and feeding behaviour of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes* 47, 203–211.
- Lucifora L.O., Garcia V.B. and Worm B.** (2011) Global diversity hotspots and conservation priorities for sharks. *PLoS ONE* 6, e19356.
- Marshall A.D., Kyne P.M. and Bennett M.B.** (2008) Comparing the diet of two sympatric urolophid elasmobranchs (*Trygonoptera testacea* Müller & Henle and *Urolophus kapalensis* Yearsley & Last): evidence of ontogenetic shifts and possible resource partitioning. *Journal of Fish Biology* 72, 883–898.
- Martínez-Ortiz J., Galván-Magaña F., Carrera-Fernández M., Mendoza-Intriago D., Estupiñán-Montaño C. and Cedeño-Figueroa L.** (2007) Seasonal abundance of sharks landing in Manta – Ecuador. In Martínez-Ortiz J.F. and Galván-Magaña F. (eds) *Tiburones en Ecuador: Casos de estudio/Shark in Ecuador: case studies*. Manta, Ecuador: EPESPO – PMRC, pp. 9–27.
- Myers R.A., Baum J.K., Shepherd T.D., Powers S.P. and Peterson C.H.** (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315, 1846–1850.
- Nava P. and Márquez-Farías J.F.** (2014) Talla de madurez del tiburón martillo, *Sphyrna zygaena*, capturado en el Golfo de California. *Hidrobiológica* 24, 129–135.
- Navia A.F., Cortés E. and Mejía-Falla P.A.** (2010) Topological analysis of the ecological importance of elasmobranch fishes: a food web study on the Gulf of Tortugas, Colombia. *Ecological Modelling* 221, 2918–2926.
- Newman S.P., Handy R.D. and Gruber S.H.** (2012) Ontogenetic diet shifts and prey selection in nursery bound lemon sharks, *Negaprion brevirostris*, indicate a flexible foraging tactic. *Environmental Biology of Fishes* 95, 115–126.
- Pauly D., Trites A., Capuli E. and Christensen V.** (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55, 467–481.
- Pauly D. and Zeller D.** (eds) (2015) *Sea Around Us: concepts, design and data*. Available at <http://www.seaaround.org>, Version (06/2016).
- Pinkas L., Oliphant M.S. and Iverson I.L.K.** (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. *California Fish and Game Fishery Bulletin* 152, 1–105.
- Rosas-Luis R., Loor-Andrade P., Carrera-Fernández M., Pincay-Espinoza J.E., Vincés-Ortega C. and Chompoy-Salazar L.** (2015) Cephalopod species in the diet of large pelagic fish (sharks and billfishes) in Ecuadorian waters. *Fisheries Research* 173, 159–168.
- Shiffman D.S., Gallagher A.J., Boyle M.D., Hammerschlag-Peyer C.M. and Hammerschlag N.** (2012) Stable isotope analysis as a tool for elasmobranch conservation research: a primer for non-specialists. *Marine and Freshwater Research* 63, 635–643.
- Smale M.J.** (1991) Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape coast of South Africa. *South African Journal of Marine Science* 11, 31–42.
- Smale M.J. and Cliff G.** (1998) Cephalopods in the diets of four shark species (*Galeocerdo cuvier*, *Sphyrna lewini*, *S. zygaena*, *S. mokarran*) from Kwazulu-Natal, South Africa. *South African Journal of Marine Science* 20, 241–253.
- Smith E.P. and Zaret T.M.** (1982) Bias in estimating niche overlap. *Ecology* 63, 1248–1253.
- Stevens J.D.** (1984) Biological observations on sharks caught by sport fishermen off New South Wales. *Australian Journal of Marine and Freshwater Research* 35, 573–590.
- Stevens J.D., Bonfil R., Dulvy N.K. and Walker P.A.** (2000) The effects of fishing on sharks, rays, and chimeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57, 476–494.
- Taibe A., Yamashiro C., Mariategui L., Rojas P. and Roque C.** (2001) Distribution and concentrations of jumbo flying squid (*Dosidicus gigas*) off the Peruvian coast between 1991 and 1999. *Fisheries Research* 54, 21–32.
- Torres-Rojas E.Y., Hernández-Herrera A. and Galván-Magaña F.** (2006) Feeding habits of the scalloped hammerhead shark, *Sphyrna lewini*, in Mazatlán waters, southern Gulf of California, Mexico. *Cybius* 30, 85–90.
- Torres-Rojas E.Y., Páez-Osuna F., Camalich J. and Galván-Magaña F.** (2015) Diet and trophic level of scalloped hammerhead shark (*Sphyrna lewini*) from the Gulf of California and Gulf of Tehuantepec, Mexico. *Iranian Journal of Fisheries Sciences* 14, 767–785.

and

**Wetherbee B., Gruber S. and Cortés E.** (1990) Diet, feeding habits, digestion and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. In Pratt H.L. Jr., Gruber S.H. and Taniuchi T. (eds) *Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of the fisheries*. NOAA Technical Report NMFS 90, 29–47.

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