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Feeding ecology of the shortfin mako shark, *Isurus oxyrinchus*, in the Ecuadorian Pacific Ocean

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Abstract

Shortfin mako shark, *Isurus oxyrinchus*, is listed as an endangered species with declining global population. Thus, studies regarding its biology and ecology are important to recommend fishery management and conservation measures. This study aimed to determine the diet composition and feeding habits of *I. oxyrinchus* in Ecuadorian waters. Samples were obtained from Santa Rosa fishing port (Ecuador). The total length (L_T), sex and sexual characteristics were recorded, and stomach contents were collected. A total of 142 individuals were recorded, comprising 81 females (104–295 cm L_T) and 61 males (127–245 cm L_T). A total of 24 prey species were identified, including crustaceans, cephalopods, teleosts and cetaceans. According to the Prey-Specific Index of Relative Importance (PSIRI), the main prey taxa were the ommastrephid squid, *Dosidicus gigas* (42.57%) and *Sthenoteuthis oualaniensis* (21.04%), followed by fish from the family Hemiramphidae (11.85%). *Isurus oxyrinchus* is a specialist predator that preferred a low number of prey ($Bi = 0.25$), both by sex (Bi; females = 0.29 and males = 0.34) and life stages (Bi; juveniles = 0.27 and adults = 0.37). The trophic overlap was medium for sexes ($J = 0.54$) and biological cycle phases ($J = 0.42$). Trophic level (TL_k) was 4.47, indicating that *I. oxyrinchus* is a tertiary predator. This information will help in fisheries management based on an ecosystem approach, where this species fulfils an ecological role, and its interactions with other species allow us to understand how the flow of nutrients and energy occurs within an ecosystem.

Introduction

Shortfin mako shark, *Isurus oxyrinchus* (Rafinesque, 1810) (Order Lamniformes; Family Lamnidae) has a circumtropical distribution in tropical and temperate seas of the Pacific, Atlantic and Indian Oceans (Compagno *et al.*, 2005). It is a large species (up to 400 cm total length, TL), with oceanic and coastal, as well as epipelagic and mesopelagic habits, extending from the surface to ~4000 m depth (Compagno, 1995; Compagno *et al.*, 2005; Robertson and Allen, 2015; Gibson *et al.*, 2021).

It is the most active and fastest-swimming shark species (Compagno *et al.*, 2005). It feeds on prey including shrimps, squid, a range of fish (ranging from herrings to elasmobranchs and tunas) and marine mammals (Rosas-Luis *et al.*, 2016a). It is a species of ecological importance as it may regulate populations of prey species at lower trophic levels.

Isurus oxyrinchus is caught in pelagic longline fisheries occurring in the main ocean basins, where it has often been either a target or marketable bycatch species (Compagno, 1995, 2001). It is also caught in some gillnet fisheries and is one of the most appreciated target species by sports fishermen. Its meat is of high commercial value and is traded fresh, frozen, smoked, salted or desiccated for human consumption. Other body parts (fins, liver, skin and jaws) have also been utilized. Globally, there is a record of landings of 257,811 t during the period 1980–2020 (FAO, 2022). In Ecuador, it is taken in both targeted fisheries and as a bycatch and is captured both by artisanal and industrial fleets. The main landing ports in Ecuador are Manta and Daniel López (Manabí province), Santa Rosa and Anconcito (Santa Elena province). The type of boats used are fiberglass boats (handmade) and wooden mother ships (industrial). The fishing gear used are shallow-set longlines and gillnets. Its meat is used for local consumption and sold fresh or frozen (Martínez-Ortiz and García-Domínguez, 2013). During the period 2010–2012, approximately 29,551 t were landed by the artisanal fleet operating from Ecuadorian ports that fish for large pelagic fish (Coello and Herrera, 2018).

Based on the life-history characteristics of *I. oxyrinchus*, such as its very slow growth (k = 0.05–0.12), average sexual maturity (females = 273–278 cm L_T and males = 180–215 cm L_T), long gestation periods between 15 and 18 months, 3-year reproductive cycle and small litter size (4–25 embryos per litter) (Stillwell, 1990; Mollet *et al.*, 2000; Compagno, 2001; Joung and Hsu, 2005; Ribot-Carballal et al., 2005; Conde-Moreno and Galván-Magaña, 2006; Liu et al., 2018), it could be categorized as having a low biological productivity compared to many other elasmobranchs. Most populations of cartilaginous fish can resist low mortality levels before they present symptoms of stock depletion and collapse (Camhi et al., 1998; Musick, 1999; Cortés, 2000), declining faster than other bony fish (Sminkey and Musick, 1995, 1996). Additionally, the landings observed by the authors in the field during the last 20 years in Ecuador indicate that the fishing exploitation levels could have affected its populations. However, the lack of biological and ecological studies does not allow us to identify its current population status in Ecuadorian waters. Also, it is important to highlight that the International Union for the Conservation of Nature (IUCN) has assessed shortfin mako as Endangered globally, and with decreasing population growth (Rigby et al., 2019).

Diet and feeding habit analyses of a species are important to evaluate its ecological role and trophic position in the ecosystem (Allan and Castillo, 2007). Stomach content analysis of fish provides information on the feeding patterns and the quantitative evaluation of its feeding habits. It is an important aspect for informing ecosystem models and the ecosystem approach to fisheries management. The diet of fish represents the integration of many relevant ecological components, which include behaviour, body condition, habitat use and energy consumption, as well as intraspecific and interspecific interactions (Sagar et al., 2018). The diet analysis of the shortfin mako shark includes information from Yatsu (1995), Velasco-Tarelo (2005), Mucientes-Sandoval and Saborido-Rey (2008), Vetter et al. (2008), López et al. (2009), Preti et al. (2012), Rosas-Luis et al. (2016a), Klarian et al. (2018) and Márquez-García (2018) in the Pacific Ocean; Stillwell and Kohler (1982), Vaske-Jr and Ricón-Filho (1998), Maia et al. (2006), Wood et al. (2009), Gorni et al. (2012, 2013) and Biton-Porsmoguer et al. (2015, 2017) in the Atlantic Ocean; and Groeneveld et al. (2014) in the Indian Ocean. However, data for the Tropical Eastern Pacific Ocean are limited.

Based on the importance of food ecology studies and the role played by this shark within tropical marine ecosystems in the Ecuadorian area, it is important to understand the relationship between predator and its prey to know how the flow of nutrients and energy occurs in this type of pelagic habitat. This study aimed to describe the composition of the diet and feeding habits of *I. oxyrinchus* in the Ecuadorian Pacific Ocean and its relationship with sex and biological cycle phases, as well as to estimate its trophic niche breadth, diet overlap and trophic level.

Materials and methods

Sampling

The fishing port of Santa Rosa is located in the Santa Elena province (02°12'56"S; 80°57'26"W), Ecuador that depends economically on fishing activity (Figure 1). It is the second most important fishing port in the country, after Manta, in number and volume of landings, which include crustaceans, cephalopods, small and large pelagic fishes, sharks, rays and demersal fishes.

Samples of *I. oxyrinchus* were collected from Santa Rosa fishing port from May to December 2004 after being landed by the artisanal fishery. The total length (L_T), fork length (L_F) and precaudal length (L_{PC}) in cm (±0.1 cm) in a natural position were measured, and sex was recorded for each individual. Life stages were characterized through sexual maturity stages that were based on Clark and Von Schmidt (1965), Stevens (1983), Mollet et al. (2000) and Costa et al. (2002). Sexual maturity stages were recorded based on the following criteria for females: the shape of the cloaca and whether it was closed or open; courtship marks on the sides of their bodies; the condition of the ovaries, oviducal gland and uterus; and the presence of embryos. For males, the size and condition of claspers (rotation, calcification, opening of the rhipidium and presence of semen); the condition of the testes and seminal vesicle, were examined. The immature individuals were considered juveniles, and mature specimens as adults (Table 1).

The stomach was also obtained, and its fullness evaluated based on reference values of the scale by Stillwell and Kohler (1982): 0 (empty), 1 (25% full), 2 (50% full), 3 (75% full) and 4 (100% full). Subsequently, the stomach contents were placed in plastic bags and kept on ice for their transfer to the laboratory to freeze them.

Laboratory analysis

Samples were unfrozen to separate, count, measure (cm) and weigh (g) prey species found in the stomachs. Prey were grouped based on their digestion rate according to Olson and Galván-Magaña (2002): state 1 (individuals that present all the complete morphological characteristics and are easily identifiable), state 2 (organisms without skin and eyes, and with muscle exposure), state 3 (headless specimens, some body parts present and axial skeleton) and state 4 (otoliths, skeletons and squid beaks).

The identification of prey items found in the stomachs of *I. oxyrinchus* was carried out based on specialized guides. The crustacean species were identified by their exoskeleton according to Hendrickx (1995). The cephalopod species were identified using their mandible ('beaks') and bodies according to Ingrid et al. (1971), Wolff (1982, 1984), Clarke (1986), Roper et al. (1995), Jereb and Roper (2010) and Jereb et al. (2014). The fish species (i.e. complete organisms, skeletons and otoliths) were identified following Clothier (1950), Clothier and Baxter (1969), Fischer et al. (1995), García-Godos (2001), Jiménez and Béarez (2004), Muñoz (2012), Robertson and Allen (2015) and Vinueza (2015). The marine mammal species were identified according to Jefferson and Leatherwood (1995).

Data analysis

The L_T of females and males were compared through the non-parametric Mann–Whitney test (W) to investigate if there were significant differences between them. The same test was used for the comparison of the diet by sex and biological cycle phases (Daniel, 1991; Celis-De la Rosa and Labrada-Martagón, 2014). Organisms were grouped according to their biological cycle phases, regardless of their sex. In addition, length–frequency distributions were made by sex, using 10 cm length groups (modified from Holden and Raitt, 1975).

The number of stomachs analysed to adequately describe the diet of this species was established using the Pielou method (Hoffman, 1979). Likewise, the coefficient of variation was obtained for each stomach and plotted as a secondary axis; such coefficient was obtained by the relationship between the standard deviation and the average diversity of prey. For this purpose, the number of stomachs was estimated through the EstimateS V.8.0 software (Colwell, 2019), in which the number of stomachs analysed was subjected to 100 permutations to eliminate bias with $\alpha = 0.05$. The selection of the respective stomach number was the one whose variation was observed to be 0.05.

The ecological indices used were the numeric methods (%N) of frequency of occurrence (%FO_i) and gravimetry (%W) (Hyslop, 1980). The importance that each species contributed

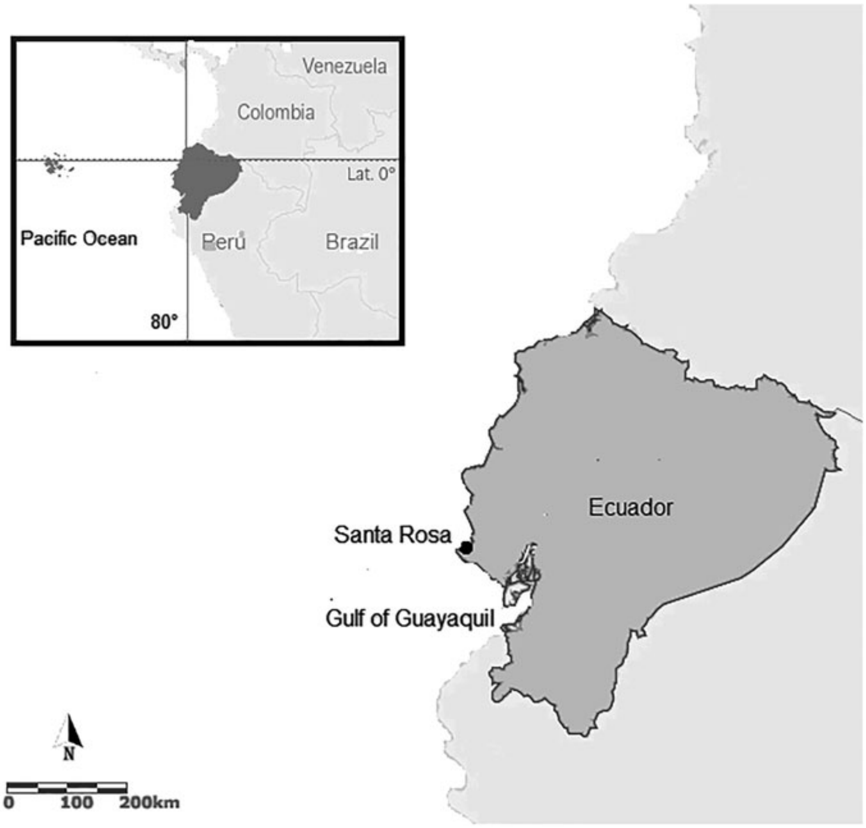

Figure 1. Location of the study area (Santa Rosa) in the Province of Santa Elena, Ecuador.

to the diet of *I. oxyrinchus* was evaluated through the Prey-Specific Index of Relative Importance (%PSIRI) (Brown *et al.*, 2011):

$$\%\text{PSIRI} = \frac{[\%\text{FOi}*(\%\text{PNi} + \%\text{PWi})]}{2}$$

where $\%PN_i$ = prey-specific numeric abundance and $\%PW_i$ = prey-specific weight abundance. These parameters were obtained from the following models:

$$\%\text{PNi} = \frac{\%\text{Ni}}{\%\text{FOi}}$$

$$\%\text{PWi} = \frac{\%\text{Wi}}{\%\text{FOi}}$$

The arrangement of the taxonomic order of the species consumed by the shortfin mako shark was completed based on Young *et al.* (2019) for cephalopods and Van der Laan *et al.* (2022) for bony fish.

The amplitude of the predator's diet was calculated through the Levin Index (*Bi*) (Krebs, 1985):

$$Bi = \frac{1}{n-1} \times \left[\left(\frac{1}{\sum P_{ij}^2} \right) - 1 \right]$$

where P_{ij} = proportion of prey j in the predator's diet i and n = number of prey species. The values of this index range from 0 to 1. Values lower than 0.6 indicate that the diet is dominated by few prey items, and thus, it would be a specialist consumer; while values equal to or greater than 0.6 suggest that consumers are generalists (Labropoulou and Eleftheriou, 1997).

The trophic overlap analysis (degree of food resource distribution) was estimated between sexes and maturity states through the Jaccard index (Krebs, 1999):

$$J = \frac{a}{a+b+c}$$

where J = Jaccard index, the same that employs the presence/absence of common prey in predators; a = number of common prey species in predators of both sexes or biological cycle phases; b = number of exclusive prey species of a predator (females or juvenile individuals); and c = number of exclusive prey species of the other predator (males or adult specimens). Values close to 0 indicate there is no overlap, while those close to 1 suggest that the use of food resources is identical. The program Past V.4.01 was used to determine this index (Hammer, 2020).

The trophic level was calculated from the equation proposed by Cortés (1999):

$$TL_k = 1 + \left(\sum_{j=1}^{n=24} Pj_x \times Tl_j \right)$$

where TL_k = trophic level of the predator, n = number of prey species, Pj_x = relative proportion of prey items that conform the consumer's diet and TL_j = trophic level of the prey. The trophic levels of the prey consumed employed in the TL_k estimates of *I. oxyrinchus* were obtained from Cortés (1999) and Froese and Pauly (2022). To categorize the trophic level of predators and prey, the scale proposed by Odum (1971) was used: TL-I: primary producers, TL-II: herbivores (fed on level I), TL-III: primary carnivores (consumed level II), TL-IV: secondary carnivores (ingested level III) and TL-V: tertiary carnivores (fed on level IV).

Given that some earlier studies had described the diet of *I. oxyrinchus* in relation to L_F or L_{PC}, the following length conversion

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Table 1. Number of sampled individuals of the shortfin mako shark, *Isurus oxyrinchus*, in Santa Rosa, Ecuador, Pacific Ocean, from May to December 2004, by sexes and biological cycle phases

Months	Females	Males	Juveniles	Adults	Total
May	8	7	11	4	15
June	12	13	18	7	25
July	11	6	16	1	17
August	15	6	20	1	21
September	12	12	21	3	24
October	5	5	8	2	10
November	16	11	22	5	27
December	2	1	2	1	3
Total	**81**	**61**	**118**	**24**	**142**

relationships were used for comparison with L_T:

$$L_F(\text{cm}) = (0.9120 \times L_T) + 5.7320 \; r^2 = 0.83$$

$$L_{PC}(\text{cm}) = (0.7647 \times L_T) + 5.5547 \; r^2 = 0.83$$

$$n = 142 \text{ lengths } = 104 - 295 \text{ cm } L_T(\bar{x} = 170.9 \pm 29.6)$$

Results

Characteristics of the sample

A total of 142 individuals were analysed, comprising 81 females (57.0%) and 61 males (43.0%). Females ranged from 104 to 295 cm L_T ($\bar{x} = 170.4 \pm 32.2$), while males ranged from 127 to 245 cm L_T ($\bar{x} = 171.7 \pm 25.9$). The largest female was 50 cm larger than the largest male but no significant differences were observed by sex ($W = 5872$; $p > 0.05$) (Figure 2). Furthermore, 118 specimens (83.1%) were juveniles and 24 (16.9%) were adults. Adult individuals were observed from 181 cm L_T onwards (males) and 216 cm L_T onwards (females).

Of the 142 stomachs analysed, 106 contained food (75%) and 36 were empty (25%). Approximately half of the studied stomachs were in state 1 ($n = 67$; 47.2%), followed by state 0 ($n = 36$; 25.4%), state 2 ($n = 18$; 12.7%), state 4 ($n = 13$; 9.2%) and state 3 ($n = 8$; 5.6%). Regarding the state of digestion of prey that composed the diet ($n = 289$), more than half were in a completely digested state (state 4; $n = 176$; 60.9%), followed by state 3 (advanced digestion; $n = 87$; 30.1%), and digestion states 1 and 2 ($n = 13$; 4.5%).

Based on the accumulative prey curve, the number of stomachs analysed in this study was sufficient to characterize the diet of *I. oxyrinchus*, given that the asymptote was reached at stomach 69. The variability of prey items decreased noticeably from stomach 54 (Figure 3).

Food composition

A total of 24 prey species or food components were identified, including shrimp remains, 12 cephalopods, 10 bony fish and one marine mammal. A total of 289 individuals that composed the diet of *I. oxyrinchus* were counted and weighed 392,079.46 g. According to the PSIRI (%), the most relevant prey species were Humboldt squid, *Dosidicus gigas* (42.57%); purpleback squid, *Sthenoteuthis oualaniensis* (21.04%); and halfbeak fish from the family Hemiramphidae (11.85%) (Table 2).

With regards to feeding by sex, the diet of females was composed of 20 species distributed in 157 individuals with a total mass of 219,332.19 g, which included shrimp remains, ten squids, eight teleosts and a marine mammal. The dominant prey species according to the PSIRI (%) were *D. gigas* (40.67%), *S. oualaniensis* (23.61%) and halfbeaks (13.34%). Likewise, males had a trophic spectrum of 17 species represented by 132 specimens with a total weight of 172,117.93 g. The most relevant prey based on the PSIRI (%) were also *D. gigas* (44.93%), *S. oualaniensis* (17.79%) and halfbeaks (9.97%) (Figure 4). There were no

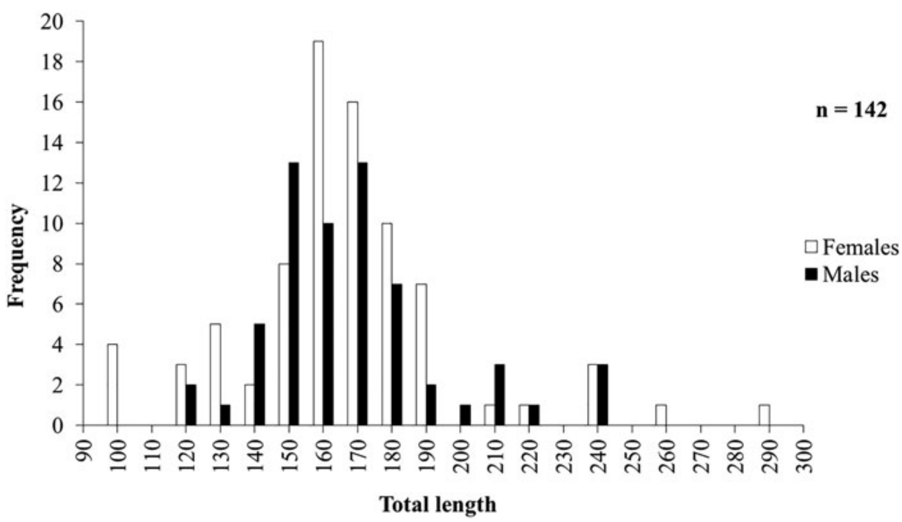

Figure 2. Size frequency distribution of the shortfin mako shark, *Isurus oxyrinchus*, landed in the Santa Rosa fishery port from May to December 2004.

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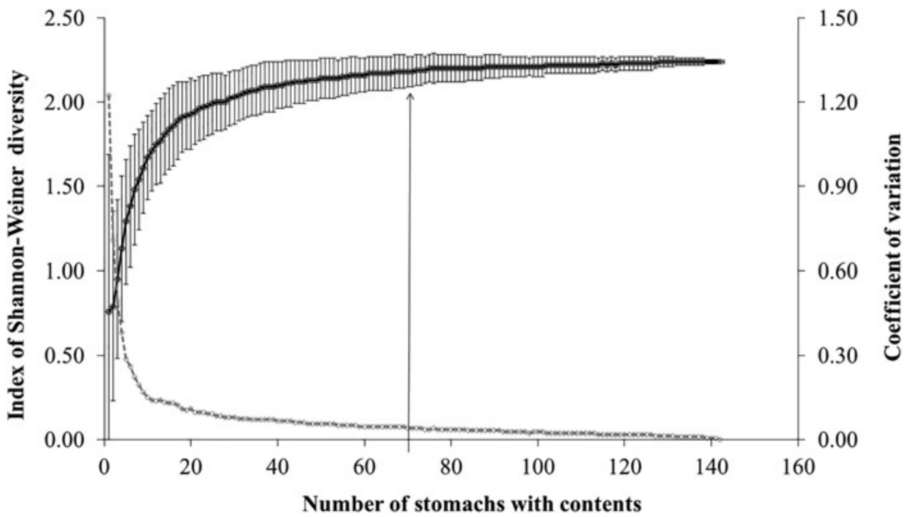

Figure 3. General cumulative curve of the prey species consumed by the shortfin mako shark, *Isurus oxyrinchus*, in Santa Rosa, Province of Santa Elena, Ecuador, Pacific Ocean. Arrow indicates the number of stomachs where the curve reached the asymptote.

significant differences between the composition of the diet of *I. oxyrinchus* by sex ($W = 589$; $p > 0.05$).

The diet of juvenile sharks was comprised of 22 species distributed in one shrimp, ten cephalopods, ten bony fish and one marine mammal, equal to 244 individuals with a total weight of 307,335.35 g. The most abundant species according to the PSIRI (%) were *D. gigas* (42.78%), *S. oualaniensis* (19.08%) and halfbeaks (12.43%). Adult sharks had a trophic spectrum of 12 species, including eight squid and four teleosts represented by 46 specimens with a total weight of 82,892.92 g. The most relevant species based on the PSIRI (%) were *D. gigas* (42.49%) and *S. oualaniensis* (30.54%) (Figure 5). No significant differences were registered between the diet of *I. oxyrinchus* by life stages ($W = 648$; $p > 0.05$).

Feeding habits

Breadth of trophic niche. Isurus oxyrinchus was a specialist predator that preferred three prey species out of the available 24 prey ($Bi = 0.25$). This behaviour remained the same in the rest of the analysed categories. Males ($Bi = 0.34$) presented a slightly higher value than females ($Bi = 0.29$). Similarly, adults ($Bi = 0.37$) registered a higher value than juveniles ($Bi = 0.27$).

Trophic overlap. The trophic overlap was moderate between females and males ($J = 0.54$), as well as for juveniles and adults ($J = 0.42$), that is, their food components were consumed regardless of their sex or life stages, so there was no defined pattern in the use of food resources.

Trophic level. The trophic level for this species was $TL_k = 4.47$, which indicated that *I. oxyrinchus* was a top predator of the secondary carnivore type. The trophic levels by sex ($TL_k = 4.46$ in females and $TL_k = 4.49$ for males), as well as by biological cycle phases ($TL_k = 4.49$ in juvenile sharks and 4.40 in adults) were similar.

Discussion

Food composition

The prey observed in this study included cephalopods, teleosts and marine mammals, with a high preference for squid, which agrees with the findings of previous studies. The diet of *I. oxyrinchus* along Ecuadorian Pacific Ocean has been poorly studied (Pincay-Espinoza, 2014; Rosas-Luis *et al.*, 2016a, 2017). However, some trophic studies in the Pacific and other oceans suggest that this species is piscivorous (Stillwell and Kohler, 1982; Vaske-Jr and Ricón-Filho, 1998; Maia *et al.*, 2006; López *et al.*, 2009; Wood *et al.*, 2009; Preti *et al.*, 2012; Biton-Porsmoguer *et al.*, 2015, 2017; Klarian *et al.*, 2018) and teuthophagous (Mucientes-Sandoval and Saborido-Rey, 2008; Vetter *et al.*, 2008; Gorni *et al.*, 2013; Rosas-Luis *et al.*, 2016b). Such observations suggest that the diet of *I. oxyrinchus* is related to geographic location, oceanic productivity and prey availability.

Even though *I. oxyrinchus* had a high preference for specific groups of prey (e.g. fish and/or cephalopods), it presents a wide trophic spectrum composed of birds (López *et al.*, 2009; Rosas-Luis *et al.*, 2016a), marine mammals (Stillwell and Kohler, 1982; Mucientes-Sandoval and Saborido-Rey, 2008; López *et al.*, 2009; Wood *et al.*, 2009; Preti *et al.*, 2012; Biton-Porsmoguer *et al.*, 2015, 2017; Rosas-Luis *et al.*, 2016a; Klarian *et al.*, 2018), sea turtles (Biton-Porsmoguer *et al.*, 2015, 2017), other elasmobranchs (Applegate, 1966; Bass *et al.*, 1975; Stillwell and Kohler, 1982; Maia *et al.*, 2006; López *et al.*, 2009; Wood *et al.*, 2009; Groeneveld *et al.*, 2014; Rosas-Luis *et al.*, 2016a) and crustaceans (Maia *et al.*, 2006; Mucientes-Sandoval and Saborido-Rey, 2008; López *et al.*, 2009; Wood *et al.*, 2009; Biton-Porsmoguer *et al.*, 2015, 2017; Rosas-Luis *et al.*, 2016a). This wide trophic spectrum indicates that the use of habitat behaves similarly regardless of its geographic area. Despite this, the selection of prey depends, to a large extent, on their availability (López *et al.*, 2009).

The similarity in the feeding behaviour of *I. oxyrinchus* in the different study areas could be related to habitat changes as a result of large vertical migrations (Wootton, 1990; López *et al.*, 2009), which can reach depths of up to 800 m during the day (Bress, 1993; Loefer *et al.*, 2005; Field *et al.*, 2007; Vetter *et al.*, 2008; Abascal *et al.*, 2011). During this time, the species shows a high preference for depths below 300 m. Conversely, this species is located between the surface and 300 m of depth during the night (Vetter *et al.*, 2008).

The bathymetric preferences of *I. oxyrinchus* indicate that this species has mesopelagic habits, which is supported by its high preference for the consumption of squids of the family Ommastrephidae (Stillwell and Kohler, 1982; Vetter *et al.*, 2008; López *et al.*, 2009; Preti *et al.*, 2012; Rosas-Luis *et al.*, 2016a, 2016b; this study). These squids occur from the surface to bathypelagic zones (0–2000 m of depth), with a high nocturnal activity between the surface and 200 m (Jereb and Roper, 2010). Additionally, it consumes epipelagic, mesopelagic and bathypelagic fish such as longfin cubehead, *Cubiceps pauciradiatus*, which is distributed vertically from 50 to 1000 m (Cervigón, 1994; López *et al.*, 2009); escolar, *Lepidocybium flavobrunneum* (200–

Table 2. Prey consumed by the shortfin mako shark, *Isurus oxyrinchus*, and its respective indices

Prey species	N	%N	%N_i	FOi	%FO_i	W	%W	%W_i	%PSIRI
Crustaceans									
Shrimp remains	1	0.35	0.36	1	0.95	1	0.00	0.00	0.17
Cephalopods									
Mastigoteuthis dentata	1	0.35	0.36	1	0.95	0.01	0.00	0.00	0.17
Ancistrocheirus lesueurii	26	9.00	0.50	19	18.10	6.81	0.00	0.00	4.50
Abraliopsis sp.	4	1.38	0.36	4	3.81	432.61	0.11	0.03	0.75
Gonatus californiensis	2	0.69	0.36	2	1.90	136.59	0.03	0.02	0.36
Histioteuthis heteropsis	3	1.04	0.36	3	2.86	3 863.08	0.99	0.34	1.01
Histioteuthis hoyle	3	1.04	0.36	3	2.86	1 708.28	0.44	0.15	0.74
Octopoteuthis sicula	1	0.35	0.36	1	0.95	1.47	0.00	0.00	0.17
Dosidicus gigas	71	24.57	0.66	39	37.14	237 480.25	60.57	1.63	42.57
Ommastrephes bartramii	5	1.73	0.36	5	4.76	3072.01	0.78	0.16	1.26
Sthenoteuthis oualaniensis	36	12.46	0.59	22	20.95	116 168.16	29.63	1.41	21.04
Onychoteuthis banksii	1	0.35	0.36	1	0.95	8 516.19	2.19	2.30	1.27
Thysanoteuthis rhombus	3	1.04	1.09	1	0.95	3	0.00	0.00	0.52
Fish									
Family Scombridae	1	0.35	0.36	1	0.95	32.50	0.01	0.01	0.18
Auxis rochei eudorax	28	9.69	0.57	18	17.14	4 552.50	1.16	0.07	5.42
Auxis thazard brachydorax	3	1.04	0.54	2	1.90	724.70	0.18	0.10	0.61
Thunnus alalunga	15	5.19	0.45	12	11.43	3 923.35	1.00	0.09	3.10
Thunnus albacares	2	0.69	0.36	2	1.90	230	0.06	0.03	0.38
Thunnus obesus	1	0.35	0.36	1	0.95	661.50	0.17	0.18	0.26
Coryphaena equiselis	11	3.81	0.40	10	9.52	4 888.25	1.25	0.13	2.53
Coryphaena hippurus	3	1.04	0.36	3	2.86	453.80	0.12	0.04	0.58
Family Hemiramhidae	65	22.49	1.69	14	13.33	4 717.70	1.20	0.09	11.85
Aluterus monoceros	2	0.69	0.36	2	1.90	261	0.07	0.03	0.38
Marine mammals									
Order Cetacea	1	0.35	0.36	1	0.95	164.70	0.04	0.04	0.19
Total	**289**	**100**				**392 079.46**	**100**		**100**

N, number; %N, percentage of number; %N_i, percentage of prey-specific abundance; FO_i, frequency of occurrence; %FO_i, percentage of frequency of occurrence; W, weight; %W, percentage of weight; %W_i, percentage of prey-specific weight; %PSIRI, percentage of prey-specific index of relative importance. The taxonomic order of the prey species is based on Young *et al.* (2019) for cephalopods and Van der Laan *et al.* (2022) for fish.

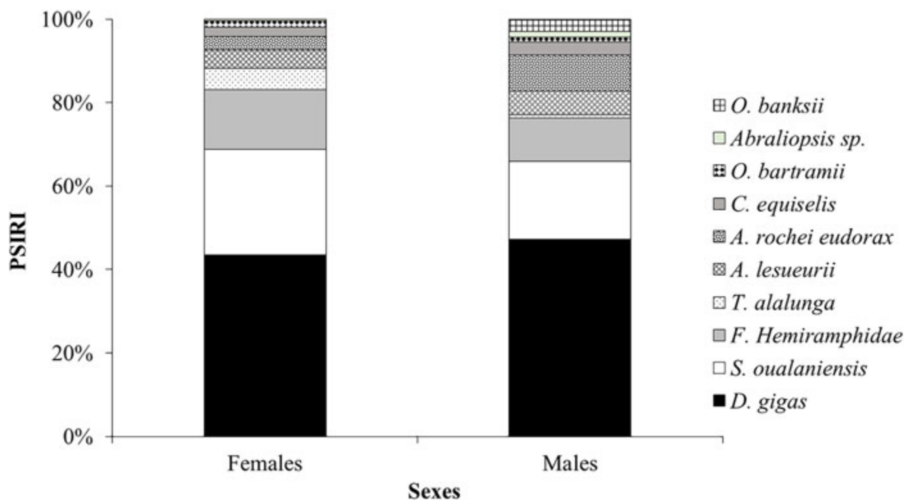

Figure 4. Values of prey-specific index of relative importance (%PSIRI) for females and males of *Isurus oxyrinchus* for each main species and others that compound its diet in the Ecuadorian Pacific Ocean.

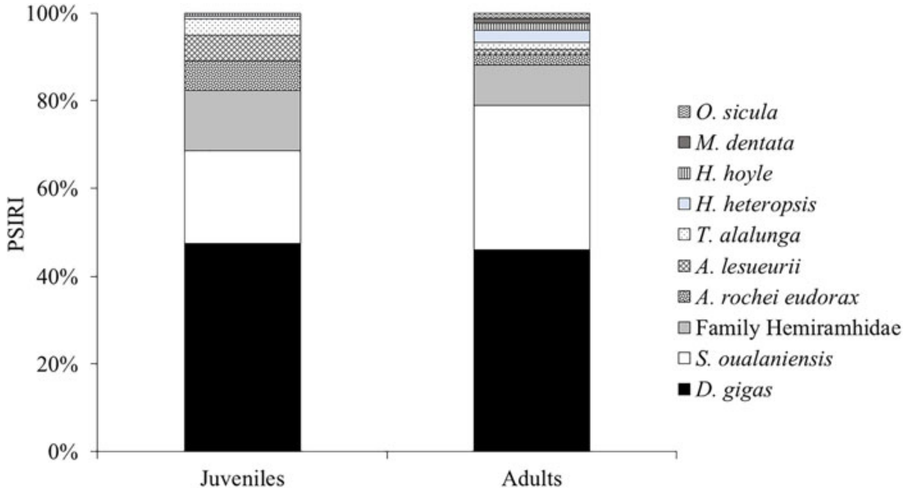

Figure 5. Values of prey-specific index of relative importance (%PSIRI) of juvenile and adult individuals of *Isurus oxyrinchus* for each main species and others that compound its trophic spectrum in waters of Ecuador.

1000 m depth; Shcherbachev, 1987; Riede, 2004; Gorni *et al.*, 2013); Atlantic saury, *Scomberesox saurus* (0–30 m depth; Wisner, 1990; Biton *et al.*, 2015); bluefish, *Pomatomus saltatrix* (0–200 m depth; Stillwell and Kohler, 1982; FAO-FIGIS, 2005); and snake mackerel, *Gempylus serpens* (0–600 m depth; Cervigón, 1994; Mucientes-Sandoval and Saborido-Rey, 2008; McMillan *et al.*, 2011). Thus, the depth ranges of the prey consumed by *I. oxyrinchus* coincide with the depths that this species frequents at different times of the day, allowing for prey selection and habitat use.

Furthermore, ontogenic shifts are influenced by habitat use, which is a characteristic documented in other shark species such as sickle fin smooth-hound, *Mustelus lunulatus* (Méndez-Macías *et al.*, 2019); blue shark, *Prionace glauca* (Estupiñán-Montaño *et al.*, 2019); scalloped hammerhead, *Sphyrna lewini* (Estupiñán-Montaño *et al.*, 2021a, 2021b); *I. oxyrinchus* (Maia *et al.*, 2006; Mucientes-Sandoval and Saborido-Rey, 2008; Preti *et al.*, 2012; Malpica-Cruz *et al.*, 2013; Klarian *et al.*, 2018; Tamburín *et al.*, 2019); and *I. paucus* (Estupiñán-Montaño and Delgado-Huertas, 2022). This condition can be explained by the results obtained in a stable isotope study at different maturity stages in shortfin mako shark (Tamburín *et al.*, 2019). These latter authors found that young-year-old embryos and juveniles of *I. oxyrinchus* (80–100 cm L_T) show isotopic signals of oceanic origin as a product of maternal transfer processes. Moreover, the study showed that larger individuals (>100 cm L_T) increase the consumption of oceanic prey, suggesting this species moves from coastal to oceanic areas changing habitats as it grows (Tamburín *et al.*, 2019), where it consumes larger prey with a higher caloric intake (Pope *et al.*, 2001).

Similar to other studies, the low incidence of dolphins observed in the present study demonstrates a low preference for this prey group in the diet of *I. oxyrinchus* (Wood *et al.*, 2009; Biton-Porsmoguer *et al.*, 2015, 2017; Rosas-Luis *et al.*, 2016a; Klarian *et al.*, 2018). Therefore, its intake could rather be the product of an opportunistic strategy by this predator (Maia *et al.*, 2006; Mucientes-Sandoval and Saborido-Rey, 2008).

Feeding habits

A total of 24 prey species composed the *I. oxyrinchus*' diet in the Ecuadorian Pacific. This is similar to previous studies that describe the diet of this species with a trophic spectrum of 17–24 prey items (Mucientes-Sandoval and Saborido-Rey, 2008; López *et al.*, 2009; Biton-Porsmoguer *et al.*, 2017; this study). Furthermore, the feeding behaviour of *I. oxyrinchus* observed in the present study is of a specialist type for all the categories analysed, due to the preferential consumption of *D. gigas*, *S. oualaniensis* and halfbeaks (Hemiramphidae). This resembles to that reported by other authors, which the feeding strategy of this species is considered specialist (Field *et al.*, 2007; Zeidberg and Robinson, 2007; Lopez *et al.*, 2012), but as somewhat opportunistic and/or generalist in some cases (Velasco-Talero, 2005; López *et al.*, 2009; Maia *et al.*, 2006; Pincay-Espinoza, 2014).

It is important to highlight the dominance of *D. gigas* in the *I. oxyrinchus*' diet may be a response to the population increase of this squid species throughout the EPO (Field *et al.*, 2007; Zeidberg and Robinson, 2007). Therefore, it is evident that *I. oxyrinchus*' foraging behaviour would be conditioned to (i) the migratory nature that allows it to forage in different types of habitats (Wootton, 1990; López *et al.*, 2009; Gibson *et al.*, 2021); (ii) the availability of prey and its abundance (López *et al.*, 2009; Pincay-Espinoza, 2014) related to spatiotemporal variability (Maia *et al.*, 2006; Mucientes-Sandoval and Saborido-Rey, 2008; Pincay-Espinoza, 2014; Biton-Porsmoguer *et al.*, 2015). For example, in North America, a high contribution of Pacific saury, *Cololabis saira*, in the diet of *I. oxyrinchus* has been recorded, which has been associated to the fact that this shark takes advantage of the high aggregations of *C. saira* during their reproductive season, given this species uses the California current to lay its eggs (Froese and Pauly, 2022); therefore, *I. oxyrinchus* takes advantage of this phenomenon to obtain easy and very abundant food (Juanes *et al.*, 1996; Salerno *et al.*, 2001). Also, ontogenetic changes may occur associated with prey consumption and habitat use (Maia *et al.*, 2006; Mucientes-Sandoval and Saborido-Rey, 2008; Preti *et al.*, 2012; Malpica-Cruz *et al.*, 2013; Klarian *et al.*, 2018; Tamburín *et al.*, 2019). This information would explain the specialist, opportunistic and/or generalist nature of this species throughout its distribution.

The diet analysis by sex and biological cycle phases indicated that there was a moderate similarity between categories, suggesting a certain degree of food competition between them. However, these estimates differ from that reported by other authors which report high values of similarity indices, $C\lambda_{\text{Sexes}} = 0.97$ (Maia *et al.*, 2006); 0.87 (Pincay-Espinoza, 2014) and $C\lambda_{\text{Maturity stages}} = 0.71$–0.98 (Maia *et al.*, 2006); 0.52–0.85 (Pincay-Espinoza, 2014).

The different estimates of trophic overlap obtained in this and other studies could indicate that *I. oxyrinchus* have segregation processes related to the habitat use and behaviour (Wearmouth and Sims, 2008), which would be explained by the greater trophic spectrum of females (20 prey species) compared to that of males (17). Therefore, we hypothesize that female *I. oxyrinchus* could prefer to use oceanic and coastal areas, potentially then interacting with more demersal prey in coastal areas, whereas males would prefer to use oceanic areas. This habitat use by the sexes of *I. oxyrinchus* could be conditioned by the availability and abundance of prey in the area, environmental and oceanographic factors, among others. Therefore, more studies are needed to validate this hypothesis, because of that, these results should be interpreted with caution.

Sharks are generally considered top predators in marine ecosystems, although this characterization is not always correct for all shark species, since their functional role in ecosystems is conditioned by factors such as maximum body length, geographic distribution, trophic breadth, vulnerability to predation by other sharks (Roff *et al*., 2016) and feeding habits (Cortés, 1999). Based on the last aspect, stomach content and stable isotope studies have estimated that *I. oxyrinchus* occupies medium and high trophic positions between 3.60 and 4.96 (Cortés, 1999; Estrada *et al*., 2003; Rosas-Luis *et al*., 2016a; Biton-Porsmoguer *et al*., 2017).

The trophic level for *I. oxyrinchus* indicated that this species was a top predator of the secondary carnivore type. This high value (trophic position) is the result of the high consumption of prey that occupy different positions in the marine trophic chain of the Ecuadorian Pacific, as is the case of *D. gigas* ($TL = 4.14$), *S. oualaniensis* ($TL = 4.09$), *Ancistrocheirus lesueurii* ($TL = 4.13$), *A. rochei eudorax* ($TL = 4.13$) and hemiramphids ($TL = 2.82$) (Froese and Paul, 2022). In addition to these food preferences, the large body size of *I. oxyrinchus*, maximum 4 m TL (Compagno, 2001), its wide range of horizontal (~2500 km) and vertical (~4000 m depth) movements (Gibson *et al*., 2021) and its diet breadth are additional characteristics that allow this species to position itself at the top of the marine food chain (Roff *et al*., 2016) and thus, consume prey from different habitats as well as from various trophic levels.

According to the previous classification and the position estimate of *I. oxyrinchus* obtained in this study, this species is considered a top predator that fulfils the functions of a carnivore. These results are similar to other species of same family Lamnidae, as the white shark, *Carcharodon carcharias*, $TL = 4.1–5.4$ (Kerr *et al*., 2006; Hussey *et al*., 2012) and longfin mako shark, *Isurus paucus*, $TL = 3.5–5.7$ (Estupiñán-Montaño and Delgado-Huertas, 2022). Therefore, this species plays an important role in the health maintenance of the Ecuadorian Pacific marine ecosystem, and may help to regulate lower trophic levels through top-down control (Navia *et al*., 2010; Bornatowski *et al*., 2014).

Data. The authors confirm that the data supporting the findings of this study are available within the article.

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