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Diet of the bull shark, *Carcharhinus leucas*, and the tiger shark, *Galeocerdo cuvier*, in the eastern Pacific Ocean

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Abstract: This study presents information on the diet of two shark species, *Carcharhinus leucas* and *Galeocerdo cuvier*, that inhabit the southeastern Pacific Ocean. The stomachs were collected from October 2003 to July 2005 in Ecuador. Stomachs of 41 *C. leucas* and six *G. cuvier* were analyzed. According to the index of relative importance (%IRI), the most important prey for *C. leucas* were fishes: family Ophichthidae (13.41%), *Tylosurus pacificus* (9.79%), *Katsuwonus pelamis* (4.54%), and fish remains (44.81%). *G. cuvier*, for its part, consumed squids: *Ancistrocheirus lesueuri* (45.14%), *Pholidoteuthis boschmaii* (7.81%), and *Octopoteuthis* spp. (5.17%), as well as turtles: *Caretta caretta* (9.7%), *Lepidochelys cf. kempii* (5%), and turtle remains (16.5%). The results show that *C. leucas* (trophic level, I_{TR}; 4.32 ± 0.13) and *G. cuvier* (I_{TR}; 4.26 ± 0.09) are tertiary consumers, occupying high positions in the food chain, but also are generalist predators that feed on a variety of prey. The high frequency of sea turtles in the stomachs of *G. cuvier* (>300 cm) suggests that this shark species is an important predator of turtles, which are commonly found along the southeastern Pacific coasts.

Key words: Top predator, feeding habits, trophic level, Ecuador, stomach contents

Sharks are apex predators in marine ecosystems and play an important role in regulating prey populations at lower trophic levels (e.g., fish, invertebrates, reptiles, mammals and birds) (Ellis et al., 1996).

The bull shark, *Carcharhinus leucas* (Müller and Henle, 1839), and the tiger shark, *Galeocerdo cuvier* (Péron and Lesueur, 1822), are common worldwide in tropical and subtropical coastal areas (Compagno, 1984). The bull shark grows to a large size (over 340 cm) (Compagno, 1984) and frequently inhabits shallow water (max. depth 30 m) (Compagno, 1984). It is one of the few shark species that is physiologically capable of spending time in fresh water (Pillans and Franklin, 2004) and has been reported in rivers and lakes (Thorson et al., 1973; Thomerson et al., 1977; Montoya and Thorson, 1982; Simpendorfer et al., 2005). The tolerance of bull sharks for low-salinity conditions allows them to frequent areas close to shore and near river mouths, where they may interact with other shark species (Carlson et al., 2010). The tiger shark reaches a larger size than the bull shark (over 550 cm) (Compagno, 1984), with a wide tolerance for different marine habitats at depths ranging from the surface to 140 m. This species is apparently nocturnal and shows a diel cycle of movement, moving inshore at night into shallow bays, estuaries, passes between islands, lagoons, and other shallow areas (e.g., Tricas et al., 1981; Alfonso and Hazin, 2015).

The species *C. leucas* and *G. cuvier* are opportunistic predators; they consume a wide variety of prey from crustaceans to cephalopods, sea turtles, teleosts, elasmobranchs, marine mammals, and fishing waste (e.g., Compagno, 1984; Snelson et al., 1984; Simpfendorfer, 1992; Lowe et al., 1996).

Fishing is one of the most important economic activities in Ecuador and often involves the capture of sharks, including *C. leucas* and *G. cuvier*, adding to the approximately 30 species caught in Ecuadorian waters. Both species are listed as "Near Threatened" in the International Union for Conservation of Nature (IUCN) Red List (IUCN, 2016). Despite this, there is a lack of knowledge about the basic biology of these sharks and few related management policies in Ecuador, apart from the National Plan of Action for the Conservation and Management of Sharks (Ministry of Foreign Trade, Industrialization, Fisheries and Competitiveness [MICIP, by its Spanish acronym], 2006) and the

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Ministerial Agreement No. 116 in 2013 (Estupiñán-Montaño et al., 2017). Some studies have focused on sharks' dietary habits (e.g., Estupiñán-Montaño et al., 2009, 2017; Polo-Silva et al., 2009, 2013; Loor-Andrade et al., 2015) and reproduction (Romero-Caicedo et al., 2014). However, no studies have examined the biology of the bull shark (*C. leucas*) and the tiger shark (*G. cuvier*) in the eastern Pacific Ocean. Thus, the aims of this paper were: (1) to describe the diet and estimate the trophic position of these two top predators in the southeastern Pacific Ocean; and (2) to contribute an implementation of the National Plan of Action for the Conservation and Management of Sharks of Ecuador.

This study analyzes the stomach contents of *C. leucas* and *G. cuvier* caught in Ecuadorian waters and landed in the port of Manta (Ecuador) between October 2003 and July 2005. The study area extended from 02°N to 02°S and from the Ecuadorian coast to 84°W (Figure 1). For each shark specimen, total length (TL in cm) was measured and sex was recorded before the digestive tract was extracted. Stomach contents were removed and filtered through a 1.5-mm mesh filter, stored in labelled plastic bags, and preserved on ice for transportation to the laboratory.

To determine the importance of prey taxa, the index of relative importance (IRI; Pinkas et al., 1971) was calculated as follows (Hyslop, 1980): IRI = (%N + %W) × (%FO) from previously calculated numerical percentage (%N), gravimetric percentage (%W, expressed in g) and frequency of occurrence (%FO), and IRI values were standardized to percentages (Cortés, 1997).

The standardized trophic level of sharks was calculated using the trophic index, I_{TR} (Cortés, 1999):

$$I_{TR} = 1 + \left(\sum_{j=1}^{n} I_{TR_j} \right),$$

where I_{TRj} is the trophic level of each prey taxa *j* and P_j is the proportion of each category of prey *j* in the predator's diet, based on weight values. The trophic levels of all prey were obtained from Cortés (1999), Hobson and Welch (1992), www.fishbase.org (Froese and Pauly, 2016), and www.seaaroundus.org (Pauly and Zeller, 2015). All calculations were performed using R software (R Core Team, 2013).

A total of 41 bull sharks (*C. leucas*) (20 females, 10 males, and 11 unsexed), with sizes ranging from 200 to 315 cm TL (mean ± SE: 267.4 ± 7.9), were examined. Food was found in 18 of these 41 individuals (31.2%), while 23 (39.9%) of them were empty. According to %IRI, the most important preys were conger eels (Ophichthidae), longtail stingrays (*Dasyatis longa*), needlefish (*Tylosurus pacificus*), skipjack tunas (*Katsuwonus pelamis*), and groupers (*Epinephelus labriformis*) (Table). The females of *C. leucas* consumed mainly sea turtles like *Lepidochelys olivacea* and fish species like *Umbrina roncador*, *Mugil cephalus*, and *Xiphias gladius*, while the males fed mainly on fish of the family Ophichthidae and the species *T. pacificus*, *K. pelamis*, and *D. longa*, as well as on sea turtles (Cheloniidae) (Figure 2; Table).

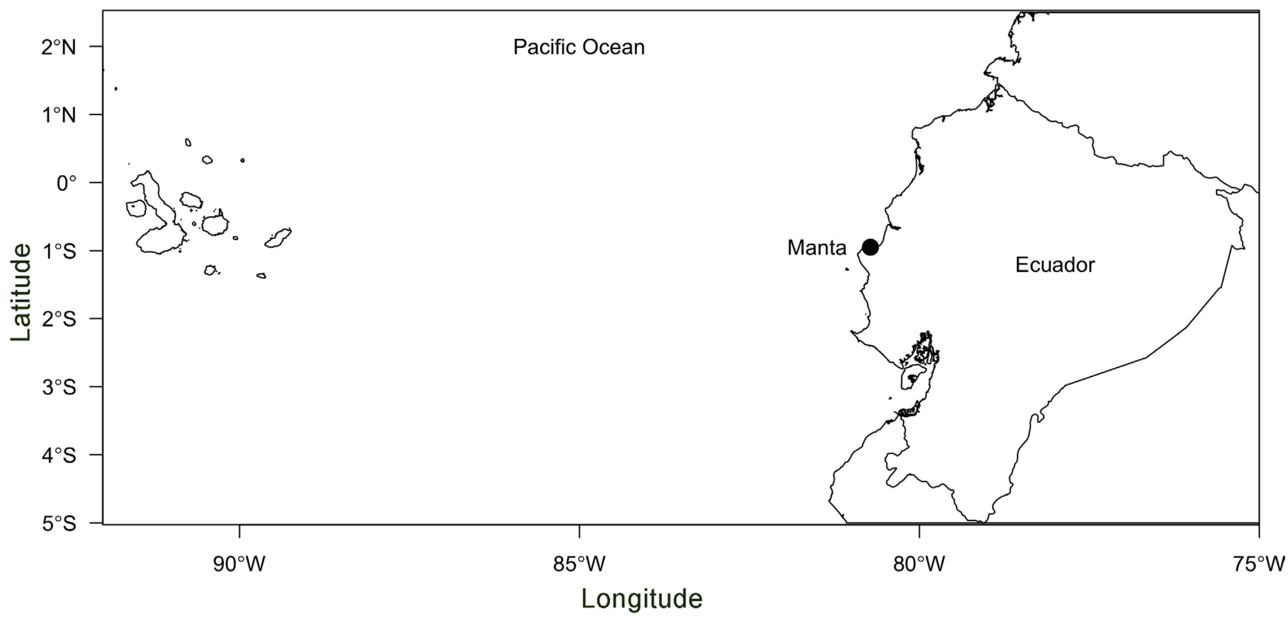

Figure 1. Landing port of the bull shark, *Carcharhinus leucas*, and tiger shark, *Galeocerdo cuvier*, caught in Ecuadorian waters.

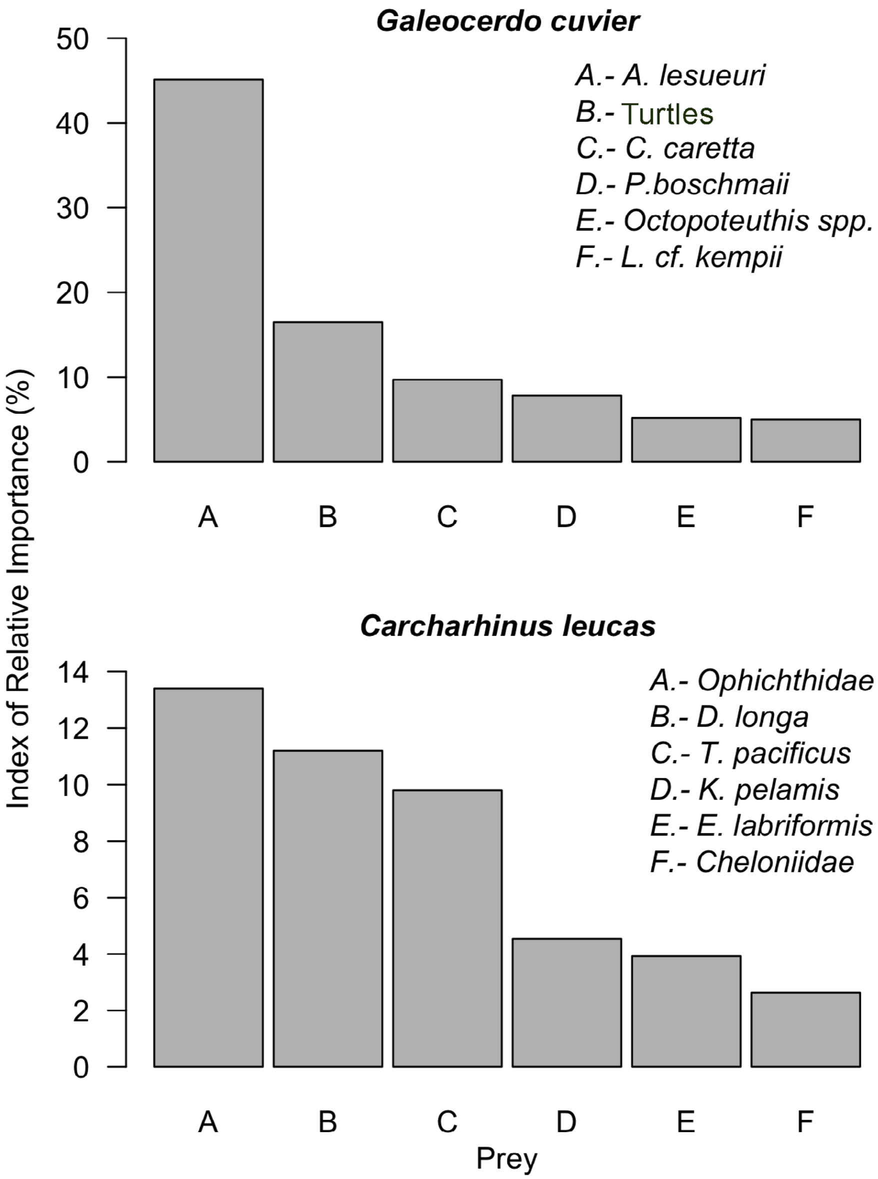

Figure 2. Trophic spectrum of the bull shark, *Carcharhinus leucas*, and tiger shark, *Galeocerdo cuvier*, in Ecuadorian waters.

Food was found in the stomach of six tiger sharks (*Galeocerdo cuvier*) (three females and three males) with sizes ranging from 139 to 450 cm TL (270.4 ± 38.5). The species consumed by this predator included some cephalopods (mainly squids: *Ancistrocheirus lesueurii* and *Pholidoteuthis boschmaii*), reptiles (sea turtles), and fishes (Figure 2; Table).

The average trophic level of *C. leucas* and *G. cuvier* was 4.32 ± 0.13 and 4.26 ± 0.09, respectively, which indicates that both species occupy a high position in the food web.

There is no information in the literature on the diet of *C. leucas* and *G. cuvier* in Ecuador. In other parts of the world, however, trophic research has been carried out for both species.

The bull shark, *C. leucas*, feeds on prey from different habitats around the world, in both marine and freshwater environments (Tuma, 1976). The species is considered a generalist predator, consuming any type of available prey (Baughman and Springer, 1950; Casey, 1964; Tuma, 1976). The bull sharks, *C. leucas*, have been found to eat echinoderms (e.g., sea urchins), mollusks (e.g., cephalopods), arthropods (e.g., crustaceans and crabs), elasmobranchs (e.g., sharks, rays, and sawfish), teleosts, marine mammals (e.g., cetaceans, porpoises, and whale remains), terrestrial organisms (e.g., dogs, cats, rabbits, and human remains), birds, and reptiles; various items like plant remains, paper, bottles, garbage, fish waste, and plastic (Nichols, 1917; Bell and Nichols, 1921; Gudger, 1932; Darnell, 1958;

Table. Trophic spectrum of the sharks *Carcharhinus leucas* and *Galeocerdo cuvier* in the southeastern Pacific Ocean, expressed numerically (%N), gravimetrically (%W), and frequency of occurrence (%FO), and index of relative importance (%IRI).

Prey	*Carcharhinus leucas*				*Galeocerdo cuvier*			
	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
Mollusca	6.78	<0.01	–	1.19	61.77	43.92	–	59.06
Ancistrocheirus lesueuri	–	–	–	–	38.24	32.12	40.00	45.14
Octopoteuthis spp.	–	–	–	–	5.88	2.17	40.00	5.17
Pholidoteuthis boschmaii	–	–	–	–	14.71	9.63	20.00	7.81
Mastigoteuthis spp.	–	–	–	–	2.94	< 0.01	20.00	0.94
Gastropods	6.78	< 0.01	5.26	1.19	–	–	–	–
Chondrichthyes	5.08	16.25	–	11.20	–	–	–	–
Dasyatis longa	5.08	16.25	15.79	11.20	–	–	–	–
Osteichthyes	82.98	71.75	–	83.29	11.76	8.08	–	8.81
Fam. Muraenidae	1.69	0.03	5.26	0.30	–	–	–	–
Herpetoichthys fossatus	1.69	1.34	5.26	0.53	–	–	–	–
Ophichthus remiger	1.69	0.13	5.26	0.32	–	–	–	–
Ophichthus spp.	23.73	14.59	10.53	13.41	–	–	–	–
Tylosurus pacificus	11.86	6.79	15.79	9.79	–	–	–	–
Opisthonema libertate	1.69	0.22	5.26	0.33	–	–	–	–
Mugil cephalus	1.69	0.73	5.26	0.42	–	–	–	–
Coryphaena hippurus	1.69	0.16	5.26	0.32	–	–	–	–
Eucinostomus currani	1.69	1.48	5.26	0.55	–	–	–	–
Umbrina roncador	1.69	0.27	5.26	0.34	–	–	–	–
Epinephelus labriformis	1.69	20.73	5.26	3.92	–	–	–	–
Katsuwonus pelamis	6.78	6.19	10.53	4.54	–	–	–	–
Sphyraena ensis	1.69	0.14	5.26	0.32				
Xiphias gladius	1.69	4.19	5.26	1.03				
Brotula spp.	1.69	< 0.01	5.26	0.30				
Balistes polyleptis	1.69	10.10	5.26	2.06	–	–	–	–
Eucinostomus entomelas	–	–	–	–	2.94	1.55	20.00	1.44
Diodon spp.	–	–	–	–	2.94	4.77	20.00	2.47
Fish remains	18.64	4.65	57.89	44.81	5.88	1.76	40.00	4.90
Reptilia	5.07	12.00	–	4.30	26.44	48.05	–	32.19
Lepidochelys olivacea	1.69	1.56	5.26	0.57	2.94	0.15	20.00	0.99
Fam. Cheloniidae	1.69	5.83	10.53	2.63	–	–	–	–
Caretta caretta	–	–	–	–	2.90	27.20	20.00	9.70
Lepidochelys cf. kempii	–	–	–	–	14.70	0.90	20.00	5.00
Turtle remains	1.69	4.61	5.26	1.10	5.90	19.80	40.00	16.50

Schuwartz, 1960; Springer, 1960; D'Aubrey, 1964; Clark and Schmidt, 1965; Sadowsky, 1971; Tuma, 1976; Snelson et al., 1984; Cliff and Dudley, 1991; Tillett et al., 2014); and even members of their own species (cannibalism) (Snelson et al., 1984).

This study agrees with observations made in previous studies, reporting similar dietary components (e.g., rays, cephalopods, teleosts, and sea turtles). These findings confirm that *C. leucas* is a generalist predator (Crow and Hewitt, 1988; Ellis and Musick, 2007; Lopez et al., 2009), with the highest number of prey consumed in coastal environments, between the sea surface and seafloor, as shown by the species' tendency for a higher consumption of fish (Table). The trophic analysis revealed no dietary pattern by sex, as both sexes consumed a large proportion of fish and sea turtles. The small number of analyzed specimens, however, does not allow inferences on the diet by sex of *C. leucas*; this result should thus be viewed with caution when drawing conclusions.

Randall (1992) reports that the tiger shark, *G. cuvier*, feeds on a wide variety of teleosts, sharks (including members of its own species), rays, sea turtles, seabirds, sea lions, dolphins, cephalopods, lobsters, crabs, gastropods, and jellyfish. It can also feed on carrion, terrestrial animals, waste, garbage, plastic, and metal, among other things. Studies following that by Randall (1992) have reported similar dietary components, but also sea snakes and manatees (Stevens and McLoughlin, 1991; Simpfendorfer, 1992; Lowe et al., 1996; Smale and Cliff, 1998; Schwartz, 2000; Simpfendorfer et al., 2001; Papastamatiou et al., 2006; Bornatowski et al., 2007, 2014a). Despite the small number of *G. cuvier* stomachs analyzed here, the results obtained agree with these previous studies, with the presence of similar groups of prey (teleosts, sea turtles, and cephalopods).

Teleost fishes, seabirds, cephalopods, and crustaceans, as well as some sharks are important prey for <300-cm TL individuals of *G. cuvier*, while those >300-cm TL consume other elasmobranchs, sea turtles, crustaceans, seabirds, and cephalopods, as well as terrestrial and marine mammals (Simpfendorfer, 1992; Lowe et al., 1996; Heithaus, 2001; Simpfendorfer et al., 2001; Papastamatiou et al., 2006; Bornatowski et al., 2007, 2014a).

The results of the present study are consistent with the prey recorded elsewhere: a 450-cm TL male of *G. cuvier* was found to have consumed a loggerhead sea turtle (*Caretta caretta*) of 2306.6 g (almost the whole of it), while six pairs of jaws of the turtle *Lepidochelys cf. kempii* and one of the turtle *L. olivacea* were identified in a 319-cm TL female. These findings suggest that sea turtles are an important component of the diet of >300-cm TL *G. cuvier* (Witzell, 1987).

In Ecuadorian waters, the presence of sea turtles in the stomachs of *G. cuvier* may indicate: (1) a possible dietary specialization (Bornatowski et al., 2007) in this group of >300-cm TL sharks; and (2) that these sharks likely feed on sea turtles at night, when they rest on the seafloor, or in the daytime, when at the surface. This shark species may be an important regulator of sea turtle populations in the Ecuadorian Pacific, which was also documented in Australia, where it was observed that sea turtles are an important dietary component of >200-cm TL *G. cuvier* (Heithaus, 2001).

Ecuador has beaches that are used as nesting areas by various species of sea turtles (Mizobe and Contreras, 2014; Ministerio del Ambiente [Ecuador's Ministry of Environment], 2014), but, in spite of this, no study to date seems to have reported the consumption of sea turtles by another predator in these waters. The high percentage of cephalopods in the diet of *G. cuvier* suggests that it is a predator with both coastal and oceanic habits; further studies are needed, however, to deepen understanding of the species' dietary patterns in Ecuador. These studies would allow confirmation of the hypotheses put forward in this paper and, by the same way, generate information that will allow the actual role of the species in the area's marine food web to be quantified.

The trophic levels estimated here for *C. leucas* (4.32) and *G. cuvier* (4.26) confirm that both species occupy a high position in the trophic web of the southeastern Pacific and the Ecuadorian Pacific coast. Being top predators makes them important in controlling lower trophic levels (Stevens et al., 2000; Myers et al., 2007; Heithaus et al., 2008; Navia et al., 2010). Thus, the reduction of their populations may result, through trophic cascade effects, in changes in marine populations (Ferretti et al., 2010; Heithaus et al., 2010).

Because they feed on a wide variety of prey along the Ecuadorian Pacific coast, *C. leucas* and *G. cuvier* are generalist predators, and because they occupy a high position in the marine food web, these sharks are important regulators of lower trophic levels. This study also suggests that *C. leucas* inhabits coastal areas, while *G. cuvier* carries out migrations between coastal and oceanic area; further *G. cuvier* is a predator of the sea turtles that are commonly found along the southeastern Pacific coasts. It seems, therefore necessary to broaden biological studies of both species, taking size, sex, and state of sexual maturity into account, as well as to study the role of these predators in ecosystems over their lifetime.

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