Environmental Biology of Fishes **47**: 203–211, 1996.

Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters

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Received 23.2.1995 Accepted 24.1.1996

Key words: Dietary analysis, Prey diversity, Predatory behavior, Elasmobranch

Synopsis

Stomach content data from 281 tiger sharks caught during shark control programs in Hawaii between 1967 and 1969, and during 1976 were analyzed to examine feeding habits and ontogenetic shifts in diet. As sharks increased in size, prey diversity and frequency of occurrence of large prey items increased. The percent occurrence of teleosts and cephalopods in stomachs decreased as sharks increased in length, while occurrence of elasmobranchs, turtles, land mammals, crustaceans, and undigestible items increased. Comparisons between the diets of tiger sharks from Hawaii and other locations indicate that ontogenetic shifts are universal in this species and that tiger sharks may be opportunistic feeders that prey heavily on abundant, easy to capture prey. Small tiger sharks may be spatially segregated from medium and large sharks and appear to be primarily nocturnal, bottom feeders. Large tiger sharks feed near the bottom at night, but also feed at the surface during the day. Prey, similar in size to humans, begin to occur in the diet of tiger sharks approximately 230 cm TL, and therefore sharks of this size and larger may pose the greatest threat to humans. Ontogenetic shifts in diet may be attributed to increased size of sharks, expanded range and exploitation of habitats of larger sharks, and/or improved hunting skill of larger sharks.

Introduction

The diet of the tiger shark, *Galeocerdo cuvier*, has received more qualitative attention and study than the diet of other shark species. This large, circumglobal shark is an opportunistic feeder, with a varied and cosmopolitan diet (Bell & Nichols 1921, Gudger 1949, Randall 1992), however, few studies have attempted to quantify the diet of tiger sharks.

Ontogenetic dietary shifts have been documented in the leopard (Talent 1976), sandbar (Springer 1960, Medved et al. 1985), soupfin (Olsen 1954), lemon (Cortés & Gruber 1990), mako (Stillwell & Kohler 1982), white (Tricas & McCosker 1984, Klimley 1985), and other sharks (Wetherbee et al. 1990), but ontogenetic changes in the diet of the tiger shark have received little attention. Rancurel & Intes (1982) suggested that small tiger sharks (< 200 cm total length) fed heavily on reef fish found in shallow lagoons of New Caledonia, while large sharks appeared to consume larger prey such as turtles and birds as well as deep water crabs and squid. Simpfendorfer (1992) found that small tiger sharks (< 150 cm TL) in Australian waters con-

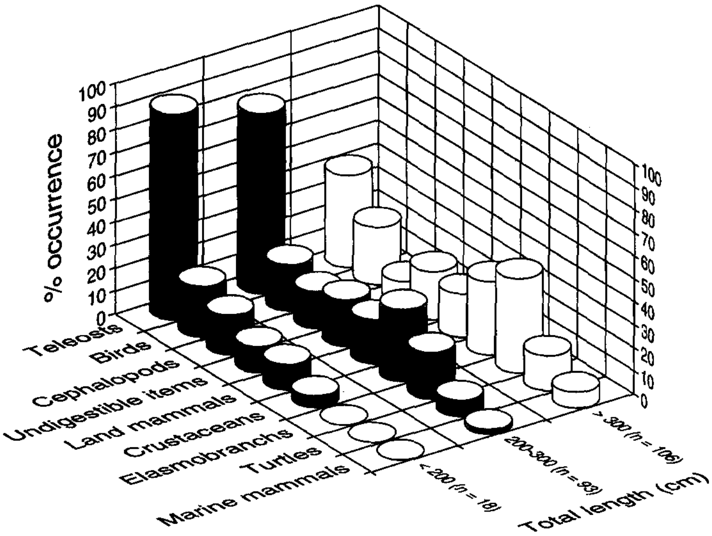

Fig. 1. Percentage of stomachs (% occurrence) containing major prey groups of three size classes of tiger sharks collected from the main Hawaiian Islands.

sumed primarily sea snakes and teleosts, while larger sharks preyed more heavily on turtles, birds, and elasmobranchs. However, neither study alluded to the possible mechanisms that may cause ontogenetic shifts in diet.

This study describes both the overall diet of tiger sharks in Hawaiian waters and ontogenetic shifts in the diet of these sharks. In addition, this study furnishes insight into the movement, distribution, and feeding behavior of tiger sharks of different ontogenetic intervals based on dietary analysis.

Methods and materials

These data were obtained from the Cooperative Shark Research and Control Program which ran from June 1967 to June 1969 (Tester unpublished). Additional data were obtained from the less extensive Shark Abatement/Student Training Program, which ran from 10 June to 20 June, 1976, and the Shark Utilization/Student Training Program, which spanned from August to September 1976. Fishing was conducted around the main Hawaiian Islands (Niihau, Kauai, Oahu, Maui, Lanai, Kahoolawe, Molokai, and Hawaii) (for review see Wetherbee et al. 1994).

Fishing effort was concentrated around Oahu, with sharks predominantly caught on longlines, although handlines were also employed (Wetherbee et al. 1994). Longlines consisted of three 800 m sections (24 hooks per section) set parallel to shore at depths ranging from 8 to 118 m, with the majority of sets in less than 30 m of water. Tiger sharks were caught, killed, and brought on the deck of the boat. Total length (TL), pre-caudal length, and sex of each shark were recorded. Stomach contents were identified to the lowest possible taxon.

For analysis of stomach content data, tiger sharks were grouped into three size classes (< 200 cm = small, 200–300 cm = medium, and > 300 cm TL = large sharks), which were chosen for comparison with data from Rancurel & Intes (1982). The frequency of occurrence of prey groups in stomachs were recorded for each size class. Stomachs containing bait or sharks noted in the records as being scavenged off the lines were not included in analyses. Human refuse or non-natural food (e.g. ham, steak, cardboard, tin foil) found in stomachs of sharks were grouped as undigestible items and were not included in dietary overlap analysis. Dietary overlaps of the three size classes were compared using the Simplified Morisita Index (C_H) (Krebs 1989). The degree of overlap was determined according to Langton's (1982) scale: low overlap, 0–0.29; medium overlap, 0.30–0.59; and high overlap, greater than

0.60. The prey diversities of the three size classes of tiger sharks were compared using the Shannon-Weiner Diversity Index (H′) (Krebs 1989).

Results

Of 281 tiger sharks stomachs examined from shark control programs, 217 (77%) contained food items. Small sharks (n = 28) were caught less frequently than sharks in the medium (n = 118) and large size classes (n = 135). Sixty-four percent of the small sharks, 79% of the medium sharks, and 78% of the large size class of sharks contained food in their stomachs.

The smallest size class of sharks contained only five major prey groups. Teleosts (89%) were the most common prey followed by birds (22%), cephalopods (17%), land mammals (5%), and crustaceans (5%). Eleven percent of stomachs of small sharks contained undigestible items (Fig. 1).

Larger sharks consumed a wider variety of prey, with both medium and large size classes consuming eight major prey groups. Teleosts (78%) were the most common prey found in the stomachs of medium size sharks followed by crustaceans (32%), birds (20%), elasmobranchs (20%), land mammals (19%), cephalopods (16%), sea turtles (7%), and marine mammals (2%). Twenty percent of stomachs of medium size sharks contained undigestible items. Elasmobranchs (42%) and teleosts (40%) were the most common prey found in stomachs of large sharks, followed by crustaceans (35%), birds (25%), land mammals (19%), turtles (15%), cephalopods (10%), and marine mammals (7%). Twenty-one percent of stomachs of large sharks contained undigestible items (Fig. 1).

Prey composition varied among the three size classes, with medium overlap between the small and medium size sharks (C_H = 0.47), and between small and large size sharks (C_H = 0.30), whereas, a high degree of overlap was observed between the medium and large size sharks (C_H = 0.79). Prey diversity also varied among the three size classes of tiger sharks. The small size class of tiger sharks had a lower prey diversity (H′ = 0.50) than the medium (H′ = 0.75) or large sharks (H′ = 0.84).

Ontogenetic shifts in the diet of tiger sharks caught in the control programs were apparent (Fig. 1). The percent occurrence of teleosts and cephalopods in stomachs decreased with increasing shark length, whereas crustaceans, turtles, land mammals, and undigestible items increased. All identifiable birds were marine or aquatic species and occurred in similar proportions in the stomachs of all three size classes of sharks (Fig. 1). Elasmobranchs, turtles, or marine mammals were only found in the stomachs of sharks exceeding 230 cm TL, and their occurrences doubled from medium to large size sharks.

Crustaceans occurred more often in larger sharks, whereas cephalopods became less common (Fig. 1). Small shark stomachs contained no lobsters, whereas 29% of medium and 32% of large shark stomachs contained lobsters (Table 1). No elasmobranchs or green sea turtles, *Chelonia mydas*, were found in the stomachs of small sharks, but their occurrences more than doubled from medium to large size sharks. The only marine mammals found in the stomachs of sharks were dolphins (Cetacea), which occurred in medium (2%) and large sharks (7%). The only land mammals found in the stomachs of small sharks were two cats, whereas medium and large-size sharks contained cats, dogs, mongooses, rats, and parts of horses, sheep, and goats. Human remains were found in the stomach of one tiger shark (335 cm TL), which was one of the larger sharks caught.

Teleost diversity increased in the diet with increasing shark size (Fig. 2). Puffer (Tetraondotidae) and porcupine fish (Diodontidae) were the most common teleosts in stomachs of all three size classes of sharks. Tetraodontids occurred most often in the smaller sharks (44%) and their occurrence decreased as sharks got larger (10% and 3% respectively). Diodontids occurred frequently in medium sized sharks (41%), but were much less common in the small (11%) or large sharks (15%). Several families of pelagic fishes, including tuna (Scombridae) and marlin (Istiophoridae) were found in stomachs of large sharks.

The occurrence of undigestible items in stomachs also changed with shark length (Table 1). Small sharks had only kitchen scraps (chicken, ham

Table 1. Number (n) and percentage of stomachs (%) of three size classes of tiger sharks from the main Hawaiian Islands which contained a specific prey group. % is the percentage of stomachs with food containing a specific prey group.

	< 200		200–300		> 300	
	n	%	n	%	n	%
Stomachs examined	28	–	118	–	135	–
Empty stomachs	10	36	25	21	29	22
Cephalopods	3	17	15	16	11	10
Unidentified cephalopod	3	17	6	6	5	5
Octopus	0	0	7	7	5	5
Squid	0	0	2	2	1	1
Crustaceans	1	5	30	32	37	35
Unidentified lobsters	0	0	8	9	16	15
Slipper lobster	0	0	11	12	12	11
Spiny lobster	0	0	8	9	6	6
Crab	1	5	3	3	2	2
Mantis shrimp	0	0	0	0	1	1
Elasmobranchs	0	0	19	20	45	42
Sharks	0	0	17	18	39	37
Rays	0	0	2	2	6	6
Teleosts	16	89	73	78	42	40
Tetraodontidae	8	44	9	10	3	3
Diodontidae	2	11	38	41	16	15
Fistulariidae	0	0	3	3	1	1
Aulostomidae	1	5	2	2	1	1
Carangidae	0	0	2	2	3	3
Balistidae	0	0	2	2	0	0
Congridae	1	5	1	1	1	1
Sphyraenidae	0	0	1	1	1	1
Muraenidae	1	5	1	1	0	0
Mullidae	1	5	0	0	0	0
Scaridae	1	5	1	1	0	0
Coryphaenidae	0	0	1	1	0	0
Labridae	0	0	1	1	0	0
Pleuronectidae	0	0	1	1	0	0
Belonidae	0	0	1	1	0	0
Pomacentridae	0	0	1	1	0	0
Monacanthidae	0	0	0	0	1	1
Acanthuridae	0	0	0	0	2	2
Scombridae	0	0	2	2	3	3
Istiophoridae	0	0	0	0	3	3
Ostraciidae	0	0	0	0	1	1
Reptiles	0	0	7	7	16	15
Chelonia mydas	0	0	7	7	16	15
Aves	4	22	19	20	27	25
Mammals	1	5	9	10	17	16
Dolphin	0	0	2	2	8	7
Horse	0	0	2	2	0	0
Goat	0	0	1	1	3	3
Sheep	0	0	2	2	0	0
Dog	0	0	0	0	2	2
Cat	1	5	0	0	0	0
Mongoose	0	0	0	0	1	1

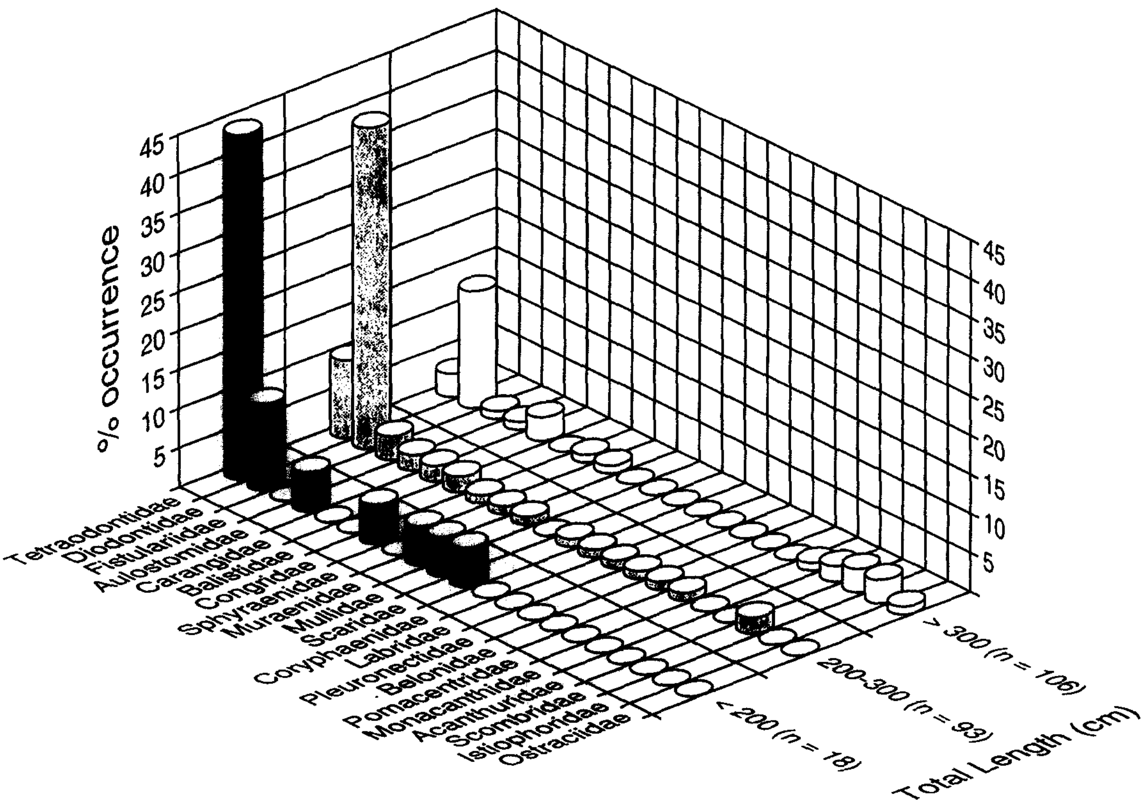

Fig. 2. Percentage of stomachs (% occurrence) containing teleost families of three size classes of tiger sharks collected from the main Hawaiian Islands.

Table I. Continued

	< 200		200–300		> 300	
	n	%	n	%	n	%
Rat	0	0	2	2	2	2
Human	0	0	0	0	1	1
Undigestible items	2	11	19	20	22	21
Kitchen scraps	2	11	7	7	3	3
Tin foil	0	0	4	4	5	5
Cellophane	0	0	1	1	4	4
Sticks	0	0	1	1	4	4
Plastic bags	0	0	2	2	0	0
Paper	0	0	3	3	5	5
Plant material	0	0	1	1	2	2
Tin cans	0	0	2	3	1	1
Cardboard	0	0	0	2	2	2
Clothing	0	0	1	0	2	2
Miscellaneous	0	0	2	3	0	0

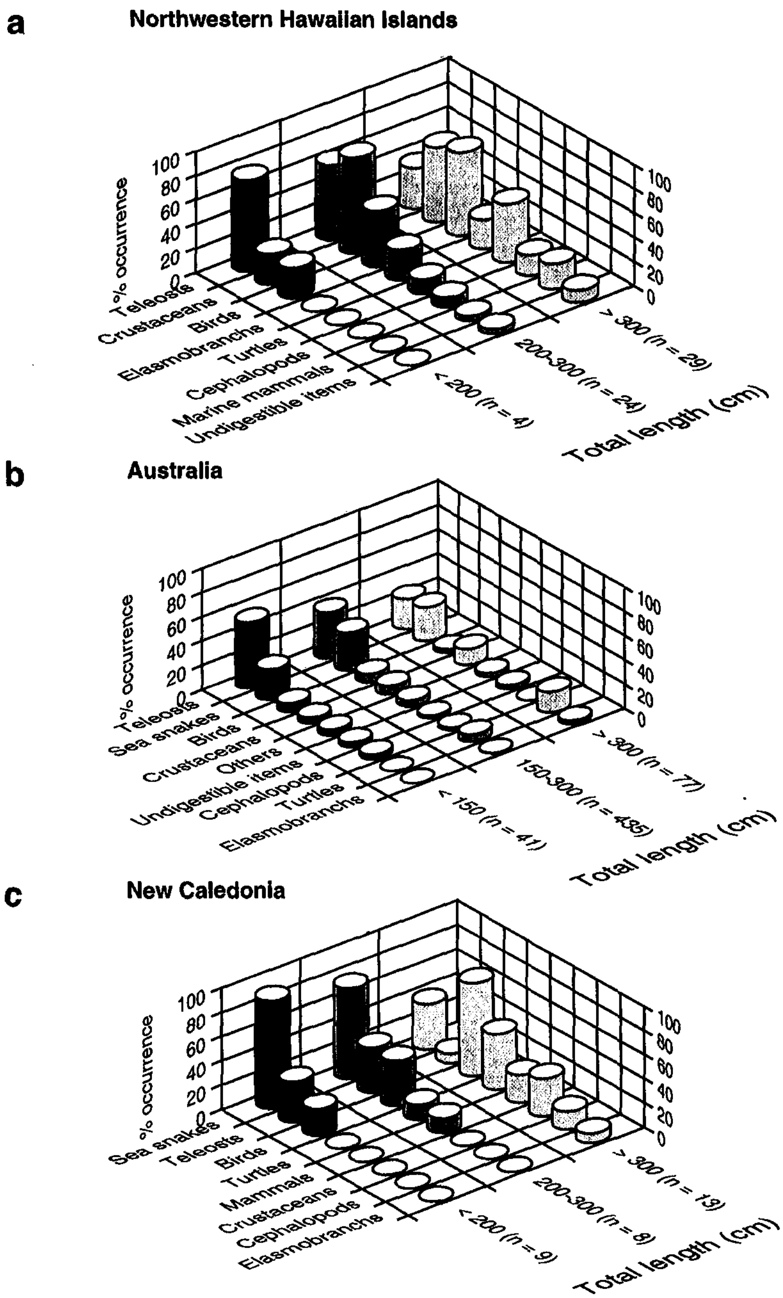

Fig. 3. Percentage of stomachs (% occurrence) containing major prey groups of three size classes of tiger sharks collected from: a – the Northwestern Hawaiian Islands (data from Taylor & Naftel unpublished and De Crosta et al. 1984), b – Australian waters (figure modified from Simpfendorfer 1992), and c – New Caledonian waters (data from Rancurel & Intes 1982).

bones, bologna sandwich, steak, Spam, and lemon and grapefruit rinds) in their stomachs (11%), whereas, medium (20%) and large size sharks (21%) contained kitchen scraps, along with other food related refuse such as tin foil, tin cans, plastic bags, cellophane, paper, and cardboard in their stomachs.

Discussion

Comparison of the diet between three size classes of tiger sharks collected around the main Hawaiian Islands (MHI) indicates that there is an ontogenetic dietary shift, particularly after sharks exceed 200 cm total length (TL). Smaller sharks (< 200 cm) contained a lower diversity of prey and fewer large prey than larger sharks.

Comparison of stomach contents from tiger sharks collected from the remote Northwestern Hawaiian Islands (NWHI) showed similar dietary trends as sharks examined from the MHI (Figure 3a). Tiger sharks collected from several of the NWHI (Nihoa, Maro, Necker, French Frigate Shoals, Midway, Pearl and Hermes, and Lisianski islands) showed large increases in the percent occurrence of birds, crustaceans, turtles, and marine mammals as sharks increased in size (data from Taylor & Naftel unpublished; De Crosta 1984). The NWHI are known as very productive seasonal breeding grounds for marine turtles, sea birds, and the Hawaiian monk seal (Polovina 1984). Tiger sharks have been observed feeding on these animals very close to shore and are believed to congregate in the lagoons surrounding these islands seasonally (W. Gilmartin personal communication). Tiger sharks may migrate to these islands from other locations to take advantage of the large seasonal influx of prey.

Apparently, ontogenetic shifts in diet occur universally in this species. Dietary analysis of tiger sharks from Australia showed an increase in sea snakes, turtles, elasmobranchs, and crustaceans as sharks increased in size (Simpfendorfer 1992) (Figure 3b). Tiger sharks from New Caledonia fed less frequently on sea snakes and teleosts as sharks increased in size, but birds, turtles, mammals, crustaceans, cephalopods, and elasmobranchs increased in occurrence (Rancurel & Intes 1982) (Figure 3c). Although different prey groups were found in the stomachs of tiger sharks from different locations, increased prey diversity and size of prey occurred in each area.

Ontogenetic changes in prey diversity and size of prey may be attributed to several factors: (1) larger sharks can feed on larger prey; (2) different size sharks may occupy different habitats; and (3) larger sharks may be more efficient hunters and capable of capturing faster prey.

The increase in prey diversity of tiger sharks with increased size may be partially attributed to the addition of larger prey types in the diet after sharks exceeded 230 cm TL. However, even small prey such as teleosts, crustaceans, land mammals, and undigestible items increased in diversity as sharks increased in size. This increase in prey diversity of smaller prey items indicates that large sharks are not merely shifting their diet to include larger prey, but are also expanding their diet by eating a wider variety of smaller prey. Larger prey may provide a greater net energetic payoff, making it more beneficial for larger sharks to capture these prey.

The varying degree of dietary overlap between the different size classes of tiger sharks may be the result of size-related changes in activity patterns. Lemon sharks were found to increase their habitat range as they increased in length (Cortés & Gruber 1990, Morrissey & Gruber 1993). Larger tiger sharks may range over and exploit a greater variety of habitats, providing them with a larger selection of prey. Larger tiger sharks contained more pelagic species of teleosts, such as scombrids, coryphaenids, and istiophorids, indicating that they may spend more time in the pelagic environment than smaller sharks. Rancurel & Intes (1982) suggested that large tiger sharks from New Caledonia fed in deeper, pelagic waters more often than small sharks, since deep water crabs (*Geryon* sp.) and pelagic squid were found in the stomachs of only the large sharks.

Small sharks may occupy habitats different from those of the larger sharks to avoid predation. Kauffman (unpublished) observed lower catch rates of small tiger sharks from Philippine waters, and suggested that the smaller sharks might be segregated to avoid predation by adults. Low catch rates of small sharks from Hawaii also suggest that tiger sharks segregate by size. Although fishing gear and bait may have selected for larger tiger sharks, small carcharhinid sharks were commonly caught on the same gear, indicating that small tiger sharks could have been caught if they were in those locations.

Ontogenetic changes in feeding behavior and acquired hunting skills (Wetherbee et al. 1990) may also result in increased prey diversity and size of prey in larger sharks. Because the larger prey types, such as turtles, elasmobranchs, marine mammals, and pelagic teleosts are more mobile than small benthic prey, sharks may have to develop special hunting skills to capture these prey. Smaller sharks may only be capable of capturing slow moving prey (tetraodontids, diodontids, cephalopods, and crabs) either because of their hunting ability, or physical limitations. Branstetter et al. (1987) stated that small tiger sharks may not be capable of rapid swimming speeds because of their thin, elongated bodies, and anguilliform swimming motion.

Foraging behavior may also change as sharks increase in size. Many of the slow moving prey found in the stomachs of small tiger sharks are nocturnally active, benthic associated prey (Hobson 1974), which suggests that small sharks spend a majority of their time foraging at night near the bottom. Stomachs of larger sharks also contained these prey, but also contained prey that are more commonly found on, or near the surface (turtles, birds, and mammals). Larger sharks may be feeding both at the surface during the day and along the bottom at night.

Ontogenetic shifts in diet of tiger sharks may provide insight into the understanding of shark attacks on humans. One theory suggests that white sharks may mistake humans for their natural prey (McCosker 1985). Klimley (1985) suggested that white sharks shift from a diet of primarily teleosts to marine mammals after attaining a size greater than 240 cm in length. Therefore, larger white sharks may pose an increased threat to humans after this shift in diet because these prey are similar in size to humans. Large tiger sharks feed on large turtles, elasmobranchs, and marine mammals, which are also similar in size to humans. In our study, these prey types were not found in any stomachs of tiger sharks less than 230 cm TL. Therefore, tiger sharks 230 cm TL or larger may pose the greatest threat to humans.

This study has demonstrated that ontogenetic shifts occur in the diet of tiger sharks in Hawaiian waters, although the mechanisms regulating these shifts are still unclear. Additional studies focusing on activity patterns, distribution, and social behavior of tiger sharks of different size classes will provide further insight useful for understanding the mechanisms responsible for ontogenetic shifts in feeding habits.

Acknowledgements

This paper is dedicated in memory of Albert Tester, who was responsible for collecting the majority of the data used in this study. We also wish to thank G. Lowe, K. Holland, E. Cortés, C. Manire, and L. Ferry for their reviews of this manuscript and J. Parrish and L. Taylor for use of their unpublished data. We thank S. Wendland-Gardner for translation of Rancurel & Intes (1982) paper. Original funding for the Hawaii Cooperative Shark Research and Control Program was provided by NSF GB-6139, Oceanic Institute, and the State of Hawaii. H.I.M.B. contribution No. 1001.

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