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ISSN 0285-3191

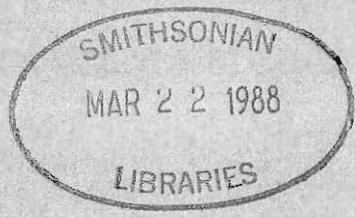
Vol. 12, No. 1

Aug. 1987

爬虫両棲類学雑誌

JAPANESE JOURNAL OF HERPETOLOGY

第12卷 第1号



日本爬虫両棲類学会
THE HERPETOLOGICAL SOCIETY OF JAPAN
KYOTO

Selective Predation on Large Cheloniid Sea Turtles by Tiger Sharks (*Galeocerdo cuvier*)

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Abstract: Tiger sharks (*Galeocerdo cuvier*) selectively prey on large cheloniid sea turtles. Of 404 tiger shark stomachs examined in eight previously published studies, 327 (80.9%) contained food; and 68 (20.8%) of those sharks with food also contained large cheloniid sea turtle remains. The literature indicates that tiger sharks are the only elasmobranch predator that consistently eats large boney turtles. Tiger sharks are able to specialize in such a diet because they share the same in-shore habitat as turtles, and have developed a unique masticating mechanism and feeding behavior. A rational tiger shark harvesting program is suggested to reduce predation on some endangered sea turtle populations.

There is little known about predation on large cheloniid sea turtles. Various sea turtle reviews have revealed little useful information other than listing "sharks" as probable predators (Hirth 1971; Marquez 1976; Witzell 1983). A cursory review of documented predators of juvenile and adult sea turtles by Stancyk (1981) listed six shark species: hammerhead (*Sphyrna* sp.), lemon (*Nagaprion brevirostris*), white (*Carcharodon carcharias*), bull (*Carcharhinus leucas*), oceanic white tip (*Carcharhinus longimanus*) and tiger (*Galeocerdo cuvier*). However, the present review of shark literature indicates that only tiger sharks prey extensively on large cheloniid sea turtles, although a large number of other shark species undoubtedly feed on smaller individuals. In order for tiger sharks to specialize on large boney prey, they have: 1) adopted the same neritic habitat as turtles, 2) evolved unique cutting teeth that have heavy, oblique cusps with coarse serrations, and 3) developed a feeding behavior that involves a rolling motion of both jaws that, combined with the specialized teeth, enables the tiger shark to cleanly cut through bone and scutes without damage to the teeth and jaws.

Accepted 13, Jul. 1987

In this paper I discuss the tiger shark as a specialized predator of large boney sea turtles using data and information obtained from an extensive literature review. During the course of this review I have attempted to limit the cases of predation to large turtles only (carapace length usually greater than 50 cm). It is hypothesized that the turtles in these cases are those turtles that can not be readily swallowed whole and, although other sharks undoubtedly do swallow small turtles, only tiger sharks are consistently willing and able to bite through the highly ossified carapace and plastral bones of the larger turtles. Turtle size was impossible to accurately determine during this study. Hence, some of the cases presented here might include some smaller turtles. Also, it is understood that several scientists recognize two species of *Galeocerdo*, *G. cuvier* and *G. rayneri*. However, pending confirmation of the validity of *G. rayneri*, the present paper is conforming to the single species (*G. cuvier*) presented in the recent review by Compagno (1984).

DIET

Wherever it occurs, the tiger shark is recognized for its apparent unselectivity of food items, eating a large variety of

fish, sharks, rays, marine mammals, sea birds, crustaceans, mollusks, carrion, and assorted debris. This shark has been called a scavenger and "... the least specialized of sharks as far as feeding is concerned" (Compagno, 1984: 505). However, because tiger sharks eat an occasional piece of wood, metal, or plastic, it does not necessarily make them unspecialized omnivores. In fact, large sea turtles appear to be a food item commonly found in tiger shark stomachs, a fact that has been well documented. The studies concerning tiger shark food habits are arbitrarily divided here into two categories: those with fewer than five stomachs examined and those with five or more. The list of studies with less than five tiger sharks examined is fairly extensive and, although the usefulness of the data in this list is limited quantitatively because of the small sample sizes, it is nonetheless indicative that tiger sharks may indeed selectively feed on large sea turtles: Coles (1919); Beebe (1937); Springer (1939, 1963); Beebe and Tee-Van (1941); Sarangdhar (1943); Gudger (1948b); Villers (1958); Travis (1959, 1967); Gohar and Mazhar (1964); Clark and von Schmidt (1965); Bustard (1972); Bryan (1973); Bass (1972).

The studies that examined the stomach contents of five or more tiger sharks show a wide range of documented predation on large sea turtles, temporally and spatially (Table 1). Summarized, Table 1 shows that of the 404 tiger sharks examined, 327 (80.9%) had food in their stomachs, and 68 (20.8%) contained the remains of large turtles. There was considerable variation from study to study as a result of: sample size, fishing technique, and differences in abundance of tiger sharks and turtles both seasonally and geographically. In spite of these variations, it is obvious that large sea turtles are an important dietary item commonly found in tiger sharks.

The exclusive nature of tiger shark pre-

dition on large boney sea turtles is also illustrated by the fact that in all major shark studies (in addition to those already cited) there is little evidence to suggest that other shark species have a preference for large turtles (Strasburg, 1958; Bass et al., 1973, 1975a, b, c; Gubanov and Grigor'yev, 1975; Stillwell and Kohler, 1982; Medved et al., 1984; Stevens, 1984). In fact, there appears to be no other shark species that regularly consumes large cheloniid sea turtles with the possible exception of the bull shark (*Carcharhinus leucas*), another large inshore shark (Gilbert and Kelso, 1971; Bass, 1972).

Tiger sharks prey on a wide variety of sea turtles around the world (Table 2). The Table indicates that tiger sharks probably eat the most abundant species of turtle available in that particular location (Groombridge, 1982), and does not reflect a preference for any one species. No conclusion can be made as to turtle species preference by tiger sharks because of poor turtle identifications and small sample sizes throughout the entire geographic range, and because the studies did not reflect the number (or quantity) of turtles eaten or killed.

An interesting footnote is that the professional shark fishermen discovered that tiger sharks definitely do prefer to eat turtle meat over the other commonly used fish baits (Gudger, 1948b; Travis, 1959, 1961). In fact, Japanese tuna long-line fishermen in the Solomon Islands reportedly take the time to open incidentally captured sharks to look for valuable hawksbill turtle shells (Vaughan, 1981).

HABITAT

Cheloniid sea turtles and tiger sharks share the same habitat, temporally and spatially (turtles—Hirth, 1971; Marquez, 1976; Groombridge, 1982; Witzell, 1983; sharks—Bigelow and Schroeder, 1948; Baughman and Springer, 1950; Castro,

TABLE 1. Frequency of sea turtles found in tiger shark (*Galeocerdo cuvier*) stomachs.

Area	Fishing* Method	N of tiger sharks examined	Tiger sharks with food	Tiger sharks with food including turtles**	Source
			N(%)	N(%)	
Southeast U.S.A.	GN	34	34 (100.0)	7 (20.6)	Bell & Nichols, 1921
Southeast U.S.A.	HL	7	7 (100.0)	5 (71.4)	Gudger, 1949
Aoutheast U.S.A.	LL	16	14 (87.5)	4 (28.5)	Doddrill, 1977
Mid-Pacific	CO	201	176 (87.5)	31 (17.6)	Balazs, 1980
Southeast Australia	CO	59	32 (54.2)	1 (4.5)	Stevens, 1984
Philippines	LL	43	22 (51.1)	13 (59.1)	Kauffman, 1950
Malaysia	HL	5	3 (60.0)	2 (66.6)	Hendrickson, 1958
South Africa	CO	39	39 (100.0)	5 (12.8)	Bass et al., 1975b
Total	—	404	327 (80.9)	68 (20.8)	—

*Fishing methods: LL is longline, RR is rod and reel, GN is gill net, HL is hook and line, CO is a combination of methods.

**Pertains only to those sharks with food and identifiable turtle remains, exclusive of those sharks with empty stomachs.

TABLE 2. The species of sea turtles found in tiger shark (*Galeocerdo cuvier*) stomachs.

Area	Sea turtle species*	Source
ATLANTIC OCEAN		
Northwest Africa	CC, CM, EI	Cadenat, 1957
Northwest Africa	EI	Villiers, 1958
Southeast U.S.A.	CC	Coles, 1919
Southeast U.S.A.	UI, CC	Bell & Nichols, 1921
Southeast U.S.A.	UI	Springer 1939, 1963
Southeast U.S.A.	CC, CM, UI	Gudger 1948a, 1949
Southeast U.S.A.	UI	Clark & von Schmidt, 1965
Southeast U.S.A.	CC	Doddrill, 1977
PACIFIC OCEAN		
Eastern Pacific	CM	Beebe & Tee-Van, 1941
Eastern Pacific	CM	Beebe, 1937
Mid-Pacific	CC, CM	Balazs, 1979, 1980
Western Pacific	CM	Bryan, 1973
Southeast Australia	UI	Gudger, 1948b
Southeast Australia	UI	Stevens, 1984
Eastern Australia	CC	Bustard, 1972
Philippines	EI, CM	Kauffman, 1950
Malaysia	CM, LO	Hendrickson, 1958
INDIAN OCEAN		
Western Australia	UI	Gudger, 1948b
Western India	CM	Sarangdhar, 1943
Seychelles	UI	Travis, 1959
East Africa	CM	Travis, 1967
Red Sea	UI	Gohar & Mazhar, 1964
South Africa	UI	Bass, 1972
South Africa	CM, EI	Bass et al., 1975b

*Sea turtle species: CM is *Chelonia mydas*, CC is *Caretta caretta*, EI is *Eretmochelys imbricata*, LO is *Lepidochelys olivacea*, UI is unidentified.

1983; Compagno, 1984). These animals are common, occurring in a wide variety of coastally pelagic habitats in tropical and warm-temperate oceans. They are generally found around coral reefs and lagoons, high relief hard-bottom banks, and large bays and estuaries. These are the normal foraging habitats and range in depth from shallow lagoonal grass flats to deep coralline banks, although they may make occasional offshore excursions. Both turtles and tiger sharks occur frequently near isolated oceanic islands, where they may take up residency for extended periods. The fact that such a large shark would inhabit this shallow coastal habitat is uncharacteristic of the Carcharhinidae, except possibly the bull shark (*Carcharhinus leucas*).

Adult sea turtles and tiger sharks are generally solitary, although each may congregate to feed or mate. Sea turtles congregate annually near nesting beaches for mating and egg laying, and it has been reported that there are also large numbers of tiger sharks that are either congregating in apparent association with the sea turtles (Fourmanoir, 1971), or they are seasonally abundant at the same time (Low and Ulrich, 1984). Interestingly, it has even been suggested that the breeding aggregations of green turtles in Hawaii reduce tiger shark predation by voluntarily beaching themselves during the day, an event extremely rare in marine turtles (Whittow and Balazs, 1982).

MASTICATING MECHANISM

Large cheloniid sea turtles are easy prey for tiger sharks because of their specialized dentition, kinetic upper jaw, and wide distendable terminal mouth. There are 18–24 similarly shaped cutting teeth in each jaw, these teeth forming a single cutting edge. The teeth have heavy cusps, forming a cockscomb shape, with prominent serrations (Fig. 1). The strong enamel cusps and serrations help strengthen the tooth structure and dissipate the

biting stresses (Preuschoft et al., 1974). No other shark has these unique dental characteristics.

The tiger shark is also unique because it has highly kinetic jaws that are exceptionally broad-based, heavily calcified, and fused at the symphyses (Moss, 1972). This allows for the single row of cusped, serrated teeth to extend out from the skull, seize the prey, and begin to saw into the bone. The broad heavily calcified jaws, aided by the extra strong symphyseal fusion, reinforce the entire jaw apparatus and enable the shark to bite through hard objects. Additionally, tiger sharks have a broad, flat head with a noticeably short, broadly rounded snout. This large, nearly terminal mouth is perfect for handling large objects.

The literature reports that sea turtles are occasionally eaten by white sharks (*Carcharodon carcharias*), the largest and most infamous of the great elasmobranch predators (Bigelow and Schroeder 1948; Castro 1983; Compagno 1984). However, there were no documented cases found of predation on large cheloniid turtles by the white shark, but there was at least one case of predation on a large, soft-shelled, leatherback turtle, *Dermochelys coriacea*, (Cropp, 1979). The serrated, triangular teeth are not designed to efficiently cut bone, but are adapted to slicing the softer skin and flesh of cetaceans and pinnipeds frequently found in white shark stomachs. Chips from white shark teeth have even been found in carcasses of sea otters, *Enhydra lutris* that were attacked off the California coast (Ames and Morejohn, 1980).

FEEDING BEHAVIOR

Tiger sharks have developed a feeding behavior that enables them to successfully prey on large turtles by utilizing a combination of stealth and speed, a strong sawing bite, and the ability to easily regurgitate large indigestible pieces of material. These sharks cruise the

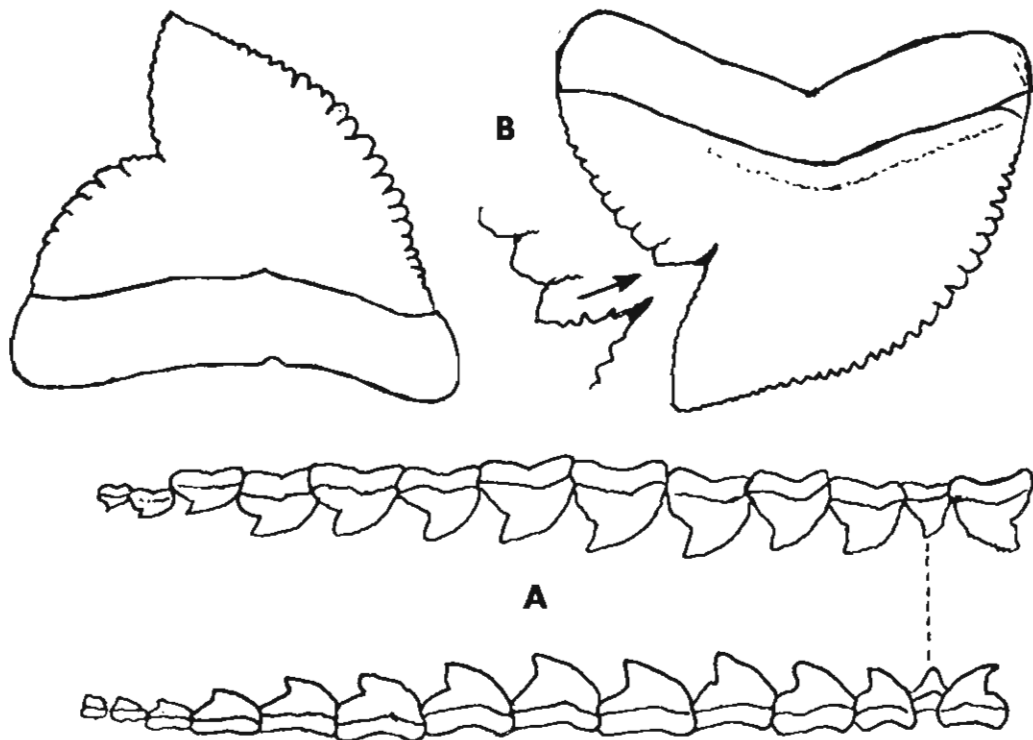


FIG. 1. (A) Right side of a typical tiger shark (*Galeocerdo cuvier*) jaw illustrating the single cutting edge formed by a single row of functional teeth. (B) Enlarged upper (left) and lower (right) teeth showing characteristic heavy cusps and strong serrations (adopted from Bigelow and Schroeder, 1948).

shallow neritic environment in a slow, sinuous motion that seems deceptively sluggish, and would not draw immediate attention to their presence and startle turtles into flight. However, when attacking prey, the tiger shark is one of the most vigorous and strong swimming of the carcharhiniid sharks, this speed-burst enabling them to quickly disable their prey before they can successfully escape.

Once the tiger shark has grasped the unsuspecting turtle in its mouth, it uses a unique method of biting described here by Springer (1939: 16): "Bites on large objects are made by a rolling motion with both jaws cutting much in the manner of a saw, and if the object is large enough to offer resistance, the tiger shark is quite capable of cutting through bone and shell". After having bitten its prey, the shark will characteristically shake its head

and body slowly, sometimes described as a spiral motion, to enable the strongly serrated cusped teeth in the kinetically fastened upper jaw to easily saw through the cheloniid's shell (Springer, 1961; Moss, 1972). Similar biting behaviors have been described by Gudger, (1948a 1949).

The tiger shark is easily able to disgorge large pieces of indigestible material by everting its stomach through its wide distendable mouth. This process has been witnessed by several authors (Radcliffe, 1916; Bell and Nichols, 1921; Gudger, 1949; Kaufmann, 1950; Balazs, 1979), and would explain how these sharks could easily remove the large amounts of turtle bone and shell from their alimentary tract after having digested the soluble protein. This could also explain why many sharks, after having

fought strenuously for several hours, may have empty stomachs.

CONCLUSIONS

Although tiger sharks may consume unusual and bizarre items, they appear to have developed a penchant for sea turtles. Stomach content analyses of 404 tiger sharks from eight published studies show that about 21% of the sharks with food in their stomachs contained pieces of large cheloniid turtles. The tiger shark is the only shark species with such a specialized diet because they share the same habitat, and have developed a unique masticating mechanism and feeding behavior.

Interestingly, fossil evidence suggests that tiger sharks had evolved as a genus (*Galeocerdo*) with the distinctive cusped teeth in the Upper Cretaceous (Bigelow and Schroeder 1948), and various species of cheloniid and toxychelliid sea turtles had also developed during this period with their distinctive dermal armor (Fenton and Fenton, 1958; Pritchard, 1979; Zangerl, 1980). Modern *Galeocerdo* and *Chelonia*, however, became fully developed in the Miocene (Caretto, 1972; Zangerl, 1980).

Predation may be severe in some local areas and conservationists desiring to control extensive predation of sea turtles should consider a fishing program targeting large tiger sharks, particularly near the nesting beaches when turtles congregate to mate. A sound harvesting program would reduce the turtle predation and also provide valuable products to coastal areas. These sharks are a valuable renewable resource and should not be indiscriminately wasted. The flesh is consumed fresh, frozen, or dried; the fins are used to make shark fin soup; the hide is used for high quality leather; and the liver is processed to make high potency vitamin oil.

ACKNOWLEDGMENTS.—This review was inspired by John Hendrickson, who knew all along that

tiger sharks had a penchant for eating sea turtles. I would also like to thank Chuck Stillwell and two anonymous reviewers for their valuable comments on the manuscript.

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要旨 イタチザメによるウミガメ科の大形カメ類に対する選択的捕食

ウェイン N. ウイツェル

イタチザメはウミガメ科の大形のカメ類を選択的に捕食する。これまでになされた8報告にある404個体分のイタチザメの胃のうち、327個(80.9%)が餌を含んでおり、また68個(20.8%)がウミガメ科の大形のカメ類を含んでいた。文献によるとイタチザメは一貫して大形で甲羅の固いカメ類を食べる唯一の板鰓類である

らしい。イタチザメは、カメ類と同じく近海に棲息域をもち、独特の咀嚼機構と摂食行動とを発達させたので、このような食性に特殊化できた。絶滅の危機にあるウミガメ個体群への捕食を減らすために合理的なイタチザメの採集案を示した。(33149 アメリカ合衆国フロリダ州マイアミ市バージニア・ビーチ・ドライブ 75 国立海産漁業施設, 東南漁業センター)