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Review of the Biology of the Tiger Shark (*Galeocerdo cuvier*)

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Systematics

The tiger shark was described by Peron and Lesueur in Lesueur (1822) from a specimen taken off the north-western coast of Australia. They named it *Squalus cuvier*. There is no type specimen. Müller and Henle (1837) proposed the genus *Galeocerdo* for the tiger shark, designating *Squalus arcticus* Faber as the type species, now known to be a junior synonym of *cuvier*. Compagno (1984) listed eight other synonyms of *G. cuvier*, among them *G. rayneri* McDonald and Barron, which some recent authors have treated as a valid species. Compagno is followed in regarding *Galeocerdo* as monotypic. The genus is one of 11 genera of the large family Carcharhinidae. It is clearly distinct from the other members of the family and deserving of subfamily status: Galeocerdinae Whitley (1934). After analysis of its morphological characters and in consideration of its ovoviviparity, Compagno (1988) concluded that the tiger shark is the most primitive of living carcharhinids. He regarded it as a transitional form between the hemigaleids and the Carcharhinidae.

Galeocerdo cuvier is one of the most distinctive of all sharks and not apt to be confused with any other species. It has a robust head and anterior body, but posterior to the abdomen the body becomes progressively more slender (Fig. 1); there is a low lateral keel on each side of the slender caudal peduncle; the upper lobe of the caudal fin is slender and pointed, with a subterminal notch but without a well developed terminal lobe; the snout is short and broadly rounded; the lateral labial furrows are very long; the spiracle is a narrow slit about one-fourth to one-third of the eye diameter; the mouth is large; the teeth are most characteristic (Fig. 2), being very strongly serrate, with the anteromedial edge convex and the posterolateral edge deeply notched; the largest serrae on the basal side of the notch are themselves secondarily serrate; there are 10 or 11 teeth on each side of the jaws that decrease greatly in size toward the corners of the mouth; there are 216–233 vertebrae, of which 100–112 are precaudal; the colour is grey, shading to white ventrally, the upper part of the body having dark grey bars or vertical rows of spots (faint or absent on large adults). The slender young are strikingly marked (Fig. 3).

Distribution

The tiger shark has a circumglobal distribution in tropical and warm temperate seas. In the western Atlantic it ranges from Cape Cod to Uruguay, including the Gulf of Mexico, Bermuda, and islands of the Caribbean; in the eastern Atlantic it is found on the West African coast from Morocco to Angola; it remains unknown from the Mediterranean Sea, but there are reports from Iceland and the United Kingdom (these were probably based on vagrants transported there during a warm year by the Gulf Stream) (Compagno 1984).

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It occurs throughout the Indo-Pacific region from the northern Red Sea to South Africa and east throughout the islands of Oceania and northern New Zealand (though not yet reported from Easter Island); in the eastern Pacific it ranges from southern California to Peru, including the Galápagos and Revillagigedo Islands.

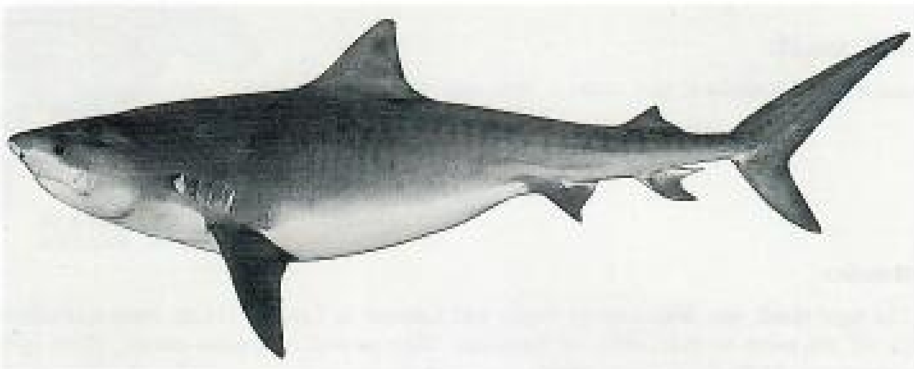

Fig. 1. *Galeocerdo cuvier*, precaudal length 241 cm, total length 305·5 cm, weight 175 kg, collected at Enewetak, Marshall Islands.

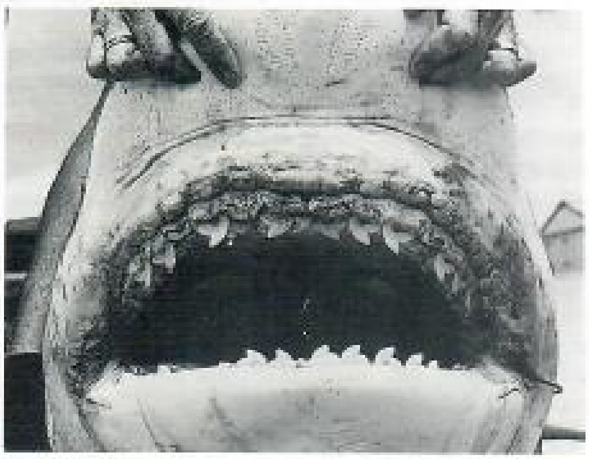

Fig. 2. Jaws of the *Galeocerdo cuvier* adult shown in Fig. 1.

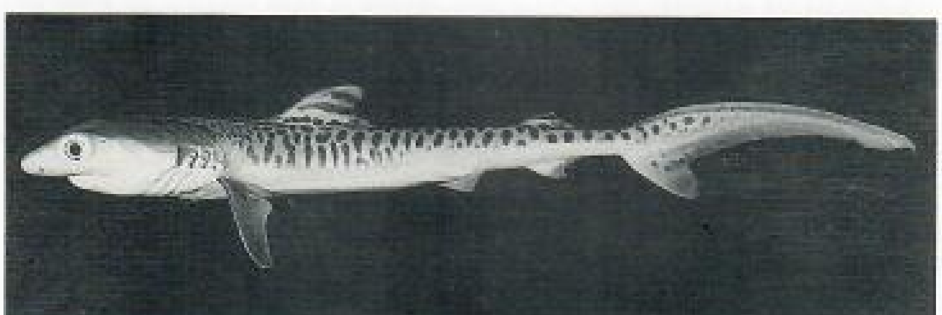

Fig. 3. Embryo of *Galeocerdo cuvier*, 52·7 cm total length, from a 360-cm female collected in the Marshall Islands.

Springer, in Gilbert (1963), wrote that the tiger shark is exceptional in many ways. From the records of the shark fishery in Florida he found no evidence of schooling, no disparity in the numbers of males and females, and no indication of absence of any size group within the population. This shark has been observed to be associated in groups of two to six or more, but such association may be transitory or merely groups assembling because of the presence of food. It is abundant in the northern Gulf of Mexico in the warm months but absent in winter. Records from the Gulf do not show segregation by size or sex, and the species does not seem to have any specific nursery area. Springer added, 'I know of no other species with such a homogeneous distribution in the shore waters of southern Florida nor of any other bottom-dwelling species so little restricted by bottom type.'

Movements

It is well known that tiger sharks may migrate into higher latitudes from tropic seas during warm months. Bigelow and Schroeder (1948), for example, stated that the species is only a summer visitor along the eastern coast of the United States north of Florida. On the basis of shark catches by sport fishers off New South Wales in Australia, Stevens (1984) found that tiger sharks were caught from September to May but were most abundant from December to April. Recent tagging studies have given us more information on tiger shark movements.

As part of a general survey of the sharks of the La Parguera region of south-western Puerto Rico in 1967, 61 sharks were tagged, of which six were tiger sharks. Incredibly, two of the tagged tiger sharks were recovered: one 4 months later within 5 km of the point of release, and the other after 5 months near Chimana Island (10°17′N,64°45′W), Venezuela, 890 km (480 nautical miles) to the south (Rivera-López 1970).

Tester (1969) reported on the tagging of 279 sharks in the Hawaiian Islands, of which there were 17 recoveries. Four of these were tiger sharks. Only one moved any appreciable distance: from the northern shore of Oahu to the southern, a distance of 45 miles, in 207 days.

The Cooperative Shark Tagging Program of the US National Marine Fisheries Service, based at the Northeast Fisheries Center in Narragansett, Rhode Island, under the direction of John G. Casey, has obtained very impressive results from its tagging of sharks. Sport fishers have accounted for most of the tag releases and recoveries, commercial fishers and fishery biologists the rest. The annual newsletter, *The Shark Tagger*, for the years 1977–89 documented the tagging of sharks in the western Atlantic. In all, 2257 tiger sharks were tagged during this period. There have been 135 recoveries; 57 of these are of sharks that travelled minimum distances of more than 100 n. miles (Table 1). Obviously, most have moved far more than the distances listed. Some have migrated surprisingly far in short periods of time. A tiger shark tagged in 1989 at Ponce Inlet on the eastern coast of Florida was recovered 17 days later at Sanibel Island on the Gulf coast of Florida, a distance of 564 n. miles. This represents an average daily movement of 32 n. miles. The longest minimum distance covered by a tagged tiger shark is 1853 n. miles; in 6 months this shark moved from Fire Island, New York, to Limón, Costa Rica.

In 1984, Casey *et al.* wrote, 'Tag returns from tiger sharks to date are difficult to interpret. Some tiger sharks seem to stay in one location, while others have travelled up to 1,850 [n.] miles. Some occur on the continental shelf (at times very close to shore), while others are found far at sea, around islands, and in a variety of oceanographic conditions. Tiger sharks that are found off Middle Atlantic States in summer may commonly overwinter off the Carolinas depending on water temperature and the abundance of food.' In August 1990, Casey (personal communication) wrote, 'More data are coming in all the time, but so far it looks like tiger sharks travel along the continental shelf and far at sea in rather random fashion.' Casey (1990) wrote, 'Tiger shark recaptures were returned after

Table 1. Recoveries of tagged tiger sharks having travelled minimum distances of more than 100 n. miles

Data are from the US National Marine Fisheries Service Cooperative Shark Tagging Program, 1977–89

Year	Tagging locality	Recapture locality	Months at liberty	Minimum n. miles travelled
1978	Fort Pierce, FL	Dominican Republic	2·5	800
1979	Jacksonville, FL	Belmar, NJ	3	708
	Dauphin I., AL	Matanilla Buoy, Bahamas	12	757
1980	Off Mississippi River	Dauphin I., AL	7	222
	Cape Hatteras, NC	Fort Pierce, FL	11	590
	Morgan City, LA	Bravo, Mexico	5	268
1981	Jones Inlet, NY	Miami Beach, FL	39	945
1982	Charlotte Harbor, FL	Cayo Coco, Cuba	8	428
	Oregon Inlet, NC	Martinique	15	1556
	Bimini Is, Bahamas	Fort Pierce, FL	7	122
1983	San Juan, PR	La Parguera, PR	25	145
	Fire Island, NY	Limón, Costa Rica	6	1853
	Marathon, FL	Isla Mujeres, Mexico	27	378
	Manasquan, NJ	Cape Hatteras, NC	1	300
1984	Barnegat Inlet, NJ	Charleston, SC	5	494
	Barnegat Inlet, NJ	Beaufort, NC	19	362
	Barnegat Inlet, NJ	Beaufort, NC	31	389
	Manasquan, NJ	Morehead City, NC	4	388
	Rudee Inlet, VA	Beaufort, NC	2	161
	Ocean City, MD	Cape Hatteras, NC	7	176
	Dauphin I., AL	Matanzas, Cuba	65	629
	Dry Tortugas, FL	New Pass, FL	37	152
	Rudee Inlet, VA	Montauk, NY	56	293
	Chincoteague, VA	Montauk, NY	3	203
1985	Block I., RI	Ocracoke, NC	5	419
	Cape May, NJ	Ponce Inlet, FL	10	637
	Cape Charles, VA	Barnegat Inlet, NJ	13	177
	Isla de la Muertos, PR	Dominican Republic	18	159
1986	Ocean City, MD	Cape Fear, NC	5	332
	Virginia Beach, VA	Fire Island Inlet, NY	1	240
	Ponce Inlet, FL	Dzilam de Bravo, Mexico	2	777
	Bimini Is, Bahamas	Flagler Beach, FL	3	242
	Montauk, NY	Ponce Inlet, FL	48	805
	Bimini Is, Bahamas	Eleuthera I., Bahamas	22	187
1987	Ponce Inlet, FL	Charleston, SC	4	197
	Stuart, FL	Shinnecock Inlet, NY	66	852
	Montauk, NY	Faro Paredon Grande, Cuba	42	1126
	Rudee Inlet, VA	Cape May, NJ	58	120
	Barnegat Inlet, NJ	Daytona Beach, FL	63	714
	Fire Island, NY	Ponce Inlet, FL	1	723
1988	Eleuthera I., Bahamas	Cape Canaveral, FL	?	322
	Ponce Inlet, FL	Cape Lookout, NC	1	352
	Point Judith, RI	Saint Augustine, FL	31	825
	Ponce Inlet, FL	Cape Point, NC	3	451
	Manasquan Inlet, NJ	Cape Hatteras, NC	48	303
	Mobile, AL	Galveston, TX	7	199
	Rudee Inlet, VA	Morehead City, NC	38	131
1989	Manasquan Inlet, NJ	Ocracoke, NC	16	331
	Indian River Inlet, DE	Cape Hatteras, NC	34	223
	Indian River Inlet, DE	Cape Hatteras, NC	19	219
	Rudee Inlet, VA	Barnegat Inlet, NJ	27	216
	Cabo San Antonio, Cuba	Trinidad, Cuba	58	335
	Ponce Inlet, FL	Sanibel I., FL	<1	564
	SE Puerto Rico	Key Largo, FL	73	862
	Norfolk, VA	Ponce Inlet, FL	16	518
	Manasquan Inlet, NJ	Andros I., Bahamas	26	1039
	Rudee Inlet, VA	Cape Lookout, NC	24	146

record times at liberty of 7·0 and 8·0 years. Many of the recaptures showed local movements off the Florida coast with some tiger sharks moving very short distances in long periods of time (e.g., 16 miles in 1·1 years, 17 miles in 1·4 years). Overall, 19 travelled more than 100 miles from their tagging location and only 8 more than 300 miles. The farthest distance travelled was by a tiger shark tagged off New Jersey and recaptured northeast of San Juan, Puerto Rico, a distance of 1228 miles.'

A number of authors have reported that tiger sharks are rarely seen in shallow water during the day but are readily caught inshore at night. In an effort to document the diel movements of a tiger shark, Tricas *et al.* (1981) tagged a 400-cm female with a telemetric device at French Frigate Shoals in the north-western Hawaiian Islands and tracked it for two 24-h periods. The shark ranged over an area of about 100 km^2, travelling a horizontal distance of about 82 km day^{-1} at a rate varying from 0·4 to 11·0 km h^{-1}. The rate at night was slightly slower than that by day, and more distance was covered by day. During the day, 68% of the shark's activity was spent deeper than the reef drop-off at 40 m (to at least 140 m, the limit of the depth sensor), whereas 83% of the shark's nocturnal activity was in depths shallower than the drop-off.

On 22 July 1981, a 3-m male tiger shark was caught in 30 m of water near Burrows Cay at the south-eastern end of Grand Bahama Island by Samuel H. Gruber and associates. A telemetric tag was attached to the shark's back between the dorsal fins. The shark's position was determined every 15 min. The shark remained within a mile of the capture locality for 4 h; then it headed west over deep water, covering 5 nautical miles (9·1 km) during the first half hour. Thereafter, the greatest movement between any two fixes was 3·5 n. miles (6·4 km), but most consecutive fixes were less than a mile part. Few series of three fixes remained on the same bearing, and most of the 15-min movements were on distinctly different headings from the preceding ones. At the end of the tracking period of 51 h and 15 min, the shark was 22 n. miles (40·2 km) WNW of the capture locality in water about 600 m deep (Gruber, unpublished data). Unfortunately, there was no depth-sounding device on the tag, so the depths for the various fixes remain unknown. However, the trackers suspected that the shark was in relatively deep water when it was offshore.

Clark and Kristof (1990, fig. 15) illustrated a female tiger shark about 250 cm in total length from a photograph taken from a submersible in 350 m of water off Grand Cayman. The shark circled the submersible's bait cage when daylight was barely visible but left when the lights were turned on.

Food Habits

Numerous papers have been written recording the food of tiger sharks, examples being Norman and Fraser (1937), Springer (1938), Whitley (1940), Bigelow and Schroeder (1948), Gudger (1948*a*, 1948*b*, 1949), Kauffman (1950), Ikehara (1960), Springer in Gilbert (1963), Gohar and Mazhar (1964), Clark and von Schmidt (1965), Randall (1967, 1980), Tester (1969), Fujimoto and Sakuda (1972), Bass *et al.* (1975), De Crosta *et al.* (1984), and Stevens (1984). Randall (1986) summarized the food habits of the species as follows: 'The Tiger Shark eats a greater variety of animals than any other shark: numerous species of bony fishes, sharks (including its own species when hooked), rays, sea turtles, sea birds, seals, dolphins, cephalopods, spiny lobsters, crabs, horseshoe crabs, gastropods, and jellyfishes. Feeds readily on carrion. Many different terrestrial animals have been found in its stomach, mostly a result of disposal in the sea by man; in addition, an incredible variety of refuse and garbage, including indigestible plastic, metal, and other items of human origin.' The ability of tiger sharks to consume large prey animals such as sea turtles, marine mammals, sharks, and rays is due to their large size and the coarse serrae of their sharp teeth, which function like a saw. Once the jaws are engaged in the prey, the rapid side-to-side twisting of the massive head and body results in swift cutting, even of seemingly indestructible tissues such as the bony carapace of a large sea turtle.

The food habits of the tiger shark vary greatly with the availability of food. Tiger sharks taken in harbours or near sites where refuse is dumped often contain a high percentage of material of human origin. Previously unreported are the stomach contents of a 300-cm female from Eilat at the northern end of the Gulf of Aqaba, Red Sea: two empty cans, one plastic bottle, two burlap sacks, one squid, and a 20-cm fish. In another 300-cm individual caught by the author off Oahu, the stomach contents were dominated by the heads of skipjack tuna, each neatly cut by a knife (hence obviously discarded by a fishing boat), and by garbage mixed with aluminium foil and plastic bags. De Crosta *et al.* (1984) opened the stomachs of 35 tiger sharks caught in the Northwestern Hawaiian Islands, 80% of which contained food. These authors found that 75% of the prey were sea-birds (sea-birds are present in enormous numbers at these largely uninhabited islands). Most of the fishes eaten were slow-swimming, 'well protected' species such as diodontids and monacanthids. Kauffman (1950) obtained 43 tiger sharks in the Philippines for stomach-content analysis, 22 of which contained food; 13 of the 32 prey items were sea turtles (11 hawksbills and two greens) and two were sea snakes. Stevens and McLoughlin (1991) found 79% of 98 tiger sharks from northern Australia with food in their stomachs. Of these, 62% contained fishes and 58% contained reptiles; the reptile prey consisted of sea turtles and sea snakes (the latter being found in a surprising 43% of the stomachs).

The author, in a 1966 unpublished report of the Oceanic Institute, Oahu, listed the stomach contents of 12 of 27 tiger sharks taken by set lines off Kawaihae, Kona, Hawaii; these data are presented in Table 2.

Table 2. Stomach contents of tiger sharks from Hawaii

Total length (cm)	Stomach contents
220	Kona crab (*Ranina ranina*)
260	Goat remains
	Cornetfish (*Fistularia petimba*) (25 cm)
273	Turtle remains
	Shark remains (including 6 embryos)[A]
299	Porcupinefish (*Diodon* sp.) (40 cm)
	Shark remains[A]
300	Fish remains (including an eel)
	Steak bone
304	Piece of cardboard
304	Jack (*Caranx* sp.) (4·5 kg)
	Sea turtle (11 kg)
	Lobster
	Three cephalopod beaks
349	Posterior part of a sea turtle
	Head of a spotted porpoise
359	Pig remains
381	Sea turtle
	Fish
400	Two large deep-water slipper lobsters
420	An entire pig

[A]Shark remains are probably a result of feeding on hooked sharks and thus may not be normal food.

Age and Growth

Galeocerdo cuvier is among those species of sharks for which estimates of age and growth have been made from growth rings of vertebrae. Using the method of Stevens (1975), De Crosta *et al.* (1984) prepared the following equation for the von Bertalanffy growth curve

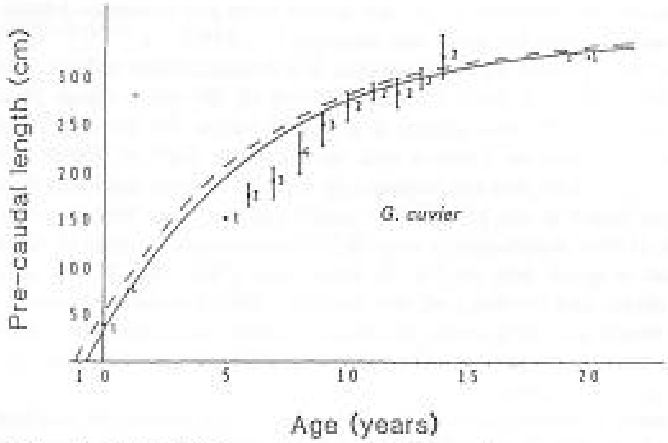

Fig. 4. Von Bertalanffy growth curves for *Galeocerdo cuvier* as calculated from vertebral age-determination data (solid line; mean lengths of year classes indicated by dots, ranges by bars, sample sizes by numbers) and from a length-frequency analysis of data from Tester (1969) (dashed line) (reproduced from De Crosta *et al.* 1984).

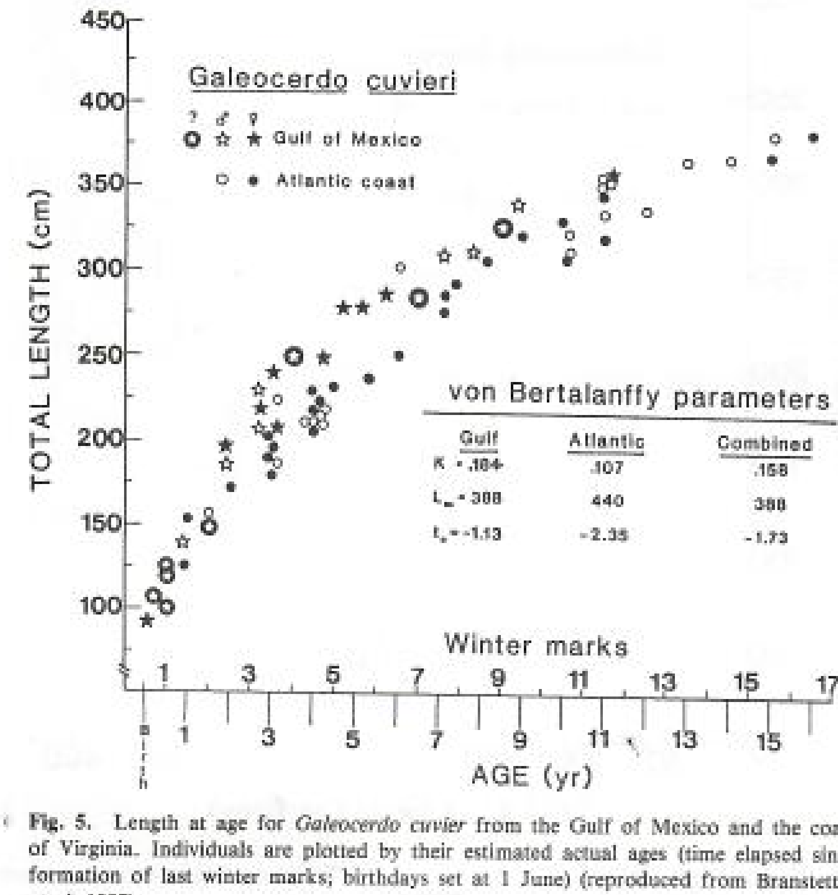

Fig. 5. Length at age for *Galeocerdo cuvier* from the Gulf of Mexico and the coast of Virginia. Individuals are plotted by their estimated actual ages (time elapsed since formation of last winter marks; birthdays set at 1 June) (reproduced from Branstetter *et al.* 1987).

from a sampling of the vertebrae of 28 tiger sharks from the Hawaiian Islands (the authors admitted to a lack of data for some age classes): $L_t = 335(1 - e^{-0\cdot155(t=0\cdot619)})$. Fig. 4 is a reproduction of their growth curve. From this, it is estimated that a shark with a precaudal length of 200 cm is about 5 years old and that one of 300 cm is about 15 years old.

Branstetter *et al.* (1987) also prepared a growth curve for the tiger shark, based on specimens from the coast of Virginia and the northern Gulf of Mexico; their curve is reproduced as Fig. 5. Note that the vertical axis of their curve is total length, not precaudal length, hence the length at any given age is notably greater than that given by the curve of De Crosta *et al.* (1984). Branstetter *et al.* (1987) also presented a figure of the length–weight relationship that is given here as Fig. 6. Kauffman (1950, fig. 2) has also presented a length–weight curve, and Stevens and McLoughlin (1991) provided equations relating fork length to total length and total length to weight. Bigelow and Schroeder (1948) pointed out that there is variation in weight at a given length with fatness and the stage of development of embryos in gravid females.

Age and growth estimates derived from vertebral rings should be confirmed by actual measurements of growth. Nearly all tagging of tiger sharks has been done while the sharks are in the sea, where only approximations can be made of their length. Branstetter *et al.* (1987) estimated that the tiger shark doubles its length in the first year of life. They stated that this estimate is supported by the growth of a full-term embryo of 69 cm total length

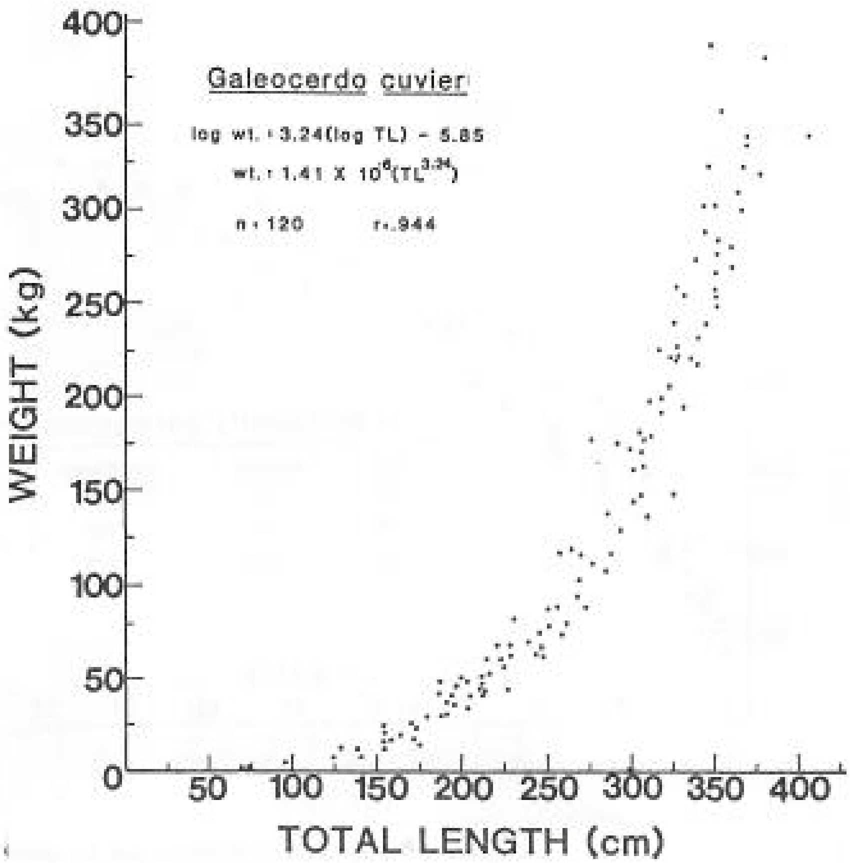

Fig. 6. Length–weight relationship for Atlantic and Gulf of Mexico *Galeocerdo cuvier* (sexes combined) (reproduced from Branstetter *et al.* 1987).

that grew to 89 cm in 12 weeks in an aquarium (Clark and von Schmidt 1965). One small tiger shark in Hawaii that was carefully measured when tagged and recovered has provided good growth data (Tester 1969). Over a period of 207 days at liberty, it grew from 131 cm total length to 173 cm, giving an annual growth of 74 cm. Casey *et al.* (1989) noted that seven tiger sharks accurately measured at both tagging and recapture have provided valuable growth data (as yet unpublished). Vertebrae were collected from three of the sharks for age determination. These workers also collected vertebrae from 13 additional tagged tiger sharks in 1990.

From their data, Branstetter *et al.* (1987) estimated a rate of growth for very large tiger sharks of 5–10 cm year^{-1}; thus, individuals of 400–450 cm total length would be 20–25 years of age. No exceptionally large tiger sharks have been aged from vertebral rings. From von Bertalanffy curves derived from back-calculated lengths, Branstetter *et al.* gave maximum ages of 45–50 years.

As with the great white shark (*Carcharodon carcharias*), there have been what appear to be exaggerated reports of the maximum length that the tiger shark can attain. Some authors have given total lengths as great as 30 feet (9·1 m). Norman and Fraser (1937), for example, wrote, 'Grows to a length of 15–20 feet, occasionally reaching 30 feet.' However, none of the reported extraordinary sizes of tiger sharks has been scientifically confirmed. The maximum length that seems authentic is one of 18 feet (5·5 m) from Cuba (Bigelow and Schroeder 1948, quoting Howell-Rivero). From two personal experiences, the author believes that a length as great as 6 m might eventually be demonstrated.

Reproduction

Male tiger sharks mature at 226–290 cm total length and females at 250–350 cm. This shark is the only one of the family Carcharhinidae that is ovoviviparous, and it is unusual in the large number of young produced (about 10 to 82 per litter). The size at birth is 51–76 cm total length. As noted by Compagno (1988), the relatively large size of tiger sharks at birth seems to be greater than could be accounted for by the amount of yolk available in the ova. It has been suggested that there is supplemental nutrition in the form of 'uterine milk' secreted from the lining of the uterus.

The gestation period has been given by Clark and von Schmidt (1965) as 13–16 months. Mating is reported to take place in the Northern Hemisphere in spring, with pupping the following spring and summer. Mating occurs again before full-term females have given birth to young. The young are very slender with a flexible body and caudal fin; they swim with an inefficient anguilliform motion. Branstetter *et al.* (1987) concluded that they are probably very vulnerable to predation at this stage, especially by sharks, including their own kind.

Importance to Humans

Norman and Fraser (1937) wrote of the tiger shark, 'From a commercial point of view this Shark is of considerable value as its skin is in great demand for leather. It is very tough, and has a tensile strength of from 6–10 times that of ox-hide.' They added that the liver gives a better yield of oil than do the livers of most other kinds of sharks. The oil often has a high vitamin A content. Tiger shark fins are of high quality for shark-fin soup. Tiger shark meat is used for human consumption in fresh, frozen, dried and salted, or smoked form. With proper refrigeration and preparation, shark meat is good food; it has gained acceptance in developed countries in recent years. Tiger shark jaws and teeth are often sold as curios. In large aquaria and oceanariums, the tiger shark is a spectacular display animal. Crow and Hewitt (1988) have presented longevity records for captive tiger sharks and notes on their management.

The tiger shark is one of seven sharks for which sportfishing world records are kept (three of the categories – hammerheads, makos, and threshers – are reported only by genus).

The all-tackle record for the tiger shark is 569·02 kg (1314 pounds). This shark was caught on 60 kg (130 lb) test line off Cape Moreton, Queensland, in 1953 (Anon. 1990).

For those who venture into the sea, the concept of the importance of the tiger shark to humans takes on a different emphasis. This shark has long been regarded as second only to the great white shark as the most dangerous in the sea. Thus, for those swimming or diving in tropical waters, it is properly regarded as the greatest threat for attack on humans. This reputation has been confirmed by records of the identity of attacking sharks. Very few sharks that have attacked humans have been identified to species level. Baldridge (1973) stated, 'At least some level of identification of the attacker was possible in 257 cases. As popular belief would have it, the great white shark (*Carcharodon carcharias*) was cited most often, with 32 known attacks to its discredit. The ubiquitous tiger shark (*Galeocerdo cuvieri*) was close behind, having been identified in 27 cases including some of the most dramatic held in the Shark Attack File.'

The word *dramatic* naturally brings to mind the famous murder case in Sydney, Australia, in 1939, in which the tatooed arm of the victim, regurgitated by a tiger shark that had recently been placed in the Coogee Aquarium, provided the evidence that the man was murdered. Dr V. M. Coppleson, an expert on shark attacks, examined the arm and was certain that it had been severed from the body of the victim by a sharp knife (Anon. 1986).

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