TECHNICAL REPORT

SHARKS OF THE FAMILY LAMNIDAE

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FOREWORD

This report summarizes the available data on some aspects of the biology of the lamnid sharks. Although much remains to be learned about this family of sharks, it is hoped that this report will be useful to other investigators.

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PREFACE

In 1944, the U. S. Navy produced a newly developed shark repellent for standard issue in survival kits. It soon became apparent, however, that the greatest value of this repellent was as a morale booster for survivors in the water, inasmuch as its efficacy as protection against sharks was questionable. To this day the development of an effective antishark device remains a pressing problem to the Navy. At a recent symposium on sharks (1958), scientists agreed that although the development of a deterrent was essential, the solution of the problem was hampered by a lack of fundamental knowledge concerning shark biology. A committee on research recommendations which met during the symposium stressed the need for more intensive research on identification and classification, distribution, abundance, behavior, and ecology of sharks, as well as continued efforts to develop a satisfactory repellent.

All three genera in the family Lamnidae are considered to be potentially dangerous to man. Of the three, *Carcharodon* and *Isurus* have been involved in authenticated attacks on man.

Since the publication in 1948 of Bigelow and Schroeder's invaluable treatise on sharks of the western North Atlantic, some new data have become available concerning the lamnid sharks. The present report is intended as a summary of available data on some aspects of their biology.

SHARKS OF THE FAMILY LAMNIDAE

HISTORY

The history of modern sharks can be traced back to the Jurassic, but fossil remains prior to this period are too scanty to determine the derivation of modern groups. The bulk of evidence consists of teeth, head spines, and fin spines, since the cartilaginous elasmobranch skeleton normally is poorly and incompletely preserved (Moy-Thomas, 1939). Available fossil material suggests that the modern sharks probably have arisen from forms such as the Hybodontii (_Hybodus_), which appear to possess characters intermediate between those of the modern Notidanoidea and Heterodontoidea. Further evidence suggests that the hybodonts can be traced through the apparently intermediate Ctenacanthi, to the Upper Devonian _Cladoselache_, the earliest known shark.

The chief distinctions in the development of modern sharks are the change from amphistyly to hyostyly, greater development of vertebral centra, and the progressive disappearance of the notochord through segmental constriction. Among the last to evolve were the lamnids, which first appeared in the Cretaceous.

CLASSIFICATION

At present, there appear to be three well-defined genera in the family lamnidae, separable according to the following key (modified from Bigelow and Schroeder, 1948):

1a. Upper teeth broadly triangular, with serrate edges.
Carcharodon A. Smith, 1838

1b. Upper teeth slender, with smooth-edged cusps.

2a. First two teeth in each jaw similar in shape to the succeeding teeth; most or all of teeth with lateral denticles in most species, and perhaps in all; origin of first dorsal about over or anterior to inner corner of pectoral when latter is laid back; anterior part of caudal fin with a secondary caudal keel on either side below the primary keel formed by the lateral expansion of the caudal peduncle.
Lamna Cuvier, 1817

2b. First two teeth in each jaw noticeably more slender and more flexuous than the others; lateral denticles absent or present only as a trace; origin of first dorsal definitely posterior to inner corner of pectoral when latter is laid back; caudal fin without secondary keels, with only the primary keels formed by the lateral expansion of the caudal peduncle.

Isurus Rafinesque, 1810

Bigelow and Schroeder (1948) placed these genera (Isuridae) in the suborder Galeoidea, along with eleven other families, accounting for the bulk of modern shark species.

Considerable variation exists in the treatment of this family by past workers. Regan (1906) placed the Lamnidae in his division Galeoidei, under the suborder Pleurotremata. Garman (1913) adopted the following classification:

Suborder: Antacea
  Group: Isuroidei (= superfamily)
    Families: Vulpeculidae
      Isuridae
      Rhincodontidae

He included the basking shark (Cetorhinus) with the Isuridae, did not distinguish between Lamna and Isurus in his generic key, and referred the species of Lamna to Isurus (the older name).

White's (1937) revision of the Galeoid sharks was based primarily on vertebral structure and other internal characters. She arrived at the following arrangement:

Subclass: Plagiostoma
  Superorder: Antacea
    Order: Galea
      Suborder: Isurida
        Superfamily: Isuroidea
          Families: Vulpeculidae
            Isuridae
            Cetorhinidae

In addition to establishing a separate family (Cetorhinidae) for the basking shark, she removed the Rhineodontidae (Rhincodontidae, the whale sharks) from Garman's grouping and placed them with the Orectoloboidea (the nurse and carpet sharks). She followed Garman in not distinguishing between Lamna and Isurus.

Berg (1940) proposed the following scheme:

Subclass: Selachii
  Order: Lamniformes (Galeoidei)
    Suborder: Lamnoidei (Isurida)
      Family: Lamnidae (Isuridae)
        Subfamilies: Alopiini
          Lamnini
          Cetorhinini

Bigelow and Schroeder (1948) included the whale sharks (Rhincodontidae) and the nurse sharks (Orectolobidae) along with the Isuridae in their suborder Galeoidea. This is the generally accepted arrangement, except that opinions are divided on the family designation. Lamnidae is the name used by some authors and is the older family name.

The validity of the designation Carcharodon A. Smith, 1838, presently depends on the stability of the designation Carcharhinus Blainville, 1816 (White, Tucker, and Marshall, 1961). The confusion centers on the designation of the type-species of Carcharhinus by Bosc (1816). Although the designation is valid, its acceptance would make Carcharhinus Blainville, 1816 a senior objective synonym of Carcharodon A. Smith, 1838. White et al. (1961) have submitted a proposal to the International Commission on Zoological Nomenclature recommending that Bosc's designation be set aside in order that both Carcharhinus and Carcharodon be stabilized in accordance with long established and current usage.

SPECIES RELATIONSHIPS

The following discussions summarize briefly current views on the affinities of species in this family.

Carcharodon -- At present, only one species, C. carcharias Linnaeus, 1758, is considered to be valid. Whitley (1939) designated the Australian - New Zealand form as C. albimors, based primarily on the form and position of the fins compared with C. carcharias. However, form and position of fins are characters that change with growth, and Bigelow and Schroeder (1948) observed that the accounts and figures of C. albimors do not seem to justify the designation of a new species.

Isurus -- Bigelow and Schroeder (1948) recognized two species, I. oxyrinchus Rafinesque, 1810 of the Atlantic, I. glaucus Müller and Henle, 1841 from the Indo-Pacific, and a third doubtful species, I. güntheri Murray, 1884, the description of which was based on a single specimen from India. None has since been taken, and Smith (1957) synonymized I. güntheri with I. tigris Atwood, 1869. He believed that the tooth count given for I. güntheri (the supposed diagnostic character for this species) was intended to mean total count in both jaws, since the number given (22/28) is "exactly double the normal range." Smith recognized three species from South African waters, I. oxyrinchus, I. glaucus, and I. tigris. From his figures, however, I. tigris appears to be more nearly intermediate between I. oxyrinchus and I. glaucus rather than distinctly separable. He based his separation primarily on shape and position of the first dorsal fin, stating that it is higher and more acute in I. tigris. As mentioned above, these characters vary with age and, in fact, Smith stated in his diagnosis of I. tigris that "the dorsal fin appears to become relatively higher and more acute with age." All the specimens of I. tigris discussed by him are large except for one taken by Murphy (1919) in New York waters. This latter specimen does not appear to differ appreciably from I. oxyrinchus and is considered to be this species by Bigelow and Schroeder (1948). Smith (1957) suggested the possibility of three geographical subspecies of I. tigris. In a still later work (Smith, 1961), he recognized I. glaucus and I. oxyrinchus as before and proposed a new species, I. africanus, as the third one occurring in South African waters.

Whitley (1929), describing a New Zealand specimen, proposed a new species, I. mako, as separable (he does not say how) from I. glaucus. Subsequently (Whitley, 1931), he designated this form as Isuropsis mako, and later (Whitley, 1940) he illustrated Isuropsis mako by using a photograph of Lamna originally published by Waite (1921) and improperly labelled as Isurus glaucus. Subsequent accounts and illustrations of the New Zealand-Australian form suggest that it does not differ from I. glaucus (Bigelow and Schroeder, 1948). Philippi (1887) described a Lamna Huidobrii from Chilean waters which, from his illustration, is clearly an Isurus, apparently close to I. glaucus.

Lamna -- In the Northern Hemisphere, two species are recognized: L. nasus Bonnaterre, 1788 from the Atlantic, and L. ditropis Hubbs and Follett, 1947 from the Pacific, the two differing primarily in snout length and coloration. In L. ditropis, the lower surface is marked with black blotches, whereas it is not so marked in L. nasus.

The relationships of these northern species with those of the Southern Hemisphere have not been definitely established. Phillipps (1935) described L. whitleyi from New Zealand waters, and Whitley (1940) considered the Australian form to be the same. Apparently, L. whitleyi differs from L. nasus in a more posteriorly positioned first dorsal fin and a longer lower caudal lobe.

Philippi (1887) illustrated L. philippii Perez Canto, 1886 from Chile. Although typically stout bodied, the figure shows no secondary caudal keel and the teeth have no lateral denticles.

Smith (1961) reported L. nasus from South African waters. Until comprehensive comparisons can be made between species of both hemispheres, the status of Southern Hemisphere forms remains uncertain.

GENERAL CHARACTERISTICS

As indicated in the generic key above, differences in dentition, relative placement of fins, and presence or absence of a secondary caudal keel are the major criteria for distinguishing these genera. All are very streamlined and characterized by a lunate caudal fin with nearly equal upper and lower lobes. The caudal peduncle is slender and markedly flattened dorsoventrally, forming the prominent primary keel typical of the family. The gill slits are particularly long, and the fifth gill opening is anterior to the origin of the pectoral fin. The dermal denticles are small and quite flattened, so that the skin, contrary to that of most other sharks, is relatively smooth to the touch.

Large size is attributed to all three genera of the Lamnidae. For Lamna, whose members are the smallest, the maximum recorded is about 10 feet (Bigelow and Schroeder, 1948; Whitley, 1940). For Isurus, Bigelow and Schroeder reported 12 feet (estimate based on teeth), Goadby (1959) 15 feet, and Whitley (1940) 13 feet. Straughan (1958) described an encounter off the Florida coast with a shark, estimated at 14 to 16 feet in length, that he believed must have been Isurus. However, his description suggests that it may have been Carcharodon.

The white shark (Carcharodon) is the largest of all predatory sharks. At least one author (Goadby, 1959) stated they grow to 40 feet in length, and the oft-quoted record, based on an estimate from teeth, is 36½ feet for an Australian specimen. However, Springer (1958), among others, is skeptical of this estimate since teeth from a measured 18-foot specimen were about the size of those from the Australian specimen. The largest reliable measurement (Bigelow and Schroeder, 1948) is 21 feet, with several others close to that figure. Several estimates of over 30 feet appear in the literature (e. g., Starks, 1917), but no accurate measurements are available to substantiate such sizes.

The tiger shark (Galeocerdo) closely approaches the white shark in size, and the maximum recorded length actually exceeds that for the white shark. Fourmanoir (1961) cited the capture of a tiger shark in Vietnamese waters which measured over 24 feet in length (7.40 meters) and weighed over 6,800 pounds (3,110 kilograms).

DISTRIBUTION

Representatives of the Lamnidae are found in boreal to tropical marine waters throughout the world. The white shark (Carcharodon carcharias) occupies a broad thermal belt. It has been reported from many localities but does not appear to be particularly abundant, except possibly in Australia and South Africa. Goadby (1959) reported it as "very prevalent" in winter along the south and east coasts of Australia, and Smith (1961) stated it is "not uncommon" around South Africa. Although it was presumed to be a truly oceanic species, Strasburg (1958) had no longline record of it for the entire central Pacific.

The white shark is reported to be quite irregular in its occurrence (Bigelow and Schroeder, 1948; and others). However, available data indicate that in certain regions it occurs fairly regularly. Postel (1958) presented catch data and stated that the white shark occurs with apparent regularity during the latter half of May in the Gulf of Tunis. Records given by Gudger (1950) and Scattergood (1962a) showed that the white shark is neither irregular nor rare along the coast of northeastern United States. Gudger gave records for the Buzzard's Bay area of Massachusetts from 1871 to 1927, and Scattergood summarized New England records (Cape Cod northward) from 1931 to 1960, including detailed data on 12 specimens taken in the Gulf of Maine, 8 of them during July and August of 1960. Backus (1957, 1960) also gave records for Massachusetts. Thus, the white shark is a regular visitor to New England waters, first appearing there in spring. During July and August it appears to achieve peak abundance and has been reported as late as November.

In the Atlantic, the white shark has been recorded from St. Pierre, Newfoundland south to Brazil, including the West Indies and the Gulf of Mexico. On the eastern side, records are available from Norway south to the Cape of Good Hope, including the offshore island groups (Belloc, 1934; Bigelow and Schroeder, 1948; Poll, 1951; Cousteau, 1953; and others).

On the Pacific coast of the United States the white shark has been reported several times from Washington (Bonham, 1942; LeMeir, 1951); Pike (1962) recently recorded it from Queen Charlotte Islands, British Columbia. Royce (1963) reported a specimen from Craig, Alaska, and gave further information on its occurrence in southeastern Alaska. Specimens occasionally are seen or taken off northern and central California (Fitch, 1949; Kenyon, 1959). Seven small ones were taken in a three-day period from the pier at Scripps Institution of Oceanography, La Jolla, California (unpublished data). There also are records from Panama (Kean, 1944) and Chile (Philippi, 1887) on the eastern side of the Pacific Ocean. Elsewhere in the Pacific, records are available from Hawaii, Bikini, Philippine Islands, Japan, China, Korea, Bonin Islands, New Caledonia, New Zealand, and Indonesian waters (Phillipps, 1927; Reeves, 1927; Fowler, 1941; Umali, 1950; Schultz et al., 1953). Fowler (1941) stated that the white shark occurs from Polynesia to the west coast of South America but did not give definite records.

Fowler (1956) also reported that there had been no record of the white shark in the Red Sea since 1775, but it has been recorded there recently (Eibl-Eibesfeldt and Hass, 1959).

The species of Isurus are inhabitants of tropical and warm temperate waters of both hemispheres, although they extend their summer range into cool temperate regions. In the Atlantic, I. oxyrinchus has been recorded from as far north as southwestern Norway as a stray, presumably because of the influence of the North Atlantic Current. It is generally oceanic but has been recorded from most island areas, such as the Azores and Canaries, as well as from the Mediterranean Sea. Coastal records from the western Atlantic are scattered, but it apparently extends from Maine (Scattergood, 1962b) south to northern Argentina (Bigelow and Schroeder, 1948). Roedel and Ripley (1950) reported I. glaucus in California waters as ranging from Monterey Bay southward to Baja California. However, Radovich (1961) reported the capture of a specimen from off the Columbia River, representing a northward extension in range. On the basis of longline records, Strasburg (1958) showed the bonito shark (I. glaucus) to be wide ranging in the central Pacific. It was never taken in great numbers, and the data showed no special centers of abundance.

Illingworth (1961) reported the New Zealand mako (I. glaucus) as occurring south to Stewart Island in southern summer, though it is normally more abundant north of Cook Strait during any season. Whitley (1940) described its distribution in Australian waters, stating that it is pelagic "and prefers colder waters." Since he illustrated the mako with a photograph of Lamna, his distributional data may apply to the latter genus, which is normally antitropical in distribution. However, I. glaucus has been taken as far south as Amsterdam Island in the Indian Ocean (Blanc, 1961); also, in a paper dealing with the sharks of Madagascar, Fourmanoir (1961) stated: "La capture d'Isurus oxyrinchus a eu lieu le 10 août 1959, elle est en relation avec le refroidissement des eaux à celle epoque." Fourmanoir also reported that Isurus accounts for as much as one-third of all sharks caught by fishermen in the Comoro Islands.

Misra and Menon (1955) recorded I. glacus from South Africa, the Red Sea, Arabia, India, Pakistan, Ceylon, and Indochina. Smith's suggestion (1953) that the range of the Atlantic I. oxyrinchus is continuous around the Cape of Good Hope is supported by Fourmanoir, as mentioned above. Thus, the range of I. oxyrinchus overlaps that of I. glaucus.

The porbeagles (Lamna) are pantemperate sharks, generally avoiding the tropics (Hubbs and Follett, 1947). In the eastern Atlantic, L. nasus occurs from northwestern Africa to southern Scandinavia.

Occasional specimens have been reported from northern Norway and the Murman coast (Bigelow and Schroeder, 1948), and it also ranges into the Baltic Sea. On the western side of the Atlantic, it is reported to be the commonest large shark in summer along the coast of Nova Scotia. Other distributional data caused Bigelow and Schroeder to suggest that the 65°F isotherm limits its normal southward occurrence.

The salmon shark of the Pacific Ocean, L. ditropis, has been reported from southern California northward to Alaska, the Bering Sea, and Japan (Hubbs and Follett, 1947; Roedel and Ripley, 1950; Clemens and Wilby, 1961). Bright (1960) reported a specimen from Alaska which he identified as L. nasus, but this appears to be a mistake in identificaton.

Sano (1960) presented seasonal catch records showing a gradual northward extension in range of the salmon shark in the northwestern Pacific. In the last decade of May, none was taken north of 52°N. The northernmost captures were made during the last decade of July in 60°-62°N, 175°E-180°. The daily average catch in the northern area was 1.2 individuals per operating boat, with more than half the total number of boats making catches. Strasburg (1958) obtained 28 longline records of the salmon shark in the central Pacific. Of these, 26 were north of 35°N, 1 was between 30°and 35°N, and the remaining record was from the Line Islands. Strasburg suggested that this last record is based on a misidentified bonito shark, I. glaucus.

Smith (1949) reported the first apparent occurrence of L. nasus from South African waters; specimens were taken in Knysna and Durban. The porbeagle is reported as "not abundant" in New Zealand waters (Illingworth, 1961), although it occurs from Cook Strait (southern winter) south to Stewart Island. Whitley (1940) recorded it from Australian waters.

HABITS

The lamnid sharks are active, vigorous swimmers, as indicated by their generally streamlined appearance and lunate caudal fin. Bigelow and Schroeder (1948) described the mackerel shark (L. nasus) as putting up feeble resistance when hooked, but the white shark and mako are highly esteemed as gamefishes. The mako particularly is known for its habit of jumping, and Goadby (1959) stated that it has been observed to clear the water by 10 feet.

Most catch records for these sharks are for surface waters, but their depth range appears to be rather variable. The Atlantic porbeagle is reported regularly down to 420-480 feet, and in winter it apparently moves farther offshore into deeper water. Phillipps (1946) reported that the New Zealand porbeagle lives in depths of 1200 feet, although young specimens are taken regularly in 180-300 feet. Strasburg (1958) took L. ditropis at depths of 160 to 500 feet in pelagic longlining operations. Toward warm-temperate regions the porbeagles normally descend to deeper levels.

The bonito shark, according to the relatively few records available, does not inhabit any particular depth between the surface and 500 feet (Strasburg, 1958). The mako apparently lives in shallower depths than its relatives and has even been known to beach itself while pursuing prey in shallow coastal waters (Illingworth, 1961).

The white shark reportedly has been taken as deep as 4,200 feet (Bigelow and Schroeder, 1948), but it has been reported most often in surface waters and has been known to enter extremely shallow coastal waters.

FOOD

The most important food source for these sharks is fishes. The species eaten are varied, generally depending upon the region inhabited by the shark. For example, herring, pilchard, and ground fish, such as the gadoids and flounders, were taken most often by Lamna nasus in the western Atlantic. It also feeds on other small sharks, such as dogfish, and on squid. Sano (1960) reported on the significance of L. ditropis as a predator on salmon, and stomachs examined by him contained Oncorhynchus nerka, O. keta, O. gorbuscha, and O. kisutch. Other fishes also were recorded, including Alepisaurus borealis, Anotopterus pharao, Pleurogrammus monopterygius, Eumicrotremus orbis, and Theragra chalcogramma.

Many kinds of fishes are taken by the mako, but the smaller schooling fishes, such as scombroids and clupeoids, are most commonly ingested. Makos are reported to feed on larger fishes too, such as snappers and yellowtail. A 120-pound swordfish (with sword) was found in one specimen and 150 pounds of swordfish flesh in the stomach of another.

The white shark has the most varied diet among the lamnids. The stomach remains of the small specimens taken off the Scripps Pier included crustaceans, squid, Mustelus californicus, and Scorpaenichthys marmoratus. Elsewhere, larger specimens have contained sharks up to 7 feet long (one contained two adults of

Carcharhinus milberti of this size), a 100-pound sea lion, seals, sturgeon, tuna, a wide variety of other fishes (including stingrays and chimaeroids), and large sea turtles. According to Goadby (1959), white sharks are attracted to the coastal whaling stations along the east coast of Australia, drawn there by the cutting in of whales, and Davies and Campbell (1962) reported a similar habit of white sharks off the South African coast.

REPRODUCTION

Relatively little is known about reproduction and development in this family, particularly of *Isurus* and *Carcharodon*. Apparently, like *Lamna*, few embryos are carried and the young are large at birth. Embryos of 18, 19, and 24 inches were found in a 5-foot female of *L. nasus*, and Hubbs (1923) described one of 20 pounds (length not given) from a 10-foot specimen. They are ovoviviparous, and the yolk sac and umbilical cord are resorbed at an early developmental stage. Until birth, embryos obtain nourishment by feeding on the unfertilized eggs present in the uterus. The stomach becomes distended into a "yolk stomach" and attains half the body length in large embryos. Yolk stomachs also have been observed in embryos of *Isurus*.

Nothing is known about the developmental stages of *Carcharodon*. Apparently, maturity is not reached until its length is about 13 feet. The smallest free-living specimen reported by Bigelow and Schroeder (1948) was about 5 feet. Smith (1951) described a 55-inch juvenile from Algoa Bay, South Africa, and Scattergood (1962a) mentioned one of 3 feet from New England waters. From time to time, several specimens in this general size range are caught in succession (such as the captures from the Scripps Pier, noted above). Coles (1919) reported the capture of four small specimens at close intervals off Cape Lookout, North Carolina. Shortly thereafter, a large female, estimated to be 22 feet long, was trapped in a net. In his opinion, this female was the mother of the 4 specimens caught earlier. If, as in *Lamna*, large young are the rule, then a 22-foot *Carcharodon* could, quite conceivably, bear young 6 to 7 feet in length.

IMPORTANCE TO MAN

Coincident with the general decline in the commercial shark fishery, these sharks no longer have a significant market value in this country. Elsewhere, particularly in Europe and Japan, the meat is well received. Sharks have a definite nuisance value to the commercial set-line fishermen, robbing the lines and frequently biting off the hook and leader in the process. The mako and the white shark are important gamefishes in many parts of the world; the largest white shark landed on rod and reel weighed 2,664 pounds (Goadby, 1959). Both these sharks are strong, vigorous fighters and dangerous as well; attacks on fishing boats by hooked specimens are not infrequent.

Of the 225 to 250 existing species of sharks, about 30, representing 9 genera, are considered as potentially dangerous to man. Size, dentition, feeding habits, and aggressiveness are the principal criteria for evaluating their danger. The white shark generally is agreed to be the most dangerous shark. It is exceeded in size only by the plankton-feeding basking shark and whale shark, possesses formidable teeth, normally feeds on large prey, and is a popular gamefish primarily because of its aggressive behavior. Attacks on humans are well documented, either through recovery of tooth fragments (e.g., Kean, 1944) or by various authenticated reports and descriptions by observers (Gudger, 1950; Coppleson, 1958; Bini, 1962; and others). A white shark was believed to have been responsible for four deaths in a 6-day period along the coast of New Jersey in 1916 (Bigelow and Schroeder, 1948). Shortly after the last attack, a specimen about 7 feet long was captured and found to contain human remains.

The species of Isurus, though possessing a milder reputation than Carcharodon, nevertheless have been incriminated in attacks on boats, swimmers, and divers. Straughan (1958) gave a vivid account of an encounter with a large mako while skin diving in Florida waters.

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