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Cetorhinus maximus (Gunnerus, 1765)

Fig. 67

Squalus maximus Gunnerus, 1765, *K. Norske Vidensk-selsk.Scr. Trondh.*: 33, pl. 2. Holotype, apparently none. Type Locality: Trondhjem, Norway.

Synonyms: ***Halsydrus pontoppidani*** Neill, 1809: 5-6; also Neill, 1809: 90-91 (*nomina nuda*; Bland and Swinney, 1978: 134). ?***Tetroras angiova*** Rafinesque, 1810a: 11. No types?, *species dubium*. Also Rafinesque, 1810b: 46; Rafinesque, 1815: 93. ***Squalus gunnerianus*** Blainville, 1810: 256, pl. 2, fig. 3; also Blainville, 1810b: 170. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus homianus*** Blainville, 1810: 257, pl. 2, fig. 1. Also Blainville, 1816: 121. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus pelegrinus*** Blainville, 1810a: 256, pl. 2, fig. 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 9853 (Eschmeyer, 1998: CD-ROM). ***Squalus peregrinus*** Blainville, 1811: 365. Also Blainville, 1816: 121. Variant and possibly emended spelling of ***Squalus pelegrinus*** Blainville, 1810. ***Squalus (Cetorhinus) Gunneri*** Blainville, 1816: 121 (*nomen nudum*). ***Squalus (Cetorhinus) Shavianus*** Blainville, 1816: 121 (*nomen nudum*). ?***Scoliophis atlanticus*** Anon., 1817: 44, cited by Sherborn (1923: 535). Listed in synonymy of ***Halsydrus maximus*** by Whitley (1939: 241) without explanation, possibly a 'sea serpent' based on a basking shark carcass? ***Halsydrus pontoppidani*** Fleming, 1817: 713. Stronsa, Orkney Islands. Holotype: National Museum of Scotland, NMSZ-1979.012, three vertebrae in alcohol and dried ceratotrichia, *fide* Herman, McGowan and Swinney (1990: 1). ***Squalus isodus*** Macri, 1819: 76, pl. 1, fig. 2. Mediterranean. No types (Eschmeyer, 1998: CD-ROM). ***Squalus rostratus*** Macri, 1819: 76, pl. 1, fig. 1, pl. 2. Mediterranean. No types known (Eschmeyer, 1998: CD-ROM). ***Squalus elephas*** Le Sueur, 1822: 350, pl. Types: Based on a large adult male specimen, about 10 m (32 ft 10 in) TL from the New Jersey coast, possibly not saved. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus rashleighanus*** Couch, 1838: 51. Type locality, Cornwall. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus rhinoceros*** Mitchell, *in* DeKay, 1842: 358 (reference to name in newspaper article by Mitchell, 1828 citation unknown). Name only, not available, Maine Coast (Eschmeyer, 1998: CD-ROM). ***Squalus cetaceus*** Gronow, 1854: 6. Type locality, Norway. No types known (Eschmeyer, 1998: CD-ROM). ***Polyprosopus macer*** Couch, 1862: 68, pl. 15, fig. 2. Type locality, Startpoint, Cornwall, England. No types known (Eschmeyer, 1998: CD-ROM). ***Cetorhinus blainvillei*** Capello, 1870: 233, 1 pl. Type locality, Portugal. Types? (Eschmeyer, 1998: CD-ROM). ***Selachus pennantii*** Cornish, 1885: 351. Type locality: Cornwall. No types known (Eschmeyer, 1998: CD-ROM). ***Tetroras maccoyi*** Barrett, 1933: 13. Types? Australia. Reference from Whitley (1934: 197) and Eschmeyer (1998: CD-ROM). ?***Tetraoras angiona*** Bigelow and Schroeder, 1948: 146. Error for ***Tetroras angiova*** Rafinesque, 1810. ***Cetorhinus maximus*** forma infanuncula van Deinse and Adriani, 1953: 309. Holland, for specimens without gill rakers. Types? Not available, according to Eschmeyer (1998: CD-ROM). ***Cetorhinus maximus normani*** Siccardi, 1960: 255, pl. 1. Syntypes (4): Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, Capital Federal, Argentina, MACN (Eschmeyer, 1998: CD-ROM). Also Siccardi, 1961: 96-97 (as species, ***C. normani***).

Other Combinations: ***Halsydrus maximus*** (Gunnerus, 1765), ***Selache maxima***, ***Selache maximus*** or ***Selache maximum*** (Gunnerus, 1765), ***Selache elephas*** (Le Sueur, 1822).

FAO Names: En - Basking shark; **Fr** - Pélerin; **Sp** - Peregrino.

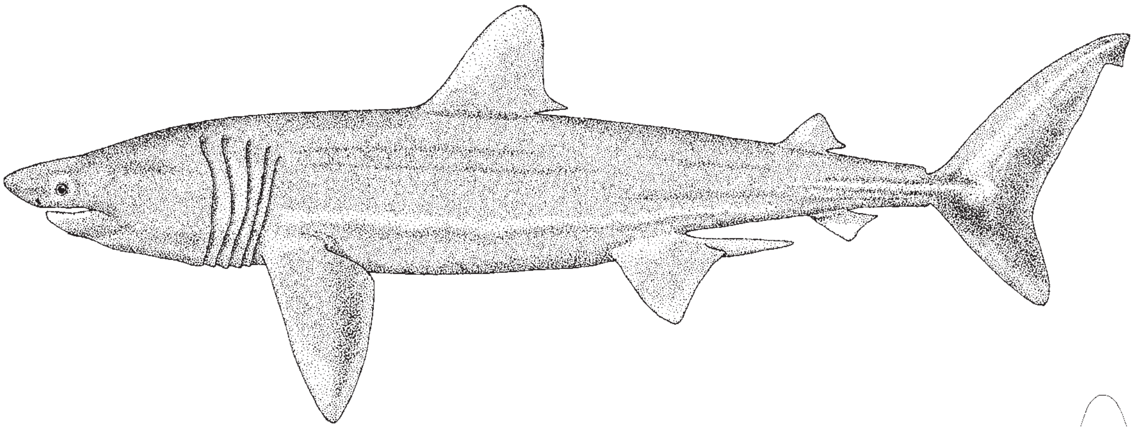
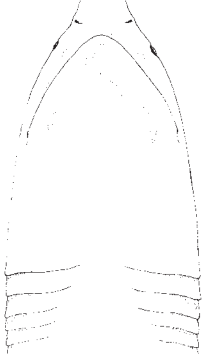


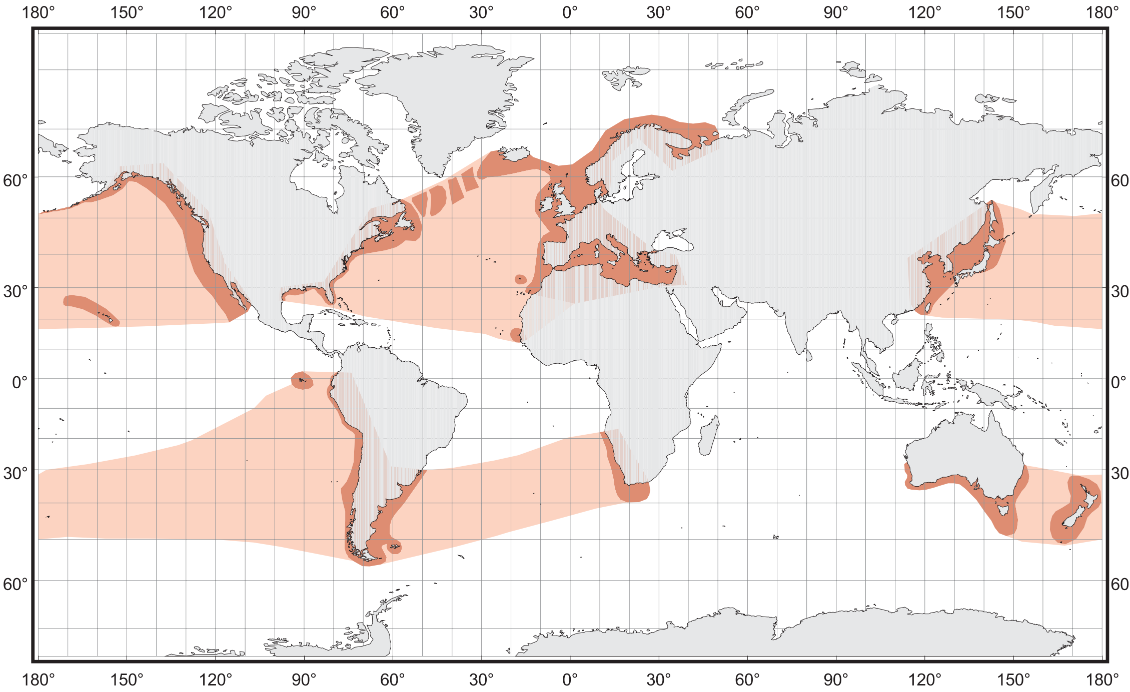
Fig. 67 *Cetorhinus maximus*



Field Marks: The great size, enormous gill slits that virtually encircle the head, dermal denticle gill rakers, pointed snout, huge, subterminal mouth with minute hooked teeth, caudal peduncle with strong lateral keels, and lunate caudal fin distinguish this shark from all others. **Colour:** blackish to grey-brown, grey or blue-grey above and below on body and fins, undersurface sometimes lighter, often with irregular white blotches on the underside of the head and abdomen; flanks sometimes with lighter linear striping and spots.

Diagnostic Features: See family Cetorhinidae above.

Distribution: Circumglobal with a wide but possibly disjunct distribution: Western North Atlantic: Canada (Newfoundland, Nova Scotia, New Brunswick) and the United States (Maine, New Hampshire, Massachusetts, Connecticut, Rhode Island, New York, New Jersey, Delaware, Maryland, Virginia, North Carolina, Georgia and Florida, also northern Gulf of Mexico), with most records in the Gulf of Maine and in the Mid-Atlantic Bight. Western South Atlantic: Southern Brazil, Uruguay and northern Argentina, Falkland (Malvinas) Islands. Eastern North Atlantic, Arctic Ocean, and Mediterranean Sea: Iceland (south and west coast), Faeroe Islands, Norway and Russia (western Barents Sea and White Sea), south to Sweden, Scotland, Ireland, England, France, Spain, and Portugal, the entire Mediterranean Sea (including Italy, Greece and Turkey), Morocco, and Senegal. Eastern South Atlantic and southwestern Indian Ocean: Namibia and South Africa (Northern and Western Cape Provinces). Western North Pacific: Japan, Korean Peninsula, Taiwan (Province of China), China. Western South Pacific: Australia (New South Wales, Victoria, Tasmania, South Australia and Western Australia), New Zealand. North-central Pacific: Hawaiian Islands (USA). Eastern North Pacific: Gulf of Alaska and Aleutian Islands to Gulf of California, including Canada (British Columbia), the United States (Alaska, Washington, Oregon, and California), and Mexico (Baja California and northern Gulf of California). Eastern South Pacific: Ecuador, Peru and Chile, Galapagos Islands.



Habitat: A coastal-pelagic and semioceanic or oceanic shark found in boreal to warm-temperate waters of the continental and insular shelves, occurring well offshore and often very close to land, just off the surf zone, and entering enclosed bays. Most individuals are observed in shallow coastal waters, but records from aerial cetacean and sea turtle surveys in the western North Atlantic, a stranding at an oceanic island chain (Hawaiian Islands), and pelagic driftnet records in the temperate North Pacific suggests that it readily ventures into the epipelagic zone. It has been sighted at the surface over the slopes from 200 to 2 000 m, and with a few sighted in the oceanic basins at 2 000 to 4 000 m. The basking shark is thought to overwinter in deep offshore waters, possibly near the bottom, and has occasionally been caught in deep bottom trawls in the Gulf of St. Lawrence and off Scotland. Off the United Kingdom, Japan and Newfoundland most records are in waters of 8 to 14°C, though off the Atlantic coast of New England sightings were in waters of 11 to 24°C with most at 16 to 24°C. Basking sharks seem to prefer ocean fronts, where differing water masses meet, and close inshore off headlands, around islands and in bays with strong fluctuation of water masses from tidal flow and where aggregations of zooplankton occur.

Biology: The sociobiology, behaviour and population biology of the basking shark are sketchily known and need further investigation. Although basking sharks are huge impressive animals that are readily accessible to underwater observation and are conspicuous to surface observers, a limited amount is known of displays, courtship, and social structure, though this is changing with intensive behavioural observation of basking sharks off the UK (Earll et al., 1992). A problem is that the basking shark is traditionally studied and viewed as a fisheries object, so that many details of its behaviour and general biology remain to be elucidated.

Basking sharks are apparently social animals as in some other lamnoids, and show some behaviours that may be intraspecific displays. This shark is often seen at or near the surface, singly, in pairs or triads or in schools up to a hundred or more individuals, basking with dorsal fins out of the water or even with bellies upward. Adults have been seen together, as have pairs with young individuals and adult females (the former assumed to be offspring). These sharks are often seen moving slowly forward or in short arcs with their mouths distended like hoops and pharynx expanded while feeding, sometimes with snouts out of the water. They also *cruise* when not feeding, with mouth partly closed and pharynx not expanded. The open-mouthed feeding posture of basking sharks is analogous to *gaping* in certain other lamnoids, although it is not established if the basking shark uses gaping in a social context apart from feeding. Surface-basking in this shark is thought to be correlated with surface concentrations of zooplankton and also with courtship and mating. Two, three or more individuals may engage in *tandem-swimming*, in a straight line or in circles, which suggests to some writers that a row of these sharks swimming together may have been mistaken for a single huge ‘sea serpent’ in the past. They also show *parallel-swimming* or *stalling* (stopping, sometimes for protracted periods), with sharks alongside one another, and sometimes make a *wedge-formation* of three individuals while feeding. Nose to tail *circling* has been described with a male and female and even a pair of males. The sharks direct their feeding along tidal lines, may circle zooplankton patches, and may swim in one direction, do a *U-turn*, then parallel their previous track. They can also stop and gulp down plankton concentrations, may stall and keep in one position, may swim very slowly, and show relatively fast dashes at the surface. They may dive suddenly when disturbed, and may flick their tails sharply before doing so. Individuals may *droop* their dorsal fins nearly 45° to one side; they also may lift their tails out of the water and do a *tail-sweep*, wagging the tail from side to side at a 45° angle in an exaggerated movement. Under provocation (particularly when harpooned) this species may defend itself by *tail-swatting*. Basking sharks may approach divers and boats quite closely, possibly out of curiosity, and swim around them or follow them.

Recent observations and photographs confirm that basking sharks *breach* or jump partway or entirely out of the water, and it has been suggested that they do so to dislodge parasites or commensals such as lampreys or remoras. In addition to the ectoparasitic copepods found on other sharks, basking sharks often have sea lampreys (***Petromyzon marinus***) attached to their skin in the North Atlantic, and although lampreys apparently are unable to cut through the formidable denticle-armoured skin of the shark, they may be enough of an irritant to evoke a reaction like breaching or rubbing on objects or the bottom (*chafing*) to dislodge them. Basking sharks may breach alone or while in groups, and breaching may also have a social significance in intraspecific communication.

Dead basking sharks are often stranded on the beach, in a state of advanced decay and damaged and partly dismembered from rolling in the surf, and they have been also occasionally lifted from the bottom by trawls on fishing boats. Several times such carcasses have been misidentified as ‘sea serpents’, plesiosaurs or other fabulous monsters, some of which have been given specific and even generic names.

Numbers of basking sharks sighted may fluctuate greatly in given areas each year, with irregular increases (‘invasions’) and decreases that are of uncertain cause. Estimates of world population numbers are unavailable, as with most other sharks, but aerial surveys suggest that numbers of basking sharks in localized areas (e.g., New England coast and Monterey Bay) may not exceed 2 000 to 6 000, nor have catches in the eastern North Atlantic much exceeded 3 000 per year when catches were highest.

The massive liver of the basking shark, contained in a long body cavity, apparently serves as a ‘hepatic float’ to adjust it to approximately neutral buoyancy.

Basking sharks are highly migratory, and noteworthy for their seasonal appearance in numbers in given localities and subsequent disappearance. Off the Atlantic seaboard of North America they appear in the southern part of their range in spring (North Carolina to New York), apparently shift northward in summer (New England and Canada), and disappear in autumn and winter. Off the eastern North Pacific basking sharks occur in greatest numbers during autumn and winter in the southernmost part of their range there (California), but shift at least in part to more northern latitudes in spring and summer (up to Washington and British Columbia). Off the United Kingdom the bulk of the population there appears in the springtime and disappears by autumn, but individuals may be present at all seasons of the year. Aerial surveys off New England suggests that basking sharks move into shallow coastal waters from deeper water in springtime as zooplankton blooms develop; sightings there indicate that basking sharks occur at the surface in the epipelagic zone in deep water, above the slopes and even in the ocean basins. Research is currently in progress in the eastern North Atlantic using satellite radio tags to resolve some of the problems of migration in this species. Priede (1984) details an early successful short-term satellite tracking effort on a radio-tagged basking shark, and plans for satellite tagging using more modern equipment are underway in the United Kingdom (Dunbar, Fowler and Denham, 1995). This space-age methodology may unravel some of the secrets of the basking shark’s seasonal migrations and movements. Adult individuals found off the United Kingdom in summertime are apparently engaged in courtship activity and copulation, as indicated by behavioural observations and courtship and mating scars found on captured individuals.

Pronounced spatial and seasonal populational segregation may be a characteristic of this species, as suggested by fisheries catches off the United Kingdom. Most individuals caught there in the summer were subadult or nonpregnant adult females, outnumbering the males by 40:1, but in the winter the few individuals caught were mostly males. Off Japan most basking sharks taken in fisheries are or were females.

Pregnant females are almost entirely unknown for the species, suggesting that such females are spatially and bathymetrically separated from those members of the population that are regularly seen basking at the surface. It is also possible that the number of pregnant females is very low relative to the number of non-pregnant adult females, with correspondingly few being taken and with extremely low fecundity for the species. Juveniles below 3 m long have been extremely rare in the literature, with a single record of a freeliving individual about 1.7 m long reported from the British Isles. More recently, field observers from the UK Marine Conservation Society have reported larger numbers of sightings of individuals between 2 and 4 m long (34%), 4 to 6 m (about 38%), and 6 to 8 m (about 18%), but with few young below 2 m (3%) or large adults above 8 m (8%) of over 3 300 individuals sized (Pollard, 1996). This suggests low local recruitment of young, but large numbers of juveniles (2 to 6 m) and smaller numbers of adults (6 to 8+ m).

A pregnant female has been reported with a litter of six young. Adult, nonpregnant female basking sharks have immense numbers of small eggs in their ovaries, which suggests that this shark has uterine cannibalism as in many other lamnoids, with embryos feeding on the small eggs (oophagy). Feeding on smaller siblings (adelphophagy) has not been demonstrated. Young below 2 m appear in waters of the United Kingdom in springtime, suggesting spring pupping.

Age of this shark has been estimated by counting vertebral rings and attempting to correlate them with supposed changes in size of individuals within a population, but this has met with limited success. It has been suggested that birth occurs after a 3.5 year gestation period, and that two calcified rings per year are laid down until maturity at between 6 and 8 years for males (Parker and Stott, 1965). The correlation of the rings with time is uncertain and controversial. Pauly (1978) initially suggested a yearly rate of ring deposition, but Pauly (in press) recently suggested that vertebral rings were unreliable for estimates of age in basking sharks due to variation in numbers of rings along the vertebral column and apparent lack of correlation of vertebral ring numbers to yearly cycles. Pauly (in press) used size frequency data to develop a von Bertalanffy growth curve for the basking shark, assuming a size at birth of 1.5 m (see below), a gestation period of about 2.6 years, and an age at greatest length (10 m) of about 50 years. There may be a possible cycle of two to three years between litters, and a possible age at maturity for males at 12 to 16 or more years and up to 20 years for females (UK CITES Authority, 1999).

The basking shark is one of the four types of large, filter-feeding elasmobranchs, the others being the megamouth and whale sharks, and the manta rays (Mobulidae). The basking shark may be unique in relying entirely on the passive flow of water through its pharynx generated by swimming for filtration; the other filter-feeders may assist the process of food ingestion by actively pumping or gulping water and food organisms into their pharynxes. The basking shark feeds on small planktonic organisms trapped on its unique gill rakers, apparently with the help of mucus secreted in its pharynx. Food items include small copepods (including calanids), barnacle, decapod, stomatopod larvae and fish eggs. On the average a half tonne of material may be present in the stomach of these sharks. While feeding the basking shark usually cruises with mouth widely open and gills distended, occasionally closing its mouth to ingest its prey. An average adult has been estimated to be capable of filtering over 2 000 t of water per hour assuming a constant cruising speed of about 2 knots. They seem to feed almost at random in low plankton densities, but are highly selective and actively search in restricted areas for high densities of zooplankton above a minimum concentration before feeding. Off southwestern England they actively seek plankton concentrations at the surface along boundaries of tidally influenced water masses or tidal fronts over bottom about 20 to 50 m deep.

The facts that the basking shark periodically sheds its gill rakers and that plankton densities seasonally fall below levels thought essential to maintain ordinary swimming and metabolic activity in this shark have spawned a controversy over whether or not the species remains active when deprived of gill rakers and high plankton densities. It has been suggested that the basking shark may hibernate on the bottom, perhaps at the edges of continental shelves or on the slopes, until its rakers are replaced and plankton blooms reoccur. Proof of hibernation has never been forthcoming, and an alternate hypothesis has been suggested that the basking shark may turn to benthic feeding when it loses its gill rakers. A possible additional factor is that the massive, oil-filled liver of this species may serve as a metabolic store to supply energy to support a reduced rate of activity (slower swimming in colder, deep water) while gill rakers regenerate and plankton supplies eventually recuperate. Estimates have been proposed that, in north European waters, the basking shark drops its gill rakers in early winter and takes about 4 or 5 months to fully replace them. An anecdotal report suggests that basking sharks may feed on small schooling fishes such as herring as a possible alternative to plankton-sieving, but this remains to be confirmed.

By far the most important enemy of this shark is humanity, primarily from fisheries but also from collisions with boats. A dead basking shark with wounds was once seen near a pod of killer whales (***Orcinus orca***), with the implication that the whales killed the shark. White sharks (***Carcharodon carcharias***) will readily consume meat from dead basking sharks, but have not been recorded as attacking living ones. A large white shark or a group of white sharks are sufficiently formidable to kill a basking shark. Lampreys, copepods and cookiecutter sharks (***Isistius***) may produce external wounds, but it is not known if they contribute to mortality.

Size: Basking sharks have been credited as reaching a maximum total length of 12.2 to 15.2 m, but even if this is correct most specimens do not exceed approximately 9.8 m. Pauly (in press), analyzing the largest North Atlantic records of basking sharks in an ‘extreme value theory plot’, suggested that individuals over 10 m long were unlikely to exist. This is supported by observational data off the UK (Pollard, 1996), in which few basking sharks (8% of over 3 300) over 8 m long were seen. Size at birth is uncertain with few pregnant females examined. An unconfirmed record of a foetus about 1.7 m long, another foetus 1.5 m long, and a 165 cm freeliving individual suggests that size at birth may be about 1.5 to 1.7 m, and hence is slightly greater than any other known ovoviviparous or viviparous shark except perhaps the common thresher and white shark. Males mature between 4 and 7 m and reach about 9 m; a late adolescent male 6.85 m long from Cape Town, South Africa (dissected by the writer) had almost fully calcified claspers; six adult males examined by Matthews and Parker (1950), Springer and Gilbert (1976), and the writer were 7.01 to 8.46 m long (average 7.83 m). Females are immature at 3.19 and 3.59 m (Springer and Gilbert, 1976, L.J.V. Compagno, unpub. data), females are mature at 8.0 to 9.8 m; six adult females examined by Matthews and Parker (1950) and Springer and Gilbert (1976) were 8.03 to 8.48 m long (average 8.27 m), suggesting that females slightly exceed males in size as with many other sharks. Pauly (in press) suggested a maximum weight of 7.5 t at 10 m using an isometric weight curve, $W(t) = 0.0075 * TL(m)^3$. The basking shark is apparently the second largest shark, neoselachian elasmobranch, and living fish-like vertebrate after the whale shark (***Rhincodon typus***), although it may be rivalled in size by the manta (***Manta birostris***).

Interest to Fisheries and Human Impact: The basking shark has been the object of small-scale targeted harpoon fisheries from small boats and small ships (some built and equipped like whale-catchers) during the eighteenth, nineteenth and twentieth centuries. In the twentieth century such fisheries operated primarily off the Norwegian coast, Ireland, Scotland, Iceland, Spain, United States (California), Peru, Ecuador, China and Japan. It has been sporadically if heavily fished due to periodic depletion of basking shark stocks or intrinsic factors of the fisheries such as falling demand for this shark. During the eighteenth and nineteenth centuries basking sharks were also harpooned from large whaling vessels in the Gulf of Maine (United States and Canada) and probably elsewhere; basking sharks in the western North Atlantic were apparently decimated by such activities. The basking shark has also been taken as discarded and utilized bycatch in net gear, including bottom anchored gill nets, floating gill nets, pelagic gill nets, bottom trawls, pelagic trawls, and even anchored fish weirs. It is caught as a rare bycatch of gill netters targeting thresher sharks and swordfish off California and was taken by squid gill netters as an uncommon bycatch in the epipelagic zone of the temperate North Pacific. It was formerly perceived as a problem to salmon gill netters off British Columbia and elsewhere in the Pacific Northwest by fouling and damaging gill nets, and was formerly subjected to a localized eradication programme in British Columbia using a modified fisheries vessel with a knife-like ram on its bow to impale and kill sharks at the surface. The activities of this vessel in the 1950s apparently decimated the basking shark locally, which has not shown signs of recovery almost fifty years later.

Meat from the basking shark is used fresh or dried-salted for human consumption. The fins of the basking shark are used for shark-fin soup and currently are extremely valuable, with the huge pectoral and dorsal fins recently (1999) sold for US$10 000 to 20 000 each. The basking shark was traditionally targeted for its liver, which is rich in oil and very large. The liver oil of the basking shark was formerly used for tanning leather and for lamp oil; it also yields vitamin A, and in modern times has been extracted for its high level of squalene which is used for medicinals and cosmetics. The hide of the basking shark is processed for leather, the cartilage for medicinals, and the carcass is sometimes rendered into fishmeal. Basking shark fisheries have not been monitored in detail except in the eastern North Atlantic and New Zealand, and catch statistics for basking sharks have been reported to FAO from New Zealand, Portugal, France and Norway. Norwegian catches were the highest reported for any nation, with catches of 2 200 to 18 700 t reported to FAO in the 1960s and 1970s, but have declined to less than 500 t in 1997 and have been caught under a quota from 1978 onward. Slightly more than 12 000 sharks were caught off the west coast of Ireland over a 29 year period, with peak catches in the 1950s and apparently no recovery in recent years. New Zealand, Portugal and France report tiny catches of 1 to 14 t at present, with the New Zealand catch strictly regulated as utilized bycatch only and with targeted fisheries not allowed.

The basking shark is usually quite tolerant of boats approaching it, which makes it easy to hunt with harpoons from small boats. Divers have been able to swim up to individuals and photograph them without invoking flight reaction. Basking sharks may approach divers quite closely, possibly out of curiosity, and swim around them. This species is regarded as ordinarily harmless and inoffensive when not provoked or molested. The immense size and power of the basking shark should invite respect by ecotouristic divers who swim with these sharks. Divers should take care in contacting the skin of basking sharks, which has large dermal denticles with sharp, hooked crowns that point forward and sideways as well as backward. As the writer can attest from dissecting large basking sharks, these denticles can inflict irritating lacerations on unprotected skin.

There is considerable and growing concern over the conservation status of the basking shark because of declining numbers caught over the last five decades, with total catches dropping from 0.5 to 0.2 of their peaks during the 1970s and with some localized fisheries depressed to less than 0.1 of their peaks in 10 to 25 years (UK CITES , 1999). Localized basking shark fisheries have a short-term boom and bust nature, and apparently are not sustainable at even moderate levels for very long due to the biological limitations of the basking shark as a fisheries species. The basking shark has proved to be extremely vulnerable to overfishing, perhaps more so than most sharks, and this can be ascribed to its slow growth rate, late maturity, long gestation period, probably low fecundity, long life, few predators when adult, probable small size of existing populations (belied by the immense size of individuals in their small schools), ready access to small fishing vessels inshore and off built-up areas, and possibly little interchange between populations or stocks. A recent and major problem is the extraordinarily high value of basking shark fins, which promotes finning of sharks caught as bycatch of other fisheries rather than the release of captured individuals alive. The fin trade also supports small-scale targeted fisheries beyond the commercial limits imposed by the lesser value of other basking shark products such as liver oil, and by the depleted stocks of basking sharks in most parts of the world. High fin prices can also promote illicit poaching and illegal trade despite local, national and international protective measures.

The basking shark has been placed on the IUCN Red List as a vulnerable species, and has received protection from exploitation in the territorial waters of the United Kingdom, Malta, New Zealand and the United States (East Coast, including separate protection by the State of Florida in its territorial waters). It was sponsored for CITES listing on Appendix II by the United Kingdom (for the 2000 CITES meeting), to promote regulation of basking shark catches and limits to international trade in fins and other products. However the CITES proposal was very narrowly defeated and the UK is going on to propose the basking shark for CITES Appendix III listing, effective from 2000 onward. The basking shark will be fully protected in the entire Mediterranean Sea once the Barcelona Convention for the Protection of the Mediterranean Sea is ratified by its Member Nations. It is listed as a strictly protected species of the Bern Convention on Conservation of European Wildlife. It is under consideration for total protection off South Africa (2000).

The basking shark has become a ‘supershark’, with a high-profile and fortunately positive public image, and has a strong and highly motivated conservationist following in the United Kingdom. This is somewhat similar to, albeit better organized than conservationists promoting the whale shark in the western Atlantic and the Indo-Pacific, which ensures public awareness of the conservation problems and interest in protecting both ‘gentle giants’. The basking shark is being monitored by three different conservation groups in the United Kingdom, with sightings by volunteers reported on standard data-cards.

Local Names: Basking shark, Giant basking shark, Elephant shark, Capidolo, Oilfish, Pelerin, Sun fish or Sunfish, Sail fish or Sailfish, Hoe mother or Homer, Bone shark, Gurry shark (English); Hoe mother, Homer (Orkneys); Heulgi (Wales); Cearban (Scotland); Sun fish, Liabhán mór, Liabhán chor gréine (Ireland); Haar moer (Scandinavia); Brugde, Brygde, Ry brigde (Norway); Brugden (Sweden); Rymer, Beinhaakal (Iceland); Brugde (Denmark); Mandelhai, Riesenhai (Germany); Reusenhaai (Belgium); Reuzenhaai (Holland); Le pélerin, Le très grand, Le squale a fanons, Poisson à volies, Elephant de mer (France); Squalo massimo, Cagnea, Selachio gigante, Cagnia, Imbestinu, Caniscu, Squalo elefante (Italy); Pixi tunnu (Malta); Carago, Peixe carago, Peixe frade (Portugal); Peregrino (Spain); Peixe frade, Tubarâo frade, Basking shark (Azores); Psina golema (Adriatic); Ubazame or Old woman shark, Teguzame [Tenguzame?] or Long-nosed shark, Bakazame or Foolish shark, Zozame or Elephant shark (Japan); Elefante (Cuba); Peje-vaca or Cow-fish (Chile); Akula gigantakaia, Akuloobraznye, Bol'shezhabernye akuly, Gigantskie akuly, Akuly nastoiaschie, Lao sha k'o (Russia); Southern basking shark (Australia); Cape basking shark, Koesterhaai (South Africa).

Literature: Garman (1913); Barnard (1925, 1937, 1947); Lahille (1928); Fang and Wang (1932); Whitley (1934, 1939, 1940, 1967); Norman (1937); Fowler (1941, 1967a); Hildebrand (1946); Bigelow and Schroeder (1948); Matthews (1950, 1956); Matthews and Parker (1950a, b); Van Deinse and Adriani (1953); Parker and Boeseman (1954); Lindberg and Legeza (1959); Siccardi (1960, 1961); Baldwin (1961); Larkins (1964); Parker and Stott (1965); Kato, Springer and Wagner (1967); Squire (1967, 1990); Lindberg (1971); Shiino (1972, 1976); Miller and Lea (1972); Hart (1973); Sadowsky (1973); Antezana (1977); Bass, D'Aubrey and Kistnasamy (1975a); Springer and Gilbert (1976); Pauly (1978, in press); Applegate et al. (1979); Konstantinov and Nizovtsev (1979); Davis (1983); Silva-Santos, Gomes and Ferreira (1983); Compagno (1984, 1990a, b); Nakaya (1984); Quero (1984); Kenney, Owen and Winn (1985); Horsman (1987); Paulin et al. (1989); Tomas and Gomes (1989); Herman, McGowan and Swinney (1990); Springer (1990); Earll et al. (1992); Hanan, Holts and Coan (1993); Izawa and Shibata (1993); Michael (1993); Bonfil (1994); Darling and Keogh (1994); Last and Stevens (1994); Dunbar, Fowler and Denham (1995); Taylor (1995); Uchida (1995); Pollard (1996); Fowler (1996); Santos, Porteiro and Barreiros (1997); Fairfax (1998); McEachran and Fechhelm (1998); Sims and Quayle (1998); Castro, Woodley and Brudek (1999); UK CITES Authority (1999); D. Ebert (pers. comm., on Namibian records); S. Fowler (pers. comm.); J. Naughton (pers. comm., on Hawaiian record); L.J.V. Compagno (unpub. data from South Africa).

2.2.7 Family LAMNIDAE

Family: Lamnoidea Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 36. Also Subfamily Lamnini Bonaparte, 1838, *Nuov. Ann. Sci. Nat., Bologna,* ser., 1, 2: 209 (Family Squalidae); Family Lamna Hasse, 1879, *Nat. Syst. Elasmobr.*, (1): 52. Emended to Family Lamnidae Müller and Henle, 1838 by Richardson, 1846, *Ichthyol. China Japan*: 195.

Type Genus: ***Lamna*** Cuvier, 1816.

Number of Recognized Genera: 3.

Synonyms: Tribe Isurina Gray, 1851 (Family Squalidae): 58. Emended and raised in rank to Family Isuridae Gray, 1851 by Gill, 1893: 130. Type genus: ***Isurus*** Rafinesque, 1810. Subfamily Carcharodontinae Gill, 1893 (Family Isuridae): 130. Type genus: ***Carcharodon*** Smith, 1838. Family Carcharodontidae Whitley, 1940: 68. Independently proposed from Gill, 1893. Type genus ***Carcharodon*** Smith, 1838. Family Lamiostomatidae Glikman, 1964: 11, 105. Type genus ***Lamiostoma*** Glikman, 1964: 105.

FAO Names: En - Mackerel sharks, Porbeagles, White sharks; **Fr** - Requins taupe; **Sp** - Jaquetones, Marrajos.

Field Marks: Large sharks with pointed snouts and spindle-shaped bodies, long mouths with large blade-like teeth, long gill slits, long pectoral fins and high first dorsal fins, small pivoting second dorsal and anal fins, large lateral keels and prominent precaudal pits on the caudal peduncle, and lunate caudal fins.

Diagnostic Features: Head moderately long but shorter than trunk. Snout moderately long pointed and conical not greatly elongated flattened or blade-like. Eyes small to moderately large, length 0.9 to 3.4% of precaudal length. Gill openings large, width of first 7.6 to 10.8% of precaudal length, extending onto dorsal surface of head; all gill openings anterior to pectoral fin bases; no gill rakers on internal gill slits. Mouth large and parabolic, ventral on head; jaws moderately protrusable but not greatly distensible laterally. Teeth large, anteriors and laterals narrow and awl-shaped or blade-like to broad, compressed and triangular, in 22 to 31/20 to 29 (43 to 60 total) rows; two rows of large anterior teeth on each side in upper jaw, separated from the smaller upper lateral teeth by one row of small intermediate teeth on each side; three rows of lower anterior teeth on each side, the first two variably enlarged but the third about as large as laterals; no symphysial teeth. Trunk fusiform and moderately slender to very stout, firm and not flabby. Caudal peduncle strongly depressed and with strong, high keels and both upper and lower crescentic precaudal pits. Dermal denticles very small and smooth, with flat crowns, small ridges and cusps and with cusps directed posteriorly on lateral denticles. Pectoral fins very long and narrow, shorter to somewhat longer than head in adults; pectoral-fin skeletons plesodic with radials extending far into fin webs. Pelvic fins small, much smaller than first dorsal fin but larger than second dorsal and anal fins; pelvic-fin skeleton aplesodic, not extending into fin web. First dorsal fin large, high, erect and angular or somewhat rounded; fin skeleton semiplesodic, extending partway into fin web. Second dorsal and anal fins minute, much smaller than first dorsal fin, with narrow pivoting bases. Caudal fin lunate, dorsal lobe moderately long, less than one third as long as rest of shark, ventral lobe long and strong, nearly as long as upper lobe. Neurocranium moderately high, not compressed, with moderately long rostrum, depressed internasal septum and widespread nasal capsules, large orbits with strong supraorbital crests, greatly enlarged stapedial fenestrae, and posteriorly expanded hyomandibular facets. Vertebral centra strongly calcified, with well-developed double cones and radii but without prominent annuli. Total vertebral count 153 to 197, precaudal count 85 to 114, diplospondylous caudal count 66 to 86. Intestinal valve of ring type with 38 to 55 turns. Size moderately large to very large with adults 1.8 to about 6 m long.

Distribution: Lamnids have a broad geographic distribution in virtually all seas except where the ice pack covers the Arctic and Antarctic Oceans. One of them, the white shark (***Carcharodon carcharias***) has one of the widest ranges of any cartilaginous fish. The salmon shark (***Lamna ditropis***) has the most limited distribution in the family, the temperate and boreal North Pacific and Arctic fringe, but lives in an enormous area.

Habitat: Lamnids are tropical to boreal or notal, littoral to epipelagic sharks in continental and insular waters from the surf line and intertidal of shallow bays to the outer shelves and open ocean and rarely down the slopes to at least 1 280 m. Lamnids are apparently intolerant of fresh water and do not ascend rivers. Salmon sharks and porbeagles (***Lamna***) are tolerant of cold and moderate water temperatures but avoid the tropics, while makos (***Isurus***) are restricted to tropical and temperate seas. ***Carcharodon*** broadly overlaps the habitats of ***Lamna*** and ***Isurus.***

Biology: The mackerel sharks are fast-swimming, active pelagic and epibenthic swimmers, some of which are capable of swift dashes and spectacular jumps when chasing their prey. Mackerel sharks are partially warm-blooded, and have a modified circulatory system that enables them to retain a body temperature warmer than the surrounding water. This permits a higher level of activity and may increase the power of their muscles as well as allow some of them to be active in cold temperatures. They feed on a wide variety of bony fishes, other sharks, rays, chimaeras, marine birds and reptiles, seals and sea lions, whales and dolphins, squid, bottom crustaceans and molluscs, carrion, and occasionally terrestrial vertebrates (rarely including humans). Development is ovoviviparous, without a yolk-sac placenta. Like other lamnoids these sharks have uterine cannibalism, in which developing foetuses feed on fertilized eggs (oophagy) for most of their gestation period. More than one foetus survives in each uterus in most species, and it is not known if intrauterine siblings will attack and devour one another as in ***Carcharias taurus***. All the living species of lamnids are of large size, with a maximum length of 3.0 to perhaps 6 m or more. A giant, rather recently extinct (late Pliocene) member of the white shark genus (the megatooth shark, ***Carcharodon megalodon***, often placed in other genera or even families by some modern palaeontologists) attained an estimated length when adult of about 11 to 20 m (Gottfried, Compagno and Bowman, 1996). It was one of the largest and most powerful predatory vertebrates ever to live, rivalled only by certain cetaceans (sperm whales, orcas and giant archaeocetes), the largest pliosaurs and mosasaurs, giant Mesozoic and Cenozoic crocodiles, and the largest terrestrial theropod dinosaurs.

Interest to Fisheries and Human Impact: These sharks are important objects of oceanic and offshore continental fisheries because of their fine meat, but are also utilized for their oil, fins, hides, fishmeal, jaws and teeth. Some species are oceanic in whole or part, and are mainly taken with pelagic longlines and gill nets. Anchored gill nets and trammel nets, fish traps, hook-and-line, harpoons, and pelagic and bottom trawls can capture these sharks.

Porbeagles and salmon sharks (***Lamna***) are apparently inoffensive and have not bitten people in the water. The shortfin mako (***Isurus oxyrinchus***) has bitten swimmers and divers on a few occasions but may often display and stage mock-charges while confronted by divers. More often shortfin makos have bitten boats, especially after being provoked by hooking. The longfin mako has never been known to bite people or boats. However, this family contains what is generally considered the most ‘dangerous’ shark, the white shark (***Carcharodon carcharias***), because of its regular if infrequent habit of biting swimmers, divers, surfers and boats.

Local Names: Mackerel sharks, Man-eater sharks, Man-eating sharks, Man-eaters, Great white sharks, Mako-sharks, Porbeagles (English); Lamie, Requin-bleu, Taupe, (France); Heringshai, T’u sha k’o; Akuly sel devye or Sel devye akuly (Russia); Nezumizame-ka (Japan); Anequins (Mozambique).

Remarks: This account follows Compagno (1984, 1990b, 1999) in recognizing a single family for the genera ***Carcharodon***, ***Isurus*** and ***Lamna***, which is termed Lamnidae or Isuridae by most authors. Lamnidae has priority, stemming from Müller and Henle’s (1838a, 1839) family Lamnoidea or Lamnae, and being recognized by numerous authors including Bonaparte (1838, 1839, subfamily Lamnini), Müller (1845), Bleeker (1859), Gill (1862b, 1872), Owen (1866), Günther (1870), Hasse (1879), Jordan and Gilbert (1883), Woodward (1889), Jordan and Evermann (1896), Regan (1906a), Goodrich (1909), Bridge (1910), Engelhardt (1913), Jordan (1923), Bertin (1939a), Berg (1940), Fowler (1947, 1967a), Berg and Svetovidov (1955), Matsubara (1955), Patterson (1967), Blot (1969), Bailey et al. (1970), Lindberg (1971), Pinchuk (1972), Compagno (1973, 1981b, 1982, 1984, 1999), Nelson (1976, 1984, 1994), Applegate et al. (1979), Gubanov, Kondyurin and Myagkov (1986), Cappetta (1987), Carroll (1988), Eschmeyer (1990, 1998), Robins et al. (1991a), and Helfman, Collette and Facey (1997). Isuridae was apparently not used until Gill (1893) essentially revived Gray’s (1851) Isurini as a family. Although an unjustified replacement of Lamnidae the family Isuridae was used by a number of influential authors, including Garman (1913), Lozano y Rey (1928), White (1936, 1937), Whitley (1940), Fowler (1941), Romer (1945, 1963), Bigelow and Schroeder (1948), Schultz and Stern (1948), Smith (1949), Arambourg and Bertin (1958), Garrick and Schultz (1963), Budker and Whitehead (1971), Bass, D’Aubrey and Kistnasamy (1975a), and Chu and Meng (1979).

Whitley (1940) separated the white shark (***Carcharodon***) in its own family Carcharodontidae as distinct from Isuridae (***Isurus*** and ***Lamna***). This was independently proposed by the innovative Soviet palaeontologist L.S. Glikman (1964, 1967), who also placed ***Lamna*** in a subfamily Lamninae of the family Odontaspididae. In addition, Glikman separated living fossil species of ***Isurus*** into two genera, ***Isurus*** and ***Lamiostoma***, and placed these respectively in the families Isuridae and Lamiostomatidae. Glikman's arrangement was followed by Rass and Lindberg (1971), while Lindberg (1971) recognized Lamiostomatidae as distinct from Lamnidae. Glikman (1964) suggested that the living lamnid genera were independently derived from the basal family Odontaspididae, and so required separate families. However, phyletic studies utilizing morphology (Maisey, 1985; Compagno, 1990b; Long and Waggoner, 1996) and DNA sequencing (Martin and Naylor, 1997; Naylor et al., 1997) suggest that the Lamnidae is a monophyletic group for the living ***Carcharodon***, ***Isurus*** and ***Lamna***, which is followed here.

Günther (1870), Regan (1906a) and Engelhardt (1913) included ***Isurus*** or its synonym ***Oxyrhina*** as a synonym of ***Lamna*** while Garman (1913), White (1936, 1937), and Fowler (1941) synonymized ***Lamna*** with ***Isurus***. Most modern authors follow Müller and Henle (1839) and more recently Bigelow and Schroeder (1948) in considering ***Isurus*** and ***Lamna*** as separate genera, which is supported by external morphology, dentition and anatomical studies (Compagno, 1990b; Long and Waggoner, 1996). Gray (1851) recognized both genera but used ***Isurus*** as a synonym of ***Lamna*** and ***Oxyrhina*** in place of ***Isurus***.

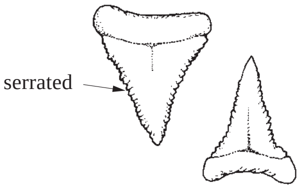
Many earlier authors included the basking shark (***Cetorhinus***) and the threshers (***Alopias***) in the family Lamnidae. Modern authors generally recognize Lamnidae (or Isuridae), Cetorhinidae and Alopiidae as distinct families, although Shirai (1996) recently demoted the Lamnidae as a subfamily Lamninae of the Alopiidae along with the subfamilies Cetorhininae and Alopiinae.

Literature: Garman (1913); Fowler (1941, 1967a); Bigelow and Schroeder (1948); Garrick and Schultz (1963); Farquhar (1963); Shiino (1972, 1976); Bass, D'Aubrey and Kistnasamy (1975a); Compagno (1984, 1990b); Alexander (1998).

Key to Genera:

1a. Teeth serrated, uppers flat and with broadly triangular cusps (Fig. 68) . . . . ***Carcharodon***

1b. Teeth smooth-edged, uppers not greatly flattened and with narrowly triangular cusps (Fig. 69a) . . . . → **2**

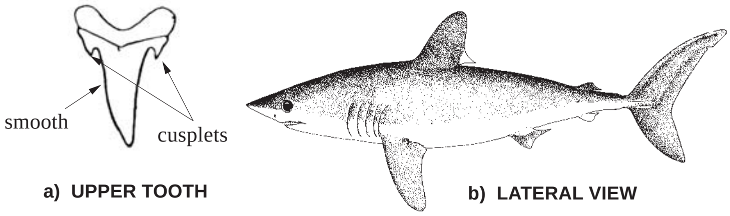


UPPER AND LOWER TOOTH

Fig. 68 ***Carcharodon***

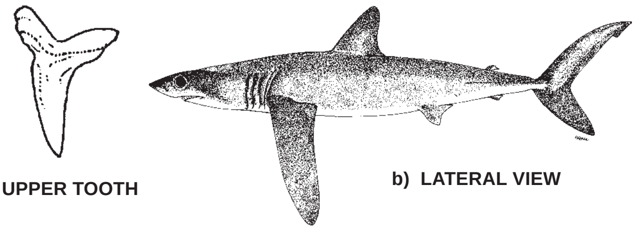
2a. Lateral cusplets present on most teeth (sometimes absent in young) (Fig. 69a); origin of first dorsal fin over or anterior to inner margins of pectoral fins; origin of second dorsal fin over origin of anal fin; a secondary keel present below main keel on caudal fin (Fig. 69b) . . . . ***Lamna***

2b. No cusplets on teeth (Fig. 70a); origin of first dorsal fin over or behind rear tips of pectoral fins; origin of second dorsal fin well in front of anal-fin origin; no secondary keel on caudal fin (Fig. 70b) . . . . ***Isurus***



a) UPPER TOOTH **b) LATERAL VIEW**

Fig. 69 ***Lamna***



a) UPPER TOOTH **b) LATERAL VIEW**

Fig. 70 ***Isurus***

Carcharodon Smith, 1838

Genus: ***Carcharodon*** Smith, *in* Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 37. Placed on the Official List of Generic Names in Zoology (Name no. 1658) by the International Commission on Zoological Nomenclature (1965, Opinion 723.3b, *Bull. Zool. Nomencl.*, 22(1): 32).

Type Species: ***Squalus carcharias*** Linnaeus, 1758, by subsequent monotypy through ***Carcharias lamia*** Rafinesque, 1810 (*International Commission on Zoological Nomenclature*, 1965, *loc. cit.*).

Number of Recognized Species: 1.

Synonyms: Subgenus ***Carcharias*** Cuvier, 1816 (Genus ***Squalus*** Linnaeus, 1758): 125, in part. Placed on the List of Rejected and Invalid Generic Names in Zoology (Name no. 811) by the International Commission on Zoological Nomenclature (1965, Opinion 723.5c: 33). Cuvier's ***Carcharias*** had only three species, ***Squalus carcharias***, ***S. vulpes*** (= ***Alopias vulpinus***), and ***S. glaucus*** (= ***Prionace glauca***). ***S. carcharias*** is the type of ***Carcharias*** Cuvier by absolute tautonymy, but is a junior homonym of ***Carcharias*** Rafinesque, 1810 (***Carcharias taurus***, type species by monotypy). ***Carcharias*** Cuvier was used extensively for carcharhinids following Müller and Henle (1839: 27). Genus ***Carcharoden*** Bleeker, 1860: 58, in combination ***Carcharoden rondeletii***. Apparent misspelling for ***Carcharodon***, as it is spelled correctly in that paper on p. 57 (***Carcharodon capensis***).

Diagnostic Features: Snout bluntly conical. Eyes small, 0.7 to 1.8% of total length. Nostrils situated adjacent to head rim in ventral view. Mouth width 1.1 to 2.3 times its length. Anterior teeth enlarged; anterior, intermediate and lateral teeth compressed and forming a continuous cutting edge; intermediate teeth enlarged and over two-thirds height of adjacent anteriors, with reversed cusps that are directed anteromesially; second lower anterior teeth moderately enlarged and about as high or usually lower than second upper anterior tooth; total tooth count 44 to 52; roots of anterior teeth broadly arched, with root lobes broad and not elongated; lateral cusplets present only on teeth of smaller sharks below about 3 m long but lost in adults; teeth with serrated edges; cusps of anterior teeth not strongly flexed. Body usually stout. First dorsal-fin origin usually over the pectoral inner margins. Anal-fin origin under or slightly posterior to second dorsal-fin insertion. Secondary caudal keels absent. Total vertebral count 170 to 187. Cranium with rostral cartilages not swollen and hypercalcified. Intestinal valve count 47 to 55. Length of adults 3.8 to almost 6 m and possibly longer. Usually a black axillary spot at pectoral fin insertions; pectoral fin tips usually abruptly black on their ventral surfaces.

Remarks: The white shark (***Carcharodon carcharias***) is apparently the sole living species of this genus although many fossil species are also recognized. The white shark was often confused with requiem sharks (Carcharhinidae) and other sharks by eighteenth and early nineteenth century writers, and was often placed in the genus ***Carcharias*** along with other large lamnoid and carcharhinoid sharks. Smith (1838a) proposed ***Carcharodon*** as a unique genus for the white shark, but without allocating any species. Müller and Henle (1839) recognized a single species, ***Carcharodon rondeletii*** Müller and Henle, 1839. The genus was accorded essentially universal recognition by subsequent authors, but the type species was questionable and was eventually stabilized by a ruling of the International Commission on Zoological Nomenclature (1965). Bigelow and Schroeder (1948), White, Tucker and Marshall (1961), and the International Commission on Zoological Nomenclature (1965) give further details of the complex nomenclatural history requiring this ruling.

There have been a few attempts to name regional species of white sharks and distinguish separate regional populations. Smith (1849) proposed a new species, ***C. capensis***, from South Africa, while Whitley (1939) separated Australian white sharks as ***C. albimors***. Neither of these were especially characterized, and are generally synonymized with ***C. carcharias***. More recently Bass, D'Aubrey and Kistnasamy (1975a) distinguished South African white sharks from those from the Northern Hemisphere by coloration and vertebral count. These authors noted that the axillary spots reported on western Atlantic white sharks (Garman, 1913; Bigelow and Schroeder, 1948) were absent in specimens they examined. At least one of the specimens examined by Bass, D'Aubrey, and Kistnasamy (1975a, fig. 10) lacked axillary spots, but Smith (1849), Smith (1951), and D'Aubrey (1964) illustrated South African white sharks with axillary spots. The writer has examined many white sharks specimens with axillary spots from South Africa and California, United States, while axillary spots were present on several live white sharks filmed at Dyer Island and Struis Bay, South Africa. Axillary spots may be absent in white sharks from Argentina (Siccardi, Gosztonyi and Menni, 1981) and were poorly defined on one examined by the writer from California. Apparently the absence of axillary spots cannot be used to distinguish South African white sharks.

Bass, D'Aubrey and Kistnasamy (1975a) suggested that lower counts of precaudal vertebral centra (100 to 108, mean = 103.2, n = 24) might distinguish white sharks from Natal as a separate population from California white sharks (103 to 108, mean = 105.2, n = 14; California data from Springer and Garrick, 1964). Further comparison of precaudal vertebrae counts for Californian and South African specimens by the author (Compagno unpub. data; n = 56) verified a small but statistically significant difference in means between the samples, but the small sample sizes, broad overlap in ranges and standard deviations in the vertebral count samples, do not rule out the differences as being a result of sampling error. Siccardi, Gosztonyi and Menni (1981) presented precaudal counts for two Argentinean white sharks (a female with 104 centra and a male with 105), which fall within the range of the South African and Californian samples.

It is not obvious from available data on morphometry, meristics, coloration and skeletal anatomy that white sharks from different 'centres of abundance' are recognizably separable. The wide distribution and habitat of the white shark suggests a single species, but discrete centres of abundance and concentration of breeding areas in warm-temperate coastal seas suggest discrete populations or subpopulations with potential genetic interchange via wide-ranging adults. There are several projects underway to compare DNA of white sharks from various areas to determine possible populational differences.

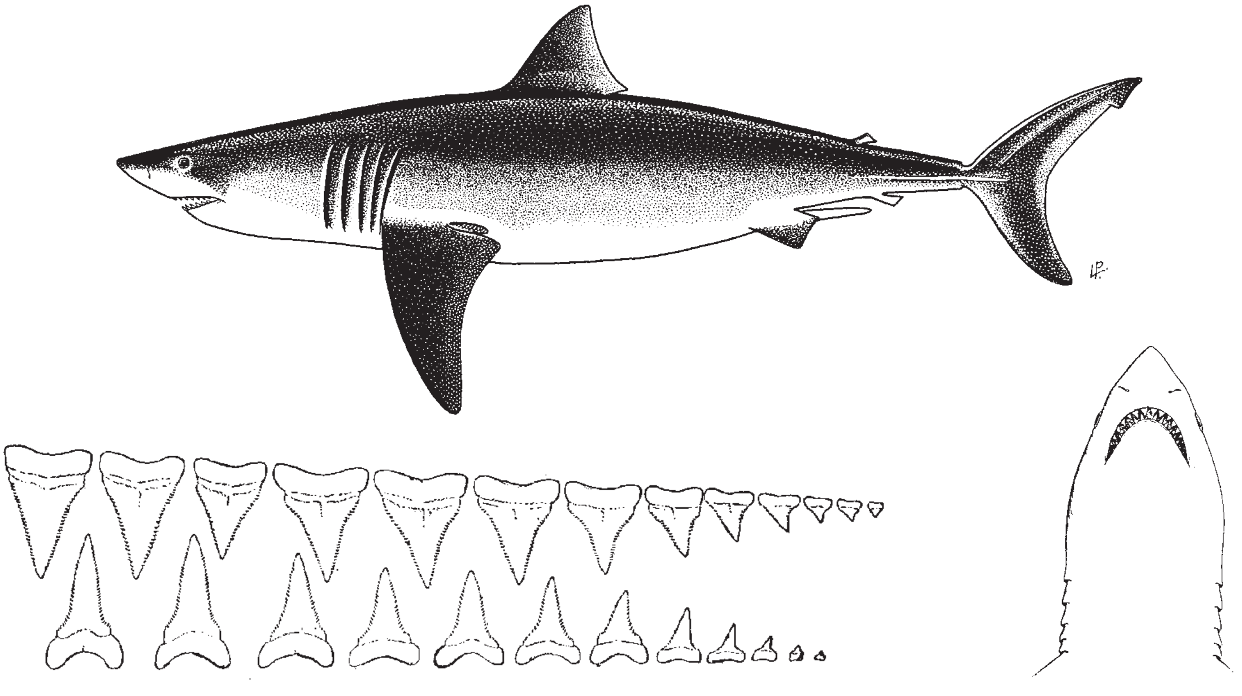
Carcharodon carcharias (Linnaeus, 1758) **Fig. 71**

Squalus carcharias Linnaeus, 1758, *Syst. Nat.*, ed. 10, 1: 235. Placed on the Official List of Specific Names in Zoology (Name no. 2056) by the International Commission on Zoological Nomenclature, (1965, Opinion 723.4b, *Bull. Zool. Nomencl.*, 22(1): 32). Holotype unknown, type locality “Europa”. Also no types known according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: ***Carcharias lamia*** Rafinesque, 1810b: 44. Type locality: Sicily. No types? Placed on the List of Rejected and Invalid Species Names in Zoology (Name no. 811) by the International Commission on Zoological Nomenclature, (1965, Opinion 723.6: 33). ?***Squalus (Carcharhinus) lamia*** Blainville, 1816: 121 (in part?). Name only. ***Carcharias verus*** Cloquet, 1817: 69. Europe. No types? ?***Squalus (Carcharhinus) lamia*** Blainville, 1825: 88, pl. 22, fig. 2 (in part?). No types? ***Carcharias rondeletti*** Bory de Saint-Vincent, 1829: 596. Europe. Types? ***Squalus (Carcharias) vulgaris*** Richardson, 1836: 288. All seas. An unexplained new name, without types, according to Eschmeyer (1998: CD-ROM). ***Carcharodon smithii*** Müller and Henle, *in* Agassiz, 1838: 91. Name only, attributed to teeth from two jaws in pl. F, fig. 3; dentition pictured shows some overlap and no intermediate, quite possibly a ***Carcharhinus***. Type locality: Possibly South Africa, presumably named after Andrew Smith and perhaps a *nomen nudum*. ***Carcharodon smithii*** was not mentioned *in* Müller and Henle (1838a, 1839, 1841) though these authors (1839: 70) note dentitional differences between a specimen collected by A. Smith and other material and suggest that there may be two species. ***Carcharodon smithii*** Müller and Henle, 1839: 9 (in synopsis, name only). Type locality: Probably South Africa, and presumably named after Andrew Smith. Apparently a *nomen nudum*. Note difference in spelling from Agassiz, 1838: 91. ***Carcharodon rondeletii*** Müller and Henle, 1839: 70. Type locality: “Mittelmeer, atlantischer Ocean, Kap, stilles Meer.”. This appears to be an original description and not merely a reallocation of ***Carcharias rondeletti*** Bory de Saint-Vincent, 1829, to ***Carcharodon***. Syntypes: A stuffed specimen (holotype of ***Carcharodon capensis***) belonging to Andrew Smith and now in the British Museum (Natural History), a specimen in the Senkenberg Museum from the Adriatic Sea, a jaw in the Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, and two specimens in the “United Services Museum” (US National Museum of Natural History, Eschmeyer, 1998: CD-ROM), from the Pacific Ocean. ***Carcharias atwoodi*** Storer, 1848: 72. Type locality, Provincetown, Massachusetts. Holotype: Museum of Comparative Zoology, Harvard, MCZ 89505 (missing), jaws may be MCZ 775-S (Eschmeyer, 1998: CD-ROM). ***Carcharodon capensis*** Smith, 1849: pl. 4 and accompanying text, pages not numbered. Holotype and only specimen: 2.135 m (7 ft) TL stuffed female, from Cape Seas, South Africa, deposited in the Museum of the Zoological Society of London, but according to Gray (1851: 61), subsequently donated to the British Museum (Natural History). The holotype, BMNH 1850.9.5:3, is still extant and in good condition and was located and examined on 10 June 1994 in the BMNH collections; current TOT (extended TL) is about 2 035 mm. ***Carcharias vorax*** Owen, 1853: 94. Holotype? No locality, identity uncertain, based on vertebrae and teeth of a 7.65 m (23 ft) specimen. ***Carcharias maso*** Morris, 1898: 412. Australia. Possible *nomen nudum* according to Eschmeyer (1998: CD-ROM). Not ***Squalus (Carcharias) maou*** Lesson, 1830 = ***Carcharhinus longimanus*** (Poey, 1861). ***Carcharodon albimors*** Whitley, 1939: 240. Holotype: Australian Museum, Sydney, AMS I.1723 (Paxton et al., 1989: 67; Eschmeyer, 1998: CD-ROM), New South Wales, Australia.

Other Combinations: None.

FAO Names: En - Great white shark; **Fr** - Grand requin blanc; **Sp** - Jaquetón blanco.


UPPER AND LOWER TEETH ON LEFT SIDE

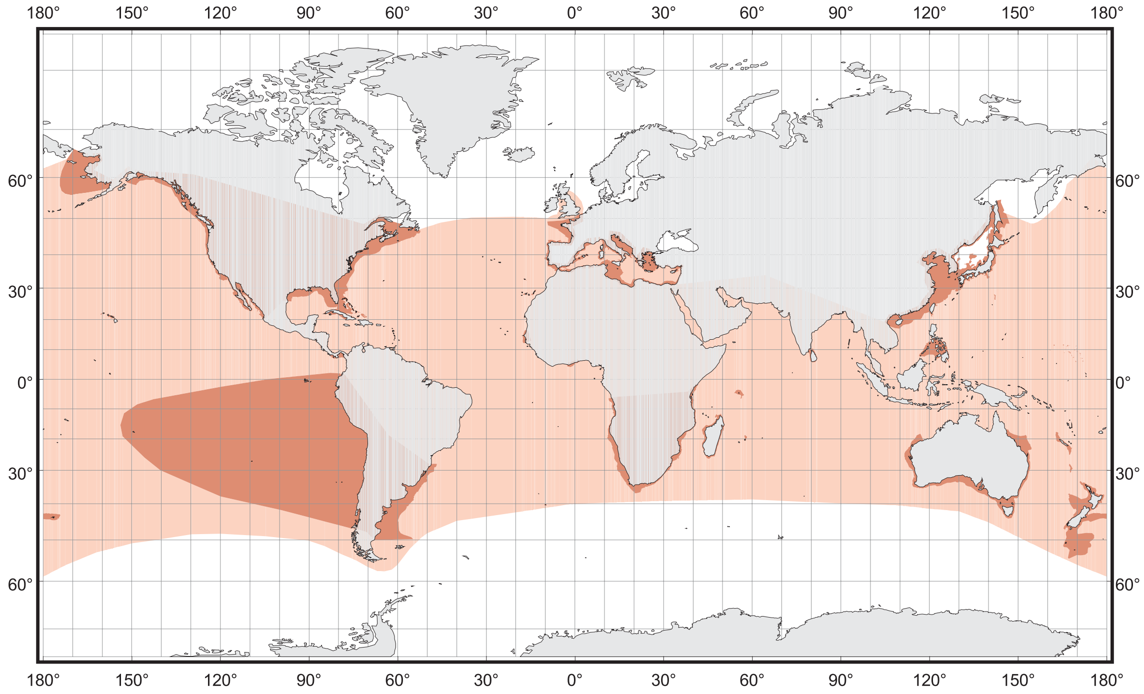
UNDERSIDE OF HEAD

Fig. 71 ***Carcharodon carcharias***

Field Marks: Heavy spindle-shaped body, moderately long conical snout, huge, flat, triangular, serrated blade-like teeth, long gill slits, large first dorsal fin with dark free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, no secondary keels on caudal base, crescentic caudal fin. **Colour:** dorsal surface lead grey or brownish grey to blackish above, ventral surface of body white, iris of eye conspicuously black, margin between dorsal dark and ventral white surfaces sharply delimited.

Diagnostic Features: See genus ***Carcharodon*** above.

Distribution: Wide-ranging in most seas. Western Atlantic: Newfoundland to Florida, Bahamas, Bermuda, Cuba, northern Gulf of Mexico; also Brazil and Argentina. Eastern Atlantic: Possibly England, also France and Bay of Biscay, to Gibraltar, the entire Mediterranean Sea (absent from Black Sea), Madeira, Canary Islands, Senegal, Gambia, Ghana, possibly Zaire, Angola, Namibia, South Africa (Northern and Western Cape Provinces); also Gough Island. Indo-West Pacific: South Africa (Eastern Cape and KwaZulu-Natal Provinces), Mozambique, Tanzania (Zanzibar), Kenya, Seychelles, Madagascar, Mauritius, possibly Red Sea and Persian Gulf (Kuwait?), Sri Lanka, possibly Indonesia, Australia (Queensland, New South Wales, Victoria, Tasmania, South and Western Australia), New Zealand (including Norfolk, Stewart, and Chatham Islands), New Caledonia, Philippines (Mindanao, Palawan), China, Taiwan (Province of China), Japan, North Korea, South Korea, Russia (Siberia, possibly Sea of Okhotsk and Bering Sea), Bonin Islands (Tanna Island). Central Pacific: Marshall Islands, Hawaiian Islands, open ocean between Polynesia and South America. Eastern Pacific: Bering Sea and Gulf of Alaska to Gulf of California, including Canada (British Columbia) and the entire Pacific coast of the USA (Washington, Oregon, California, Alaska), and much of Mexico, also Panama, Ecuador, Peru, Chile, and Galapagos Islands.



Habitat: This huge and formidable shark is best known as a coastal and offshore inhabitant of the continental and insular shelves in temperate seas, but it readily penetrates the epipelagic zone and occurs in the inshore equatorial tropics and at high latitudes. The presence of large individuals off oceanic islands far from land and where breeding does not occur (e.g., Hawaiian Islands, Gough Island, Mauritius, Seychelles) as well as recent open-ocean gill net records in the North Pacific suggest that it regularly occurs in the epipelagic zone although less commonly than smaller, more abundant species of ***Isurus*** and ***Lamna***. It is seldom recorded from pelagic longline catches unlike other lamnids. This may be a function of relative rarity in the epipelagic zone and gear selectivity, with larger animals breaking off gangions and the species seldom being caught or reported in the past.

The white shark often occurs close inshore to the surfline and even penetrates shallow bays, estuaries and the intertidal zone in continental coastal waters, but also frequents offshore continental and oceanic islands (especially those with pinniped colonies) and inshore and offshore fish banks. The white shark can be found at the surface down to the bottom in epicontinental waters but rarely ranges down the continental slope, where it was once caught on a bottom longline at 1 280 m along with the large sixgill shark (***Hexanchus griseus***). More recently it has been taken in bottom trawls on the outer shelf down to 130 m off South Africa. It is often seen by divers off rocky reefs and near shipwrecks but in the tropics it is occasionally sighted on coral reefs. The white shark has one of the widest habitat and geographic ranges of any fish-like vertebrate, and readily tolerates temperature extremes from the Bering Sea and sub-Antarctic islands to the inshore tropics. It apparently does not occur in fresh water, but can be expected to occur in most marine environments if only sporadically.

Biology: This species is a very active, nomadic, social shark with a fluid, powerful, scombroid-like mode of cruising that allows it to efficiently cruise and manoeuvre for long periods at a relatively slow speed. Tracking of white sharks off the east coast of the United States and south Australia with sonic tags indicated an average cruising speed of about 3.2 kph, with one shark covering 190 km in 2.5 days. The white shark is capable of sudden high-speed dashes and drastic manoeuvres. It sometimes jumps (*breaches*) right out of the water in pursuit of prey, and jumps to attack prey at the surface, in midair, or even on rocks above the water. It can shoot straight out of the water like a dolphin for no obvious reason.

The white shark is most commonly reported from cold and warm temperate ‘centres of abundance’, though there are enough tropical continental and oceanic records to suggest that at least larger individuals have a wide temperature range and readily penetrate the tropics. Smaller individuals, below 3 m long, may be mostly restricted to temperate continental seas, and the distribution of presumably newborn individuals in the 100 to 160 cm size range suggest that pupping and nursery grounds for the species are also in temperate to subtropical coastal and mostly continental waters. Known centres of abundance, including nursery and probably breeding areas, include the west coast of the United States (California), Mexico (Baja California, possibly Gulf of California), the Mid-Atlantic Bight off the USA (New England and Mid-Atlantic States), the Mediterranean Sea, the east coast of South Africa (from False Bay to KwaZulu-Natal), southern Australia, New Zealand, and Japan.

White sharks are endothermic and by development of countercurrent vascular heat exchangers maintain higher temperatures in their body musculature, brains, eyes and viscera than the surrounding water (Carey and Teal, 1969; Carey et al., 1982, 1985; Carey, 1982, 1990; Tricas and McCosker, 1984; Block and Carey, 1985; McCosker, 1987; Goldman et al., 1996; Goldman, 1997). Body muscle may run 3 to 5°C higher than ambient (with few sharks measured and possible problems with measuring gear), but stomach temperatures can be 10 to 14°C above ambient and relatively constant in cold water. The heat retention system of the white shark (and possibly its large size) may be particularly advantageous in allowing it to function efficiently as a fast, agile predator in cold water, and to hunt active large prey.

Relatively little is known of the abundance of this species, except that it is uncommon to rare compared to most other sharks where it lives, even in temperate coastal waters. Catches in some areas have been as many as 50 to 100 per year (South Africa and South Australia) in the past but mostly less in others. There have been unsubstantiated claims that the species is increasing in numbers in some areas (off central California and South Africa), as a result of increasing numbers of pinnipeds. There is no hard evidence to prove this, and increasing fishing pressure and injuries from targeted and bycatch fisheries in such areas may be very well having the reverse effect. Declines in shark-meshing catches of white sharks have occurred off Queensland and New South Wales, and reductions in sightings of white sharks in Spencer Gulf, South Australia may have been related to commercial and sports fishing mortality.

Pronounced periodicity in white shark abundance may occur in some areas, apparently correlated with temperature and to some extent with life stage, or by movements of individuals or groups in response to prey concentrations or other stimuli. Also, shifts may occur in size and gender composition of white sharks off ‘white shark sites’ such as fish banks or seal colonies where the sharks congregate. In colder, higher latitudes at the periphery of its range in North America, the white shark moves into more northern areas when water masses warm up in the summertime. Off KwaZulu-Natal, South Africa, it was believed that individuals below 2.8 m long segregated themselves from larger individuals and moved out of the area when temperatures rose above 22°C, but this was proven wrong by more extensive data presented by Cliff, Dudley and Davis (1989). Essentially both size classes are present all year round in the area, although numbers of both fluctuated by time of year and area. In central California (Monterey Bay) white sharks are present year round but are slightly commoner when water temperatures rise to 14 to 15°C than when it is below 11°C.

Observation of white sharks at ‘white shark sites’ suggest that they are nomadic and may spend relatively short periods of less than a day at a given site, but at least some individuals revisit these sites periodically, from a few days to over several years. Recognizable individuals have been photographed and resighted for several years off the Farallon Islands, California. Streamer and plate tagging off Australia and South Africa, and sonic tagging off Australia also revealed short to moderately long-term site specificity of some individuals. Tagging of white sharks and photographing of dorsal fins and body patterns (‘bodyprinting’) have shown fairly long-range movements, including between northern and southern California (over 700 km, Anderson and Goldman, 1996) and between Dyer Island and Mossel Bay (about 300 km) or from Dyer Island to KwaZulu-Natal, South Africa (over 1 100 km, M. Marks and L.J.V. Compagno, unpub. data). So far there have been no intercontinental resightings or recaptures of tagged or photographed sharks, but given the size and strong swimming abilities of this shark and scattered records in the tropics and off oceanic islands these are to be expected and may be revealed by usage of improved tracking technologies and by development of ‘bodyprint’ libraries that could be made widely available via the Internet.

The white shark occurs singly or in pairs but is apparently a social animal that can be found in aggregations or congregations of 10 or more; polarized schooling possibly does not occur (apart from parallel swimming of two individuals) but sharks in a group may mill about and interact socially while showing various behaviours, often one-on-one but sometimes with more individuals involved. White sharks are ‘inquisitive’ animals, and often closely and repeatedly investigate human activities (including divers). Behaviour and sociobiology of this species is sketchily known at present but it is apparently at least as complex as the better-known bonnethead shark (***Sphyrna tiburo***), with most of the noncourtship, social and asocial behaviours reported by Myrberg and Gruber (1974) being present in the white shark along with several additional behaviours not observed in the bonnethead. A detailed account of these behaviours will be published elsewhere. A possibly agonistic behaviour commonly directed at people underwater or above the surface is *gape*, a graded distension and protrusion of jaws also seen in the shortfin mako (Strong, 1996). *Spy-hopping*, in which the shark raises its head out of the water (often alongside a boat), and *tail-slap*, in which the shark raises its tail and caudal fin out of the water and smashes it against the surface, are common behaviours. Klimley, Pyle and Anderson (1996) suggest the latter is a social signal between contesting sharks over a prey item, which is plausible from their evidence although tail-slapping also occurs in situations of ambiguity as when a shark has a bait pulled out of its grasp and may also be directed toward inanimate objects or even people. White sharks will *hunch*, arching their backs and depressing their pectoral fins in a possibly agonistic display as in bonnetheads and grey reef sharks (***Carcharhinus amblyrhynchos***). One white shark may closely *follow another*, and two approaching white sharks on a collision course may *give-way*, with one shark avoiding the other, or both may give-way almost simultaneously (*stand-back*). *Follow give-way* is sometimes seen at baits, where a shark approaching a bait is followed by a second (sometimes larger); the first shark suddenly aborts its approach and the second eats the bait, or a third shark may follow and displaces the second. Courtship behaviour is poorly known in the white shark but rows of limited tooth marks on the pectoral fins of large adult female sharks suggests that complex courtship behaviour may be present as in the sand tiger shark (***Carcharias taurus***; Gordon, 1993).

Territoriality in the white shark (as contrasted with site specificity) cannot be demonstrated at present, but there is some evidence for sorting of individuals into a partly size-related hierarchy around food sources such as dead whales, pinniped colonies or feeding stations provided by people. White shark tooth scratches and inhibited bite marks are seen on individuals of all sizes, both sexes, and all postnatal maturity stages. They have been interpreted as evidence of intraspecific conflict, possibly in competition for food resources, but they probably have a broader context of social interactions. In certain areas (southern Australia, the south coast of South Africa, and central California), white sharks may have habituated to human-provided food sources and may have learned to seek out fishing boats to exploit hooked fish or the baits provided by shark cage-dive operators and film-makers.

The white shark is ovoviviparous (aplacental viviparous) and practices uterine cannibalism as do many other lamnoids, apparently in the form of embryos and foetuses eating large numbers of nutritive eggs (oophagy). The gestation period is not known at present but could be a year or more, and may or may not include taking a year off to recuperate. There are few records of pregnant females and litter size, which varies from 2 to possibly 14 young. Females mature between 4 and 5 m long and 12 to 14 years old and reach at least 23 years old, while males mature between 3.5 and 4.1 m long and 9 or 10 years old (ageing from growth rings on vertebral centra, assumed to be annual); the maximum age of either sex is unknown but has been roughly estimated at about 27 years from a von Bertalanffy growth model (Cailliet et al., 1985) assuming a maximum size of 7.6 m and indeterminate growth to that size.

The rarity of pregnant female white sharks could be explained in part by spatial separation from other white sharks during pregnancy (without evidence, however) and their sheer size that precludes capture by most fishing gear. However, it is possible that adult female white sharks are uncommon (more so than adult males), and possible also that they may have very low fecundity, with only a few adult females being pregnant at any one time and with an interval of a few years between pregnancies.

The white shark readily scavenges on available carrion, garbage, and fish caught on lines. This species probably obtains most of its prey by killing it, but is highly opportunistic as with terrestrial apex predators. Its diet in different areas may vary according to the availability (including abundance) and vulnerability of suitable prey, as well as by motivation of the predator. Live prey of individual white sharks is mostly marine vertebrates and invertebrates smaller than itself, ranging in size from small schooling fishes and squid to elephant seals and grey whale calves. The chief prey categories of the white shark are ray-finned bony fishes (Actinopterygii), cartilaginous fishes, marine mammals, marine birds, cephalopods, and crustaceans, with marine reptiles (sea turtles) and gastropods being relatively unimportant.

Bony fish prey of the white shark includes a wide range of large and small, demersal and pelagic forms, such as sturgeon (Acipenseridae), menhaden and pilchards (Clupeidae), salmon (Salmonidae), sea catfish (Ariidae), lings (Gadidae), hake (Merluccidae), flounders and halibut (Paralichthyidae), rockfish (***Sebastes* spp.**, Scorpaenidae), cabezon (***Scorpaenichthys marmoratus***, Cottidae), lingcod (***Ophiodon elongatus***, Hexagrammidae), barracuda (Sphyraenidae), striped bass (***Morone saxatilis,*** Percichthyidae), bluefish (Pomatomidae), butterfish (Stromateidae), grunters (Pomadasyidae), croakers (Sciaenidae), garrick and maasbanker (***Lichia*** and ***Trachurus***, Carangidae), porgies or sea bream (Sparidae), mackerels and tuna including bluefin tuna (***Thunnus thunnus***, Scombridae), swordfish (***Xiphias gladius***, Xiphiidae), and ocean sunfish (***Mola mola***, Molidae). White sharks are known to congregate at concentrations of schooling bony fishes such as pilchards and bluefish, and follow the KwaZulu-Natal sardine (***Sardinops***) run off South Africa.

Chondrichthyan prey of the white shark includes other sharks such as shortfin mako (***Isurus oxyrinchus***, Lamnidae), sand tiger sharks (***Carcharias taurus***, Odontaspididae), catsharks (Scyliorhinidae), houndsharks (***Galeorhinus***, ***Mustelus***, Triakidae), requiem sharks (***Carcharhinus***, ***Prionace***, ***Rhizoprionodon***, Carcharhinidae), hammerheads (***Sphyrna***, Sphyrnidae), and spiny dogfish (***Squalus***, Squalidae). Basking shark (***Cetorhinus***) meat has been found in several white sharks, apparently taken as carrion from harpooned sharks. Whale shark (***Rhincodon***) remains were found in one shark taken in a beach meshing net. It is presently unknown if the white shark ever attacks adult basking or whale sharks though smaller juveniles of both might be readily killed and eaten. Batoid prey includes giant guitarfish (***Rhynchobatus***, Rhynchobatidae), guitarfish (***Rhinobatos***, Rhinobatidae), skate egg cases (Rajidae), stingrays (Dasyatidae), and eagle rays (***Myliobatis*** and ***Pteromylaeus***, Myliobatidae). Chimaeras (Chimaeriformes) are eaten and include shortnose chimaeras (Chimaeridae), and elephantfish (Callorhinchidae). No small white sharks have been found in white shark stomachs, although large white sharks will eat shortfin makos and other very fast prey, will attack hooked, injured conspecifics, and will deliver inhibited bites to other white sharks. The writer suspects that white sharks have behavioural inhibitions on cannibalization under ordinary circumstances, as reflected by known prey records and from social interactions of small and large white sharks within aggregations.

Sea turtles are occasionally eaten by the white shark, including loggerhead and green turtles (Carettidae) and leatherback turtles (Dermochelyidae) but apparently not to the degree that the tiger shark (***Galeocerdo***) preys on them (Fergusson, Marks and Compagno, 2000).

Marine birds fall prey to white sharks and include cormorants (Phalacrocoracidae), gannets (Sulidae), gulls (Laridae), giant petrels (***Macronectes***, Procellariidae), pelicans (Pelicanidae), and penguins (Spheniscidae). Jackass penguins (***Spheniscus demersus***) are commonly grabbed, cut or slashed by white sharks off South Africa and are often killed but seldom eaten. White sharks also use their snouts to flip or bounce seabirds on the surface without eating them, and victims have included gulls (Laridae) and shearwaters and fulmars (Procellariidae).

Marine mammals can be an important food source for white sharks in some areas, and these include a number of cetaceans and pinnipeds. Those cetaceans killed and eaten include harbor porpoises (***Phocaena phocaena***, Phocaenidae), common dolphins (***Delphinus delphis***) and bottlenose dolphins (***Tursiops*** sp., Delphinidae), and even a grey whale calf (***Estrichtius robustus***). White shark inhibited bite marks have been seen on striped dolphins (***Stenella caerulalba***) from South Africa and on a pygmy sperm whale from California (Long, 1991). White shark predation on odontocetes is more difficult to study than pinniped predation, though careful study of stranded cetaceans can reveal greater diversity of cetacean predation, scavenging, and non-predatory biting by white sharks. Dead baleen whales and other large cetaceans may contribute a significant amount to the white shark's diet in some areas (Long and Jones, 1996), but such food is sporadically available at best.

True, earless or 'hair' seals (Phocidae) taken by white sharks include harbor seals (***Phoca vitulina***), grey seals (***Halichoerus grypus***) and northern elephant seals (***Mirounga angustirostris***), with predation suspected for leopard seals (***Hydrurga leptonyx***), Hawaiian and Mediterranean monk seals (***Monachus***), and southern elephant seals (***Mirounga leonina***). Eared seals (Otariidae) taken include Steller's sea lion (***Eumetopias jubata***), California sea lions (***Zalophus californianus***), South African fur seals (***Arctocephalus pusillus pusillus***), Australian fur seals (***A. p. doriferus***), South American fur seals (***A. australis***), northern fur seals (***Callorhinus ursinus***), and probably several other species. Sea otters (***Enhydra lutris***, Mustelidae) are commonly killed by white sharks off California, but have yet to be found as stomach contents. Mammalian carrion from slaughterhouses and other sources, including mutton, pig, horse, dog, cattle, and rarely human, has been found in the white shark's stomach also. Terrestrial mammals probably do not figure as a significant part of the white shark's diet.

Larger white sharks above 3 m long tend to prey more readily on marine mammals than smaller sharks below 2 m long which feed more readily on bony fishes and sharks (although the young of smaller pinnipeds can be taken by small white sharks). This and other observations have lead to the belief that large white sharks are virtually dependent on pinnipeds for prey. However, large white sharks are not restricted to pinniped prey (even in areas with pinniped colonies and abundant seals), but also catch large teleost fishes, sharks and rays, birds, dolphins and marine reptiles, and are presumably capable of subsisting on such other small to large prey, in areas where seals are uncommon or absent (Mediterranean Sea, Spencer Gulf in South Australia, Brazil). One 4.4 m specimen from the USA (Washington State) had 150 crabs (Cancridae) as well as salmon, hake, rockfish and seal hides in its stomach (LeMier, 1951). Pinnipeds may be especially important prey for white sharks where they occur together, especially at seal colonies where pinnipeds are highly vulnerable. An observational problem is that seal predation by white sharks at concentrated seal colonies can be more easily studied than their interactions with other prey items. Rather than comprising a simple growth-related switch from fish to mammal prey as some authors have assumed, the prey spectrum of the white shark is more likely to increase with growth in maximum prey size and in diversity. Only larger white sharks are apparently able or motivated to kill large pinnipeds, dolphins, bony fish, sharks, rays and turtles while retaining the ability to capture smaller prey.

Recent observations and filming of white sharks at Dyer Island, South Africa, suggest that larger animals are anything but inept, clumsy predators. The slow cruise speed and deliberate investigation of boats and baits by large white sharks belies their high dash speed and ability to chase, overhaul, and kill fast, agile prey such as Cape fur seals, sometimes after multiple jumps. Large, live, active prey may be taken by a sudden, swift rush at high speed, sometimes from below but also at the surface or even after jumping into the air. The white shark is inconspicuously coloured when viewed from above and below, and may take advantage of its cryptic coloration to stalk potential prey (as with apical terrestrial predators), but it also will cruise through Cape fur seal rafts and suddenly attack a selected victim. If the shark misses its prey, a fast chase (including jumping) may ensue. Attachment of sonic tags (Strong et al, 1992) and self-contained remote cameras ('crittercams', I. Fergusson and G. Marshall, pers. comm., and supplied footage) to white sharks show slow patrolling just below the surface and near the bottom, punctuated by occasional fast dashes (apparently after prey), with little time spent in midwater.

Invertebrate prey includes squid (Loliginidae), abalone (***Haliotis***) and other gastropods, bivalves, and crabs (Cancridae). Inedible garbage is occasionally taken from the stomachs of white sharks, but apparently this species is not fond of swallowing oddities as does the tiger shark.

Much speculation has occurred on the predatory behaviour of white sharks, particularly in the context of biting people. The white shark is clearly capable of inflicting mortal wounds on a human with a single bite, but often merely clamps lightly onto a diver or swimmer without completing its bite and releases them after a short time. Such inhibited biting behaviour has been interpreted as a predation tactic ('bite and spit') of an inept, ambush predator to avoid injury from prey, but is unlikely because of the nature of full-fledged white shark predation bouts on large active, potentially injurious prey such as seals. A white shark generally delivers a powerful bite (or bites) to immobilise, incapacitate or kill the prey item outright, then may continue biting while feeding, may resume biting after a short to long interval, or may leave without consuming more of the victim. The presence of other white sharks near a kill may influence the predator's activities via social interactions. An 'exsanguination' predation tactic has been suggested for white sharks (Klimley, 1994), in which the shark bites to kill a victim by bleeding it to death. However, white shark bites often cause severe or mortal injury (including decapitation and removal of limbs) apart from blood loss. The predation tactic used by white sharks on large, active prey is more likely the rapid infliction of 'massive trauma' to halt and kill its victim, which also begins the feeding process (somewhat as in pack-hunting terrestrial carnivores that run down their ungulate prey and eat them to death). Smaller prey items including neonate Cape fur seals may be swallowed whole by large white sharks without powerful biting or chasing (sometimes after slowly following them at the surface), and this may be likewise with large sharks eating small bony fish, crabs, and other small, defenceless prey.

Non-feeding, inhibited bites on people may be agonistic, such as possibly happens in contact encounters among white sharks, or alternatively exploration, displacement (displaced aggression), or even play. Inhibited bites have been explained as 'mistaken identity' predation bouts, in which the shark bites its victim after mistaking it for a seal or turtle and then aborts its activity after biting. Observation on free-ranging white sharks suggests that white sharks are highly selective visual predators and may be readily able to distinguish prey from divers or surfers and will react accordingly. Mistakes are possible, however, when visibility is impaired. Full-fledged predation bouts in which the white shark repeatedly bites and dismembers a human victim have been reported, but fortunately these are extremely rare compared to inhibited bites, and are very rare compared to episodes of human predation by large terrestrial carnivores, particularly tigers and the largest macropredatory crocodilians.

Ironically, ***Homo sapiens*** is the chief *known* predator and cause of mortality to white sharks, through targeted and bycatch fisheries. A large orca (***Orcinus orca***) was recently seen to kill a white shark off the Farallon Islands, California, United States, but little is otherwise known of the interactions between these apical predators. Orcas and white sharks broadly overlap in distribution and take much the same prey (except for large baleen whales occasionally killed by orcas), but complement each other ecologically and possibly displace each other in different areas. Colder seas near the poles tend to have more killer whales, cool to warm-temperate seas more white sharks, while both can occur in the tropics. The behavioural and ecological relationships of killer whales and white sharks are little understood. Large pinnipeds and other species of large, macropredatory sharks are potential predators or sources of injuries to white sharks, but without much evidence except occasional seal bite-marks on sharks. White sharks will also cut and bite one another in possible dominance-related aggressive interactions, and adult male white sharks may bite females during courtship. The injuries are often minimal and apparently inhibited and it is not known what the contribution of such injuries are to white shark mortality. Nothing is known of white shark bacterial or viral diseases, or if common parasites such as the large copepods on the maxillary valve of white sharks or the intestinal cestode fauna are a source of problems for them. Sometimes large white sharks are found dead on beaches with no obvious external or internal injuries.

Size: Maximum total length to about 6 m, and possibly to 640 cm or more; the largest free-swimming individuals commonly captured are between 500 and 580 cm (mostly adult females). Records of white sharks 6.4 to 7 or even 9 m long are difficult or impossible to verify. A much quoted record of an 11 m (36 ft) shark from Australia is erroneous and based on a jaw from a shark 4.9 to 5.5 m long in the British Museum of Natural History (Natural History Museum). Size at birth is assumed as being between 109 and about 165 cm, with term foetuses at 100 to 165 cm and free-living young down to 109 to 129 cm. Male white sharks mature at a smaller size than females and reach a smaller maximum size. Size at maturity for males is about 350 to 410 cm, with adolescence roughly between 250 and 400+ cm, and with small but fully adult males at 356, 368 and 380 cm; maximum length for males is between 501 and at least 517 cm and possibly 550 cm. Females mature somewhere between 400 and 500 cm, with females 441, 470 and 490 cm being immature or early adolescent (Florida, United States, and South Africa) and adults reported at 420 to 580 cm; maximum size of females possibly about 6 m.

Several length-weight equations are available for the white shark. See Mollet and Cailliet (1996) for a detailed review of length-weight methodology.

Compagno (1984): $W(kg) = 4.34 \times 10^{-6}\, TL(cm)^{3.14}$ (n = 98, TL = 127 to 554 cm, mostly from California)

Tricas and McCosker (1984): $W(kg) = 3.8 \times 10^{-6} \times TL(cm)^{3.15}$ (n = 127)

Casey and Pratt (1985): $W(kg) = 4.804 \times 10^{-6} \times TL\ (cm)^{3.095}$ (n = 200, from the western North Atlantic)

Cliff, Dudley and Davis (1989): $W(kg) = 1.84 \times 10^{-5} \times PCL(cm)^{2.97}$ (n = 309, from South Africa)

Cliff, Dudley and Jury (1996): $W(kg) = 2.14 \times 10^{-5} \times PCL(cm)^{2.944}$ (n = 383, from South Africa)

Kohler, Casey and Turner (1995): $W(kg) = 7.5763 \times 10^{-6} \times FL(cm)^{3.0848}$ (n = 125)
where $FL(cm) = 0.9442 \times TL - 5.7441$ (n = 112, from the western North Atlantic)

Compagno (update from 1984): $W(kg) = 3.026 \times 10^{-6} \times TL(cm)^{3.188}$ (n = 156, from California and South Africa).

Interest to Fisheries and Human Impact: The importance of the white shark as a fisheries species is limited because of its low abundance wherever it occurs, which restricts targeted commercial fisheries for conventional bulk fisheries products such as meat or liver oil. However, the high value of its jaws, teeth and fins makes it a viable target of small-scale targeted commercial fisheries as well as an added value to bycatch. It is mostly caught as a bycatch of fisheries for other sharks and other marine organisms (including bony fishes and cephalopods), by many forms of gear utilized by modern marine fisheries including longlines, specialized heavy line gear, rod-and-reel, fixed bottom gill nets, floating inshore gill nets, pelagic gill nets, fish traps, herring weirs, trammel nets, harpoons, bottom and pelagic trawls, and purse seines. Its tendency to investigate human activities (including fishing operations) and to scavenge from fishing gear, as well as the value of its jaws and fins, makes it very vulnerable to being killed and captured despite its size and strength. It is subject to targeted sports fisheries for game-fishing records and trophy jaws because of its great size, notoriety, and powerful resistance to capture. It is also targeted by small-scale and erratic commercial fisheries in several countries.

The meat of the white shark is or has been utilized fresh, fresh-frozen, dried-salted, and smoked for human consumption, although the extremely high mercury content of the meat limits its utility. The flesh has been used in traditional medicine in South Africa. White shark meat has been sold as ‘shark’ in California, but in the 1980s at least one market got higher values by marketing it as white shark meat. The liver of the white shark has been extracted for vitamin oil. Presumably white shark cartilage is processed for medicinals but the writer has no evidence of it. White shark carcasses have been processed for fishmeal, but also frozen or preserved whole for exhibit in oceanaria and museums. White shark specimens are also cast and modelled whole for oceanarium and museum exhibits and for trophies. The skin of the white shark has been utilized for leather, although rarely at present.

White shark teeth and jaws are used for trophies, decorations and collectibles. Properly prepared white shark jaws may bring an inflated price, essentially what the upscale international private collector’s market will bear, with greatest value for the jaws and teeth of large sharks over 5 m long. In South Africa, offers of US$20 000 to 50 000 have been made for white shark jaws, and US$600 to 800 for individual teeth.

Apart from their size, white shark fins are boosted in value because of notoriety. A fin set from a large white shark may be valued at over US$1 000. Unfortunately, as with rhino horns and elephant tusks the high value of white shark products encourages poaching, clandestine trade, and flouting of protective laws.

Live white sharks have been avidly sought by public aquaria and oceanaria for exhibits, but capture trauma usually insures that the sharks perish after a day or a few days in captivity. White sharks were mostly caught for display during the 1970s and 1980s, but seldom are taken at present.

The white shark has for the last few decades been the subject of commercial underwater cage-diving operations in South Australia allowing sport SCUBA and snorkel divers to view and film white sharks, as well as intensive and sometimes oral-obsessive filming of these sharks by professional film crews. This activity also started in South Africa in the early 1990s, continues unabated at present, and has engendered some problems for the sharks and for researchers trying to study them. Regulation of capture and ecotouristic access to white sharks was seriously debated in Australia and South Africa, and licensing and guidelines have been imposed to limit access to white shark sites and methods of attracting white sharks to boats. A flurry of shark-bite incidents off South Africa in the late 1990s spawned a high-profile media-hyped controversy on the assumption that exposure of white sharks to cage diving in the Western Cape somehow caused them to bite people elsewhere.

The white shark is feared by many people as the most ‘dangerous’ living shark; more instances of white sharks biting swimmers, divers, surfers, and boats have been reported than for any other shark. Although much has been made of white shark encounters with people and boats in the popular news and entertainment media, including the JAWS motion pictures that established the white shark as a Hollywood science-fiction monster, the white shark is not very ‘dangerous’ when compared to other causes of injuries and fatalities to people. Most white shark bites are nonfatal and may not be predatory (see above). The rate of white shark bite incidents averaged about three per year worldwide between 1952 and 1992 (range 0 to 8, with an 18% fatality rate) and a slowly increasing trend from about 1.5 per year between 1952 and 1962 to 5.3 per year between 1983 and 1992 (data in part from Ellis and McCosker, 1992; see also Burgess and Callahan, 1996). During the last decade (1990 through 1999) unprovoked incidents averaged 6.9 per year (69, range 0 to 12 per year, with a 16% fatality rate), with most occurring off the United States and South Africa (G. Burgess, International Shark Attack File, pers. comm.). This is far less than drownings, diving accidents, automobile accidents, deaths from lightning strokes, injuries or deaths from terrestrial animals including tigers, large crocodilians, and even domestic livestock, or other calamities that afflicted humans in the countries where white shark incidents occurred.

Most injuries and fatalities from white shark encounters have occurred off California (United States), southern Australia, New Zealand, South Africa, and Japan, but about 80% of reported shark biting incidents have occurred in the tropics, where white sharks are rare or uncommon but where large carcharhinid sharks predominate. There might very well be tropical and warm-temperate carcharhinoids, particularly the tiger and bull sharks, that may be responsible for more shark bite incidents than the white shark, but this remains to be verified.

Several surfers and paddleboarders have been bitten by white sharks or knocked off their boards. The sharks have sometimes destroyed the boards or held, shook, and released the boards without harming the surfers. Boats may be bitten, particularly if boaters provoke the sharks by landing fish out of their grasp or try to ram the sharks. For some reason False Bay, South Africa, was the site of more boat incidents involving white sharks than all other places combined between 1940 and 1980, although hardly since then. White sharks have on a few occasions persistently bitten at boats until they sank, and in a few instances leapt into a boat or punched through the hull like a torpedo.

Despite the frightful, JAWS-inflated reputation of the white shark there is accumulating evidence that the presence of a white shark near people (especially divers) does not necessarily mean that the shark will automatically bite (much less kill and eat) them. Numerous incidents have been reported where these sharks swim up to divers as close as a few feet and depart without biting or without displaying possible agonistic behaviours such as *gape* or *hunch*, and these have been followed up by deliberate encounters by film-makers with white sharks outside shark cages without adverse affects. Numerous close, deliberate, and systematic encounters involving divers without a cage in proximity to numerous white sharks ranging in size from about 2 to over 5 m long have shown very little agonistic behaviour by the sharks, although they were inquisitive, were sometimes present in groups, and often came very close to the diver (M. Marks pers. comm. and videos). This is definitely not recommended for ordinary divers seeking recreational thrills, and should be seen as deliberate and calculated risk in support of science comparable to behavioural observation of large, potentially harmful terrestrial carnivores and large ungulates.

World catches of white sharks from all causes are difficult to estimate. Compagno (1984) noted that off California 10 to 20 or more white sharks were killed each year as a bycatch of various fisheries, vs. 0.13 humans per year killed by white sharks. These figures were over a period of about three decades up to the early 1980s, and protection of the white shark in the 1990s may have reduced the catch since then.

Conservationists have been concerned with the vulnerability of the white shark to possible extinction, and it is currently considered a *vulnerable* species in the IUCN Red List. This seems warranted given that this species has a relatively low intrinsic rebound potential (a relative measure of the ability to recover from fishing; Smith, Au and Show, 1998). Threats to the white shark include: 1. Targeted commercial and sports fisheries for jaws, fins and game fish records. 2. Anti-shark measures to protect beaches. 3. Ad-hoc media-fanned campaigns to kill white sharks after a biting incident occurs. 4. Long-term increases in use and efficiency of commercial and artisanal fishing gear that have an impact on white sharks. 5. Degradation of inshore habitats used by white sharks for pupping and nurseries. 6. Increased demand for shark products in general, including vastly inflated values of white shark jaws, fins and teeth. 7. The tendency of white sharks to investigate human activities, which can be fatal to them. 8. Lack of knowledge on many crucial aspects of white shark biology, and limited interest on investigating them. 9. The negative JAWS image, which invites neglect, killing of sharks, and disregard of conservation measures. 10. Slow maturation and low fecundity. 11. Proximity of concentrations of white sharks to highly-developed coastal areas such as those of California, the Mid-Atlantic Bight, and the Mediterranean Sea. 12. Inadequate catch data in most places where the white shark occurs.

Numbers of white sharks have been thought to be declining off Australia due to sports and commercial fisheries and anti-shark nets. The white shark is currently protected in Australia (nationally and statewise), South Africa, Namibia, Israel, Malta and the United States (statewise off California and Florida and with directed fisheries prohibited off all coasts). Protective laws are strict, but loopholes and inadequate enforcement may cause problems including promoting a black market for high-value white shark products. The United States and Australia proposed the white shark for CITES I and II listing at the 2000 CITES Conference to ban trading in white shark parts, but the proposals were not approved. These countries are currently proposing the white shark for a CITES III listing while Australia has developed a comprehensive and multidisciplinary recovery plan for white sharks in its waters (Environment Australia, 2000b).

Local Names: Sarda (Canary Islands); Jaquetón de ley (Cuba); Uptail, Tommy, White death shark, White death, Great white death, Death shark, White pointer (Australia); Great white shark, White shark (AFS), Maneater or man-eater shark, (England and USA); Ami, Lamea, Lamie, Lameo, Le Carcharodonte lamie, Le grand requin, Pei can, Requin blanc (France); Menschen fresser, Menchenhai, Merviel fras, Weisshai (Germany); Ca mari, Marraco, Salroig, Salproig, Salproix, Taburo, Tiburo, Tiburón blanco, Tauró blanc (Spain); Tubarâo branco, White shark (Azores); Carcarodonte, Cagnia, Cagnesca grande, Cagnia, Caniscu, Carcarodonte lamia, Carcarodonte di rondelet, Damiano [sic] or Demon shark, Imbestinu, Lamia, Mastinu feru, Mangia alice or Anchovy-eater, Pesce cane, Pesca can, Pescecane, Pesce can grande, Pesciu can, Pici bistinu, Pisci cani or Can grossu, Pisci mastinu, Squalo bianco, Tunnu palamitu di funnu or Tuna shark (Italy); Hohojirozame, Hitokiuzame, Oshirozame (Japan); Psina ljudozdera (Yugoslavia); Gab doll, Kelb Il-bahar, Kelb-il-bahar abjad, Huta tax-xmara (Malta); Taniwha, Mango-tuatini, Hare hongi (New Zealand); Haa skieding (Norway); Tabarao (Portugal); Gench, Kersch (Red Sea); Blue pointer, White shark, Great white shark, Springhaai or Jumping shark, Witdoodshaai, Withaai, Cowshark, Mudshark, Sarda (South Africa); Niuhi (Hawaiian Islands); Tanifa (Samoa).

Literature: Linnaeus (1758); Müller and Henle (1839); Smith (1849); Garman (1913); Barnard (1925, 1937); Fowler (1936, 1941); Springer (1939); Whitley (1940); Bonham (1942); Bigelow and Schroeder (1948); Smith (1949, 1951); LeMier (1951); Herre (1953); Schultz et al. (1954); Strasburg (1958); Farquhar (1963); Smith and Smith (1963); Garrick and Schultz (1963); Limbaugh (1963); Stead (1963); Follett (1966); Squire (1967); Case (1968); Carey and Teal (1969); Mundus and Wisner (1971); Arnold (1972); Randall (1973, 1987); Springer (1973); Bass, D'Aubrey and Kistnasamy (1975a); Ellis (1976); Allen and Allen (1978); Wallett (1978); Penrith (1978); Ames and Morejohn (1980); Ainley et al. (1981, 1985); Miller and Collier (1981); Carey (1982, 1990); Carey et al. (1982, 1985); le Boeuf, Riedman, and Keyes (1982); Pratt, Casey and Conklin (1982); Brodie and Beck (1983); Compagno (1984, 1990a, b, d, 1991); Engaña and McCosker (1984); Quero (1984); Tricas and McCosker (1984); Block and Carey (1985); Cailliet et al. (1985); Pratt and Casey (1985); Klimley (1985); Taylor (1985); Tricas (1985); Tricas and McCosker (1985); McCosker (1985); Bass (1986); deSilva (1986); Corkeron, Morris and Bryden (1987); Nakano and Nakaya (1987); Stafford-Deitsch (1987); Randall, Randall and Compagno (1988); Uchida et al. (1988); Paxton et al. (1989); Cliff, Dudley and Davis (1989); Cockcroft, Cliff and Ross (1989); Paulin et al. (1989); Fulgosi (1990); Strong (1990, 1996); Springer (1990); Cousteau and Richards (1991); Ellis and McCosker (1991); Long (1991, 1996); Bruce (1992, 1995); Klimley et al. (1992); Strong et al. (1992, 1996); Francis and Randall (1993): Hanan, Holts and Coan (1993); Michael (1993); Compagno and Fergusson (1994); Klimley (1994); Seret (1994); Last and Stevens (1994); Bonfil (1994); Fergusson (1994, 1996); Nakaya (1994, 1996); Anderson and Goldman (1996); Burgess and Callahan (1996); Cliff, Dudley and Jury (1996); Collier, Marks and Warner (1996); Goldman et al. (1996); Francis (1996); Gadig and Rosa (1996); Klimley, Pyle and Anderson (1996); Long and Jones (1996); Long and Waggoner (1996); Long et al. (1996); Mollet and Cailliet

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