

(1996); Mollet et al. (1996); Pratt (1996); Strong (1996); Uchida et al. (1996); Goldman (1997); Smale and Heemstra (1997); Compagno, Marks and Fergusson (1997); Santos, Porteiro and Barreiros (1997); McEachran and Fechhelm (1998); Smith, Au and Show (1998); Cliff et al. (2000); Environment Australia (2000b); Fergusson, Marks and Compagno (2000); D. Ainley (pers. comm.); R. Alexander (pers. comm.); D. Allen (pers. comm.); G. Burgess (pers. comm.); G. Cailliet (pers. comm.); S. Cook (pers. comm.); D. Ebert (pers. comm.); A.P. Klimley (pers. comm.); R. Lea (pers. comm.); M. Marks (pers. comm.); S. Smith (pers. comm.); I. Fergusson (pers. comm.); G. Zorzi (pers. comm.).

Isurus Rafinesque, 1810

Genus: *Isurus* Rafinesque, 1810a, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 11.

Type Species: *Isurus oxyrinchus* Rafinesque, 1810, by monotypy.

Number of Recognized Species: 2.

Synonyms: Genus *Oxyrhina* Agassiz, 1838: 86, pls. 33-34. Type species: "*Lamna oxyrhina* Cuvier and Valenciennes, MS." by absolute tautonymy, a junior synonym of *Isurus oxyrinchus* Rafinesque, 1810. Genus *Oxyrrhina* Bonaparte, 1846: 17. Type species: *Oxyrhina gomphodon* Müller and Henle, 1839, a junior synonym of *Isurus oxyrinchus* Rafinesque, 1810. Genus *Plectrostoma* Gistel, 1848: 10. Replacement name for *Oxyrhina* Agassiz, 1835, and thereby taking the same type species, *Lamna oxyrhina* Cuvier and Valenciennes, 1838, a junior synonym of *Isurus oxyrinchus* Rafinesque, 1810. Genus *Isuropsis* Gill, 1862b: 397. Type species: *Oxyrhina glauca* Müller and Henle, 1839, by original designation. Genus *Plectrosoma* Bigelow and Schroeder, 1948: 123 (error for *Plectrostoma* Gistel, 1848). Genus *Lamiosstoma* Glikman, 1964: 105. Type species: *Lamiosstoma belyaevi* Glikman, 1964, by original designation.

Diagnostic Features: Snout bluntly to acutely conical. Eyes large, 1.3 to 3.1% of total length. Nostrils situated adjacent to head rim in ventral view. Mouth width 0.9 to 1.5 times its length. Anterior teeth enlarged; anterior and intermediate teeth not compressed but upper lateral teeth more or less compressed, teeth not forming a continuous cutting edge; intermediate teeth very small and less than half height of adjacent anteriors, with normal cusps directed posterodistally or nearly vertical; second lower anterior teeth greatly enlarged and taller than second upper anterior tooth; total tooth count 43 to 54; roots of anterior teeth deeply arched, with root lobes narrow and elongated; lateral cusplets absent from teeth at all stages; teeth smooth-edged; cusps of anterior teeth weakly to strongly flexed. Body usually fairly slender. First dorsal-fin origin usually behind the pectoral-fin free rear tips. Anal-fin origin under second dorsal-fin midbase or slightly posterior to second dorsal-fin insertion. Secondary caudal keels absent or present and weak. Total vertebral count 182 to 197. Cranium with rostral cartilages neither swollen nor hypercalcified. Intestinal valve count 47 to 54. Length of adults 2.0 to 4.2 m. Usually a black axillary spot at pectoral-fin insertions; pectoral-fin tips usually abruptly black on their ventral surfaces.

Local Names: Makos, Mako sharks, Mackerel sharks, Awozame-zoku (Japan).

Remarks: The systematics of makos (genus *Isurus*) was formerly chaotic, with a few regional species recognized on growth changes within a single species, *Isurus oxyrinchus* (Garman, 1913; Fowler, 1941; Bigelow and Schroeder, 1948; Smith, 1957). Guitart (1966) described a second, highly distinctive macroceanic mako, *I. paucus* from Cuba, which Garrick (1967) independently described as *I. alatus* from the central Pacific. Garrick (1967) sorted out the growth change problems and his arrangement and synonymy for *I. oxyrinchus* were followed by Bass, D'Aubrey and Kistnasamy (1975a), Pinchuk (1983), Compagno (1984), and Moreno and Morón (1992b), who recognized two living species, *I. oxyrinchus* and *I. paucus*. Moreno and Morón presented detailed comparisons of eastern Atlantic makos from extensive fisheries samples and confirmed the differentiation of *I. oxyrinchus* and *I. paucus* on morphometry, external morphology including coloration, and dentitional characters. They noted, however, that *I. oxyrinchus* specimens caught around the Azores closely agreed with other eastern Atlantic specimens in morphometrics, morphology and dentition, but had a dusky snout and mottled or all-dark underside as in *I. paucus*. They suggested that the Azores mako represented a distinct, localized population or 'population variant' of *I. oxyrinchus*. This is plausible but needs further research, including molecular studies, and is of some urgency as the Azores mako is possibly declining due to overfishing. The Azores mako may have an analogy within the genus *Lamna*, in which the North Pacific *L. ditropis* differs from the North Atlantic *L. nasus* in having a dusky or mottled underside, but Southern Hemisphere 'black-faced' *L. nasus* have similar dark undersides and have been mistaken for *L. ditropis*. Compagno (1990b) noted chondrocranial differences between *Isurus oxyrinchus* and *I. paucus*.

Key to Species:

1a. Snout usually acutely pointed; cusps of upper and lower anterior teeth flexed, with tips reversed; pectoral fins considerably shorter than head, relatively narrow-tipped in young and acutely pointed in adults (Fig. 72); underside of snout and mouth white in adults (dusky in Azores' 'marrajo criollo') ***Isurus oxyrinchus***

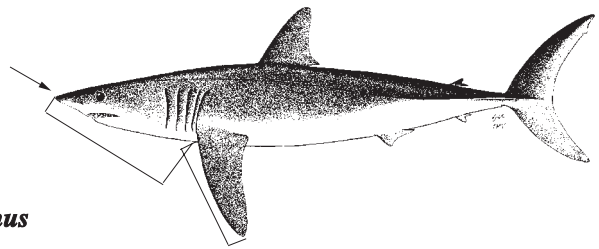


Fig. 72 *Isurus oxyrinchus*

1b. Snout narrowly to bluntly pointed, usually not acute; cusps of upper and lower anterior teeth straighter, with tips not reversed; pectoral fins about as long as head or longer (Fig. 73), relatively broad-tipped in young and adults; underside of snout and mouth dusky in adults ***Isurus paucus***

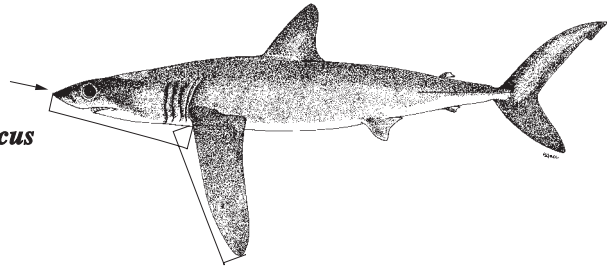


Fig. 73 *Isurus paucus*

<i>Isurus oxyrinchus</i> Rafinesque, 1810
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Fig. 74

Isurus oxyrinchus Rafinesque, 1810a, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 12, pl. 13, fig. 1. Also Rafinesque, 1810b, *Indice Ittiol. Sicil.*: 45. Holotype unknown, type locality Sicily, Mediterranean Sea. Variant spellings include *Lamia oxyrhincus* Bory de St. Vincent, 1829, and *Isurus oxyrhynchus* Jordan and Evermann, 1896.

Synonyms: *Isurus spallanzanii* Rafinesque, 1810b: 45, 60. Type locality: Sicily. No types known according to Eschmeyer (1998: CD-ROM). *Squalus (Lamna) cepedii* Lesson, 1830: 93. Holotype: 1.83 m individual, Equatorial Atlantic, 6°S, 27°W; according to Eschmeyer (1998: CD-ROM) the whereabouts of this specimen is unknown. *Lamna oxyrhina* Cuvier and Valenciennes, in Agassiz, 1838: 86. Manuscript name only cited by Agassiz, but without a species description. Types uncertain: Agassiz mentioned a set of jaws in the collection of the Museum National d'Histoire Naturelle, Paris, without specific data. A tooth set from a mako was illustrated by him (Agassiz, 1835, pl. G, fig. 2, as *Lamna*) and may be from the Paris specimen. *Oxyrhina gomphodon* Müller and Henle, 1839: 68, pl. 28. Holotype, Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB 4528, a stuffed adult male 1 650 mm +, without head, jaws separate according to Paepke and Schmidt (1988: 163), from "Ocean". *Oxyrhina glauca* Müller and Henle, 1839: 69, pl. 29. Syntypes, three stuffed specimens, Rijksmuseum van Natuurlijke Historie, Leiden, RMNH 2529, 1 020 mm TL male (a lectotype, designated by Garrick, 1967: 675), RMNH 2533, 750 mm TL male, RMNH 2587, 660 mm TL male, and two jaws of uncertain deposition, possibly Berlin (not mentioned in Paepke and Schmidt, 1988). Type locality originally stated as Java, but actually Japan according to Garrick (1967). *Lamna latro* Owen, 1853: 96. Locality unknown. Types? *Isuropsis dekayi* Gill, 1862: 409. Based on *Lamna punctata* DeKay, 1839, not *Oxyrhina daekayi* Gill, 1862b, (= *Lamna nasus*). *Carcharias tigris* Atwood, 1865: 81. No distinguishing features; also Atwood, 1869: 268. Types: None, according to Eschmeyer (1998: CD-ROM), from Gulf of Mexico and Massachusetts, Provincetown, Cape Cod. *Lamna guentheri* Murray, 1884: 349. Type locality, Kurrachee (= Karachi), Pakistan. Original spelling *Lamna güntneri*. Holotype: a 2 580 mm specimen according to Garrick (1967: 665-667). Disposition of holotype uncertain, presumably in the British Museum (Natural History); Garrick (*loc. cit.*) and Eschmeyer (1998: CD-ROM) had no information. *Lamna huidobrii* Philippi, 1887: 548, pl. 3, fig. 1. Holotype: 2.90 m female (possibly stuffed) in collection of Universidad de Chile, Departamento de Biología Celular y Genética, Santiago, Chile (Eschmeyer, 1998: CD-ROM), possibly lost (S. Kato, pers. comm.), type locality, Santiago Province, Chile. *Isurus mako* Whitley, 1929: 101. A new name based on the account of *I. glaucus* by Phillipps, 1932: 268, off Manaukau Bar, Auckland, New Zealand. No types according to Eschmeyer (1998: CD-ROM). *Isurus bideni* Phillipps, 1932: 227, fig. 2. According to Phillipps (*loc. cit.*) and Eschmeyer (1998: CD-ROM), the holotype is a South African specimen in the Australian Museum, Sydney, AMS IA.4311 (jaws and photographs) sent to Mr G.P. Whitley by Mr C. Leo Biden of Cape Town and possibly from the Western Cape Province, South Africa. *Isurus tigris africanus* Smith, 1957: 96, pl. 1, fig. 1. Holotype: J.L.B. Smith Institute of Ichthyology, RUSI 426, jaws from 2 540 mm TL adult male. Type locality, Algoa Bay, South Africa.

Other Combinations: *Isurus* or *Isuropsis glaucus* (Müller and Henle, 1839), *Isurus guentheri* (Murray, 1884).

FAO Names: **En** - Shortfin mako; **Fr** - Taupe bleu; **Sp** - Marrajo dientuso.

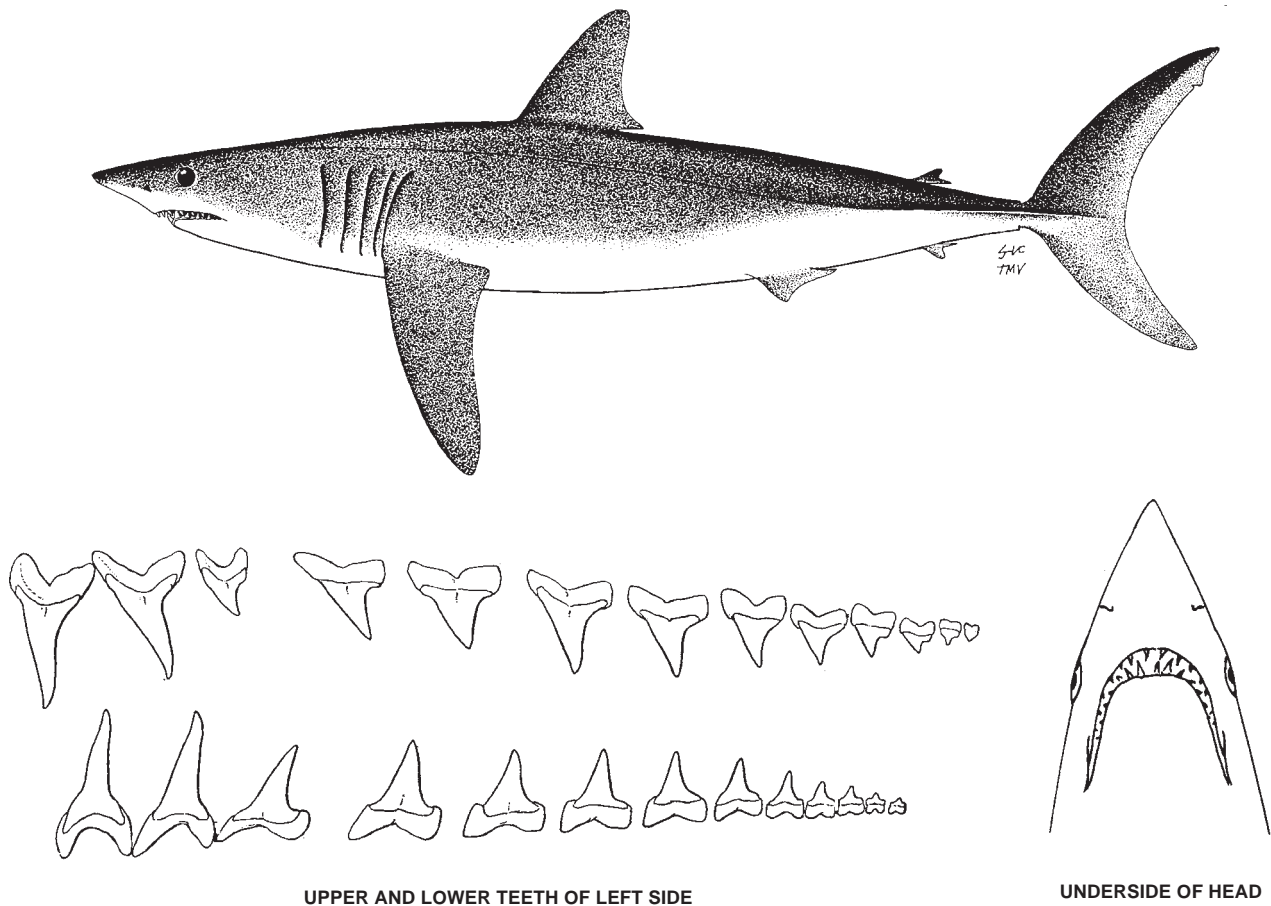
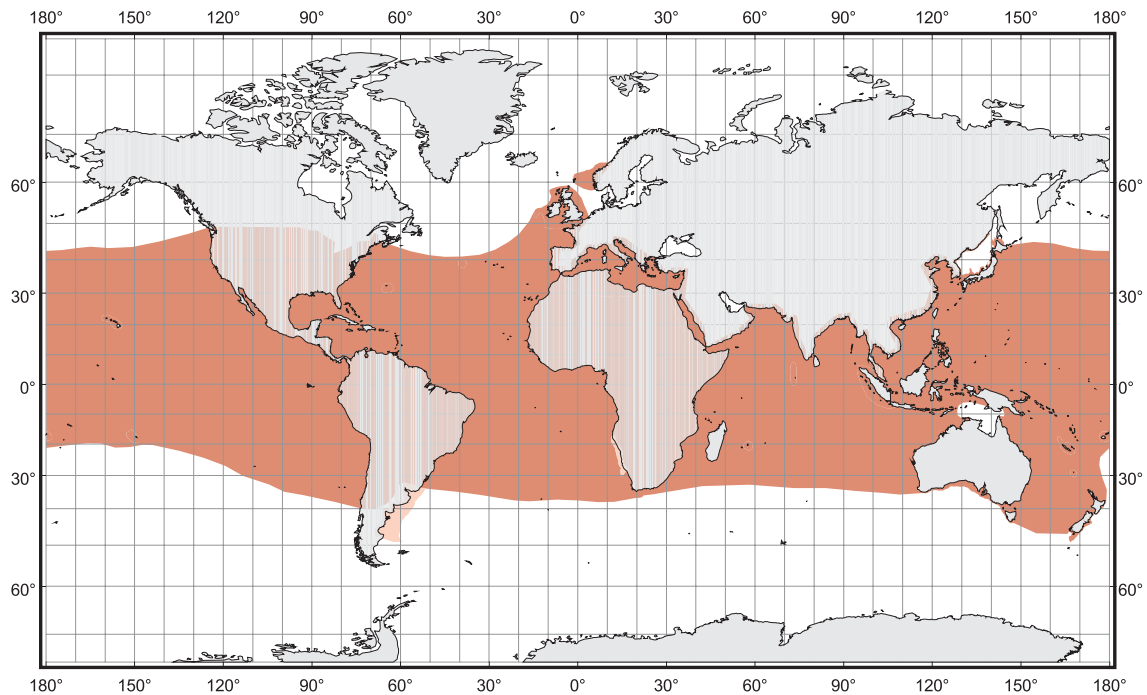


Fig. 74 *Isurus oxyrinchus*

Field Marks: Spindle-shaped body, long, acutely conical snout, large blade-like teeth without cusplets or serrations, pectoral fins rather narrow-tipped and with anterior margins less than head length, large first dorsal fin and minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, no secondary keels on caudal base, crescentic caudal fin, ventral surface of body usually white.

Diagnostic Features: Snout acutely pointed. Eyes relatively small. Mouth U-shaped. Lower anterior teeth strongly protruding and horizontal on jaws even when mouth is closed; anterior teeth with narrow, more oblique cusps with flexed tips; cusps of first upper anterior teeth with incomplete cutting edges; intermediate teeth with curved oblique distally hooked cusps. Body moderately slender but more fusiform than in *Isurus paucus*. Pectoral fins semifalcate and with tips relatively narrow, anterior margins about 16 to 22% of total length and shorter than head length. Origin of first dorsal fin over or just behind the pectoral free rear tip; first dorsal-fin apex broadly rounded in young but more angular and narrowly rounded in large juveniles and adults; first dorsal-fin height greater than base length in large individuals but equal or smaller in young below 185 cm. Total vertebral count 182 to 195, mostly below 190. **Colour** (except Azores 'marrajo criollo'): dorsolateral coloration brilliant blue or purplish in life, white below underside of snout in young and adults; dark colour of head partially covering gill septa, lower part of second and third gill septa white; dark colour of flanks not extending ventrally onto abdomen; pelvic fins dark on anterior halves, white on posterior halves, undersides white and sometimes with thin dark margin; first dorsal fin with pale centre (more obvious in young than adults); anal fin dark only on anterior half and white on posterior half.

Distribution: Coastal and oceanic, circumglobal in all temperate and tropical seas. Western Atlantic: Gulf of Maine to southern Brazil and possibly northern Argentina, including Bermuda, Gulf of Mexico and Caribbean. Eastern Atlantic: Norway, British Isles and Mediterranean to Morocco, Azores, Western Sahara, Mauritania, Senegal, Côte d'Ivoire, Ghana, southern Angola, probably Namibia, and South Africa (west coast). Indo-West Pacific: South Africa (east coast), Mozambique, Madagascar, Mauritius and Kenya north to Red Sea and east to Maldives, Iran, Oman, Pakistan, India, Indonesia, Viet Nam, China, Taiwan (Province of China), North Korea, South Korea, Japan, Russia (Primorskiyi Krai), Australia (all states and entire coast except for Arafura Sea, Gulf of Carpentaria and Torres Strait), New Zealand (including Norfolk Island), New Caledonia, Fiji. Central Pacific: From south of Aleutian Islands to Society Islands, including Hawaiian Islands. Eastern Pacific: USA (Washington and California) south to Mexico, Costa Rica, Ecuador, Peru and central Chile.



Habitat: The shortfin mako is a common, extremely active, offshore littoral and epipelagic species found in tropical and warm-temperate seas but seldom occurring in waters below 16°C. This shark occurs from the surface down to at least 500 m. It occurs well offshore but penetrates the inshore littoral just off the surf zone in places such as parts of KwaZulu-Natal, South Africa, where the continental shelves are very narrow. Shark meshing data off South Africa suggests that this species prefers clear water to turbid water and is caught at a range of water temperatures from 17 to 22°C. In the western North Atlantic it prefers a similar range of temperatures, and only moves onto the continental shelf when surface temperatures exceed 17°C. In the eastern North Pacific juveniles range into southern California waters and tend to stay near the surface, with little tendency to descend into cold subsurface waters, and use these offshore continental waters as nursery areas. Telemetered small sharks in this area tended to stay near the surface above 20 m depth and in waters 20 to 21°C, and mostly avoided the thermocline and cold deeper waters (Holts and Bedford, 1992).

Biology: The peregrine falcon of the shark world, the shortfin mako may be the fastest shark and one of the swiftest and most active fishes. It is famed as a jumper, leaping several times its length from the water, and is capable of extreme bursts of speed when hooked and in pursuit of prey. Sonic telemetry of small (1.7 to 1.8 m and 32 to 36 kg) makos off southern California showed a relatively slow cruise speed (Holts and Bedford, 1992) between 1.3 and 2.6 km/h, with short increases up to 4.5 and 5.6 km/h and slowing to less than 1 km/h at night. No fast dashes were recorded during the periods monitored. Similar speeds were recorded over a track of 280 km off Florida by a larger (about 180 kg) shortfin mako (Casey and Kohler, 1992).

Shortfin makos are endothermic and maintain higher temperatures than surrounding water temperatures in their body musculature, brains, eyes and viscera with countercurrent vascular heat exchangers (Carey and Teal, 1969; Carey et al., 1972; Carey, 1982, 1992; Block and Carey, 1985). Body muscle may run 1 to 10°C higher than ambient temperature. Central temperatures in the body musculature of the shortfin mako are highest relative to water temperature in cooler water (between 19 and 25° in water 15°C), but approach ambient in warm water (27 to 29° in water 27°C). Endothermy is particularly advantageous in maintaining elevated swimming, visual, central nervous system and digestive functions when the makos are in cooler waters in higher latitudes or when diving below the thermocline in warm waters.

The shortfin mako is highly migratory and in the extreme northern and southern parts of its range, has a tendency to follow movements of warm water masses polewards in the summer. Off South Africa catches in the KwaZulu-Natal shark nets indicate inshore movements from deeper water over the continental slopes, which in the area is relatively close to shore because of the narrow shelves.

Long-range movements of this shark are not well known and are being slowly elucidated by conventional tagging in the North Atlantic. Casey and Kohler (1992) reported on 2 459 shortfin makos tagged off the western North Atlantic coast of the USA between 1962 and 1989, with a recapture rate of 9.4% to date. About 64% were recaptured within 500 km of where they were tagged, but 13% travelled over 1 600 km with several recaptures in the Azores and one even travelling about 4 000 km to Spain. Casey and Kohler suggested that makos may travel up the Gulf Stream and around the Sargasso Sea to return to the East Coast of North America, with few crossing the Mid-Atlantic Ridge and reaching European waters. The authors hypothesized that the western North Atlantic makos form a separate population or stock to those in the eastern Atlantic although intermixing is possible as shown by crossings to the Azores and Europe. There are problems in understanding the population structure of western North Atlantic makos because large adults, particularly females, are little-known in the area although juveniles are abundant.

This species is ovoviviparous and a uterine cannibal (oophagous), with 4 to 25 and possibly 30 young (mostly 10 to 18) in a litter, with larger females having larger litters. Sex ratios from beach-meshed sharks off KwaZulu-Natal, South Africa, varied monthly, with male-female ratios ranging from 0.6:1 to 2.5:1 and with males more abundant than females for most of the year except January and August; with a sample of 171 sharks, males were significantly more abundant than females with an overall ratio of 1.4:1. Birth occurs mostly in late winter to midsummer in both hemispheres. Off KwaZulu-Natal birth occurred offshore in late spring (November), and mating occurs in autumn (March to June). Estimates of gestation period vary, but recent estimates suggest it may be 15 to 18 months within a reproductive cycle of three years (including a year break between pregnancies; Mollet et al., 2000). Adult males show seasonal changes in gonadosomatic index (gonad weight as % of body weight), with males having the heaviest gonads in the summer and the lightest in winter. Gonadosomatic index is positively correlated with hepatosomatic index (liver weight as % of body weight) in adult females, with females with large ovaries having larger livers than those with small ovaries.

Makos may mature at a minimum age of 7 to 8 years old, based on yearly addition of growth rings on vertebral centra, with the oldest known with 18 rings corresponding to at least 18 years at 321 cm, and an estimated maximum age of 45 years (Cailliet et al., 1983). Pratt and Casey (1983) assumed that two growth rings were formed each year on the vertebral central of shortfin makos, though Cailliet et al. (1983) suggested that one ring per year was formed. Stillwell (1990) suggested that makos were faster-growing, and achieved adult size in 4.5 years for males and 7 years for females.

The shortfin mako primarily feeds on other fishes, with a wide variety of prey recorded. Prey items are typically much smaller than the mako, and off South Africa range between 10 and 35% of the length of the predator. However, Stillwell (1990) suggested that large makos shifted to large prey near their own size, with swordfish (*Xiphias*) weighing 180 kg or more being commonly taken by large and presumably adult makos (males about 136 kg and females 337 kg) in the western North Atlantic.

The mako eats both pelagic and demersal bony fishes, including freshwater eels (Anguillidae), eel-pouts (Zoarcidae), anchovies (Engraulidae), menhaden, sardines and other herring (Clupeidae), grunts (Haemulidae), lancetfish (Alepisauridae), needlefish (Belonidae), sauries (Scomberesocidae), cod, ling, whiting and other cod-like fishes (Gadidae), hake (Merlucciidae), alfonosinos (Berycidae), croakers (Sciaenidae), mullet (Mugilidae), Australian salmon (*Arripis*), butterfishes (Stromateidae), bluefish (*Pomatomus saltatrix*, Pomatomidae), yellowtails, jack mackerel and other jacks (Carangidae), sea bass (Serranidae), porgies or sea breams (Sparidae), scabbardfish (Trichiuridae), snake mackerel (Gempylidae), swordfish (*Xiphias gladius*, Xiphiidae), sailfish (*Istiophorus platypterus*, Istiophoridae), mackerel, tuna, bonito, skipjack, and other scombrids (Scombridae), medusafishes (Centrolophidae), rockfish (*Sebastes*, Scorpaenidae), sea robins (Triglidae), and even seahorses (Syngnathidae), puffers (Tetraodontidae), porcupine fish (Diodontidae), and boxfish (Ostraciidae). In the western North Atlantic, bluefish are the most important food and comprise about 78% of the shortfin mako's diet (Stillwell and Kohler, 1982), but the same species (called taylor in Australia) was not recorded from makos off New South Wales (Stevens, 1984).

Elasmobranchs taken by the shortfin mako include blue sharks (*Prionace glauca*), grey sharks (*Carcharhinus obscurus*, *C. brevipinna*, *C. sealei* and *C. limbatus*), milk sharks (*Rhizoprionodon acutus*), hammerheads (*Sphyrna lewini* and *S. zygaena*), skates (Rajidae), spotted eagle rays (*Aetobatus narinari*, Myliobatidae), and cownose rays (Rhinopterae). Off KwaZulu-Natal, South Africa, small sharks less than 1.3 m long including the young of large species such as *Carcharhinus obscurus* are more important food items for the mako than large sharks and rays, which is a function possibly of high availability as well as preference for smaller prey items. Off South Africa elasmobranchs were the most important prey, followed by teleosts and cephalopods (squid), but in the western North Atlantic and New South Wales teleosts were the most important prey while elasmobranchs were virtually unrepresented.

Cephalopods are important prey and include a variety of inshore and oceanic and deep-benthic squids including *Loligo* (Loliginidae), *Ancistrocheirus* (Ancistrocheiridae), *Lycoteuthis* (Lycoteuthidae), *Octopoteuthis* (Octopoteuthidae), *Histioteuthis* (Histioteuthidae), Gonatidae, and *Illex* and other ommastrephids (Ommastrephidae), as well as cuttlefish (*Sepia*, Sepiidae). Other food includes sea turtle heads (uncertain if these were scavenged or if the turtles were decapitated by the makos), unidentified small cetacean material (including a pelagic dolphin), salps, isopods, penaeid shrimp, sponges, sargassum weed, and occasional stones and other detritus. Marine mammals are rarely reported in the diet of the shortfin mako and may be scavenged, but very large individuals occasionally catch small pelagic cetaceans (dolphins). Very large shortfin makos over 3 m long have somewhat broader, more flattened and triangular upper teeth, perhaps more suitable for handling small cetaceans than the awl-shaped teeth of smaller makos. Pinnipeds have not been recorded as mako food so far (although they could be eaten in places where their distribution overlaps that of large makos), and makos have not been seen scavenging on dead whales as with white sharks or tiger sharks.

From prey types and other information, makos apparently feed at or near the surface and well below it, and may feed on bottom prey when close inshore. Stillwell and Kohler (1982) estimated that a 68 kg mako might consume about 2 kg of prey per day, and could eat about 8 to 11 times its body weight per year. Stillwell (1990) suggested that makos might consume up to 15 times their weight per year.

This is a bold and responsive shark when a feeding stimulus (such as speared fish or a bait station) is present, and individuals have charged divers repeatedly at high speed (usually veering off at the last moment) as well as chasing off less dominant (possibly smaller?) conspecifics from baits. About a fourth of some 156 makos examined from the shark nets off KwaZulu-Natal, South Africa, had injuries, including missing fin tips, clasper tips, and mako bite patterns on the belly, flanks, pectoral fins, and gill regions. Some injuries were due to scavenging by other sharks, but mako-induced tooth cuts are likely

to be both from combat and mating, as with similar cuts on white and sand tiger sharks, including pectoral fin injuries that may be due to a male holding onto a female with its mouth during courtship. Open-mouth *gaping* at divers by these sharks may be a threat display as in the white shark. Another possible threat display under non-baited conditions may be *porpoising* or low short leaps at the surface, followed by *figure 8 looping* at speed. Behaviour is otherwise sketchily known, but it is suspected that a variety of behavioural elements, including varied social interactions, may be present in this species as in the white shark. Shark netting data off South Africa suggests that makos were generally caught singly off beaches, though two occurred in the same net on the same day and a small group of five was caught in adjacent nets over nine days.

The shortfin mako apparently has relatively few natural predators, perhaps because of its high activity level, speed and large size. Their chief predators are humans, in the form of commercial fisheries. It is not immune from predation by its larger cousin the white shark, which is very fast when chasing prey or conspecifics. Off California and in the Mediterranean Sea small (less than 2 m long) makos have been found in white shark stomachs. In South Africa the fresh head of a mako (cut off at the pectoral fins) was found on a beach with unmistakable white shark wounds indicating a predation bout and no evidence of scavenging from fishing gear such as hook or net injuries. A live South African mako was caught with injuries suggesting that a white shark grabbed it by the caudal fin and either lost it or let it go. Sailfish and swordfish may stab makos with their beaks, presumably in self-defence; one adult female South African mako was found with a beak of a small sailfish sticking out of one eye. Makos caught in the KwaZulu-Natal shark nets were mostly dead (only 6% still alive when examined), vs. 16% alive for white sharks and 33% for spotted ragged-tooth sharks (*Carcharias taurus*). This probably reflects different activity levels and oxygen requirements, with the mako (presumably with obligate ram-ventilation of its gills) having the highest levels and the more sluggish ragged-tooth (which can hover motionless) the least.

Size: Maximum about 396 cm, estimated maximum total length about 408 cm. Size at birth between 60 and 70 cm, with free-living individuals as small as 71 cm. Males adolescent at about 140 to 199 cm and maturing between 203 and 215 cm and reaching about 296 cm; females adolescent at about 233 to 286 cm, maturing at about 275 to 293 cm and reaching at least 394 cm. Females apparently mature at smaller sizes in the Southern Hemisphere than in the western North Atlantic (Mollet et al., 2000). Several length-weight equations exist for this species and include:

Stevens (1983): $W(\text{kg}) = 4.832 \times 10^{-6} \times \text{TL}(\text{cm})^{3.10}$ (n = 80, TL = 58 to 343 cm, Australia)

Guitart (1975): $W(\text{kg}) = 1.193 \times 10^{-6} \times \text{TL}(\text{cm})^{3.46}$ (n = 23, TL = 160 to 260 cm, Cuba)

Strasburg (1958): $\log W(\text{lb}) = -4.608 + 2.925 \times \log \text{TL}(\text{cm})$ (Central Pacific)

Cliff, Dudley and Davis (1990): $W(\text{kg}) = 1.47 \times 10^{-5} \times \text{PCL}(\text{cm})^{2.98}$ (n = 143, PCL = 84 to 260 cm, South Africa)

Kohler, Casey and Turner (1995): $W(\text{kg}) = 5.2432 \times 10^{-6} \times \text{FL}(\text{cm})^{3.1407}$ (n = 2081, western North Atlantic)
where $\text{FL}(\text{cm}) = 0.9286 \times \text{TL}(\text{cm}) - 1.7101$ (n = 199)

Mollet et al. (2000): $W(\text{kg}) = 7.2999 \times \text{TL}(\text{m})^{3.224}$ (n = 63, for females TL = 2.0 to 3.7 m, western North Atlantic)

and $W(\text{kg}) = 6.824 \times \text{TL}(\text{m})^{3.137}$ (n = 64, for females TL = 2.0 to 3.4 m, Southern Hemisphere).

Interest to Fisheries and Human Impact: The shortfin mako is an important species for pelagic longline fisheries wherever it occurs, because of its relative abundance and high quality meat, but is also caught in fisheries using drifting and set gill nets, and is taken by hook-and-line. It is taken as a utilized bycatch of tuna and swordfish longline fisheries worldwide, with carcasses as well as fins being retained for market. The meat is utilized fresh, frozen, smoked and dried-salted for human consumption; the oil is extracted for vitamins; the fins used for shark-fin soup; the hides are processed into leather and the jaws and teeth are used for ornaments.

Considerable fisheries for shortfin mako exist or existed in the Mediterranean Sea, off Cuba, in the Gulf of Mexico and Caribbean, off southern California, and in the western and central Pacific. It has been estimated that the Spanish longline fleet caught about 750 t/y of shortfin makos in the Atlantic Ocean and Mediterranean Sea in the early 1990s (Bonfil, 1994). Off California, early juvenile shortfin makos were targeted by a short-lived experimental drift longline fishery and are a very welcomed bycatch in the driftnet fishery for swordfish (Cailliet et al., 1993). Up to 475 t of shortfin makos were taken jointly by these fisheries in 1987, and although CPUE did not show a declining trend concerns over the heavy exploitation of immature fish prompted the closure of the experimental longline fishery in 1992 (O'Brien and Sunada, 1994). The total bycatch of shortfin makos in the former high-seas driftnet fisheries in the North Pacific in the early 1990s was estimated at about 360 t/y (Bonfil, 1994). This species is apparently very common in the tuna fisheries of Indonesia: unconfirmed reports indicate that landings of shortfin makos from Indonesian waters attained 5 200 t in 1995 and that the estimated potential is about 16 000 t/y (Priyono, 1998). The Brazilian longlining fleet based in Santos landed between 13.3 and 138.3 t of shortfin makos annually between 1971 and 1990 (Costa et al., 1996). Despite increasing fishing effort during this period, the CPUE of shortfin makos has remained relatively stable with an initial slight decreasing trend followed by a slight increasing trend.

Despite the role of shortfin makos in worldwide pelagic fisheries, catches are currently poorly reported to FAO at least. Brazil, New Zealand and the United States reported very small catches (2 to 76 t) to FAO from 1987 to 1997 (FAO FishStat Plus database, 2000).

Big-game sports angling for mako sharks is widespread, with New Zealand and South Africa being traditional places for offshore sports fishing for makos with heavy gear. The International Game Fish Association lists the shortfin mako as a record game fish. In the 1980s mako angling became popular in the USA off southern California, with numerous anglers involved and mako tournaments rivalling competitive angling for marlin.

Makos rarely bite divers and swimmers and few biting incidents are reliably reported. This suggests that the mako is not normally inclined to bite people without an exciting stimulus or provocation and does not normally eat marine mammalian prey (except perhaps large females preying on small pelagic dolphins), however it should be treated with respect. The mostly offshore habitat of this species probably prevents it from coming in contact with recreational swimmers except under exceptional circumstances such as places where makos visit the vicinity of beaches with a narrow continental shelf. Its speed, power, large teeth, and boldness when a feeding stimulus is present should be cause for divers, especially spearfishers, to treat the mako with caution and observe what it is doing if it approaches. Divers should not dispute it for possession of a shot fish and should back off if it is directing *gapes* their way, swimming in *figure-8s*, or giving bluff-*charges*. The shortfin mako tends to respond vigorously when hooked or harassed, and it should not be speared or otherwise provoked underwater. A defensive response by this animate torpedo when provoked may be far too quick for directed anti-shark weapons such as powerheads or repellent squirters to be effective. Steel-mesh armour suits were penetrated by the powerful jaws and teeth of these sharks in tests. Electronic shark repellent devices worn by divers may be effective in thwarting oral contact by these sharks but may not be needed if the shark's activities are correctly gauged.

Makos occasionally bite boats, and mako boat incidents are second in number only to those involving the white shark. Most of these incidents have occurred while makos were being played by anglers and should be regarded as human-provoked and abnormal. The angling and popular literature is rife with 'mako stories', in which these sharks bite, jump into, or even smash right through the boats of their assailants. Anglers who suddenly find themselves sharing a boat with an aroused and vigorous mako have been known to leap into the water!

Makos have become the subject of ecotouristic diving in recent years, with most of the mako dive sites being off southern California from the Los Angeles Basin to San Diego, but with sites also in South Africa and the Maldives. The sight of this sleek, beautiful, graceful shark underwater may be one of the high points for the shark-watching diver. The writer does not know offhand of any attempts to display shortfin makos in public oceanaria, but small makos have been kept for physiological research in hydrodynamic tunnels at Scripps Institution of Oceanography in southern California (United States).

The conservation status of the shortfin mako is of moderate concern despite its relative abundance and vast distribution. It has been preliminarily assessed as a *Lower Risk/Near Threatened* species by the IUCN Shark Specialist Group. The shortfin mako was found to have a midrange intrinsic rebound potential (a measure of its ability to recover from exploitation) among 26 shark species analysed (Smith, Au and Show, 1998). Fisheries are regulated and limited in the United States and New Zealand, but not elsewhere where intensive epipelagic longline fisheries can have a major impact on it. Obviously international and regional management is needed to maintain sustainable catches. It is not known what the effects of the former pelagic gill net fishery for scombroids was on makos and other oceanic sharks. Declines in landings have been recorded off the United States (east and west coasts) and in the eastern Atlantic by the Azorean 'marrajo' fleet, but trends are little known elsewhere. Castro, Woodley and Brudek (1999) suggest that although it is very difficult to assess the conservation status of this shark because it is caught in numerous fisheries worldwide, it is reasonable to assume that decreases are occurring in those areas for which there is limited data or none whatsoever.

Local Names: Mako (original Maori name for this species, New Zealand); Shortfinned mako shark, Mako shark, Mako, Atlantic mako shark, Pacific mako shark, Pacific bonito shark, Pacific mako, Mackerel shark, Blue shark, Sharp nosed, Sharpnosed or Sharp-nosed mackerel shark, Mackerel porbeagle, Mediterranean mackerel shark (English); Ossirina dello spallanzani, Meanto, Pisci tunnu, Piscicani, Cani di mari, Cane di mare di Messina, Cagnia (Italy); Psina cavlozuba, Psina dugonoska (Adriatic); Anequin (Portugal); Marracho, Rinquim, Mako, Shortfin mako, Marrajo criollo (Azores); Sobraig, Sobratg, Ludia marraco, Marraquet, Marrajo, Tiburón (Spain); Alecrín (Mexico); Dentudo, Dientuso azul (Cuba); Ganumu sorrah (India, Tamil); Blue pointer, Mako shark, Snapper shark (Australia); Porpoise shark, Blue porpoise shark, Sharpnose mako, Mambone, Moro (South Africa); Aozame, Morozame, Awozame (Japan); Bonito shark (California); Anequin barbatana curta (Mozambique).

Remarks: Moreno and Morón (1992b) give detailed descriptions of the coloration of typical *I. oxyrinchus* and the Azores 'marrajo criollo' mako, which was long recognized by Azores fishermen as a separate form as distinguished from typical *I. oxyrinchus* or marrajo, and marrajo negro or *I. paucus*. Apparently Cuban and Japanese fishermen recognized the longfin and shortfin makos as being distinct long before scientists were aware of their existence.

Literature: Garman (1913); Barnard (1925); Fowler (1936, 1941); Whitley (1940); Bigelow and Schroeder (1948); Smith (1949, 1957d); Strasburg (1958); Farquhar (1963); Stead (1963); Garrick and Schultz (1963); Randall (1963); Applegate (1966, 1977); Guitart (1966, 1975); Garrick (1967); Carey and Teal (1969); Lineaweaver and Backus (1970); Mundus and Wisner (1971); Carey et al. (1972); Gubanov (1974, 1978); Bass, D'Aubrey and Kistnasamy (1975a); Ellis (1976); Penrith (1978); Glikman and Dolganov (1980); Cadenat and Blache (1981); Stillwell and Kohler (1982); Cadenat and Blache (1981); Carey (1982, 1990); Pratt and Casey (1983); Gilmore (1983); Stevens (1983, 1984, 1990, 1992); Cailliet and Bedford (1983); Compagno (1984, 1990a, b); Nakaya (1984); Block and Carey (1985); Compagno, Ebert and Smale (1989); Quero (1984); Paulin et al. (1989); Springer (1990); Fischer et al. (1990); Cliff, Dudley and Davis (1990); Stillwell (1990); Compagno, Ebert and Cowley (1991); Casey and Kohler (1992); Moreno and Morón (1992b); Holts and Bedford (1992); Anderson and Ahmed (1993); Cailliet, Holts and Bedford (1993); Francis and Randall (1993); Michael (1993); Bonfil (1994);

Last and Stevens (1994); Seret (1994); Costa et al. (1996); Priyono (1998); Smith, Au and Show (1998); Castro, Woodley and Brudek (1999); Mollet et al. (2000); H. Mollet (pers. comm.).

***Isurus paucus* Guitart, 1966**

Fig. 75

Isurus paucus Guitart, 1966, *Poeyana*, Ser. A, (15): 3, figs. 1, 2A, 3A, 3C. Syntypes: 2 260 mm PCL adult female, 2 030 mm PCL adult male, and 1 955 mm PCL adult female, possibly in the Instituto de Biología or Instituto de Oceanología, Cuba, collected in the Caribbean near Cuba. No types known according to Eschmeyer (1998: CD-ROM).

Synonyms: ?*Lamiostoma belyaevi* Glikman, 1964: 105. Syntypes: a set of fossil tooth crowns from the bottom of the West-Central Pacific at 5 120 m depth, 13°00' N, 176°04' E. Syntypes doubtfully referred to the living species (see remarks below). *Isurus alatus* Garrick, 1967: 677. Holotype: US National Museum of Natural History, USNM-197427, 1 233 mm TL immature male, Indo-Pacific, no precise locality. Status confirmed by Howe and Springer (1993: 3).

Other Combinations: None.

FAO Names: En - Longfin mako; Fr - Petit taupe; Sp - Marrajo carite.

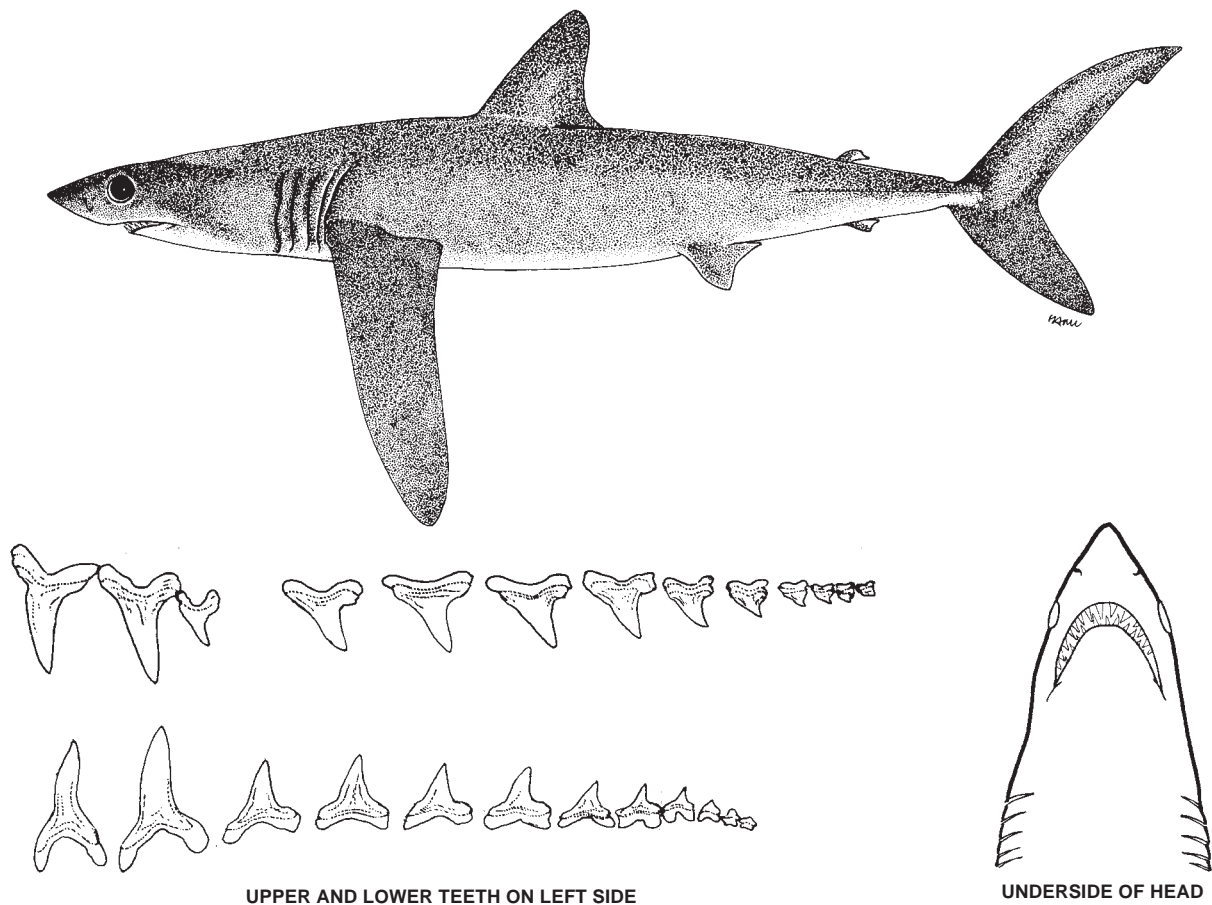


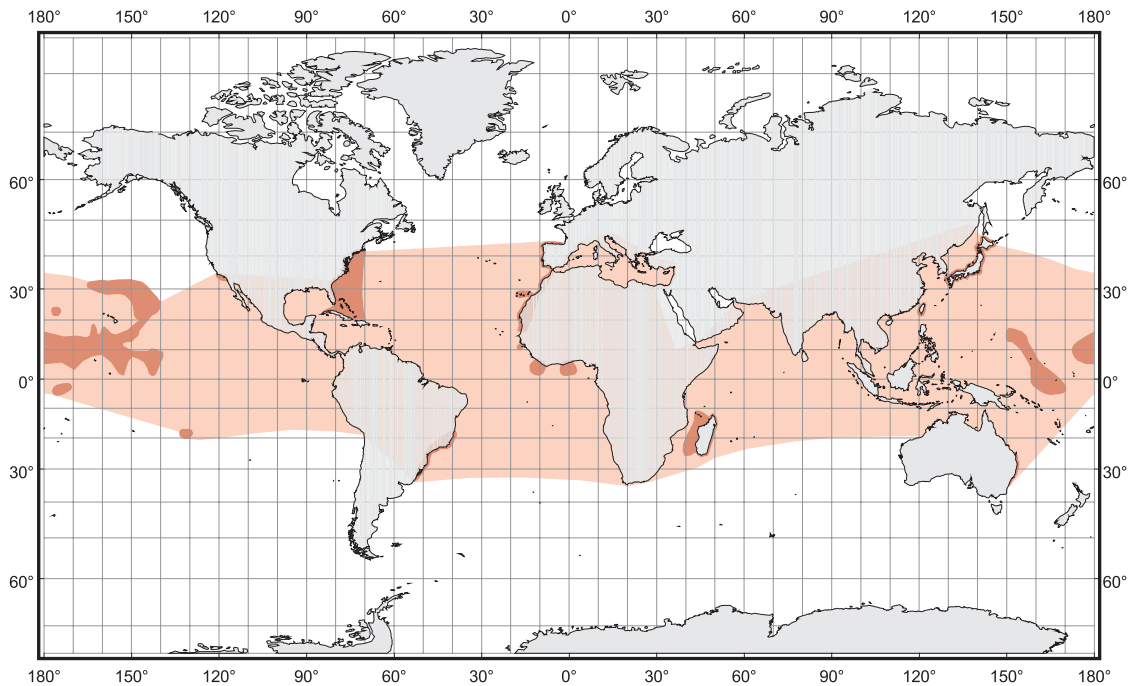
Fig. 75 *Isurus paucus*

Field Marks: Slender, spindle-shaped body, moderately long conical snout, large blade-like teeth without lateral cusplets or serrations, long gill slits, pectoral fins broad-tipped and as long or longer than head, large first dorsal fin with light free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, short secondary keels on caudal base, crescentic caudal fin, ventral surface of body dusky on underside of head.

Diagnostic Features: Snout broadly pointed. Eyes relatively large. Mouth parabolic in shape. Lower anterior teeth slightly protruding from jaws and in line with the laterals; anterior teeth with relatively broad, nearly straight cusps with unflexed tips; cusps of first upper anterior teeth with complete cutting edges; intermediate teeth with nearly straight or slightly hooked cusps. Body slender and elongated. Pectoral fins nearly straight and very broad-tipped, anterior margins about 23 to 31% of total length and equal to or greater than head length. Origin of first dorsal fin well behind the pectoral free rear tip; first dorsal-fin apex broadly rounded and hardly angular at all stages; first dorsal-fin height greater than base length at all stages

(smaller in term foetuses). Vertebral total count 195 to 197. **Colour:** dorsolateral coloration dark slaty blue or grey-black in life, underside white but with underside of snout and jaws dark in adults and large juveniles though not in young; dark colour of head entirely covering gill septa; dark colour of flanks extending ventrally onto abdomen in adults; pelvic fin completely dark, underside white with prominent dark margin; first dorsal fin as dark as back; anal fin dark except for white free rear tip and posterior margin.

Distribution: Oceanic and tropical, probably circumtropical but records sporadic and distribution sketchily known, probably often mistaken for the apparently far more common *Isurus oxyrinchus* or included with records for it. Western Atlantic: Florida, Gulf Stream off eastern USA, Cuba, southern Brazil. Eastern Atlantic: Spain, Portugal, probably Mediterranean, Morocco, Western Sahara, Canary Islands, Mauritania, Guinea-Bissau, Liberia, Ghana, ?Cape Verde Islands. Western Indian Ocean: ? South Africa, Madagascar. Western Pacific: Japan, Taiwan (Province of China), Australia (Queensland and northern New South Wales, also possibly off northern Australia). Central Pacific: Northeast of Micronesia, between Solomon and Nauru Islands, area south of Johnston and Hawaiian Islands, near Phoenix Island, and north of Hawaiian Islands. Eastern Pacific: United States (southern California).



Habitat: A little-known epipelagic, tropical and warm-temperate shark, apparently common in the western Atlantic and possibly in the Central Pacific, but rare elsewhere. Said to be deep-dwelling but bathymetric data was not available.

Biology: The biology of the longfin mako is poorly known. In the eastern Atlantic this species is possibly rare compared to *I. oxyrinchus*, and landings of longfin mako in Spanish fishing ports sampled by Moreno and Morón (1992) included only 51 specimens compared with 45 679 shortfin mako (0.1%). The often slimmer build and broad, long pectoral fins of this shark suggest that it is slower and less active than its better-known relative, the shortfin mako (J. Casey, pers. comm.). Its macroceanic morphology suggests similar slow cruising in the epipelagic zone as in the oceanic whitetip (*Carcharhinus longimanus*) and the blue shark (*Prionace glauca*) rather than the more active, scombroid-like swimming of *Isurus oxyrinchus*. The longfin mako is apparently endothermic, with countercurrent vascular heat exchangers for its body musculature, eyes, brain and viscera as in other lamnids (Carey, 1982), but the levels of temperature elevation it can achieve above ambient conditions have apparently not been measured.

The longfin mako is ovoviviparous, with uterine cannibalism; foetuses are larger than those of *I. oxyrinchus*, are full-term at 92 to 120 cm, and occur as a litter of 2 to 8 young. It may approach land to give birth.

Food of this shark is presumably schooling fish and pelagic cephalopods. Michael (1993) noted that one was found with a swordfish sword stuck in its abdomen, though it is not known if swordfish are an important item of this mako's diet as with the shortfin mako.

Size: Maximum reported 417 cm; size at birth between 97 and 120 cm; a male (Central Pacific) was adult at 245 cm; adult females (western North Atlantic) were 245 to 417 cm long.

Interest to Fisheries and Human Impact: Probably taken regularly in tropical pelagic longline fisheries for tuna and swordfish as bycatch (with some marketed in Tokyo). Historically it was often taken in the Cuban longline fishery for sharks off the north coast of Cuba and averaged about a sixth of the total weight of sharks caught there in 1971-1972. Whether it is still as common there at present is unknown. It is utilized fresh, frozen and dried-salted for human consumption but the meat is of lower quality than the shortfin mako and it is often finned and discarded at sea. In addition to longlines, the species is taken with hook-and-line and with anchored gill nets.

This species has not bitten people or boats and has not, to the writer's knowledge, been observed underwater or kept in captivity.

The conservation status of this species is uncertain but needs urgent investigation. It has probably been captured as bycatch in oceanic fisheries wherever it occurs and is a minor bycatch of fisheries targeting shortfin makos in the eastern Atlantic. No trends are obvious for the species as there are no catch statistics for it except off Cuba and the United States and these are not long-term. The United States reported small catches (2 to 12 t in 1987 to 1997) to FAO (FAO FishStat Plus database, 2000). Problems for the longfin mako include the rarity or uncommonness of this shark in most places (except perhaps the western Atlantic in the 1970s at least); limited knowledge of its biology; large maximum size; apparently lower fecundity than the shortfin mako; and occurrence as a limited but complementary bycatch of high-intensity oceanic fisheries targeting shortfin makos, other sharks, and pelagic scombroid fishes. These problems should arouse the concern of conservation and fisheries organizations, because of increased mortality of an uncommon or rare species due to finning and possibly capture trauma.

Local Names: Longfinned mako shark, Taupe longue aile (France); Dientuso prieto (Cuba); Marrajo negro (Azores); Bake-aozame (Japan).

Remarks: Garrick (1967), Compagno and Vergara (1978), and Compagno (1981a) thought that the species *Lamiostoma belyaevi* Glikman, 1964 might prove to be an earlier name for *I. paucus*, particularly because a stuffed *Isurus* illustrated in a photograph in Glikman (1964, figs 31-32) and labelled *L. belyaevi* appeared to be a longfin mako. This may be irrelevant even if correct. A translation of Glikman's description of *L. belyaevi* (pp. 105, 132-133) by Mrs L.J. Dempster with the aid of Dr V.V. Barsukov (noted in Compagno, 1984) revealed that Glikman deliberately refrained from naming the stuffed *Isurus* as holotype of *L. belyaevi* but instead picked one lot of teeth crowns dredged from the ocean bottom 5 120 m deep at RV VITYAZ station 5128, 13°00' N, 176°04' E in the Central Pacific southwest of the Hawaiian Islands (Glikman, 1964, pl. 31, figs 13, 14, 18, 19) for this role. Examination of Glikman's photos did not convince Compagno (1984) that the shark or sharks represented by these teeth were necessarily conspecific with *I. paucus* and were not conspecific with *I. oxyrinchus* or even some extinct *Isurus* species. Hence the substitution of the species name *belyaevi* for *paucus* was rejected, especially because the former is based on such poor material. It is uncertain if the stuffed specimen illustrated by Glikman is *I. paucus* also, because some of the characters ascribed to it (snout very long and acute, pectoral fins falcate, and pectoral fin length slightly less than the distance from snout tip to upper margin of first gill opening, vs. snout short and bluntly conical, pectoral fins not strongly falcate, and pectoral-fin length much longer than the distance from snout tip to upper margin of first gill opening in *I. paucus*) indicate that it might be a specimen of *I. oxyrinchus* instead.

Literature: Glikman (1964); Guitart (1966, 1968, 1975); Garrick (1967); Bass, D'Aubrey and Kistnasamy (1975a); Fourmanoir and Laboute (1978); Dodrill and Gilmore (1979); Gilmore (1983, 1993); Pinchuk (1983); Compagno (1984); Nakaya (1984); Quero (1984); Sadowsky, Amorim and Arfelli (1986); Killam and Parsons (1986); Joung, Wu and Chen (1989); Springer (1990); Moreno and Morón (1992); Michael (1993); Seret (1994); Stevens and Scott (1995); Stevens and Wayte (1998); Castro, Woodley and Brudek. (1999); Mollet et al. (2000); R. Bonfil (pers. comm.); H. Mollet (pers. comm.); D. Ebert (pers. comm. on California record).

Lamna Cuvier, 1816

Genus: Subgenus *Lamna* Cuvier, 1816 (Genus *Squalus* Linnaeus, 1758), *Reg. Anim.*, ed. 1, 2: 126.

Type Species: *Squalus cornubicus* Bloch and Schneider, 1801 by monotypy, equals *S. cornubicus* Gmelin, 1788: 1497, and a junior synonym of *S. nasus* Bonnaterre, 1788.

Number of Recognized Species: 2.

Synonyms: Genus *Lamia* Risso, 1827: 123. Type species, "*L. cornubicus* L" = *Squalus cornubicus* Gmelin, 1788 by monotypy. A junior homonym of *Lamia* Fabricius, 1775 in Coeloptera (Insecta). Genus *Selanonius* Fleming, 1828: 169. Type species, *Selanonius walkeri* Fleming, 1828 by monotypy (Eschmeyer, 1998: CD-ROM), junior synonym of *Squalus nasus* Bonnaterre, 1788. Genus *Exoles* Gistel, 1848: ix. Replacement name for *Lamia* Risso, 1827, and hence taking the same type species, *Squalus cornubicus* Gmelin, 1788.

Diagnostic Features: Snout very bluntly conical to acutely conical. Eyes large, 1.6 to 2.8% of total length. Nostrils situated medial to horizontal head rim in ventral view. Mouth width 1.4 to 2.3 times its length. Anterior teeth not enlarged; anterior and intermediate teeth not compressed but upper lateral teeth somewhat compressed, teeth not forming a continuous cutting edge; intermediate teeth small and about half height of adjacent anteriors, intermediate teeth with normal cusps directed posterodistally or vertically; second lower anterior teeth moderately enlarged and taller than second upper anterior tooth. Total tooth count 49 to 60; roots of anterior teeth deeply arched, with narrow short lobes; lateral cusplets present on teeth at all stages except newborn sharks; teeth smooth-edged; cusps of anterior teeth not strongly flexed. Body very stout. First dorsal-fin origin over or just behind the pectoral-fin insertions. Anal-fin origin about under second dorsal-fin origin.

Secondary caudal keels present and strong. Total vertebral count 150 to 173. Cranium with rostral cartilages more or less expanded and hypercalcified. Intestinal valve of ring type with count 38 to 41. Length of adults 1.5 to at least 3.1 m. No black axillary spot at pectoral-fin insertions; pectoral-fin tips not abruptly black on their ventral surfaces but sometimes with dark margins.

Local Names: Porbeagles, Mackerel sharks, Salmon sharks.

Remarks: As with the makos (*Isurus*) there has been confusion in the past as to the number of valid species of mackerel sharks (*Lamna*). Material examined by the writer and the accounts of Bigelow and Schroeder (1948), Nakaya (1971), Stevens, Dunning and Machira (1983), and Compagno (1984, 1990b, c), suggest that there are only two species, *L. ditropis* and *L. nasus*, with *L. philippi* from Chile and *L. whitleyi* from New Zealand and Australia most probably being synonyms of *L. nasus*. *Lamna ditropis* was compared in detail to *L. nasus* by Nakaya (1971) and the two are readily separable in external morphology and coloration. Nakaya (1971) also noted differences between the dentitions of the two species, with *L. ditropis* having more oblique-cusped upper first lateral teeth. This needs to be confirmed by a comprehensive study of the dentition of *Lamna* from different areas, as some Southern Hemisphere *L. nasus* have upper first lateral teeth about as oblique-cusped as *L. ditropis*. Compagno (1984 and this volume) noted differences in the colour of the first dorsal rear tip and the flanks between the two species (see below), while Compagno (1990b) described and illustrated striking differences in their cranial morphology.

Pillai and Honma (1978) reported *L. ditropis* from the southern Indian Ocean without data confirming their identification. Compagno (1984) suggested that the species in question was *L. nasus*, and had examined a specimen from the southern Indian Ocean (open sea between Kerguelen and St. Paul Islands, ANTON BRUUN Cruise 5, Sta. 309, 960 mm immature female, 42°23'S, 74°56'E, in collections of the California Academy of Sciences). There are also records from near Kerguelen Island (Duhamel and Ozouf-Costaz, 1982). Records of *L. nasus* from sub-Antarctic seas were summarized by Duhamel and Compagno (1985) and Compagno (1990c).

A few specimens of large *L. nasus* (1.6 to 2.1 m long) have subsequently been examined by the writer from the Southern Hemisphere, off the Western Cape, South Africa, off Marion Island, and between the Prince Edward and Crozet Islands. These specimens agreed with *L. nasus* from the North Atlantic in having more elongated snouts, moderately hypercalcified rostra, no light flank markings, and a light first dorsal rear tip, but agree with *L. ditropis* in having dusky or blackish faces with dark coloration on the underside of the head and a spotted, dusky abdomen. Stevens, Dunning and Machira (1983) illustrated a similar colour pattern in a porbeagle from the Tasman Sea. These 'black-faced' porbeagles resemble the 'marrajo criollo' makos from the Azores (*Isurus oxyrinchus*), which have a colour pattern similar to *I. paucus* (see above). It may be that black-faced *Lamna nasus* have been misidentified as *L. ditropis* in the Southern Hemisphere, but it is not known if large southern *L. nasus* are exclusively dark-faced, or if this dark form is geographically restricted within the vast southern range of the porbeagle. Apparently it is necessary to conduct comparative studies of porbeagles from different areas, including molecular research, to sort out these problems. One aspect of this is to determine if separate populations or subpopulations exist for *L. nasus*, within contiguous ranges and north or south of the Equator.

It is an interesting irony of nomenclature that the names *Lamna* Cuvier, 1816 and its synonym *Lamia* Risso, 1827, based on the classical *Lamia* (*Carcharodon carcharias*) and connoting a frightful anthropophagous monster, should be used for the rather less assertive porbeagles and salmon sharks.

Key to Species:

1a. Snout relatively long, distance from snout tip to eye 50% or more of the distance from eye to first gill opening (Fig. 76); free rear tip of first dorsal fin abruptly white; sides above pectoral-fin bases dark, without an extension of the white abdominal area *Lamna nasus*

1b. Snout shorter, distance from snout tip to eye 40% or less of the distance from eye to first gill opening (Fig. 77); free rear tip of first dorsal fin dark; sides above pectoral-fin bases marked with a white patch extending forward from the abdominal area *Lamna ditropis*

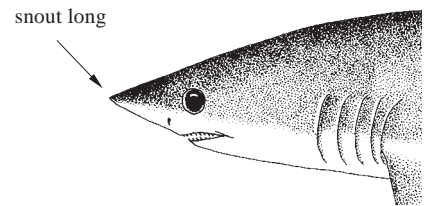


Fig. 76 *Lamna nasus*

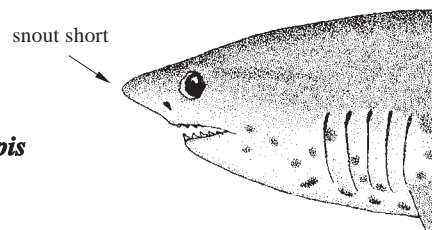


Fig. 77 *Lamna ditropis*

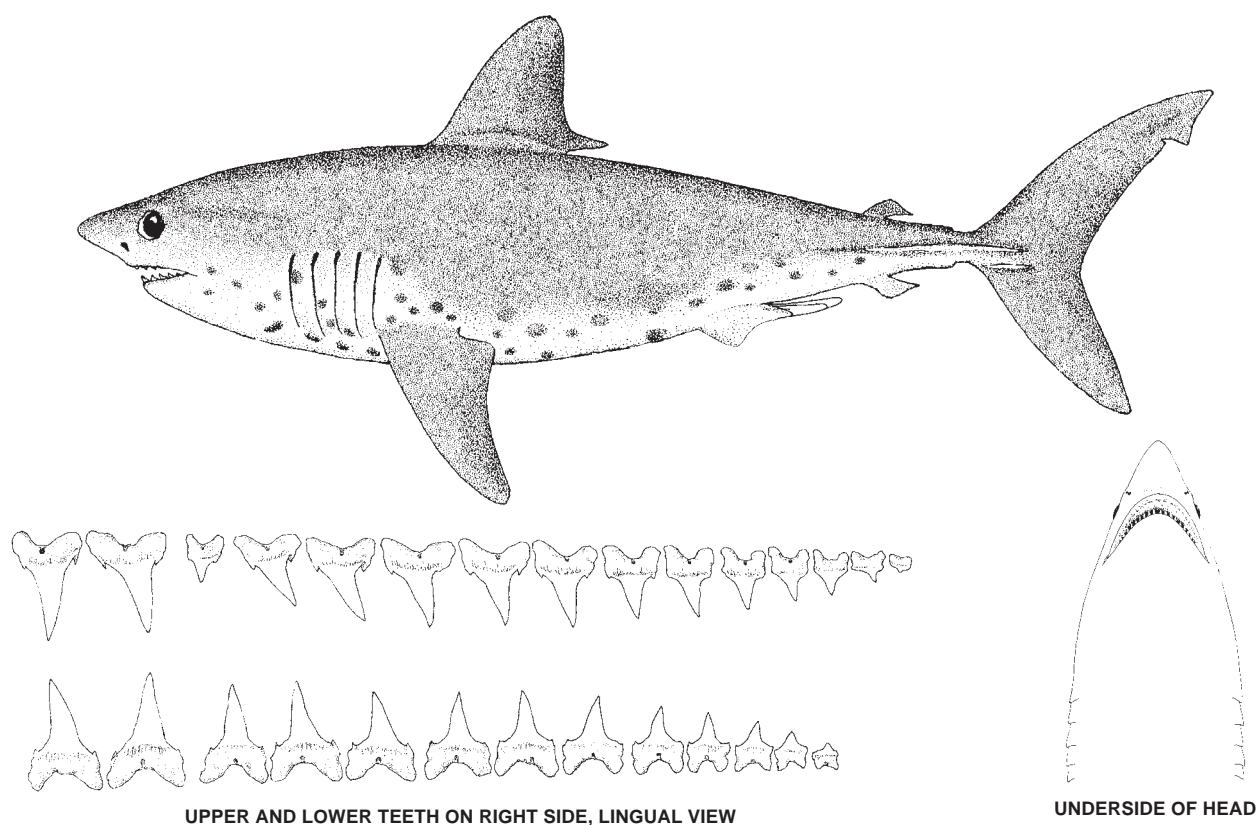
Lamna ditropis* Hubbs and Follett, 1947*Fig. 78**

Lamna ditropis Hubbs and Follett, 1947, *Copeia*, 1947(3): 194. Holotype, Museum of Comparative Zoology, Harvard University, MCZ-36471, adult male (partial specimen, size uncertain); type locality, La Jolla, California, 92 to 107 m off the La Jolla Beach Club in shallow water.

Synonyms: None.

Other Combinations: None.

FAO Names: **En** - Salmon shark; **Fr** - Requin-taupo saumon; **Sp** - Marrajo salmón.



UPPER AND LOWER TEETH ON RIGHT SIDE, LINGUAL VIEW

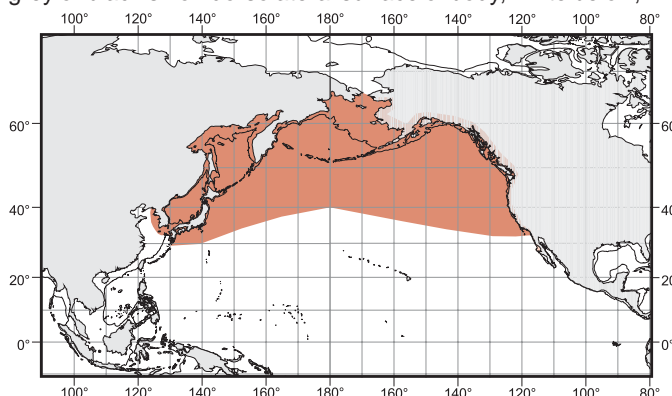
UNDERSIDE OF HEAD

Fig. 78 *Lamna ditropis*

Field Marks: Heavy spindle-shaped body, short conical snout, moderately large blade-like teeth with lateral cusplets, long gill slits, large first dorsal fin with dark free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, short secondary keels on caudal base, crescentic caudal fin, underside of preoral snout dark, often dusky blotches on ventral surface of body and white patches over pectoral bases.

Diagnostic Features: Snout short and bluntly pointed, with preoral length 4.5 to 7.6% of total length (adults 4.5 to 5.0%), space from eye to first gill slit 1.3 to 1.9 times preorbital length. First upper lateral teeth with oblique cusps. Total vertebral count 170, precaudal vertebral count 103. Cranial rostrum expanded as a huge hypercalcified knob which engulfs most of the rostral cartilages except bases in adults. **Colour:** dark grey or blackish on dorsolateral surface of body, white below, with white abdominal colour extending anteriorly over pectoral bases as a broad wedge-shaped band; first dorsal fin without a white free rear tip; ventral surface of head dusky and abdomen with dusky blotches in adults but not in young.

Distribution: Coastal and oceanic. North Pacific: Japan (including Sea of Japan), North Korea, South Korea, and the Pacific coast of Russia (including Sea of Okhotsk) to Bering Sea and the eastern Pacific coast of the USA and Canada (Alaska south to British Columbia, Washington, Oregon, and southern California) and probably Mexico (northern Baja California).



Habitat: A common coastal-littoral, offshore and epipelagic shark with a preference for boreal to cool temperate waters, found at depths from the surface to below 152 m. One was photographed at 255 m near the bottom in Monterey Canyon using an underwater camera, while a diver in a submersible saw one at 224 m off Alaska. Salmon sharks are common in continental offshore waters but range inshore to just off beaches; they also are abundant far from land in the North Pacific Ocean basin, along with their pelagic fish prey.

Biology: Salmon sharks are common and are often encountered by oceanic and coastal fisheries but are sketchily known biologically. Behaviour and sociobiology are little-known. They occur singly and in schools or feeding aggregations of several individuals and in some areas are seen at or near the surface. Water temperatures where salmon sharks were caught ranged from 2.5° to 24°C. They are swift-swimming sharks, maintaining a body temperature well above ambient water temperature. Recent studies suggest that salmon sharks may have the highest body temperature of any shark. Body temperature elevations of 8° to 11°C above that of the surrounding water have been reported for smaller specimens, while elevations up to 13.6°C have been recorded in larger ones (Smith and Rhodes 1983; Goldman and Human, *in press*). Salmon sharks are migratory, with segregation by size and sex, and with larger sharks ranging more northerly than young. In the western North Pacific large sharks migrate from Japanese waters (where they breed) in the wintertime, move north to the Sea of Okhotsk and the western Bering Sea when the water warms, and return to Japan in the autumn or early winter (for a one-way distance of 3 220 km). In the eastern Pacific females apparently migrate south to pup in the spring off Oregon and California, USA, as suggested by commercial fish catch records, washed up (beached) young of the year and anecdotal information. A strong sexual segregation appears to exist across the Pacific Ocean basin, with males dominating the western North Pacific and females dominating the eastern North Pacific (K.J. Goldman and J. A. Musick, pers. comm.).

This shark reproduces by aplacental viviparity, with uterine cannibalism (oophagy); litter size is 2 to 5 young. Length of gestation period might be nine months; length of entire reproductive cycle unknown. Breeding occurs in late summer and into autumn, and females bear young in spring. Breeding and nursery areas may be localized in the offshore western North Pacific between about 156° and 180°E in the open ocean, off the southern Kuril region, and in the Sea of Okhotsk, where young below 60 cm (possibly newborn) occur and juveniles up to 110 to 120 cm long also are found. Age 0 and 1 salmon sharks occur off California, USA, suggesting that a breeding and nursery ground might exist in the eastern North Pacific (K.J. Goldman and J.A. Musick, pers. comm.). Males may mature at 5 years and about 182 cm TL, and females at 8 to 10 years and about 221 cm TL (Tanaka, 1980). Females in the eastern North Pacific live to at least 20 years of age, males to at least 27 years; preliminary indications are that female salmon sharks mature at an earlier age and are heavier in the eastern North Pacific relative to those living in the western North Pacific (K.J. Goldman and J.A. Musick, pers. comm.).

Salmon sharks are opportunistic feeders and eat a variety of pelagic and demersal bony fishes including Pacific salmon and steelhead trout (Salmonidae), herring and sardines (Clupeidae), pollock, Alaska cod and tomcod (Gadidae), lancetfishes (Alepisauridae), daggerteeth (Anopteridae), sauries (Scombrosocidae), lanternfishes (Myctophidae), pomfrets (Stromateidae), mackerel (*Scomber*, Scombridae), lumpfishes (Cyclopteridae), sculpins (Cottidae), possibly rockfish (*Sebastes*, Scorpaenidae), possibly sablefish (Anoplopomatidae), and Atka mackerel (*Pleurogrammus*, Hexagrammidae). Salmon sharks also feed on spiny dogfish (*Squalus acanthias*, Squalidae) and several species of pelagic squid, and have been attracted to bycatch offal dumped by shrimp trawlers.

The salmon shark is generally considered to be one of the principal predators of Pacific salmon (*Oncorhynchus*) apart from humans and is depicted as voraciously feeding on salmon. This is apparently the case around the Aleutians and the Gulf of Alaska, where peaks in abundance in salmon sharks follow maximum catches of salmon and the distribution and migrations of the two appear to be strongly correlated as predator and prey. Salmon sharks caught by Japanese pelagic salmon gill netters in this area have had salmon in their stomachs and little else. However Blagoderov (1994) suggested that this relationship is highly unlikely, and cited major differences in areal distribution between salmon and salmon sharks in the western North Pacific, with most salmon sharks concentrated south of the main migration path of salmon and very few within it. In the western North Pacific these sharks congregate in areas with breeding aggregations of herring and sardines and may be selecting these fishes rather than salmon.

Size: Maximum total length about 305 cm; anecdotal accounts mention sizes of 3.7 to 4.3 m TL but cannot be confirmed, and confusion with the larger white shark is possible and has happened. Size at birth between 40 and 50 cm and 85 cm TL, with the largest fetuses at least 70 cm long and the smallest free-ranging young between 40 and 50 cm. Males maturing at about 182 cm TL (5 years) and females at about 221 cm TL (8 to 10 years); both sexes adult over about 210 to 220 cm TL.

Interest to Fisheries and Human Impact: This species has been fished in the North Pacific in the past by Japanese coastal and oceanic longliners. Salmon sharks are commonly caught by Japanese, United States and Canadian offshore salmon gill netters as bycatch but are generally discarded (except for fins). They are also caught in salmon seines, by salmon trollers towing hooks, and possibly by bottom trawlers off Alaska; Russian research vessels have regularly caught them in pelagic trawls in the western North Pacific. They are occasionally trammel-netted by halibut fishermen off California and have showed up in numbers as bycatch in gill nets set for swordfish and threshers off California but have usually not been marketed there. Sports anglers in Alaska and Canada catch salmon sharks using rod and reel much like porbeagle anglers in the North Atlantic.

Salmon sharks are generally considered a nuisance for the damage they do to salmon nets and other fishing gear. A commercial fishery was initiated off Alaska but this did not succeed. FAO catch statistics for recent salmon shark landings were not available (FAO FishStat Plus database, 2000) but available data (Makihara, 1980) indicates that Japanese fishers landed 100 to 41 000 t during 1952-1978 (with one very high catch year, 41 000 t in 1954, but mostly below 10 000 t and

averaging about 6 900 t). Bycatch of salmon sharks in the flying squid and large-mesh driftnet fisheries of the North Pacific in 1990, just before high-seas driftnets were internationally banned was estimated to be about 5 400 t and 71 t respectively.

The flesh of the salmon shark is used fresh for human consumption in Japan, where it is processed into various fish products, and to a lesser extent in Alaska and California, United States, where it is seldom marketed and has in the past (California) been occasionally sold as swordfish. Presumably its flesh is less desirable than that of the shortfin mako. Its oil, skin (for leather), and fins (for shark fin soup) are utilized also. The heart of the salmon shark is highly appreciated in a local sashimi dish in the northern fishing port of Kesenuma, where most of the landings of salmon sharks occur in Japan (R. Bonfil, pers. comm.).

The salmon shark has been regarded as potentially injurious to people because of its large size and relationship to other species that occasionally bite people, but has never been positively identified in shark-bite incidents. There are a few unsubstantiated incidents reported for the species, but possibly by confusion with the white shark. Salmon sharks are reported as occasionally circling, approaching and bumping fishing vessels and sports boats off southeastern Alaska (Paust and Smith, 1985), but their identity needs to be confirmed to eliminate white sharks as being involved in such activities. Divers have seen and photographed schools of adult salmon sharks underwater, with no agonistic overtures on the part of the sharks (R. Lea, pers. comm.). An ecotouristic dive site at Roca Partida, Socorro Islands, Mexico has reported "*Lamna nasus*", but it is not known if salmon sharks or other lamnids are being viewed there. The salmon shark is not currently held in captivity in large oceanaria, nor does the writer know of any attempts to keep salmon sharks in the past.

Recently (1997) there has been numerous strandings of small salmon sharks, ca. 1 m long, off north-central and southern California (R. Lea, pers. comm.), which was of rare occurrence in the 1970s and 1980s. Whether this has to do with human-induced environmental problems such as pollution or unusual water conditions is not known.

The conservation status of this species is of concern because it is heavily fished as largely discarded but complementary bycatch (with finning) in major pelagic fisheries in the North Pacific. Unlike *Lamna nasus*, this species has limited fisheries statistics (with no country reporting catch statistics to FAO in 1997) and no regulation of the largely pelagic fishery in international waters, so that trends in abundance are unknown. It also has a negative image as an abundant and low-value pest that avidly eats or damages valuable salmon and wrecks gear, which encourages fishers to kill it and add to mortality from finning and capture trauma. Knowledge of its biology is limited despite its abundance, which invites neglect, but its fecundity is very low and probably cannot sustain current fishing pressure for extended periods.

The Alaska Board of Fisheries has closed all commercial shark fishing and has heavily regulated the sport fishery in Alaska state waters since 1997 in view of the lack of biological information at a time when there was a small amount of commercial fishing and a large increased interest in sport fishing for salmon sharks (Goldman and Human, *in press*). The North Pacific Fishery Management Council is currently considering closure of commercial fishing for sharks in Federal waters as no Federal Management plan exists specifically for sharks in the Gulf of Alaska and the Aleutian Islands. Currently, salmon sharks are allowed as bycatch, and are included in the commercial bycatch TAC (Total Allowable Catch) for Alaska Federal waters. Sport fishing regulations in Alaska include EEZ waters and are two sharks per person per year, one in possession at any time (one per day).

Local Names: Nezumizame, Mokazame, Radukazame, Sakezame, Japanese mackerel shark (Japan); Salmon shark, Porbeagle, Mackerel shark (English).

Literature: Hubbs and Follett (1947); Bigelow and Schroeder (1948); Roedel and Ripley (1950); Strasburg (1958); Lindberg and Legeza (1959); Sano (1962); Farquhar (1963); Larkins (1964); Kato, Springer and Wagner (1967); Nakaya (1971, 1984); Miller and Lea (1972); Hart (1973); Makihara (1980); Tanaka (1980); Urquhart (1981); Smith and Rhodes (1983); Compagno (1984); Paust and Smith (1986); Paust (1987); Brodeur (1988); Applegate et al. (1989); Hanan, Holts and Coan (1993); Blagoderov (1994); Bonfil (1994); Nagasawa (1998); Castro, Woodley and Brudek (1999); Goldman and Human, (*in press*); K.G. Goldman and J. A. Musick (pers. comm.); S. Kato (pers. comm.); R. Lea (pers. comm.); T. Neal (pers. comm.); H. Mollet, (pers. comm.).

***Lamna nasus* (Bonnaterre, 1788)**

Fig. 79

Squalus nasus Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris*: 10, pl. 85, fig. 350. Holotype unknown, type locality probably Cornwall, England (Eschmeyer, 1998: *Cat. Fish.*: CD-ROM).

Synonyms: *Squalus glaucus* Gunnerus, 1768: 1, pl. 1. Type locality, Norway. A junior homonym of *S. glaucus* Linnaeus, 1758 (= *Prionace glauca*). *Squalus cornubicus* Gmelin, 1788: 1497. No types known according to Eschmeyer (1998: CD-ROM). Type locality: Cornwall, England. *Squalus pennanti* Walbaum, 1792: 517. Type locality: Atlantic. No types according to Eschmeyer (1998: CD-ROM). *Squalus monensis* Shaw, 1804: 350. Based on the 'Beaumaris Shark' of

Pennant, a 2.33 m (7 ft) shark observed and reported by the Rev. Hugh Davies, of Beaumaris, Isle of Anglesey, Wales. No types known according to Eschmeyer (1998: CD-ROM). Shaw thought that his *S. monensis* might be the same as *Squalus cornubicus* Gmelin, 1788 (= *Lamna nasus*), and that differences between them might be attributable to sexual dimorphism. *Squalus cornubiensis* Pennant, 1812: 152. Type locality: Cornwall. Variant spelling of *S. cornubicus* Gmelin, 1788 according to Eschmeyer (1998: CD-ROM). *Squalus selanonus* Leach, 1818: 64, pl. 2, fig. 2. Holotype: University of Edinburgh, ca. 2.6 m TL adult male, Lochfyne, Scotland (also, Eschmeyer, 1998: CD-ROM). *Selanonius walkeri* Fleming, 1828: 169. Argyll, Scotland. Based on *Squalus selanonus* of Walker, 1769 (manuscript name) according to Eschmeyer (1998: CD-ROM). *Lamna punctata* Storer, 1839: 185, pl. 3, fig. 2. Also Storer, 1839: 534, pl. 8. New combination for and misinterpretation of *Squalus punctatus* Mitchill, 1815 (= *Carcharhinus isodon*), itself a junior homonym of *S. punctatus* Bloch and Schneider, 1801 (= *Ginglymostoma cirratum*). Type locality: Massachusetts Bay; cf. Eschmeyer (1998: CD-ROM). *Lamna pennanti* Desvaux, 1851: 23. Possibly new combination based on *Squalus pennanti* Walbaum, 1792. *Oxyrhina daekayi* Gill, 1862a: 60. New name for *Lamna punctata* Storer, 1839 according to Eschmeyer (1998: CD-ROM). *Isuropsis dekayi* Gill, 1873: 813 (emended spelling of specific name). *Lamna philippi* Perez Canto, 1886: 1. Type locality, Chile. Types? *Lamna whiteleyi* Phillipps, 1935: 239, fig. 3. Syntypes: Whereabouts unknown according to Eschmeyer (1998: CD-ROM). Type Locality, Island Bay, Wellington, New Zealand.

Other Combinations: *Lamna cornubica* (Gmelin, 1788).

FAO Names: En - Porbeagle; Fr - Requin-taube commun; Sp - Marrajo sardinero.

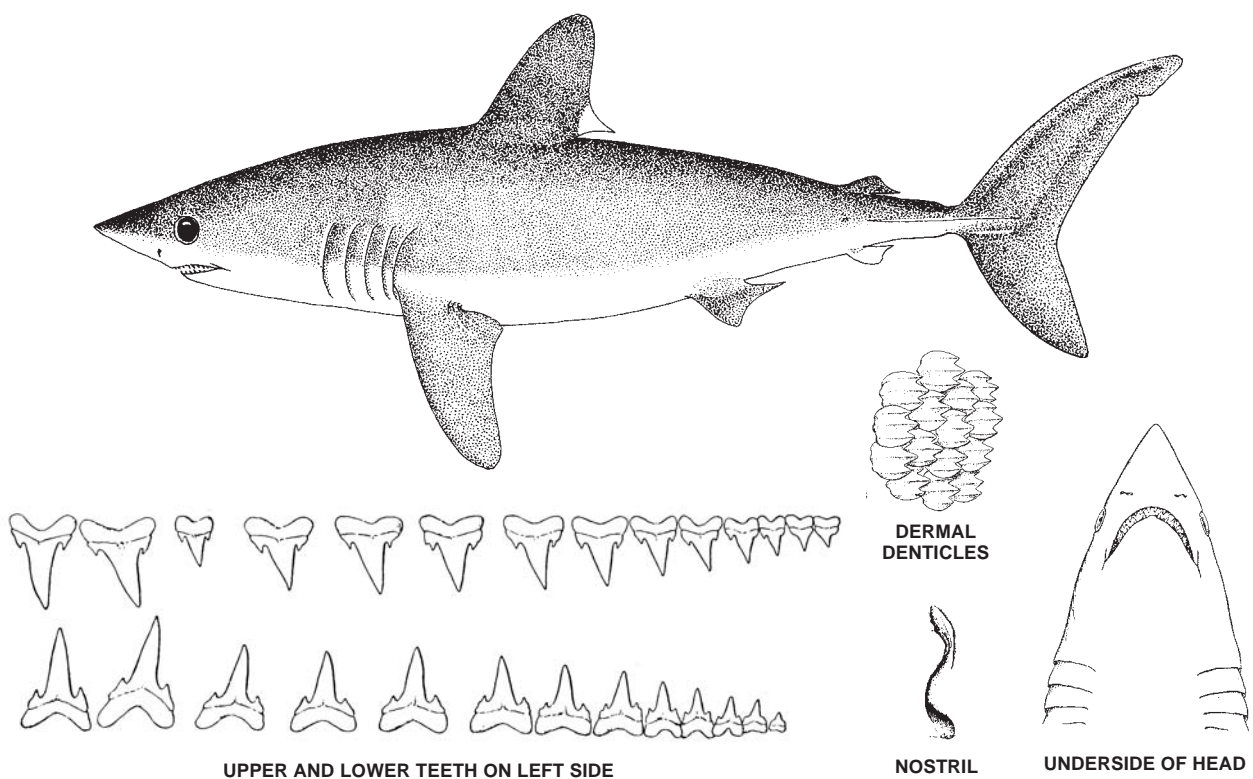
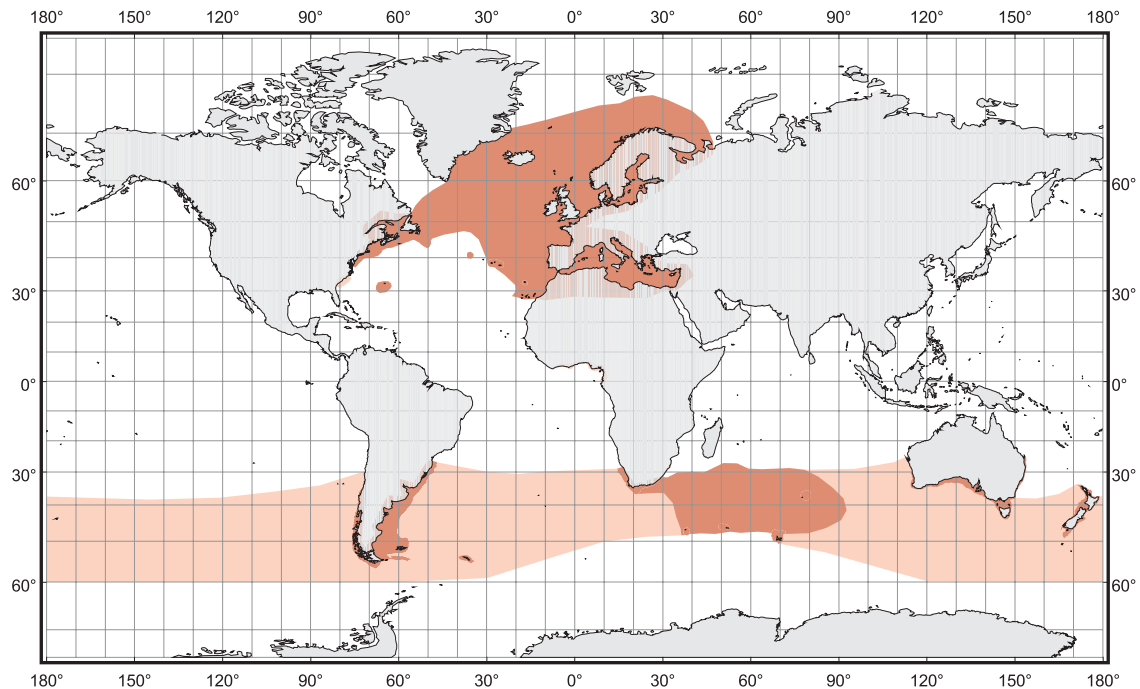


Fig. 79 *Lamna nasus*

Field Marks: Heavy spindle-shaped body, moderately long conical snout, moderately large blade-like teeth with lateral cusplets, long gill slits, large first dorsal fin with abruptly white free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, short secondary keels on caudal base, crescentic caudal fin, ventral surface of body white and not extending over pectoral bases as white patches.

Diagnostic Features: Snout long and sharply pointed, with preoral length 5.9 to 9.0% of total length (adults 5.9 to 7.3%) and space from eye to first gill slit 1.7 to 2.5 times preorbital length. First upper lateral teeth with nearly straight cusps. Total vertebral count 150 to 162, precaudal vertebral count 85 to 91. Cranial rostrum with enlarged but discrete hypercalcified rostral cartilages, not forming a massive knob. **Colour:** grey or bluish grey to blackish above, white below, with white abdominal colour terminating at rear end of pectoral bases; first dorsal fin with an abruptly white or greyish white free rear tip; ventral surface of head white and abdomen without dusky blotches in adults of typical Northern Hemisphere porbeagles, but underside of head dark and abdomen blotched in some Southern Hemisphere adults.

Distribution: Coastal and oceanic, amphitemperate, with centres of distribution in the North Atlantic and in a circumglobal band of temperate water of the southern Atlantic, southern Indian Ocean, southern Pacific and Antarctic Ocean. Western Atlantic: Greenland, Canada (Newfoundland Banks, Gulf of St. Lawrence and Nova Scotia), United States (Maine, Massachusetts, Rhode Island, rarely New York, New Jersey and possibly South Carolina), and Bermuda; southern Brazil and Uruguay to southern Argentina. Eastern Atlantic: Iceland and western Barents Sea to Baltic and North Seas, English Channel, Straits of Gibraltar, and Mediterranean Sea, including Russia, Norway, Sweden, Denmark, Germany, Holland, Scotland, England, Wales, Ireland, the Orkney Islands, France, Portugal, Spain, and Gibraltar; entire coast of Mediterranean Sea but not in Black Sea; Morocco, Madeira, Azores, possibly the Gulf of Guinea, and off South Africa (Western Cape). Indo-West Pacific: South-central Indian Ocean from South Africa (Eastern Cape and possibly KwaZulu-Natal) eastward to between Prince Edward and Crozet Islands, between Kerguelen and St. Paul Islands, and the southern coast of Australia (southern Western Australia and South Australia, Victoria, Tasmania, New South Wales and southern Queensland), New Zealand (including Stewart Island). Subantarctic waters off South Georgia, Marion, Prince and Kerguelen Islands. Eastern South Pacific: southern Chile south to Cape Horn.



Habitat: A common littoral and epipelagic shark, most abundant on the continental offshore fishing banks but also found far from land in ocean basins and occasionally close inshore. It was recently caught at the mouth of a brackish estuary in Argentina but does not penetrate fresh water. This shark usually occurs in cold water, less than 18°C and down to 1°C, but was once recorded in water 23°C. It does not occur in equatorial seas as far as is known. The porbeagle ranges in depth from the surface and inshore waters less than 1 m deep down to at least 700 m.

Biology: The porbeagle is described as very active and strong-swimming in pursuit of prey or when viewed by divers underwater but does not engage in spectacular leaps like the shortfin mako (*Isurus oxyrinchus*) when hooked. Behaviour and sociobiology are poorly known, and most data available has a fisheries context.

The porbeagle is found at the surface down to the bottom, singly and in schools and feeding aggregations. Porbeagles may come inshore and to the surface in summer, but will winter offshore and beneath the surface. Fisheries catches in Europe indicate that the porbeagle has populational segregation by size (age) and sex.

Porbeagles of the western North Atlantic seem to constitute a single stock that undertakes extensive migrations between southern Newfoundland (Canada) in summer to at least Massachusetts (USA) in the winter. Longterm tagging data suggest there is no mixing between this population and that of the eastern North Atlantic.

Porbeagles breed on both sides of the North Atlantic, off the Atlantic coast of Europe and the British Isles, where females have embryos during most of the year except July through September, and off North America from Massachusetts to Maine, where females can be found with young at all times of year. Young are apparently born in the spring off Europe, in either winter-spring or late summer off North America, and probably from April to September (peak June-July [winter]) in the Southern Hemisphere. Mating in European waters occurs in late summer, and breeding there probably occurs every year. An extended mating period seems to exist for Southern Hemisphere populations around Australia and New Zealand.

The porbeagle is ovoviviparous and a uterine cannibal (oophagous), with litters of 1 to 5 young but the majority of litters are of four young. The foetuses grow enormously by feeding on fertilized eggs, and develop grotesquely expanded abdomens and branchial regions. Small porbeagle embryos possess fang-like functional teeth to tear open egg capsules and release the contained ova; the fangs are shed at 34 to 38 cm FL (Francis and Stevens, 2000). The gestation period has been estimated at about 8 or 9 months for North Atlantic and South Pacific populations. The length of the entire reproductive cycle is not known. Pupping and nursery areas may be in continental waters, but are little-documented. In the western North Atlantic, mating is believed to take place off southern Newfoundland.

Tag-recapture data and tetracycline injected sharks at liberty have been used to validate age determinations for porbeagles in the western North Atlantic up to age 10, but longevity could be as much as 30 to 45 years (Natanson, Mello and Campana, in press). Preliminary studies in this region suggest that males mature at about 175 cm FL (~ Age 7) and females at around 212 cm FL (~ Age 14) (Campana et al. 1999). Newborn porbeagles grow an estimated 15 to 20 cm per year (FL) during the first three years of life in the South Pacific. Prior to the intensive fishery that greatly reduced the numbers of this shark in European waters, the annual mortality for the species was an estimated 18% under low human exploitation and probably minimal predation pressure from other species. Recent research in Atlantic Canada indicates that the instantaneous natural mortality rate of porbeagles is about 0.1.

This shark is a proverbially voracious feeder on small to moderate-sized pelagic schooling fishes, including mackerel (*Scomber*, Scombridae) and pilchards and herring (Clupeidae), but also feeds on demersal fishes including various gadoids such as cod, haddock, cusk, whiting (Gadidae) and hake (Merlucciidae), icefishes (Channichthyidae), and John dories (Zeidae). Chondrichthyan prey include dogfish (*Squalus acanthias*, Squalidae) and tope sharks (*Galeorhinus galeus*, Triakidae). Cephalopod prey includes squid and cuttlefish. It will scavenge hooked fishes including cod from longlines.

Predators of the porbeagle are little known (apart from humans). A small specimen from Argentina had tooth marks suggestive of a carcharhinid, perhaps *Carcharhinus brachyurus*, but it is uncertain if these were from a predation bout or agonistic encounter. The white shark and orca are obvious candidates for porbeagle predators, but records of predation by either on porbeagles are not known to the author.

Size: Maximum total length 300+ cm, possibly to 370 cm but most smaller; size at birth between 60 and 75 cm TL (69 to 80 cm TL in South Pacific); males maturing at about 150 to 200 cm TL (196 cm TL in the western North Atlantic) and reaching at least 262 cm; females maturing at about 200 to 250 cm TL (with one reported at only 152 cm), to possibly 370 cm (with most less than 300 cm). Females mature at about 237 cm TL in the western North Atlantic and at about 185 to 202 cm TL in the South Pacific. There are several morphometric and L-W equations for porbeagles:

Kohler, Casey and Turner (1995): $W(\text{kg}) = 1.4823 \times 10^{-5} \times \text{FL}(\text{cm})^{2.9641}$ (n = 15, western North Atlantic)
 where: $\text{FL}(\text{cm}) = 1.7939 + 0.8971 \times \text{TL}(\text{cm})$ (n = 13)

Campana et al. (1999): $W(\text{kg}) = 0.5 \times 10^{-4} \times \text{FL}(\text{cm})^{2.713}$ (n = 286, western North Atlantic)
 where: $\text{FL}(\text{cm}) = 0.99 + 0.885 \times \text{TL}(\text{cm})$ (n = 361)

Campana et al. (1999): $\text{FL}(\text{cm}) = 4.96 \times \text{IDL}(\text{cm})^{0.901}$ (n = 358)

Campana et al. (1999): $\text{FL}(\text{cm}) = 1.7 + 1.12 \text{PCL}(\text{cm})$ (n = 360)

Francis and Stevens (2000): $\text{PCL}(\text{cm}) = -1.366 + 0.907 \text{FL}(\text{cm})$ (n = 866, FL = 61 to 223 cm, New Zealand)

Francis and Stevens (2000): $\text{TL}(\text{cm}) = 4.165 + 1.098 \text{FL}(\text{cm})$ (n = 173, FL = 63 to 180 cm, Australia)

Interest to Fisheries and Human Impact: This species has been heavily fished commercially and utilized for human consumption in the temperate North Atlantic and the Mediterranean, but is also caught as bycatch in the Southern Hemisphere where it is the second most common shark as bycatch of the New Zealand longline fishery. World catches of porbeagles have been reported to FAO by a number of countries, including Canada, Denmark, the Channel and Faeroe Islands, France, Germany, Iceland, Malta, New Zealand, Norway, Portugal, Spain, Saint Pierre and Miquelon Islands, Sweden, the United Kingdom, and the United States. World catches per annum ranged from 346 to 9 674 t from 1951 through 1997 (mean 2 102 t) with 1 736 t reported in 1997 (FAO FishStat Plus database, 2000). The major peak was in the middle 1960s and was followed by a declining trend with peaks and declines in the 1970s and 1980s to a level between 1 000 and 2 500 t in the 1990s.

Stocks in the North Atlantic have shown signs of serious overfishing in the form of greatly declining catches. Scandinavian fishers have caught porbeagles since the early nineteenth century, but only intensively during the twentieth century. Norway and to a lesser extent Denmark have been the principle fishers of porbeagles in the North Atlantic. Norwegian catches have varied wildly during the twentieth century, increasing from 279 t in 1926 to 3 884 t in 1933, then declining steadily to low levels during the second world war. Intensive fishing resumed in 1945 and peaked at 2 824 t in 1947, but then steadily declined to 207 t in 1970 and only 25 t in 1994. Porbeagles became scarce off Europe and the Norwegian fishery spread to the western North Atlantic, but eventually the fishery shifted to other species such as shortfin mako and swordfish. Small regulated catches exist at present for Norway (200 t allocated in European Community waters per year) and New Zealand, with the species protected in United States waters and regulated in the European Community. Canadian catches of

porbeagles were less than 100 t/y until 1990 but landings increased in 1992 and catches have oscillated around 1 300 t/y since 1994. The western Atlantic stock is currently considered overexploited, with declining catch rates, and a fishing mortality beyond the replacement level. A Canadian management plan that limits the number of licenses, types of gear, fishing areas and seasons, prohibits finning, and restricts recreational fishing to catch-and-release only, has been in force since 1995. A TAC of 1 000 t/y was introduced in the commercial fishery for the period 1997-1999 pending better scientific information about resource status. In the past porbeagles were considered a nuisance to commercial fishermen because they wrecked light gear set for bony fishes (such as cod nets) and bit fish off hooks, but probably not so much at present with greatly depleted porbeagle stocks and decimated stocks of some of its prey species (including cod).

A considerable bycatch fishery for porbeagle by Japanese longliners and probably the pelagic fishing fleets of other countries has existed in the southern Indian Ocean and probably elsewhere in the Southern Hemisphere. The catch is poorly known and may be little-utilized except for fins. It has figured as complementary bycatch (fins utilized) of the Japanese longline fishery for southern bluefin tuna off Tasmania. It is used fresh and dried-salted for human consumption; for oil and fishmeal for fertilizer; and for fins for shark-fin soup. The species is primarily caught with pelagic longlines; also pelagic and bottom trawls, handlines and gill nets. It has recently showed up as bycatch of demersal longlines for Patagonian toothfish (*Dissostichus eleginoides*, Nototheniidae) in the southern Indian Ocean. Statistics for the Southern Hemisphere porbeagle fishery are only reported to FAO by New Zealand (21 t in 1997), which suggests that the southern catch is largely unreported.

This species has been described as a relatively less active game fish compared to the shortfin mako and white shark. However, the porbeagle has been regularly sought by sportsfishing anglers in the United Kingdom, Ireland and the United States and is a strong fighter (especially on light tackle from a small boat). It is listed as a record game fish by the International Game Fish Association.

The porbeagle seldom if ever bites people in the water or boats (unlike its close relatives the shortfin mako and white sharks). An older anecdotal account mentions a provoked encounter by a porbeagle that leapt at and bit a piece of clothing from a fisherman who was attempting to capture it. A swimmer was reported as being bitten by a 'mackerel shark', but this was not confirmed and could have resulted from mistaking a white shark or shortfin mako for a porbeagle or mackerel shark. Recently adult porbeagles have been filmed underwater making fast rushes at divers servicing oil platforms in the North Sea, with the sharks sometimes brushing the divers and making light contact without hurting them (I. Fergusson, pers. comm.). The motivation of this activity is uncertain but is apparently nonpredatory and possibly agonistic or exploratory. To the writer's knowledge porbeagles have not figured in ecotouristic diving, nor have they been kept in captivity.

The conservation status of the porbeagle is of major concern because of the drastic decline in catches from targeted fisheries in the North Atlantic and continuing exposure of the species to intensive high-seas pelagic longline fisheries (with finning and capture trauma contributing to mortality) wherever it occurs. North Atlantic fisheries are relatively well-documented and under regulation, but not those of the Southern Hemisphere with the exception of New Zealand.

Local Names: Mackerel shark, Common porbeagle, Porbeagle shark, Atlantic mackerel shark, Common Atlantic mackerel shark, Salmon shark, Atlantic porbeagle, Swordfin, Blue dog, American porbeagle, Beaumaris shark, Blue shark, Bottle-nosed shark (England and USA); Le squale nez, Le lamie long nez, Lamie, Nez, Touille, Touilele boeuf taupe, Requin long nez, Loutre de mer, Nas llarg, Melantoun (France); Neushaai (Holland); Sillhaj or Herring shark, Sildehaaen (Denmark); Morgi mawr (Wales); Haabranden, Haamar (Sweden); Smeriglio, Lamna smeriglio, Isuro muso acuto, Cagnia, Smeriglio, Sorglio pisci tunnu, Pesci cani, Cani di mer (Italy); Psina atlantska (Adriatic); Calderon, El marrago, Ludia, Marraco, Marraquet, Marraix, Marrajo, Taulo (Spain); Anequim, Arrequim, Marracho, Sardo (Portugal); Marracho, Porbeagle (Azores); Requim, Nequim (Madeira); Akula sel devaia (Russia); Haringhaai (South Africa).

Literature: Shann (1911, 1923); Garman (1913); Lahille (1928); Fowler (1936, 1941); Whitley (1939, 1940); Bigelow and Schroeder (1948); Smith (1949); Aasen (1961, 1963); Farquhar (1963); Garrick and Schultz (1963); Templeman (1963); Kato, Springer and Wagner (1967); Nakaya (1971); Stevens (1973); Baldrige (1974); Schwartz and Burgess (1975); Sadowsky and Amorim (1977); Svetlov (1978); Duhamel and Ozouf-Costaz (1982); Stevens, Dunning and Machida (1983); Compagno (1984, 1990b, c); Quero (1984); Duhamel and Compagno (1985); Sadowsky, Arfelli and Amorim (1985); Paust and Smith (1986); Stevens (1990); Last and Stevens (1994); Santos, Porteiro and Barreiros (1997); Lucifora and Menni (1997); O'Boyle et al. (1998); Castro, Woodley and Brudek (1999); Campana et al. (1999); Francis and Stevens (2000); Natanson, Mello and Campana, (in press); I. Fergusson, (pers. comm.).