**Alopias pelagicus** Nakamura, 1935


**Synonyms:** None.

**Other Combinations:** *Alopias vulpinus* (not Bonnaterre, 1788).

**FAO Names:** En - Pelagic thresher; Fr - Renard pélagique; Sp - Zorro pelágico.

**Field Marks:** Long upper caudal lobe nearly as long as rest of shark, relatively small eyes, very narrow head with arched dorsal profile, straight broad-tipped ‘oceanic’ pectoral fins, first dorsal fin somewhat closer to pectoral-fin bases than pelvic-fin bases, very slender caudal-fin tip, body colour deep blue or grey above, white below, white colour of abdomen not extending over pectoral-fin bases.

**Diagnostic Features:** Head narrow in dorsal and ventral views, with a convex, arched dorsolateral profile. Snout moderately long, conical. Eyes moderately large in adults but very large in newborn and foetuses, not expanded onto dorsal surface of head and without a vertical, binocular field of view; interorbital space broadly convex. Labial furrows absent. Teeth very small, in 41 to 45/37 to 38 rows (total for both jaws 75 to 86 rows); posterior tooth rows 5 to 11; symphysial and intermediate tooth rows usually present. Weak nuchal grooves present above branchial region. Pectoral fins of ‘macroceanic’ type with straight and very broad tips. Claspers moderately slender and not whip-like. First dorsal-fin midbase about equidistant between pectoral and pelvic-fin bases or closer to pectoral-fin bases. Caudal tip very slender with very narrow terminal lobe. Ribs of monospondylous precaudal vertebrae fused ventrally to form a canal extending nearly to the occiput. Total vertebral count 453 to 477. Intestinal valve count 37 to 40. **Colour:** body deep blue to grey on upper surface with sides silvery and underside white, white colour of abdomen not extending over pectoral-fin bases; no white dot on upper pectoral-fin tips.

**Distribution:** Oceanic and wide-ranging in the Indo-Pacific. Indian Ocean: South Africa (KwaZulu-Natal), Red Sea, Gulf of Aden, Arabian Sea (off Somalia, between Oman and India, and off Pakistan), Australia (northwest Western Australia), Western North Pacific: China, Taiwan (Province of China), Japan (southeastern Honshu), Western South Pacific: New Caledonia, eastern Micronesia, Tahiti, Central Pacific: Hawaiian Islands, equatorial waters north of Howland and Baker, Phoenix and Palmyra Islands. Eastern Pacific: USA (California) and Mexico (Baja California, Gulf of California), equatorial waters northwest of French Polynesia, and off Galapagos Islands.
Habitat: Primarily an oceanic, epipelagic, circumtropical species, but sometimes caught near shore on beaches with a narrow continental shelf, ranging in depth from the surface to at least 152 m. Sometimes seen by divers near coral reefs, near dropoffs and in large lagoons, and on sea mounts.

Biology: A little-known, active, strong-swimming species, probably migratory but with movements little-known. In the eastern North Pacific there is a possible population centre off central Baja California, which tends to shift northward (along with other oceanic sharks) during strong El Niño events. Behaviour and sociobiology is poorly known. Michael (1993) has seen this species repeatedly leap (breach) out of the water.

Ovoviviparous, with uterine cannibalism as in other species of *Alopias*. Embryos subsist on their yolk-sacs up to about 12 cm, after which they become oophagous, feeding on unfertilized eggs. No evidence of adelphophagy (embryo-eating) was reported by Liu et al. (1999), who examined 233 embryos from 167 pregnant females. Litter size is two, with one foetus per uterus and with sex ratio 1:1. Gestation period uncertain because females give birth all year long without a definite birth season. Liu et al. suggest that the gestation period may be less than a year as with *A. vulpinus*, but because most adult females were pregnant throughout the year there may be an annual cycle with no resting period between pregnancies. Pupping may also occur in winter in the Gulf of Aden (R. Bonfil, pers. comm.). This species presumably feeds on small fishes and squid but no details are known.

Vertebral growth rings are laid annually in vertebral centra; females mature at about 8 or 9 years old and males at about 6 to 9 years old, with up to 16 growth rings for females and 14 for males for a minimal age of 14 to 16 years old and a maximum age estimated from von Bertalanffy growth curves as 20 years for males and 29 years for females. Assuming birth of two young every year a female might produce about 40 young during her lifetime. This species has unusually large young, with the largest known foetus 43% of the length of the largest adult female. The large size of the young may help to reduce postnatal predation (presumably by other large sharks), but the relatively small size of the adults combined with the low fecundity imposed by large foetal size may in turn require annual breeding.

Size: Maximum total length at least 365 cm. Size at birth uncertain but presumably between about 130 and 160 cm and possibly up to 190 cm. The largest term foetus examined by Liu et al. (1999) off Taiwan (Province of China) was 158 cm and their smallest specimen was 190 cm long and a year old; a freeliving specimen from the western Indian Ocean that was examined by the author was 137 cm long. A term or near-term foetus 96.5 cm long attributed to this species by Nakamura (1935) is probably *A. vulpinus*. Off Taiwan (Province of China) males were immature at about 174 to 283 cm, adolescent at about 239 to 305 cm, and adult at 259 to 323 cm; onset of maturity was at about 267 cm, with 50% mature at 267 to 276 cm. Females from Taiwan (Province of China) were immature at 176 to 294 cm, adolescent at 253 to 321 cm, and adult at 265 to about 365 cm; onset of maturity was at about 273 cm, with 50% mature at 282 to 292 cm. Elsewhere males were adolescent at 192 to 318 cm and adult at 276 cm, while females were immature or adolescent at 277 to 233 cm, adult at 264 to 330 cm, while pregnant females were 264 to about 300 cm. This is apparently a smaller species than *A. superciliosus* or *A. vulpinus*.

Length-weight equations are given by Liu et al. (1999) for Taiwanese specimens:

Females: \[ W(kg) = 4.61 \times 10^5 \times TL(cm)^{2.494} \quad (n = 230) \]

Males: \[ W(kg) = 3.98 \times 10^5 \times TL(cm)^{2.52} \quad (n = 230) \]
Interest to Fisheries and Human Impact: This species was formerly exploited by the longline fishery in the northwestern Indian Ocean (primarily by the former USSR), but it is also fished in the Central Pacific. It is an important catch off Taiwan (Province of China) with about 222 t landed yearly. It enters the commercial thresher catch off California and is sometimes caught in considerable numbers off the Pacific coast of Mexico and Gulf of California. Also caught by shark fishermen in the Red Sea and Gulf of Aden (R. Bonfil, pers. comm.). Utilized for its meat (for human consumption), liver oil for vitamin-A extraction, hides for leather, and fins for shark-fin soup. Apparently seldom caught by anglers, but listed as a record fish along with other threshers by the International Game Fish Association. It is rarely caught by anti-shark nets off KwaZulu-Natal, South Africa. Harmless to people, seldom encountered by divers and not kept in aquaria as far as is known. Divers have viewed and photographed this shark on coral reefs and seamounts in the Gulf of California and the Red Sea, Indonesia and Micronesia, but it is not a regular subject of ecotouristic diving. According to Michael (1993) it is shy and difficult to approach underwater. The conservation status of this shark is uncertain, but Liu et al. (1999) considered it extremely vulnerable to overexploitation and in need of close monitoring because of its very low fecundity and relatively high age at maturation.

Local Names: Pelagic thresher, Thresher shark, Whiptail shark, Fox shark; Onagazame, Nitara (Japan); Zorro pelagico (Mozambique).

Remarks: Nakamura (1935) described *A. pelagicus* from three large specimens 270 to 330 cm TL, for which he presented measurements. He also gave an illustration (pl. 1, fig. 2) of a large female specimen, one-twentieth life size. It is uncertain if the specimen illustrated is one of the three large individuals described, as scaling up the drawing (204 mm long) gives a size of 408 cm. He also included a separate description (p. 5) and illustration (pl. 3) of a foetus 96.5 cm long as *A. pelagicus*. All of these specimens are apparently syntypes of *A. pelagicus*. Nakamura did not designate types for *A. pelagicus* and did not indicate if one of the three large specimens measured or the large female illustrated was the mother of the illustrated foetus or if the latter was separately obtained.

The large *A. pelagicus* specimen illustrated by Nakamura is apparently conspecific with *A. pelagicus* of Bass, D'Aubrey and Kistnasamy (1975a), Compagno (1984), and Last and Stevens (1994), as shown by its fin shapes, fin positions, colour pattern (including lacking a white patch over its pectoral base), oblique teeth, and possibly by lacking labial furrows. However, the illustrated foetus is apparently *A. vulpinus* and is recognizable by its small eyes, broad head with a strongly convex dorsal profile, short snout, presence of labial furrows, and falcate pectoral fins. Compagno (1984) and Eschmeyer (1998) were unable to provide information on whether or not the syntypes of this species still exist or for that matter if they were ever preserved and deposited in a research collection. Nakamura only mentioned that the specimens were drawn by him from life. It may be necessary to designate a neotype for *A. pelagicus* based on Taiwan (Province of China) material. The name *A. pelagicus* is used here in the sense of Bass, D'Aubrey and Kistnasamy (1975a), Compagno (1984), and Last and Stevens (1994), who served to revise the concept of this species by restricting it to the species represented by Nakamura's illustrated adult.

*Alopias pelagicus* has commonly been mistaken for *A. vulpinus*. For example, Gohar and Mazhar (1964, Red Sea), Kato, Springer and Wagner (1967, eastern Pacific), Fourmanoir and Laboute (1976, New Caledonia), Johnson (1978, Tahiti), and Faughnan (1980, Hawaiian Islands) all published illustrations of this species under the name *A. vulpinus*. This species is probably more wide-ranging than present records show, although it has not been found in the Atlantic Ocean nor Mediterranean Sea and may be absent there.

Literature: Nakamura (1935); Gohar and Mazhar (1964, Red Sea), Kato, Springer and Wagner (1967, eastern Pacific), Fourmanoir and Laboute (1976, New Caledonia), Johnson (1978, Tahiti), and Faughnan (1980, Hawaiian Islands) all published illustrations of this species under the name *A. vulpinus*. This species is probably more wide-ranging than present records show, although it has not been found in the Atlantic Ocean nor Mediterranean Sea and may be absent there.

*Alopias superciliosus* (Lowe, 1840)  
*Fig. 65*


Synonyms: *Alopias profundus* Nakamura, 1935: 2, pl. 1, fig. 1, pl. 2. Syntypes: Three large specimens, 332, 352 and 366 cm TL, a large female illustrated and of uncertain size (Nakamura, 1935, pl. 1, fig. 1); also a 72 cm foetus, presumably the same as illustrated (Nakamura, 1935., pl. 2); all specimens from Suô fish market, Taiwan (Province of China). Whereabouts of syntypes unknown according to Eschmeyer (1998: CD-ROM), possibly never accessioned in a research collection.

Other Combinations: None.
FAO Names: En - Bigeye thresher; Fr - Renard à gros yeux; Sp - Zorro ojón.

**Field Marks:** Long dorsal caudal lobe nearly as long as rest of shark, notched or helmeted contour of head, huge eyes extending onto dorsal surface of head, falcate but rather broad-tipped pectoral fins.

**Diagnostic Features:** Head broad in dorsal and ventral view, with a notched dorsolateral profile. Snout moderately long, bulbous. Eyes greatly enlarged in young and adults, expanded onto dorsal surface of head and with a vertical, binocular field of view; interorbital space nearly flat. Labial furrows absent. Teeth large and in 22 to 27/20 to 24 rows (total for both jaws 42 to 51 rows); no symphysial or intermediate teeth. Strong nuchal grooves present above branchial region. Pectoral fins falcate with curved and moderately broad tips. Claspers moderately slender and not whip-like. First dorsal midbase closer to pelvic-fin bases than to pectoral-fin bases. Caudal tip broad with wide terminal lobe. Ribs of monospondylous precaudal vertebrae fused ventrally to form a canal extending nearly to the occiput. Total vertebral count 219 to 319. Intestinal valve count 43 to 45. **Colour:** body purplish grey or grey-brown on upper surface and sides with underside grey to white, light colour of abdomen not extending over pectoral-fin bases; no white dot on upper pectoral-fin tips.

**Distribution:** Oceanic and coastal, virtually circumglobal in tropical and temperate seas. Western Atlantic (including Gulf of Mexico): USA (Atlantic coast from New York to Florida, Gulf of Mexico off Florida, Mississippi and Texas), Mexico (Veracruz to Yucatan), Bahamas, Cuba, Venezuela, central and southern Brazil. Eastern Atlantic: Portugal, Spain, Madeira, near Azores, Morocco, Canary Islands, Senegal, Guinea to Sierra Leone, Angola, South Africa (Western Cape): also western and central Mediterranean Sea. Indian Ocean: South Africa (Eastern Cape and KwaZulu-Natal), Madagascar, Arabian Sea (Somalia), Gulf of Aden, Maldives, Sri Lanka. Western Pacific: Southern Japan (including Okinawa), Taiwan (Province of China), Viet Nam, between northern Mariana Islands and Wake Island, Northwestern Submarine Rise, New Caledonia, Australia (northwestern coast), New Zealand. Central Pacific: Area between Wake, Marshall, Howland and Baker, Palmyra, Johnston, and Hawaiian Islands; north and south of Hawaiian Islands, off east of Line Islands, and between Marquesas and Galapagos Islands. Eastern Pacific: USA (California), Mexico (Gulf of California) and west of Galapagos Islands (Ecuador); possibly off Peru and northern Chile.

**Fig. 65 Alopias superciliosus**

DORSAL VIEW OF HEAD
Habitat: Found in coastal waters over the continental shelves, sometimes close inshore in shallow waters, and on the high seas in the epipelagic zone far from land; also caught near the bottom in deep water on the continental slopes. Ranges from the surface and in the intertidal to at least 500 m deep, but mostly below 100 m depth.

Biology: An epipelagic, neritic, and epibenthic shark, apparently strong-swimming but little-known behaviourally. Ovoviviparous, with uterine cannibalism (oophagy), number of young usually two per litter, but sometimes with 3 or 4. Sex ratio of foetuses 1:1. Larger females apparently do not have larger term foetuses than smaller females. Birth may occur throughout the year although in the eastern Atlantic more females may give birth in autumn and winter than other times of year. The gestation period may be 12 months long but remains uncertain because of lack of birthing seasonality. In the eastern Atlantic a nursery area occurs off the Straits of Gibraltar, but similar areas no doubt occur elsewhere in the vast range of this species. Bigeye threshers have been aged with annular growth rings in vertebral centra, assuming one ring per year (Liu, Chiang, and Chen, 1998). Males mature at about 9 or 10 years old and females at about 12 or 13 years old. Maximum number of growth bands, and maximum known age, about 19 for males and 20 for females.

The bigeye thresher feeds on pelagic fishes, including lancetfishes (Alepisauridae), herring (Clupeidae), mackerel (Scombridae), and small billfishes (Istiophoridae) and bottom fishes including hake (Merluccidae); also squids (Ommastrephidae). Apparently this species stuns its prey with its long caudal fin, as individuals are often tail-hooked on longlines. The arrangement of the eyes, with keyhole-shaped orbits extending onto the dorsal surface of the head, suggest that this species has a dorsal, vertical binocular field of vision (unlike other threshers) which may be related to fixating on prey and striking them with its tail from below. Michael (1993) observed sea lampreys attached near the cloaca of a bigeye thresher.

Size: Maximum total length about 461 cm. Size at birth 100 to 140 cm, with full term foetuses at 105 or 106 cm and free-swimming individuals down to 155 cm. Males immature up to 316 cm, maturing at about 279 to 300 cm; adult males as small as 276 cm and reaching about 410 cm with an estimated maximum of 421 cm. Females immature up to 350 cm, and maturing at about 294 to 355 cm; adult females as short as 341 cm and reaching at least 458 cm. Length-weight equations for this species are given by Kohler, Casey and Turner (1995) for fork length:

\[ W (kg) = 9.1069 \times 10^{-6} \times FL (cm)^{3.0802} \quad (n = 55; \text{both sexes}) \]

where \( FL (cm) = 0.5598 \times TL (cm) + 17.666 \quad (n = 56) \)

Liu, Chiang, and Chen (1998) give equations for total length:

Females: \( W (kg) = 1.02 \times 10^{-5} \times TL (cm)^{3.78} \quad (n = 175) \)

Males: \( W (kg) = 3.73 \times 10^{-5} \times TL (cm)^{3.57} \quad (n = 65) \)

Interest to Fisheries and Human Impact: Caught or formerly caught in the oceanic longline fisheries operated by the former USSR, Japan, Taiwan (Province of China), Spain, the USA, Brazil, Uruguay, Mexico, and probably other countries. Especially important areas for these fisheries are the northwestern Indian Ocean, western and Central Pacific, eastern North Pacific, and North Atlantic. The bigeye thresher was formerly a very important component of the Cuban longline fishery, and more recently has been taken in considerable numbers by longliners off the northeastern USA and by gill net vessels off southern California (USA) and the eastern Atlantic (by Spanish vessels), and by longliners off Taiwan (Province of China; where about 220 t per year are landed). This species is also taken as incidental bycatch in fixed bottom and pelagic gill nets, in trawls, and as a rare catch of anti-shark nets off KwaZulu-Natal, South Africa. It has been caught by anglers with sportfishing gear (rod-and-reel) in the USA, South Africa, and New Zealand, in some instances by anglers targeting swordfish at night and using luminous lures. It is listed as a record fish along with other threshers by the International Game Fish Association. Its meat is utilized fresh, smoked and dried-salted for human consumption, its liver oil is processed for vitamin A, its skin for leather, and fins for shark-fin soup. Apparently harmless to people, and not known to have been encountered by divers underwater.

Local Names: Big-eyed thresher, Zorro (Cuba); Zorro ojón (Mexico); Tubarão raposo, Bigeye thresher (Azores); Deepsea bigeye thresher, Bigeye, Bigeyed thresher shark, Big-eyed thresher, Hachiware (Japan); Grootoog-sambokhaai (South Africa); Zorro olho grande (Mozambique).

Remarks: This account follows Bass, D’Aubrey and Kistnasamy (1975a), Gruber and Compagno (1981), and Compagno (1984) in synonymizing *Alopias profundus* with this species. See Gruber and Compagno (1981) for a detailed discussion of the synonymy of *A. profundus* and for a general review of the biology of *A. superciliosus*.

Literature: Nakamura (1935); Springer (1943); Bigelow and Schroeder (1948); Cadenat (1956c); Fitch and Craig (1964); Bass, D’Aubrey and Kistnasamy (1975a); Stillwell and Casey (1976); Blasco and Chapuli (1981); Gruber and Compagno (1981); Cadenat and Blache (1981); Branstetter and McEachran (1983); Gilmore (1983, 1993); Fulgosi (1983); Compagno (1984, 1990b, 1994); Compagno and Smale (1986); Ivanov (1986); Moreno and Morón (1992a); Hanan, Holts and Coan (1993); Michael (1993); Last and Stevens (1994); Eilner (1995); Kohler, Casey and Turner (1995); Bonfil (1997); Santos, Porteiro and Barreiros (1997); Chen, Liu and Chang (1997); Castillo-Geniz et al. (1998); Liu, Chiang and Chen (1998).
**Alopias vulpinus** (Bonnaterre, 1788)


**Other Combinations:** *Alopias vulpes* (Gmelin, 1788), *Alopecias vulpes* (Gmelin, 1788), *Carcharias vulpes* (Gmelin, 1788).

**FAO Names:** En - Thresher shark; Fr - Renard; Sp - Zorro.

**Field Marks:** Long curving dorsal caudal lobe about as long as rest of shark, relatively small eyes, falcate pointed pectoral fins, white colour of abdomen extending over pectoral-fin bases.

**Diagnostic Features:** Head broad in dorsal and ventral view, with a strongly convex dorsolateral profile. Snout relatively short, conical and pointed. Eyes moderately large at all sizes, not expanded onto dorsal surface of head and without a vertical, binocular field of view; interorbital space broadly convex. Labial furrows present. Teeth smaller with 32 to 52/25 to 50 rows (total for both jaws 58 to 102 rows); posterior tooth rows 2 to 10; symphysial and intermediate tooth rows usually present. No nuchal grooves present above branchial region. Pectoral fins falcate and with curved and narrow tips. Claspers extremely slender and whip-like. First dorsal-fin midbase closer to pectoral-fin bases than to pelvic fin bases. Caudal tip moderately slender with moderately broad terminal lobe. Ribs of monospondylous precaudal vertebrae lateral and not fused ventrally as a canal. Total vertebral count 339 to 364. Intestinal valve count 33 to 34. **Colour:** body blue-grey to dark grey or blackish above with sides silvery or coppery and underside white, white colour of abdomen extending dorsally and anteriorly over pectoral-fin bases as a conspicuous patch; white dot often present on upper pectoral-fin tips.

**Distribution:** Oceanic and coastal, virtually circumglobal in tropical to cold-temperate seas but commonest in temperate waters. Western Atlantic (including Gulf of Mexico): Canada (Newfoundland, Nova Scotia, New Brunswick, and Quebec, north to the Bay of Chaleur, Gulf of St. Lawrence), USA (entire Atlantic Coast but rare south of New England; Gulf Coast off Florida, Mississippi and Texas), Cuba, Mexico (Veracruz to Campeche), Venezuela, Brazil to Argentina. Eastern Atlantic: Norway and British Isles to Mediterranean and Black Seas, Morocco, Madeira, the Azores, Ghana, Côte d’Ivoire, Angola, Namibia, and South Africa (Western Cape and probably Northern Cape). Indo-West Pacific: South Africa (Eastern Cape and KwaZulu-Natal), Tanzania, Somalia, Maldives, Chagos Archipelago, Gulf of Aden, possibly Oman, Pakistan, India, Sri Lanka, Sumatra, Japan, Republic of Korea, China, Taiwan (Province of China), Australia (Queensland, New South Wales, Victoria, Tasmania, South Australia), New Zealand, New Caledonia. Central Pacific: Society Islands, Fanning Islands, Hawaiian Islands. Eastern Pacific: Canada (British Columbia), the USA (Washington, Oregon and California) and Mexico (Baja California), south to Panama and Chile.
**Habitat:** Coastal over the continental and insular shelves and epipelagic far from land in temperate to tropical waters, most abundant near land; young often close inshore and in shallow bays. Depth range from the surface and the intertidal to at least 366 m, often near the surface.

**Biology:** An active, strong-swimming shark, sometimes leaping out of the water. Thresher sharks in the northwestern Indian Ocean and off the west coast of North America show spatial and depth segregation by sex. Off the west coast of North America (and probably elsewhere) the species is seasonally migratory, and moves northward from Baja California into California waters during the spring, with adult males tending to travel farther northward than females and reaching the coast of British Columbia. Juveniles are mostly found in shallow warm-temperate inshore waters, particularly off southern California where an important nursery area occurs. Juveniles may be less cold-tolerant than adults, and seldom range north of central California. Both adults and juveniles congregate in inshore waters of southern California, primarily during spring and summer. Behaviour is otherwise poorly known, and little is known of sociobiology and behaviour patterns.

Transoceanic migrations have not been demonstrated, and there may be separate populations with slightly different fecundity and size at maturity in the eastern Pacific and western Indian Ocean, and possibly elsewhere, but this remains to be determined.

Ovoviviparous and apparently a uterine cannibal (oophagous), number of young 2 to 4 and rarely 6 in a litter off California (usually 2 to 4, commonly 4), and 3 to 7 in the eastern Atlantic. This species apparently uses inshore nursery areas in temperate waters (east coast of the United States, California, South Africa, the northeastern Atlantic and western Mediterranean, and probably elsewhere), with young sharks occurring in shallow bays (California, South Africa). In the eastern North Pacific (California) the species mates in summer, has a gestation period of nine months and gives birth during the spring. This shark matures between 3 and 8 years old, with a maximum age estimated at 45 to 50 years (Cailliet et al., 1983).

Feeds mostly on small schooling fishes but also bottom fishes, including herring, sardines, shad, pilchards and menhaden (Clupeidae), anchovies (Engraulidae), lanternfishes (Myctophidae), lancetfishes (Alepisauridae), needlefishes (Belonidae), scad (Trachurus, Carangidae), mackerels (Scombridae), plaice and flounder (Pleuronectidae) and sole (Soleidae); also squids, octopi and pelagic crustaceans, and rarely seabirds. Herds and stuns its prey with its long, whip-like caudal fin, and is often caught on longlines by being tailhooked. It swims in narrowing circles around schools of small fishes, splashing water with its caudal fin and compressing the school, then strikes and injures fishes with the caudal. Two threshers may cooperate on bunching and killing small fish.

**Size:** The largest thresher. Maximum total length at least 573 cm and possibly to over 610 cm, with an estimated maximum at 651 cm from growth curves and older unconfirmed records up to 760 cm. Size at birth 114 to 160 cm, with term foetuses up to 139 to 156 cm and small freeliving specimens down to 117 to 145 cm. Immature males up to at least 252 cm, while an adolescent male examined was 288 cm and adult males are 314 to at least 420 cm. Females maturing at about 315 to 400 cm, with immature or adolescent females up to 395 cm and adult females 376 to at least 549 cm. A length-weight equation is given by Kohler, Casey and Turner (1995) for fork length:

\[ W(kg) = 1.8821 \times 10^{-4} FL(cm)^{2.198} \quad (n = 88; \text{both sexes}) \]

where:

\[ FL(cm) = 0.5474 \times TL(cm) + 7.0262 \quad (n = 13) \]
Interest to Fisheries and Human Impact: Widely caught or formerly caught in offshore longline and pelagic gill net fisheries including those of the former USSR, Japan, Taiwan (Province of China), Spain, the USA, Brazil, Uruguay, Mexico, and other countries. Especially important areas for these fisheries are the northwestern Indian Ocean, the western, central, and eastern Pacific, and the North Atlantic. Also fished with anchored bottom and surface gill nets, and accidentally caught in other gear including bottom trawls and fish traps. The species became the object of an important targeted pelagic gill net fishery off the west coast of the United States (particularly California but also Washington and Oregon) in the late 1970s, peaking at about 1 000 t in 1982 and declining due to overfishing to less than 300 t by the late 1980s. The targeted fishery was ended by 1990 but the species was still caught as bycatch of the swordfish gill net fishery and may be sold for higher prices in the market than swordfish. The meat is highly prized fresh for human consumption (cooked) but is also eaten smoked and dried-salted; the fins are valuable for shark-fin soup; the hide is usable for leather and the liver oil can be processed for vitamins.

Sports anglers seek these sharks in the USA, South Africa, and elsewhere with rod and reel. These sharks fight strongly when hooked and may jump out of the water. This and other threshers are listed as record fishes by the International Game Fish Association.

Apparently harmless to people, though the size of adults of this species should invite respect. There is an unconfirmed anecdotal account of a fisherman on the western North Atlantic coast of the USA that was decapitated by a tailstroke from a big adult thresher (Mundus and Wisner, 1971). A few assaults on boats are doubtfully attributed to this species. Small specimens have been seen underwater by divers, at the surface or close to the bottom, and have circled them at the limit of visibility without acting aggressively. Michael (1993) notes that this species is shy and difficult to approach underwater, but mentions an incident where a thresher of this species was aggressive toward a spearfishing diver off New Zealand. To the writer’s knowledge, this species has seldom if ever been kept in captivity and is not currently the subject of ecotouristic shark-diving.

The conservation status of this shark is little known but is of some concern despite its midrange intrinsic rebound potential (a measure of the capacity to recover from fishing pressure; Smith, Au and Show, 1998) because of the history of the eastern Pacific thresher fishery (which declined quickly despite a relatively small and localized catch), and its exposure to high-intensity offshore fisheries virtually wherever it occurs.

Local Names: Common thresher, Fox shark, Thresher shark, Long-tailed shark, Sea fox, Sea ape, Slasher (England); Whiptail shark, Thintail thresher, Fynstert-sambokhaai (South Africa); Luynog mor (Wales); Renard, Singe de mer, La fauq, Poisson épée, Péi aspasu ratou, Touille à l'épée (France); Rabosa, Peix espasa, Zorra de mar, Pez zorro, Zorro blanco (Spain); Aremquim, Peixe alicer, Peixe raposo, Peixe zorra (Portugal); Peixe rato, Peixe cavalo (Madeira); Tubarão raposo, Romano, Romão, Thresher shark (Azores); Pesce volpe, Pesce sorcio or Pavone, Pesce bandiera, Pesce pavone, Pesce bannera, Volpe di mare, Pescio rato, Allopia coda lunga, Allopia volpe marina, Pavone di mare, Pisce surci, Pisci coda longa, Pisci cuduto, Pisci scibula turca (Italy); Pas sabljás (Adriatic); Raefhajen (Sweden); Onagazame, Nadebuka, Nezumezame, Ma-onaga (Japan); Zorro (Cuba); Lisitska morskayia (Russia); Zorro cauda longa (Mozambique).

Remarks: This account follows Bass, D’Aubrey and Kistnasamy (1975a) and Compagno (1984) in combining several regional species of threshers from Chile, New Zealand and Australia into one wide-ranging species, *A. vulpinus*. Threshers examined by the writer from the west coast of the USA and South Africa agree closely in morphology and meristics.

Literature: Garman (1913); Bigelow and Schroeder (1948); Gubanov (1972, 1978); Bass, D’Aubrey and Kistnasamy (1975a); Hixon (1979); Gruber and Compagno (1981); Cailliet et al. (1983); Cailliet and Bedford (1983); Compagno (1984, 1990b); Cailliet, Radtke and Welden (1986); Pascoe (1986); Bedford (1987); Cailliet and Radtke (1987); Moreno, Parajua and Morón (1989); Cailliet, Holts and Bedford (1993); Hanan, Holts and Coan (1993); Michael (1993); Last and Stevens (1994); Kohler, Casey and Turner (1995); Eitner (1995); Smith, Au and Show (1998).
Diagnostic Features: Head moderately long but much shorter than trunk. Snout moderately long, pointed and conical, not depressed, flattened or blade-like. Eyes small with length 0.8 to 1.3% of precaudal length. Gill openings extremely large, width of first 17.7 to 29.2% of precaudal length, extending onto dorsal and ventral surfaces of head; all gill openings anterior to pectoral-fin bases; gill rakers present on internal gill slits, in the form of hair-like modified dermal denticles with extremely elongated crowns. Mouth large and arcuate, ventral on head; jaws hardly protrusable but greatly distensible laterally. Teeth very small, hook-like, not blade-shaped, and in 203 to 255/225 to 230 (432 to 480 total) rows. Several rows of small anterior teeth in upper jaw, separated from the similar-sized laterals by a broad gap but without intermediate teeth; no symphysis teeth. Trunk fusiform and moderately stout, firm and not flabby. Caudal peduncle depressed and with strong lateral keels and upper and lower crescentic precaudal pits. Dermal denticles large and rough, with erect hooked crowns, strong cusps and ridges, with cusps of lateral denticles pointing in several directions. Pectoral fins long and moderately broad, much shorter than head in adults; pectoral skeleton plesodic with radials extending far into fin webs. Pelvic fins smaller than first dorsal fin but larger than second; fin skeleton aplesodic, not extending into fin web. First dorsal fin large, high, erect and angular; fin skeleton semiplesodic, extending partways into fin web. Second dorsal and anal fins moderately large but less than half size of first dorsal, with broad, non-pivotal bases. Caudal fin lunate, dorsal lobe moderately long but less than one-third length of rest of shark, ventral lobe nearly as long as dorsal lobe. Neurocranium with a high cranial roof but otherwise low, not compressed, with long rostrum, depressed internasal septum and widespread nasal capsules, small orbits with strong supraorbital crests, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified, with well-developed double cones and radii and prominent annulli. Total vertebral count 109 to 116, precaudal count 50 to 54, diplospondyloid caudal count 55 to 62. Intestinal valve of ring type with 47 to 51 turns. Size gigantic with adults 5 to 10 m and possibly to 12 to 15 m long.

Remarks: This family includes the single living genus *Cetorhinus* Blainville, 1816, and possibly a single living species, the basking shark, *C. maximus* (Gunnerus, 1765) as well as several fossil species (Woodward, 1889; Cappetta, 1987). Publication of *Cetorhinus* Blainville and its synonym *Selache* Cuvier in the same year caused confusion, with several prominent nineteenth century authors using *Selache* or the emended *Selachus* instead of *Cetorhinus*. After synonymizing (1810) genus *Tetroras* (and its variant *Tetroras*) was hard to identify from its generic description, with Rafinesque’s claim that *Tetroras* has four gill openings being probably erroneous (unless the specimen examined was abnormal). Rafinesque’s description of *Tetroras angiova*, the only species in the genus, does indeed suggest a basking shark in certain details ("denti in forma di raspa... ha gli occhi piccolissimi, e le aperture delle branche bastantemente larghe."). However, even if more evidence was available to prove that *T. angiova* actually was a basking shark, the substitution of *Tetroras* for *Cetorhinus* would not serve the stability of zoological nomenclature due to universal usage of *Cetorhinus* for the basking shark at present.

Couch (1862) proposed the genus *Polypropus* as separate from *Cetorhinus* and including two species apparently based on large basking sharks. *Polypropus* was recognized by Gill (1862b) but was synonymized with *Cetorhinus* or *Selache* by Dumeril (1865), Günther (1870) and subsequent authors.

Following Müller and Henle (1839) and Bonaparte (1838, 1839), *Cetorhinus* or *Selache* were often placed in the family Lamnidae or Isuridae (Gray, 1851; Bleeker, 1859; Dumeril, 1865; Woodward, 1889; Regan, 1906a; Goodrich, 1909; Garman, 1913; Engelhardt, 1913; Berg, 1940; Norman, 1966; Bailey et al., 1970; Nelson, 1976, 1984). Gill (1862b) proposed a subfamily *Cetorhininae* within *Isuridae* (Gray, 1851; Bleeker, 1859; Dumeril, 1865; Woodward, 1889; Cappetta, 1987). Following Müller and Henle (1839) and Bonaparte (1838, 1839), *Cetorhinus* or *Selache* were often placed in the family Lamnidae or Isuridae (Gray, 1851; Bleeker, 1859; Dumeril, 1865; Woodward, 1889; Regan, 1906a; Goodrich, 1909; Garman, 1913; Engelhardt, 1913; Berg, 1940; Norman, 1966; Bailey et al., 1970; Nelson, 1976, 1984). Gill (1862b) proposed a subfamily *Cetorhininae* within the Lamnidae for *Cetorhinus*; the *Cetorhininae* as a subfamily of Lamnidae was recognized by Berg and Svidoviz (1955). Günther (1870) proposed a group *Selachina* within Lamnidae for *Selache*, which was followed by Hasse (1879). Gill (1872) elevated *Selachinae* to the family *Cetorhinidae*, which has been recognized by most modern authors (Jordan and Gilbert, 1883; Gill, 1893; Jordan and Evermann, 1896; Bridge, 1910; Jordan, 1923; Lozano y Rey, 1928; White, 1936, 1937; Bertin, 1939a; Romer, 1945, 1946; Bigelow and Schroeder, 1948; Matsubara, 1955; Arambourg and Bertin, 1958; Glikman, 1964, 1967; Fowler, 1967a; Patterson, 1967; Blot, 1969; Budker and Whitehead, 1971; Linden, 1971; Hass and Linden, 1971; Pinchuk, 1972; Compagno, 1973, 1981b, 1982, 1984, 1990b, 1999; Applegate et al., 1979; Chu and Meng, 1979; Gukanov, Kondyurin and Myagkov, 1986; Cappetta, 1987; Carroll, 1988; Eschmeyer, 1990, 1998; Robins et al., 1991a; Nelson, 1994; Helfman, Collette and Facey, 1997). Shirai (1996) in contrast placed *Cetorhinus* in a subfamily *Cetorhininae* of the family *Alopiidae*. Whitlcy (1940), Fowler (1941), and Smith (1949) substituted the family *Halsydridae* for *Cetorhinidae* after synonymizing *Cetorhinus* with *Halsydrus* (see above). Maisey (1985) synonymized the megamouth family Megachasmidae with *Cetorhinidae*, which was followed by Robins et al. (1991a). As noted by Springer and Gilbert (1976) and Compagno (1990b), *Cetorhinus* is very distinct. It may be the sister group of the family Lamnidae (Compagno, 1990b) but is apparently not closely related to Megachasmidae on its anatomy. Martin and Naylor (1997) suggested that Lamnidae and *Cetorhinidae* are sister groups on gene similarities from cytochrome b DNA, while Long and Waggoner (1996) suggested that *Megachasma* and *Cetorhinidae* are sister groups on dental morphology.

Most authors recognize only one species of living basking shark (summarized in Garman, 1913; Bigelow and Schroeder, 1948; Springer and Gilbert, 1976; and Compagno, 1984), but Siccardi (1960, 1961) suggested that there are four species (or subspecies) of *Cetorhinus*, two from the North Atlantic and Mediterranean (*C. maximus* and *C. rostratus*), one from southern Australia (*C. macropyi*) and one from the western South Atlantic (*C. normani*), based on morphometric, morphological and meristic differences. Characters included differences in head length, numbers of functional-tooth rows, gill opening width, body height, prepectoral...
length, trunk shape, interdorsal space, position of the dorsal and anal fins, vertebral numbers, and size. Apart from Argentinean material of C. normani which she examined, Siccardi’s morphometrics were based on available literature accounts of basking sharks from other areas. More recently Tomés and Gomes (1989) suggested that two specimens of Brazilian basking sharks they had examined differed morphologically from those from the North Atlantic.

Springer and Gilbert (1976) suggested that there was insufficient evidence at present to separate the four Cetorhinus species on the basis suggested by Siccardi, with which Compagno (1984) concurred. The ‘small’ species C. rostratus seems to represent juveniles of C. maximus, and C. maccocyri, and C. normani as defined by Siccardi differed in characters that need more detailed analysis and consistent collection of data from basking sharks from various parts of the world to factor out individual variation, allometry, sexual dimorphism, and data idiosyncrasies. The question of allopatric species, subspecies, or populations within Cetorhinus needs further study. A problem with conventional morphological studies is the lack of sufficient data for adequate comparisons, as well as the existence of data sets (including morphometrics and illustrations) that are difficult to compare. This stems in part from the great size of the basking shark, which makes data-collecting (particularly of morphometrics, as the writer can attest) and illustration difficult and prone to error, as well as low and sporadic interest in basking shark variation, limited opportunities to collect data, and lack of agreement on data protocols for morphometrics, meristics and descriptive morphology.

Even if the basking shark comprises a single species, its known distribution suggests that there may be isolated populations in temperate and boreal waters with potentially limited genetic interchange. Records of occasional basking sharks from warm-temperate to tropical inshore waters suggest, however, that interchange by crossing the tropics in deep water is possible if infrequent. Populations or subpopulations of basking sharks could include a North Pacific population (with possible eastern and western North Pacific subpopulations?); a North Atlantic population (with possible western North Atlantic, eastern North Atlantic and Mediterranean subpopulations?); a temperate American population (with possible eastern South Pacific and western South Atlantic subpopulations?); a southern African (Namibia and South Africa) population (‘Cape basking shark’), and an Australian-New Zealand population (if not forming separate New Zealand and Australian subpopulations?). Some efforts are being made to collect tissue samples from Northern Hemisphere basking sharks for DNA comparisons (UK CITES proposal, 1999), which should be extended to Southern Hemisphere sharks. Lack of recovery of basking shark numbers following intensive localized fisheries suggests isolated, geographically limited populations or subpopulations that are not readily replaced through immigration. Some of these populations may be very small; basking sharks occurring off southern Africa and possibly Brazil and Argentina are apparently present in very small numbers compared to northern hemisphere localities.

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**Cetorhinus Blainville, 1816**
