		
CHAPTER 2.2.1.4: THRESHER	AUTHORS: MAS F., DOMINGO A., FORSELLEDO R. and MILLER P.	LAST UPDATED: August 2022 Original: Spanish

2.2.1.4 Description of the thresher shark (ALV)

1. Names

1.a. Classification and taxonomy

Species name: *Alopias vulpinus* (Bonnaterre, 1788)

Etymology: According to Castro (2011), *Alopias* is an abbreviation of the Greek word *alopekias*, derived from *alopex*, the name of the thresher shark, which in turn is derived from *alopos*, meaning fox. In addition, *vulpinus* comes from Latin and means “similar to a fox”, derived from *vulpes*, meaning fox.

Synonyms: *Squalus vulpinus* (Bonnaterre, 1788), *Squalus vulpes* (Gmelin, 1788), *Alopias vulpes* (Gmelin, 1788), *Alopecias vulpes* (Gmelin, 1788), *Carcharias vulpes* (Gmelin, 1788), *Alopias macrourus* (Rafinesque, 1810), *Squalus alopecias* (Gronow, 1854), *Alopecias barrae* (Perez Canto, 1886), *Alopecias chilensis* (Philippi, 1902), *Alopecias longimana* (Philippi, 1902), *Vulpecula marina* (Garman, 1913), *Alopias caudatus* (Phillipps, 1932), *Alopias greyi* (Whitley, 1937).

ICCAT species code: ALV

ICCAT names: Thresher shark (English), Requin renard (French), Tiburón zorro (Spanish).

According to the ITIS (Integrated Taxonomy Information System), the thresher shark is classified as follows:

- Phylum: Chordata
- Subphylum: Vertebrata
- Superclass: Gnathostomata
- Class: Chondrichthyes
- Subclass: Elasmobranchii
- Superorder: Euselachii
- Order: Lamniformes
- Family: Alopiidae
- Genus: *Alopias*

1.b. Common names

List of vernacular names used in different countries, according to ICCAT, FAO, Fishbase (www.fishbase.org) and Compagno (2001). The list of countries is not exhaustive and some local names may be missing.

Albania: Peshkaqenibishtshpatë, Peshkaqenidhelpër, Peshkdhelapën, Peshkdhelapër, Peshkudhelpër

Australia: Atlantic thresher, Common thresher, Fox shark, Thresher shark, Thintail thresher

Azores: Romano, Romão, Thresher shark, Tubarãoraposo

Brazil: Cação-pena, Cação-raposa, Rabilongo, Tubarão-raposa

Canada: Swingletail, Swivetail, Thresher shark

Canary Islands: Coletto, Pejerrabo, Zorro

Chile: Pejezorro

China: 狐鲛, 长尾鲨, 长尾沙, 长尾鲨, 弧形长尾鲨, 弧形长尾鲨

Chinese Taipei: 狐鲛

Congo: Tchissouéndji

Croatia: Lisica, Morskalisica, Pas lisica, Pas macun, Pas sabljās, Pas sabljaš, Sabljorep

Cuba: Common thresher, Fox shark, Pezzorro, Swiveltail, Thrasher, Thresher Shark, Zorro
Czech Republic: Žralokmlatecobečný
Denmark: Almindeligrævehaj, Rævehai, Rævehaj, Tærsker
Ecuador: Zorro de mar
Faroe Islands: Revaháur, Revahávur
Finland: Kettuhai
France: Faux, La faux, Pèis rato, Poisson-épée, Péiaspasuratu, Renard, Renard de mer, Requin-renard, Requin-renardcommun, Singe de mer, Thonblanc, Touille à l'épée
French Polynesia: Requin renard
Germany: Drescher, Drescherhai, Fuchshai, Langschweif, Seefuchs
Ghana: Katsi polley
Greece: Αλεπούτηςθάλασσης, Αλεπούσκυλος, Αλεπόσκυλος, Aleposkylos, Alepouskylos, Alepoúskylos, Σκυλόψαρο, Skylópsaro
Hawaii: Mano 'ula
India: Nigudigumiyaru, Threshershark
Italy: Peiratu, Pesciurattu, Piscibandiera, Piscibannera, Piscicuda longa, Piscicudutu, Piscisciabula turca, Piscisurci, Ratto, Sorcio, Squalovolpe, Surci 'mperiali, Volpe di mare, Volpe, Topo, Volpe de mar
Japan Mao-naga, Onagazame, Nadebuka,Nezumezame
Kiribati: Te bakoa, Te kimoa
Korea: 흰배환도상어
Madagascar: Santira
Malta: Budenb, Pescevolpe, Pixxivolpi, Threshershark
Mexico Coludo, Coludo pinto, Grillo, Tiburón zorro, Zorro threshershark
Montenegro: Lisica
Morocco Kalb
Mozambique: Zoro cauda longa
Namibia Fynstert-sambokhaai
Netherlands: Voshaai
New Zealand: Mango-ripi, Threshershark
Nicaragua Tiburón zorro
Norway: Rævehai, Revehai
Oman: Jarjur, Qatwa al bahar, Watwaalbahar
Peru: Peje zorro, Tiburón zorro común
Philippines: Pating
Poland: Kosogon
Portugal: Raposo, Tubarão-raposo, Tubarão-zorro, Tubarão-zorra, Zorro, Zorra, Arequim, Peixealecrim
Romania: Rechin-vulpe
Russia: акулапелагическая, акула-лисица, Lisitskamorskaya
Serbia: Lisica, Pas lisica, Psinalisica
South Africa: Fynstert-sambokhaai, Thintail thresher, Whiptail shark
Spain: Chichi espada, Guadaña, Guilla, Peje sable, Peje zorra, Pez zorro, Pichirata, Rabo de zorra, Raposa marina, Tiburón zorro, Tiburón zorro común, Zorra de mar, Zorro, Zorro blanco
Sweden: Rävhaj, Raefhagen
Tahiti: Ma'oaero
Tanzania: Karage, Papa kinengo, Papa kinengwe
Türkiye: Sapan, Sapan balığı
United Kingdom: Big-eye thresher, Fox shark, Grayfish, Sea fox, Slasher, Swiveltail, Thintail thresher, Thresher, Thresher shark, Whip-tailed shark
United States: Common thresher, Fox shark, Sea fox, Swiveltail, Thrasher, Thrasher shark
Uruguay: Azotador, Threshershark
Vietnam: CáNhàmđuôidài
Wales: Lluynog mor

2. Identification (based mainly on Gubanov, 1972; Moreno *et al.*, 1989; Compagno, 2001).

Characteristics of *Alopias vulpinus* (see Figure 1).

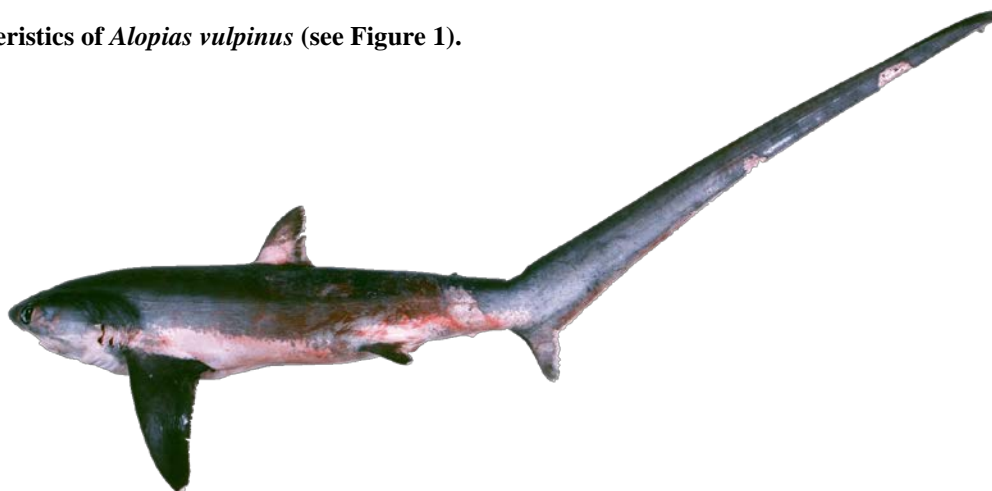


Figure 1. Thresher (*Alopias vulpinus*) (Bonnaterre, 1788). Photo: CSIRO Marine and Atmospheric Research, Australia.

Length

References to length throughout this document consistently relate to total length (TL), unless otherwise specified (e.g. fork length: FL, and precaudal length: PCL). For specimens caught in the Atlantic Ocean whose size is reported in FL, the corresponding TL is reported in brackets, calculated using the conversion equation of Gervelis and Natanson (2013) (**Table 2**).

According to Compagno (2001) the maximum length of *A. vulpinus* would be at least 573 cm and possibly 610 cm. In the North-eastern Atlantic and western Mediterranean, the maximum lengths recorded corresponded to 3 females measuring 451, 456, and 472 cm (Moreno *et al.*, 1989), while in the eastern Mediterranean Megalofonou *et al.* (2005a) reported a maximum length of 514 cm. Barrull *et al.* (1999) reported a maximum length of 431 and 501 cm for males and females, respectively, based on catches taken by the Catalanian fisheries in the North-western Mediterranean. Kabasakal (1998) reported a female of 453 cm in the South-eastern Black Sea. In the South-western Atlantic, Berrondo *et al.* (2007) reported a maximum length of 400 cm, while Mancini and Amorim (2006) reported the length of 470 cm for a female, estimated from the length of its carcass (188 cm and 224 kg). For the North-western Atlantic, Natanson (2002) reported a maximum length of around 488 cm. In the Pacific, the maximum length reported was 573 cm (Cailliet and Bedford, 1983).

Colouring

Greyish blue to dark grey on the dorsum, silver or copper flanks. White belly, spreading across the bases of the pectoral fins forming a conspicuous patch (**Figure 1**).

External characteristics

Relatively tapered head, short and pointed trunk. The head differs from that of *A. superciliosus* in that does not have prominent lateral furrows on the dorsum. Labial furrows present. Moderately small eyes, round sockets and convex interorbital space. Caudal fin about as long as the rest of the body. Base of the first dorsal fin closer to the base of the pectoral fins than of the pelvic fins. Curved pectoral fins with narrow tips. Males with thin whip-like claspers.

Internal characteristics

Small teeth, without secondary cusps, and similar in both jaws, with smooth edges and narrow cusps slightly inclined towards the commissures of the mouth. From 32 to 52 rows of teeth in the upper jaw and from 42 to 57 in the lower jaw. The third tooth of the upper jaw is notably smaller and straighter than the rest. Symphyseal teeth present at least at the embryonic stage (Shimada, 2002). Two to three rows of functional teeth on each jaw. Backbone composed of between 339 and 364 vertebrae. Spiral valve with 33 to 34 turns. Unlike the other species in the genus, the aerobic red muscle is internalised, in epaxial position and near the backbone (Bernal and Sepulveda, 2005; Sepulveda *et al.*, 2005; Patterson *et al.*, 2011).

3. Distribution and population ecology

3.a. Geographic distribution

Alopias vulpinus has a circumglobal distribution in tropical and temperate waters (**Figure 2**). In the western Atlantic it is found in Canada (Compagno, 2001; Kneebone *et al.*, 2020), the United States (Bigelow and Schroeder, 1948; Castro, 2011), Gulf of Mexico (Kneebone *et al.*, 2020), Mexico (from Veracruz to Campeche), the Caribbean Sea (Tavares and Arocha, 2008), Brazil (Amorim *et al.*, 1998; Gadig, 2001), Uruguay (Berrondo *et al.*, 2007; Forselledo and Domingo, 2015) and Argentina (Cuevas and García, 2015). In the eastern Atlantic, it is found in the Azores archipelago (Santos *et al.*, 2020), Scandinavian waters (Fries *et al.*, 1892), the British Isles and the North Sea (de Jong *et al.*, 1995; Ellis, 2004; Heessen and Ellis, 2006; Quigley *et al.*, 2008; Howes, 2017), Bay of Biscay and Iberian waters (Muñoz-Chápuli, 1985; Moreno *et al.*, 1998), Mediterranean Sea (Kabasakal, 2007; de Maddalena *et al.*, 2016; Panayiotou *et al.*, 2020; Serena *et al.*, 2020), Black Sea (Kabasakal, 1998; Serena *et al.*, 2020) Western Sahara (Muñoz-Chápuli, 1985), Morocco (Cadenat and Blanche, 1981; Muñoz-Chápuli, 1985; Moreno *et al.*, 1998), Canary Islands (Muñoz-Chápuli, 1985; Moreno *et al.*, 1998), Mauritania and Senegal (Muñoz-Chápuli, 1985), Madeira (Cadenat and Blanche, 1981), Ghana, Côte d'Ivoire, Angola, Namibia and South Africa (Cadenat and Blanche, 1981; Bass *et al.*, 1975; Compagno, 2001; Petersen *et al.*, 2008; Rigby *et al.*, 2019; Ebert *et al.*, 2021; Sekey *et al.*, 2022). Within its family, *A. vulpinus* is the species whose geographic distribution reaches higher latitudes, at least in the Atlantic Ocean.

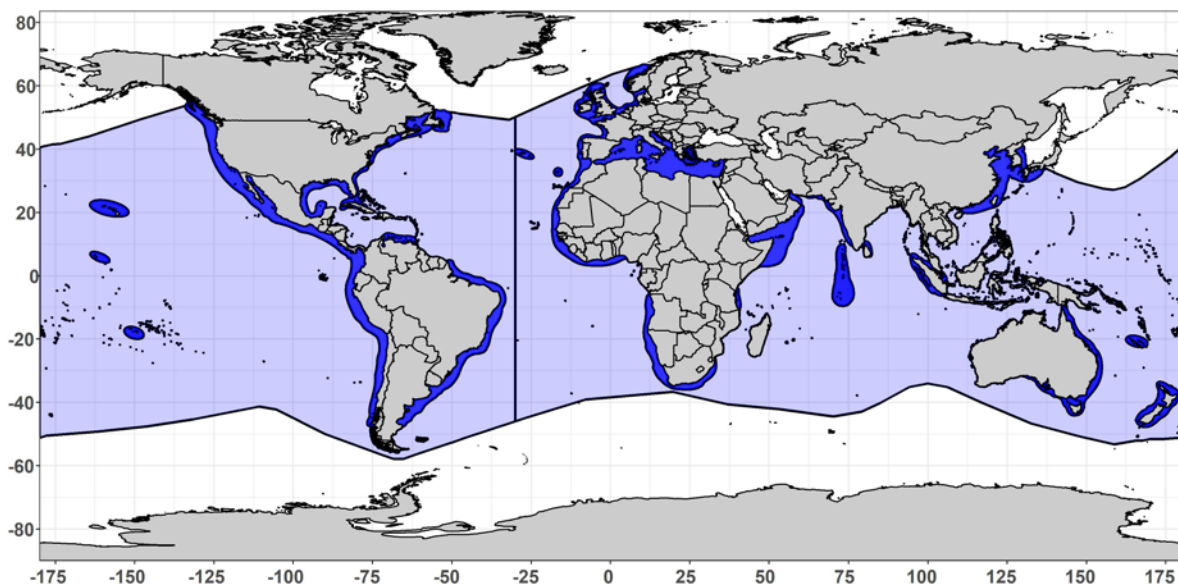


Figure 2. Geographic distribution of *Alopias vulpinus* in the Atlantic. Taken and modified from the International Union for Conservation of Nature (IUCN) (IUCN SSC Shark Specialist Group 2018. *Alopias vulpinus*. The IUCN Red List of Threatened Species. Version 2021-1).

3.b. Habitat preferences

Alopias vulpinus inhabits tropical and temperate neritic and oceanic waters, although it appears to be more abundant in waters on the continental shelf (Gubanov, 1972; Moreno *et al.*, 1998; Compagno, 2001; Berrondo *et al.*, 2007; Anon., 2008; Smith *et al.*, 2008; Kneebone *et al.*, 2020). Moreno *et al.* (1998) reported that the largest longline catches were taken no further than 40 miles off the North-eastern Atlantic coast, while in the Central Pacific, Strasburg (1958) noted that catches were virtually nil beyond 40 miles off the coast. Moreno *et al.* (1989) also referred to the occurrence of the species near the coast (from a few metres up to 8-9 nautical miles, nm), associated with the presence of large schools of fish, while Tudela *et al.* (2005) reported catches in driftnets 1-2 nm off the coast, taken by the Moroccan fisheries. More recent studies appear to indicate that space is used differently by the different age classes, which is likely related to the characteristics of the species' reproductive cycle. In the North-East Pacific, according to Smith and Aseltine-Neilson (2001), after birth and during the first years of life, juveniles are present near the coast and in shallow bays while larger individuals (> 300 cm) are generally more widely distributed and further off the coast. The use of acoustic telemetry tools in the same region has provided new evidence on the preference of sub-adults and adults for waters outside the continental shelf (>120 cm FL; Cartamil *et al.*, 2010a), and how almost all juveniles remain on the shelf (Cartamil *et al.*, 2010b).

While the monitoring times with this technique are limited, these data, in conjunction with high productivity on the continental shelf, suggest that these waters are possibly used as a breeding and pupping area (Cartamil *et al.*, 2010b). Further empirical evidence has been provided recently through use of satellite telemetry on juveniles within the area (Cartamil *et al.*, 2016). Catches of this species in the Northeast Pacific and Northwest Atlantic demonstrate that the progressive use of deeper waters is linked to ontogeny. Juveniles more frequently occupy shallow waters while adults and sub-adults expand their distribution to reach deeper waters on the external continental shelf, slope and oceanic waters (Smith *et al.*, 2008; Kneebone *et al.*, 2020).

A. vulpinus inhabits tropical and temperate waters of all oceans (Compagno, 2001). While telemetry studies indicate its preference for using upper parts of the water column, including surface waters, and occupying waters above the thermocline for most of the time, there is sound evidence that the species is capable of performing extensive vertical migrations (Heberer *et al.*, 2010; Stevens *et al.*, 2010; Cartamil *et al.*, 2011, 2016). In the North-East Pacific, acoustic and satellite telemetry data indicate that the species is preferentially found above the thermocline (<20 m) at night, while during the daytime it is found at significantly greater depths and frequently carries out vertical migrations under the mixed layer, to a recorded maximum of 320 m (Cartamil *et al.*, 2010a, 2011; Heberer *et al.*, 2010). While limited by the shallower depth of the shelf waters, juvenile individuals also display a different use of the water column during the day and at night (Cartamil *et al.*, 2010b; Cartamil *et al.*, 2016). A specimen monitored by satellite telemetry in eastern Australia spent 80.3% and 8.9% of the time at depths less than 100 m during the night and daytime, respectively (Stevens *et al.*, 2010). These authors also reported behaviour more similar to night-time behaviour at dusk (51% of the time at <100 m), and more similar to daytime behaviour at dawn (31% of the time at <100 m). The maximum depth reached by this individual (640 m) (Stevens *et al.*, 2010) is twice that reported for the Northeast Pacific (Cartamil *et al.*, 2011). Heard *et al.* (2017) tagged a specimen measuring 175 cm FL in southern Australia and also observed that the individual used the water column differently during the day and at night.

The differential use of the water column during the daytime and at night has been reported for other shark species (e.g. *Alopias superciliosus*, Weng and Block, 2004; *Carcharodon carcharias*, Nasby-Lucas, *et al.*, 2009; *Isurus oxyrinchus*, Vetter *et al.*, 2008). Cartamil *et al.* (2010a) suggested that the frequent vertical migrations performed during the daytime would indicate increased activity of the individuals during this period, possibly food related. Since the species inhabits a vast proportion of the water column, as a product of their vertical migrations, it experiences a wide range of temperatures, which are colder during the daytime and warmer at night (Cartamil *et al.*, 2010a, 2011; Stevens *et al.*, 2010). Telemetry studies carried out in the Northeast Pacific indicate that the species frequents surface temperatures of between 16 and 21.7°C, experiencing temperatures down to 9.1°C during their vertical migrations (Cartamil *et al.*, 2010a, 2011). For its part, the only individual monitored by Stevens *et al.* (2010) experienced a temperature range of between 11.0 and 27.0°C, spending most of its time between 15.0-17.5°C or 22.5-25.0°C.

In the Northwest Atlantic and Gulf of Mexico, Kneebone *et al.* (2020) analysed *A. vulpinus* catch in several fisheries, including pelagic longline, bottom longline, trawl net, purse seine, gillnet and recreational fishing. Catches were taken over a wide range of surface temperatures (4-31°C), although more frequently between 12 and 18°C. Although the species was caught in areas with an extensive bathymetric range (1 to 5,427 m), 47% took place in waters 10-25 m deep, and 98% of juveniles in their first year of life were caught at depths of less than 50 m. In waters off the State of Florida, United States, Castro (2011) reported catches at surface temperatures of 16.5-19.8°C. Cao *et al.* (2011) studied the ambient preferences of *A. vulpinus* in waters close to the Marshall Islands, in the West Pacific, based on 69 longline fishing sets directed at bigeye tuna (*Thunnus obesus*). The authors reported the preferred ranges for depth (160-240 m), temperature (18-20°C), salinity (34.5-34.9) and dissolved oxygen (1.0-1.5 ml/l). However, given the setting and haul-back times of the fishing gear during this study, the ranges of the ambient variables presented by the authors would only correspond to the species' habitat use during the daytime.

3.c. Migrations

The information on movements of *A. vulpinus* is scarce. Based on data from the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program, Kohler and Turner (2019) reported a 2% recapture rate of the total tagged specimens (n=203). Based on these data, the maximum distance travelled was 271 km and the maximum time at liberty was 8 years. Sepulveda *et al.* (2015) reported that distances of 425 and 446 km were travelled in a time at liberty of 90 and 81 days, respectively, in the Northeast Pacific, while in the Indian Ocean Gubanov (1976) reported a distance travelled of 1,556 km based on tagging and recapture.

In the North-eastern Atlantic, more precisely on the Iberian and Moroccan coasts, while *A. vulpinus* is caught all year round, catches are more frequent between spring and early autumn (Moreno *et al.*, 1989). It is believed that a migration occurs in July and August towards more coastal waters, where aggregations mainly of neonate pups and gravid females are found (Moreno *et al.*, 1989). These authors also reported a large abundance of specimens between July and August a few metres off the coast, and up to 8-9 miles offshore between Chafarinas and Cape Quilates (Northeast Morocco).

In the Northwest Atlantic, Kneebone *et al.* (2020) reported catches from Florida in the United States up to Canada, and indicated the seasonal nature of these catches throughout the year. According to these authors, juveniles and adults made periodic north-south and south-north migrations. Furthermore, catches were particularly scarce to the south of 37°N in summer and to the north of this latitude in winter. These movements are related to water temperature, but other biological (size, sex) and ecological (feeding, reproduction) factors likely affect the timing and direction of these migrations (Kneebone *et al.*, 2020, Kinney *et al.*, 2020).

In the Northeast Pacific there is evidence of a latitudinal migration throughout the year. According to this hypothesis, the species would migrate North, from Baja California to southern Californian waters, in early spring, where presumably pupping would take place and there would be a nursery area (Holts, 1988; Hanan *et al.*, 1993; Smith and Aseltine-Neilson, 2001; Cartamil *et al.*, 2010b; Cartamil *et al.*, 2016; Kinney *et al.*, 2020). Sub-adults would remain in the region in summer, moving towards the coast and reaching waters as far North as San Francisco. For their part, adults (mainly males) would continue their northbound course, reaching waters of the State of Oregon, Washington and even Vancouver Island in late summer and early autumn (Bedford, 1985; Holts, 1988; Hanan *et al.*, 1993; Smith and Aseltine-Neilson, 2001; Cartamil *et al.*, 2010b; Kinney *et al.*, 2020). Finally, it is thought that the species would retract its distribution in autumn towards more southerly waters, spending winter in waters off Mexico (Smith and Aseltine-Neilson, 2001; Anon., 2008; Smith *et al.*, 2008; Cartamil, 2009; Kinney *et al.*, 2020).

4. Biology

4.a. Growth

Studies on age and growth of *A. vulpinus* are particularly scarce (**Table 1**) and restricted to the Northwest Pacific (Cailliet *et al.*, 1983; Smith *et al.*, 2008) and North-western Atlantic (Natanson, 2002; Gervelis and Natanson, 2013; Natanson *et al.*, 2015). These papers generally agree that *A. vulpinus* is a large, slow growing species. However, compared with other thresher species (*Alopias pelagicus* and *A. superciliosus*), *Alopias vulpinus* has a relatively faster growth rate, a lower age of maturity and a larger maximum length (Smith *et al.*, 2008).

Table 1. Growth parameters for *Alopias vulpinus* (according to the Von-Bertalanffy growth model. L_{∞} : Maximum asymptotic length (cm), k : growth coefficient (years⁻¹), t_0 : theoretical age at length 0 (years)).

Growth parameter			Area	Reference	Sex	Method
L_{∞}	k	t_0				
225 (FL)	0.17	81 (FL)*	North-western Atlantic	Gervelis & Natanson (2013)	Males	Vertebrae
274 (FL)	0.091	-4.82	North-western Atlantic	Gervelis & Natanson (2013)	Females	Vertebrae
256 (FL)	0.11	-3.99	North-western Atlantic	Natanson <i>et al.</i> (2015) ^f	Both	Vertebrae/BRC
493 (TL)	0.215	-1.416	North-East Pacific	Cailliet <i>et al.</i> (1983)	Males	Vertebrae
636 (TL)	0.158	-1.021	North-East Pacific	Cailliet <i>et al.</i> (1983)	Females	Vertebrae
651 (TL)	0.108	-2.362	North-East Pacific	Cailliet <i>et al.</i> (1983)	Both	Vertebrae
416 (TL)	0.189	-2.080	North-East Pacific	Smith <i>et al.</i> (2008)	Males	Vertebrae
464 (TL)	0.124	-3.350	North-East Pacific	Smith <i>et al.</i> (2008)	Females	Vertebrae
465 (TL)	0.129	-2.879	North-East Pacific	Smith <i>et al.</i> (2008)	Both	Vertebrae

TL: total length; FL: fork length; BRC: bomb radiocarbon. * A modified version of Von-Bertalanffy was used with a fixed size at birth of 81 cm FL.^c According to the authors, the Schnute model exhibited slightly greater adjustment than the Von-Bertalanffy model, but the latter is presented in the table for the purpose of comparison with other published models.

In the North-western Atlantic, Gervelis and Natanson (2013) reported specimens of up to 22 and 24 years of age for males (~413 cm) and females (~445 cm), respectively, and estimated that the species could achieve a longevity of up to 31 years. According to these authors, males and females display similar growth until 8 years of age, from which point the male growth rate decreases. Females do not carry out this migration until they have reached the age of 12 (Gervelis and Natanson, 2013). Based on generated growth curves and unpublished NMFS data, Gervelis and Natanson (2013) estimated a median age-at-maturity of 8 and 12 years for males and females, respectively.

Natanson *et al.* (2015) used the bomb radiocarbon technique for the first time in this species to validate the frequency of growth band deposition. The results of this study confirmed annual deposition for the species. However, the authors highlighted that classic band count methods can accurately determine age only up to 14 years of age, as the band count tends to underestimate the real age of more long-lived individuals. Natanson *et al.* (2015) reported a maximum age of 38 years, which demonstrates that longevity is considerably higher than previously believed. The authors updated growth curves for this species, changing classic vertebra count techniques up to 14 years of age (Gervelis and Natanson, 2013) in conjunction with specimens dated using radiocarbon. According to the results, the age at maturity of males remained unchanged at 8 years, while the age at maturity of females increased from 12 to 13 years. More recently, the annual frequency of band formation was also partially validated in the Northeast Pacific based on the recapture of samples that had been tagged with oxytetracycline (Spear, 2017).

In the North-East Pacific, the individuals with the longest lifespan dated by Cailliet *et al.* (1983) reached 15 years of age (510 and 539 cm), although extrapolating data based on growth curve, the authors estimated an age of 50 years for reaching maximum asymptotic length (651 cm). Two decades later, Smith *et al.* (2008) incorporated new data into those used by Cailliet *et al.* (1983) and used a more precise alternative length conversion (distance between the origin of the first and second dorsal fin) to total length than that used previously. These authors dated a maximum age of 22 years in a female of 480 cm, but given that its length was considerably less than the maximum length reported for the species, they suggested that the species could achieve a lifespan of up to 25 years. The underestimation of the maximum asymptotic length reported by Smith *et al.* (2008) with respect to maximum lengths communicated for the Pacific (see section 2) could be due to the small number of large size individuals included in the study. In the North-East Pacific males of this species reach maturity at an estimated age of 4.8 years, while for females it is around 5.3 years (Smith *et al.*, 2008). Cailliet *et al.* (1983), like Smith *et al.* (2008), indicated similar growth for both sexes within the range of ages analysed. Comparing the results of Smith *et al.* (2008) and Natanson *et al.* (2015), specimens of *A. vulpinus* in the North-East Pacific would reach reproductive maturity at an earlier age than their counterparts in the Northwest Atlantic.

4.b. Length-weight relationship

There are few length-weight relationships for this species in literature. **Table 2** details those found in the current bibliographic review.

Table 2. Length-weight relationships published for *Alopias vulpinus*. TW: total weight (kg); GW: gutted weight (without the head, guts or fins; kg); TL: total length (cm); FL: fork length (cm).

Equation	N	Length range (cm)	R ²	Area	Reference
$TW = 1.8821 \times 10^{-4} \times (FL)^{2.5188}$	88	154-262	0.88	North-western Atlantic	Kohler <i>et al.</i> (1995)
$GW = 1.066 \times 10^{-7} \times (FL)^{2.81}$	-	-	-	North-East Pacific	Bedford (1985)
$TL = 60.7 \times (GW)^{0.351}$	18	-	0.99	Mediterranean Sea	Megalofonou <i>et al.</i> (2005a)
$TW = 4.0 \times 10^{-5} \times (FL)^{2.8156}$	693	145-263	0.93	North-western Atlantic	Gervelis & Natanson (2013)
$TW = 6.0 \times 10^{-3} \times (TL)^{2.824}$	21	142-415	0.80	Adriatic Sea	Colombelli & Bonanomi (2022)

4.c. Conversion factors

Published length-length relationships for several areas of the Atlantic are shown in **Table 3**.

Table 3. Published length-length relationships for *Alopias vulpinus*. TL: total length (cm); FL: fork length (cm); PCL: precaudal length (cm).

Equation	N	Length range (cm)	R ²	Area	Reference
$FL = 0.5474 \times (TL) + 7.0262$	13	291-450	0.89	North-western Atlantic	Kohler <i>et al.</i> (1995)
$TL = 1.687 \times (FL) + 20.483$	22	-	0.93	North-eastern Atlantic	Buencuerpo <i>et al.</i> (1998)
$FL = 1.118 \times (PCL) - 2.29$	22	-	0.99	North-eastern Atlantic	Buencuerpo <i>et al.</i> (1998)
$TL = 1.707 \times (FL) + 20.2$	24	-	0.95	Mediterranean Sea	Megalofonou <i>et al.</i> (2005a)
$FL = 0.5168 \times (TL) + 16.466$	173	150-262	0.84	North-western Atlantic	Gervelis & Natanson (2013)

4.d. Reproduction

The reproductive biology of the *A. vulpinus* has been relatively little studied at global level, and most information gathered to date is from the North-East regions of the Pacific and Atlantic, and western region of the Mediterranean Sea.

Gestation and pupping

Oophagy is a common feeding mechanism during embryo development in Lamniformes (Gilmore, 1993; Gilmore *et al.*, 2005) and its occurrence has already been observed in *A. vulpinus* (Gubanov, 1972; Moreno *et al.*, 1989; Natanson and Gervelis, 2013). According to Moreno *et al.* (1989), the embryos arrange themselves indistinctly in both uteri in alternate position, without significant predominance of either of the sexes, with the caudal fin retracted. They are covered with foetal grease in the final stages of development which would appear to be lost during or immediately after birth. In embryos, the first row of teeth lie flat (except in at term embryos), and are shorter than the subsequent rows, which is why it is thought that they would not be functional (Moreno *et al.*, 1989). Based on the absence of these teeth inside the maternal uterus and of the digestive tract of the embryos, Moreno *et al.* (1989) suggested that these are replaced shortly after birth. For his part, Gilmore (1993) refers to the presence of small, erect embryonic teeth, with a different morphology compared to adult teeth, in two specimens of 59 and 61.5 cm, which would appear to be used to break egg capsules and consume their contents. While it has been suggested that the species could display intrauterine cannibalism (Compagno, 1984), there are no reports to date that confirm this behaviour takes place (Gilmore, 1993; Natanson and Gervelis, 2013). In a more recent study on reproduction, Natanson and Gervelis (2013) observed a turning point in embryos' feeding at a length of around 70 cm FL (~ 104 cm TL), at which point ovulation stops and embryos continue to grow thanks to the yolk they have already consumed and accumulated in their digestive tract.

The gestation period of *A. vulpinus* is estimated at 9 months in the Pacific (Bedford, 1985; Hanan *et al.*, 1993; Smith and Aseltine-Neilson, 2001) and, unlike what is estimated for *A. superciliosus* (e.g. Chen *et al.*, 1997), this species would appear to display a pupping and mating period that is more defined in time. The reproductive frequency of *A. vulpinus* would be around 12 months (Cailliet and Bedford, 1983; Bedford, 1985). In the Northwest Atlantic, Natanson and Gervelis (2013) noted that gestation and vitellogenesis occur sequentially over time, and hypothesized a biennial reproductive cycle with a gestation period of approximately one year and a rest stage lasting for the same period of time. Nonetheless, inconclusive results suggest that the cycle could even be triennial. The authors' sample, albeit exhaustive, was limited to specimens caught in a single period of the year (mainly from June to August), which highlights the need for more extensive sampling in order to reach more solid conclusions. According to these authors, the mating period would occur in the autumn.

Based on the presence of gravid at-term females and post-partum females, Natanson and Gervelis (2013) reported that in the Northwest Atlantic pupping would take place between May and June, and could even extend to August. The authors also suggested that pupping would take place in coastal areas between the states of Delaware and Massachusetts, United States. Kneebone *et al.* (2020) observed that 99% of individuals in the first year of life were caught on the continental shelf and to the north of 35°N, which suggests that the waters of the state of North Carolina could play an important role for the species as a nursery area. In the Northeast Atlantic (Cádiz and Northwest Morocco), Moreno *et al.* (1989) reported the presence of a large number of neonates and gravid females carrying at-term embryos under 40 nm from the coast between May and August, which suggests that the pupping peak may also take place in May, as reported for the Northwest Atlantic. In the Mediterranean, Finotto *et al.* (2016) suggested that the northern Adriatic Sea could represent a pupping and/or nursery area for the species, based on catches of juveniles in midwater trawl nets. In the Southwest Atlantic, more precisely in Southeast Brazil, although the occurrence of this species is infrequent (Amorim *et al.*, 1998; Gadig *et al.*, 2001), the presence of gravid females with embryos in late stages of development and reports of neonates and juveniles in coastal waters between April and July led Mancini and Amorim (2006) to suggest that at least part of the reproductive cycle of *A. vulpinus* could take place in this region during the austral summer. In the same region, Barcellos (1957) reported the catch of two individuals measuring 123 and 131 cm between April and May, Gadig *et al.* (2002) reported the catch of a 150 cm specimen during the winter, and Sadowsky (1967) and Gadig *et al.* (2001) reported the occasional catch of specimens between 176 and 190 cm from July to November. Piva Silva *et al.* (2008) reported the catch of a female carrying four at-term embryos (115.5-118.8 cm) at the end of November in Southeast Brazil (36°00'S and 33°00'-34°00'W). In Uruguayan waters, Silveira *et al.* (2018) reported the catch of a small *A. vulpinus* juvenile measuring 190 cm in winter off the Atlantic coast of the Department of Rocha, while neonates and juveniles measuring between 110 and 150 cm are occasionally caught in Uruguay's artisanal fisheries between the summer and the beginning of autumn (DINARA, unpublished data). Overall, information from various areas of the Southwest Atlantic, suggests that the pupping season would mainly take place during summer and at the start of autumn, similarly to the Northwest Atlantic (Natanson and Gervelis, 2013), in coastal waters off Southeast Brazil and the East coast of Uruguay.

In the Northeast Pacific, sub-adults and adults gather annually in coastal waters of southern California in spring and summer (Cailliet and Bedford, 1983; Bedford, 1985; Hanan *et al.*, 1993). Several authors refer to a large presence of gravid females and neonates in the months of spring (March to June), suggesting that pupping would take place in that season. Mating could occur soon after birth, during summer (Cailliet and Bedford, 1983; Bedford, 1985; Smith and Aseltine-Neilson, 2001; Cartamil, 2009). According to Cartamil (2009), the nursing area of *A. vulpinus* within the Northeast Pacific would extend from Point Conception, California, to Punta Eugenia, Baja California, Mexico. More recent data provide new evidence in favour of this hypothesis (Cartamil *et al.*, 2016). In the North-western Indian Ocean, between January and May, Gubanov (1972) reported a disproportionate presence of females, of which 93% were gravid.

The species' size-at-birth appears to be variable. For the Indo-Pacific, Last and Stevens (1994) reported sizes at birth of 114 and 160 cm, while Gubanov (1972) reported a size of 110 cm for the Indian Ocean. Cailliet and Bedford (1983) and Bedford (1985) reported for the North-East Pacific a length range of between 150 and 158 cm, while a more recent study within the same region (Smith *et al.*, 2008) reported a wider length range (114-156 cm). In the Northeast Atlantic, Moreno *et al.* (1989) found broad overlap between the lengths of the largest embryos observed (156 and 159 cm) and the lengths of the smallest neonates (120, 122 and 126 cm). These authors concluded that natality may not be closely linked to embryo length, but rather to morphological changes that occur throughout their development (erection of the first row of teeth and loss of foetal grease), therefore suggesting a broad spectrum of lengths at birth (120-160 cm), similar to that indicated by Smith *et al.* (2008) for the North-East Pacific. Barrull *et al.* (1999) reported a minimum length of 125 cm in the Northwest Mediterranean Sea, which tallies with the minimum lengths reported by Moreno *et al.* (1989). Based on a sample of 48 specimens in 14 distinct litters, Natanson and Gervelis (2013) reported a maximum embryo size of 81 cm FL (~125 cm TL) in the Northwest Atlantic. In addition, the smallest neonates observed by these authors were between 78 and 89 cm FL (~119 and 140 cm TL), which suggests an average size at birth of 80 cm FL (~123 cm TL). This is consistent with sizes reported for other areas of the Atlantic and other oceans.

Maturity

Information on length at maturity of *A. vulpinus* in the Atlantic Ocean is particularly scarce. Moreno *et al.* (1989) reported a length of 384 cm for the smallest adult female in the Northeast Atlantic, but it was not possible to estimate a length at maturity for males. The reporting of a gravid female of 385 cm by Buencuerpo *et al.* (1998) in the same region is consistent with the estimate of Moreno *et al.* (1989). Natanson and Gervelis (2013) studied the reproductive biology of this species, based on a sample of 130 males and 256 females caught in the Northwest Atlantic. The results of this study reported a median size at maturity 188 cm FL (~332 cm TL) for males and 216 cm FL (~386 cm TL) for females. The smallest adult reported by these authors was 181 cm FL (~318 cm TL). It should be noted that mature sperm was found in the testicles and epididymides of all juvenile and adult individuals that were subjected to histological techniques, which suggests that the presence of sperm alone is not sufficient to determine the stage of maturity of male individuals (Natanson and Gervelis, 2013). The smallest gravid female recorded was 221 cm FL (~395 cm TL), while the smallest adult was 208 cm FL (~371 cm TL). According to updated growth curves for the same region, males and females would reach the median size at maturity at an age of 8 and 13 years, respectively (Natanson *et al.*, 2015).

Compagno (1984) mentioned a length at maturity of 319 and 376 cm for males and females, respectively, which is generally consistent with the figures reported by Natanson and Gervelis (2013). Estimates of length at maturity of this species have been reported for the North-East Pacific, however, several studies report different estimates. According to Cailliet and Bedford (1983), males would reach sexual maturity at around 330 cm and females between 260 and 315 cm. Bedford (1985) reported a length at maturity for females of 230 cm FL (413 cm TL), corresponding to an age of 7 years based on the growth curves of Cailliet *et al.* (1983). A more recent study establishes a length at maturity of 293-311 cm and 303 cm for males and females, respectively (Smith *et al.*, 2008). According to these authors, both sexes would reach maturity at around 5 years of age. For the Indian Ocean, Gubanov (1972) suggested a size at maturity for females of approximately between 260 and 330 cm.

The minimum sizes reported for gravid females are 221 cm FL (~ 396 cm TL, Natanson and Gervelis, 2013) in the Northwest Atlantic, 385 cm in the Northeast Atlantic (Buencuerpo *et al.*, 1998) and 298 cm in the Indian Ocean (Gubanov, 1972).

Sex ratio

The sex ratio between embryos from a given litter does not significantly differ from the ratio 1:1 (Moreno *et al.*, 1989; Natanson and Gervelis, 2013). However, there is evidence of sex segregation at spatial level, which is mainly associated with migrations towards more coastal waters in the context of the reproductive cycle of the species (Gubanov, 1972; Holts, 1988; Bedford, 1985; Moreno *et al.*, 1989; Hanan, 1993; Smith and Aseltine-Neilson, 2001; Cartamil, 2009; Kinney *et al.*, 2020).

Fecundity

The litter size of *A. vulpinus* tends to range from 2 to 4 embryos, generally being 4 (2 embryos per uterus) (Gubanov, 1972; Cadenat and Blanche, 1981; Cailliet and Bedford, 1983; Compagno, 1984; Bedford, 1985; Buencuerpo *et al.*, 1998; Smith and Aseltine-Neilson, 2001; Mancini and Amorim, 2006; Smith *et al.*, 2008; Natanson and Gervelis, 2013). However, Holts (1988) reported litter sizes of up to 6 embryos in the North-East Pacific, while Moreno *et al.* (1989) reported a maximum of 7 embryos in the North-East Atlantic and in the western Mediterranean Sea, even mentioning a possible record of 8 embryos in a single litter based on fishers' anecdotes. Based on a study of 12 gravid females in the Northwest Atlantic, Natanson and Gervelis (2013) reported litters of between 1 and 4 embryos, with an average of 4 embryos per litter.

4.e. Diet

Thresher sharks use the whip-like dorsal lobe of their caudal fin to hit, disorientate and stun their prey (Compagno, 2001; Smith *et al.*, 2008; Aalbers *et al.*, 2010), which is probably why it is relatively common to observe specimens hooked by this fin in longline fisheries (Gubanov, 1972; Strasburg, 1958; Gubanov, 1972; Stillwell and Casey, 1976; Gruber and Compagno, 1981; Smith *et al.*, 2008; Castro, 2011). In the North-East Pacific, some sport fishers make the most of this aspect of the species' behaviour by using a special type of lure to catch them directly by their caudal fin (CalCOFI, 2009; Heberer *et al.*, 2010).

In general, the diet of *A. vulpinus* mainly consists of bony fish and cephalopods, although on occasions some crustaceans, chondrichthyans and even birds have been recorded (Gubanov, 1972; Compagno, 1984, 2001; Pascoe, 1986; Cortés, 1999; Bowman *et al.*, 2000; Preti *et al.*, 2001, 2004). The most detailed and comprehensive studies of the diet of *A. vulpinus* have been carried out in waters of the Northeast Pacific. According to these studies, *A. vulpinus* covers a broad spectrum of species, feeding mainly on pelagic fish, but also mesopelagic and demersal species, with the diet composition showing significant differences at latitudinal scale and under different oceanographic conditions (Preti *et al.*, 2001, 2004, 2012). In particular, Preti *et al.* (2004) provided solid evidence of a significant change in the trophic spectrum used by the species, both in number of taxa and species composition, during the influence of El Niño (warm waters, 20 taxa) and La Niña (cold waters, 8 taxa).

Bowman *et al.* (2000) analysed the stomach contents of 12 specimens of *A. vulpinus* in the Northeast Atlantic and found that the diet mainly comprised pelagic fish (97.1%), the remainder being cephalopods (2.9%). A previous study carried out by Cortés (1999) compares the results of Bowman *et al.* (2000). By compiling information from different studies, and based on the analysis of 399 stomachs, Cortés (1999) reported greater dominance of cephalopods (71.8%) in comparison with bony fish (26.7%). By analysing stable isotopes in several tissues, MacNeil *et al.* (2005) reported that *A. vulpinus* would display a generalist diet that is consistent throughout the year within the Northwest Atlantic. However, given the small number of samples analysed (n=5), these results should be viewed with caution. Finotto *et al.* (2016) reported a correlation between *A. vulpinus* catches and sardine (*Sardina pilchardus*) catches in the Adriatic Sea, which suggests a trophic relationship between these species. In southern Australia, Rogers *et al.* (2012) examined 17 stomachs with contents and only found small pelagic fish, in particular anchovies (*Engraulis astralis*) and sardines (*Sardinops sagax*). These authors suggested that *A. vulpinus*'s diet could be highly specialised in small pelagic fish.

Below is a list of species referred to in the diet of *A. vulpinus* based on the literature review (Compagno, 1984, 2001; Bowman *et al.*, 2000; Preti *et al.*, 2001, 2004, 2012; Rogers *et al.*, 2012):

Teleosts: Alepisauridae sp., *Ammodytes dubius*, *Atherinops affinis*, *Citharichthys sordidus*, Clupeidae sp., *Cololabis saira*, Belonidae sp., Engraulidae sp., *Engraulis astralis**, *Engraulis mordax**, Exocoetidae sp., *Genyonemus lineatus*, *Leuresthes tenuis*, *Luarus imperialis*, *Magnisudis atlantica*, *Merluccius productus**, Myctophidae sp., Paralepididae sp., *Peprilus simillimus*, Pleuronectidae sp., *Pomatomus saltatrix**, *Sarda chiliensis*, *Sardinops sagax**, Scombridae sp., *Scomber japonicus**, *Scomberesox saurus*, *Sebastes* sp., *Sebastes jordani*, *Seriphus politus*, *Sphyræna argentea*, *Trachurus symmetricus*.
Cephalopods: *Dosidicus gigas*, *Gonatus* sp., *Illex illecebrosus*, *Loligo opalescens**, Ommastrephidae sp., Teuthoidea sp.
Crustaceans: *Pleuroncodes planipes*.

* Dominant species in the composition of the diet (in weight or number).

4.f. Physiology

Existing evidence that several sharks of the Lamniformes order are capable of maintaining their body temperature above that of the surrounding water through generation of metabolic heat (regional endothermy; Carey and Teal, 1969; Block and Carey, 1985; Block and Finnerty, 1994; Bernal *et al.*, 2001, 2005), historically suggested the possibility that this ability is shared by thresher sharks (Alopiidae) (e.g. Gruber and Compagno, 1981; Weng and Block, 2004; Smith *et al.*, 2008; Amorim *et al.*, 2009). However, detailed studies of the physiology of these sharks show that only *A. vulpinus* possess the physiological specialisations necessary to generate metabolic heat and maintain it, thus enabling generation of a regional endothermy (Bernal and Sepulveda, 2005; Sepulveda *et al.*, 2005; Patterson *et al.*, 2011). Unlike all other species of this genus, in *A. vulpinus* the aerobic red muscle is internalised in an epaxial position close to the spinal column, which drastically reduces loss of the heat generated (Bernal and Sepulveda, 2005; Sepulveda *et al.*, 2005; Patterson *et al.*, 2011).

For *A. superciliosus* in particular, Weng and Block (2004) reported the presence of a network or plexus of arteries and veins that almost run in contact and in the opposite direction in the cephalic region and suggested that this species could be capable of generating a cranial endothermy, maintaining only the eye and brain temperatures above the ambient temperature. This capacity would enable the species to feed more efficiently even at low temperatures during their extensive vertical migrations (Weng and Block, 2004). In a previous paper, Block and Carey (1985) located this network in *A. superciliosus* and *A. pelagicus*, but not in *A. vulpinus*. In shark in which the cranial endothermy has been observed (e.g. *I. oxyrinchus* and *Lamna nasus*), the internal carotid artery is narrow, while in sharks lacking this ability this artery is the main blood supply to the brain (Block and Carey, 1985). The internal carotid artery does not pass through the network or plexus, and therefore sends cold blood to the brain (Block and Carey, 1985). According to the paper by Block and Carey (1985) none of the thresher species has a narrow internal carotid artery. Therefore, in the absence of *in vivo* measurements of cranial temperature, it is not yet possible to confirm the cranial endothermy in this family (Weng and Block, 2004).

Wootton *et al.* (2015) performed a detailed analysis of the gills of three species from the *Alopias* genus and concluded that, unlike *A. superciliosus*, neither *A. vulpinus* nor *A. pelagicus* have the necessary physiological adaptations to efficiently exploit the mesopelagic niche and tolerate hypoxic conditions for prolonged periods. This explains the more epipelagic habits of *A. vulpinus* and *A. pelagicus* compared to *A. superciliosus*.

4.g Mortality

Bedford (1985) reported the presence of two neonates of *A. vulpinus* in the stomach of a shortfin mako (*I. oxyrinchus*) of approximately 210 cm. However, given the long length at birth (120-160 cm), the survival rate of neonates of this species can generally be expected to be high (Bedford, 1985), as has also been suggested for *A. superciliosus* (Gilmore, 1993; Chen *et al.*, 1997). Similarly, due to the large size of this species, it likely has few natural predators over the course of its life. In the waters of New Zealand, Visser (2005) reported that orcas (*Orcinus orca*) occasionally attacked and consumed *A. vulpinus* of between 150 and 300 cm.

Knowledge regarding catch and post-catch mortality is limited for this species. Sepulveda *et al.* (2015) used archival transmitters to assess post-catch mortality of specimens caught by recreational fishing in California, the United States. Although the number of samples was limited, the authors observed apparent differences in post-catch mortality depending on whether the individuals had been hooked by the mouth or using a special technique that aims to hook the caudal fin. The 7 tagged specimens hooked by the mouth survived for at least 10 days after they were caught and released, while only 3 of the 9 tagged specimens hooked by the caudal fin survived. Two of the 3 specimens caught by the Portuguese longline fleet in the Atlantic were found to be dead at haulback (Coelho *et al.*, 2012).

5. Fisheries biology

5.a. Stocks/ stock structure

Based on mitochondrial DNA (control region), Trejo (2005) found greater genetic interpopulation variation than intrapopulation even within the same region (Indo-Pacific, Atlantic), suggesting that *A. vulpinus* has a lower dispersion ability compared to its next of kin (*A. superciliosus* and *A. pelagicus*). Based on the results of pair-wise ranking, Trejo (2005) raised the existence of at least 6 populations, or management units, that are genetically differentiated (Oregon-Washington-California; Chinese Taipei; New Zealand; South Africa; Northwest Atlantic and France). The presence of haplotypes shared between populations of the Indo-Pacific (New Zealand and South Africa) and the Atlantic (Gulf of Mexico, Northwest Atlantic and France) suggested that, either they are shared ancestral traits, or there is some genetic flow between the two ocean basins (Trejo, 2005). However, based on the presence of *A. vulpinus* in South African waters, the author suggests that a certain genetic exchange could exist between the basins. Moreover, given that Trejo (2005) did not analyse samples from the South Atlantic, there is no reliable proof of genetic exchange between the Indo-Pacific and the Atlantic. Similarly, given that within the Atlantic Ocean the number of samples was small and restricted only to the North Atlantic, it is not yet possible to assert the existence of distinctive stocks between hemispheres. However, given the apparently limited dispersion ability of the species and the existence of genetically heterogeneous populations in several regions, the existence of distinctive stocks between the North and South Atlantic is at least likely.

5.b. Description of fisheries

A. vulpinus is caught by different fishing methods such as trawl and driftnet, gillnet, purse seine, rod and reel, bottom-set longline and surface pelagic longline (Maguire *et al.*, 2006; Rigby *et al.*, 2019; Kneebone *et al.*, 2020; Seidu *et al.*, 2022). At global level, thresher sharks (*A. pelagicus*, *A. superciliosus* and *A. vulpinus*) are traded internationally for their meat, skin and fins (Camhi *et al.*, 2008; Rigby *et al.*, 2019; Dent and Clarke, 2015). Although it is commonly considered to be a bycatch species in the pelagic fisheries, *A. vulpinus* is usually retained, even being considered as a secondary target species in some cases (CalCOFI, 2009, 2010; Rigby *et al.*, 2019).

This species is caught virtually throughout its distribution range within the Atlantic, including Canada (Hurley, 1998), United States (Berkeley and Campos, 1988; Beerkircher *et al.*, 2002; Passerotti *et al.*, 2010; Lynch *et al.*, 2018), the Gulf of Mexico and the Caribbean Sea (Arocha *et al.*, 2002; Tavares and Arocha, 2008), Brazil (Amorim, *et al.* 1998; Mancini and Amorim, 2006; Hazin *et al.*, 2008), Uruguay (Berrondo *et al.*, 2007; Forselledo and Domingo, 2015), South Africa (Basson *et al.*, 2007; Petersen *et al.*, 2008), North Africa (Moreno *et al.*, 1989), the Iberian Peninsula (Moreno *et al.*, 1989; Buencuerpo *et al.*, 1998), the Mediterranean Sea (Moreno *et al.*, 1989; Hattour and Nakamura, 2004; Megalofonou, *et al.* 2005a, b; Cavanagh and Gibson, 2007; Kabasakal, 2007; Finotto *et al.*, 2016), the Black Sea (Kabasakal, 1998), and around the British Isles, including the North Sea (Ellis, 2004; Heesen and Ellis, 2006; Quigley, *et al.* 2008; Howes, 2017).

In the longline fishery, catches of *A. vulpinus* vary between regions, but in no case do they appear to constitute a substantial proportion of the total shark catch. In Venezuela, this species represented 1.6% of the total shark catch of the Venezuelan longline fleet between 1994 and 2000 (Arocha *et al.*, 2002). In Southeast Brazil, *A. vulpinus* constituted less than 5% of the total shark catch of the Santos longline fleet between 1974 and 1997 (Amorim *et al.*, 1998). Within the Uruguayan Exclusive Economic Zone, and based on information obtained through the Observers Programme, this species represented around 0.5% of total shark catch of the pelagic longline fleet between 1998 and 2009 (Mas, 2012). Between 1998 and 2005, 2.2% of the total shark catch of the South African longline fleet comprised *A. vulpinus* (Petersen *et al.*, 2008). In the United States, this species was caught infrequently, representing, in conjunction with another 9 shark species, 4.2% of total catch of the longline fleet between 1992 and 2000 (Beerkircher *et al.*, 2002). According to Kneebone *et al.* (2020) the species is caught in several fisheries in the Gulf of Mexico, the East coast of the United States and Canada. The various population components are caught differently depending on the fishery. Neonates and small juveniles account for the majority of catches taken with gill nets and trawls, whereas adults are more common in pelagic longline and recreational rod and reel fisheries.

In the Mediterranean Sea, different pelagic shark species are taken as bycatch and targeted by driftnet, surface and bottom-set longline, trawl net and purse seine fisheries, *Prionace glauca*, *I. oxyrinchus* and *A. vulpinus* being the dominant species in catch (Tudela, 2004; Tudela *et al.*, 2005; Megalofonou *et al.*, 2005a; Panayiotou *et al.*, 2020). Tudela *et al.* (2005) reported that, on occasions, when the target species are scarce, the Moroccan fleet targeting swordfish casts their driftnets 1-2 miles off the coast, where the likelihood of catching pelagic sharks, and especially *A. vulpinus*, is greater. According to Megalofonou *et al.* (2005a), the magnitude of shark discards in general within the Mediterranean Sea is low due to the demand of the European market (considering longline and driftnet fisheries).

5.c. Stock status

In general, pelagic sharks, including *A. vulpinus*, tend to use their energy initially in somatic growth, delaying sexual maturity and living longer than small coastal sharks. In addition, they grow at a faster rate, reach maturity earlier and live shorter than the large coastal species (Cortés, 2000, 2002; Smith *et al.*, 2008). In particular, *A. vulpinus* is considered to be one of the more productive pelagic shark species (Cortés, 2008; Smith *et al.*, 2008). Based on the results of the ecological risk assessment in Atlantic pelagic longline fisheries carried out by Cortés *et al.* (2015), *A. vulpinus* was identified as a species with relatively low vulnerability, ranking 11th out of the 20 stocks and 16 species of pelagic elasmobranchs. However, since the species is essentially caught across the age classes and length spectrum by different fishing methods (Kneebone *et al.*, 2020), and given that to date the magnitude of unreported catches is not known, it is prudent to consider that this species is fully exploited or even overexploited at global level (Maguire *et al.*, 2006). In addition, the possibility that the species may have a biennial reproductive cycle could negatively affect the results obtained by Cortés *et al.* (2015), which considered an annual reproductive cycle.

For the Northwest Atlantic, Baum *et al.* (2003) reported a sizeable reduction in the abundance of a large number of shark species with respect to the levels prior to expansion of the industrial fishery, indicating, in particular for thresher sharks (*A. superciliosus* and *A. vulpinus* combined), a decrease of around 80%. Although these results have caused great controversy (e.g., Burgess *et al.*, 2005a, b; Maunder *et al.*, 2006), there is consensus that the abundance of many shark species has decreased, to a greater or lesser degree, compared to the past (e.g. Cortés *et al.*, 2007; Dulvy *et al.*, 2008). In the Northwest Atlantic, Cortés *et al.* (2007) reported an apparent stabilisation in the catch per unit of effort (CPUE) of *Alopias* sp. (*A. superciliosus* and *A. vulpinus* combined) and even a slight increase between the late 1990s and 2005, depending on the data source used. However, due to the infrequency of *A. vulpinus* in the catches of the United States longline fleet, these results are likely more reflective in trends of *A. superciliosus* (Cortés *et al.*, 2007). A more recent study performed in the same region reported a dramatic decrease in the catches of the US longline fleet from the end of the 1980s, followed by apparently stable catch yields (although 4 times lower than in the 1980s) until the end of the analysis period in 2013 (Lynch *et al.*, 2018). More recently, Pacoureaux *et al.* (2021) analysed abundance trends for 18 pelagic chondrichthyan species. According to the authors, global abundance of these species would have decreased by 46.1% in the Atlantic Ocean, 67.0% in the Pacific Ocean, and 84.7% in the Indian Ocean between the 1970s and 2018. At the global level, the estimations made by Pacoureaux *et al.* (2021) would indicate a 60% decrease in the relative abundance of *A. vulpinus*.

In the Mediterranean, Ferretti *et al.* (2008) estimated that, due to the intense fishing activity in recent decades, *A. vulpinus* would have experienced decreases of >80% in biomass and abundance in some regions of the Mediterranean, including the Adriatic Sea and Ionian Sea. In the Northeast Pacific, *A. vulpinus* has been a target species alongside swordfish (*Xiphias gladius*) in drift gillnet fisheries (Cailliet and Bedford, 1983; Bedford, 1985; Holts, 1988; Hanan, 1993; Smith and Aseltine-Neilson, 2001; CalCOFI, 2009; Teo *et al.*, 2018). Following its collapse in the late 1980s, *A. vulpinus* was included in a management plan in the West coast of the United States that included catch limits, restrictions on gillnet use and time closures (Maguire *et al.*, 2006; CalCOFI, 2009; Rigby *et al.*, 2009). Currently, this species is still caught incidentally and as a secondary target species in drift gillnet fisheries targeting swordfish (Maguire *et al.*, 2006; Rigby *et al.*, 2009) and continues to be the most frequently landed shark species (CalCOFI, 2009, 2010). According to Teo *et al.* (2018), the population has been showing signs of recovery since 2006, and it is unlikely that the stock is overexploited or overfished. The species is also valued in sport fishing, particularly in this region (Anon., 2008; CalCOFI, 2009; Heberer *et al.*, 2010; Sepulveda *et al.*, 2015).

Globally, *A. vulpinus* is classified as “Vulnerable” on the red lists of the International Union for the Conservation of Nature (IUCN; Rigby *et al.*, 2019). More local character assessments classify the species as “Endangered” in the Mediterranean Sea and Northeast Atlantic (Ellis *et al.*, 2015, 2016). Within the United States waters of the Atlantic, *A. vulpinus* is part of a management unit called “pelagic sharks” together with oceanic sharks (*Carcharhinus longimanus*), shortfin mako (*I. oxyrinchus*), blue shark (*P. glauca*) and porbeagle (*L. nasus*), but to date it has not been individually assessed (NMFS, 2010). According to Kneebone *et al.* (2020), there is no minimum sale size for this species in US waters of the Atlantic, while observer programme data indicate that at least some small juveniles are retained for sale.

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