

		<h1>ICCAT Manual</h1> <p>INTERNATIONAL COMMISSION FOR THE CONSERVATION OF ATLANTIC TUNAS</p>			
CHAPTER 2.2.1.2 SHORTFIN MAKO		AUTHORS: DOMINGO A., FORSELLEDO R., MAS F. & MILLER P.		LAST UPDATE: August 2022 ¹ Original: Spanish	

2.2.1.2 Description of Shortfin Mako (SMA)

1. Names

1.a Classification and taxonomy

Species name: *Isurus oxyrinchus* Rafinesque, 1810

Etymology: from the Greek *isos-ourá* meaning “equal-tail”, in reference to the almost homocercal tail, and the Greek *oxys-rhynchos*, meaning “pointed-snout”

Synonyms: *Isurus glaucus* (Müller and Henle, 1839)

ICCAT species code: SMA

ICCAT names: Shortfin mako (English), Taupe blue (French), Marrajo dientuso (Spanish)

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

- Kingdom: Animalia
- Phylum: Chordata
- Subphylum: Vertebrata
- Superclass: Gnathostomata
- Class: Chondrichthyes
- Subclass: Elasmobranchii
- Superorder: Euselachii
- Order: Lamniformes
- Family: Lamnidae
- Genus: *Isurus*

1.b Common names

List of vernacular names used in various countries according to ICCAT, FAO and Fishbase (www.fishbase.org). The list of countries is not exhaustive, and some local names might not be included.

Albania: Peshkagen tonil.

Argentina: Marrajo.

Australia: Blue pointer, Mackerel shark, Mako shark, Shortfin mako, Snapper shark.

Azores Islands: Mako, Marracho, Rinquim, Shortfin mako, Marrajo crioulo.

Bahamas: Mako.

Brazil: Anequim, Cação-anequim, Cação-atum, Cação-atun, Cação-moro, Mako, Sombreiro, Tubarão-sombreiro.

Cambodia: Chlarm.

Canary Islands: Janequín, Marrajo.

Cape Verde: Anequim, Marracho, Peixe-ruim, Tubarão, Tubarão-anequim, Tubarão-azul.

Chile: Marrajo, Mako.

China Main: 灰鯖鲨, 尖吻鯖鲨, Hui qing sha.

¹ This chapter was originally created by J. Valeiras and E. Abad in September 2006, and was updated by A. Domingo and R. Forselleo in September 2009.

Chinese Taipei: 灰鯖鯪.

Colombia: Mako.

Congo: Moussodji.

Cuba: Atlantic mako, Cane de mare, Dentuda, Dentuse, Dientuso azul, Mackerel porbeagle, Pesce tondo.

Cyprus: Skyllopsaro.

Czech Republic: Zralok mako kritkoploutvý. **Denmark:** Almindelig makohaj, Makrelhaj, Sildehaj. **Ecuador:** Tinto.

Egypt: Deeba.

Finland: Makrillihai.

France: Lamie, Mako, Marache, Requin-taupe bleu, Taupe bleu, Taupe bleue.

Germany: Blauhai, Mako, Makohai, Makrelenhai.

Greece: Ρυγχοκαρχαρίας, Καρχαρίας, Carcharias, Rynchocarcharias, Rynchokarcharias, Σκυλόψαρο.

Guyana: Pointed nose shark, Sharp-nosed shark, Sharpnose mackerel shark.

India: Ganumu sora, Ganumu sorrah, Ganumu-sorrah, Shortfin mako, Shortfin shark.

Iran: Kooseh-e-vahshi.

Israel: Amlez.

Italy: Cagna, Cagnia, Cagnizzo, Canesca, Cani di mari, Cani di mari de Messina, Caniscu, Cranicia, Meanto, Muanto, Ossirina, Ossirina dello apallanzani, Pesci tunnu, Piscicani, Squalo mako, Tunnu palamitu.

Japan: Aozame, Morozame, Awozame.

Korea, Rep: Ch'ong-sang-a-ri.

Lebanon: Qarsh.

Malta: Pixxiplamptu, Pixxitondu, Shortfin mako, Squalo mako.

Mauritius: Bleu pointu, Blue shark, Mako, Peau bleue, Requin bleu, Requin maquereau, Requin-tigre.

Mexico: Mako, Tiburón marrajo.

Morocco: Al karch.

Mozambique: Anequin barbatana curta.

Namibia: Kortvin-mako.

Netherlands Antilles: Mako, Spitsnuitmakreelhaai, Tribon blou, Tribon mula.

Netherlands: Haringhaai, Kortvinmakreelhaai.

New Zealand: Mako, Mako shark, Ngutukao, Shortfin mako.

Nicaragua: Marrajo dientuso.

Niue: Mako paala, Mako shark.

Norway: Makrellhai.

Papua New Guinea: Shortfin mako.

Peru: Mako, Tiburón bonito.

Philippines: Pating.

Poland: Rekin ostronosy.

Portugal: Marracho-azul, Tubarao-anequim, Tubarão-anequim.

Puerto Rico: Mako, Tiburon carite.

Romania: Rechin macrou.

Samoa: Aso-polota.

Senegal: Gisandoo, Guissando, Requin maquereau, Sidi, Walandol.

Somalia: Cawar.

South Africa: Kortvin-mako, Shortfin mako, Porpoise shark, Blue porpoise shark, Sharpnose mako, Mambone, Moro.

Spain: Atunero, Cane de mare, Diamante, Dientuso, Maco, Marrajo, Marrajo dientuso, Solraig, Tiburón azujelo, Tiburón bonito, Tiburón carito, Tinto.

St. Helena: Dog shark, Mackerel shark, Shortfin mako.

Suriname: Haai, Sartji.

Sweden: Mako, Makrillhaj.

Tahiti: Ma'o a'ahí.

Tanzania: Papa nyamarasi, Papa nyamzani, Papa sumbwi.

Trinidad Tobago: Sharp-nosed shark, Sharpnose mackerel shark.

Türkiye: Canavar baligi, Dikburun, Dikburuncanavar baligi, Sivriburuncanavar baligi.

United Kingdom: Atlantic mako, Bonito shark, Sharp-nose mackerel shark, Sharp-nosed mackerel shark, Shortfin mako, Shortfined mako.

United States: Blue pointer, Mackerel shark, Mako, Mako shark, Shortfin mako, Bonito shark.

Uruguay: Moro, Mako.

Venezuela: Tiburón carite.

Vietnam: Ci Nhim môm nhom.

2. Identification



Figure 1. Shortfin mako (*Isurus oxyrinchus*). Image taken from Domingo *et al.*, 2010. Photo: National on-board observer programme of the Uruguayan tuna fleet (PNOFA) DINARA/Uruguay.

Characteristics of *Isurus oxyrinchus* (see Figure 1 and Figure 2).

The estimated maximum size of shortfin mako reaches 500 cm in total length (TL) (Lopez-Mirones *et al.*, 2020). Although size records above 400 cm are rare and many are estimations, Kabasakal & De Maddalena (2011) used photographs to estimate the size of an *I. oxyrinchus* caught in the Aegean Sea at between 577-619 cm TL, the largest length estimated on record to date.

Sexual dimorphism is characteristic in this species, both in terms of size and life cycle characteristics. In some cases, this suggests sexual segregation based on ontogenetic differences (Mucientes *et al.*, 2009; Semba *et al.*, 2011).

Colour:

- Brilliant blue of purplish coloration on the dorsal and flanks, the laterals are a softer metallic colour.
- Ventral surface of body usually white.
- Head: White under the snout in young and adults. Dark colour of head partially covering the gill septa; lower part of second and third gill septa, white.

External characteristics:

- Robust body, shape similar to a dolphin.
- Conical snout, long and acute.
- Large first dorsal fin, and small second dorsal and anal fins.
- Origin of first dorsal fin over or just behind the free rear tip of the pectoral fin.
- Pectoral fins rather narrow-tipped, with anterior edges of smaller size than the length of the head.
- Strong keel on caudal peduncle, no secondary keels.
- Large blade-like teeth without cusps, smooth.
- Fine lower anterior teeth, very prominent and horizontal in the jaws even when mouth is closed.

Internal characteristics:

- Vertebrae: 182 to 195, the majority below 190.
- Cranium with rostral cartilages neither swollen nor hypercalcified.
- Intestinal valve count, 47 to 54.

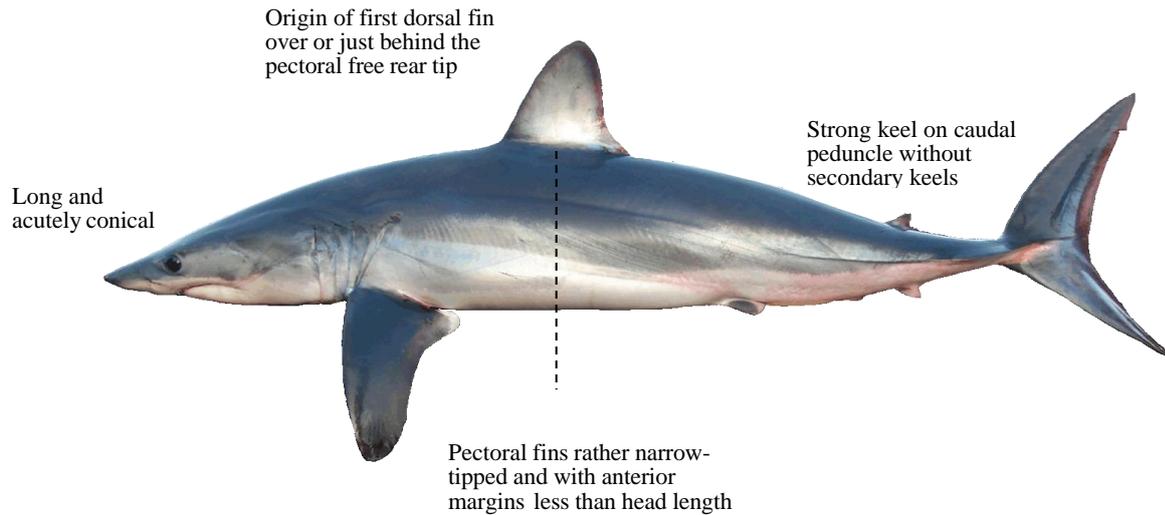


Figure 2. Summary of the shortfin mako’s (*Isurus oxyrinchus*) most distinguishing characteristics.

3. Distribution and population ecology

3.a Geographic distribution

The shortfin mako is a highly migratory oceanic and epipelagic species, which is distributed throughout all oceans in tropical, subtropical and temperate waters between 60°N and 50°S (**Figure 3**). In the western Atlantic its distribution extends from the Gulf of Maine, United States, down to Argentina. In the East Atlantic from 60°N to South Africa, including the Mediterranean Sea (Compagno 1984, 2001; Coelho *et al.*, 2017).

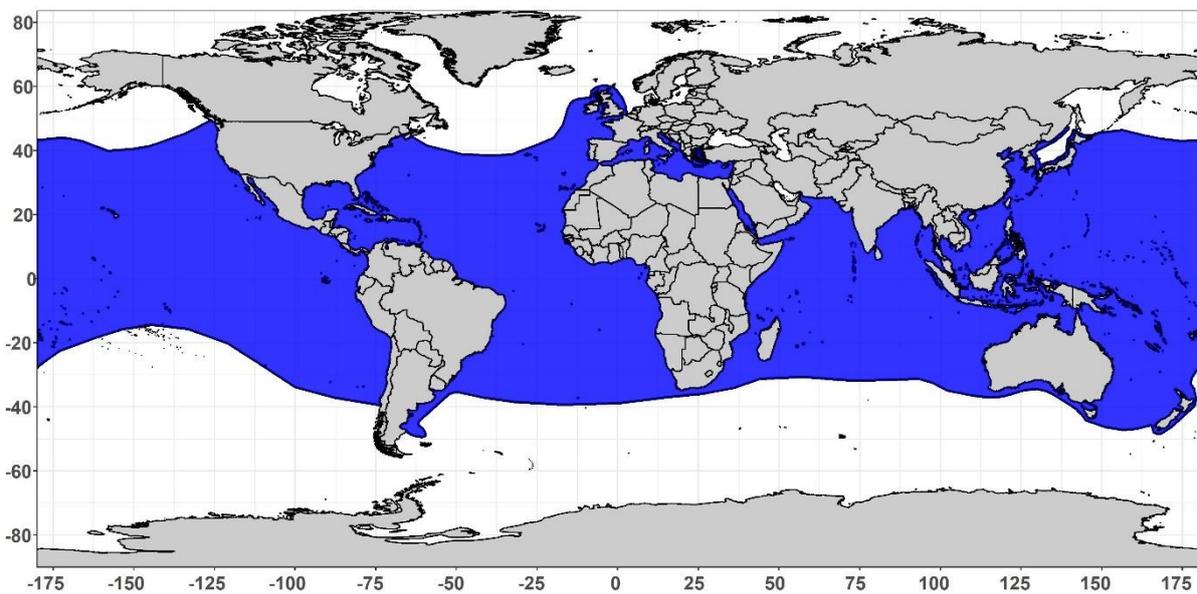


Figure 3. Map of the geographical distribution of *Isurus oxyrinchus*. Taken and modified from the IUCN (IUCN SSC Shark Specialist Group 2018. *Isurus oxyrinchus*. The IUCN Red List of Threatened Species. Version 2021-1).

3.b *Habitat preferences*

Shortfin mako is an epipelagic species that occurs in both tropical and warm and temperate waters between 5.2 and 31.7°C, with a preferred temperature range between 17 and 27°C. The shortfin mako is distributed from the surface 1.064 m (Mucientes-Sandoval *et al.*, 2012; Mejuto *et al.*, 2013; Vaudo *et al.*, 2016; Santos *et al.*, 2018, 2021; Francis *et al.*, 2019; Gibson *et al.*, 2021).

It is a very active and highly migratory shark, with records of horizontal movements spanning several thousands of kilometres, over 9,000, in short periods of time (Mejuto *et al.*, 2013). Tagging studies have shown that some sharks make oceanic movements over long distances, but that they tend to stay within specific regions of oceanic basins (Francis *et al.*, 2019). In many cases, they spend a large part of their time in Exclusive Economic Zones and the shelf, presumably due to high coastal productivity and access to abundant prey. These results challenge the conventional view that shortfin mako are wandering nomads and suggest that both the local and regional scale should be considered in management of this species (Francis *et al.*, 2019; Santos *et al.*, 2021). They swim between the surface up to a depth of around 900 m, with an average depth of 67 m, and spend the majority of their time both during the day and at night at depths above the thermocline 0-90 m (Casey & Kohler 1992; Loefer *et al.*, 2005; Stevens *et al.*, 2010; Abascal *et al.*, 2011; Vaudo *et al.*, 2016; Santos *et al.*, 2018, 2021).

3.c *Migrations*

It is a very active and highly migratory species with extensive horizontal migrations. Tagging programmes observed that shortfin mako performs large migrations (Anon. 2021; Santos *et al.*, 2021). There is a record of a shark that travelled ~ 25,550 km through the Indian Ocean from the Great Australian Bight to an area SE of Madagascar over a period of 18 months (Rogers *et al.*, 2015). To our knowledge, this is the largest published migration reported for shortfin mako. Conclusions on horizontal movements appear to be conditioned to a certain extent by the tagging scheme applied in each tagging programme or experiment (González-González *et al.*, 2017). Based on conventional tagging carried out over several decades, migrations and large and extensive mixes of individual, at least in each hemisphere of the Atlantic, have been described (Casey & Kolher 1992; Kolher & Turner 2019; Mejuto *et al.*, 2005).

Conventional tagging data obtained in the Atlantic would indicate that migration is limited to within each hemisphere or in the vicinity thereof and, in general, no large-scale trans-equatorial migrations have been observed. Migrations only occur in areas close to the equatorial limits (Mejuto *et al.*, 2005). With regard to electronic tagging, movements have been observed from the equatorial area to the temperate south-eastern Atlantic along the African continent, crossing the hemispheres. This was seen in a small female (185 cm FL) tagged in November 2017 and tracked over a 4-month period. (Anon. 2018; Santos *et al.*, 2021). Although the majority of tagging data does not appear to contradict the current assumption that stocks are divided (North and South Atlantic stocks, separated at a latitude of 5°N), there are some cases of individuals that cross these limits and more research is required in this regard (Santos *et al.*, 2021). Satellite tagging data suggest that shortfin mako can swim quickly, although horizontal movement is estimated at an average of 27 km per day (Mejuto *et al.*, 2013).

Using satellite tagging in the Gulf of Mexico, a large female was seen to show high loyalty to this region throughout the continental shelf throughout the majority of the year, while mature males carried out extensive large-scale migrations that cross several management jurisdictions, leaving the Gulf at the end of summer or beginning of autumn and returning at the end of autumn or beginning of winter every year (Gibson *et al.*, 2021). These movements were different from those observed by Santos *et al.*, (2021) in the northwest Atlantic, that did not approach the Gulf of Mexico region and followed general northwards movements towards shelf and slope waters off the coast of the United States at the end of winter. Great site loyalty was observed in other areas such as the southwestern Atlantic off the coast of Uruguay and North Argentina, probably due to the large amount of nutrients resulting from the confluence of water masses between the warm Brazil current and the cold Malvinas / Falkland current (the Subtropical Convergence) (Santos *et al.*, 2021).

4. **Biology**

4.a *Growth*

There are few studies on the age and growth of shortfin mako in Atlantic waters and there are still several knowledge gaps in these parameters. Shortfin makos are born with a size of approximately 60 – 70 cm TL (Castro 1983, Mollet *et al.*, 2000, Compagno *et al.*, 2001) and grow to about 400 cm TL (Bigelow & Schroeder 1948; Compagno *et al.*, 2005). Age estimates were obtained for the northwest Atlantic by Pratt & Casey

(1983), although these have not yet been validated. For these estimates, four methods were used (size- month seasonal analyses, tag/recapture data, size frequency data, and vertebral ring counts). Based on consistency between methods, it was assumed that two growth rings were formed each year on the central vertebrae area of shortfin makos, although Cailliet *et al.*, (1983) suggested that one ring per year was formed. Some studies use the hypothesis of one marker per year, while others assume the formation of two rings per year (e.g., Bishop *et al.*, 2006; Semba *et al.*, 2009; Doño *et al.*, 2014). The theory of the biannual periodicity of rings in lamnoids has been the subject of continued debate and it is being reviewed again using updated techniques and larger sample sizes with an emphasis on obtaining validation (Natanson 2002). Studies using radiocarbon markers on the vertebral growth ring of one *Isurus oxyrinchus* sample supported the hypothesis that two rings per year are produced (Campana *et al.*, 2002). Other researchers that also worked with radiocarbon tags in individuals from the North Atlantic backed this interpretation for the first years of growth but understand that their findings do not indicate that the early growth pattern can be extrapolated to more advanced ages (Ardizzone *et al.*, 2006).

The results of Campana *et al.*, (2005) regarding age determination indicate that the species grows slower than previously reported.

The results of the ICCAT Shark Species Group's collaborative study on age and growth for SMA in the South Atlantic indicate a size-at-birth of approximately 63 cm (FL), with the resulting growth parameters of $L_{inf} = 218.5$ cm FL for males and $L_{inf} = 263.1$ cm FL for females. These preliminary results seem to underestimate the asymptotic size. Consequently, both the authors and the ICCAT Shark Species Group do not recommend that these growth curves be used for the South Atlantic (Anon. 2018; Rosa *et al.*, 2018).

Studies on age and growth of shortfin mako shark in the North Pacific Ocean, caught by Japanese longline vessels (Semba 2009) support the hypothesis of a pair of rings per year, but the resulting growth curve was in between the existing hypothesis (Takeuchi *et al.*, 2005). Wells and collaborators (2013), in southern California, based on validation studies with oxytetracycline, using direct and indirect methods in their work, indicate rapid growth of juvenile shortfin mako sharks with two annual depositions during the first 5 years of life. Later, Kinney *et al.*, (2016) suggested that male *I. oxyrinchus*, in the northeastern Pacific (California), experience rapid growth and biannual deposition of banded pairs as juveniles, followed by slower growth and annual deposition of banded pairs as adults. The exact point at which this transition may occur is still uncertain but is probably after the first 5 years and near the age of sexual maturity.

Cailliet *et al* (1983) estimated the longevity of shortfin mako at 45 years, although the oldest individual sampled by Pratt & Casey (1983) was 17 years old.

Table 1. Growth parameters for shortfin mako according to the Von-Bertalanffy growth curve. L_{∞} : maximum asymptotic length (cm), k : growth coefficient (years⁻¹), t_0 : theoretical age at length 0 (years), L_0 : size at birth.

<i>Growth parameters</i>			<i>Area</i>	<i>Reference</i>	<i>Sex</i>	<i>Method</i>
L_{∞}	k	t_0 / L_0				
302 (FL)	0,266	-1	Northwest Atlantic	Pratt y Casey (1983)	Males	Vertebrae ²
345 (FL)	0,203	-1	Northwest Atlantic	Pratt y Casey (1983)	Females	Vertebrae ²
253,3 (FL)	0,125	71,6 (FL)	Northwest Atlantic	Natanson <i>et al.</i> , (2006)	Males	Vertebrae ¹ / OTC
432,2 (FL)	0,043	81,2 (FL)	Northwest Atlantic	Natanson <i>et al.</i> , (2006)	Females	Vertebrae ¹ / OTC
416 (FL)	0,03	-6,18	Southwest Atlantic	Doño <i>et al.</i> , (2014)	Males	Vertebrae ¹
580 (FL)	0,02	-7,52	Southwest Atlantic	Doño <i>et al.</i> , (2014)	Females	Vertebrae ¹
328,7 (FL)	0,08	-4,47	South-western and central Atlantic	Barreto <i>et al.</i> , (2016)	Males	Vertebrae ¹
407,6 (FL)	0,04	-7,08	South-western and central Atlantic	Barreto <i>et al.</i> , (2016)	Females	Vertebrae ¹
340,2 (FL)	0,14	-2,75	South-western and central Atlantic	Barreto <i>et al.</i> , (2016)	Males	Vertebrae ²
441,6 (FL)	0,07	-3,98	South-western and central Atlantic	Barreto <i>et al.</i> , (2016)	Females	Vertebrae ²
291,5 (FL)	0,2	-2,38	South-western and central Atlantic	Barreto <i>et al.</i> , (2016)	Males	Vertebrae ³
309,8 (FL)	0,13	-3,27	South-western and central Atlantic	Barreto <i>et al.</i> , (2016)	Females	Vertebrae ³
350,6 (FL)	0,064	-3,1	Atlantic	Courtney <i>et al.</i> , (2017)	Females	Estimated average
241,8 (FL)	0,136	-2,2	Atlantic	Courtney <i>et al.</i> , (2017)	Males	Estimated average
298 (FL)	0,07	-3,75	Northeast Pacific	Cailliet y Bedford (1983)	Both	Vertebrae ¹
267 (FL)	0,31	-0,95	South-western Pacific	Chan (2001)	Males	Vertebrae ²
349 (FL)	0,15	-1,97	South-western Pacific	Chan (2001)	Females	Vertebrae ²
321,8 (FL)	0,04	-6,07	North-western Pacific	Hsu (2003)	Males	Vertebrae ¹
403,6 (FL)	0,04	-5,27	North-western Pacific	Hsu (2003)	Females	Vertebrae ¹
411 (TL)	0,05	-4,7	North-eastern Pacific	Ribot-Carballal <i>et al.</i> , (2005)	Both	Vertebrae ¹
302,2 (FL)	0,05	-9,04	South-western Pacific	Bishop <i>et al.</i> , (2006)	Males	Vertebrae ¹
820,1 (FL)	0,01	-11,3	South-western Pacific	Bishop <i>et al.</i> , (2006)	Females	Vertebrae ¹
325,3 (TL)	0,076	-3,18	South Pacific	Cerna y Licandeo (2009)	Females	Vertebrae ¹
296,6 (TL)	0,087	-3,58	South Pacific	Cerna y Licandeo (2009)	Males	Vertebrae ¹
231 (PCL)	0,16	59,7 (PCL)*	North-western and Central Indian Ocean	Semba <i>et al.</i> , (2009)	Males	Vertebrae ¹
308 (PCL)	0,09	59,7 (PCL)*	North-western Indian Ocean	Semba <i>et al.</i> , (2009)	Females	Vertebrae ¹
285 (FL)	0,113	90,4 (FL)	South-western Indian Ocean	Groeneveld <i>et al.</i> , (2014)	Both	Vertebrae ¹
267,6 (CFL)	0,123	-2,487	South Indian Ocean	Liu K. Ming <i>et al.</i> , (2018)	Both	Vertebrae ¹

FL: Fork length; TL: Total length; CFL: Curved Fork Length; PCL: Precaudal length; *: A modified version of Von-Bertalanffy was used with size at birth fixed at 59.7 cm CFL.

¹ One growth band pair per year;

² Two growth band pairs per year;

³ Two growth band pairs per year in the first 5 years of life, one band pair per year in the following years.

4.b Length-weight relationship

Published length-weight relationships for several worldwide oceanic areas are shown in **Table 2**.

Table 2. Published weight-length, weight-weight and length-length relationships published for *Isurus oxyrinchus*.

Equation	N	Range (cm)	Area	Reference
$RW = 5.243 \times 10^{-6} \times (FL)^{3,1407}$	2081	65-338 (FL)	Northeast Atlantic	Kohler <i>et al.</i> , (1995)
$W = 7.2999 \times (TL)^{3,224}$	63		Northeast Atlantic	Mollet <i>et al.</i> , (2000)
$W = 6.824 \times (TL)^{3,137}$	64		Southeast Atlantic	Mollet <i>et al.</i> , (2000)
$DW = 2.808 \times 10^{-6} \times (FL)^{3,202}$	17	70-175 (FL)	Northeast Atlantic	García-Cortes y Mejuto (2002)
$DW = 1.222 \times 10^{-5} \times (FL)^{3,895}$	166	95-250 (FL)	East Atlantic	Tropical García-Cortes y Mejuto (2002)
$DW = 2.52 \times 10^{-5} \times (FL)^{2,76}$	22	120-185 (FL)	Central Atlantic	Tropical García-Cortes y Mejuto (2002)
$DW = 3.114 \times 10^{-5} \times (FL)^{2,724}$	97	95-240 (FL)	Southwest Atlantic	García-Cortes y Mejuto (2002)
$W = 5.2432 \times 10^{-6} \times (FL)^{3,1407}$			Atlantic	Courtney <i>et al.</i> , (2017)
$GW = 1 \times 10^{-5} \times (TCL)^{2,517}$	170	84-273 (FL)	Indian Ocean	Liu <i>et al.</i> , (2018)
$RW = 1.1527 \times (GW)$	34		South Atlantic	Mejuto <i>et al.</i> , (2008)
$RW = 1.4369 \times (DW)$	34		South Atlantic	Mejuto <i>et al.</i> , (2008)
$GW = 0.8674 \times (RW)$	34		South Atlantic	Mejuto <i>et al.</i> , (2008)
$DW = -0.760 + 0.7093 \times (RW)$	34		South Atlantic	Mejuto <i>et al.</i> , (2008)
$DW = -0.7573 + 0.8176 \times (GW)$	34		South Atlantic	Mejuto <i>et al.</i> , (2008)
$FL = 0.9286 \times (TL) - 1.7101$	199		Northwest Atlantic	Kohler <i>et al.</i> , (1995)
$TL = 1.127 \times (FL)$	1020	88-264 (TL)	South Atlantic	Mas <i>et al.</i> , (2014)
$TL = 1.239 \times (CPL) + 2.651$	1021	87-264 (TL)	South Atlantic	Mas <i>et al.</i> , (2014)
$FL = 1.069 \times (CPL) + 5.292$	1369	70-270 (TL)	South Atlantic	Mas <i>et al.</i> , (2014)
$CPL = 2.04 \times (DL) + 12.1$ (Males)	55		Pacific	Semba <i>et al.</i> , (2009)
$CPL = 2.18 \times (DL) + 7.79$ (Females)	76		Pacific	Semba <i>et al.</i> , (2009)
$CPL = 0.84 \times (TL) - 2.13$	131		Pacific	Semba <i>et al.</i> , (2009)
$CPL = 0.91 \times (FL) - 0.95$	130		Pacific	Semba <i>et al.</i> , (2009)
$FL = 0.913 \times (TL) - 0.397$			North Pacific	NOAA-SWFSC
$CPL = 0.816 \times (TL) + 0.784$	1240		Northwest Pacific	Joung y Hsu (2005)
$FL = 0.89 \times (TL) + 0.952$	1236		Northwest Pacific	Joung y Hsu (2005)

RW: Round weight
W: Total weight
DW: Dressed weight
GW: Gutted weight
FL: Fork Length
DL: Distance between the base of the first and second dorsal fin
TL: Total Length
TCL: Total Curved Length
CPL: Caudal Peduncle Length

4.c Reproduction

Certain aspects related to reproduction are known in several areas, such as size-at-maturity, size-at-birth and litter size. Results suggest that there is sexual dimorphism in terms of size, with females being larger than males. Females give birth between winter and spring to litters of between 4 and 26 embryos with total lengths of between 65 and 75 cm (TL) in the Atlantic Ocean (Pratt & Casey 1983), and between 70 and 80 cm (TL) in the Pacific Ocean (Stevens 1983; Duffy & Francis 2001; Joung & Hsu 2005; Semba *et al.*, 2011), although Duffy & Francis (2001) observed individuals giving birth in summer. By contrast, there is relatively little information on the mating period (Joung & Hsu 2005; Semba *et al.*, 2011) and wide variation in gestation period estimates, ranging from 9 months (Semba *et al.*, 2011) to 25 months (Joung & Hsu 2005). As the details of the rest period remain unclear, no consensus has been reached on whether the reproductive cycle lasts for two (Semba *et al.*, 2011) or three years (Mollet *et al.*, 2000; Joung & Hsu 2005). The difficulty of studying reproductive characteristics - especially the gestation, rest and mating period - is due to scarce records on adult females worldwide. Nonetheless, individuals of sizes between 52 (FL) and 57 cm (TL) have been caught in both the Caribbean Sea and the North Atlantic, which could indicate that the size-at-birth is lower than reported (Rosa *et al.*, 2018; Tagliafico *et al.*, 2021), in the case of the North Atlantic, the individuals were caught over the course of several months, between March and September.

Parturition

Shortfin mako is an aplacental viviparity shark, with oofagy (form of intrauterine cannibalism whereby the embryos in the uterus feed on other eggs produced by the mother) (Snelson *et al.*, 2008). A seasonal analysis of the index of the expansion of the uterus and of the gonado-somatic index of pregnant and postpartum females indicated a gestation period of 15 to 18 months (Mollet *et al.*, 2000, 2002). Parturitions generally occur from the end of the winter to spring in both hemispheres and could extend up to summer. In this case, the reproductive cycle could be three years (Duffy and Francis 2001).

Maturity

It has been suggested that there are geographical differences in size-at-maturity for both sexes (Semba & Yokawa 2014). The estimated median size at maturity (50%) in the North Atlantic is 182 cm (173-187 FL) for males and 280 cm (263-291 FL) for females (Maia *et al.*, 2006, Natanson *et al.*, 2020). This length is larger than the figure estimated for females from the southern hemisphere (252 cm FL) (Mollet *et al.*, 2000). Mas *et al.*, (2017) estimated smaller sizes at maturity (50%) for males in the South Atlantic (166 cm TL). For the Pacific, Francis & Duffy (2005) reported in New Zealand a size at maturity (TL) of 197-202 cm for males and 301-312 cm for females. Stillwell (1990) suggested that male shortfin makos reached adult size at 4.5 years, while females reach adult size at 7 years. More recent data observed in New Zealand, just as in the North and South Atlantic, suggest that males are mature at the age of 7-8 years and females at the age of 12-19 years (Campana *et al.*, 2005; Bishop *et al.*, 2006; Natanson *et al.*, 2006; Doño *et al.*, 2014; Barreto *et al.*, 2016).

Fecundity

Litter size generally varies between 4 and 25 pups, with a maximum of 30, and is related to the size of the female (Mollet *et al.*, 2000, 2002; Compagno *et al.*, 2005; Mejuto *et al.*, 2013).

Sex ratio

With data obtained from tagging studies in the northwest Atlantic, a 1:1 sex ratio was found. However, this ratio changes with size from 240 cm FL, where a predominance of females is observed (Casey & Kohler 1992). On the other hand, according to that reported by Mejuto & Garcés (1984) for the northeast Atlantic, in the area between Spain and the Azores Islands the sex ratios for shortfin mako show a higher percentage of males with sizes over 200 cm FL (1:0.4 ratio). In the western Mediterranean, the sex ratio is close to 1:0.9, with a minor predominance of females (de la Serna *et al.*, 2002). Information on adults over 240 cm FL is scarce, but from the West Atlantic (Casey & Kohler, 1992) and the East Atlantic (Mejuto, 1984), there have been some reports of some specimens over this size.

This species segregates by size and sex various times during its life history (juveniles, adult females and males) (Kohler *et al.*, 2002).

4.d Diet

Shortfin mako is an opportunistic and generalist predator with similar customs to white sharks (Maia *et al.*, 2006).

In the northwest Atlantic and Australia, it primarily feeds on other bony fish and celaphopods (Stillwell and Kohler 1982; Stevens 1984), whereas in Natal, South Africa, the main prey were other elasmobranchs (Cliff *et al.*, 1990). Celaphopods comprise important prey and include a variety of squid, both *Loligo* in some areas of the north-eastern Pacific, and the jumbo squid (*Dosidicus gigas*) is an important item in the shortfin mako's diet (Vetter *et al.*, 2008). Other foods include sea turtles, marine mammals and invertebrates (Storai *et al.*, 2001; Lyons *et al.*, 2015; Porsmoguer *et al.*, 2015). In a study based on individuals between 64 and 290 cm (FL), Maia *et al.*, (2006) discovered that teleosts were the main component of shortfin mako's diet in the North Atlantic, as they were found in 87% of stomachs and represented 90% of the content in terms of weight. Crustaceans and cephalopods were also relatively important in this species' diet, while other elasmobranchs were only present in smaller percentages. In the northwest Atlantic, bluefish (*Pomatomus salatrix*) constitute the most important food and represents about 78% of the diet (Stillwell & Kohler 1982). Analyses of stable isotopes in tissues have demonstrated a shift in the shortfin mako diet, from cephalopods to bluefish in spring (MacNeil 2005). Other studies observed that the bluefish continues to be the major food item for shortfin mako, consuming 4.6% of their body weight to meet demands for energy. Based on this, it was calculated that on average a shortfin mako consumes 500 kg annually of this species (Wood *et al.*, 2009). This was also confirmed by other studies where teleosts represented 82.4% of the prey consumed by shortfin mako in the northeast Atlantic (Porsmoguer *et al.*, 2014). All these prey are much smaller than the shortfin mako. However, Stillwell (1990) suggested that the large makos prefer large prey, almost their same size, with swordfish (*Xiphias gladius*) being the most common prey for the large makos in the northwest Atlantic.

In the south-western Atlantic to the south of Brazil, analyses of the stomach contents of shortfin mako showed that bony fish such as *Brama brama* and *Lepidocybium flavobrunneum* were predominant in the diet (Vaske-Junior & Rincon-Filho 1998). Other studies in the same area of Southeast-South Brazil identified 144 food items belonging to 11 taxons. Following the calculations, the most important food category is comprised of teleost fishes, followed by cephalopod molluscs. Crustaceans and other groups were of little importance in the species' diet (Gorni *et al.*, 2012).

4.e Physiology

This species are endothermic and maintain higher temperatures than that of the surrounding waters in musculature, brain, eyes and viscera, with countercurrent vascular heat exchangers (Carey & Teal 1969; Carey *et al.*, 1981, 1985; Carey 1982; Block & Carey 1985). Body muscle may run 1 to 10°C higher than ambient temperature depending on the waters, which makes it one of the most active and powerful fishes and probably the fastest shark, while the stomach could be between 6 and 8°C above ambient temperature (Carey *et al.*, 1981). The mechanisms used to regulate heat transfer in shortfin mako are very similar to those used in tunas (Bernal *et al.*, 2001). Moreover, the shortfin mako has greater digestive enzyme activity than other sharks, which should result in higher food processing rates and could represent a selective advantage for the species, in addition to visceral endothermy (Newton *et al.*, 2015).

The shortfin mako has an enlarged midbrain that represents approximately 23% of its brain. This hypertrophy of the midbrain has been attributed to the importance of vision and its effect on foraging (Yopak *et al.*, 2007).

4.f Mortality

The parameter of natural mortality (M) is extremely rarely estimated for sharks. It can be inferred from information on the life cycle, using relationships derived from longevity, growth or size. Common methods are based on age determination and are calculated from theoretical longevity, length relationships by age and weight by age, and/or Von Bertalanffy growth function parameters. These estimations are sensitive to the level of uncertainty in age determination for elasmobranchs, where longevity in particular can be systematically underestimated. Underestimation of maximum age results in overestimation of M using methods based on life history. Estimations of M based on the life cycle of pelagic sharks are very low compared to other fish species, which suggests that natural mortality events are rare (Bowlby *et al.*, 2021). From the survival mixture model and a single natural mortality event, Bowlby *et al.*, (2021) estimated the probability of M in shortfin mako in the North Atlantic using information from satellite tags. For the estimated rate ($M = 0.101$), approximately 1.5% of the population is expected to live until the maximum age of longevity for shortfin mako (41 years old). This estimation is within the expected longevity range of 20 to 52 years observed in other studies (Bowlby *et al.*, 2021). Moreover, the M value obtained by Bowlby *et al.*, (2021) is within the range of values estimated by methods based on longevity and growth (0.068-0.318) for males and females combined, which attributes the natural mortality values currently used in the ICCAT stock assessment.

There are records of natural mortality due to predation by orcas (Visser *et al.*, 2000) and the white shark (Fergusson *et al.*, 2000) in New Zealand.

5. Fisheries biology

5.a Stocks/Stock structure

Casey & Kohler (1992) suggested that the central distribution of shortfin mako in the northwest Atlantic stretches from 20-40° N and borders the Gulf Stream to the west and the Mid-Atlantic Ridge to the east. It is also hypothesised that shortfin mako in the northwest and northeast Atlantic are separate populations or stocks. In the north-eastern Atlantic, the Strait of Gibraltar is presumed to be a nursery area (Buencuerpo *et al.*, 1998; Tudela *et al.*, 2005). The area between 17° and 35° S off the coast of Brazil appears to be a pupping, nursery and mating area in the southwest Atlantic (Amorim *et al.*, 1998). Coelho *et al.*, (2018) extended previous observations as the entire temperate northern and central Atlantic appears to be an area of juveniles of this species, particularly the areas closest to the continental shelf and island waters. In the South Atlantic, the southeast and southwest areas also appear to be nursery areas for this species due to the large proportion of juveniles.

Heist *et al.*, (1996) and Heist (2008) carried out genetic studies on stocks based on samples of mitochondrial DNA of individuals from the North and South Atlantic and the Pacific. Their results do not support the presence of different genetic stocks, although the North Atlantic stock seems to be separated from that of the South Atlantic.

The work of Schrey & Heist (2003) using microsatellites does not provide solid evidence of a population structure or the existence of independent separate management units for shortfin mako. Therefore, microsatellite data do not support that need for independent management of populations of this species. More recent studies performed in the framework of collaborative activities between scientists from the ICCAT Shark Species Group concur with the findings of Heist (2008) and observe no differences in the genetic structure of individuals obtained in the Atlantic, with the exception of some individuals obtained off the coast of Uruguay and in the south-western Atlantic. In order to better assess these differences, second-generation sequencing technologies are being used to analyse mitochondrial DNA and improve the information, which allows for a stricter definition of stocks of this species in the North Atlantic. The main uncertainty is related to differences between the southeast and southwest Atlantic, especially with regard to differences in the Uruguayan samples. For this reason, the possibility of including samples from the south-eastern Pacific (e.g., from Chile) has been considered to see if there is some kind of relationship with the southeast Atlantic (Anon. 2018).

Schrey & Heist (2003) concluded that females are probably more philopatric based on the differences found in mtDNA inherited from the mother, and that males disperse more widely based on weak differentiation in nuclear DNA markers. Although evidence is not entirely conclusive for shortfin mako, this type of sex-biased dispersal has also been reported for other shark species (Campana *et al.*, 2006) and males have often been seen to move more than females (see 3.c Migrations).

In the North Atlantic size structure, a trend for smaller sizes can be observed in northern areas (e.g., ICES and NAFO), for slightly larger specimens in more tropical areas of the central-western Atlantic, and for larger specimens in the southwest Atlantic region (Santos *et al.*, 2013).

5.b Description of fisheries: Catches and effort

Shortfin mako constitutes an important part of the bycatch caught by longline fisheries targeting tunas, billfish and swordfish. They are caught by various gears in the Atlantic Ocean, Gulf of Mexico, the Caribbean, and the Mediterranean Sea including seine, gillnet, handline, rod and reel, trawl, troll, and harpoon, but they are mostly caught in pelagic drift longline fisheries.

It is also caught in the recreational fisheries of some countries such as Canada, the United Kingdom, Ireland, Mexico, France and the United States. Catches of sharks, including shortfin mako, have increased in recent years in the United States (Anon. 2005; Babcock 2013). In terms of volume, it is the second most common shark species taken as by-catch in tuna fisheries of the ICCAT area (Rosa *et al.*, 2018).

The recent updates made to ICCAT Task 1 (several catch series rebuilt and recovered) on the three major shark species (SMA, BSH and POR), in particular for the last 3 decades, have improved the knowledge of the ICCAT Shark Species Group on the extent to which fishing activity in the ICCAT convention area has impacted the stocks of these three major shark species. There is still much work to be done in the process of reconstructing historic catches, especially for the 1950-1990 period. Moreover, knowledge on the level of shortfin mako discards and estimations as regards the condition of individuals upon release (alive or dead) are scarce. ICCAT nominal annual landings reached 4,171 t in 2019. Average landings from 1990 to 2019 are estimated at 5,975 t (**Figure 4**).

During 2019, six ICCAT Contracting Parties landed 97% of the shortfin mako from the North Atlantic (EU-Spain, EU-Portugal, Morocco, Canada, the USA and Senegal), and five Contracting Parties landed 97% of the shortfin mako from the South Atlantic (EU-Spain, Brazil, EU-Portugal, Japan and South Africa) (Anon. 2021).

In recent years the demand for and value of shark products has increased mainly due to changes in the market, and consequently higher catches of pelagic sharks have been recorded in the ICCAT Convention area.

Catch data indicate that the smallest specimens are mainly found in more temperate waters of the North and South Atlantic, while larger specimens are more commonly caught in tropical and equatorial regions. This is similar to the patterns found for other pelagic sharks such as the blue shark (Coelho *et al.*, 2018).

The majority of shortfin mako catches from the North Atlantic are landed by the European Union (EU) fleet, with Spanish boats registering the highest landing figures, followed by Portuguese boats. Around 9% of catches from the North Atlantic are attributed to vessels flagged to the United States (USA) (Rosello *et al.*, 2021). Some fleets such as the Portuguese fleet often use a pelagic drift longline to target swordfish (*Xiphias gladius*). Even so, this is a multispecies fishery where some other bony fish are frequently caught, in addition to pelagic sharks (mainly the blue shark *Prionace glauca* and shortfin mako *Isurus oxyrinchus*) (Santos *et al.*, 2013). In the North Atlantic area, this fishery began to develop mainly after 1986, while it gained importance in the South Atlantic from 1989 (Santos *et al.*, 2002).

In recent years, the decrease in swordfish catches has been offset by the adoption of operational adaptations by some fleets to opportunistically catch pelagic sharks, which have seen favourable market conditions (Rosello *et al.*, 2021).

In the Atlantic area to the south of Morocco, it is generally taken as by-catch as in all fisheries, although at times the fishery seems to target this species. This fishery is executed on a part of the population predominantly consisting of juveniles of lengths between 135-200 cm, which represent 90% of catches (Baibbat *et al.*, 2017).

In the Mediterranean Sea, shortfin mako is taken as by-catch in swordfish fisheries and is one of the most abundant species after the blue shark (Megalofonou *et al.*, 2005).

Since its inclusion in CITES Appendix II in 2019, discards are estimated to have increased (Santos *et al.*, 2021).

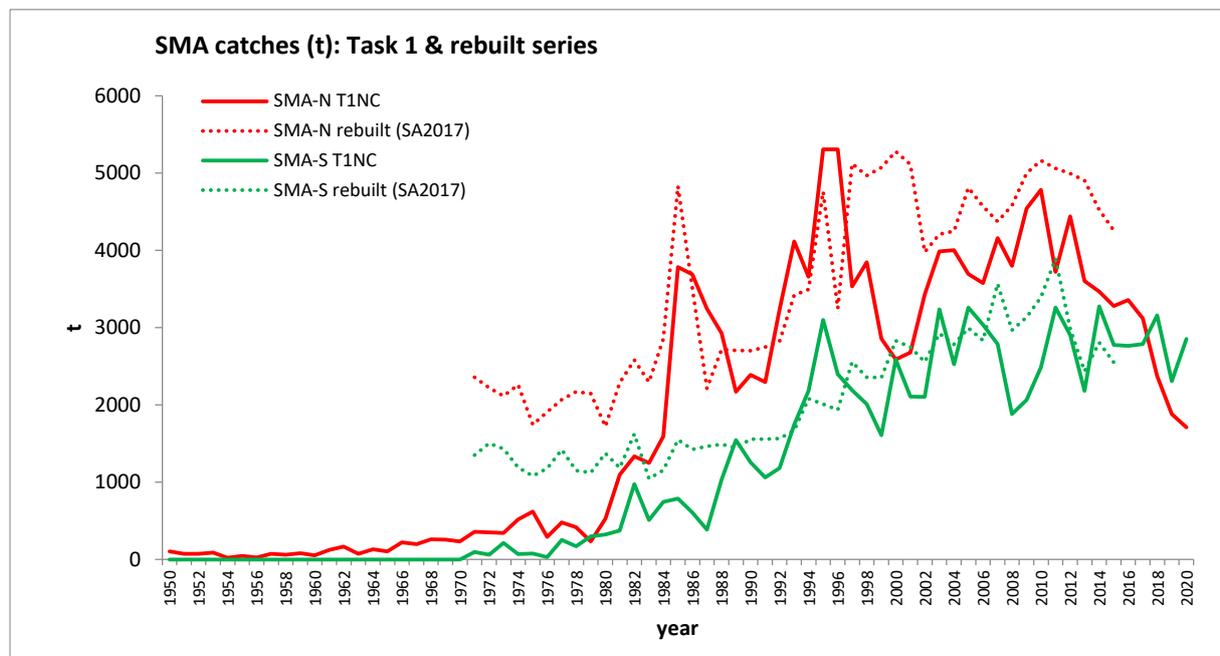


Figure 4. Total catches (t, landings and dead discards) by stock and year. Task 1 ICCAT nominal catches (T1NC, continuous lines) and the historical reconstruction used in the 2017 assessment (SA2017, dotted lines).

5.c State of stocks

Considerable progress has been made since the 2012 assessment on the integration of new data sources (size data by sex) and modelling approaches (model structure). Uncertainty in data inputs and model configuration has been explored through sensitivity analysis.

In the 2019 North Atlantic stock assessment, scenarios estimated that the stock was overfished (B2015/BRMS=0.57 to 0.85) and that overfishing was occurring (H2015/HRMS = 1.93 to 4.37). The probability of the stock being overfished and experiencing overfishing was 82.1 – 99.9% according to various models. Estimates obtained with the final run of the Stock Synthesis model (SS3) predicted that the stock was probably overfished (SSF2015/SSFRMS = 0.95, where SSF is spawning stock fecundity), and that overfishing was occurring (F2015/F_{MSY}=4.38, CV=0.11) with a probability of 56.1% of being overfished and experiencing overfishing. The combined probability from all the models of being in an overfished state while still experiencing overfishing was 90%. The results obtained in this evaluation are not comparable with those obtained in the last

assessment in 2012 because the input data and model structures have changed. Catch time series are different (they start in 1950) and are derived using various assumptions. Some of the biological data used in the model were changed and are now specific for each sex, and additional size composition data is available. Additionally, in 2012 only the production model and a catch-free age-structured production model were used. The 2019 assessment represents a significant improvement in the understanding of the North Atlantic stock's status.

The production models in the South had difficulty fitting the increasing trends in the CPUE series combined with increasing catches. The results obtained from these models for this region were implausible as there is conflict between the data and the model assumptions.

For the South Atlantic stock, the combined model results indicated a probability of 19% that the stock is both overfished and experiencing overfishing. The results regarding the status of the South Atlantic stock were very uncertain. There were many differences between models and in the different scenarios for each model. Despite this uncertainty, it is not possible to discount that in recent years the stock may have been at, or already below, BMSY and that fishing mortality has exceeded F_{MSY} . (Anon. 2020).

Cortés *et al.*, (2015) carried out an ecological risk assessment for the Atlantic Ocean, which considered shortfin mako to be one of the most susceptible species to pelagic longline fisheries. It was also among the five most vulnerable species due to its high susceptibility and low productivity (Cortés *et al.*, 2015).

Since its inclusion in CITES Appendix II in 2019, this species has received greater attention from RFMOs and the international community as regards the condition of its populations and the various aspects related to conservation of the species.

5.d Relationship with the environment

As a top predator and an oceanic, highly migratory species, the shortfin mako can be used as an environmental sentinel given that various chemical pollutants from the persistent organic pollutants (POP) family can be detected in individuals, including polychlorinated compounds, perfluorinated compounds and various trace and heavy metals. One of the most widely studied and regulated of these pollutants is mercury deposited in the sea, mainly coming from the energy industry, coal and waste incineration, as well as from mining. Its transport capacity means that it can be found very far from the area where it was produced. Once deposited in water, bacteria can convert mercury (Hg) into methylmercury (CH₃Hg), which poses an even greater risk as it can be absorbed through membranes in this state and accumulate in tissues. This causes biomagnification of Hg throughout the trophic chain, leading to significant levels of this element in the muscle tissue of some top predators such as the shortfin mako. This effect increases on a par with the size and weight of individuals (Alves *et al.*, 2016; Biton-Porsmoguer *et al.*, 2018).

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