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| CHAPTER 2.2.1.3: PORBEAGLE | AUTHORS: R. FORSELLEDO, A. DOMINGO, F. MAS and P. MILLER | LAST UPDATE: August 2022¹ Original: Spanish |

2.2.1.3 Description of porbeagle (POR)

1. Name

1.a. Classification and taxonomy

Species name: *Lamna nasus* (Bonnaterre, 1788)

Ethymology: The genus name *Lamna* is derived from the Greek “*lamna-es*” which refers to a voracious fish, whilst the species name *nasus* is of Latin origin, meaning “nose”.

The common species name in English “porbeagle” is derived from Cornish (Brittonic Celtic language) “porgh-bugel” and probably derives from a combination of “porpoise”, with reference to the shape of its body which is similar to that of a dolphin or porpoise, and “beagle” (dog breed), with reference to its hunting abilities (Compagno 2001; Roman n.d.).

Synonyms: *Isurus nasus* (synonym), *Lamna cornubica* (Gmelin, 1789), *Lamna pennanti* (Walbaum, 1792), *Lamna philippii* (Pérez Canto, 1886), *Lamna punctata* (Storer, 1839), *Lamna whitleyi* (Phillipps, 1935), *Oxyrhina daekayi* (Gill, 1861), *Selanonius walkeri* (Fleming, 1828), *Squalus cornubicus* (Gmelin, 1789), *Squalus cornubiensis* (Pennant, 1812), *Squalus monensis* (Shaw, 1804), *Squalus nasus* (Bonnaterre, 1788), *Squalus pennanti* (Walbaum, 1792), *Squalus selanonus* (Leach, 1818).

ICCAT species code: POR

ICCAT names: Porbeagle (English), Requin-taupe commun (French), Marrajo sardinero (Spanish)

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

- Phylum: Chordata
- Subphylum: Vertebrata
- Infraphylum: Gnathostomata
- Superclass: Chondrichtyes
- Class: Chondrichtyes
- Subclass: Elasmobranchii
- Superorder: Euselachii
- Order: Lamniformes
- Family: Lamnidae
- Genus: *Lamna*

1.b. Common names

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

Albania: Tonil.

Australia: Mackerel shark, Porbeagle.

Azores: Marracho, Porbeagle.

Brazil: T. Golfinho, Cavalha, Cação, Marracho.

Canada: Maraîche.

¹ Original version created in September 2006 by J. Valeiras and E. Abad (Spanish Institute of Oceanography, Spain).

Cabo Verde: Anequim, Arrequim, Marracho, Peixe-cão, Sardo, Tubarão.

Canada: Maraîche, Porbeagle.

China (Mandarin Chinese): 鼠鯊.

Croatia: Kučina, Morski pas.

Crozet Islands: Requin taupe, Taupe.

Czech Republic: Žralok makrelový.

Denmark: Almindelig sildehaj, Sildehaj.

Estonia: Harilik heeringahai.

Faroe Islands: Hemari.

Finland: Sillihai.

France: Requin taupe, Requin-taupe commun, Lamie, Lamie, Taupe, Touille, Le squalé nez, Le lamie long nez, Lamie, Nez, Touille, Touillele boeuf taupe, Requin long nez, Loutre de mer, Nas llarg, Melantoun Sbrigliulu (corso).

Germany: Heringshai.

Greece: Λάμια, Καρχαρίας, Karharías, Lamia, Σκυλόψαρο, Skylopsaro.

Iceland: Hámeri.

Ireland: A craosaire, Porbeagle shark.

Isle of Man: Porbeagle.

Italy: Smeriglio.

Japan: Mōka-zame.

Kerguelen Islands: Requin taupe.

Madeira: Marracho.

Malta: Pixxiplamptu, Pixxiplamtu, Porbeagle shark, Smeriglio.

Montenegro: Kučina.

Morocco: Kalb.

Netherlands: Haringhaai, Neushaai.

New Zealand: Porbeagle.

Norway: Håbrand, Håbrann.

Poland: Żralacz sledziowy.

Portugal: Tubarão-sardo.

Romania: Rechinul scrumbiilor.

Russia: Aatlanticheskaya seldevaya akula, Акула сельдевая, акула атлантическая.

Senegal: Ndiagadar.

Serbia: Kučina, Psina atlantska.

South Africa: Haringhaai, Porbeagle, Porbeagle shark.

Spain: Calderon, El marrago, Ludia, Marraco, Marraquet, Taulo, Cailón, Cailón marrajo, Marraix, Marrajo, Marrajo sardinero.

Sweden: Håbrand, Håbrandshaj, Sillhaj.

Türkiye: Dikburun karkarias, Dikburunkarkarias baligi.

United Kingdom: Beaumaris shark, Porbeagle.

United States: Blue dog, Porbeagle.

Uruguay: Moka, Porbeagle.

Wales: Morgi mawr.

2. Identification (Based mostly from Compagno 2001).

Characteristics of *Lamna nasus* (Figure 1).



Figure 1. Porbeagle (*Lamna nasus*) (Bonnaterre, 1788). Image taken from Domingo *et al.*, 2010. Credit for photograph: CSIRO Marine and Atmospheric Research, Australia.

Lengths

References to size throughout this document consistently relate to total length (TL) in centimetres, unless otherwise specified (e.g. fork length: FL and precaudal length: PCL).

Porbeagle maximum reported size is 302 cm FL (Francis *et al.*, 2008). In the Northwest Atlantic the maximum sizes reported for males and females are 262 and 317 cm FL, respectively. In the Southwest Atlantic, females reach a maximum size of 278 cm and males 253 cm FL. In the Southwest Atlantic, the reported sizes were 221 cm FL for females and 226 cm FL for males (Forselledo, 2012). The maximum sizes reported in the Southwest Pacific are 228 cm FL for males and 208 cm FL for females (Francis and Stevens, 2000), which suggests that both sexes reach a smaller size in the Southern Hemisphere than in the Northern Hemisphere (Francis *et al.*, 2008).

Colour

Dorsal bluish grey, grey or dark grey. Ventral surface of body white, which does not extend over the pectoral bases. Ventral surface of head and abdomen white. Adults in the Southern Hemisphere may have a dark colour on the lower area of the head, and the abdomen may have blackish spots. The free rear tip of the first dorsal fin has a white patch that is characteristic of this species. The ventral surface of the pectoral fin tips is dark.

External characteristics

The porbeagle has a robust, fusiform body with a moderately long conical snout. Large dark eyes without nictitating membrane. Very large gill slits. The fins are quite stiff. First dorsal fin large, with a rounded form, with an almost straight posterior tip, and a white spot on the free rear tip. Origin of first dorsal fin over or just behind the insertions of the pectoral fin. Very small and pivoting second dorsal fin and anal fin. The origin of the anal fin is under the origin of the second dorsal fin. It presents strong keels on caudal peduncle and shorter secondary keels, under the former, on the base of the caudal. Large, half-moon shaped caudal fin, with upper and lower lobes of a similar size (Compagno, 2001; McMillan *et al.*, 2019; Roman n.d.).

Internal characteristics

On both jaws, large teeth with almost straight cusps, and small lateral cusps on both sides, in the lower jaw. The size and shape of teeth of species from the order Lamniformes vary considerably depending on their position in the jaw. They exhibit the so-called “lamnioid tooth pattern”, which refers to large anterior teeth, very small intermediate teeth, medium-to-large lateral teeth and small posterior teeth. This species has no symphyseal teeth. The dentary formula is variable with 12 to 16 teeth on either side of the upper jaw and 11 to 16 on either side of the lower jaw (Shimada, 2002; Purdy and Francis, 2007). Cranial rostrum with enlarged but discrete hypercalcified rostral cartilages, not forming a massive protuberance. The spinal column is made up of 150 to 162 vertebrae, 85 to 91 of which are located in the precaudal region (Compagno, 2001).

3. Distribution and population ecology

3.a. Geographic distribution

It has antitropical distribution, and is found in the North Atlantic, Mediterranean Sea and in the Southern Hemisphere in a circumglobal band in waters of the Atlantic, Indian and Pacific approximately between 30° and 60°S (**Figure 2**) (Last and Stevens, 1994; Compagno, 2001; Ebert *et al.*, 2013). Semba *et al.* (2013) showed that porbeagle has continuous distribution between the South Pacific and Southeast Indian Ocean, and between the Southwest Indian Ocean and the Southeast Atlantic. Based on information from fishing records, scientific observer data and satellite transmitters, Bowlby *et al.* (2020a) updated the species' distribution range in the Northwest Atlantic. It is found from Greenland and Canada, in the Labrador Sea, along the United States coast, to Puerto Rico, including the Gulf of Mexico. In the Northeast Atlantic, it is found from Iceland, to the West of the Barents Sea, including the North Sea and the Baltic Sea, to Morocco, including the Azores, Madeira, Cabo Verde and the Canary Islands (Compagno, 2001; Ebert and Stehmann, 2013; ICES, 2017; Biscoito *et al.*, 2018), and possibly the Gulf of Guinea (Compagno, 2001; ICES, 2017). It is present throughout the Mediterranean Sea, but not in the Black Sea (Bauchot, 1987; Compagno, 2001; Serena, 2005). In the Southwest Atlantic, porbeagles are distributed from 26°45'S, in southern Brazil, including Uruguay, southern Argentina, to 60°S, including the South Georgia Islands (Sadowsky *et al.*, 1985; Compagno, 2001; Domingo *et al.*, 2002, Cortés and Waessle, 2017; Rigby *et al.*, 2019). In the Southeast Atlantic, porbeagles are found in waters of Namibia and South Africa, up to approximately 50°S (Compagno, 2001; Basson *et al.*, 2007; Rigby *et al.*, 2019). Mejuto *et al.* (2020) recently reported catches of this species in intertropical areas of the East Atlantic, between 20°N and 20°S, some near the Gulf of Guinea. The authors indicate that these catches are possibly associated with low sea temperatures due to the presence of upwellings and cold superficial currents that cover the coast of the African continent and, therefore, some individuals of this species could sporadically reach these areas. The authors also mention that these “rare” occurrences have also been reported by Compagno (2001). In light of this new information, the ICCAT Shark Species Group recommended in the 2020 stock assessment of the species that more data are needed on fisheries in the equatorial area (between 20° South and 20° North) to confirm the presence of the species in this area (Anon., 2020). New reports of the species in this area from Ghanaian artisanal fisheries have been indicated by Seidu *et al.* (2022), with 3 individuals being caught. The map contained in **Figure 2** has been modified to represent the distribution of the species detailed in this section, including the work of Bowlby *et al.* (2020a) and Mejuto *et al.* (2020).

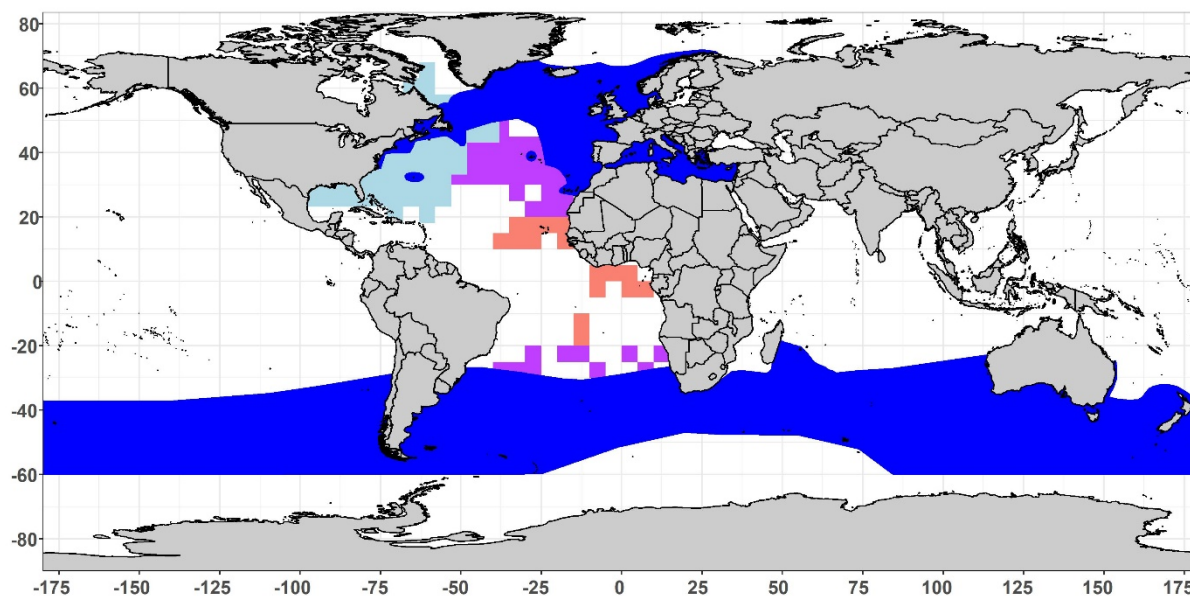


Figure 2. Map of porbeagle distribution (*Lamna nasus*). Taken and modified from the International Union for Conservation of Nature (IUCN) (IUCN SSC Shark Specialist Group 2018). *Lamna nasus*. The IUCN Red List of Threatened Species. Version 2021-1). The data taken from Bowlby *et al.* (2020a) are in light blue, and those from Mejuto *et al.* (2020) are shown in violet and salmon pink. To distinguish, the data from intertropical areas of the East Atlantic between 20°N and 20°S are indicated in salmon pink.

3.b. Habitat preferences

Porbeagle is an epipelagic species that mainly inhabits continental shelves and the open ocean, occasionally occurring in areas close to the coast (Compagno, 2001; Francis *et al.*, 2008). Catch data have shown that the species has a wide longitudinal distribution in pelagic waters of the Southern Hemisphere (Semba *et al.*, 2013). This species' antitropical distribution probably originated in the glacial periods when tropical areas were narrower, which allowed this species to cross between hemispheres through the tropics (Stevens, 2010).

In general, porbeagle is distributed from the surface to depths of 200 m, although there are reports of porbeagle on the coast at a depth of 1 m and reports at depths between 350 and 700 m (Last and Stevens, 1994; Lucifora and Menni, 1998; Francis and Stevens, 2000; Compagno, 2001; Campana *et al.*, 2010). It occurs in a wide range of temperatures, in the Southern Hemisphere, it is found from 2 to 23°C, preferring the range between 8°C and 20°C and its abundance decreases upwards of 19°C (Francis and Stevens, 2000). In the Southwest Atlantic, based on scientific observer data of the Uruguayan longline fleet, catches of the species were recorded in surface temperatures between 10.6°C and 22.7°C, the highest values of catch per unit effort (CPUE) being observed at temperatures between 11° and 12°C and a negative correlation between the CPUE and the sea surface temperature (SST) (Forselledo, 2012). In the Northwest Atlantic, Campana and Joyce (2004) observed catches of this species at temperatures between -1 and 15°C, with a preference between 5 and 10°C. This difference in temperatures between studies is mainly due to the fact that Campana and Joyce (2004) use temperature data taken at catch depth. Satellite telemetry studies in the Northeast Atlantic have indicated that the species lives in waters with temperatures between 9° and 19° C and appear from the surface to 700 m deep. The authors observed variability between individuals in vertical movements, even in the same oceanographic conditions (Pade *et al.*, 2009; Saunders *et al.*, 2011).

3.c. Migrations

Porbeagle is a highly migratory species. It is found on the surface, on the bottom, alone, and in schools. Catch information from various fisheries in the Atlantic and Pacific indicate segregation by size (age) and sex (Campana, 1999; Francis and Stevens, 2000; Francis *et al.*, 2008; Forselledo, 2012).

Time-area variations in species abundance are observed in the North Atlantic. Movements of this species in the North Atlantic are known from tagging data obtained from conventional and satellite tagging programmes (Stevens, 1990; Campana *et al.*, 1999; Kohler *et al.*, 2002; Campana *et al.*, 2010; Pade *et al.*, 2009; Saunders *et al.*, 2011; Biais *et al.*, 2017; Kohler *et al.*, 2019). Campana *et al.* (1999) summarizes the annual movements of porbeagle in the Canadian Atlantic and informs that this species is present in January-February in the Gulf of Maine, Georges Bank and South of the Scotian shelf, and shifts towards the Northeast, along the Scotian shelf in spring, and then appears off the South coast of Newfoundland and in the Gulf of St Lawrence in the summer and autumn. Catches in late autumn suggest a return movement towards the Southwest. Tagging data support this annual migration where tags applied in the first half of the year tended to be recovered in more easterly and northern locations, while the reverse would occur for tags applied in the summer and autumn (Campana *et al.*, 1999). These tagging programmes showed that in the North Atlantic, the majority of the sharks tagged travel short to moderate distances (up to 1,500 km) on the continental shelves (Kohler *et al.*, 1998; Pawson and Vince, 1998; O’Boyle *et al.*, 1998; Campana *et al.*, 1999, Cavanagh, 2005). Of the individuals tagged, only one crossed the Atlantic, travelling 4,260 km from Ireland to Canada where it was caught after more than 10 years at liberty (Cameron *et al.*, 2018). In the North Atlantic, it was observed that individuals move northwards along the coast during spring and early summer and remain there until late autumn, when they return (Mejuto, 1985; Campana and Joyce, 2004). These migratory patterns have been confirmed in recent studies based on satellite telemetry, in which extensive annual migratory cycles are observed, with a proven species site fidelity (Pade *et al.*, 2009; Saunders *et al.*, 2011; Biais *et al.*, 2017).

In the Southern Hemisphere, interactions with fisheries suggest a higher rate of juveniles in areas to the North of the southern distribution (Semba *et al.*, 2013), and most of the species’ movements appear to take place in a North-South latitudinal direction (Francis *et al.*, 2015). Migration to the North in winter and to the South in summer was observed in both the Southwest Atlantic and Southwest Pacific (Francis and Stevens, 2000; Francis *et al.*, 2007; Forselledo, 2012).

4. Biology

4.a. Growth

Biological data on age and growth of porbeagle in Atlantic waters are incomplete and several characteristics remain unknown.

Growth parameter estimates were calculated for porbeagle in the Northwest Atlantic using ring counts on vertebral annuli, size-frequency analysis, and tag-recapture data (Natanson *et al.*, 2002). The periodicity of two annual rings up to 11 years was validated, by injecting oxytetracycline and sharks of known age. Age estimates were validated up to 26 years (Campana *et al.*, 2002a; Natanson *et al.*, 2002).

Table 1. Growth parameters for porbeagle (L_{∞} in cm, K in y^{-1} , t_0 in y).

| Growth parameter | | | Area | Reference | Sex | Method |
|------------------|-------|-------|-----------------------|-------------------------------|---------|-----------|
| L_{∞} | k | t_0 | | | | |
| 289.4 (FL) | 0.07 | -6.06 | Northwest Atlantic | Natanson <i>et al.</i> (2002) | All | Vertebrae |
| 309.8 (FL) | 0.06 | -5.9 | Northwest Atlantic | Natanson <i>et al.</i> (2002) | Females | Vertebrae |
| 257 (FL) | 0.08 | -5.78 | Northwest Atlantic | Natanson <i>et al.</i> (2002) | Males | Vertebrae |
| 276.6 (FL) | 0.045 | 8.0 | Northeast Atlantic | Jung <i>et al.</i> (2010) | All | Vertebrae |
| 182.2 (FL) | 0.112 | -4.75 | New Zealand | Francis <i>et al.</i> (2007) | Males | Vertebrae |
| 233.0 (FL) | 0.060 | -6.86 | New Zealand | Francis <i>et al.</i> (2007) | Females | Vertebrae |

4.b. Length-weight relationships

Published length-weight relationships in the Atlantic are showed in **Table 2**.

Table 2. Published length-weight relationships for porbeagle (*Lamna nasus*). N: No. of individuals. This column also provides detailed information if the relationship has been made for combined sexes (C), males (M) or females (F). TW: Total weight (kg); TL: Total length (cm); PCL (precaudal length) (cm); FL: Fork length (cm); CFL: Curved fork length (cm).

| Equation | N | Size range | R ² | Area | Referencr |
|--|----------|----------------|----------------|--------------------|------------------------------|
| $TW = 1.48 \times 10^{-5} \times (FL)^{2.9641}$ | 15 (C) | 106 – 227 (FL) | 0.944 | Northwest Atlantic | Kohler <i>et al.</i> (1995) |
| $TW = 5 \times 10^{-4} \times (FL)^{2.713}$ | 286 | N/A | 0.980 | Northwest Atlantic | Campana <i>et al.</i> (1999) |
| $TW = 1.292 \times 10^{-4} \times (TL)^{2.4644}$ | 71 (C) | 104 – 187 (TL) | N/A | Northeast Atlantic | Ellis & Shackley (1995) |
| $TW = 2.77 \times 10^{-4} \times (FL)^{2.3958}$ | 39 (M) | 136 – 248 (FL) | 0.941 | Northeast Atlantic | Mejuto & Garcés (1984) |
| $TW = 3.90 \times 10^{-6} \times (FL)^{3.2070}$ | 26 (F) | 116 – 210 (FL) | 0.983 | Northeast Atlantic | Mejuto & Garcés (1984) |
| $TW = 1.07 \times 10^{-5} \times (TL)^{2.99}$ | 17 (C) | 84 – 163 (TL) | 0.990 | Northeast Atlantic | Stevens (1990) |
| $TW = 3 \times 10^{-5} \times (CFL)^{2.8164}$ | 245 (M) | 100 – 230 | N/A | Northeast Atlantic | Jung (2009) |
| $TW = 5 \times 10^{-5} \times (CFL)^{2.7290}$ | 283 (F) | 100 – 236 | N/A | Northeast Atlantic | Jung (2009) |
| $TW = 4 \times 10^{-5} \times (FL)^{2.7316}$ | 564 (M) | 88 – 230 | N/A | Northeast Atlantic | Hennache & Jung (2010) |
| $TW = 3 \times 10^{-5} \times (FL)^{2.8226}$ | 456 (F) | 93 – 249 | N/A | Northeast Atlantic | Hennache & Jung (2010) |
| $TW = 4 \times 10^{-5} \times (FL)^{2.7767}$ | 1020 (C) | 88 – 249 | N/A | Northeast Atlantic | Hennache & Jung (2010) |

4.c. Conversion factors

Table 3 presents the published length-length relationships for the species' distribution areas, with particular emphasis on the Atlantic Ocean.

Table 3. Published length-length relationships for porbeagle (*Lamna nasus*). N, number of individuals. In this same column it is indicated whether the relationship is for both sexes combined (C), males (M) or females (F). TL: total length (cm); PCL: precaudal length (cm); FL: fork length (cm); CFL: curved fork length (cm), IDL: interdorsal length (cm).

| Equation | N | Size range | R ² | Area | Reference |
|-----------------------------------|---------|----------------|----------------|--------------------|------------------------------|
| $FL = 0.885 \times (TL) + 0.99$ | 361 | N/A | 0.990 | Northwest Atlantic | Campana <i>et al.</i> (1999) |
| $FL = 1.120 \times (PCL) + 1.7$ | 360 | N/A | 0.990 | Northeast Atlantic | Campana <i>et al.</i> (1999) |
| $FL = 2.755 \times (IDL) + 26.3$ | N/A | N/A | 0.980 | Northeast Atlantic | Campana <i>et al.</i> (1999) |
| $FL = 0.897 \times (TL) + 1.794$ | 13(C) | 106 – 227 (FL) | 0.987 | Northeast Atlantic | Kohler <i>et al.</i> (1995) |
| $PCL = 0.907 \times (FL) - 1.366$ | 866 | 61 – 223 (FL) | 0.995 | New Zealand | Francis y Stevens (2000) |
| $TL = 1.098 \times (FL) + 4.165$ | 173 | 63 – 180 (FL) | 0.967 | New Zealand | Francis y Stevens (2000) |
| $FL = 0.95 \times (CFL) + 0.90$ | 172 | N/A | 0.997 | New Zealand | Francis <i>et al.</i> (2007) |
| $FL = 1.103 \times (PCL) + 2.250$ | 983 (C) | 66 – 226 (FL) | 0.995 | Southwest Atlantic | Mas <i>et al.</i> (2014) |
| $FL = 1.102 \times (PCL) + 2.619$ | 638 (M) | 66 – 226 (FL) | 0.995 | Southwest Atlantic | Mas <i>et al.</i> (2014) |
| $FL = 1.102 \times (PCL) + 2.082$ | 329 (F) | 67 – 214 (FL) | 0.995 | Southwest Atlantic | Mas <i>et al.</i> (2014) |
| $TL = 1.147 \times (FL) + 0.742$ | 700 (C) | 67 – 214 (FL) | 0.997 | Southwest Atlantic | Mas <i>et al.</i> (2014) |

4.d. Reproduction

Biological data on the reproduction of porbeagles in Atlantic waters are incomplete and several aspects remain unknown.

Gestation and parturition

The porbeagle is viviparous, placental with oofagy (type of cannibalism whereby the embryos in the uterus feed on other eggs produced by the mother) (Francis and Stevens, 2000; Jensen *et al.*, 2002). Nursery areas are found on both sides of the North Atlantic, off the coast of Europe and the British Isles and also off North America, from Maine to Canada. There is reported presence of embryos from Maine to Massachusetts and in Atlantic Canada (Bigelow and Schroeder, 1948; Jensen *et al.*, 2002). The juveniles are bred in all their ranges in the East Atlantic (Bigelow and Schroeder, 1948). O'Boyle *et al.* (1998) suggest that, based on data published on the Northeast Atlantic, mating takes places in the autumn and birth in the spring when porbeagle swim up from deep water to the surface to feed intensively. Size and sex segregation is common in pregnant females that, according to what has been reported, move to remote areas during gestation and birth and remain separated from males and juveniles in discrete breeding areas (O'Boyle *et al.*, 1998; Jensen *et al.*, 2002).

In the Northwest Atlantic, Jensen *et al.* (2002) observed that all the females sampled in winter were gravid, suggesting that there is no extensive rest period between one breeding and another, and that the reproductive cycle of the females lasts one year. Recent studies observed the presence of mature females in a resting stage, which suggests that this species has a biennial reproductive cycle like other species from the family Lamnidae (Natanson *et al.*, 2019). After an extensive mating period in the autumn (September-November), females give birth in the spring, starting in April, with an average of four pups (Jensen *et al.*, 2002). Gestation is estimated between 8-9 months (Aasen, 1963; Jensen *et al.*, 2002), while in the Northeast Atlantic it is considered to be one year (Gauld, 1989).

Maturity

In the Northwest Atlantic, males matured between 162 and 185 cm FL, and 50% are mature at 174 cm FL. Females matured between 210 and 230 cm FL, and 50% mature at 218 cm FL (Jensen *et al.*, 2002). Other estimates of maturity include that by Aasen (1961), in the Northwest Atlantic, of males between 136-181 cm FL and females between 181-226 cm FL. Males mature at an age between 6 and 10 years, with 50% maturing at the age of 8 years. Females mature at an age between 12 and 16 years, with 50% maturing at the age of 13 years (Jensen *et al.*, 2002; Natanson *et al.*, 2002). In the Northeast Atlantic, the smallest size mature male measured 140 cm FL and the L50 for males was estimated at 169.5 cm FL. The L50 size for females was estimated at 199.5 cm FL, however the authors mentioned that this value was estimated based on the low number of mature females, therefore this figure should not be extended to all the population (Jung *et al.*, 2009).

In the Southwest Atlantic, Uruguay, it was observed that the relation between FL and the clasper length (CLI) shows a sigmoidal type curve with rapid growth of the claspers between 120 and 150 cm. According to this, males would reach maturity approximately between 150 and 160 cm. This size is closer to that observed in the Southwest Pacific (140-150 cm FL) by Francis and Duffy (2005) than that observed in the Northwest Atlantic (174 cm FL) by Jensen *et al.* (2002) and Forselleo *et al.* (2012).

Sex ratio

Kholer *et al.* (2002) found a sex ratio for males and females of 1:1 in the Northwest Atlantic and of 1:0.25 in the Northeast Atlantic. Aasen (1963) found a sex ratio of 1:1 in the Northwest Atlantic and observed an increase in the size of porbeagle from the West to the East. In the Northeast Atlantic, in the Azores, a sex ratio of approximately 1:0.5 was observed, this being the highest difference in the sex ratio observed (Mejuto, 1985; Mejuto and Garcés, 1984). Gauld (1989) observed a ratio of males to females of 1:1.3 off the Shetland Islands in Scottish waters. Likewise, in the Northeast Atlantic, Jung *et al.* (2009) observed a general ratio of 1:0.89, this proportion varying depending on the areas studied, and in some areas found ratios in favour of females of 1:1.08.

In the Southwest Atlantic, it was found that the sex ratio (males:females) was 2:1, showing different ratios by season, decreasing from autumn to summer (autumn: 3.7:1; winter: 2.0:1; spring: 0.9:1; summer 1:1). These differences in the sex ratios are explained in part by a greater presence of small individuals during the spring and summer months, since different sex ratios were also observed by size (Forselleo, 2012; Forselleo *et al.*, 2020). Males were observed to exceed females with a ratio of 2.8:1 in individuals over 145 cm (Forselleo, 2012).

Fecundity

Usually the litter size is four embryos, but it fluctuates between 1 and 5 (Bigelow and Schroeder, 1948; Gauld, 1989; Francis and Stevens, 2000; Jensen *et al.*, 2002; Forselleo, 2012). The average number of pups in the Southwest Pacific, Northeast Atlantic, and Northwest Atlantic was 3.75, 3.70, and 4, respectively (Gauld, 1989; Francis and Stevens, 2000; Jensen *et al.*, 2002; Francis *et al.*, 2008). Sex frequency in the embryos is not significantly different from 1 (Francis and Stevens, 2000; Jensen *et al.*, 2002). Generally, size at birth is between 60 and 75 cm TL in the North Atlantic (Aasen, 1963; Compagno, 1984). In the Southwest Pacific the size at birth is 58-67 cm FL (Francis and Stevens, 2000). Based on sizes of embryos observed and the smallest individuals caught in the Southwest Atlantic, this species has an estimated size at parturition of 66-67 cm (Forselleo, 2012).

4.e. Diet

There are few studies on this species' diet, and currently records are mainly anecdotal. It is an opportunistic predator, and its diet may include a wide range of prey, including small to moderate sized pelagic species such as mackerel, sardine, herring, squid and cuttlefish. However, porbeagle also feed on demersal fish, including cod, haddock, cusk, whiting, hake, icefishes and St. Peter's fish. This species' prey also includes some Chondrichthye species, including *Squalus acanthias* and *Galeorhinus galeus*. In contrast to other species from the family Lamnidae, there is no record of the remains of marine mammals or large fish being found in stomach contents (Stevens, 1973; Gauld, 1989; Compagno, 2001; Joyce *et al.*, 2002). The stomach contents of a 100 cm individual were analysed off the West Irish coast, and only the remains of many euphausiaceans and some polychaeta were observed (Henderson *et al.*, 2003).

Joyce *et al.* (2002) performed a detailed study of this species' diet in the Northwest Atlantic, providing a quantitative description thereof, based on an analysis of the stomach contents of 1,022 individuals measuring between 85 and 264 cm. The species' diet was seen to be mainly composed of bony fish and cephalopods. In terms of frequency of occurrence, squid beaks and bony fish topped the list. Based on the percentage of total stomach contents, demersal fish are the most significant element. Diet composition changes seasonally following a migration from deep to shallow waters, with a larger presence of demersal fishes in autumn, while pelagic fish and cephalopods comprised made up most of the diet in spring.

Based on an analysis conducted in the Northeast Atlantic, it was observed in 93 stomachs that the diet of porbeagle is mainly composed of two taxa: teleosts and cephalopods which are present in 61.3% and 17.2% of stomachs. The other taxa, echinoderms, annelids, gasteropods and crustaceans are present in very small proportions. Among bony fish, the major species were *Scomber scombrus*, *Merlangius merlangus*, *Micromesistius poutassou* and *Trachurus trachurus*. Authors observed that prey varies depending on catch area of the individuals analyzed, and that each main prey corresponds to a species present in abundance in the fishing area. These results confirm the ubiquitous nature of porbeagle shark, which feed both in open waters and near the sea floor near the continental shelf (Jung *et al.*, 2009).

In the Southwest Atlantic, the species' diet was analysed, based on 413 individuals caught incidentally in a trawl fishery that mainly catches *Macruronus magellanicus* and operates in Argentinian waters, between 52° and 56° S. Based on the stomach contents, it was observed that porbeagle feeds mainly on fish (88.3%), *M. magellanicus*, *M. australis* and *Sprattus fuegensis* being the main species found. Cephalopods came second in terms of importance (5.8%) and crustaceans third (4.3%). 24.9% of the stomachs were empty. In light of these results, the estimated trophic level for the species in this region was 4.35 (Belleggia *et al.*, 2021). These authors also observed that smaller individuals feed on large and small bony fish, while larger individuals feed exclusively on large bony fish (Belleggia *et al.*, 2021).

A study of the stomach contents of individuals caught in the Kerguelen Islands reported the presence of 15 squid species (mainly based on beak identification) and several mesopelagic and pelagic species of bony fish from the continental shelf. Of all the squid species, two were observed to be an important part of porbeagle's diet: *Histioteuthis atlantica*, accounting for 46% of the total number of beaks found, and *Todarodes angolensis*, accounting for 32.5%. Based on the reconstructed cephalopod mass, the latter species represented 56.5% of total cephalopod mass. According to this study, the species is a predominantly pelagic predator in the waters of the Kerguelen Islands as demersal species are not an important element (Cherel and Duhamel, 2004).

4.f. Physiology

Like other members of the Lamnidae family, porbeagle have the ability to maintain their body temperature considerably higher than the temperature of the surrounding water by generating metabolic heat (regional endothermy; Carey and Teal, 1969; Block and Carey, 1985; Block and Finnerty, 1994; Bernal *et al.*, 2001, 2005). In particular, body temperatures between 7° and 11°C above ambient temperature have been recorded for this species, and it has also been reported that porbeagle is as effective as the shortfin mako (*Isurus oxyrinchus*) in maintaining the temperature of its visceral organs (Carey and Teal, 1969; Carey *et al.*, 1981, 1985). Among the pelagic shark species, porbeagle is one of the most tolerant of the cold, which could suggest that it has evolved to take advantage of its capacity to thermoregulate, thus allowing them to search for and feed on abundant cold-water prey (Campana and Joyce, 2004).

4.g. Mortality

Natural mortality (M) is one of the most important parameters for a stock assessment, however it is one of the most difficult parameters to estimate, and direct estimation is extremely rare for sharks. Thus, M is often indirectly estimated from the life history traits, using relations derived from lifespan, sizes, growth parameters, in general assuming that there is no variation in size, age and time. From the information published on growth parameters, Chen and Yuan (2006) estimated that the natural mortality for the Northeast Atlantic for this species was 0.113 years⁻¹. During the last stock assessment carried out by ICCAT, Cortés and Semba (2020) presented an estimation of population parameters for the species, where the M value was estimated for the Northwest and South Atlantic, based on different models that use life cycle parameters. For the Northeast Atlantic, M value was estimated for all the ages between 0.05 and 0.13 years⁻¹, while the M value by age varied between 0.18 to 0.21 year⁻¹ for sharks aged 0, and 0.09 to 0.10 year⁻¹ for sharks aged 25 years. For the South Atlantic the constant M value was estimated for all the ages between 0.06 and 0.19 years⁻¹, while the M value by age varied between 0.18 to 0.22 year⁻¹ for sharks aged 0, and 0.09 to 0.12 year⁻¹ for sharks aged 25 years.

As regards catch mortality, Coelho *et al.* (2012) reported a 30% mortality for the pelagic longline fishery, however based on a very low number of individuals caught (n = 10). In the Northwest Atlantic, studies carried out in the Canadian longline fleet, reported 27% mortalities (10% for individuals that were healthy when taken on board, and 75% for injured) (Campana *et al.*, 2016). More recently, these data have been updated, resulting in post-catch mortalities of 14% (6% for healthy individuals and 40% for injured individuals). Authors suggested that this difference in the proportion of individuals that die is related to handling characteristics during tagging, which switched from bringing animals on board to tagging the individuals in the water (Bowly *et al.*, 2020b). In the same area, a study on post catch mortality of porbeagle in the rod and reel fishery observed that 100% of the individuals survived after release (Anderson *et al.*, 2021).

Mas *et al.* (2020) analyzed information on longline catch mortality in the Southwest Atlantic through the fitting of a Generalized Additive Mixed Model (GAMM) taking into account biological, environmental and operative covariables. The results showed that deep longline (targeting tuna) have lower hooking mortality compared to surface longline (targeting swordfish and sharks). The size, sea surface temperature and sex were also important covariables and the hooking mortality increased with size and temperature, being lower in females than males. Authors suggest that the differences observed in hooking mortality between deep longline and surface longline could be related to the ganglion lengths. Deep longline use longer branch lines which could offer less restricted movement to specimens caught. On the other hand, shorter branch lines for surface longline could restrict movement to the point of limiting the capacity of specimens to ventilate adequately, ultimately reducing their survival possibilities. Authors also recognized that soaking time for fishing gear constitutes an important variable which should be included in future analyses.

5. Fisheries biology

5.a. Stocks / Stock structure

Within ICCAT, the structure of porbeagle stocks has been addressed and discussed in the latest assessments carried out (Anon., 2010; Anon., 2020). According to the available information, there are four stocks for this species: Northwest, Northeast, Southwest and Southeast. The limits defined in the ICCAT Manual are used to delimit these stocks (see: ICCAT geographical definitions, Version: 2016.02, ICCAT 2006-2016).

Several authors have reported genetic differentiation between individuals in the Northern and Southern Hemispheres (Kitamura and Matsunaga, 2010; Testerman, 2014; González *et al.*, 2021). Testerman (2014) proposed that the Northern and Southern Hemispheres be managed as two separate and genetically distinct stocks.

In the North Atlantic, tagging and recapture data from conventional (Stevens, 1990; Campana *et al.*, 1999; Kohler and Turner, 2001; Kohler *et al.*, 2002; Kohler and Turner, 2019) and satellite tags (Campana *et al.*, 2010; Pade *et al.*, 2009; Saunders *et al.*, 2010; Biais *et al.*, 2017) support the view of restricted movements between individuals from the Northwest and Northeast Atlantic, clear evidence that they are two separate stocks (Anon., 2020). Although Testerman (2014) found no genetic evidence to differentiate between Northeast and Northwest Atlantic porbeagle stocks, the data suggested approximately 30 to 150 migrants per generation between the two stocks, or 2 to 12 migrants per year. Although no genetic differentiation was found between the Northeast and Northwest stock, gene recruitment between these areas is low and they should be considered as two stocks (Testerman, 2014).

Regarding the South Atlantic, there is little to no information available from conventional or satellite tagging studies to help define stocks. In addition, results based on genetic analyses are inconclusive in terms of defining the existence of one or more subpopulations (Kitamura and Matsunaga, 2010; Testerman, 2014). Information from data obtained by observers on Japan's longliner fleet and from research campaigns in the Atlantic, Pacific, and Indian Oceans indicate that the species is continuously distributed throughout these three oceans and extends from a latitude of 20° and 60° South (Semba *et al.*, 2013). Despite this continuous distribution, spatial variations were observed in population index trends (Hoyle *et al.*, 2017a), and the spatial scale of the Southern Hemisphere was observed to be very large in relation to the observed movement rates (Francis *et al.*, 2015). Given these factors, it was already suggested that it was unlikely that the population comprises a single well-mixed stock for management purposes and that it would be preferable to model the general population as separate assessment units, defined by longitude (Hoyle *et al.*, 2017b). The result of this study subdivides the Southern Hemisphere into five subpopulations: West Atlantic Ocean, East Atlantic/West Indian Ocean, East Indian Ocean, West Pacific Ocean and East Pacific Ocean (Hoyle *et al.*, 2017b).

During the 2020 ICCAT assessment meeting, the information available on this species in the South Atlantic suggesting the existence of a single stock was evaluated and discussed. In fact, it was suggested that there may be a single southern stock that extends across the Atlantic, Indian and Pacific Ocean basins. Despite this, the ICCAT Sharks Species Group recommended leaving the management units as currently defined in two stock units: Southeast and Southwest. Likewise, it was suggested that more research on stock structure is needed to determine an appropriate stock unit (Anon., 2020).

5.b. Description of fisheries

Porbeagle (*Lamna nasus*) is caught with a variety of fishing gears throughout its distribution range. In the Atlantic Ocean, it is caught by surface, deep and bottom longline, pelagic and bottom trawl, gillnet, handline, sport fisheries, and is mainly taken as bycatch in the pelagic longline fisheries targeting tuna and swordfish (Bonfil, 1994; Anon., 2005). Historically, this was one of the shark species of greatest commercial value in Europe (Gauld, 1989). Thus, it has been exploited commercially since the early 1800s, mainly by Scandinavian fishermen in North Atlantic waters (Gauld, 1989; Compagno, 2001; Cavanagh, 2005).

In the Northeast Atlantic, fisheries targeting *L. nasus* in the North Sea and off the Scottish coasts have mainly been conducted by Norwegian and, to a lesser extent, Danish vessels, and by French vessels in southern and western England by French vessels (Cavanagh, 2005). The Norwegian fishery was active in the 1930s and 1940s and was the main fishery for *L. nasus* in the Northeast Atlantic after the Second World War (Gauld, 1989), but since the 1960s, has declined significantly (ICES, 1995; Cavanagh, 2005). In the Bay of Biscay and the Celtic Sea, fisheries targeting this species were also conducted (Pawson and Vince, 1999). Landings in the ICES area decreased since the late 1940s, remaining relatively stable between the mid-1960s and 2010. In 2010, the Total Allowable Catch (TAC) was reduced to 0 and EU vessels were prohibited from landing porbeagle taken in international waters (ICES, 2019). Since 2015, it is prohibited for EU vessels to land porbeagle taken in any area (EU, 2019).

The porbeagle stock in the Northwest Atlantic Ocean supported annual catches of up to 9,000 t in the early 1960s, before the fishery collapsed in 1967. Low and apparently sustainable catches of about 350 t in the 1970s and 1980s allowed the stock to partially rebuild before a new fishery arose in the early 1990s. Canadian and U.S. fishermen began targeting this species in the early 1990s (O'Boyle *et al.*, 1998). The response of the stock to the renewed fishing pressure is unclear but an analysis of the population dynamics suggests that stock abundance has declined once more (Campana *et al.*, 2002b), and collapsed for the second time (Campana *et al.*, 2008).

In the South Atlantic, the species has been taken by various fleets operating in those waters, mainly as bycatch in pelagic longline fisheries, but in most cases was retained on board for trade (Amorim *et al.*, 1998; Domingo *et al.*, 2002; Basson *et al.*, 2007; Semba *et al.*, 2013; Forselledo *et al.*, 2017; Anon., 2020; Mejuto *et al.*, 2020). The species is also taken as bycatch in bottom and mid-water longline and trawl fisheries (Forselledo and Domingo, 2015; Cortés and Waessle, 2017).

Figure 3 presents nominal catches (t) of porbeagle in the Atlantic Ocean, reported to ICCAT in Task 1 for the period 1950-2020 (SHK Executive Summary). It is highly likely that the values are underestimated, as there continue to be unreported landings of this species, and dead discards continue to be very limited (Anon., 2020). Catches of this species have decreased throughout the Atlantic Ocean due mainly to the management measures imposed. In 2019, the catches reached just over 16.2 t for all ICCAT Convention areas, 15.6 t corresponding to the Northeast stock.

5.c. State of the stocks

Many shark fisheries have been associated with ‘boom and bust’ (Stevens *et al.*, 2005). One of the best-known examples is the North Atlantic porbeagle fishery; a decade after reaching a maximum of 11,000 t in 1964, catches dropped below 2,000 t approximately, and following partial recovery of the fishery, it collapsed again for the second time (Compagno, 1990; O’Boyle *et al.*, 1998; Campana *et al.*, 2002b; Campana *et al.*, 2008).

In 2009, the ICCAT Shark Species Group, together with ICES, conducted a porbeagle stock assessment, concluding that according to the available information, the populations of this species in the North Atlantic Ocean have dropped below the Maximum Sustainable Yield (MSY). Furthermore, while countries such as Canada have established a conservative catch regime, it is estimated that due to the low productivity of this species, it will take decades for the stock to recover (Anon., 2010). In the assessment it was concluded that the existing data for the South Atlantic are too limited to provide a robust indication of the status of the stock. Data indicate a potential decline in abundance below MSY, therefore adoption of precautionary measures should be considered (Anon., 2010).

ICCAT conducted a new stock assessment for porbeagle in 2020 (Anon., 2020). The results of the stock assessment are presented below. In this process, two modelling approaches were used to assess stock status. Firstly, a sustainability assessment for fishing effects (SAFE) was used to assess whether stocks in the North and South Atlantic were experiencing overfishing. Secondly, an incidental catch model (ICM) was used to assess whether the Northwest Atlantic stock was currently overfished and to determine the stock’s capacity for future removals.

The results of the SAFE approach indicated that porbeagle stocks in both the North and South Atlantic were not experiencing overfishing. It was noted that, while this is a data-poor approach, the overfishing status results were robust in relation to the assumed selectivity curve and the post-release mortality value used in the computation of post-catch mortality. The Group observed that the results for the South Atlantic are in line with those found in the Southern Hemisphere assessment and that the values of F/F_{MSY} of both studies are of relatively similar magnitude (0.063, range: 0.046 to 0.083 for 2006-2014 in the Southern Hemisphere assessment compared to 0.107-0.19 for 2010-2018 in the SAFE analysis).

All formulations of the ICM model indicated a rebuilding trend since 2001 for the Northwest stock, although biomass in 2018 was only 57% of biomass at the SPRmer reference point and the stock was predicted to be overfished, with a probability of 98%.

There are conflicting signs regarding the overfished status (the SAFE approach indicates that there is no overfishing and the exploratory method based on size suggesting overfishing), but with the large reduction of recent removals, the Group does not consider probable that the stock experiencing overfishing if the total removals (landings, dead discards and mortalities following unreported releases) do not greatly exceed what the Group had estimated as removals. However, given that the magnitude of dead discard specimens continues to be uncertain and that mortalities, following release, are not incorporated in the release, there remains uncertainty regarding the overfishing status.

Considering the underreporting of removals and the current low Northwest stock status, the Group recommends that catches do not exceed the current levels to allow for stock recovery. Although the Kobe matrix could suggest that some increases in catches could allow for possible recovery in the long-term, the assessment suggests that the stock is sufficiently productive to recover in a much shorter period if the catches are maintained

at lower levels. This is coherent with Rec. 11-13 where overfished stocks should recover in the shortest possible period. However, the delegates of the Commission should be aware that the real removals (particularly of dead discard specimens and mortalities following the release of live specimens) are greater than the information that has been reported, and the Kobe matrix is very optimistic, insofar as the removals that go unreported. Regarding the South Atlantic stocks, the Group could not reach a conclusion as regards their overfished state.

As to porbeagle in the Southern Hemisphere, the results of the stock assessment presented in 2017 in the Western and Central Pacific Fisheries Commission (WCPFC), show low fishing mortality rates in the three regions comprising the assessment area and low risk from commercial pelagic longline for porbeagle shark over the spatial domain of the assessment. These results are consistent with the trends observed in catch rate indicators over the entire range of the porbeagle shark population in the Southern Hemisphere, which in most cases show stable or increasing catch rates (Hoyle *et al.*, 2017b).

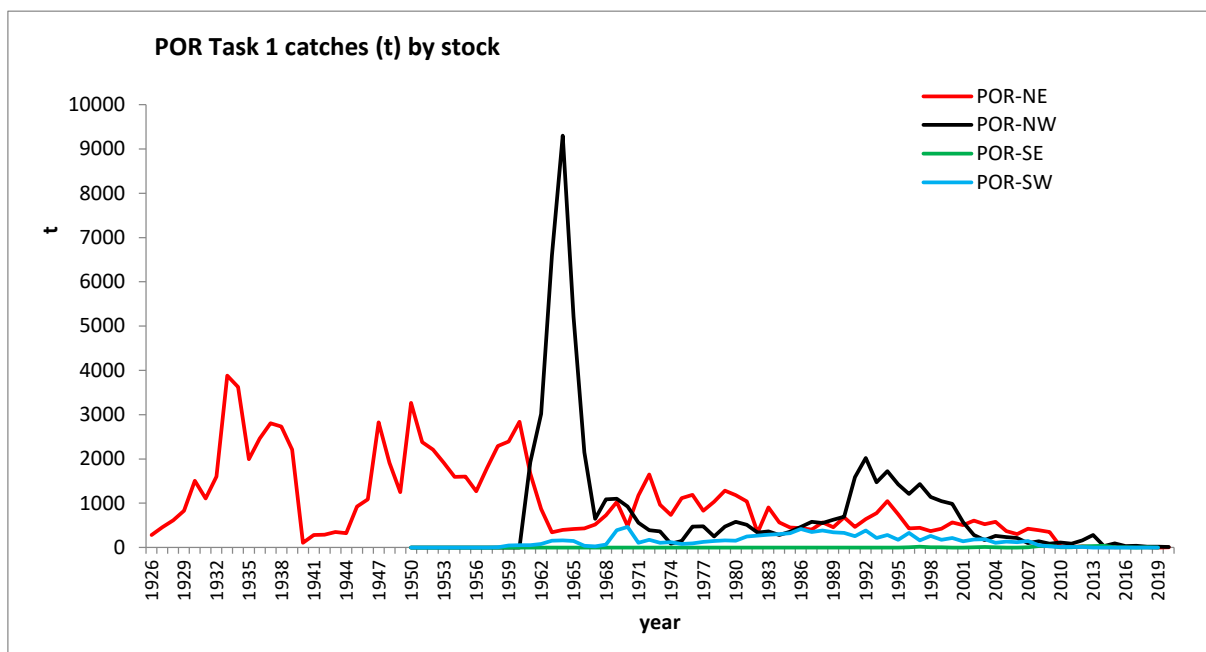


Figure 3. Nominal catch of porbeagle (t) in each of the 4 stocks considered in the Atlantic Ocean, reported to ICCAT in Task 1 for the period 1950-2020 (Anon., 2022).

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