

STOCK DELINEATION OF NORTHEAST ATLANTIC PORBEAGLE *LAMNA NASUS*

Jim R. Ellis¹, Graham Johnston² and Rui Coelho³

*The recent benchmark assessment for North-east Atlantic porbeagle *Lamna nasus* necessitated further consideration of stock identification. The published information reviewed suggests seasonal, ontogenetic and sexual differences in movements and distribution, including (i) northward movements of larger porbeagle (including large females) along the shelf to overwinter north of Scotland, (ii) southward movements of smaller porbeagle (including males) to overwinter in Iberian waters and northern parts of FAO Area 34, and (iii) westward movements of some porbeagle into oceanic waters. Whilst different parts of the population may undertake different seasonal migrations, the wide-ranging movements and mixing in the North-east Atlantic support the single-stock hypothesis within this area. The stock extends to the northern parts of FAO Area 34, and the southern boundary of the stock unit considered by ICES should extend southwards to 5°N, as used by ICCAT. It is hypothesised that porbeagle in the Mediterranean relate to occasional incursions from the Atlantic, given their wintertime presence in adjacent Atlantic waters, and that their presence in the Mediterranean is temporally sporadic and generally restricted to the cooler parts of the Mediterranean.*

RÉSUMÉ

*La récente évaluation de référence du requin-taube commun (*Lamna nasus*) de l'Atlantique Nord-Est a nécessité l'examen plus approfondi de l'identification du stock. Les informations publiées examinées suggèrent des différences saisonnières, ontogénétiques et sexuelles dans les mouvements et la distribution, y compris (i) des mouvements vers le Nord des grands requins-taupes communs (y compris de grandes femelles) le long du plateau pour hiverner au Nord de l'Écosse, (ii) des mouvements vers le Sud des petits requins-taupes communs (y compris les mâles) pour hiverner dans les eaux ibériques et les parties septentrionales de la zone 34 de la FAO et (iii) des mouvements vers l'Ouest de quelques requins-taupes communs dans les eaux océaniques. Bien que différentes parties de la population puissent entreprendre des migrations saisonnières différentes, les mouvements et les mélanges de grande envergure dans l'Atlantique Nord-Est soutiennent l'hypothèse d'un stock unique dans cette zone. Le stock s'étend aux parties septentrionales de la zone 34 de la FAO, et la limite méridionale de l'unité de stock considérée par le CIEM devrait s'étendre vers le sud jusqu'à 5°N, comme l'utilise l'ICCAT. On suppose que la présence du requin-taube commun en Méditerranée est liée à des incursions occasionnelles en provenance de l'Atlantique, compte tenu de sa présence hivernale dans les eaux atlantiques adjacentes, et que sa présence en Méditerranée est temporellement sporadique et généralement limitée aux parties plus fraîches de la Méditerranée.*

RESUMEN

*La reciente evaluación de los niveles de referencia del marrajo sardinero (*Lamna nasus*) del Atlántico nororiental requirió una mayor consideración de la identificación del stock. La información publicada que se ha revisado sugiere diferencias estacionales, ontogenéticas y sexuales en los movimientos y la distribución, incluyendo (i) movimientos hacia el norte del marrajo sardinero de mayor tamaño (incluidas las hembras grandes) a lo largo de la plataforma para pasar el invierno al norte de Escocia, (ii) movimientos hacia el sur del marrajo sardinero de menor tamaño (incluidos los machos) para pasar el invierno en aguas ibéricas y en las partes septentrionales de la zona 34 de la FAO, y (iii) movimientos hacia el oeste de algunos marrajos sardineros hacia aguas oceánicas. Aunque diferentes partes de la población pueden emprender*

¹ Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK. (email: jim.ellis@cefass.co.uk)

² Marine Institute, Rinville, Oranmore, Co. Galway, H91 R673, Ireland.

³ Portuguese Institute for the Ocean and Atmosphere (IPMA), Av. 5 de Outubro s/n, 8700-305 Olhão, Portugal.

diferentes migraciones estacionales, los amplios movimientos y la mezcla en el Atlántico nororiental respaldan la hipótesis de un solo stock en esta zona. E stock se extiende hasta las partes septentrionales de la zona 34 de la FAO, y el límite meridional de la unidad de stock considerada por ICES debería extenderse hacia el sur hasta los 5°N, tal como la utiliza ICCAT. Se plantea la hipótesis de que la presencia del marrajo sardinero en el Mediterráneo está relacionada con incursiones ocasionales desde el Atlántico, dada su presencia invernal en las aguas atlánticas adyacentes, y que su presencia en el Mediterráneo es temporalmente esporádica y generalmente se limita a las partes más frías del Mediterráneo.

KEYWORDS

Fishery biology, geographical distribution, habitat, migrations, population structure, porbeagle, shark fisheries, stock identification

1. Introduction

Recent discussions at the 2022 benchmark workshop for porbeagle *Lamna nasus* in the North-east Atlantic (ICES stock code por.27.nea) indicated a need to reappraise and clarify the stock structure and delineation of this stock. ICES (2021) stated “WGEF has traditionally considered that there is a single stock of porbeagle *Lamna nasus* in the Northeast Atlantic. The stock occupies the entire ICES area (subareas 1–14) and extends from the Barents Sea to Northwest Africa. For management purposes the southern boundary of the stock is 36°N and the western boundary at 42°W”. ICCAT (2009) also assume there to be a single stock in the North-east Atlantic, extending southwards to 5°N.

However, there have been several new sources of published information since the initial consideration of the stock delineation of porbeagle in the Atlantic, including tagging data and genetic analyses. A review of these studies and a more robust consideration of earlier data can be used, therefore, to reappraise stock delineation and stock structure.

2. Tagging studies

Pade *et al.* (2009), using pop-up satellite archival tags (PSATs), tagged and released four individuals (160–185 cm fork length, L_F) caught in the Bristol Channel (ICES Division 7.f) during July. All were found to have spent August and September in the Southwest Approaches (Bristol Channel, Celtic Sea and western Channel), a time of the year where porbeagle are known to have been exploited (Ellis and Shackley 1995). The individual providing the most days of data moved offshore to the shelf edge and moved northwards in October.

Saunders *et al.* (2011) tagged and released three individuals (91–154 cm L_F) caught off north-west Ireland (ICES Division 6.a) during September 2008, with all tags programmed to pop-off in January 2009 (122 days later). Whilst the largest individual tagged (154 cm L_F female) stayed in oceanic waters west of Ireland (at latitudes of ca. 52–56°N), the two smaller individuals moved south over winter. One of these (a 143 cm L_F female) moved to the northern Bay of Biscay and the smallest individual (a 93 cm L_F male) moved even further south, to the waters between western Morocco and Madeira (ca. 33.8°N).

Biais *et al.* (2017) tagged and released nine individuals (197–265 cm total length; 171–234 cm L_F ; all but one being female) caught in the Bay of Biscay. Data were available for 128–265 days at liberty ($\bar{x} = 292$), during which time they moved an estimated 3871–13 352 km ($\bar{x} = 7846$ km). Whilst most stayed in shelf seas and/or displayed latitudinal movements along the shelf edge (<20°W), three individuals (shark 4, 199 cm L_F ; shark 5, 172 cm L_F ; and shark 6, 207 cm L_F) undertook more oceanic excursions (but staying within the stock boundary, being east of 42°W). Of the remaining sharks, three individuals (shark 2, 234 cm L_F ; shark 3, 180 cm L_F ; and shark 9, 206 cm L_F) spent the autumn and winter at more northerly latitudes (including off Scotland, Faroes and Norway), whilst one individual (shark 8, 218 cm L_F) moved into more oceanic water, another stayed in the Celtic Sea/western Channel (shark 7; 202 cm L_F) and the smallest individual (shark 1, a 171 cm L_F male) overwintered in the Cantabrian Sea. Whilst differing movement patterns were observed, the overall range of the reconstructed tracks were from Morocco/Madeira to northern Norway, with the largest individual overwintering off Norway, and the smallest individual overwintering further south (Biscay).

In terms of conventional tagging (i.e. mark-recapture tags), Stevens (1976) provided initial mark-recapture data for porbeagle, with two (20%) of the ten porbeagle tagged in the western English Channel recaptured - one from Denmark and the other from Spain. Stevens (1990) subsequently provided further data based on six further recaptures of tagged porbeagle, of which five were at liberty for >1 year. Of these, two were recaptured in the English Channel (Isle of Wight and Cherbourg peninsula), two from the Bay of Biscay, whilst the largest individual (253 cm) was recaptured off Norway.

Cameron *et al.* (2019) summarised conventional tagging data from Ireland, based on data from the Inland Fisheries Ireland (IFI) coordinated National Marine Sport Fish Tagging (MSFT). Of the 268 individuals tagged, nine (3.4%) were recaptured, including one individual reported from the North-west Atlantic (see below). Of the eight individuals recaptured in the North-east Atlantic, these had been at liberty from 71–3946 days and were recaptured in areas extending from the northern Bay of Biscay to the Faroe Islands (47.4–61.4°N).

Cameron *et al.* (2018) reported on a putative transatlantic movement of a porbeagle that was tagged off Ireland (in 1972) and that was recaptured by a Faroese vessel from off south-east Newfoundland (in 1982). Whilst the authors acknowledged that “*The recapture location could not be independently verified from secondary sources*”, it should be recognised that species such as spurdog *Squalus acanthias*, which are considered to have separate North-east and North-west Atlantic stocks, have also shown very occasional transatlantic movements (Holden 1967, Templeman 1976), and so the occasional transatlantic movement of porbeagle is likely, especially when noting the oceanic excursions observed (Biais *et al.* 2017). Whilst such transatlantic movements could lead to a degree of genetic mixing (see González *et al.* 2021), the degree of exchange should also consider other sources of information. For example, Kohler *et al.* (2002) summarised conventional (mark-recapture) tagging data derived from the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program (CSTP). This study reported that, between 1962–2000, a total of 1300 porbeagle were tagged and released in the North-west Atlantic, with 143 (11.0%) recaptured. These individuals, which had travelled distances of up to 1005 nm (=1861 km) and been at liberty for up to 9.2 years, were all recaptured in the North-west Atlantic. Consequently, the reported transatlantic movement may be considered as an occasional event, and that the North-east and North-west Atlantic stocks are primarily separate for assessment and management purposes.

More recently, Skomal *et al.* (2021) reported on electronic tagging data from porbeagle (n = 20; 128–153 cm L_F) tagged in the North-west Atlantic, with all found to have remained in the North-west Atlantic. In general, the behaviour of porbeagle was seasonal, being described as “*shelf-oriented during the summer and early fall with more expansive offshore radiation in the winter and spring*”.

ICCAT regularly publishes statistical bulletins that summarizes information that is submitted by ICCAT Contracting Parties, including tagging data (ICCAT 2020a). The latest available information for the conventional tagging of porbeagle, and associated recaptures, is shown in **Figure 1**. Between 1961–2017, a total of 2368 porbeagle were released with conventional tags, of which 346 (14.6%) were recaptured between 1 and 15+ years later. All the porbeagles released in the North-west and North-east Atlantic that were subsequently recaptured were reported from the same respective area, with no transatlantic crossings reported.

3. Genetic studies

A recent study by González *et al.* (2021) found very different haplotype networks between southern hemisphere populations compared to the North Atlantic, ‘high gene flow’ within hemispheres, and these authors also found no “*evidence of genetic structure between porbeagle populations*” in the North-east and North-west Atlantic. Previous studies have also confirmed the genetic differentiation between the North and South Atlantic (Kitamura and Matsunaga 2010).

4. Factors affecting the distribution of porbeagle

Whilst movements from tagging studies can be used to inform on stock units and delineation, such data need to be interpreted in line with other relevant data that can inform on seasonality in the distribution, as well as any ontogenetic or sex-related differences in distribution and behaviour. Furthermore, as a pelagic predator, porbeagle distribution may be influenced by oceanographic conditions, including any shifts in the distribution of pelagic prey. Indeed, as Biais *et al.* (2017) concluded, “*the dynamics and life-history processes of porbeagle sharks are spatially structured and complex*”.

In terms of seasonality, Muñoz-Chápuli (1985) observed that porbeagle occurred during the winter in the southernmost part of the North-east Atlantic distribution, stating that “*Una comunidad de aguas frías, formada por una sola especie, L. nasus, escualo especialista en la explotación de la porción más septentrional del gradiente y, según las observaciones realizadas, sólo en los meses de invierno, cuando la temperatura superficial media del agua baja de los 16.7°C*” [“A cold-water community, made up of a single species, *L. nasus*, a shark that specializes in exploiting the northernmost portion of the gradient and, according to observations, only in the winter months, when the average surface water temperature drops below 16.7°C”].

Mejuto and Garcés (1984) and Mejuto (1985) provided data on porbeagle caught by longline from the fishing grounds between the Iberian Peninsula and the Azores. The three main areas were (a) North-west Spain (ca. 40–45°N, 8–17°W), (b) west of Portugal (ca. 35–42°N, 13–20°W) and (c) North-east Azores (ca. 40–45°N, 18–30°W). The catch-per-unit-effort (CPUE) of porbeagle was observed to be higher in September–November (Mejuto and Garcés 1984, Mejuto, 1985), with a peak in January to March also observed in another year (Mejuto 1985).

These findings of these studies (Mejuto and Garcés 1984, Mejuto 1985, Muñoz-Chápuli 1985) would be indicative of porbeagle migrating to the southern parts of FAO Area 27 and northern parts of FAO Area 34 to overwinter. However, sexual segregation should also be considered, with skewed sex ratios reported in two successive years by Mejuto and Garcés (1984; F : M = 1 : 1.71) and Mejuto (1985; F : M = 1 : 1.98) on the fishing grounds west of the Iberian Peninsula, which may indicate that parts of the female population may display different distributions and/or behaviours. In terms of the size distribution, data from Mejuto and Garcés (1984) and Mejuto (1985) indicate that a majority of the porbeagle measured were <200 cm L_F .

Seasonality in porbeagle catches was also reported in the French longline fishery that operated in the Bay of Biscay and Celtic Sea area. The fishery was described as being from March to October (Le Gall and Mallet 1972), with subsequent studies indicating it peaking in quarters 2–3 (Lallemand-Lemoine, 1991; 1985–1990 fishing seasons) or from March to August (Jung 2008, based on data from the 2007 fishing season), with many of the fish caught <200 cm L_F (Jung 2009). Obviously, the fishing season in any one year can be impacted by a range of factors, including catch rates, market value, fishing opportunities for other species and weather.

Further north, Gauld (1989) reported on the seasonality of porbeagle captures in Scottish waters. These data indicate a peak in the occurrence of porbeagle from August to December (**Table 1** and **Table 2**). The seasonal presence of porbeagle in more northern areas was noted previously by Parnell (1838; “*it is said to occur more frequently during autumn on the northern coast*”) and Sim (1903; “*I have often seen this species brought on shore in mid-winter*”).

A comparison of those data given by Lallemand-Lemoine (1991) and Gauld (1989) indicate a seasonal shift in peak landings (**Figure 2**), which would be indicative of a northward shift in the stock. Gauld (1989) also reported that catches in Scottish waters showed a preponderance of females (M:F = 1:1.3), and the available data on the length distribution of males ($n = 592$; 81–288 cm total length L_T ; $\bar{x} = 206$ cm L_T) and females ($n = 776$; 91–317 cm L_T ; $\bar{x} = 214$ cm L_T) indicated that catches contained a greater proportion of larger individuals (>200 cm L_T).

Overall, available data indicate that there are various potential migratory patterns displayed by porbeagle in the North-east Atlantic. These include a northward movement of larger porbeagle, including large females, to overwinter in the waters north of Scotland, whilst smaller porbeagle, including males, may overwinter in the southern parts of FAO Area 27 and northern part of FAO Area 34. In addition to these latitudinal shifts, some parts of the population may make more oceanic excursions in winter.

5. Southern extent of the stock boundary and occurrence in FAO Area 34

Muñoz-Chápuli (1985) examined the pelagic shark catches from longline fisheries operating from 15–40°N, with data allocated to five fishing zones. Porbeagle was reported from the three most northerly zones, which ranged from 31–40°N

Given the findings of Muñoz-Chápuli (1985) and the tagging data presented by Biais *et al.* (2017), the southern limit of the North-east Atlantic porbeagle stock should certainly be extended southwards from the current latitude (36°N) to at least 31°N, thus extending south from FAO Area 27 and into the northern parts of FAO Area 34. Whilst the presence of porbeagle around the Canary Islands has been questioned (Brito *et al.* 2002), data from the Spanish longline fishery show occasional captures of porbeagle further south, including from the ICCAT statistical squares extending as far south as 10°N (Mejuto *et al.* 2010, 2020; **Figure 3**).

Consequently, the stock definition currently used by ICES should be extended southwards to 5°N, therefore covering ICCAT areas BIL94B and BIL94C, as used during ICCAT porbeagle assessments (ICCAT 2009, 2020b).

6. Occurrence of porbeagle in the Mediterranean Sea (FAO Area 37)

There is great uncertainty regarding the stock delineation of several pelagic fish stocks that occur in the Atlantic and the Mediterranean Sea (FAO Area 37). Indeed, some recent studies have questioned whether the Strait of Gibraltar is a phylogeographic barrier for a number of marine species (Patarnello *et al.* 2007), which has implications for considering stock units.

Porbeagle is known to occur in the Mediterranean Sea, but records are generally infrequent and sporadic (Marconi and De Maddalena 2001, Storai *et al.* 2005, Scacco *et al.* 2012, Lipej *et al.* 2016, Keramidas *et al.* 2019). Storai *et al.* (2005) collated records of 33 porbeagle caught in Italian waters (1871–2004, with multiple captures in some years and some protracted periods with no records), with length (or approximate length) available for 29 specimens. Of these, four specimens were <100 cm L_T (86.7–91 cm L_T), 14 specimens were 138–187 cm L_T , eight specimens ca. 200–206 cm L_T and three specimens were larger, measuring 236–250 cm L_T . Subsequent records of porbeagle in the area have included males of 150–200 cm L_T (Scacco *et al.* 2012) and juveniles of 91–104 cm L_T (Lipej *et al.* 2016, Keramidas *et al.* 2019).

Interestingly, most reported records of porbeagle in the Mediterranean Sea appear to come from Italian waters, primarily the Ligurian, Tyrrhenian, and Adriatic Seas, with few records elsewhere. Regarding porbeagle in Spanish waters, Lozano Rey (1928) noted that “*Se encuentra en todo el litoral ibérico. No obstante, en algunos casos pude haber, sido denunciado su presencia por equivocación. De mí sé decir que no he vistol un sole ejemplar de este género, procedente de nuestras costas mediterráneas, que n estuviere mal clasificado. Todas figuraban como Isurus cornubicus, pero todo eran I. oxyrinchus*” [“It is found throughout the Iberian coast. However, in some cases, their presence may have been reported by mistake. I can say that I have not seen a single specimen of this genus, from our Mediterranean coasts, that was not misclassified. They were all listed as *Isurus cornubicus*⁴, but all were *I. oxyrinchus*⁵“]. Similarly, Barrull *et al.* (2000) reviewed the sharks off the Catalonian coast of Spain, for which there was a single nominal report of *L. nasus* (caught in 1911), whilst Capapé *et al.* (2000) did not find any evidence of porbeagle in the waters of Languedoc (southern France).

Further south, Quignard and Capapé (1971) noted that one earlier account listed *L. nasus* in Tunisian waters, but they doubted the presence of the species from that area. Megalofonou *et al.* (2005a) did not report porbeagle as a bycatch in the swordfish and albacore longline fisheries in the eastern Mediterranean Sea (with only 15 porbeagle specimens measured after being taken as bycatch across the wider Mediterranean Sea; Megalofonou *et al.* 2005b), with only very occasional reports from the eastern basins (e.g., Kabasakal and Kabasakal 2004).

When interpreting the presence and distribution of porbeagle in the Mediterranean Sea, this could usefully consider water temperature. Porbeagle is a boreal species, with recent electronic tagging data from the North-east Atlantic indicating that it occurs in waters of 9.8–18.5°C (Pade *et al.* 2009) or 9–17°C (Saunders *et al.* 2011), whilst Muñoz-Chápuli (1985) postulated that it occurred in the southern parts of the North-east Atlantic range when waters were <16.7°C. Whilst the species has been reported over a wider temperature range in the North-west Atlantic (2–26°C), this study also noted that 97% of records were from waters of 6–20°C. Considering the water temperature in the Mediterranean Sea (e.g. Macias *et al.* 2013), Sea Surface Temperature (SST) is generally outside the preferred range for porbeagle over much of the southern parts of the Mediterranean Sea, though there are areas of slightly lower temperature which may be more suitable (e.g. Alboran Sea, Golfe du Lions, Ligurian Sea, Adriatic Sea).

Given that much of Mediterranean Sea may be too warm for porbeagle (with most records from the slightly cooler Adriatic and Ligurian Seas), it may be that there is a discrete, relict population in the central Mediterranean Sea or that there is occasional ingress of Atlantic porbeagle into the Mediterranean Sea, with some of these individuals then moving towards cooler parts of this basin. Given the sporadic nature of reports, the latter is arguably the more likely hypothesis. This would imply that FAO Area 37 (and ICCAT area BIL95) should be included in the stock area, though the limited data from the Mediterranean Sea would have little bearing when assessing the main Atlantic part of the stock range.

⁴ Junior synonym for *Lamna nasus*

⁵ Unaccepted older synonym for *Isurus oxyrinchus*

7. Summary

The seasonal distributions and movements of porbeagle may display ontogenetic and sexual differences. Available data indicate that there are various plausible patterns in seasonal movements of North-east Atlantic porbeagle, including (i) northward movements of larger porbeagle (including large females) along the shelf to overwinter in the shelf waters north of Scotland; (ii) southward movements of smaller porbeagle (including males) to overwinter in the southern parts of FAO Area 27 and northern part of FAO Area 34; and (iii) westward movements of some porbeagle into more oceanic waters.

Whilst different parts of the population may undertake different seasonal migrations, there are wide-ranging movements along the North-east Atlantic shelf and so the single-stock hypothesis for North-east Atlantic porbeagle should be maintained. Based on observed tag returns from Scandinavia to Spain, Stevens (1990) first suggested that there would be a single stock in the North-east Atlantic, and this perception was also accepted during the DELASS project (Heessen 2003, Pawson and Ellis 2005).

Nevertheless, it should be recognised that the spatio-temporal distribution of porbeagle may have changed in relation to oceanographic conditions, as has been inferred with other pelagic species in the area, such as bluefin tuna *Thunnus thynnus* (Tiews 1978). The latter study highlighted the decline in reported landings of bluefin tuna from the North Sea and Skagerrak during the 1960s and early 1970s. Consequently, the interpretation of available data (e.g., landings and commercial catch rates) could usefully consider other sources of information (e.g. relating to environmental conditions and the distribution of prey species) when inferring population-level trends.

The southern boundary of the stock unit considered by ICES should be extended southwards to 5°N, as the information summarised here highlights that the stock occurs in the northern parts of FAO Area 34. This would also ensure consistency between ICES and ICCAT stock boundaries.

Though there are no tagging data to demonstrate that Atlantic porbeagle move into the Mediterranean Sea, such movements have been observed for other sharks, including tope *Galeorhinus galeus* (Colloca *et al.* 2019) – a species which has a degree of co-occurrence with porbeagle (Muñoz-Chápuli 1985). It may be hypothesised that porbeagle in the Mediterranean Sea are the results of occasional incursions from the Atlantic, given that porbeagle shows a wintertime presence in the adjacent Atlantic waters, and that the reported temporal presence of porbeagle in the Mediterranean Sea is sporadic and that most captures have been restricted to the coolest parts of the Mediterranean Sea. That porbeagle in the Mediterranean Sea are likely connected to the North-east Atlantic population has also been proposed in a recently published study by Haugen *et al.* (2022).

Acknowledgements

This paper was based on an ICES Working Document presented to the recent benchmark workshop on porbeagle (WKELASMO 2022) and we thank our scientific colleagues from ICCAT and the ICES Working Group on Elasmobranch Fishes for their comments.

References

- Barrull, J., Mate, I. and Bueno, M. 2000. Observaciones de tiburones (Chondrichthyes Euselachii) en aguas de Catalunya (Mediterráneo NO), con algunos aspectos generales de su ecología. *Scientia Gerundensis*, 24: 127–151.
- Biais, G., Coupeau, Y., Séret, B., Calmettes, B., Lopez, R., Hetherington, S. and Righton, D. 2017. Return migration patterns of porbeagle shark (*Lamna nasus*) in the Northeast Atlantic: implications for stock range and structure. *ICES Journal of Marine Science*, 74: 1268–1276.
- Brito, A., Pascual, P.J., Falcón, J.M., Sancho, A. and González, G. 2002. Peces de las Islas Canarias. Catálogo comentado e ilustrado. Francisco Lemus Editor, La Laguna.
- Cameron, L.W., Roche, W., Green, P., Houghton, J.D. and Mensink, P.J. 2018. Transatlantic movement in porbeagle sharks, *Lamna nasus*. *Fisheries Research*, 207: 25–27.

- Cameron, L.W., Roche, W.K., Houghton, J.D. and Mensink, P.J. 2019. Population structure and spatial distribution of porbeagles (*Lamna nasus*) in Irish waters. *ICES Journal of Marine Science*, 76: 1581–1590.
- Capapé, C., Tomasini, J.A., Quignard, J.P. 2000. Les elasmobranches pleurotrèmes de la côte du Languedoc (France méridionale): observations biologiques et démographiques. *Vie et Milieu*, 50: 123–133.
- Colloca, F., Scannella, D., Geraci, M.L., Falsone, F., Batista, G., Vitale, S. and Di Lorenzo, M. 2019. British sharks in Sicily: records of long distance migration of tope shark (*Galeorhinus galeus*) from North-eastern Atlantic to Mediterranean Sea. *Mediterranean Marine Science*, 20: 309–313.
- Ellis, J.R. and Shackley, S.E. 1995. Notes on porbeagle sharks, *Lamna nasus*, from the Bristol Channel. *Journal of Fish Biology*, 46: 368–370.
- Gauld, J.A. 1989. Records of porbeagles landed in Scotland, with observations on the biology, distribution and exploitation of the species. *Scottish Fisheries Research Report*, No. 45; 15 pp.
- González, M. T., Sepúlveda, F.A., Zárate, P.M. and Baeza, J.A. 2021. Regional population genetics and global phylogeography of the endangered highly migratory shark *Lamna nasus*: Implications for fishery management and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 620–634.
- Haugen, J.B., Skomal, G.B., Curtis, T.H. and Cadrin, S.X. 2022. Interdisciplinary stock identification of North Atlantic porbeagle (*Lamna nasus*). *Journal of Northwest Atlantic Fisheries Science*, 53: 1–18.
- Heessen, H.J.L. (Ed.) 2003. Development of elasmobranch assessments DELASS. Final report of DG Fish Study Contract 99/055, 605 pp.
- Holden, M.J. 1967. Transatlantic movement of a tagged spurdogfish. *Nature*, 214 (5093): 1140–1141.
- ICCAT. 2009. Report of the 2009 porbeagle stock assessments meeting. ICCAT SCRS/2009/014 – Sharks Stock Assessment SCI-032/2009. Copenhagen, Denmark, June 22 to 27, 2009.
- ICCAT. 2020a. ICCAT Statistical Bulletin. Vol 46 (1950-2018). Available online at: <https://www.iccat.int/sbull/SB46-2020/index.html>
- ICCAT. 2020b. Report of the 2020 porbeagle shark stock assessment meeting. 15–22 June 2020. Available at: https://www.iccat.int/Documents/Meetings/Docs/2020/REPORTS/2020_POR_SA_ENG.pdf
- ICES. 2021. Working Group on Elasmobranch Fishes (WGEF). *ICES Scientific Reports*. 3:59. 822 pp. <https://doi.org/10.17895/ices.pub.8199>
- Jung, A. 2008. A preliminary assessment of the French fishery targeted porbeagle shark (*Lamna nasus*) in the Northeast Atlantic Ocean: Biology and catch statistics. ICCAT SCRS/2008/152.
- Jung, A. 2009. Preliminary results on the French fishery that targeted porbeagle shark (*Lamna nasus*) in the northeast Atlantic Ocean: Biology and catch statistics. *ICCAT Collective Volume of Scientific Papers*, 64(5): 1693–1702.
- Kabasakal, H. and Kabasakal, E. 2004. Sharks captured by commercial fishing vessels off the coast of Turkey in the northern Aegean Sea. *Annales, Series Historia Naturalis*, 14: 171–180.
- Keramidas, I., Ugarković, P., De Maddalena, A. and Giovos, I. 2019. An additional record of *Lamna nasus* (Bonnaterre, 1788) from Croatia, Adriatic Sea. *Journal of Black Sea/Mediterranean Environment*, 25: 87–92.
- Kitamura, T. and Matsunaga, H. 2010. Population structure of porbeagle (*Lamna nasus*) in the Atlantic Ocean as inferred from mitochondrial DNA control region sequences. *ICCAT Collective Volume of Scientific Papers*, 65(6): 2082–2087.

- Kohler, N.E., Turner, P.A., Hoey, J.J., Natanson, L.J. and Briggs, R. 2002. Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. ICCAT Collective Volume of Scientific Papers, 54(4): 1231–1260.
- Lallemand-Lemoine, L. 1991. Analysis of the French fishery for porbeagle *Lamna nasus* (Bonnaterre, 1788). ICES CM 1991/g:71; 10 pp.
- Le Gall, J.Y. and Mallet, G. 1972. Technique de pêche à la Palangre du Requin Sonneur (*Lamna nasus* Bonnaterre) et de l'Espadon (*Xiphias gladius* Linnaeus) en Atlantique Nord-Est. Bulletin de la Société franco-japonaise d'océanographie, 10: 174–177.
- Lipej, L., Uhan, J., Mavrič, B. and Vujčić-Karlo, S. 2016. A record of porbeagle, *Lamna nasus* (Bonnaterre, 1788), in the Gulf of Trieste with discussion on its occurrence in the Adriatic Sea. Acta Adriatica, 57: 305–313.
- Lozano Rey, L. 1928. Fauna Ibérica: Peces. Madrid, Spain: Museo Nacional de Ciencias Naturales.
- Macias, D., Garcia-Gorrioz, E. and Stips, A. 2013. Understanding the causes of recent warming of Mediterranean waters. How much could be attributed to climate change? PloS one, 8(11), p.e81591.
- Marconi, M. and De Maddalena, A. 2001. On the capture of a young porbeagle, *Lamna nasus* (Bonnaterre, 1778), in the western Adriatic Sea. Annales: Series Historia Naturalis, 11: 179–184.
- Megalofonou, P., Damalas, D. and Yannopoulos, C. 2005a. Composition and abundance of pelagic shark by-catch in the eastern Mediterranean Sea. Cybium, 29: 135–140.
- Megalofonou, P., Yannopoulos, C., Damalas, D., De Metrio, G., Deflorio, M., de la Serna, J.M. and Macias, D. 2005b. Incidental catch and estimated discards of pelagic sharks from the swordfish and tuna fisheries in the Mediterranean Sea. Fishery Bulletin, 103: 620–634.
- Mejuto, J. 1985. Associated catches of sharks, *Prionace glauca*, *Isurus oxyrinchus*, and *Lamna nasus*, with NW and N Spanish swordfish fishery, in 1984. ICES CM 1985/H:42; 16 pp.
- Mejuto, J. and Garcés, A.G. 1984. Shortfin mako, *Isurus oxyrinchus*, and porbeagle, *Lamna nasus*, associated with longline swordfish fishery in NW and N Spain. ICES CM 1984/G:72; 10 pp.
- Mejuto, J., A. Ramos-Cartelle, B. García-Cortés, and J. Fernández-Costa. 2020. Size and area distribution of porbeagle (*Lamna nasus*) inferred from a data mining in the Spanish longline fishery targeting swordfish (*Xiphias gladius*) in the Atlantic for the 1987–2017 period. ICCAT Collective Volume of Scientific Papers, 77(6): 89–117.
- Mejuto, J., Ortiz, M., García-Cortés, B., Ortiz de Urbina, J. and Ramos-Cartelle, A. 2010. Historical data and standardized catch rates of porbeagle (*Lamna nasus*) caught as by-catch of the Spanish surface longline fishery targeting swordfish (*Xiphias gladius*) in the Atlantic Ocean. ICCAT Collective Volume of Scientific Papers, 65(6): 2006–2030.
- Muñoz-Chápuli, R. 1985. Análisis de las capturas de escaulos pelágicos en el Atlántico nororiental (15°–40° N). Investigación Pesquera, 49: 67–79.
- Pade, N.G., Queiroz, N., Humphries, N.E., Witt, M.J., Jones, C.S., Noble, L.R. and Sims, D.W. 2009. First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: area fidelity, wider-scale movements and plasticity in diel depth changes. Journal of Experimental Marine Biology and Ecology, 370: 64–74.
- Parnell, R. 1838. Fishes of the district of the Firth of Forth. Edinburgh: Wernerian Natural History Society.
- Patarnello, T., Volckaert, F.A. and Castilho, R. 2007. Pillars of Hercules: is the Atlantic–Mediterranean transition a phylogeographical break? Molecular Ecology, 16: 4426–4444.
- Pawson, M.G. and Ellis, J.R. 2005. Stock identity of elasmobranchs in the Northeast Atlantic in relation to assessment and management. Journal of Northwest Atlantic Fishery Science, 35: 173–193.

- Quignard, J.P. and Capapé, C. 1971. Liste commentée des Sélaciens de Tunisie. Bulletin de l'Institut national scientifique et technique d'océanographie et de pêche de Salammbô, 2(2): 131–141.
- Saunders, R.A., Royer, F. and Clarke, M.W. 2011. Winter migration and diving behaviour of porbeagle shark, *Lamna nasus*, in the Northeast Atlantic. ICES Journal of Marine Science, 68: 166–174.
- Scacco, U., Consalvo, I., DiMuccio, S. and Tunesi, L. 2012. On the by-catch of two porbeagle sharks *Lamna nasus* in the central Adriatic Sea. Marine Biodiversity Records, 5.
- Sim, G. 1903. The vertebrate fauna of “Dee”. Aberdeen: D. Wyllie & Son.
- Skomal, G., Marshall, H., Galuardi, B., Natanson, L., Braun, C. and Bernal, D. 2021. Horizontal and vertical movement patterns and habitat use of juvenile porbeagles (*Lamna nasus*) in the western north Atlantic. Frontiers in Marine Science, 8, p.16.
- Stevens, J.D. 1976. First results of shark tagging in the north-east Atlantic, 1972–1975. Journal of the Marine Biological Association of the United Kingdom, 56: 929–937.
- Stevens, J.D. 1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom, 70: 707–720.
- Storai, T., Celona, A., Zuffa, M. and De Maddalena, A. 2005. On the occurrence of the porbeagle, *Lamna nasus* (Bonaterre, 1788)(Chondrichthyes: Lamnidae), off Italian coasts (northern and central Mediterranean Sea): a historical survey. Annales: Series Historia Naturalis, 15: 195–202.
- Templeman, W. 1976. Transatlantic migrations of spiny dogfish (*Squalus acanthias*). Journal of the Fisheries Board of Canada, 33: 2605–2609.
- Tiews, K. 1978. On the disappearance of bluefin tuna in the North Sea and its ecological implications for herring and mackerel. Rapport et Procès-verbaux des Réunions du Conseil international de l'Exploration de la Mer, 172 : 301–309.

Table 1. The numbers of porbeagle *Lamna nasus* landed in Scotland (1954–1987) and reported to the Marine Laboratory at Aberdeen. Source: Gauld (1989).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1954			1	87	3	5	1	5	6	6	1	5	120
1955				1	3	5	7	20	4	4	5	8	57
1956		2	1		3	7	20	16	16	5	11	9	90
1957	4	1	2	1	18	11	18	42	27	19	12	10	165
1958	6	2	2	2	11	6	11	33	8	11	1	29	122
1959	9	9	32	10	37	8	7	12	14	16	13	15	182
1960	8	10	2	1	10	3	7	21	11	12	15	13	113
1961	1	1	5		4	2	11	15	16	9	22	17	103
1962	9	10	6	4	19	12	18	45	64	22	20	13	242
1963	10	16	1	7	2	1	13	47	19	11	9	11	147
1964	7	6	3	2	3	1	2	3	2	10	4	11	54
1965		8	1		3		3	5	5	9	7	1	42
1966					2	1	1		6	19	8	2	39
1967	2	3		8	7	1	7	5	2	6	8	2	51
1968	1	2	1	5	12	6	3	5		1	9	2	47
1969									1	1	3	6	11
1970		7	1	1	1		4	2	9	9	5	4	43
1971									7		9	10	26
1972	10	10		1	28	8	4	12	11	20	20	2	126
1973	8	3	1	2	2	3	2	6	9	8	8	1	53
1974	4	3		1	3		2	11	4	8		9	45
1975	6	1		3		1			3	2	2	3	21
1976	2		2				1	1	2	1	2	12	23
1977	10		1			1		1	1	6			20
1978			1		2	1	3	2			2	3	14
1979	3	1			6	3		3	4	3	7	1	31
1980		1			3	1		8	8	1	6	3	31
1981					1				2	7	3	1	14
1982	2								3	1	3		9
1983									1	2			3
1984		1					7	3	5	1			17
1985					2					3			5
1986								1	2	1			4
1987		1	1							2	23	302	329

Table 2. Monthly occurrence of porbeagle *Lamna nasus* in Scottish waters, giving the mean percentage by month (1954–1987) and the overall percentage by month from aggregated (1954–1987) data.

Month	Mean percentage by month (for the years 1954–1987)	Overall percentage by month (aggregated data for the years 1954–1987)
Jan	5.9%	4.3%
Feb	3.8%	4.1%
Mar	2.0%	2.7%
Apr	4.2%	5.7%
May	7.5%	7.7%
Jun	3.2%	3.6%
Jul	6.3%	6.3%
Aug	11.5%	13.5%
Sep	14.1%	11.3%
Oct	15.9%	9.8%
Nov	11.9%	9.9%
Dec	13.8%	21.1%

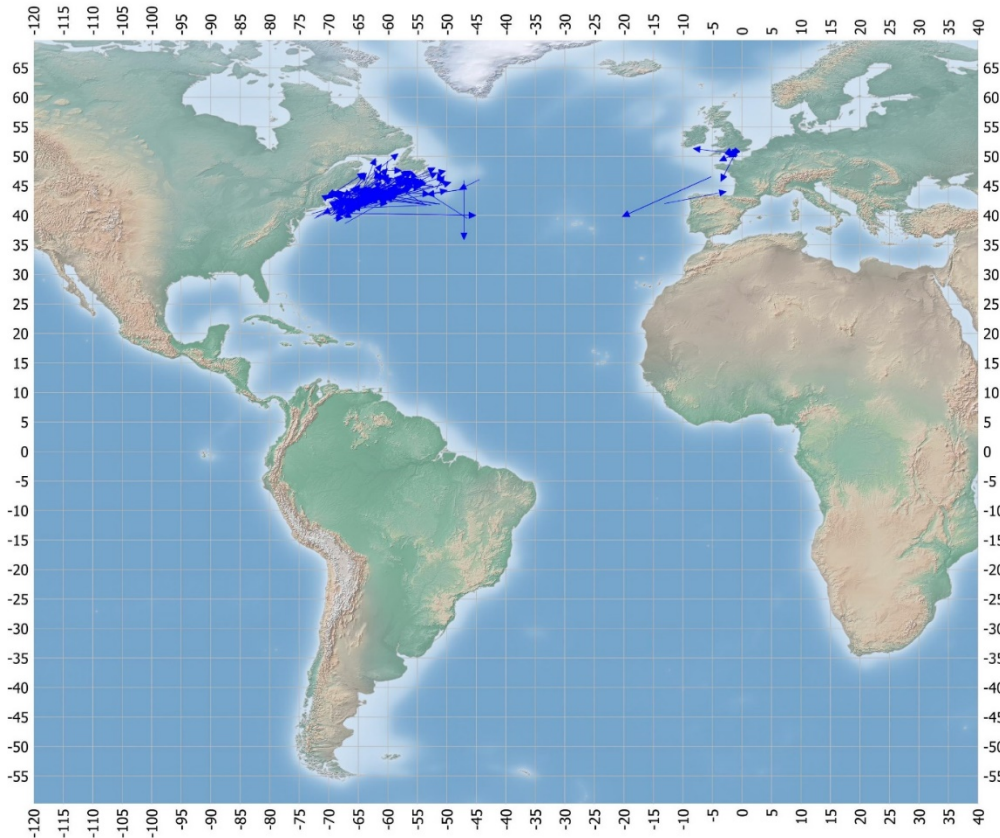


Figure 1. Conventional tagging data for porbeagle *Lamna nasus* in the North Atlantic that have been reported to ICCAT (ICCAT, 2020a). Data shown refers to 346 porbeagles recaptured between 1 and 15+ years after tagging.

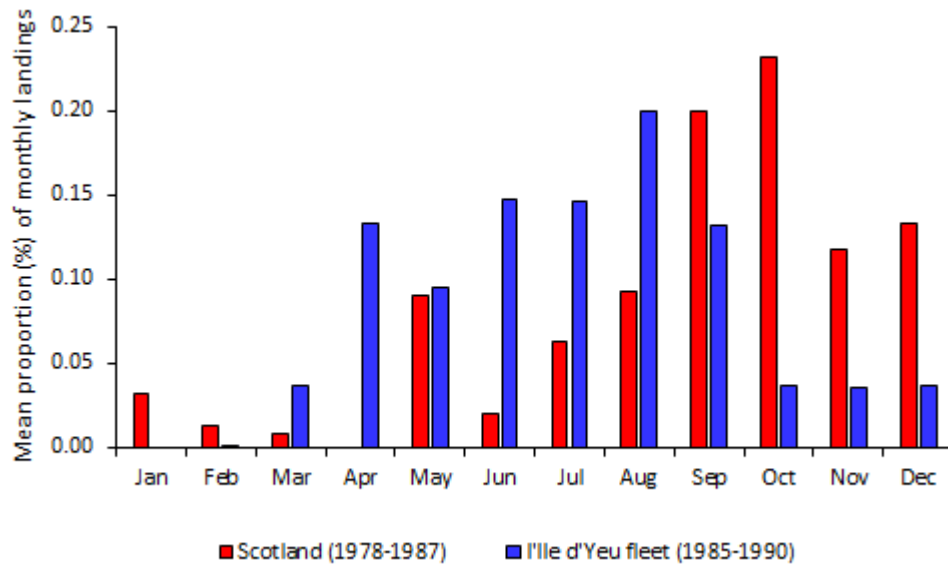


Figure 2. Seasonality in catches of porbeagle *Lamna nasus* in the Bay of Biscay and Celtic Sea showing the average proportion caught by month by the l'Ile d'Yeu fleet (blue columns) and in Scottish waters (red columns). Adapted from data presented by Gauld (1989) and Lallemand-Lemoine (1991).

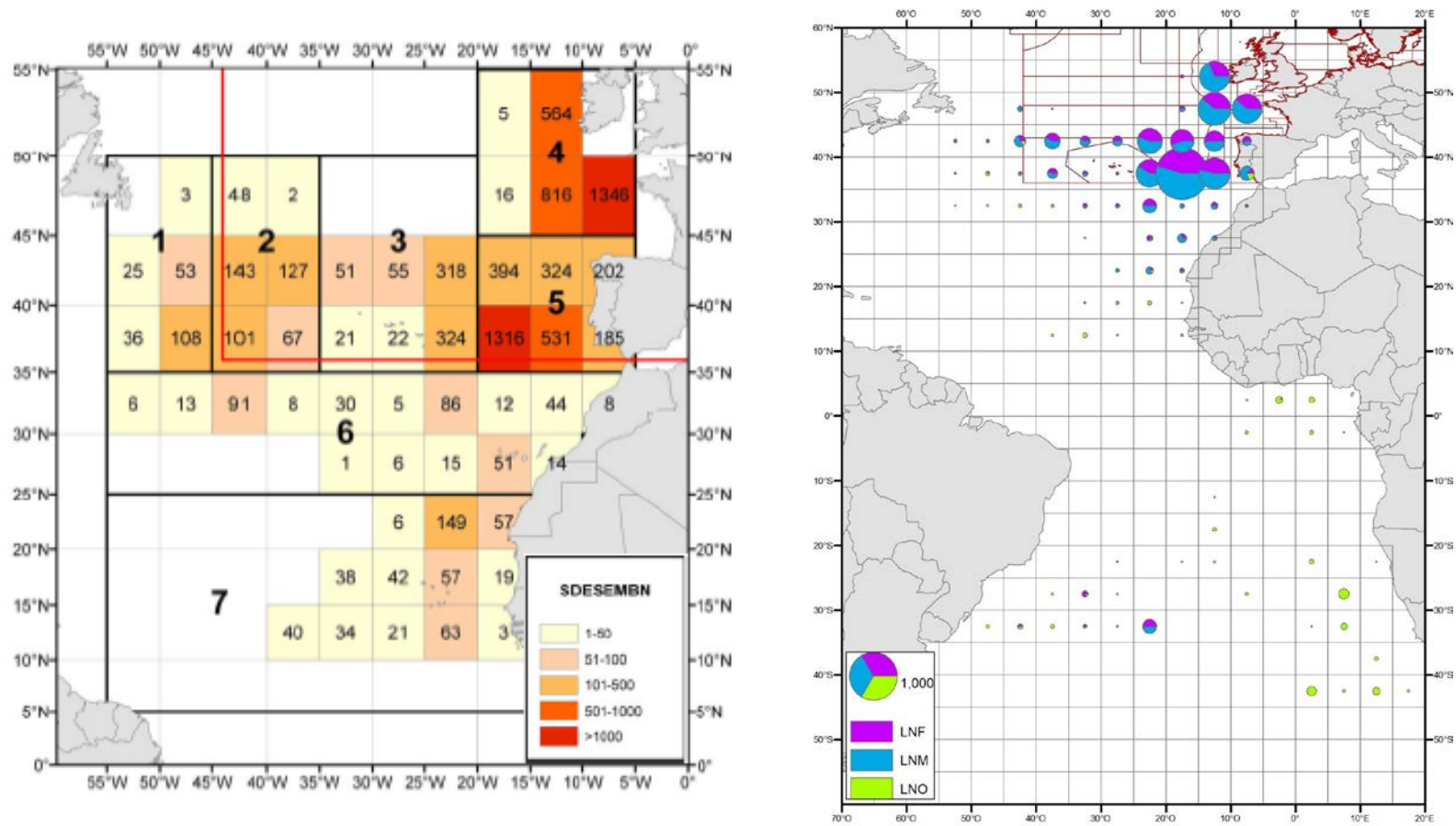


Figure 3. Total number of porbeagle *Lamna nasus* observed in Spanish observer trips (1986–2007) in those areas to the north of 5°N (Left; from Mejuto *et al.*, 2010), and the number of length observations of porbeagle collected during Spanish observer trips (1987–2017) in the Atlantic (right; from Mejuto *et al.*, 2020).