Fisheries Research 275 (2024) 107007

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Full length article

Transboundary movements of porbeagle sharks support need for continued cooperative research and management approaches

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ARTICLE INFO

Handled by Ivone Figueiredo Rosa

Keywords:
Telemetry
Transboundary
Management
Elasmobranch
Biologging

ABSTRACT

Distribution of species across jurisdictional and physical boundaries poses a challenge to management and research, and these transboundary species tend to suffer more-severe population declines from fisheries exploitation. Large pelagic sharks like the porbeagle shark, *Lamna nasus*, are particularly vulnerable to anthropogenic pressures due to their life history characteristics and their highly migratory behaviour. However, limited knowledge of their precise spatio-temporal movements is particularly challenging for management in situations where jurisdictional boundaries change over small spatial scales. We used satellite tags to demonstrate that porbeagle sharks tagged in the northern Northeast (NE) Atlantic (n = 3), display inter-individual variation in behaviour. Tagged sharks undertook rapid horizontal movements (up to 100 km per day) while transiting through multiple physical habitats and management jurisdictions in a matter of days along different paths. The spatial scale of these movements is important now that the population is deemed in recovery and a new catch advice for porbeagle sharks has been issued by ICES for the first time since 2009 in the NE Atlantic. These movement data highlight the value of existing, and need for continued, regional collaboration to inform sustainable fisheries and conservation management. This is achieved by maximising research impact through cross border funding mechanisms to fill knowledge gaps of species' life-history and ecology, and, in turn, improve respective outcomes for vulnerable and highly mobile shark species.

1. Introduction

Fisheries management relies on the spatial delineation of resources and knowledge obtained from applied research into the use of these resources by organisms. Many commercially important marine species have transboundary distributions on various scales, spanning across at least two management boundaries (e.g. Regional Fisheries Management Organisations – RFMOs, Exclusive Economic Zones – EEZs; Palacios-Abrantes et al., 2020; ICES, 2021; ICCAT, 2022; Junge et al., 2019), adding complexity to the management of their fisheries. Challenges to this are increasingly compounded by climate change, which can lead to range shifts of species potentially resulting in their increased vulnerability, while at the same time they are being exposed to additional fisheries and potentially overexploitation (Gullestad et al., 2020; Hammerschlag et al., 2022; Rodriguez-Burgos et al., 2022). This could necessitate additional or restructuring of existing management measures, such as reassessment of stock structure and connectivity across space, revisions or re-allocations of quotas, or shifts from static to dynamic spatial closures (Koubrak and VanderZwaag, 2020; Palacios-Abrantes et al., 2020; Lédée et al., 2021). These management

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https://doi.org/10.1016/j.fishres.2024.107007
Received 9 October 2023; Received in revised form 21 March 2024; Accepted 24 March 2024

and ultimately conservation challenges are clearly exemplified among highly mobile species whereby individuals transit multiple jurisdictional boundaries and management zones (Rooker et al., 2019; Ketchum et al., 2020). Even though knowledge of these movement patterns and their linkages to important life-history events (e.g., reproduction, parturition) remains key to informed management decisions, such knowledge is often incomplete or lacking altogether (Wearmouth and Sims, 2008; Yokoi et al., 2017; Daly et al., 2018; Jacoby et al., 2022; Lubitz et al., 2022). Issues like these may, at least partially, explain why highly migratory species with transboundary distributions seem to experience greater population declines than many other species (Palacios-Abrantes et al., 2020).

A large pelagic shark, the porbeagle shark, *Lamna nasus* (Bonnaterre, 1788), is globally considered *Vulnerable* by the International Union for Conservation of Nature (IUCN) Red List (Rigby et al., 2019) and was assessed as *Critically Endangered* in 2015 for European waters (Ellis et al., 2015). Porbeagle sharks are currently split into the following units for assessment and management: (1) the North Atlantic (split into two stocks: the Northwest (NW) and Northeast (NE) Atlantic), and (2) the Southern Hemisphere (Kitamura and Matsunaga, 2010; Testerman, 2014; Curtis et al., 2016; González et al., 2021). The NE Atlantic population is now increasing after having previously been estimated to have declined by 50–79% over ~ 60 years, though full recovery to sustainable levels has not yet been reached highlighting the need for continued conservation and research efforts (Rigby et al., 2019; ICES, 2022). Some data are available on the movements of individual porbeagle sharks in the NE Atlantic, but this information tends to rely on broad scale reconstructions of satellite tracks or low-resolution spatial inference based on conventional mark-recapture tags (Kohler et al., 2002; Pade et al., 2009; Saunders et al., 2010; Bendall et al., 2013; Biais et al., 2017; Cameron et al., 2019; ICCAT-ICES, 2022) that can be difficult to relate to precise locations of different management zones and/or habitat types due to greater location uncertainties. These transboundary movements can further promote the need for international research collaboration and data pooling, particularly when long research timelines and limited resources are taken into account (Bendall, et al., 2012; ICES, 2021; ICCAT-ICES, 2022). Collecting data on vertical and horizontal movements and environmental conditions, is a key step in addressing existing knowledge gaps for this species. Examples include, (i) the location of essential habitats (Fowler et al., 2004) (ii) their reproductive cycle in the North Atlantic (Francis et al., 2008), (iii) general life history knowledge globally (ICCAT Shark Species Group, 2020), (iv) stock structure, including mixing (are stocks connected, and if yes how connected?) between NW, NE Atlantic and the Mediterranean (ICCAT Shark Species Group, 2020; ICCAT-ICES, 2022), and (v) temporal and spatial distribution of porbeagle sharks in relation to environmental and ecosystem features, as well as fisheries and other human activities (ICCAT Shark Species Group, 2020).

To gain more knowledge on the migration of porbeagle sharks in the NE Atlantic, and improve our understanding of horizontal and vertical movements using different tagging methodologies, we tagged three individuals. While PSATs can deliver high-resolution information on depth, temperature, and light-level, all of which can be used to approximate geolocation, SPOTs yield fine-scale information on horizontal movements when animals are at the surface. The different combinations of use of these tags help us identify areas and locations of interest for further study and management under collaborative frameworks.

2. Materials and methods

The following work was conducted under the Irish Health Products Regulatory Authority (HPRA) Project Authorisation (AE19136/P127) and the Norwegian Food Safety Authority animal experimentation permit (FOTS ID 27484). A research fishing permit was obtained from the Norwegian Directorate of Fisheries for work carried out in Norway.

Three porbeagle sharks were captured using baited rod and line. Two individuals were captured in collaboration with recreational anglers off the coast of Malin Head, County Donegal, Ireland on the 15th of April 2022. These individuals were brought onboard, and a seawater hose was placed in the sharks' mouths to ventilate their gills. A wet towel was placed over their eyes to reduce stress. The third individual was captured from a chartered recreational angling vessel off the coast of Vesterålen, County Nordland, Norway on the 19th of August 2022. It was kept in-water, alongside the boat, using only a smooth multifilament rope which was tied around the belly posterior to the pectoral fins and anterior to the first dorsal fin.

Sharks 1 and 2 were tagged with a SPOT (SPOT 258**,** Wildlife Computers (WC), Inc., Redmond, WA, USA) and a PSAT tag (miniPAT 348, WC) each (Hueter et al., 2013; Coffey et al., 2017; Drymon and Wells, 2017; Renshaw et al., 2023). Anti-biofouling paint was applied to each tag prior to deployment (Renshaw et al., 2023). SPOT tags were attached near the tip of the dorsal fin using nylon bolts, and miniPATs were anchored adjacent to the insertion point of the dorsal fin, using titanium anchor darts with six-inch monofilament tethers (Hammerschlag et al., 2011; Renshaw et al., 2023). Shark 3 was tagged with a PSAT (miniPAT 348, WC) which was attached using a silicon-tube covered monofilament loop which was threaded through a drilled hole in the cartilaginous part of the dorsal fin (Musyl et al., 2011). All sharks were then measured. Sharks 1 and 2 were measured over the curve of the body for total length (TL) while they on the deck of the boat with the tail in line with the body. Shark 3 was measured as a straight line above the animal while it remained in the water, Sharks 1 and 2 were also measured for fork length (FL), and blood sampled.

Messages are transmitted when fin-mounted SPOT tags break the surface of the water. Transmitted messages that are received by polar orbiting ARGOS satellites, when overhead, are used to estimate shark locations based on doppler shift calculations. Each transmission is assigned a quality rating (3, 2, 1, 0, A, B and Z, from best to worst) defining the precision of the location from a radius of a few kilometres down to 250 m. We confined our analysis to quality 3–1 locations, representing a <1500 m error radius. Tracks were determined by interpolating the minimum straight-line distance between each location. Minimum horizontal swimming speed was calculated as the distance between two successive positions divided by time elapsed.

During deployment, the PSAT tags measure ambient light (irradiance at 550 nm), depth (0.5 m resolution, ±0.005 m accuracy) and temperature (0.05°C resolution, ±0.1° C accuracy), which are relayed via satellite after the detachment from the animal as a 10-minute summary time series. Resulting data were aggregated into depth and temperature bins for each 4-day period to investigate the depth and temperature space exploited by each shark. Analyses were performed using the open-source R Statistical Software (v4.3.3; R Core Team, 2023) and RStudio (R Studio Team, 2021).Track maps and hexagonal heatmap of 2D bin counts plots were produced using the package "ggplot2" (Wickham, 2016). The most probable track was estimated with the Global Position Estimator, Version 3 software (GPE3, WC; Pedersen et al., 2011) informed by twilight estimates, sea surface temperature, dive depth and a cruising speed of 2 m/s in line with Skomal et al. (2021).

3. Results

Three female porbeagles were caught and tagged ((#1) tag ID 20P2561, 244 cm total length (TL); (#2) tag ID 20P2560, 280 cm TL; and ((#3) ID20P1240, 260 cm TL; Table 1). All three were assumed mature based on their lengths (Jensen et al., 2002). Locations from the SPOT tags were received for 348 days (Shark 1; Table 1) and 374 days (Shark 2; Table 1). The PSATs remained on sharks 1 and 2 until programmed release from the animal 6 months (180 days) after tagging. The tag from shark 3 detached prematurely after 118 days as the maximal safety depth of 1700 m, as suggested by the manufacturer, was exceeded.

Table 1
Summary data of the three L. nasus tagged with miniPATs (N=3) and SPOT tags (N=2) off northwest Ireland and northern Norway.

Shark	Tagging Date	Sex	Fork Length (cm)	Total Length (cm)	Tagging Location	miniPAT Pop-up Date	miniPAT Pop-up Latitude	miniPAT Pop-up Longitude	Last Recorded SPOT Latitude	Last Recorded SPOT Longitude	Last Recorded SPOT date
1	15-Apr-22	Female	210	244	Donegal Ireland	13-Oct-22	73.1574	20.1411	34.08241	-17.8929	29-Mar-23
2	15-Apr-22	Female	249	280	Donegal Ireland	13-Oct-22	53.3297	0.6332	58.57976	-5.30996	24-Apr-23
3	19-Aug-22	Female	NA	260	Nordland Norway	14-Dec-22	30.7813	-23.0174	NA	NA	NA

3.1. Migration routes

Full tracks derived from the filtered SPOT tag positions of sharks 1 and 2 are presented in Fig. 1. Over their time at liberty, shark 1 transmitted an average of 3.42 (± 4.13 SD) SPOT tag locations per day and shark 2, an average of 2.05 (± 2.36 SD) locations per day. Two weeks after tagging, shark 1 commenced a complete circumnavigation of Ireland, swimming at least 1500 km in approximately 85 days total. While at liberty, the shark passed through UK and Irish EEZs several times, before continuing northward to come within 40 km of the Danish-Faroese EEZ, and then entering the Norwegian EEZ on August 5th 2022, where the tag continued to transmit (Fig. 1). During its circumnavigation of Ireland, the individual travelled parallel to both EEZs in the Irish Sea, frequently crossing borders (min. five times), before residing in a discrete area of the Celtic Sea for two months (Fig. 1). It spent a total of 11.45% of its total SPOT track time within the Irish EEZ and 22.51% in the British EEZ (Supplementary Table). The latter part of the shark's journey was rapid, travelling around 1500 km in 18 days at an average speed of at least 85 km d^{-1} (but included periods of ~100 km per day) and crossing into the Arctic circle on August 12th 2022. This shark then resided around the Lofoten-Vesterålen Archipelago in the Norwegian EEZ for the next month (25.83% of its total SPOT track time (Supplementary Table), before continuing along a North-easterly trajectory, reaching a maximum latitude of 76.0 N at the end of October, placing the shark within the Svalbard Fisheries Protection Zone (SFPZ) where it spent a total of 4.02% of its total SPOT track time (Supplementary Table). It then began a return southward journey along a similar trajectory and speed (85 km per day) in early November and entered international waters on November 17th 2022; Danish-Faroese waters on November 21st; UK waters between the 27th and the 30th November; Irish waters on December 3rd; international waters south of Ireland on December 8th (16.77% of its total SPOT track time; Supplementary Table); continued travelling south in international waters passing between the Azores and Madeira between the 25th and 30th December 2022; it reached the southernmost point of its migration on 5th January 2023 in the high seas 500 km west of the Canary Islands (latitude of 30.02 N). From there, it began a return northward trajectory reaching 250 km NW of the Iberian Peninsula on 29th March 2023, its last transmitted location. Shark 3 undertook a similar migration (Fig. 2). Tagged in mid-August off the Lofoten-Vesterålen Archipelago, it started migrating south towards the Shetlands and the Celtic shelf edge along the continental shelf break and through the Rockall Trough in September, travelling about 2220 km in 33 days, at an average speed of 82 km per day. It continued further south, passing between the Azores and Madeira in early December. This shark spent 45.86% of its total track time in Areas Beyond National Jurisdictions (ABNJ; Supplementary Table). The miniPAT released from the shark at 30.78°N, 23.0174°W on the 14th of December.

In contrast, shark 2 remained within 60 km of the tagging site for two months, crossing between Irish and UK EEZs on four occasions. In mid-June, this shark initiated a northward trajectory, travelling 500 km between the Inner and Outer Hebrides, reaching the Orkney Islands in nine days (~55 km per day) and subsequently travelling down the eastern coast of Britain (Fig. 1). Here, the shark resided for approximately three months (mid-July – mid-October), before continuing on a northern trajectory, reaching the Moray Firth in mid-November with an average transit speed of 20–30 km per day. From mid-November 2022 to late April 2023, shark 2 remained in northern Scotland, moving between the Moray Firth and Cape Wrath where its last location was transmitted on 24th April 2023. This individual spent 84.93% of its total SPOT track time within the British EEZ and 15.07% in the Irish EEZ (Supplementary Table).

A comparison of SPOT and PSAT tracks for sharks 1 and 2 (Fig. 3) reveals local scale differences in track locations in parts exceeding 200 km (shark 1). A comparison of shark 1's PSAT track and SPOT track clipped to the same dates reveals up to 6.68% of proportion of time spent in the different EEZs (Supplementary Table). SPOT tag tracks of shark 2 showed the shark travelling around Scotland through the inner channel on the east side of the Outer Hebrides whereas PSAT tracks place it over 100 km west, offshore. When comparing the proportion of time spent in the British and Irish EEZs between the PSAT track and the SPOT track clipped to the same dates of shark 2, this represents a difference of 22.23% (Supplementary Table).

3.2. Depth and temperature niche

The PSAT data, with a deployment between April and October, showed sharks 1 and 2 to be generally surface oriented, spending a majority of their time between 0 and 100 m depth (Fig. 4, Shark 1 and Shark 2). However, as shark 1 moved northward, it regularly occupied progressively deeper water, and frequently exceeded 400 m depth in the northern extent of the Norwegian EEZ and the southern extent of the SFPZ. During the first half of its migration, this individual experienced water temperatures ranging from approximately 10° to 18°C and shifted to cooler temperatures (spending considerable time in temperatures below 5°C) in the second half (Fig. 4, Shark 1). In contrast, shark 2 remained in shallower waters (< 200 m) throughout the deployment period, and, between July to October, experienced higher - and a broader range - of temperatures of 7.5° to 20.5°C corresponding to its residency off the eastern coast of Britain (Fig. 4, Shark 2). Shark 3 spent the first part of its track (in Norway) occupying depths between 0 and 600 m and temperatures between 2 and 12 °C. Then, in a second part corresponding to its time along the Celtic Shelf and in the Shetlands in September, it spent a majority of its time in depths beyond 500 m, often exceeding 800 m, and in temperatures from 8 to 10°C, within a range of 6–18 °C. When moving into waters further south from October to December, shark 3 stopped surfacing and occupied depths from 50 down to 1867 m depth at which point the tag detached from the fin prematurely. During this period, it experienced temperatures from 4 to 24 °C (Fig. 4, Shark 3).

4. Discussion

The three porbeagle sharks tagged in the NE Atlantic showed inter-individual variation in their horizontal and vertical space use. Spatial use included rapid, extensive movements across multiple jurisdictional and environmental boundaries in the NE Atlantic over short periods of time. This is in line with previous research that also showed wide-

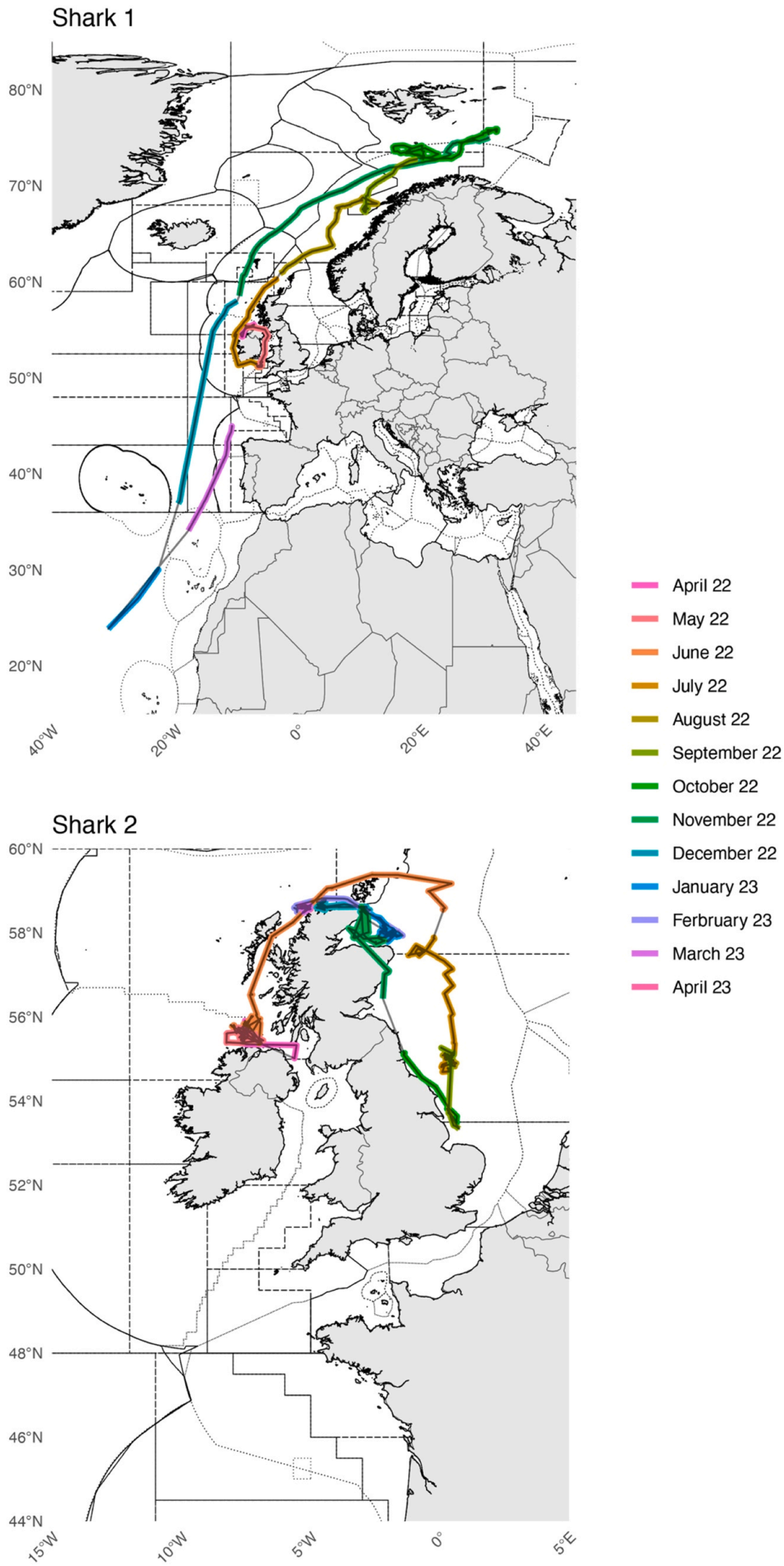

Fig. 1. Individual tracks colored by month for Sharks 1 and 2 tagged off Ireland in April 2022 and tracked until April 2023 using SPOT tag locations. Gaps in color overlays indicate long gaps in transmission from the tags. Dotted lines: EEZs; dashed lines: ICES areas; solid lines: ICES ecoregions.

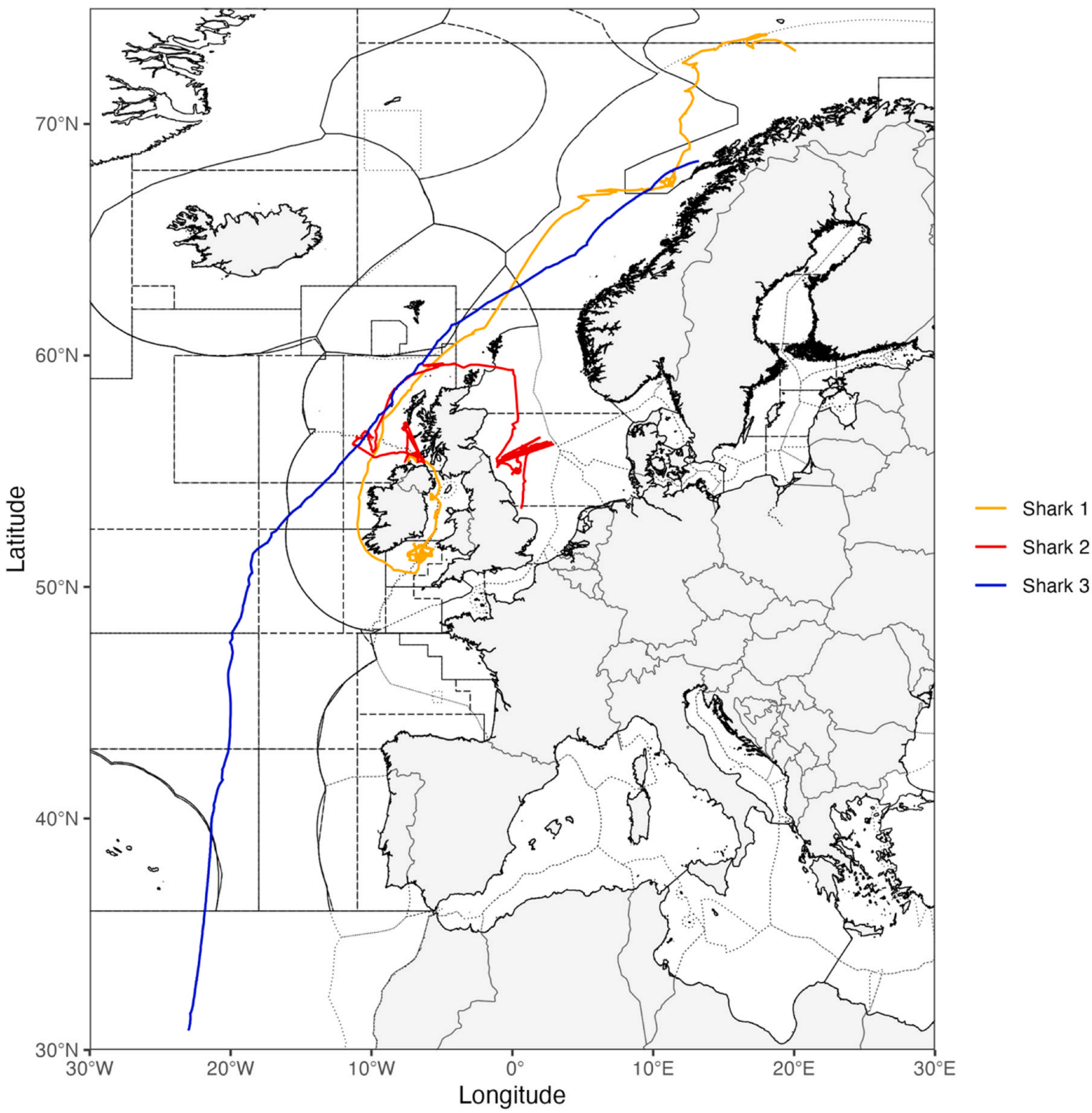

Fig. 2. Most probable tracks obtained from all three individual sharks using PSAT derived geolocation. Dotted lines: EEZs; dashed lines: ICES areas; solid lines: ICES ecoregions.

ranging movements and inter-individual variation (Pade et al., 2009; Saunders et al., 2010; Biais et al., 2017; ICCAT-ICES, 2022). In the south-west Pacific, mature female porbeagle sharks have been shown to undertake pronounced latitudinal migrations (Francis et al., 2015), yet they may travel less extensively than their North Atlantic counterparts that can travel large distances between summer and winter months (Campana, 2016; Biais et al., 2017; Skomal et al., 2021). However, the limited tracking data for this globally distributed species is insufficient to generalise these conclusions.

4.1. Added value through double-tagging and international collaboration

Previous studies on porbeagle shark movements have largely relied on reconstructed paths based on PSATs (Pade et al., 2009; Saunders et al., 2010; Francis et al., 2015; Campana, 2016; Biais et al., 2017; Skomal et al., 2021). Our study extends this approach by using a combination of SPOT and PSAT tags, providing both horizontal movement and vertical habitat-use data at high resolution. SPOT tags typically provide location error on the order of <1.5 km, whereas errors associated with geolocation from PSATs may exceed 100 km, especially around the equinoxes and at high latitudes (Teo et al., 2004; Braun et al., 2018; Wilflife Computers 2022, pers. comm., 8 November 2022). Comparison of tracks 1 and 2 obtained from both tags revealed differences in locations sometimes exceeding 200 km (Fig. 3) and in residency time differences of over 22% in the case of EEZs, over 10% in the case of ICES areas and over 20% for OSPAR regions (Supplementary Table). However,PSATs, in turn, allow us to investigate the vertical space use, which is a key, but often neglected, component in understanding the ecological niches of sharks and their exposure to anthropogenic pressures (Andrzejaczek et al., 2022). Thus, while PSATs are powerful for studying large scale migrations and deliver temperature and depths data, SPOT tags deliver migration data on a finer horizontal scale, as long as individuals surface frequently.

To our knowledge, this is the first use of fin-mounted SPOT tags for porbeagle sharks and results suggest the species may be well suited for it with long retention and frequent surfacing, but further testing under different conditions (location, sex, season) is necessary to confirm this. We acknowledge that the use of SPOT tags is, therefore, species dependent and, in some case where animals surface rarely, PSATs alone, or with Fastloc-GPS tags (Dujon et al., 2014), may be the more

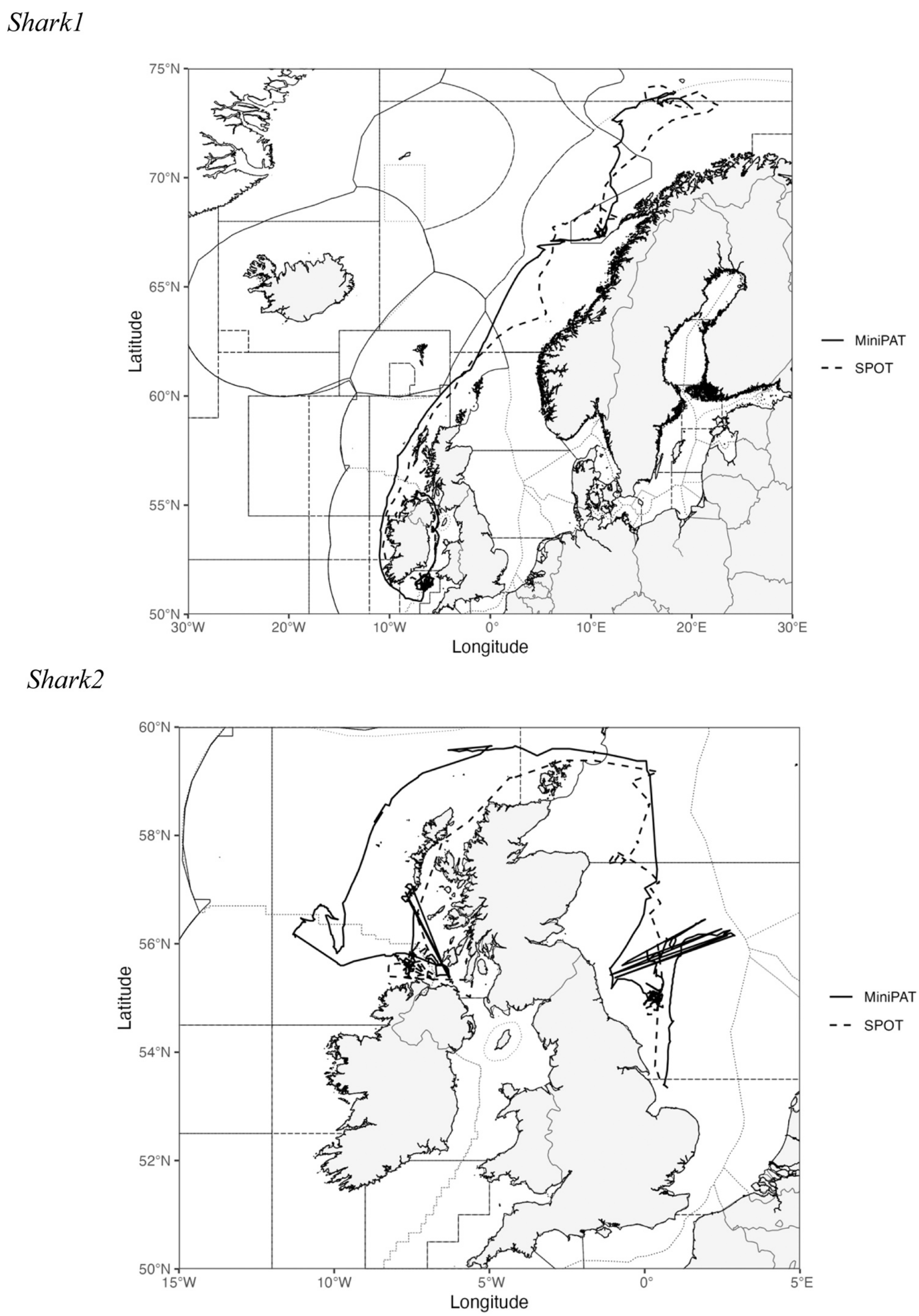

Fig. 3. Comparison of tracks obtained from PSAT light-derived geolocations (solid line) and SPOT GPS and ARGOS satellite locations (dashed line) for Shark 1 and Shark 2. SPOT tracks are shown only for the time period for which PSAT data were available. Background dotted lines: EEZs; dashed lines: ICES areas; solid lines: ICES ecoregions.

appropriate and advantageous option. Thanks to the combination of both tags, the data presented here is therefore much more extensive, allowing for example for swimming speed calculation, which can cross-inform the processing of PSAT derived tracks where SPOT data is absent, as shown in this study. Further, such double tagging could allow us to better define the space use of individual porbeagle sharks including areas of prolonged residence or migration corridors, as well as associated habitat characteristics. In the face of resource limitations, tagging with a combination of single SPOT, single PSAT deployments, together with double-tagged individuals can thus prove an effective way of collecting high-resolution data in both the horizontal and vertical dimension (Teo et al., 2004; Stevens et al., 2010; Siders et al., 2022). Improvements are also currently being made to geolocation models (Nielsen and Tribuzio, 2023) which will further refine resolution of satellite tracks.

These efforts are particularly effective if they can build on collaborative and transboundary research networks – reflecting the highly migratory nature of this species – and maximise data collection from each individual when taking into consideration the species' elusive behaviour, inter-individual variations, along with the many other challenges that present themselves when studying a wide-ranging, pelagic, threatened species. This study involved researchers from different institutions and countries as well as the support from the ICCAT Shark Research and Data Collection Programme (SRDCP) and its

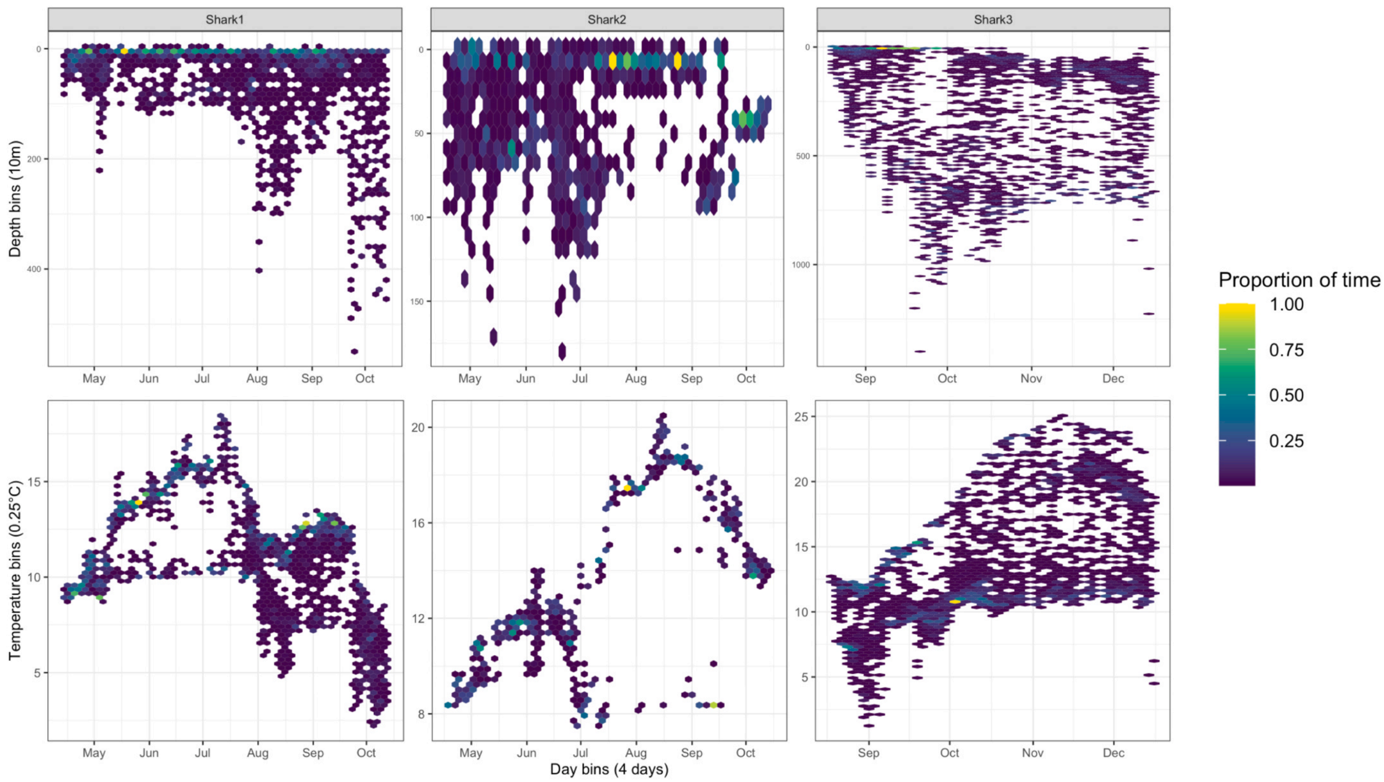

Fig. 4. Hexagonal heatmap showing the frequency of occurrences in depth and temperature bins for all three sharks based on relayed 10-minute time-series data. Bins are aggregated over a 4-day period. Depth is aggregated as 10-meter bins and temperature in 0.25°C bins.

associated researchers. This partnership allowed us to obtain high resolution information on the environmental space use for three individuals at different parts of their migration routes; an undertaking which requires open collaboration, data and knowledge exchange, and lays the groundwork for larger future collaborative efforts.

With this high-resolution data, we contribute to the existing porbeagle shark tracking dataset in the NE Atlantic (Pade et al., 2009; Saunders et al., 2010; Biais et al., 2017). Although data from previous studies range across sexes, ages and tagging periods, sample sizes of published telemetry data to this date are low, and access to the data may be limited or restricted. This makes it difficult to infer movement trends between classes. Therefore, more comprehensive and collaborative tagging efforts as well as data sharing initiatives are needed to provide a more holistic picture of migration routes and critical habitats for this species to inform management.

4.2. Management implications across borders and habitats

The management challenges presented by transboundary marine species are increasingly recognised (Hooker et al., 2011; Campana, 2016; Daly et al., 2018; Junge et al., 2019; Rooker et al., 2019; Palacios-Abrantes et al., 2020), and these data allow us to build on previous work, generating more-precise confirmation that individual porbeagle sharks transit through multiple EEZs, management zones (e.g. ICES, ICCAT, OSPAR) and ABNJs in a relatively small area and over short periods.

The population status of NE Atlantic porbeagle sharks, including its moderate intrinsic rate of increase, as well as their low rates of biological productivity (Campana et al., 2015), coupled with data on transboundary movements, highlight the need for continued robust cooperative management, and research strategies to inform them. This need is compounded when considering the apparent likelihood that the population is predominantly constituted of mature (possibly pregnant) females (Biais et al., 2017; Cameron et al., 2018) which are a key demographic group for the conservation of slow-growing species with low reproductive output. The NE Atlantic stock is currently defined as overfished but overfishing is no longer occurring (ICCAT, 2016; ICCAT-ICES, 2022). Due to effective international management measures, including the prohibition of fisheries along with abundance and tagging surveys (OSPAR, 2014; ICCAT, 2016; ICES, 2021), the stock seems in recovery and a small fishing quota for porbeagle shark has been advised by ICES for the entire NE Atlantic (ICES, 2022), for the first time since 2009. However, the robustness of measures could be improved (particularly on the high seas) by a continued effort to fill in knowledge gaps in porbeagle shark ecology, biology, life-history and physiology. Identification of essential habitats (areas used for foraging, resting, shelter from predators, reproduction, parturition etc) and knowledge of movements undertaken to connect these locations is particularly key to guiding the design of area-based management practices such as MPAs and spatio-temporal fisheries management measures (Barnett et al., 2019; Sheaves et al., 2021; Hyde et al., 2022; IUCN Species Survival Commission Shark Specialist Group, 2022; Moore and Fowler, 2022).

The movement patterns observed in this study include and extend the known latitudinal (76° – 30°N, shark 1) and vertical (0–1867 m, shark 3) ranges for porbeagle sharks in the Northeast Atlantic (Rigby et al., 2019). Porbeagle sharks not only transit between EEZs but also beyond international management zones responsible for the management and conservation of this population such as ICES and OSPAR (southern boundaries at 36°N). With respect to ICCAT, two of the three individuals transitioned out of the Northern Temperate Atlantic Ecoregion into the Tropical Atlantic Ecoregion, both of which were recently proposed as a candidate ICCAT ecoregions (Jordá et al., 2022). These long migrations in addition to an extensive use of the water column makes them vulnerable to encountering a range of fishing gears and varying levels of fishing pressure (Cortés et al., 2010; Dulvy et al., 2014). Large pelagic sharks are particularly prone to being bycaught in international and national waters of the Iberian, French as well as Celtic parts of the continental shelf due to high efforts with drifting longlines in those areas (Queiroz et al., 2019; Kroodsma et al., 2022; Welch et al., 2022) (see also Fig. 4). The sharks in this study conducted movements through regularly and rapidly changing physical habitats, characterised by depth and temperature, crossing temperature boundaries as low as 2.5°C and up to 24.5°C. These movements through different physical landscapes not only raise concerns related to their exposure to current anthropogenic threats and activities (Cortés et al., 2010; Queiroz et al., 2016; Andrzejaczek et al., 2022), but also to the effects of changing ocean conditions and habitat degradation on their movements (Lowerre-Barbieri et al., 2019; Vedor et al., 2021). This emphasises the need for governance at appropriate spatial scale and of critical habitats informed by new and continuing research into migration patterns and spatial distribution of the life cycle of this species (Lowerre-Barbieri et al., 2019).

4.3. Essential habitats and future work

Anecdotal evidence suggests Ireland, in addition to being an important summer aggregation site for juvenile porbeagle sharks (Cameron et al., 2019), may be an important reproductive area for the species (Clarke et al., 2016). Results from our study therefore contribute additional clues as to locations worthy of further investigation to identify essential habitats for the species including to the north of the island of Ireland; the Celtic Deep in the Irish sea (matching tracks from Pade, 2009); the North and East coast of Britain; and the Norwegian Shelf Edge and the seas around the Macaronesian archipelagos, where our individuals spent extensive periods of time. Further, the Rockall Trough could act as an important migration corridor for extended migrations such as observed with shark 1 and 3. Expanded, multi-year studies in conjunction with other tools such as genetic studies (e.g. Junge et al., 2019; Lieber et al., 2020) are needed to confirm potential inter-annual site fidelity (Biais et al., 2017) and consistency or class differences in migration routes and movement patterns.

5. Conclusion

In this study, we report high-resolution SPOT tracks and PSAT geolocation tracks of two adult female porbeagle sharks tagged off Ireland in spring, as well as light and SST-based geolocation tracks for one adult female tagged off Northern Norway in autumn. We demonstrate for the first time the value in using fin-mounted SPOT tags in this species, particularly when combined with PSAT tags. The tracks obtained from these individuals highlight rapid, transboundary movement patterns across a wide range of distances, depths and habitats within the NE Atlantic, but beyond the ICES ecoregions and statistical fishing areas, as well as across and beyond other management zones, underscoring the need for urgent cross-border, regional and international research collaborations to support and ensure continued effective management of this vulnerable porbeagle shark population in the NE Atlantic and beyond.

CRediT authorship contribution statement

Claudia Junge: Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing. **Keno Ferter:** Investigation, Methodology, Resources, Writing – review & editing. **Adam Barnett:** Resources, Writing – review & editing. **Otte Bjelland:** Resources, Writing – review & editing, Investigation, Methodology. **Neil Hammerschlag:** Resources, Writing – review & editing. **Austin J Gallagher:** Resources, Writing – review & editing. **Jenny Rose Bortoluzzi:** Conceptualization, Data curation, Visualization, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing, Validation. **William K Roche:** Resources, Writing – review & editing. **Grace E McNicholas:** Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing, Investigation. **Nicholas L Payne:** Conceptualization, Resources, Validation, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Antonia Klöcker:** Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. **Andrew Lloyd Jackson:** Supervision, Visualization, Writing – original draft, Writing – review & editing, Conceptualization, Data curation, Funding acquisition, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

Irish work was funded by Science Foundation Ireland (18/SIRG/5549) and with significant support from Irish anglers. Tagging in Norwegian waters was financed by the Norwegian Research Council as part of the Sharks on the Move project (NRC #326879). The PSAT tag deployed by Norway was kindly provided by ICCAT through the Shark Research and Data Collection Programme (SRDCP), which is supported through the ICCAT Science Envelop. The latter is funded by ICCAT regular budget and the voluntary contribution by the European Union through the grant agreement - *Strengthening the scientific basis on tuna and tuna-like species for decision-making in ICCAT*. The content of this paper does not necessarily reflect ICCAT's point of view or that of any of the other sponsors, who carry no responsibility. In addition, it does not indicate the Commission's future policy in this area The miniPAT tags provided by Dr Neil Hammerschlag were funded by the Ruta Maya Coffee, Isermann Family Foundation.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107007.

References

Andrzejaczek, S., Lucas, T.C.D., Goodman, M.C., Hussey, N.E., Armstrong, A.J., Carlisle, A., Coffey, D.M., et al., 2022. Diving into the vertical dimension of elasmobranch movement ecology. Sci. Adv. 8, eabo1754.

Barnett, A., McAllister, J.D., Semmens, J., Abrantes, K., Sheaves, M., Awruch, C., 2019. Identification of essential habitats: including chimaeras into current shark protected areas. Aquat. Conserv.: Mar. Freshw. Ecosyst. 29, 865–880.

Bendall, V.J., Ellis, J.R., Hetherington, S.J., McCully, S.R., Righton, D., Silva, J.F., 2013. Preliminary observations on the biology and movements of porbeagle Lamna nasus around the British Isles. Collect. Vol. Sci. Pap. ICCAT 69, 1702–1722.

Biais, G., Coupeau, Y., Séret, B., Calmettes, B., Lopez, R., Hetherington, S., Righton, D., 2017. Return migration patterns of porbeagle shark (Lamna nasus) in the Northeast Atlantic: implications for stock range and structure. ICES J. Mar. Sci. 74, 1268–1276.

Braun, C.D., Galuardi, B., Thorrold, S.R., 2018. HMMoce: an R package for improved geolocation of archival-tagged fishes using a hidden Markov method. Methods Ecol. Evol. 9, 1212–1220.

Cameron, L.W., Roche, W., Green, P., Houghton, J.D., Mensink, P.J., 2018. Transatlantic movement in porbeagle sharks, Lamna nasus. Fish. Res. 207, 25–27.

Cameron, L.W.J., Roche, W.K., Houghton, J.D.R., Mensink, P.J., 2019. Population structure and spatial distribution of porbeagles (Lamna nasus) in Irish waters. ICES J. Mar. Sci. 76, 1581–1590.

Campana, S., Fowler, M., Houlihan, D., Joyce, W., Showell, M., Simpson, M., Miri, C., et al., 2015. Recovery potential assessment for porbeagle (Lamna nasus) in Atlantic Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 41, 45.

Campana, S.E., 2016. Transboundary movements, unmonitored fishing mortality, and ineffective international fisheries management pose risks for pelagic sharks in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 73, 1599–1607.

Clarke, M., Farrell, E., Roche, W., Murray, T., Foster, S., and Marnell, F. 2016. Ireland Red List No. 11: Cartilaginous fish [sharks, skates, rays and chimaeras].

Coffey, D.M., Carlisle, A.B., Hazen, E.L., Block, B.A., 2017. Oceanographic drivers of the vertical distribution of a highly migratory, endothermic shark. Sci. Rep. 7, 10434.
Cortés, E., Arocha, F., Beerkircher, L., Carvalho, F., Domingo, A., Heupel, M., Holtzhausen, H., et al., 2010. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Aquat. Living Resour. 23, 25–34.
Curtis, T., Cortes, E., DuBeck, G., and McCandless, C.T. 2016. Statues review report: porbeagle shark (Lamna nasus).
Daly, R., Smale, M.J., Singh, S., Anders, D., Shivji, M., K., Daly, C.A., Lea, J.S.E., et al., 2018. Refuges and risks: evaluating the benefits of an expanded MPA network for mobile apex predators. Divers. Distrib. 24, 1217–1230.
Drymon, J.M., Wells, R.J.D., 2017. Double tagging clarifies post-release fate of great hammerheads (Sphyrna mokarran). Anim. Biotelemetry 5, 28.
Dujon, A.M., Lindstrom, R.T., Hays, G.C., 2014. The accuracy of Fastloc-GPS locations and implications for animal tracking. Methods Ecol. Evol. 5, 1162–1169.
Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., et al., 2014. Extinction risk and conservation of the world's sharks and rays. eLife 3, e00590.
Ellis, J., Farrell, E., Jung, A., McCully, S., Sims, D., Soldo, A., 2015. Lamna nasus. IUCN Red. List Threat. Species.
Fowler, S., Raymakers, C., and Grimm, U. 2004. Trade in and conservation of two shark species, porbeagle (Lamna nasus) and spiny dogfish (Squalus acanthias).
Francis, M.P., Natanson, L.J., Campana, S.E., 2008. The biology and ecology of the porbeagle shark, Lamna nasus. Sharks Open Ocean.: Biol. Fish. Conserv. 105–113.
Francis, M.P., Holdsworth, J.C., Block, B.A., 2015. Life in the open ocean: seasonal migration and diel diving behaviour of Southern Hemisphere porbeagle sharks (Lamna nasus). Mar. Biol. 162, 2305–2323.
González, M.T., Sepúlveda, F.A., Zárate, P.M., Baeza, J.A., 2021. Regional population genetics and global phylogeography of the endangered highly migratory shark Lamna nasus: implications for fishery management and conservation. Aquat. Conserv.: Mar. Freshw. Ecosyst. 31, 620–634.
Gullestad, P., Sundby, S., Kjesbu, O.S., 2020. Management of transboundary and straddling fish stocks in the Northeast Atlantic in view of climate-induced shifts in spatial distribution. Fish Fish 21, 1008–1026.
Hammerschlag, N., Gallagher, A.J., Lazarre, D.M., 2011. A review of shark satellite tagging studies. J. Exp. Mar. Biol. Ecol. 398, 1–8.
Hammerschlag, N., McDonnell, L.H., Rider, M.J., Street, G.M., Hazen, E.L., Natanson, L. J., McCandless, C.T., et al., 2022. Ocean warming alters the distributional range, migratory timing, and spatial protections of an apex predator, the tiger shark (Galeocerdo cuvier). Glob. Change Biol. 28, 1990–2005.
Hooker, S.K., Cañadas, A., Hyrenbach, K.D., Corrigan, C., Polovina, J.J., Reeves, R.R., 2011. Making protected area networks effective for marine top predators. Endanger. Species Res. 13, 203–218.
Hueter, R.E., Tyminski, J.P., de la Parra, R., 2013. Horizontal movements, migration patterns, and population structure of whale sharks in the Gulf of Mexico and northwestern Caribbean Sea. Plos One 8, e71883.
Hyde, C.A., Notarbartolo di Sciara, G., Sorrentino, L., Boyd, C., Finucci, B., Fowler, S.L., Kyne, P.M., et al., 2022. Putting sharks on the map: a global standard for improving shark area-based conservation. Front. Mar. Sci.: 1660.
ICCAT Shark Species Group 2020. Report of the 2020 porbeagle shark stock assessment meeting, ICCAT.
ICCAT. 2016. Report of the 2016 intersessional meeting of the shark species group. ICES Document SCRS P/2016/020. 27 pp.
ICCAT-ICES. 2022. Report of the joint ICES-ICCAT benchmark workshop in advance of the North-Eastern Atlantic porbeagle stock assessment. ICES Document SCRS/2022/002: 79. 60 pp.
ICES 2021. Working Group on Elasmobranch Fishes (WGEF).
ICES. 2022. Porbeagle (Lamna nasus) in subareas 1–10, 12, and 14 (the Northeast Atlantic and adjacent waters).
IUCN Species Survival Commission Shark Specialist Group. 2022. Important Shark and Ray Area (ISRA): Guidance document on criteria application.
Jacoby, D.M., Watanabe, Y.Y., Packard, T., Healey, M., Papastamatiou, Y.P., Gallagher, A.J., 2022. First descriptions of the seasonal habitat use and residency of scalloped hammerhead (Sphyrna lewini) and Galapagos sharks (Carcharhinus galapagensis) at a coastal seamount off Japan. Anim. Biotelemetry 10, 1–11.
Jensen, C.F., Natanson, L.J., Pratt Jr., H.L., Kohler, N., and Campana, S.E. 2002. The reproductive biology of the porbeage shark (Lamna nasus) in the western North Atlantic Ocean.
Jordá, M.J., Nieblas, A., Hanke, A., Tsuji, S., Andonegi, E., Di Natale, A., Kell, L., et al., 2022. Report of the ICCAT workshop on the identification of regions in the ICCAT convention area for supporting the implementation of the ecosystem approach to fisheries management. Collect. Vol. Sci. Pap. ICCAT 79, 178–211.
Junge, C., Donnellan, S.C., Huveneers, C., Bradshaw, C.J.A., Simon, A., Drew, M., Duffy, C., et al., 2019. Comparative population genomics confirms little population structure in two commercially targeted carcharhinid sharks. Mar. Biol. 166, 16.
Ketchum, J.T., Hoyos-Padilla, M., Aldana-Moreno, A., Ayres, K., Galván-Magaña, F., Hearn, A.R., Lara-Lizardi, F., et al., 2020. Shark movement patterns in the Mexican Pacific: a conservation and management perspective. Adv. Mar. Biol. 85 (1), 1–37.
Kitamura, T., Matsunaga, H., 2010. Population structure of porbeagle (Lamna nasus) in the Atlantic Ocean as inferred from mitochondrial DNA control region sequences. Collect. Vol. Sci. Pap. ICCAT 65, 2082–2087.
Kohler, N.E., Turner, P.A., Hoey, J.J., Natanson, L.J., 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. Collect. Vol. Sci. Pap. ICCAT 54, 1231–1260.
Koubrak, O., VanderZwaag, D.L., 2020. Are transboundary fisheries management arrangements in the Northwest Atlantic and North Pacific seaworthy in a changing ocean? Ecol. Soc. 25.
Kroodsma, D.A., Hochberg, T., Davis, P.B., Paolo, F.S., Joo, R., Wong, B.A., 2022. Revealing the global longline fleet with satellite radar. Sci. Rep. 12, 21004.
Lédée, E.J.I., Heupel, M.R., Taylor, M.D., Harcourt, R.G., Jaine, F.R.A., Huveneers, C., Udyawer, V., et al., 2021. Continental-scale acoustic telemetry and network analysis reveal new insights into stock structure. Fish Fish 22, 987–1005.
Lieber, L., Hall, G., Hall, J., Berrow, S., Johnston, E., Gubili, C., Sarginson, J., et al., 2020. Spatio-temporal genetic tagging of a cosmopolitan planktivorous shark provides insight to gene flow, temporal variation and site-specific re-encounters. Sci. Rep. 10, 1661.
Lowerre-Barbieri, S.K., Kays, R., Thorson, J.T., Wikelski, M., 2019. The ocean's movescape: fisheries management in the bio-logging decade (2018–2028). ICES J. Mar. Sci. 76, 477–488.
Lubitz, N., Bradley, M., Sheaves, M., Hammerschlag, N., Daly, R., Barnett, A., 2022. The role of context in elucidating drivers of animal movement. Ecol. Evol. 12, e9128.
Moore, A.B., Fowler, S.L., 2022. Important Shark Areas: rationale and need. Aquat. Conserv.: Mar. Freshw. Ecosyst. 32, 710–711.
Musyl, M.K., Brill, R., Curran, D.S., Fragoso, N.M., McNaughton, L., Nielsen, A., Kikkawa, B.S., Moyes, C.D., 2011. Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. Fish. Bull. 109, 341.
Nielsen, J.K., Tribuzio, C.A., 2023. Development and parameterization of a data likelihood model for geolocation of a bentho-pelagic fish in the North Pacific Ocean. Ecol. Model. 478, 110282.
OSPAR 2014. OSPAR Recommendation 2014/6 on furthering the protection and conservation of the porbeagle shark (Lamna nasus) in the OSPAR maritime area. *In* OSPAR Recommendation 2014/06. Ed. by O. Commission. Cascais.
Pade, N.G., Queiroz, N., Humphries, N.E., Witt, M.J., Jones, C.S., Noble, L.R., 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. J. Exp. Mar. Biol. Ecol. 370, 64–74.
Palacios-Abrantes, J., Reygondeau, G., Wabnitz, C.C.C., Cheung, W.W.L., 2020. The transboundary nature of the world's exploited marine species. Sci. Rep. 10, 17668.
Queiroz, N., Humphries, N.E., Mucientes, G., Hammerschlag, N., Lima, F.P., Scales, K.L., Miller, P.I., et al., 2016. Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. Proc. Natl. Acad. Sci. U. S. A. 113, 1582–1587.
Queiroz, N., Humphries, N.E., Couto, A., Vedor, M., Da Costa, I., Sequeira, A.M., Mucientes, G., et al., 2019. Global spatial risk assessment of sharks under the footprint of fisheries. Nature 572, 461–466.
R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
R Studio Team, 2021. RStudio: Integrated Development Environment for R. RStudio. PBC, Boston, MA.
Renshaw, S., Hammerschlag, N., Gallagher, A.J., Lubitz, N., Sims, D.W., 2023. Global tracking of shark movements, behaviour and ecology: a review of the renaissance years of satellite tagging studies, 2010–2020. J. Exp. Mar. Biol. Ecol. 560, 151841.
Rigby, C., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M., Herman, K., et al. 2019. Lamna nasus-Porbeagle. The IUCN Red List of Threatened Species 2019.
Rodriguez-Burgos, A.M., Briceño-Zuluaga, F.J., Ávila Jiménez, J.L., Hearn, A., Peñaherrera-Palma, C., Espinoza, E., Ketchum, J., et al., 2022. The impact of climate change on the distribution of Sphyrna lewini in the tropical eastern Pacific. Mar. Environ. Res. 180, 105696.
Rooker, J.R., Dance, M.A., Wells, R.J.D., Ajemian, M.J., Block, B.A., Castleton, M.R., Drymon, J.M., et al., 2019. Population connectivity of pelagic megafauna in the Cuba-Mexico-United States triangle. Sci. Rep. 9, 1663.
Saunders, R.A., Royer, F., Clarke, M.W., 2010. Winter migration and diving behaviour of porbeagle shark, Lamna nasus, in the Northeast Atlantic. ICES J. Mar. Sci. 68, 166–174.
Sheaves, M., Mattone, C., Connolly, R.M., Hernandez, S., Nagelkerken, I., Murray, N., Ronan, M., et al., 2021. Ecological constraint mapping: understanding outcome-limiting bottlenecks for improved environmental decision-making in marine and coastal environments. Front. Mar. Sci.: 1133.
Siders, Z.A., Westgate, A.J., Bell, K.R., Koopman, H.N., 2022. Highly variable basking shark (Cetorhinus maximus) diving behavior in the lower Bay of Fundy, Canada. Front. Mar. Sci. 9, 976857.
Skomal, G., Marshall, H., Galuardi, B., Natanson, L., Braun, C., Bernal, D., 2021. Horizontal and vertical movement patterns and habitat use of juvenile porbeagles (Lamna nasus) in the Western North Atlantic. Front. Mar. Sci. 8, 624158.
Stevens, J.D., Bradford, R.W., West, G.J., 2010. Satellite tagging of blue sharks (Prionace glauca) and other pelagic sharks off eastern Australia: depth behaviour, temperature experience and movements. Mar. Biol. 157, 575–591.
Teo, S.L., Boustany, A., Blackwell, S., Walli, A., Weng, K.C., Block, B.A., 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Mar. Ecol. Prog. Ser. 283, 81–98.
Testerman, C.B. 2014. Molecular ecology of globally distributed sharks.
Vedor, M., Queiroz, N., Mucientes, G., Couto, A., Costa, I. d, Santos, A. d, Vandeperre, F., et al., 2021. Climate-driven deoxygenation elevates fishing vulnerability for the ocean's widest ranging shark. eLife 10, e62508.
Wearmouth, V.J., Sims, D.W., 2008. Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Adv. Mar. Biol. 54, 107–170.

Welch, H., Clavelle, T., White, T.D., Cimino, M.A., Van Osdel, J., Hochberg, T., Kroodsma, D., Hazen, E.L., 2022. Hot spots of unseen fishing vessels. Sci. Adv. 8, eabq2109.

Wickham, H., 2016. Data analysis. ggplot2. Springer, pp. 189–201.

Yokoi, H., Ijima, H., Ohshimo, S., Yokawa, K., 2017. Impact of biology knowledge on the conservation and management of large pelagic sharks. Sci. Rep. 7, 1–14.