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Migration and space use by porbeagle sharks *Lamna nasus* in the northeast Atlantic

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ABSTRACT: The porbeagle shark *Lamna nasus*, a top predator in the North Atlantic, is vulnerable to anthropogenic stressors due to its life history characteristics. Understanding its biology, abundance and spatial ecology is crucial for underpinning effective conservation and management strategies. We collected satellite tag data from 10 porbeagle sharks caught off the north coast of Ireland to study migration behaviour and space use. Data from pop-up satellite archival tags and platform terminal telemetry tags collected between July 2010 and February 2014 (for deployments up to ~9 mo) showed long-distance (1479—25 707 km), seasonal migrations, with autumnal movements along the shelf-break to regions around Portugal, the Bay of Biscay and the Azores via the Mid-Atlantic ridge. Migrations to waters off Norway and the Faroe/Shetland Islands were also evident prior to these autumnal southward migrations. In spring, some sharks returned northwards, and there was evidence of site fidelity for shelf waters around the northern Irish coast and western Scotland and the Celtic Sea in summer. Porbeagles exhibited seasonal changes in vertical space use as they traversed various habitats during migration, with deeper occupancy of the water column in winter than in summer. There was a distinct day—night pattern in porbeagle depth distribution during their off-shelf residency in winter, consistent with diel vertical migrations between deep waters in daytime and the surface layers at night. Nocturnal depth distribution was closely associated with the lunar cycle, with deeper residency/diving occurring during periods of full moon. Porbeagles occupied and traversed both the open ocean and coastal areas of high fishing activity, highlighting the challenge of managing this stock because of large-scale migratory behaviour.

KEY WORDS: Porbeagle shark · Satellite tag · Migration · Diving behaviour · North Atlantic

1. INTRODUCTION

The porbeagle shark *Lamna nasus* is a large (~2 to 3 m in length), predatory, endothermic shark that inhabits the temperate seas of the North and South Atlantic, as well as the Mediterranean and Baltic Seas (Campana & Joyce 2004, Francis et al. 2008). Like most pelagic sharks, the species has relatively slow growth, low fecundity and late age at sexual maturity, making it vulnerable to population depletion by fisheries (Campana et al. 2002, Jensen et al. 2002, Cameron et al. 2019, Colonello et al. 2024). Porbeagles are also commercially valuable and, consequently, the species has had a history of heavy exploitation by commercial fisheries since the 1930s (Campana et al. 2008), with evidence of significant population declines in both the northeast and northwest Atlantic around the mid- to late-20th century (DFO 2005, Curtis et al. 2016, ICES 2024a). Globally, the species is currently listed as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Rigby et al. 2019), and as Critically Endangered in the northeast Atlantic (Ellis et al. 2015, ICES 2024a). Directed fishing for porbeagles has been prohibited

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by Norway since 2007 and by the European Union since 2010, although the risk of incidental bycatch in other commercial fisheries remains substantial. There is evidence that the population in the northeast Atlantic is increasing, although recovery to sustainable levels for commercial fishing has yet to be achieved and there remain large uncertainties over the true state of the stock (ICES 2024a). It has been estimated that the porbeagle fishery would need to be closed for 15 to 34 yr from 2010 in order for stock biomass to recover to levels where sustainable harvesting is possible (ICES 2024a). Therefore, there is a requirement for continued research and conservation effort in this region and across its distributional range.

Developing a greater understanding of the species' spatial ecology is central to this research and conservation focus. For management and assessment purposes, porbeagles are divided into 2 stocks in the North Atlantic, one on each side of the 42° W meridian. This stock separation is supported by limited information from mark-and-recapture studies, which suggests that porbeagles inhabit regions around the continental shelf, where they may undertake apparent short- to medium-scale (500–1000 km) seasonal migrations, but they seldom leave the continental shelf/shelf-break and cross the Atlantic Ocean (Stevens 1990, Kohler & Turner 2001, Cameron et al. 2019). More detailed information from tagging studies using pop-up satellite archival tags (PSATs) support these general findings, but the technology is also revealing new insights into the spatial ecology of the species on both sides of the Atlantic (Pade et al. 2009, Campana et al. 2010, Saunders et al. 2011, Biais et al. 2017, Skomal et al. 2021, Bortoluzzi et al. 2024). The emerging picture is that, despite apparent inter-individual variation in behaviour, porbeagles undertake regular long-distance (>5000 km) seasonal migrations between sub-tropical (winter) and sub-polar waters (summer), which encompass seasonal transitions between coastal, shelf-break and oceanic habitats.

In the northeast Atlantic, these migrations extend between waters off Madeira and northwest Africa to the waters around the Arctic Circle off western Norway, with frequent periods of residency around the Bay of Biscay, northwest Ireland and the Celtic Sea (Saunders et al. 2011, Biais et al. 2017, Bortoluzzi et al. 2024). The European shelf-break appears to be an important corridor for these seasonal migrations, which includes heavily fished coastal areas for a range of commercially targeted species, although there is emerging evidence that the oceanic waters of the Mid-Atlantic Ridge also comprise an important habitat (Biais et al. 2017). During their long-distance migrations, it is increasingly clear that porbeagles regularly cross multiple international management zones and jurisdictions, necessitating the need for international coordination and cooperation to ensure effective management and conservation measures (Bortoluzzi et al. 2024).

Despite recent satellite tagging studies on porbeagles in the northeast Atlantic, the available data (<30 sharks) do not allow an exhaustive analysis of their migration behaviour and space use, and there is a requirement for more data. In particular, little is known about smaller-scale patterns in site fidelity, primarily because too few individuals have been tagged with PSATs, but also because PSATs use light-based geolocation methods that are associated with high positional error bounds (typically >1° of latitude and longitude due to dive-induced shifts in recorded light levels) that limit the precision of small-scale analyses of porbeagle space use (Saunders et al. 2011, Biais et al. 2017). There is preliminary evidence that porbeagles exhibit high site fidelity to regions around the Bay of Biscay, Celtic Sea and northwest Ireland, with some individuals returning annually to their initial PSAT tagging sites in the Bay Biscay and relatively high spatial congruency in porbeagle mark-and-recapture locations around Ireland (albeit after several years) (Biais et al. 2017, Cameron et al. 2019). Furthermore, it has been hypothesised that these locations are important parturition grounds for the species in the northeast Atlantic based on a few observations of females (n = 7) and newborn pups (n = 9) in coastal waters around Scotland, the Celtic Sea, the English Channel and the Bay of Biscay shelf (Biais et al. 2017). However, it has thus far not been possible to comprehensively quantify site fidelity, residency times and common space-use patterns that porbeagles have in such regions during their wider seasonal migrations.

Compared to the light-based geolocation methods of PSATs, platform terminal telemetry (PTT) tags offer far greater precision in their location estimates because they transmit a radio signal into space upon surfacing and the position is calculated from the doppler shift as satellites pass overhead. This enables the monitoring of porbeagle movement patterns and site fidelity at relatively small spatial scales (~200–1500 m). Indeed, Bortoluzzi et al. (2024) demonstrated the utility of using both PSATs, which collect additional high-resolution data on depth and temperature, together with PTTs to provide greater accuracy and precision in estimates of movements and space use. However, PTT data from only 2 porbeagles have been published to date (Bortoluzzi et al. 2024). Furthermore, the existing analyses on these data were based solely on simple linear interpolations between transmitted location points, which may not adequately account for positional errors or the sharks' true movement behaviour between location fixes that can be spatially and temporally far apart during extended periods below the sea surface (Saunders et al. 2011). The application of state-space models can therefore potentially improve the use of PTT data for examining the movement ecology of porbeagles (Johnson et al. 2008).

In this study, we used a combination of PSATs and PTT tags deployed on porbeagles caught off the northwest Irish coast between 12 July 2010 and 25 February 2014 to assess the possibility of return migrations, patterns in horizontal and vertical space use and site fidelity around the European continental shelf. We tagged 13 sharks (5 with PSATs, 6 with PTTs and 2 with both PSATs and PTTs) in total and used state-space models to robustly quantify porbeagle movement patterns. Our study provides new information on the movement ecology of porbeagles in the northeast Atlantic that will help contribute to addressing existing knowledge gaps on essential porbeagle habitats, particularly their reproductive grounds, spatial connectivity of stocks, areas of fisheries overlap and the environmental drivers of porbeagle space use, which are essential prerequisites for future conservation and management strategies.

2. MATERIALS AND METHODS

2.1. Field sampling

Thirteen porbeagles were caught by rod and lines with baited hooks off northwest Ireland between 12 July 2010 and 25 February 2014 (Table 1). All animals were brought on-board for measuring body size (total length, fork length and girth) and tagging. Once a shark was onboard, a seawater hose was placed in its mouth to ventilate the gills and a damp towel was placed over the eyes to reduce stress. We tagged 5 female porbeagles with Microwave Telemetry PTT-100 archival pop-up tags (PSATs). Each PSAT was attached via a short nylon tether (encased in a silicone tube) to a urethane dart at the base of the dorsal fin. The PSATs were programmed for an 8–9 mo deployment, collecting ambient light (for geolocation), temperature (±0.1°C) and depth (±0.5 m) data at a sampling rate of once every 15 min. To optimise

Table 1. Summary data for 13 sharks tagged off northwest Ireland. Estimates of weight were derived from allometric equations of Natanson et al. (2002). PSAT: pop-up satellite archival tag; PTT: platform terminal telemetry tag. Sharks that were double-tagged with PSATs and PTTs are marked with an asterisk (*). Dates are given as d/mo/yr. Est: estimated; –: not applicable

Shark tag	Type	Sex	Total length (m)	Fork length (m)	Girth (m)	Weight (kg)	Tagging date	Tagging location (°N)	Tagging location (°W)	Pop-up or end transmission date	No. days tagged	Pop-up end (°N)	Pop-up end (°W)	Est. trip length (km)	Est. mean movement (km d^{-1})	Total no. PTT transmissions	Mean no. PTT transmissions d^{-1} (SD)
39428	PSAT	F	1.93	1.78	1.00	67.1	12/07/2010	55.305	7.634	11/04/2011	270	44.636	10.577	2961	11	–	–
38633	PSAT	F	1.63	1.43	0.86	40.1	12/07/2010	55.305	7.634	19/07/2010	7	55.391	7.356	–	–	–	–
108960	PSAT	F	1.86	1.7	0.94	53.1	06/08/2012	55.288	7.874	06/04/2013	243	55.831	11.992	20344	84	–	–
108777	PSAT	F	1.32	1.15	0.72	22.7	08/10/2012	55.372	7.800	13/03/2013	156	46.963	6.695	9790	63	–	–
111694	PSAT	F	1.4	1.27	0.89	37.6	09/10/2012	55.374	7.784	09/06/2013	243	64.689	7.682	25707	106	–	–
111693	PSAT	*F	1.4	1.24	0.81	30.4	13/10/2012	55.393	7.808	13/06/2013	243	55.85	7.856	13936	57	–	–
111697	PTT									29/04/2013	98	54.243	10.847	9008	92	649	5.45 (3.66)
111695	PSAT	*F	1.46	1.3	0.83	33.6	14/10/2012	55.374	7.859	14/06/2013	243	48.356	8.247	12026	49	–	–
111696	PTT									23/10/2013	9	54.048	10.735	1479	164	53	5.30 (5.01)
129736	PTT	F	1.63	1.45	0.81	33.1	18/06/2013	55.324	7.433	26/12/2013	191	57.924	11.183	8861	46	1025	7.77 (5.29)
129735	PTT	F	2.02	1.93	1.11	87.1	10/07/2013	55.298	7.544	No data	–	–	–	–	–	–	–
129740	PTT	M	2.04	1.95	1.12	88.9	10/07/2013	55.298	7.544	11/01/2014	185	50.181	34.222	8915	48	455	5.29 (4.20)
129738	PTT	M	1.97	1.78	1.00	66.7	11/07/2013	55.326	7.544	No data	–	–	–	–	–	–	–
129737	PTT	M	1.91	1.62	0.97	57.6	12/07/2013	55.333	7.491	30/11/2013	141	48.75	11.659	14640	104	1652	14.62 (11.41)
129739	PTT	F	1.82	1.72	0.96	59	20/07/2013	55.358	7.473	25/02/2014	220	49.882	7.837	8016	36	1005	8.82 (6.31)

data retrieval via the Argos satellite system, these tags use a 'fuzzy logic' algorithm to give at least 1 complete data return per 60 min interval over the archived time-series, with the number of additional returns per interval fulfilled subsequently depending on battery capacity. Our PSATs had the capacity to measure water temperature from 0 to 35°C, depth to 1280 m and ambient light levels at 550 nm wavelength. The tags were programmed to detach from the sharks if they reached 1250 m in depth (±5 m), or if a constant depth (±2.5 m) was maintained for 4 d, indicative of animal mortality. Following detachment and pop-up to the sea surface, the archived data were transmitted to Argos receivers on NOAA polar-orbiting satellites. We also tagged 6 sharks (3 male and 3 female) with Wildlife Computers SPOT5 PTT tags. These tags were attached to the top of the dorsal fin using nylon bolts and were configured to transmit location-only messages to satellite-borne Argos receivers upon surfacing. This was done to extend the battery life to maximise the possible deployment time to periods >12 mo. In addition, 2 female sharks were tagged with both a PSAT and a PTT tag to facilitate an intercomparison of movement tracks.

2.2. PSAT movement track processing

PSATs function optimally for geolocation estimation when situated in the upper 100 m of the water column where light attenuation is lowest (Block et al. 2011). Inspection of the initial geolocation positions calculated by the proprietary tag software (using light levels at dusk and dawn) revealed many anomalous estimates resulting from predominantly deep-water residency (>100 m) and dive-induced shifts in light intensity. Location estimates were therefore produced by the Collecte Localisation Satellite (CLS) 'Track and Loc' service that is based on the geolocation models described by Royer & Lutcavage (2009). This state-space modelling approach estimates a daily position of the tracked animal between the tag deployment and the detachment position, using tag-derived light-based geolocation positions (where possible), as well as tag-derived depth and temperature records, satellite-derived sea surface temperature (SST) and local bathymetry data input.

For this procedure, a simple spatial model was built to predict the likely distribution of a given shark per day using a random walk model with a uniform movement kernel starting at the tag release point. These initial daily predicted probability densities (calculated for 0.1° × 0.1° grid cells) were used in a hidden Markov model, with estimates of tag-derived daily positions (where light data were robust), SST and maximum depth used as positional constraints in relation to satellite-derived SST measurements and underlying local bathymetry (see Pedersen et al. 2008 for details on constructing such a hidden Markov model). In this case, the model was fitted assuming a maximum horizontal movement speed of 100 km d^{-1} and a maximum absolute SST error of ±0.5°C. The final location estimation was then determined using a recursive Bayesian estimation technique which is consistent with the Kalman filter that is used widely in satellite tracking studies of marine animals (Nielsen et al. 2006, Royer & Lutcavage 2009). Following Neilson et al. (2014), this Bayesian filtering process employs 2 steps to determine daily location measurements. At each sampling time, the method first predicts initial positions by numerically solving the advection—diffusion equation for the 2D probability densities of the shark's presence. Positional corrections are then applied to the predicted probability densities using data recorded by the PSAT to produce the final distribution of the shark. This correction step uses the available light-based tag location estimates to retain the most likely predicted probability densities, with additional selection constraints based on both bathymetry (i.e. the presence of a shark in a cell will only be probable if the maximum depth of the shark is less than the maximum water depth within that cell) and satellite-based SST (by minimising the deviation of this SST at the updated location from the daily tag-derived SST). In this way, the constrained probability of the shark's presence is estimated spatially for each grid point (0.1° × 0.1° resolution) at each time step, and best estimates of daily location are calculated as the mean of the daily grid locations weighted by their probability.

All movement tracks were processed using the same model parameters, where the diffusion coefficient of the isotopic random walk model was set to 5000 km^2 d^{-1}, the standard deviation of the light-based tag geolocation used in the correction step was set to 1° of longitude and 3° of latitude, and the standard deviation of the SST error was set to 0.5°C. For all models, we used daily SST estimates from Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) with a resolution 0.05° (https://data.marine.copernicus.eu/product/SST_GLO_SST_L4_NRT_OBSERVATIONS_010_001/description) and the ETOPO2 bathymetry (www.ngdc.noaa.gov/mgg/global/etopo2.html) data set with 2 min resolution.

2.3. PTT movement track processing and spatial analysis

PTTs transmit radio signals to transceivers on polar-orbiting Argos satellites when the dorsal fin breaks the surface of the water and the shark's position is calculated from the doppler shift as the satellites pass overhead. Each transmission is assigned a quality rating (3, 2, 1, 0, A, B and Z, from best to worst) to define the precision of the calculated location from a radius of a few kilometres to ~250 m (Vincent et al. 2002). Our analysis used quality 3—0, A and B locations (which are often similar in accuracy to 1 and 0 locations and can be accommodated in state-space models), representing an approximate error radius of <1.5 km. Erroneous locations of >8 km h^{-1} were removed using the McConnell speed filter (McConnell et al. 1992), and the state-space model R package 'crawl' was subsequently applied to estimate a shark's movement tracks (Johnson et al. 2008, Johnson 2022). Essentially, this package fits continuous-time correlated random walk models with time indexed covariates to PTT data, providing a more realistic view of spatial movement than simple linear travel between recorded PTT fixes, since uncertainty relating to both observation errors in the positions and process errors arising from variations in possible movement between each position are incorporated. This is particularly advantageous for porbeagles that may travel long distances and undergo extended periods without surfacing (Saunders et al. 2011). Inspection of our data showed that gaps between PTT transmissions rarely exceeded 15 d, although on a few occasions there were large periodic gaps between 28 and 50 consecutive days (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m755p095_supp.pdf). The likelihood of reliably interpolating accurate positions within the 'crawl' model framework was therefore relatively high for most of the data. However, the accuracy of the modelled positions was considerably lower between periodic gaps exceeding 28 d, so the movement tracks in these few instances should be treated with caution. The model was fitted using the Kalman-Filter on the state-space version of the continuous-time stochastic movement process (Johnson et al. 2008). Hourly location and movement speed predictions were calculated from the model to obtain the best fit movement track for each shark between the deployment time and final transmitted PTT tag message.

To enable estimates of porbeagle site fidelity and common space use, the model was used to simulate 1000 movement tracks for each shark within the inherent data and model uncertainty structure. This enabled spatially gridded probability densities to be computed that were then used to calculate maps of percentage time spent across a 0.2° resolution grid. The time spent at each location was summed across all sharks to calculate an overall map of percentage time spent for the whole porbeagle population tagged with PTTs in the study (n = 6 sharks with recovered data sets). Since 'crawl' incorporates uncertainty from both observation and process errors, the approach is more robust than the alternative of using kernel density estimation (KDE), which would treat each point as an accurate measure and use linear interpolation to derive positions at a fixed time interval. This modelling of uncertainty introduces a degree of smoothing to the surface comparable to that achieved with KDEs, but without the necessity of using an arbitrary or estimated smoothing parameter. However, a 2-dimensional KDE was performed (in ArcMap, Esri ArcGIS) subsequently to improve visualisation of porbeagle spatial hotspots from the 'crawl' output. Prior to the analysis, we removed the first 2 d of data for each shark following tag deployment to account for post-tagging acclimatisation. We recognise that not all tags transmitted for the same period of time and were deployed at roughly the same position, which may create higher space-use of areas near to where the sharks were tagged. However, we consider our approach to be the best available until such time that more comprehensive PTT tagging programmes eventuate across the wider European continental shelf break.

2.4. Depth distribution analyses

Since only partial data sets are retrieved from PSATs via the Argos system (see Section 2.1), we aggregated our depth and temperature data at a minimum resolution of 60 min (using their mean) to reduce gaps in the time-series. The R package 'RchivalTag' was used to partition the data into periods of day and night, which estimates times of sunrise, sunset and nautical twilight events based on positional data and algorithms provided by NOAA. Mean daily values for both day and night periods were then calculated to investigate diurnal variations in depth distribution.

We also investigated cyclical patterns in night-time depth distribution in relation to lunar cycles using a combination of fast Fourier transform (FFT) analysis, cross correlational analysis and the Pearson correlation. FFT has been used widely in shark behaviour studies to identify rhythmic patterns, or periodicities, in vertical distribution and diving patterns within complex time-series data (Graham et al. 2006, Shepard et al. 2006, Tyminski et al. 2015). Essentially, FFT breaks down a stream of time-series data into a constituent spectrum of sinusoidal (or cosine) components of different frequencies and periodicities. The power of each periodic component is identified by the magnitude of its corresponding spectral peak in the frequency spectrum (periodogram; see Graham et al. 2006 for further details). Given the likely inherent variability in space use and behaviour between sharks, the correlation analyses were performed subsequently to substantiate the underlying relationship between lunar phase and depth distribution influencing any observed patterns in nocturnal cyclicity. For these analyses, information on lunar phase, expressed here as the fraction of the moon illuminated per day, was taken from the US Naval Observatory Astronomical Applications Department. The FFT analyses were executed using a MATLAB FFT routine (MathWorks) and were conducted for the whole time-series data and for data partitioned into periods of on-shelf and off-shelf residency where possible.

3. RESULTS

3.1. Tagging effort and tag performance

The sampled population comprised 10 female and 3 male sharks, which were between 1.32 and 2.04 m in size (total length, Table 1). Five female sharks were tagged solely with PSATs, and 6 sharks (3 male, 3 female) were tagged only with PTTs. Two females were double-tagged with both PSATs and PTTs (Table 1).

Data were not acquired for all tagged sharks, and the tags varied in performance. Of the PSATs deployed, 5 remained attached for the full programmed period (243 and 270 d), including the 2 deployed on the doubled-tagged sharks, whilst 2 detached prematurely after 7 and 156 d due to attachment failure. Between 76 and 93% of the total archived data set per tag was retrieved through the Argos system, and a complete archived data set was obtained for tag 108960 after it was retrieved from a beach off Stornoway on the Isle of Lewis, Scotland (on 4 November 2016 at 58.193° N, 6.339° W). Two PTT tags failed to transmit any data after deployment. The remaining PTTs functioned for periods between 9 and 220 d despite having the capacity for a deployment period >18 mo. Whilst at liberty, the average (±SD) number of received PTT positional transmissions ranged between 5.29 ± 4.20 and 14.62 ± 11.42 per day (Table 1). Most of these positional messages were transmitted to the satellite-borne Argos receivers at night, with peak numbers occurring at times around sunrise and sunset (Fig. 1). Our analysis revealed that this pattern was not related to diurnal patterns in satellite passes in the region (Fig. 1).

3.2. PSAT migration patterns

The total estimated distance travelled by PSAT-tagged sharks ranged between 2961 and 25 707 km for deployment periods lasting between 156 and 270 d, with a mean daily distance travelled of 62 km (range: 11–106 km d^{-1}; Table 1). The reconstructed PSAT geolocation tracks suggested that most sharks were predominantly associated with the shelf and shelf-break off northwest Ireland during the late summer/

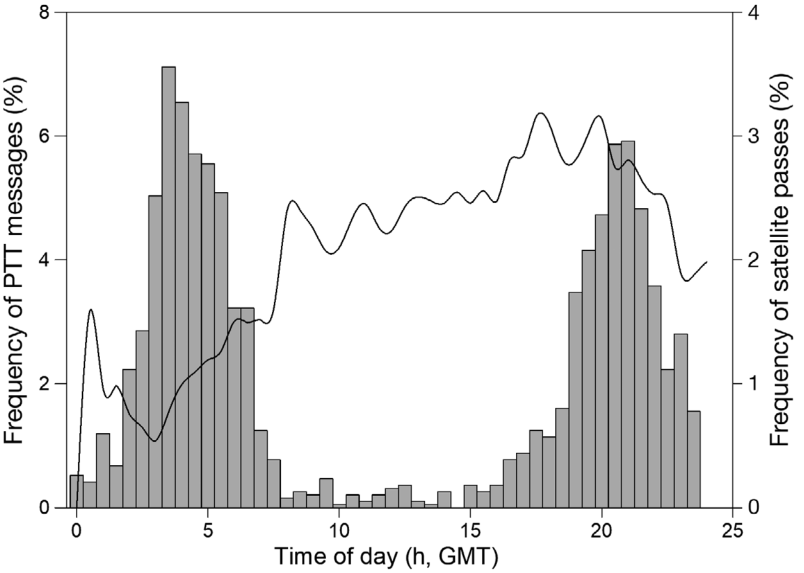

Fig. 1. Percentage frequency of platform terminal telemetry tag (PTT) messages received by polar-orbiting Argos satellites per 30 min time intervals between 10 July 2013 and 25 February 2014 (bars). Data are from 6 tagged porbeagle sharks. The percentage frequency of satellite passes at the deployment location for this period is also shown (black line)

autumn period, the exception being 1 shark (111694) that moved to waters around the Mid-Atlantic Ridge (Fig. 2). Clear seasonal migrations were apparent for all sharks, with southward migrations to either the Bay of Biscay, western Portugal, or to the Azores around November where they subsequently spent most of the winter period (December–February). Apart from the shark that moved to the Mid-Atlantic Ridge, the sharks stayed close to the shelf-break during this migration, before occupying deeper oceanic waters in winter. Following the onset of spring (March–April), 4 sharks migrated back northwards. Shark 111 695 migrated to the English Channel, whilst shark 11194 migrated northwards along the Mid-Atlantic Ridge before moving to southwest Norway via the Celtic and Irish Seas. Two sharks (108960 and 111693) migrated back to the northern coast of Ireland, close to where they were tagged. Again, the sharks were mostly associated with the western European shelf-break during this northward migration. A return seasonal migration was not apparent for sharks 39428 and 108777, possibly due to insufficient PSAT monitoring time.

3.3. PTT migration patterns

The PTTs provided a more precise view of the porbeagle distribution and movement patterns than the PSATs (Fig. 3). The total estimated distance travelled by PTT-tagged sharks ranged between 1479 and 14 640 km for deployment periods between 9 and 220 d, with a mean daily distance travelled of 82 km (range: 36–164 km d^{-1}; Table 1). The overall trends in movement pattern were broadly similar to those from the PSAT-tagged sharks, albeit over shorter time periods (Fig. 3, Table 1). The data showed that the sharks were predominantly associated with shelf-

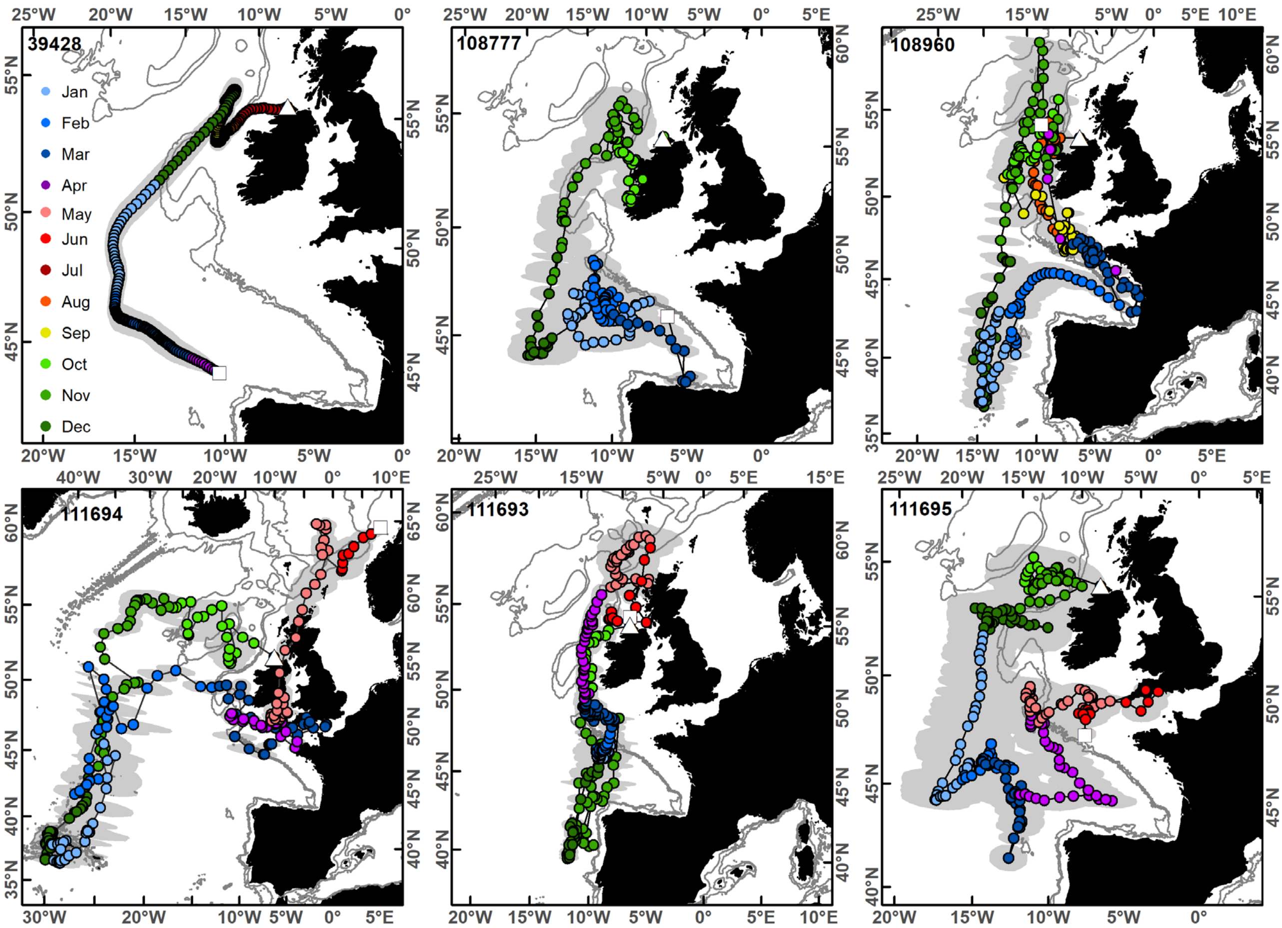

Fig. 2. Estimated geolocation tracks for 6 female sharks tagged with pop-up satellite archival tags (PSATs). Shark IDs are in the top left corner of each plot. Triangles and squares show tagging and pop-up locations, respectively. The grey-shaded area represents the 50% confidence intervals of the calculated positions. Note that PSAT 111693 and PTT 111697 were deployed on the same shark, as were PSAT 111695 and PTT 111696 (see Table 1)

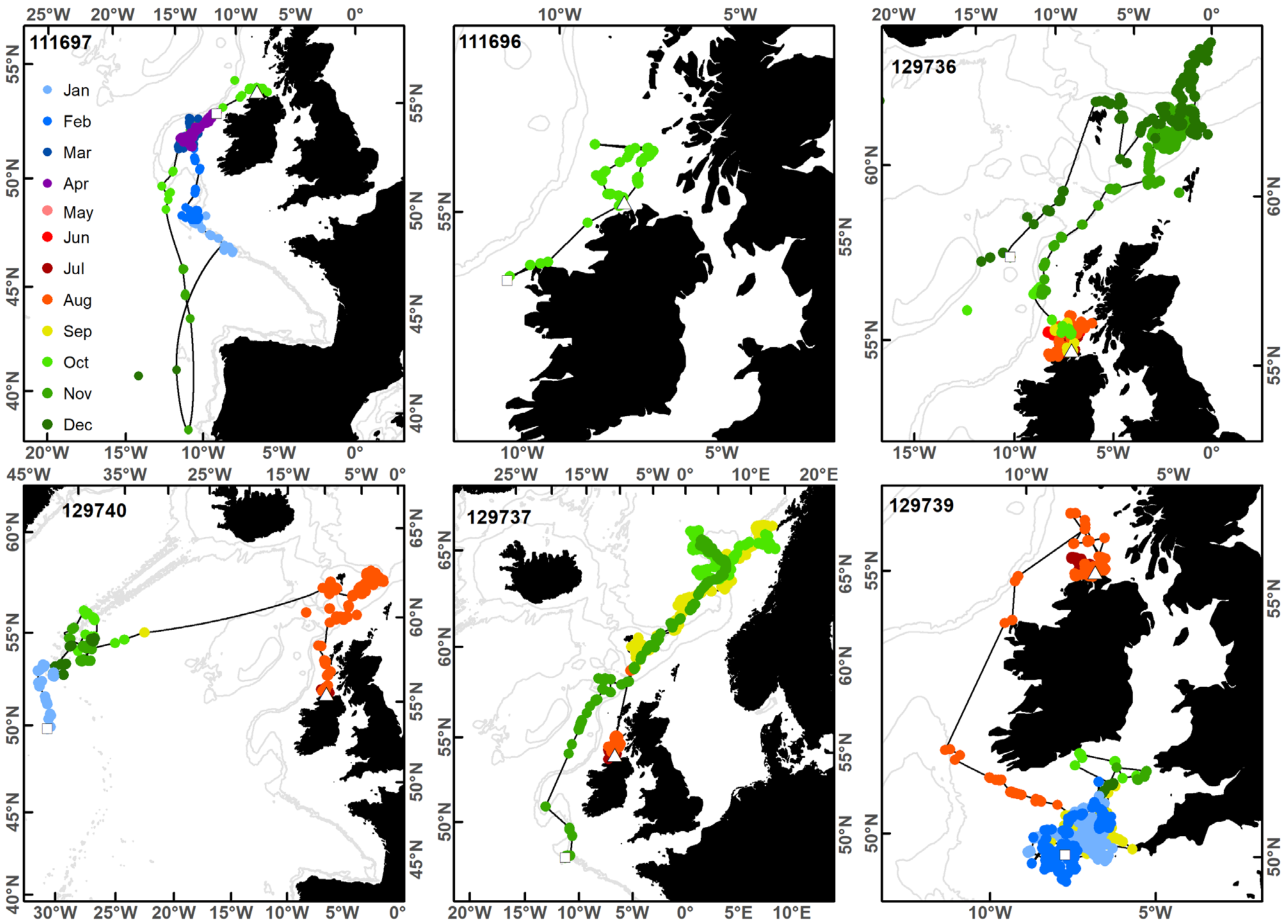

Fig. 3. Movement tracks of 6 sharks tagged with platform terminal telemetry (PTT) tags. All sharks were female except for 129740 and 129737 (shark IDs are in the top left corner of each plot). Coloured dots are the transmitted data points, and the solid lines show the modelled movement tracks. Note that modelled movement tracks between prolonged (28–50 d; Fig. S1) gaps in PTT transmissions should be treated with caution (see Section 2.3). Triangles and squares show tagging and last transmission locations, respectively. The 500, 1000 and 2000 m depth contours are also shown. Note that PSAT 111693 and PTT 111697 were deployed on the same shark, as were PSAT 111695 and PTT 111696 (see Table 1)

break and on-shelf waters around northwest Ireland during the summer period (July–August/early September). Again, clear seasonal migrations were apparent, but there were differences in behavioural patterns between individuals. Two of the PTT-tagged sharks migrated northwards to waters around the Faroe–Shetland Islands (129736 and 129740) in late summer (September–October), where they resided for ~1–2 mo before making their winter migration southwards back along the western European shelf-break (129736), or via the Mid-Atlantic Ridge (129740). Shark 129737 also migrated northwards along the shelf-break to waters of western Norway in August–September, before migrating back south to waters around the Porcupine Bank in October. In contrast, shark 129739 migrated southwards to the Celtic Sea and English Channel region in August where it resided for ~5 mo over the winter before the tag failed towards the end of February. Since the tags stopped working prematurely, it was not clear where the other sharks overwintered, although the available data suggest that shark 129740 occupied waters of the Mid-Atlantic Ridge during this period.

The data set was small for shark 111696, although the available data suggest a possible southward migration along the Malin Shelf close to Ireland, which is consistent with less accurate observations from the concurrent PSAT data deployed on this shark (111 695; Fig. 2). The movement patterns derived from PTT 111697 and PSAT 111693 on the other double-tagged shark were broadly similar during congruent attachment times, with a southward winter migration and northward return migration in spring, although the degree of accuracy on the reconstructed PSAT track was much lower and positions were more spatially variable (by approximately 50–500 km; Fig. S2 in the Supplement).

3.4. Site fidelity

The available PTT tracks showed high variability in movement patterns and space use between individuals around the northeastern European shelf-break during the late-summer to spring period (Fig. 4). All 6 sharks were highly migratory and, although most individuals frequented waters around the shelf-break at some stage, there was little temporal and spatial overlap between individuals across their wide migratory range. However, aside from these long-distance migrations, the sharks exhibited a degree of site fidelity for the region between the northern coast of Ireland and the Scottish Outer Hebrides in summer and autumn. In this region, some sharks remained resident for up to ~1 mo prior to their autumn–winter migrations where there was spatial and temporal overlap between 4 individuals between July and August 2012. The Celtic Sea also appeared to be an area of extended residency (~5 mo, late August to late February) for one shark, and waters around the Porcupine Bank and Bight were occupied for periods between ~2 and 6 wk by another shark in late winter and spring (February–April).

3.5. Depth distribution, habitat and diving behaviour

All sharks had a broad vertical distribution between 0 and 800 m and a temperature range between ~5 and 20°C (Fig. 5). Although there were distinct variations in diving behaviour between individuals across the time-series, there was a clear seasonal pattern in the depth distributions of all sharks whereby they occupied the shallower on-shelf waters above 50–100 m in summer (May–October) and then transitioned to the deeper off-shelf waters below 200 m in late autumn and winter (November–March). The range of vertical movement across the water column was greatest during winter, with frequent migrations from depths between 50 and 600 m. The deeper residency depths were most likely associated with local bathymetry at this time. All sharks undertook prolonged periods where they seldom occupied surface waters above 50 m during the winter. This was particularly evident for the shark that occupied the Mid-Atlantic Ridge waters around the Azores (111 694) and for shark 111 695 that overwintered in waters to the west of the Bay of Biscay.

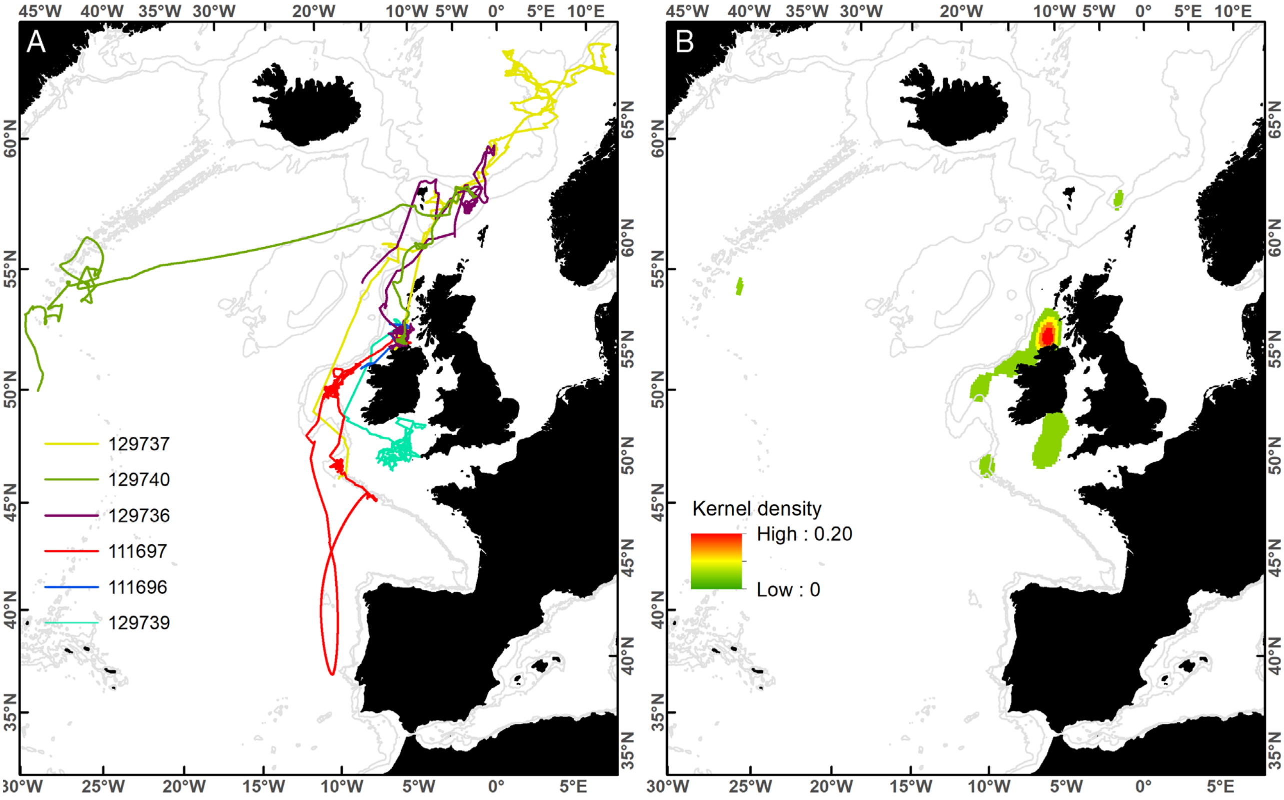

Fig. 4. (A) Movement tracks of all sharks tagged with platform terminal telemetry (PTT) tags combined and (B) a kernel density estimate plot the of percentage time spent per 0.2° × 0.2° gridded area for all PTT-tagged sharks collectively

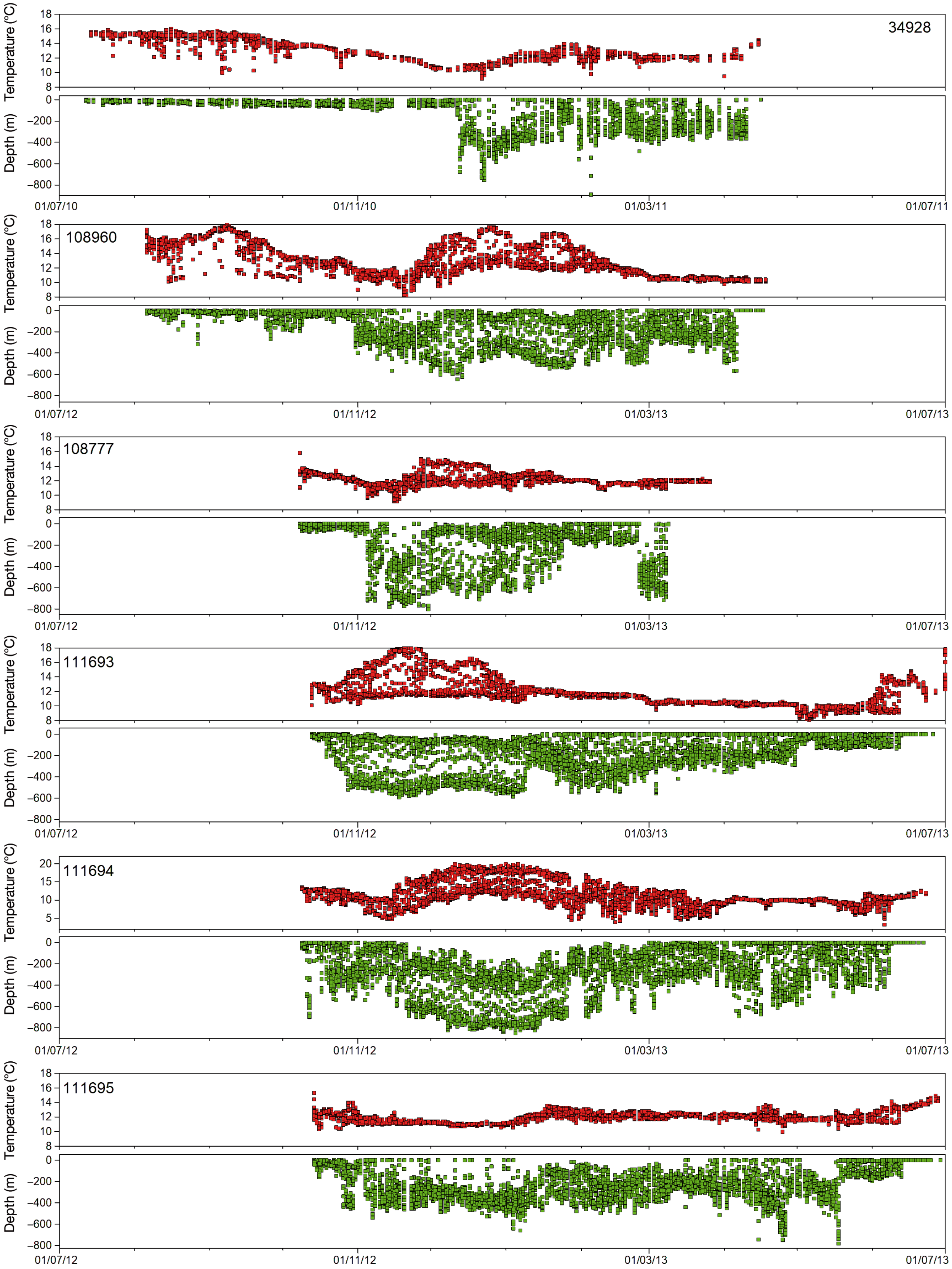

Fig. 5. Time-series of depth (green) and temperature (red) for sharks tagged with pop-up satellite archival tags. Data are at a 60 min resolution. Shark IDs are in the top left or right corner of each temperature plot

Across their seasonal migrations and transitions from on-shelf to oceanic habitats, the sharks transited through both mixed and stratified waters (Fig. 5). The seasonal decline in shelf and near shelf-break water temperatures was apparent between July and mid-November during the sharks' southward (34 928, 108 960 and 108 777) and westward (111 694) migrations to latitudes lower than ~50° N, whereupon ambient water temperatures subsequently increased, and most sharks dived through strongly stratified waters typical of oceanic habitats. Sharks 34 928 and 111 695, which remained longer at latitudes above ~50° N, remained predominantly below the thermocline and seldom occupied the surface layers (0–50 m) during their migrations and winter residency at depth. Interestingly, there was evidence that deeper winter diving behaviour was associated with higher water temperatures and greater thermal stratification, particular for sharks that reached waters below ~42° N (108 960, 11 193 and 111 694). The seasonal decline in surface waters and the breakdown of the thermocline in the overwintering habitats was apparent between January and March for most sharks as they returned northwards.

There were distinct day–night differences in the daily mean depth distribution of each shark following their seasonal transition from on-shelf to oceanic habitats (Fig. 6). Whilst the sharks were on-shelf during summer and autumn (July to November), they occupied similar mean depths within the upper ~50 m during both day and night. However, the sharks resided substantially deeper (by ~200–400 m) in the water column during the day than during the night following their movement to oceanic waters around November and December. The extent of this daily vertical separation decreased with the onset of spring (around March), as the sharks migrated north and back up the shelf break towards their on-shelf summer habitats. When the sharks occupied thermally stratified waters, these diurnal vertical movements corresponded to diurnal patterns in mean daily temperature, with temperature maxima occurring at night during residency in the warmer surface layers, and temperature minima occurring predominantly during the day when the sharks resided in the cooler deep layers.

Our analyses also revealed that the night-time depth distributions of the sharks in the epipelagic zone (0–200 m) were closely associated with the monthly lunar cycle (Fig. 7, Table 2; Fig. S3 in the Supplement). Although there was considerable variation in nocturnal depth distribution and diving behaviour between sharks across the time-series, there were distinct periods where either deep diving events or deeper occupancy of the water column occurred around full moon periods for all sharks. In contrast, shallower depth distributions occurred consistently around new moon periods. These circalunar patterns were consistent over periods of between 3 and 9 mo and were apparent in both on-shelf/shelf-break and off-shelf waters, in different seasons (summer–autumn, winter and early spring) and in different regions of the northeast Atlantic. Furthermore, FFT analysis revealed periodicities of between ~25 and 31 d (but predominantly around 28–29 d) in the nocturnal depth distribution time-series of each shark, approximately the same periodicity of a complete lunar cycle (~29 d: new moon to full moon). Cross-correlation analysis also revealed a significant ($p < 0.05$) correlation between brighter moon phase and deeper depth distribution for all sharks (Table 2), substantiating the circalunar trends within the variable data.

4. DISCUSSION

4.1. Migration patterns

Our study showed that porbeagles undertake large-scale (1479–25 707 km) seasonal migrations in the northeast Atlantic. Despite considerable inter-individual variation in both their horizontal and vertical space use, the emerging common pattern is that porbeagles inhabit waters around the northern European shelf/shelf-break in summer and autumn (July–October), particularly the regions north of 52° N around Ireland and western Scotland, but also extending farther north (>62° N) to the Faroe–Shetland Islands and sub-Arctic waters off Norway. Following the onset of winter (November–December), there is a clear southward migration towards waters below 43° N, particularly to regions around the Bay of Biscay, Portugal, Maderia and the Azores, where they overwinter in oceanic waters before returning northwards in spring (March–April). The European shelf-break appears to be a common highway for these seasonal migrations, although they may extend westwards to the Mid-Atlantic Ridge, which also appears to be an important habitat and migration pathway. These results are broadly congruent with previous porbeagle tagging studies in the region, based on relatively small numbers (n < 15) of tags deployed around Ireland, Bay of Biscay and Norway (Saunders et al. 2011, Biais et al. 2017, Bortoluzzi et al. 2024). Furthermore, our results are consistent with those from the southern hemisphere, where porbeagles also undertake north–south migrations to

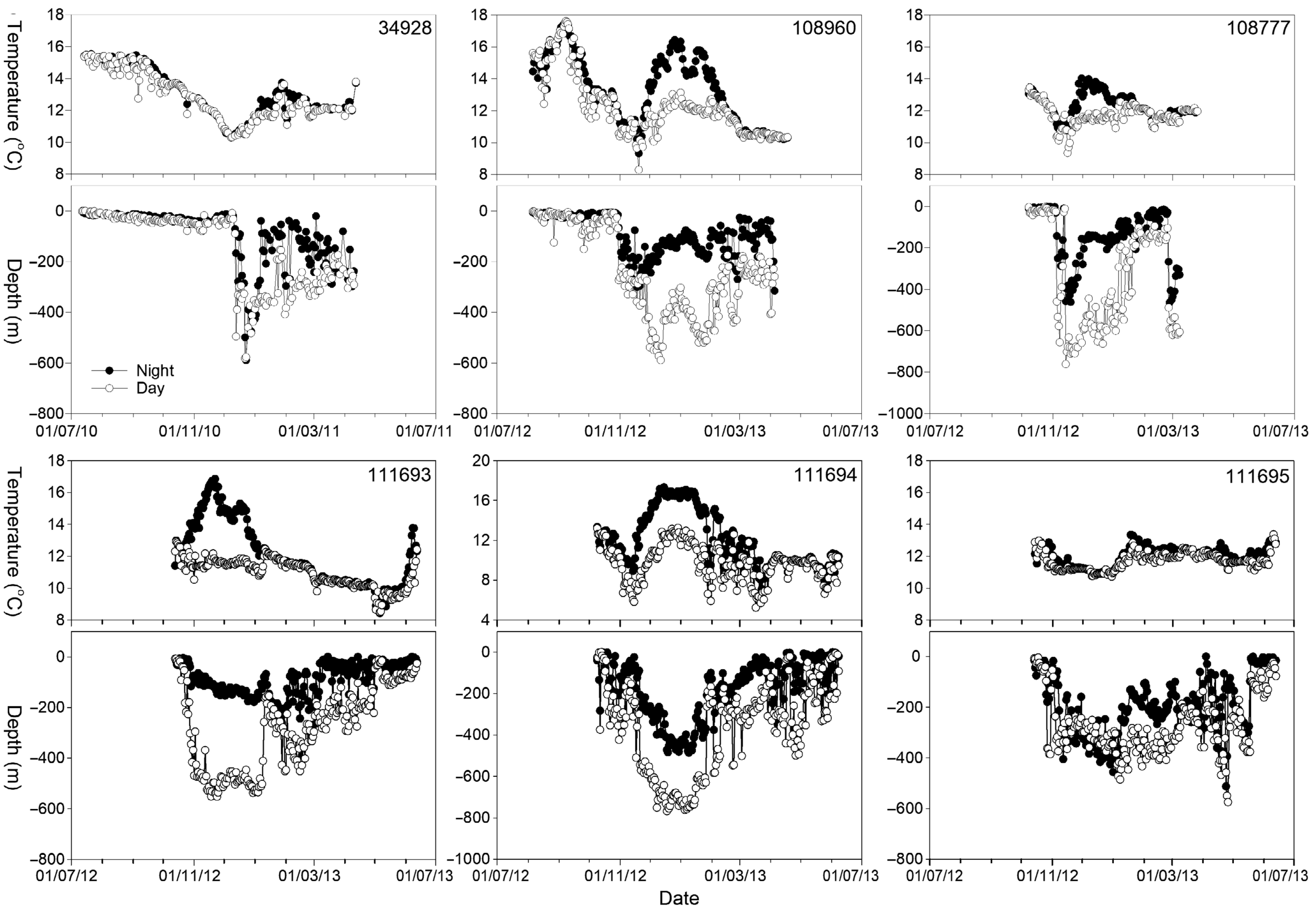

Fig. 6. Time-series of mean depth and mean temperature partitioned by day (white dots) and by night (black dots) for sharks tagged with pop-up satellite archival tags between 12 July 2010 and 14 June 2013. Shark IDs are in the top right corner of each plot

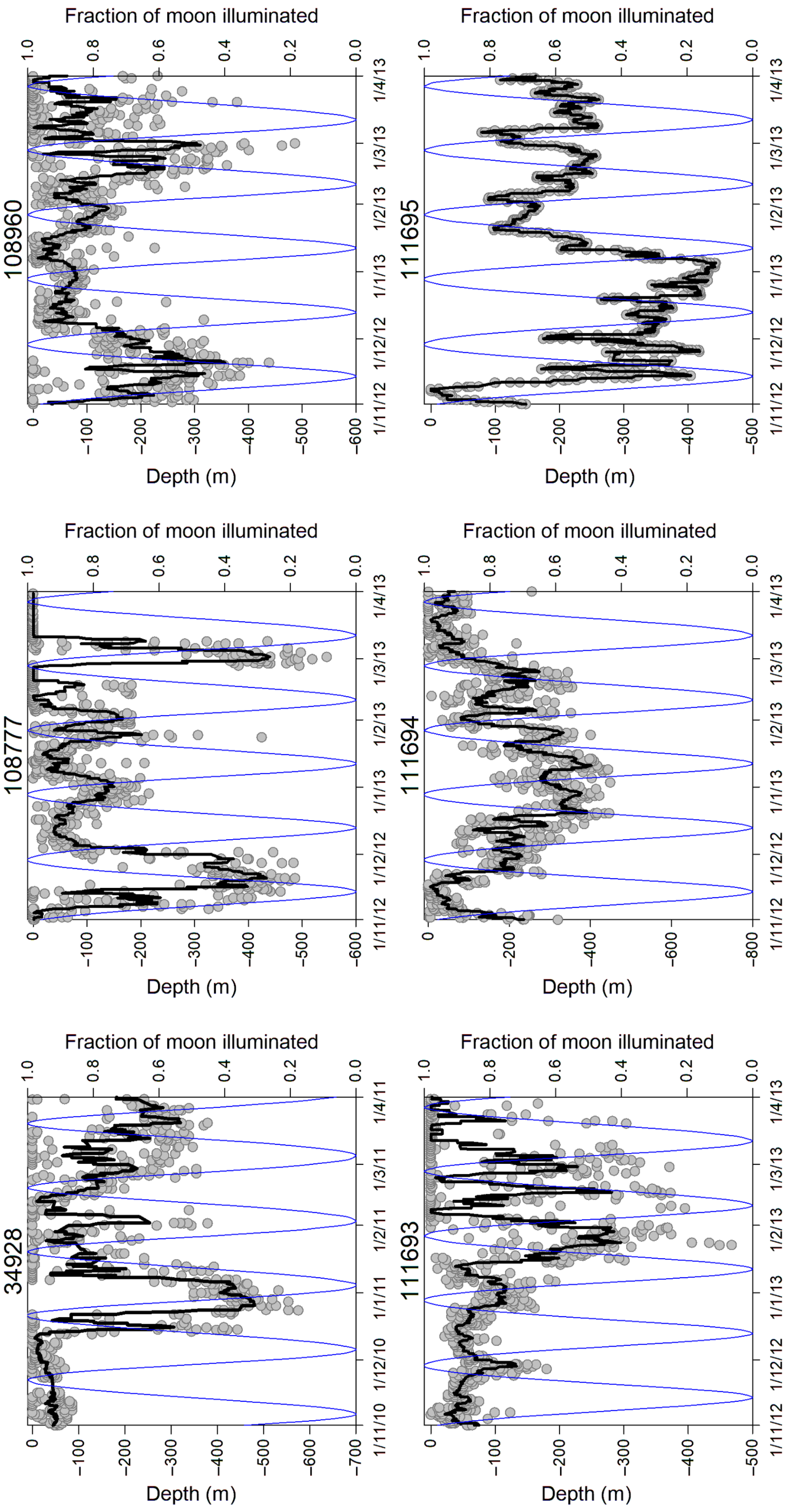

Fig. 7. Examples of changes in the nocturnal depth distribution of 6 porbeagles (grey dots) in relation to the lunar cycle (blue line) between 1 November 2010 and 30 April 2013. The thick black line is a nightly running mean of the 8 hourly depth distribution points per day. The lunar cycle is expressed as the fraction of moon illuminated per day. See Fig. S3 for the full time-series

occupy lower latitudes in winter than in summer (Francis et al. 2015), and with results from the northwest Atlantic where east—west migrations between summer coastal habitats and oceanic winter habitats are apparent (Skomal et al. 2021).

Similar migratory behaviour is also apparent for other lamnid shark species. For example, the salmon shark *Lamna ditropis*, which is the North Pacific counterpart to the porbeagle, undertakes long-distance (>2000 km) seasonal migrations between oceanic waters and the productive Alaskan coast (Weng et al. 2005), whilst the shortfin mako *Isurus oxyrinchus* likewise migrates (>2500 km) between temperate and tropical habitats in the western North Atlantic (Vaudo et al. 2016, Gibson et al. 2021). Similarly, return seasonal migrations have been reported in different parts of the globe for the lamnid white shark *Carcharodon carcharias* (Bonfil et al. 2005, Jorgensen et al. 2010, Skomal et al. 2017, Bruce et al. 2019, Bastien et al. 2020, Franks et al. 2021) and the non-lamnid tiger shark *Galeocerdo cuvier* (Lea et al. 2015, Ajemian et al. 2020) and oceanic whitetip shark *Carcharhinus longimanus* (Howey-Jordan et al. 2013).

Interestingly, Biais et al. (2017) reported frequent annual return migrations and site fidelity for porbeagles in waters around the Bay of Biscay between late winter and spring (February—June), but little

Table 2. Summary results for analyses of porbeagle depth distribution in relation to the lunar cycle. For each shark, the periodicity (d) in the 1 h resolution nighttime depth data was identified by fast Fourier transform (FFT) analysis. A cross-correlation analysis was also undertaken between time-series of mean nightly depth distribution and the fraction of the moon illuminated at midnight per day for each shark. Lags: number of cross-correlation lags; CF: Pearson correlation coefficient. Statistical significance is indicated with asterisks (*$p < 0.05$, ***$p < 0.001$)

Shark ID	Approx. period	Main location	Main habitat	FFT periodicity (d)	Lags (d)	CF	df	*t*	Significance
34928	Jul–Apr	NW of Bay of Biscay	Off-shelf	28.5	3	−0.18	197	2.58	*
108777	Oct–Apr	NW of Bay of Biscay	Off-shelf	29.0	0	−0.20	158	2.48	*
108960	Aug–Nov	West of Ireland	On-shelf/shelf-break	29.3	0	−0.31	58	2.31	*
108960	Dec–Apr	West of Portugal	Off-shelf	29.0	0	−0.14	181	−1.9	*
111693	Oct–Jun	SW to NW Bay of Biscay	Off-shelf	31.6	0	−0.25	249	4.11	***
111694	Oct–Apr	Mid-Atlantic Ridge	Off-shelf	25.0	0	−0.15	252	2.31	*
111695	Jan–Jun	NW of Bay of Biscay	Off-shelf	28.5	0	0.38	137	4.85	***

evidence of site fidelity in more northern regions (>52° N) in summer and autumn (June–October). Indeed, porbeagles tagged around the Bay of Biscay rarely frequented the coastal waters around Ireland and Scotland during their summer migrations, instead migrating either northwards or westwards through more oceanic waters. This is in contrast with our study, where there was evidence of porbeagle site fidelity and occasional near-annual return migrations to the shelf waters around Ireland during this time, particularly in regions off the north Irish coast and Celtic Sea. This contrast suggests a degree of spatial structuring of the northeast Atlantic porbeagle population. Such site fidelity in the region is consistent with reports from both recreational anglers and mark-and-recapture studies around Ireland that show relatively frequent captures of juvenile to earlier adult porbeagles during summer, including marked individuals caught near their initial tagging sites (albeit after several years) (Stevens 1976, 1990, Cameron et al. 2019). Evidence of coastal site fidelity in the Irish Sea, Celtic Sea and English Channel during summer was also reported for 3 satellite-tagged porbeagles (over ~3 mo periods) by Pade et al. (2009). Collectively, the available data suggest that porbeagles exhibit complex and dynamic patterns in site fidelity across their broad migratory range that requires further investigation across all demographic components of the population. Nevertheless, our study further demonstrates that, in addition to the oceanic habitats around the Bay of Biscay (Biais et al. 2017), the coastal and shelf-break waters around Ireland are important habitats for the species, particularly in summer, and they are regions where future research focus is required.

The observed patterns in migrations and site fidelity are most likely related to feeding and reproductive activity, as discussed previously for porbeagles (Saunders et al. 2011, Chapman et al. 2015, Biais et al. 2017, Skomal et al. 2021, Colonello et al. 2024) and other lamnid shark species (Weng et al. 2005, Jorgensen et al. 2010, Vaudo et al. 2016, Franks et al. 2021, Gibson et al. 2021). Our data support the general notion that porbeagles in the northeast Atlantic undertake seasonal migrations to waters along the northern European shelf to the sub-Arctic to exploit the abundant concentrations of Atlantic herring *Clupea harengus*, Atlantic mackerel *Scomber scombrus* and blue whiting *Micromesistius poutassou* that occur in shelf-break and coastal waters in these regions during spring–summer (Molloy 2004, 2006). In doing so, porbeagles frequently return annually to similar locations of predicable food abundance, although the northeast Atlantic population is probably widely distributed and formed of components that return to spring–summer feeding areas that are widely separated (Biais et al. 2017). Seasonal changes in temperature may partly facilitate these migration patterns, as hypothesised previously (Campana & Joyce 2004). It is also possible that there are sex-related differences in migration behaviour, as proposed for other pelagic species (Lea et al. 2015, Franks et al. 2021), although there are currently insufficient data from male porbeagles to examine this (Francis et al. 2015, Biais et al. 2017). Our data suggest that residency time in these food hotspots around Ireland and Scotland appears to be around 1 to 2 mo before undertaking further migrations northwards up to the onset of autumn, before returning to their overwintering, off-shelf habitats south of the Bay of Biscay where deeper food resources associated with the deep-scattering layer (DSL) may be predictably available at this time. Zooplankton and nekton, as well as their predators such as dolphins and tunas, appear to be particularly abundant around the seamounts and bathymetric features of the Mid-Atlantic ridge and around the Azores (Cascão et al. 2017), whilst the Bay of Biscay region is an important region for other predators such as bluefin tuna *Thunnus thynnus*, albacore tuna *T. alalunga* and blue sharks *Prionace glauca* that feed on prey similar to that of porbeagles (Queiroz et al. 2005, Stokesbury et al. 2007, Cosgrove et al. 2008, 2014, Vandeperre et al. 2014, Ferter et al. 2024). Site fidelity may also be linked to reproductive behaviour (Jorgensen et al. 2010, Chapman et al. 2015), but for most lamnid sharks, including porbeagles in the northeast Atlantic, the evidence for mating and parturition sites currently remains unclear and further data are required. Nevertheless, it has been hypothesised from limited observational information from the northeast Atlantic that the Celtic Sea—Bay of Biscay region and the northern coast of Ireland may be important parturition sites for porbeagles between May and June (Biais et al. 2017, Cameron et al. 2019). Further satellite tagging studies of mature and gravid females may cast new light on the role of reproduction in porbeagle site fidelity behaviour.

4.2. Tag performance

Our study further demonstrates the relative merits of PSATs and PTTs for monitoring the spatial ecology of porbeagle sharks (Pade et al. 2009, Saunders et al. 2011, Biais et al. 2017, Bortoluzzi et al. 2024). PSATs collect both horizontal and vertical movement data, although the error bounds on the positional data are large due to the predominantly deep residency of the porbeagles which results in unreliable light-based geolocation data. This uncertainty restricts studies of small-scale movement patterns and site fidelity, despite the application of movement models to reconstruct movement tracks and reduce errors. However, PSATs perform well over sub-annual time scales, with a relatively high success rate in tag attachment and subsequent data acquisition (Biais et al. 2017, present study). In contrast, PTTs provide locations at a finer spatiotemporal resolution and higher accuracy, particularly when used in conjunction with state-space models, but over shorter deployment periods in our study (<9 mo). Tag performance over the winter period was poor for our PTTs, which may have been due to mechanical damage (e.g. detachment of the fin tag mountings or antennae breakage) due to additional drag stress when the sharks entered their deep-water habitats and migrated more extensively through the water column. Alternatively, biofouling may have been responsible for tag failure. Bortoluzzi et al. (2024) reported better success rates with their more contemporary PTTs (Wildlife Computer SPOT 258 tags) and better anti-biofouling measures, with deployments of around 1 yr, although only 2 tags were used in that study, and the sharks occupied predominantly coastal and shelf-break waters, including during winter. Nevertheless, functioning PTTs are likely to provide a more limited view of porbeagle movement patterns in the winter when fewer and more temporally disparate transmissions are obtained due to predominantly deep-water residency at this time. State-space models improve the accuracy of interpolations between gaps in PTT fixes, but estimates may become less reliable over long periods (>15 d; Fig. S1) in winter.

For future applications, the acquisition of data over time scales >1 yr will be crucial for assessing the extent of return migrations and site fidelity in porbeagles (Biais et al. 2017). To date, the current generation of satellite tags appears to fall short of this requirement and there remain uncertainties regarding the extent to which porbeagles remain in the locations where they were initially tagged following their return migrations. Since deployment times are mostly limited to timescales <1 yr, the timing of porbeagle tagging fieldwork is an important consideration for future research efforts. For example, most porbeagle tagging in the northeast Atlantic has been constrained to the summer months in coastal regions, such that the following early spring to summer period is sparsely covered due to early tag expiration or premature pop-up. This is particularly true for tagging efforts off Ireland. Extending fieldwork to periods closer to the winter, and to other locations across the migratory range of porbeagles (e.g. Bay of Biscay, Azores, Maderia and NW Africa), may help increase our window of observation into the spatial ecology of porbeagles off Ireland in the future. Such efforts could also help overcome potential issues with 'release effects' associated with concentrated tagging efforts in limited porbeagle hotspot areas, although the acquisition of sufficiently comprehensive, randomised and temporally congruent data to address this remains challenging at the scale of the European Shelf break. Nevertheless, our study supports the notion of Bortoluzzi et al. (2024) that the use of both PTTs and PSATs, particularly when used in tandem, provide crucial data for monitoring the spatial ecology of porbeagle sharks in a conservation and management context.

4.3. Diurnal and seasonal depth distribution

Consistent with previous studies, there was a distinct day–night difference in porbeagle depth distribution that was consistent with diel vertical migration (DVM) behaviour (Pade et al. 2009, Saunders et al. 2011, Biais et al. 2017). Although there are regional and inter-specific differences, such behaviour is relatively common in pelagic sharks across the globe, particular in lamnid species (Andrzejaczek et al. 2022). Our study further compliments the existing knowledge base by demonstrating that DVM appears to be seasonal, occurring more frequently, and over a wider depth range, in their offshore winter habitat than during their residency in more coastal habitats. Furthermore, porbeagles resided deeper in the water column during winter than in summer and seldom occupied the surface layers during this time. With the onset of spring, the extent of DVM and range of porbeagle overall depth distributions decreased as they appeared to migrate back up the shelf-break to their summer coastal habitat. These changes in distribution pattern and behaviour could be a response to spatio-temporal changes in vertical distribution and community composition of planktivorous fish prey across seasons and habitats (Carey & Scharlod 1990, Sims et al. 2005, Benoit-Bird et al. 2009). For example, the depth distribution and DVM of prey, such as mackerel and herring, may be constrained by bathymetry in the summer when they aggregate in the more productive coastal waters (Parrish & Saville 1965). In deeper off-shelf waters, diel vertically migrating fish, particularly mesopelagic fish (e.g. Myctophidae) tend to be associated with the DSLs that typically occur around 300–400 m depth, which may deepen further in winter (Sutton 2013, van Haren & Compton 2013, Proud et al. 2017). Porbeagles may therefore occur deeper in the water column in winter to exploit these food resources.

This tendency appeared to be particularly so for the shark that moved to warmer waters at latitudes below ~42° N via the Mid-Atlantic Ridge, where the shark was found deeper in the water column than elsewhere, and its increased winter depth distribution seemed to be associated with increasing temperature along this southward migration. We hypothesise that the depth of the DSL (hence available food resources) decreased latitudinally (Proud et al. 2017), possibly due to temperature and a locally deeper thermocline (Palma et al. 2012), although thermal effects on porbeagle physiology during long-distance migration may also be important (Weng et al. 2005). For example, salmon sharks predominantly remain below the thermocline and seldom surface during their long-distance migrations between sub-Arctic and sub-tropical waters (spanning temperatures between ~2 and 24°C) in the North Pacific, suggesting that increased swimming activity in the cooler layers below the thermocline may be physiologically beneficial during long-distance migrations (Campana & Joyce 2004, Weng et al. 2005). Similar effects also appear apparent in shortfin makos that inhabit more tropical habitats (Vaudo et al. 2016). Congruent with observations from white sharks (Lee et al. 2021), porbeagles have been reported to be associated with fronts and certain waters masses, so it is possible that the shark in our study followed the base of the thermocline during its southward migration (Campana & Joyce 2004).

A lack of food resources in the surface layers in winter may also explain the absence of porbeagles in waters shallower than 50 m at this time. This contrasts markedly with the situation in summer, where porbeagles frequently occupied surface waters, particularly during times of dawn and dusk when there was greater tendency for individuals to swim directly at the surface with their dorsal fins out of the water (to enable PTT transmissions). This behaviour is highly consistent with that of blue sharks in the region, where 'knifing' behaviour (swimming with the dorsal fin above water) is pronounced during times of dawn and dusk (Doyle et al. 2015). It has been proposed that such behaviour may be a strategy to maximise foraging opportunities, since surface-dwelling prey are more dispersed and silhouetted by ambient light conditions during twilight periods, making individual prey more visible (Doyle et al. 2015).

4.4. Circalunar depth distribution patterns

Six porbeagles tagged in this study exhibited vertical distribution patterns and diving behaviour that was associated closely with the monthly lunar cycle. These results extend the findings of Saunders et al. (2011), who reported the same circalunar relationship for a porbeagle that migrated from northwest Ireland to the west coast of Morrocco over a ~6 mo period. Our study suggests that such behaviour is common in the species, and that it occurs over prolonged periods (up to ~9 mo) when porbeagles occupy the epipelagic waters of the northeast Atlantic, including those in both coastal and oceanic regions. Elucidating such circalunar patterns in vertical space use contributes to a better understanding of the ecological role of pelagic sharks and their exposure to anthropogenic stressors, which may aid both local and global management and monitoring strategies (Andrzejaczek et al. 2022).

Correlations between lunar phase and swimming depth have been demonstrated for several large pelagic fish and shark species. For example, swimming depths have been found to be notably deeper around the full moon for bluefin tuna (Wilson et al. 2005), swordfish *Xiphias gladius* (Carey & Robinson 1981), school sharks *Galeorhinus galeus* (West & Stevens 2001), grey reef sharks *Carcharhinus amblyrhynchos* (Vianna et al. 2013) and whale sharks *Rhincodon typus* (Graham et al. 2006). Such behaviour in porbeagles possibly reflects shifts in the vertical distribution of prey resources under different levels of lunar illumination. Porbeagle prey such as pelagic fish (herring, horse mackerel *Trachurus trachurus* and blue whiting), mesopelagic fish (Myctophidae) and squid typically undertake DVM, whereby they descend to the deep layers of the ocean during the day and ascend to the surface layers at night (Boden & Kampa 1967, Blaxter 1974). This behaviour usually occurs in synchrony with surface light intensities and is considered to be a strategy for feeding in the productive surface waters whilst minimising the risk of mortality from visually searching predators (Tarling et al. 2000, Langbehn et al. 2019). However, during full moon nights, surface light intensities are around 3 orders of magnitude higher than during new moon nights (Kaartvedt et al. 2019). Therefore, prey species may halt their upward migration at greater depths during these periods, as it is more risky for them to migrate to the surface (Benoit-Bird et al. 2009).

4.5. Conclusions

Our study improves on the existing knowledge base of porbeagle spatial ecology in the northeast Atlantic and provides data that are important for porbeagle conservation and ecosystem-based fisheries management strategies. We demonstrate further that porbeagles undertake regular, long-distance seasonal migrations that span several international fishing zones, which necessitates international coordination and cooperation for future stock assessments and conservation measures. Furthermore, our data substantiate that porbeagles either traverse or show site fidelity for regions of high commercial fisheries activity, such as blue whiting, bluefin tuna and swordfish fisheries (ICCAT 2024, ICES 2024b), where they are potentially at risk as bycatch, which also requires further consideration of such measures. Acquisition of more comprehensive fisheries bycatch data in the region will be crucial for this conservation and management effort. In conclusion, this study contributes towards a more holistic understanding of the horizontal and vertical space use by pelagic sharks that may aid management and monitoring strategies at both a regional and global scale.

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