



## Return migration patterns of porbeagle shark (*Lamna nasus*) in the Northeast Atlantic: implications for stock range and structure

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Biais, G., Coupeau, Y., Séret, B., Calmettes, B., Lopez, R., Hetherington, S., and Righton, D. 2016. Return migration patterns of porbeagle shark (*Lamna nasus*) in the Northeast Atlantic: implications for stock range and structure. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsw233.

Received 8 June 2016; revised 18 November 2016; accepted 23 November 2016.

During two surveys in 2011 and 2013, we deployed pop-up satellite archival tags (PSATs) on subadult or adult porbeagles at the Bay of Biscay shelf break. We collected data that enabled the reconstruction of nine migrations (eight females, one male) that uncover the large spatial extent of these sharks in the Northeast Atlantic. The mean duration of each deployment was 292 d, with four reaching 365 d. The reconstructions show that, after migrations that extended up to 2000 km away from the point of release, the tagged porbeagles returned to their location of tagging. All the reconstructed migrations followed the same general pattern of a migration away from the Bay of Biscay in late summer, and a return in spring the following year. The total distance of the migrations was estimated at 5000–13 000 km for PSATs deployed for a full year ( $n = 4$ ), with examples of migration to the Arctic Circle, southward to Madeira and westward to the mid-Atlantic Ridge. The observed site fidelity to the Bay of Biscay and the common migration pattern of all females provide evidence of complex spatial structure and dynamics that encompasses both the open ocean and heavily fished coastal areas, and highlights the challenge of assessing and managing the porbeagle stock in this area.

**Keywords:** habitat use, Lamnidae, migration, movement, population structure, pop-up satellite archival tag, shark, site fidelity.

### Introduction

The porbeagle (*Lamna nasus*) is a large pelagic shark found throughout the North Atlantic, between 30° and 75°N (Aasen, 1961; Compagno, 2001), and circumglobally between 25° and 60°S in the southern hemisphere, although it is absent from the North Pacific Ocean (Francis *et al.*, 2008; Semba *et al.*, 2013). Its distribution encompasses the high seas, coastal shelf, and inshore areas; porbeagles have even been reported from rivers (Matheson, 1928). They are born at 60–90 cm total length (TL) [fork length (FL) values are converted to TL in this article using the 1.12 ratio

given by Campana *et al.*, 2013], (Aasen, 1963; Jensen *et al.*, 2002), and reach 170 cm TL at 5–6-years old (Natanson *et al.*, 2002). Maximum recorded lengths are over 340 cm TL (Templeman, 1963; Kohler *et al.*, 2002), with males in the Northeast Atlantic reaching maturity at 190 cm TL and females at above 223 cm TL (Hennache and Jung, 2010). Porbeagle sharks have a fusiform body shape, providing a powerful swimming capacity and the potential for long-distance migrations. Like all lamnid sharks, porbeagles have the capacity to raise their body temperature above ambient by conserving metabolic heat (Carey and Teal, 1969),

which enables tolerance of cool waters and occupation of the relatively high latitudes where the species is found (Campana and Joyce, 2004).

Porbeagles have been exploited in Europe since the 1930s. Market demand led to the development of a Northeast Atlantic porbeagle fishery based initially in Norway (ICES, 2015a). After the Second World War, Danish vessels began to target porbeagle, and landings rose to a peak during the late 1940s. As catches declined through the 1950s, the porbeagle fishery remained predominantly Scandinavian and located in Northern European waters (Norwegian Sea, North Sea, Northwest Scotland and Faroe region) but expanded into Western European waters (Bay of Biscay, Southwest Ireland, Celtic Sea), in the early 1960s before landings declined further when the Norwegian interest in the Northeast Atlantic fishery waned (Rae, 1962). French vessels exploiting porbeagle in western European waters became the dominant source of fishing mortality in the 1970s. However, landings of porbeagle continued to decline through the 1980s and 1990s, eventually leading to concerns in the early 21st century that the North-eastern Atlantic stock was at risk. In consequence, Norway banned directed fishing for porbeagle in 2007 before the European Union prohibited all catches in 2010. However, at present, the true state of the stock still remains unknown (ICES, 2015a) because a full assessment of stock status is not possible, predominantly because abundance indices for the stock are not available at the time the fishery was at its peak (ICCAT, 2009; ICES, 2015b). Developing a greater understanding of porbeagle biology and ecology is therefore desirable.

For management and assessment purposes, two porbeagle stocks are considered in the North Atlantic (ICES, 2007; ICCAT, 2009); one to each side of the 42°W meridian. This stock separation is supported by mark-recapture experiments. In the Northwest Atlantic, tag recaptures show that movement occurs between fishing areas all along the North American coast ( $n = 209$  returns from  $\sim 2000$  releases; Kohler *et al.*, 2002; Campana *et al.*, 2013). In the northeast Atlantic, the pattern is similar, with recaptures mainly along the western European coast rather than across the ocean ( $n = 15$  returns from 165 releases, one east to west transoceanic trip reported; Stevens, 1990; Kohler and Turner, 2001; Kohler *et al.*, 2002; ICES, 2007). However, the limited number of tag recoveries does not allow an exhaustive analysis of spatial extent or migratory patterns. Furthermore, because observed movements are dependent on the distribution of fishing effort, mark-recapture data can only ever provide a limited insight into movements or distribution.

Pop-up satellite archival tags (PSATs) provide a method for collecting direct and detailed evidence of the migrations and distributions of species that are not fished across their geographic range, or which are tagged and recovered only rarely. This technology is now a routine research tool (e.g. Block *et al.*, 2011). PSATs were first deployed on porbeagle in the Northwest Atlantic from 2001 to 2008 (Campana *et al.*, 2010). In the Northeast Atlantic, PSATs have been deployed in 2007 in the Celtic Sea (Pade *et al.*, 2009) and off Northwest Ireland in 2008–2009 (Saunders *et al.*, 2011). In the southern hemisphere, PSATs have also been deployed off New Zealand (Francis *et al.*, 2015). Overall, these deployments have shown that male and female porbeagles may undertake large migrations in the open ocean, whether immature, sub-adult or mature. However, the time at liberty for tagged porbeagles rarely reaches one year (only one tag, deployed on a shark in the Northwest Atlantic, has reported 348 d after release, the other deployments are

10 months long or less) and, consequently, the annual migratory cycle is not well understood for porbeagles in any part of their geographic range. Furthermore, despite the value of the PSAT deployments in the Northeast Atlantic, the number of individuals from which data have been collected is particularly limited ( $n = 4$  and 3 from Pade *et al.*, 2009 and Saunders *et al.*, 2011 respectively), and the duration of the observations, at fewer than 4 months, is relatively short. Tagged individuals have also generally been small, falling in the range 102–207 cm TL (91–185 cm FL), including three mature males but no mature females, leaving an important gap in our knowledge of the seasonal movements or the extent of adult migrations.

To address this gap, we undertook a PSAT tagging programme to study the migrations of adult porbeagle, with an emphasis on mature females. Between 2011 and 2013 we tagged 13 large porbeagles (1 male and 12 females 197–265 cm TL) in the region of the Bay of Biscay. Our results show that porbeagles migrate widely across the Northeast Atlantic, but also that they exhibit site fidelity, a behaviour that is shown for the first time for porbeagle sharks.

## Material and methods

### Shark tagging

Two tagging surveys were carried out in 2011 and 2013 using a chartered commercial long-lining vessel. The fishing area was the Bay of Biscay shelf break between latitudes 46°N and 48°N. The goal of each survey was to deploy PSATs on females preferably larger than 230 cm TL (a length at which they are likely to be reproductively mature; Hennache and Jung, 2010). Pelagic longlines were used to catch porbeagles; line lengths and set durations were limited to ensure hooked sharks were in the best possible condition for tagging. The long-line was set at 200–300 m depth at locations over the continental slope (700–3600 m seabed depths).

To achieve the best tag attachment, all sharks were brought on board for tagging. Sharks were supported on a foam block, their eyes were shielded with a damp towel, and their gills were irrigated with running seawater at all times during the procedure. Wildlife Computers Mk10 or MiniPat (both of which record light intensity, depth and temperature) were attached to each shark by inserting a urethane anchor (Wildlife Computer's "Wilton dart") about 10 cm into the pterygiophores below the dorsal fin and at one-third of its length from the posterior end. A stainless steel anchor attached to a nylon ring was also inserted behind the dorsal fin to bridle the tag and stream it alongside the body. Tags were programmed to release after 365 d (for large females) and after 190 d (for the male) with an aim to obtain information on potential parturition and mating locations and on the relevant locations and times for future surveys. Depth ( $\pm 0.5$  m), temperature ( $\pm 0.1$  °C) and light intensity were recorded every 10 s. The data were internally binned by 6 h (7 PSAT), 12 h (one PSAT in 2011) or 24 h (one PSAT in 2011 with depth time series generation each 10 min enabled) intervals. PSAT were programmed to release from the shark if a constant depth ( $\pm 2.5$  m) was maintained for 4 d, indicating mortality due to the absence of depth change. Shark tagging was conducted in accordance with the guidelines of the Animal Care Committee of France.

### Track reconstruction

We aimed to estimate one location per day that best explained the daily observed light intensity, depth and temperature data

recovered from the PSAT (number of days with observations in [Supplementary Table S1](#)). The process relies on a state-space formulation of the tracking problem. In essence, the daily location is the unknown state of a dynamic system governed by a dynamic model (random walk), which means that the sequence of daily state follows a Markov chain. This (hidden) location is directly linked by an observation model to the light, depth, and surface temperature records.

Within this framework, the effective resolution resorts to a discretization of the state space in grid cells ( $0.1 \times 0.1$  degrees) to infer the probability density of the (hidden) location, given the sequence of observations. This approach was first introduced in the field of fish tracking by [Thygesen et al. \(2009\)](#) and it is known as Grid Filter in the geolocation literature ([Neilson et al., 2014](#)). It is a recursive Bayesian estimation technique, in line with the widespread Kalman filter (e.g. [Nielsen et al., 2006](#); [Royer and Lutcavage, 2009](#)). In this Bayesian filtering, the daily measurement assimilation is a two-step process. At each sampling time, the method performs a position prediction step by numerically solving the advection-diffusion equation for the 2D probability of animal's presence. A position update step is then performed to combine the predicted probability density with information recorded by the tag to produce the posterior distribution of the animal. Thus, at each time step the probability of presence of the fish is obtained on each point of the grid. The daily location is computed as the average of the grid locations weighted by their probability. The track of each tag is obtained by connecting the daily position estimates. The standard deviation of a daily location estimate in 2D representations is an ellipse. The orientation angle, the semi-major and semi-minor axis lengths of the ellipse are then deduced from the error covariance matrix of the daily distribution. We implemented a modified version of the geolocation method described in [Neilson et al. \(2014\)](#). First, the positions update step uses the raw locations derived from light intensity as the observed data (obtained with the Wildlife Computers Software "GPE2"). The update step is constrained by the bathymetry as in [Thygesen et al. \(2009\)](#) (i.e. the depth at the updated location must be greater than the daily recorded maximum depth) but also by the satellite-based sea surface temperature SST (by minimizing the deviation of this SST at the updated location from the daily recorded SST). Additionally, the first location of the track is assumed to be the deployment position of the tag and the last location is the pop-up position provided by ARGOS. If the detachment of the tag was premature, the tag will drift 4 d until reporting its position, according to PSAT parameter settings.

The tracks were estimated using the same model parameters for all the PSATs: (i) the diffusion coefficient of the random walk model is set empirically to  $1000 \text{ km}^2 \text{ d}^{-1}$  because this value minimizes the SST root mean square error (satellite observed vs tag recorded) calculated along the track (a posteriori error), (ii) the standard deviation of the raw light-based location of the update step is set to  $1^\circ$  in longitude and  $3.5^\circ$  in latitude and (iii) the standard deviation of the error in SST is set to  $0.5^\circ \text{ C}$  (a priori error). The satellite-based sea surface temperature at the updated location is obtained from Ostia (Operational Sea Surface Temperature and Sea Ice Analysis, see [http://ghrsst-pp.metoffice.com/pages/latest\\_analysis/](http://ghrsst-pp.metoffice.com/pages/latest_analysis/) – spatial resolution: 0.05 degrees – temporal resolution: daily) and the depth is given by the ETOPO02 bathymetry model (see <http://www.ngdc.noaa.gov/mgg/global/etopo2.html> – spatial resolution: 2 min).

## Results

Despite setting longlines at locations where large porbeagles had been reported in commercial catches in previous years, catching and tagging females larger than 230 cm TL proved to be difficult. In total, eight large females (197–265 cm TL) and one large male (199 cm TL) were tagged ([Table 1](#)), for which tags were retained for over 4 months (mean 292 d; range 128–365 d). In addition, three porbeagles were tagged from which long-term data were not recovered; one porbeagle was captured, while two other tags detached prematurely (shark fate unknown). One tag did not transmit any data. The ratio of long-term tag deployments to premature release shows that our deep and precise insertion of the PSAT anchor and the addition of a ring to bridle the tag alongside the body was extremely successful.

### Migrations and daily horizontal movements

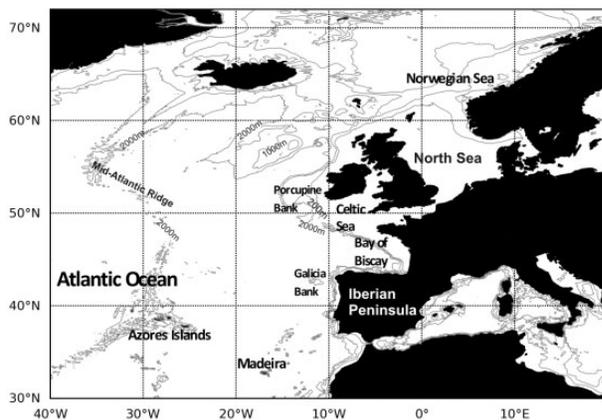
Reconstructions of migrations showed that porbeagles migrated to a range of distant locations; from the Bay of Biscay, northward to the Arctic Circle, southward to Madeira and westward to the Mid-Atlantic Ridge ([Figures 1 and 2](#) and [Supplementary Material S1](#)). The confidence limits of the most probable tracks are relatively large (the mean width of the 50% confidence interval area is  $\sim 250$  km). However, despite the low precision, the direction and extent of the migrations were clear.

The mean daily distance travelled was 28 km, ranging from  $<1$  km to nearly 200 km ([Figure 2](#)). The total estimated travel distance ranged between 3800 and 13 400 km ([Table 1](#)), with a maximum distance of  $\sim 2400$  km between release position and tag pop-up. However, when the pop-up time of the tag was 365 d after release (four of the nine sharks), the tags reported a pop-off position within 400 km of release; two of these were within 50 km.

In general, sharks at liberty for 9 months or more showed a movement back towards the point of tagging, strongly suggesting a spring (April–June) return to the Bay of Biscay. The pattern of this round-trip was similar between sharks, as follows. They resided at the shelf break of the Bay of Biscay after tagging or when returning the next year (April–September), where daily movement rates were often low. In August–October, all but one (shark no. 7) of the female porbeagles moved in a northwesterly migration along the shelf break to West Ireland (generally on the west side of the Porcupine Bank), before eventually reaching a latitude of  $54\text{--}55^\circ \text{ N}$ . This migration from the Bay of Biscay was generally rapid, but it was sometimes punctuated by short-term residences on the continental slope (sharks nos. 3, 5, 9 on or near Porcupine Bank, no. 8 in the West of Brittany) or an incursion on the continental shelf (no. 6). Sharks nos. 1 and 2 undertook this northward migration slightly earlier than others, and were located to the west of Scotland in August. From this latitude, two routes were identified. Some porbeagles (nos. 1, 2, 3, and 9) travelled northeast to the West of Scotland, the Faroe region, the North Sea or the Norwegian Sea, remaining in residence for up to 5 months. Others (nos. 4–6) adopted a general westerly direction, reaching the mid-Atlantic Ridge, where they stayed for up to 6 weeks. At the end of the autumn period and beginning of winter, all sharks turned to the south. The rate of movement was rapid in some cases (sharks nos. 4 and 9), with sharks eventually reaching latitudes as far south as  $33^\circ \text{ N}$  (shark no. 3 close to Madeira) or  $36^\circ \text{ N}$  (shark no. 4 in Azores region) between mid-February to the beginning of April. A

**Table 1.** Tagging summary for the nine tagged porbeagles used for track reconstructions.

Shark	Sex	TL (cm)	FL (cm)	Tagging Date	Tagging Lat. (°N)	Tagging Long. (°W)	Pop-up date	Days at liberty	Tagging to pop-up distance (km)	Estimated mean daily move (km)	Estimated trip length (km)
1	M	199	171	23 Jun 2011	47°47,1'	8°44,1'	30 Dec 2011	190	475	34	6512
2	F	265	234	26 Jun 2011	47°30,8'	7°24,0'	08 Feb 2012	227	2408	30	6778
3	F	204	180	28 Jun 2011	47°49,1'	8°05,7'	27 Jun 2012	365	311	37	13 352
4	F	233	199	03 Jul 2011	46°54,1'	5°36,1'	02 Jul 2012	365	12	26	9331
5	F	197	172	09 Jun 2013	47°08,5'	5°58,6'	03 May 2014	328	863	24	7905
6	F	235	207	10 Jun 2013	47°09,6'	5°54,0'	28 Mar 2014	291	911	27	7857
7	F	233	202	10 Jun 2013	47°09,8'	5°54,7'	10 Jun 2014	365	384	15	5594
8	F	250	218	11 Jun 2013	47°08,9'	5°49,6'	17 Oct 2013	128	864	30	3871
9	F	228	206	13 Jun 2013	46°42,5'	5°08,4'	13 Jun 2014	365	41	26	9410
Mean	F	231	202	–	–	–	–	304	724	27	8012
Mean	M+F	227	199	–	–	–	–	292	697	28	7846

**Figure 1.** North East Atlantic Ocean. 200, 1000, and 2000 m depth contours and area names cited in the text are shown.

return to the Bay of Biscay was observed in March–April each time that the tags remained deployed 12 months.

The migration pattern of the adult male (no. 1) was similar to that of the females but the timings of the large-scale movements differed slightly. The shark moved north after release, but turned to the south earlier than the females at the beginning of September and returned to the area of its initial release. It remained in the Bay of Biscay off the northern coast of Spain for 2 months before moving northward again in mid-November, when the track was terminated by the pop-off date.

Porbeagles tagged in 2011 migrated further north than those sharks tagged in 2013 and an exception to the large offshore general trip was observed for one shark (no. 7, 230 cm TL). This shark remained in the Bay of Biscay and adjacent waters for its entire period at liberty (365 d). However, it still exhibited the general north–south migration pattern of the other sharks; residing in more northerly waters in autumn (September–December), migrating rapidly to waters off north Portugal in January–February before returning to the Bay of Biscay in spring (April–June).

### Vertical habitat use

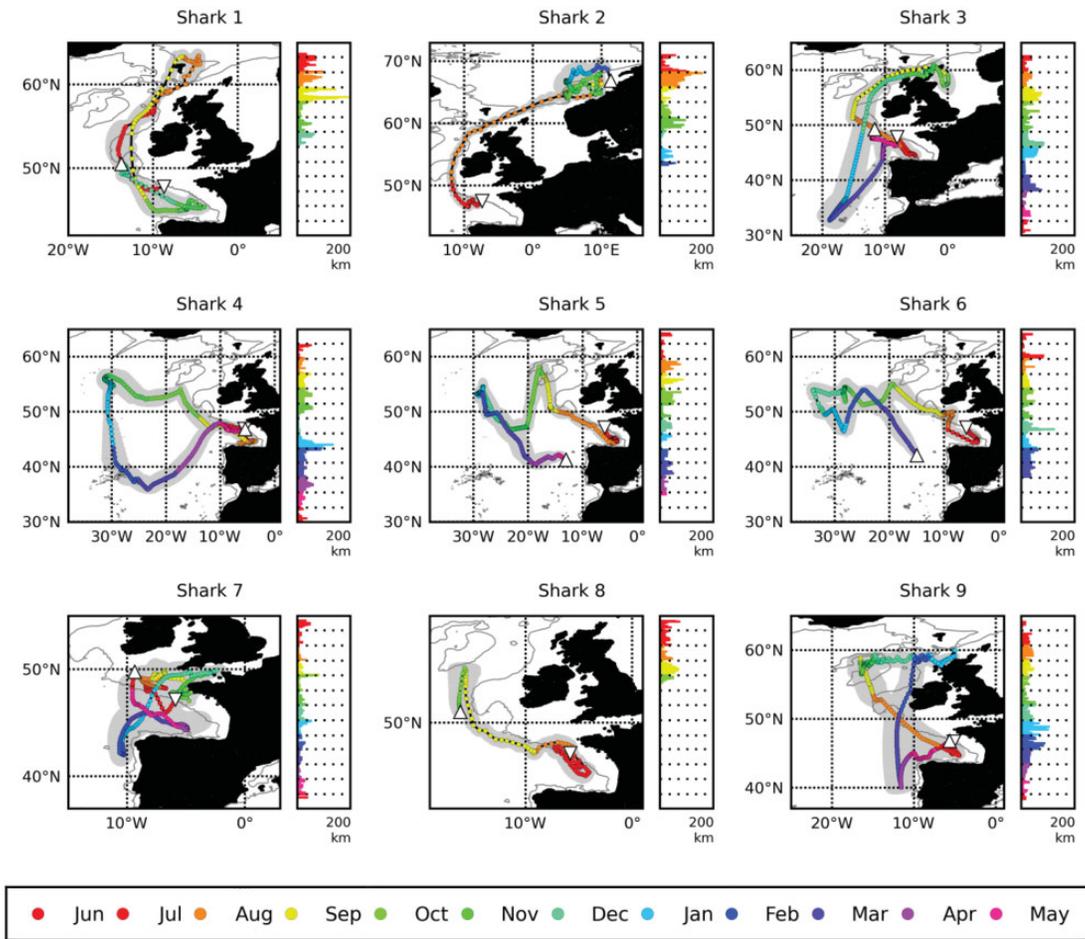
Porbeagles ranged between the surface and 1600 m depth during their time at liberty, but rarely ventured deeper than 700 m (Figure 3). All sharks occupied the upper 200 m of the water column predominantly (monthly average time percentage: 59%

$\pm 11$ ), but they all spent time in the mesopelagic zone ( $>200$ m), with some individuals (nos. 1, 3, 4, and 9) exhibiting an affinity for deeper waters. The timing of deep diving occurred in spring (February to April) for sharks nos. 3, 4, and 9 (respectively in Madeira, Azores, and Galicia Bank areas) and in September for shark no. 1 to the west of Scotland.

Patterns of depth occupation were bimodal, with individuals splitting their time between surface waters (0–50 m and sometimes 50–100 m) and depth zones below 200 m, with the exception of shark no. 2 (Figure 3). The mean percentage in the 0–50 m surface waters was  $38\% \pm 9$  rising to  $47\% \pm 9$  in summer (July–September) when the sharks were typically in the Bay of Biscay or off southwest Ireland. This bimodal occupation of different ocean layers is partly driven by changes in vertical habitat during the migration. Thus, when sharks resided in the Norwegian Sea (no. 2 in December–February), Madeira (no. 3 in February), the Mid-Atlantic Ridge in the Azores Region (no. 4 in February), they remained in the lower part of the epipelagic layer or in the mesopelagic layer (Figure 3). The method of data transmission from the PSATs (depth records were binned by 6, 12 or 24 h with no time-series information, except shark no. 1) does not permit a detailed examination of diel vertical movements, but the bimodal pattern of depth was also likely a consequence of daily movements between shallow and deep water; time at depth histograms by quarter show this diel pattern clearly (Supplementary Figure S2). The use of the mesopelagic layer increased during the periods that include more daylight hours (6–18 GMT), and generally largely, with few exceptions mostly in quarter 4 (sharks nos. 2, 3, 7).

### Discussion

The reconstructions shown here provide evidence that sub-adult and mature female porbeagles undertake large annual cyclical migrations. The general pattern we observed was a northward movement in summer–autumn (August–October) followed by a northward or westward extension in autumn–winter (September–February), and continued later on by a movement to south of  $43^\circ\text{N}$  in winter–spring (January–April). Porbeagles rarely moved north of  $62^\circ\text{N}$  but a period of residence north of  $52^\circ\text{N}$  in autumn–winter (September–February) was observed in almost all reconstructed migrations. Returns to the Bay of Biscay and southwest Ireland shelf break in spring (March–June) were observed in four of the sharks that were tracked for a full year. The observation of site fidelity is even more



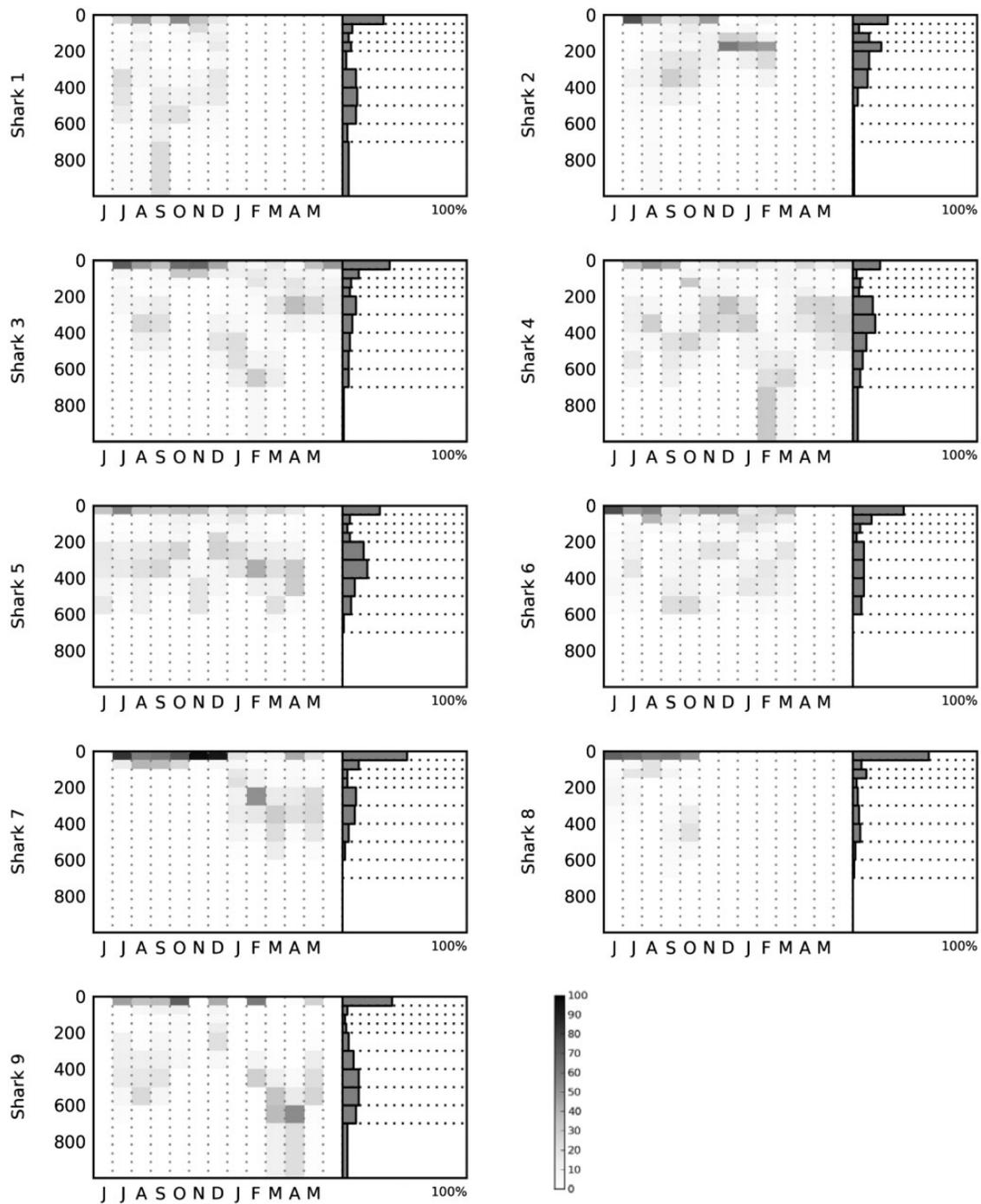
**Figure 2.** Reconstructed tracks (left) and daily estimated movement distance (right) of the 9 porbeagles tagged in the Bay of Biscay in June–July 2011 (nos. 1–4) and June 2013 (nos. 5–9). 50% CIs are displayed as light grey ellipses and 1000 m depth contours are shown. Downward and upward triangles denote the tagging and pop-up locations, respectively.

remarkable because our data provide evidence that, in some cases, large females moved 1900–2200 km away from the point of release as far south as 33°N (shark no. 3) and as far west as 31°W (shark no. 4).

The migratory paths and general pattern of movements exhibited by the porbeagles in this study are consistent with those described elsewhere for porbeagle in the Northeast Atlantic (Pade *et al.*, 2009; Saunders *et al.*, 2011). In previous studies, sharks were tagged close to the coastal shelf in summer or in early autumn and migrated to the shelf break and offshore areas in autumn and winter when deployments were long enough to observe this migration. In Saunders *et al.*, 2011 extensive migrations to the south were observed during winter, similar to sharks tagged in our study. However, unlike those studies, we observed migrations to high latitudes and the mid-Atlantic ridge in the late summer, before the southward migrations occurred. This may indicate that larger sharks have a greater capacity for large migratory movements although it should be noted that one shark of 91 cm FL tagged in Saunders *et al.*, 2011 migrated to the west coast of Morocco over a period of 6 months. Tag retention in Pade *et al.* (2009) was too low to provide the same information (<90 d; mean 44 d). A recent study on porbeagle in the southern hemisphere also showed also that sharks move predominantly

north–south to occupy lower latitudes in winter than in summer (Francis *et al.*, 2015). This study provides 10 tracks (deployment durations 72–300 d; median 221 d) that show that most of the porbeagles remained in offshore waters (depth > 1000 m) adjacent to New Zealand; one immature male (140 cm LF) performed a long circular migration in 300 d. Deployment durations did not provide evidence of site fidelity as clearly as in our study but Francis *et al.* (2015) as well as Saunders *et al.* (2011), show that small and immature porbeagles may also undertake north–south migrations with a presumption of site fidelity. Further studies will shed light on this phenomenon.

The use of the water column by porbeagles in our study was also similar to that described in other studies. Typically, porbeagles predominantly used the epipelagic zone in summer, before switching to greater use of the mesopelagic zone from autumn to spring, a result reported by Saunders *et al.*, 2011 and Francis *et al.* (2015). Porbeagles that had migrated further offshore tended to make greater use of the mesopelagic zone, likely related to the greater productivity of these areas in winter, or in areas of ocean in proximity to seabed features known to attract biomass (e.g. seamounts). Further work to establish the drivers of vertical migration is necessary to develop a greater understanding of the links between migration and habitat use.



**Figure 3.** Time at depth distribution by month (left part of each panel) and overall (right) of the nine porbeagles tagged in the Bay of Biscay in June–July 2011 (nos. 1–4) and June 2013 (nos. 5–9). Layers limits from top to down are 50, 100, 150, 200, 300, 400, 500, 600, 700, and >700 m. Time at depth data are shaded to indicate proportion of time at each depth band, while overall depth distribution is shown as a percentage along the x-axis.

The annual migration cycle is likely to be linked to critical times for feeding and reproductive activity. For example, based on records of historical porbeagle catches, Rae (1962) describes the annual arrival of porbeagle in the North Sea as “an invasion” beginning in May and reaching a peak in August, in synchrony with catches of spawning herring, suggesting that the availability of this food resource is related to the increase in abundance of

porbeagle. Herring (*Clupea harengus*) is the species that is most commonly observed in porbeagle stomachs (Gauld, 1989) in northern European waters. The occurrence of spawning herring aggregations off the northeast Scottish and Shetland coasts during August to September and in the central North Sea during August to October is likely a factor in the increase in porbeagle abundance in the North Sea in summer. In western European waters,

the fishery typically began in March–April, peaked between May to August, and ended in September–October; large porbeagles (FL > 200 cm) were caught throughout this period (Lallemant-Lemoine, 1991; Hennache and Jung, 2010). The porbeagle diet in the Bay of Biscay is dominated by horse mackerel (*Trachurus trachurus*) and blue whiting (*Micromesistius poutassou*) (Hennache and Jung, 2010). These two preys are abundant during spring and summer on the shelf break (Certain *et al.*, 2011). These timings correspond to the periods when the tagged porbeagles in our study remained close (or returned) to the coastal shelf and predominantly occupied epipelagic depths. Since the historic porbeagle fishery had a broad spatial extent, and none of the tagged sharks exhibited migration from west European waters in spring to north European waters in summer, it seems likely that spatially separate fisheries were exploiting a widely dispersed population. Therefore the evidence for site fidelity in our study suggests that the porbeagle population in the North-East Atlantic may be formed by components which return to spring–summer feeding areas that are widely separated. Similar behaviours are seen in other shark species. For example, the salmon shark *Lamna ditropis*, a lamnid shark which replaces porbeagle in the North Pacific Ocean (Francis *et al.*, 2008), also makes long distance migration before returning to the productive Alaskan coast (Weng *et al.*, 2008). This behaviour is suggested to improve foraging success of migratory sharks by reducing the cost of research of suitable feeding areas as suggested for the white shark *Carcharodon carcharias* (Jorgensen *et al.*, 2010), the oceanic whitetip *Carcharhinus longimanus* (Howey-Jordan *et al.*, 2013) or the tiger shark *Galeocerdo cuvier* (Lea *et al.*, 2015).

Site fidelity may also be linked to reproductive ecology but, for many shark species it is not fully described even if there are evidence that it is common for sharks (Chapman *et al.*, 2015). Within the lamnid sharks, fidelity to mating sites is suggested for the white shark (Jorgensen *et al.*, 2010; Domeier and Nasby-Lucas, 2013) and the salmon shark (Weng *et al.*, 2008). Natal philopatry is also suggested for these two species (Bonfil *et al.*, 2005; Weng *et al.*, 2008), with the possibility of two parturition areas for the salmon shark. One of them is a highly productive region (the California Current) but the other one is the Subtropical Gyre, which is an oligotrophic region. However, this latter fact remains to be demonstrated, particularly because the advantage of locating pupping grounds in an oligotrophic region is questionable. Similarly, from observations of migration in the Western Atlantic, Campana *et al.* (2010) suggested that porbeagle pupping grounds might be in the southern part of their annual migration to the Sargasso Sea, which is also a low productivity region of the ocean. This inference of a pupping ground in subtropical waters (south of latitude 35°N) was strongly based on the observation that the southward migration is only made by female longer than 218 cm FL at which 50% of porbeagle females are mature (FL<sub>50</sub>) (Jensen *et al.*, 2002). In our study, six of the tagged females that remained at liberty for more than 9 months (mean TL 222 cm) were at or larger than the size at maturity estimated by Hennache and Jung (2010). The reconstructed tracks do not provide evidence of any incursion into tropical waters; the most southerly location recorded was 33°N, raising the possibility that pupping grounds of the stock of porbeagles in the Northeast Atlantic might also be located in temperate waters. Observations of several large embryos and small free-swimming specimens and the captures of gravid females provide evidence of this possibility. For example, in June 1960, a large female porbeagle was caught off

Jersey (Western Channel) containing an 89 cm TL embryo (Caunter, 1961). More recently, a catch of four gravid females with a total of 12 embryos, each about 80 cm long (TL), were reported in May 2008 on the south Celtic Sea shelf break (Hennache and Jung, 2010). Two catches of gravid females containing large embryos (60–63 and 66–76 cm TL) were also reported in East-Scotland and around Shetland in May and June (Gauld, 1989). Further evidence of parturition close to the western European shelf was recently provided by the captures of 9 newborn pups on the Bay of Biscay shelf break in May 2015 and July 2016, during an anchovy sentinel survey ( $n = 1$ ; 74 cm FL; E. Duhamel, pers. comm.) and a new porbeagle tagging survey carried out in June–July 2016 by some authors of this paper ( $n = 8$ ; 74–90 cm FL).

Based on these observations, the parturition period may begin as early as May, and extend to at least July. This matches the spring–summer residency period of large female porbeagles in the Celtic Sea and the Bay of Biscay shelf and shelf-edge. This area is also a habitat of major importance to juvenile porbeagle (77% of 2008–2009 French catches < 170 cm TL in Celtic Sea–Bay of Biscay; Hennache and Jung, 2010), raising the possibility that mature females and their offspring occupy the same summer–spring feeding area and suggesting natal philopatry (Hueter *et al.*, 2004; Feldheim *et al.*, 2014; Chapman *et al.*, 2015). To what extent the male population might conform to the same migration patterns and consequently might form a discrete demographic unit with the females remains unknown although our single mature male track (shark no. 1) suggests that it might be possible. Genetic and wider tagging studies are required to test this hypothesis, as well that of philopatry behaviour, which remains speculative at the present time. However, our findings provide evidence that the dynamics and life-history processes of porbeagle sharks are spatially structured and complex. The porbeagle stock structure definition in the Northeast Atlantic therefore remains an issue to tackle for assessments and management of this stock.

## Supplementary data

Supplementary material is available at the ICESJMS online version of the article.

## Acknowledgements

We thank the skipper, Adrien Delavaud, and the crew of the fishing vessel ‘Fille du Suet’ for their commitment to the success of the two tagging surveys that we carried out with them. We are thankful to José Jouaneau and to Fanny Brivoal, respectively Chairman and General Secretary of the Pays de la Loire fishermen Committee, and to Marie-Bénédicte Peyrat, Head of Scientific affairs office at the Directorate for Marine Fisheries of the Ecology, sustainable development and energy French Ministry, for their support.

## Funding

This work was funded by the French state (Directorate for Marine Fisheries), the Pays de la Loire Regional Council, the Pays de la Loire fishermen Committee and the UK Department for Environment, Food and Rural Affairs (MB5201).

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Handling editor: Caroline Durif