

Winter migration and diving behaviour of porbeagle shark, *Lamna nasus*, in the Northeast Atlantic

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The porbeagle is one of the top marine predators in the North Atlantic. However, little is known about its biology, abundance, or spatial ecology there. Results are presented on the migration and behaviour of three porbeagles tagged with archival pop-up tags off Ireland between September 2008 and January 2009. One shark migrated >2400 km to the northwest of Morocco, residing around the Bay of Biscay for approximately 30 days. The other two remained more localized in off-shelf regions around the Celtic Sea/Bay of Biscay and off western Ireland. The sharks occupied a broad vertical depth range (0–700 m) and a relatively limited temperature range (~9–17°C), with notable variations in diving behaviour between individual sharks. There were distinct day–night differences in depth distribution, each shark being positioned higher in the water column by night than by day. Night-time depth distribution also appeared to be driven by the lunar cycle during broad-scale migration through oceanic waters. Our results show that porbeagles occupy and traverse regions of high fishing activity where they are potentially vulnerable to population depletion. Such large-scale movement outside the ICES Area underlines the need for international coordination in their assessment and management.

Keywords: diving behaviour, lunar cycle, migration, porbeagle shark, satellite tag.

Introduction

The porbeagle shark (*Lamna nasus*) is a predatory, endothermic shark that typically inhabits waters between 5 and 20°C in temperate seas of the North and South Atlantic, as well as the Mediterranean and Baltic Seas (Campana and Joyce, 2004). Like most pelagic sharks, it is vulnerable to overexploitation and population depletion by fisheries owing to its relatively slow growth rate, low fecundity, and late age at sexual maturity (Campana *et al.*, 2002; Jensen *et al.*, 2002; Natanson *et al.*, 2002). Porbeagles are valuable commercially, so they have been heavily exploited by targeted and non-targeted fisheries in the Northeast Atlantic since the 1930s (Campana *et al.*, 2008). In the late 1950s, the Northeast Atlantic porbeagle fishery apparently collapsed, resulting in a major shift in European fishing activity to the Northwest Atlantic off the coast of Canada. By 1967, the Northwest Atlantic fishery suffered large decreases in catches, indicative of a substantial population crash. It has been estimated that population numbers of mature porbeagles there were reduced to 14–21% by the early 1990s as a consequence of unsustainable fishing effort (DFO, 2005).

In the Northeast Atlantic, ICES has considered the sparse information available and has consistently advised that there should be no targeted fishing for the species (Clarke, 2009). This advice was based on the precautionary approach, considering the biological vulnerability of the species and trends in catch rates. The ICES advice applies to the ICES Area (Figure 1) only. However, the species is also present in the Mediterranean, off west Africa, and in the Northwest Atlantic (Quero, 1984), and the relationship between populations in these areas and the ICES Area remains

unknown. Recent proposals for conservation listing and international management of the species (e.g. Appendix II of the Convention on International Trade in Endangered Species, CITES) were rejected primarily because of insufficient biological data (Pade *et al.*, 2009). In particular, there are few data on the spatial ecology of porbeagles, and little is known about its migratory behaviour and habitat preference, especially in the Northeast Atlantic. Acquisition of such data is therefore key to the conservation of the species and for establishing robust, ecosystem-based management strategies (Stevens *et al.*, 2000).

Much of the current understanding of the spatial ecology of porbeagle sharks comes from conventional tagging and mark-recapture studies, mainly in the Northwest Atlantic. The results of these studies have suggested that porbeagle sharks predominantly inhabit coastal and shelf-break regions, where they remain localized for prolonged periods of time (Kohler and Turner, 2001; Francis *et al.*, 2008). Tagging studies in the Northwest Atlantic have revealed apparent seasonal, annual, and sex-specific migration of mature sharks in Canadian waters, but individuals appear to traverse only short- to medium-range distances along the continental shelf (500–1000 km; Campana and Joyce, 2004; Campana *et al.*, 2008; Francis *et al.*, 2008). The few studies conducted in the Northeast Atlantic have also shown that the horizontal movement of porbeagles is often limited to such distances. Porbeagles tagged off southwestern England and northern France were recaptured close to their release sites, with just one recaptured, after several years, far to the north (2370 km; Stevens, 1976, 1990). There has been only one

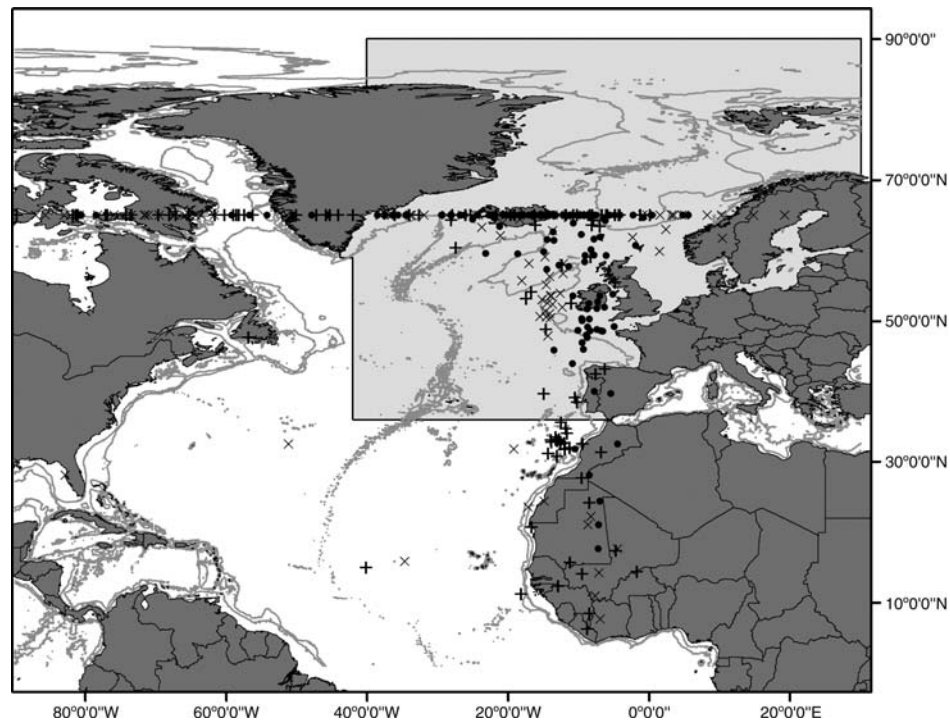


Figure 1. Initial (i.e. pre-screened) geolocation positions derived from the PTTs. Plus signs and crosses denote positions from sharks 1 and 2, respectively, and dots the positions from shark 3. The 200 and 2000 m depth contours are also shown, and the shaded region is the standard ICES assessment/management zone. Details of the screening process by which erroneous geolocations were removed are given in the Methods section.

Table 1. Summary data for three porbeagles tagged with PTTs off the northwest coast of Ireland, with estimates of weight calculated using the allometric equations of Natanson *et al.* (2002).

| Shark ID | Sex | Fork length (m) | Girth (m) | Weight (kg) | Tagging date | Tagging location (°N) | Tagging location (°W) | Pop-up date | Days tagged | Pop-up latitude (°N) | Pop-up longitude (°W) |
|----------|--------------|-----------------|-----------|-------------|-------------------|-----------------------|-----------------------|-----------------|-------------|----------------------|-----------------------|
| 1 | 34653 Male | 0.91 | 0.62 | 13.1 | 20 September 2008 | 55.417 | 7.906 | 19 January 2009 | 122 | 33.832 | 13.044 |
| 2 | 34655 Female | 1.54 | 0.91 | 48.1 | 24 September 2008 | 55.366 | 7.829 | 25 January 2009 | 122 | 52.754 | 13.797 |
| 3 | 34656 Female | 1.43 | 0.88 | 41.4 | 25 September 2008 | 55.357 | 7.775 | 26 January 2009 | 122 | 48.787 | 9.135 |

published study of a porbeagle shark migrating across the Atlantic (4260 km from Ireland to Canada; Kohler and Turner, 2001), but it is difficult to assess the extent to which such migrations take place, because so few individuals have been tagged in the Northeast Atlantic.

Pop-up, satellite-transmitting archival tags are used extensively to study a wide range of marine species, including squid, turtles, seals, tunas, and sharks (Arnold and Dewar, 2001; Boustany *et al.*, 2002; Hays *et al.*, 2006; Stokesbury *et al.*, 2007; Stainiland and Robinson, 2008). Information from these tags has provided new insight into the spatial dynamics, habitat utilization, behaviour, physiological ecology, and fisheries interactions of these species. To our knowledge, there has been just one study that has used such an approach to investigate the spatial ecology of porbeagles in the Northeast Atlantic. Pade *et al.* (2009) tagged four porbeagles off Cornwall, southwest England, and tracked them for a period of 22–90 d during summer. Their results showed the porbeagles tending to occupy localized areas on the continental shelf throughout summer, with the possibility of larger-scale movement to more off-shelf regions around Ireland towards autumn. Pade *et al.* (2009) also observed considerable plasticity in diving behaviour as a function of regional bathymetry.

In our study reported here, we used archival pop-up tags to investigate further the spatial ecology of porbeagles in the Northeast Atlantic, and to test whether porbeagles exhibited large-scale movements to more oceanic regions during autumn/winter. We also investigate the hypothesis that there are variations in porbeagle depth distribution and diving behaviour as a function of such migration and as a function of regional changes in the underlying oceanography.

Material and methods

Three porbeagles were tagged with PTT-100 Archival Pop-up Tags (Microwave Telemetry, MD, USA; hereafter PTT) off Northwest Ireland in September 2008 (Table 1). The sharks were caught using rod and line and were brought on board for measuring body length and tagging. Each tag was attached via a short nylon tether to a dart at the base of the dorsal fin. The tags can measure water temperature from 0 to 35°C ($\pm 0.17^\circ\text{C}$) and depth to 1280 m (± 5.3 m), as well as ambient light levels at 550 nm wavelength. The PTTs were programmed to detach 122 days after deployment and sampled at a rate of once every 15 min.

Following detachment, each tag floated to the sea surface and transmitted the archived data to Argos receivers on NOAA polar-

orbiting satellites. Initial geolocation positions were calculated by the tag manufacturer using light levels at dusk and dawn. Anomalous estimates resulting from dive-induced shifts in the estimated timings of dawn and dusk were removed following comparisons with standard light curves. Geolocation estimates were also excluded if there was movement of $>1^\circ$ latitude or longitude in a single day, or if movement between locations was deemed excessive. Archival pop-up tags function optimally when situated within the upper 100 m of the water column where light levels are greatest. Inspection of the retrieved data showed that the sharks mainly remained deeper than 100 m during daylight, so many of the estimated times of dusk and dawn, and hence the estimates of latitude and longitude, were erroneous (Figure 1). Location estimates and individual tracks were therefore produced by Collecte Localisation Satellite (CLS) using geolocation models described in Royer and Lutcavage (2009) that incorporate sunrise/sunset times, tag-derived depth and temperature records, satellite-derived sea surface temperature (SST) data, and local bathymetry data as input.

Because of the large number of obvious outliers (e.g. some sunset/sunrise time records showed variations of more than 100 min), an *ad hoc* cleaning procedure was proposed. A simple spatial model was built to predict the likely distribution of a given animal per day using a movement model constrained solely by its maximum sustainable speed (100 km d^{-1}). This is analogous to a random walk with a uniform movement kernel starting at the tag release point. These initial, daily predicted probability densities were used in a hidden Markov model that incorporated a maximum allowable error in SST and the maximum depth reached by the shark for each day as hard constraints: see Pedersen *et al.* (2008) for detail on building such a hidden Markov model. In this case, the model was fitted using a maximum horizontal movement speed of 100 km d^{-1} and assuming a maximum absolute SST error of $\pm 0.5^\circ\text{C}$. Daily SST fields optimally interpolated were built from the blended microwave + infrared product (resolution 9 km) provided by Remote Sensing Systems. The ETOPO2 dataset (resolution 2 min) was used as bathymetry data.

The model was run forward then backward in time, starting from the pop-off location to yield a set of refined daily probability densities that were used as conservative bounds for the presence of the sharks. Each probability surface in state space (i.e. in latitude/longitude coordinates) was propagated into observation space (i.e. converted to sunrise/sunset time coordinates) and used to estimate the likelihood of the actual pairs of sunrise/sunset times provided by each tag for each day. The tag-derived records were then ranked according to the likelihood of each sunrise/sunset pair in the context of this simple model, and only plausible data were selected. After this scrutiny with the modelled daily probability distributions, just $\sim 20\%$ of the sunrise/sunset data points per tag were deemed viable and selected for construction of the sharks' movement tracks. Although this procedure requires some selectivity in determining the percentage of records to retain, it does provide a more objective alternative to fully user-driven data-selection criteria in the current scenario. Finally, the shark-movement tracks were determined using a standard state-space model that incorporated the most robust sunrise/sunset pairs, together with the daily SST and maximum depth as constraints (Royer and Lutcavage, 2009). A Metropolis–Hastings re-sampling step was used to tackle the non-linear bathymetric constraints of proximity to coast and the large bathymetry

gradients. Shark movement was modelled using a random-walk model with a diffusion coefficient of $5000 \text{ km}^2 \text{ d}^{-1}$, and a twilight-timing error was assumed to be Gaussian distributed with a standard deviation of 20 min.

Results

One male and two female porbeagle sharks were tagged off north-western Ireland (Table 1). Each tag surfaced on schedule after 122 d and transmitted a full archived dataset to the Argos satellites within a two-week period. The tag from Shark 1, a relatively small male, popped up between the western coast of Morocco and the island of Madeira (Figure 2a), indicating a southerly straight-line migration of more than four months. It apparently travelled mainly along the shelf break to the northwestern Bay of Biscay, where it stayed for ~ 30 d between 29 October and 8 December 2008, then moved to more-open waters during its migration farther south. The second tag detached off the west coast of Ireland and shark 2 remained mainly in oceanic waters around the shelf edge (Figure 2b). Shark 3 also migrated south from the tagging site to the Celtic Sea and northwestern Bay of Biscay, where it occupied regions in proximity to the shelf break for much of the deployment period (Figure 2c).

All three sharks had a broad vertical distribution (0–700 m) and a relatively limited temperature range (c. $9\text{--}17^\circ\text{C}$), with distinct variations in depth distribution and diving behaviour between individuals (Figure 3). At the start of the time-series, shark 1 tended to remain between the surface and 200 m, making occasional dives to depths of ~ 400 m (Figure 3a). Then, after 19 October 2008, it was seldom closer than 30 m to the surface, staying mainly around c. 40–120 m deep, but with frequent dives to below 400 m. This pattern is consistent with the shark residing mainly around the shelf break at the start of the series, then moving to more oceanic regions during its residence in the Bay of Biscay and its subsequent migration south. The maximum dive depth for shark 1 was 608 m. Shark 2 was mainly distributed between 0 and 250 m throughout the time-series, but made several dives to depths of ~ 300 m (Figure 3b), reaching a maximum depth of 430 m. Shark 3 occupied mainly the upper 60 m of the water column between 25 September and 11 October 2008, before making several deep dives to $\sim 600\text{--}700$ m over a period of three days (12–15 October 2008; Figure 3c). Subsequently, it remained between the surface and 200 m for the remainder of the time-series, and there was no further evidence of deep-diving. These patterns are consistent with sharks 2 and 3 residing in off-shelf regions close to the shelf break.

The water temperatures experienced by each shark varied, but in general all three dived through strongly stratified water during late summer/autumn (Figure 3). In the regions occupied by sharks 2 and 3, the thermocline appeared to break down around 30 October 2008 and 18 October 2008, respectively, and those animals resided in relatively isothermal waters throughout winter (Figure 3b and c). In contrast, shark 1 occupied thermally stratified water continually throughout its time-series and the maximum water temperature increased from 22 November 2008 on, indicative of the animal moving south through regions of increasing SST (Figure 3a).

There was distinct evidence of day–night differences in the mean daily depth distribution of each shark (Figure 4). After 19 October 2008, shark 1 was distributed significantly ($p < 0.01$; Student's *t*-test) higher in the water column at night (above

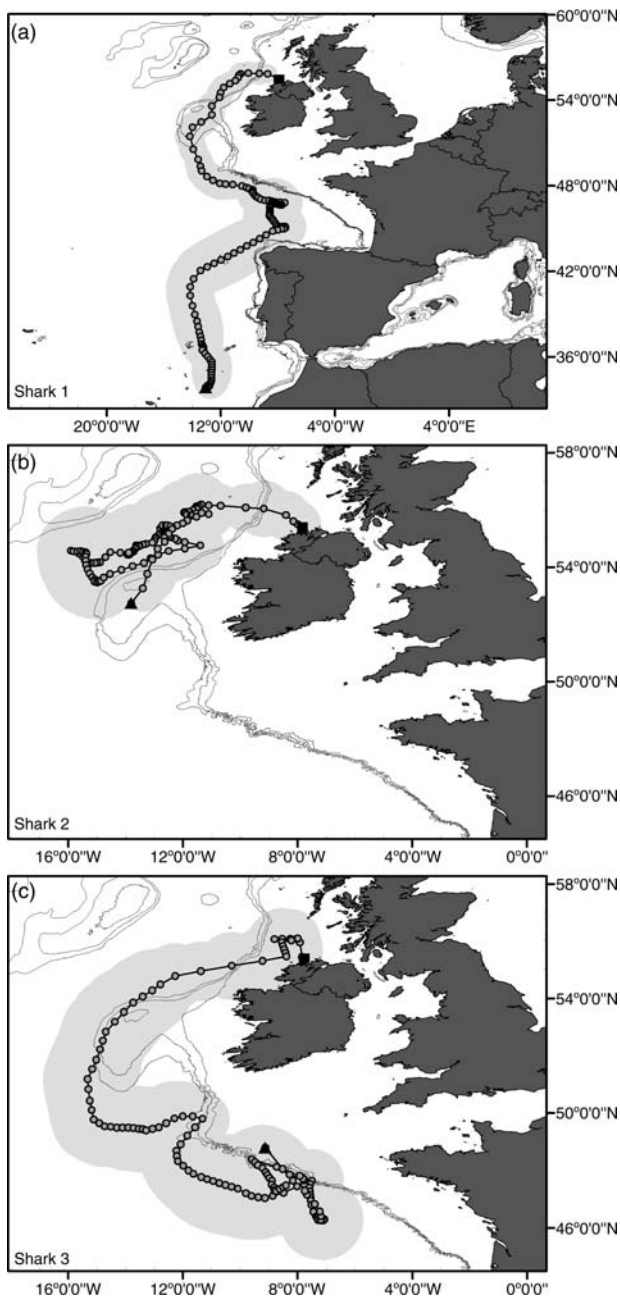


Figure 2. Movement of three porbeagles, *L. nasus*, tagged with PTTs: (a) shark 1 (male); (b) shark 2 (female); and (c) shark 3 (female). Black squares and triangles denote the tagging and pop-up locations, respectively. The shaded area represents the 50% confidence interval of the calculated positions. The 200, 500, and 1000 m depth contours are also shown. The southernmost boundary of the ICES management zone is delimited at 36°N.

~110 m) than by day (below ~150 m) with the deepest dives made by day (Figure 4a). A similar trend was observed for shark 2 after 1 October 2008 ($p < 0.01$; Figure 4b), but the extent of vertical separation between the two periods was not as great as that of shark 1. Shark 3 occupied relatively shallower regions of the water column by day than sharks 1 and 2, but its depth preferences were still significantly ($p < 0.01$) greater by night (above ~90 m) than by day (Figure 4c). Mean daily temperature data calculated by night and day corresponded well with these trends when the

waters were stratified. Temperature maxima were recorded mainly at night when the sharks occupied the warmer, upper layers of the water column, and temperature minima were recorded by day when the sharks occupied the cooler layers deeper down (Figure 4). A distinct monthly cycle in nocturnal depth distribution was observed for shark 1, the shark being found higher in the water column at both the start and end of the month than during the middle of the month (e.g. 50 m on 1 December 2008 vs. 102 m on 15 December 2008; Figure 5). Power-spectrum analysis (Fourier-transform analysis) conducted on the data revealed maximum power at 29.7 d, almost exactly the same periodicity of a complete lunar cycle, or one lunar 'month' (29.5 d; new moon to full moon). Cross-correlation analysis revealed a highly significant ($r = -0.49$, $p < 0.001$) negative correlation between moon phase (expressed as a fraction of the moon illuminated at midnight per day; US Naval Observatory) and nocturnal depth distribution. The shark was therefore distributed deeper in the water column when the moon was fullest, and its vertical distribution in the water column appeared to be driven largely by the changes in moon phase. Such a trend was not observed for the other two sharks, which made comparatively smaller horizontal migrations and occupied regions in proximity to the shelf break.

Discussion

To our knowledge, this is the first study to track the horizontal and vertical movement of porbeagle sharks in the Northeast Atlantic in autumn and early winter using archival pop-up tags.

Light-based, geolocation techniques are problematic for deep-living species such as pelagic sharks, which spend considerable portions of their time in regions where light levels are low, particularly during winter when periods of daylight are shorter and ambient light levels are often masked by heavy cloud cover. The diving behaviour of the porbeagles proved particularly challenging to the sunrise/sunset geolocation method used in the current generation of archival pop-up tags, with many obvious outliers in the datasets retrieved. Using such data directly in a standard filtering procedure (Royer and Lutcavage, 2009) would most likely have given erroneous results as a result of asymmetric errors in the estimated sunrise/sunset times, caused by the marked diving behaviour. To make the most of the datasets, therefore, an *ad hoc* selection procedure was used based on a simple movement model and hard constraints that incorporated SST and depth. Daily probability surfaces were calculated, then used to compute the likelihood of the actual sunset/sunrise records from each tag, so that the data could be ranked and scrutinized. Although not totally objective, the ranking procedure and the use of a conservative movement model driven solely by a maximum daily speed eased the task of selecting plausible data and minimized selection bias. As with any user-driven selection criteria in data analysis, further calibration and validation of the procedure is required, and analyses are ongoing. However, we did use the hardest possible constraints and thresholds in a robust modelling framework to maximize objectivity and produce valid movement tracks based on the available data.

Although the horizontal movement tracks of this study are associated with relatively high error bounds (50% confidence interval), our results do provide valuable insight into porbeagle spatial ecology, and they demonstrate the feasibility of monitoring the species with archival pop-up tags on a long-term basis. Our results show that porbeagles inhabit shelf-break and off-shelf

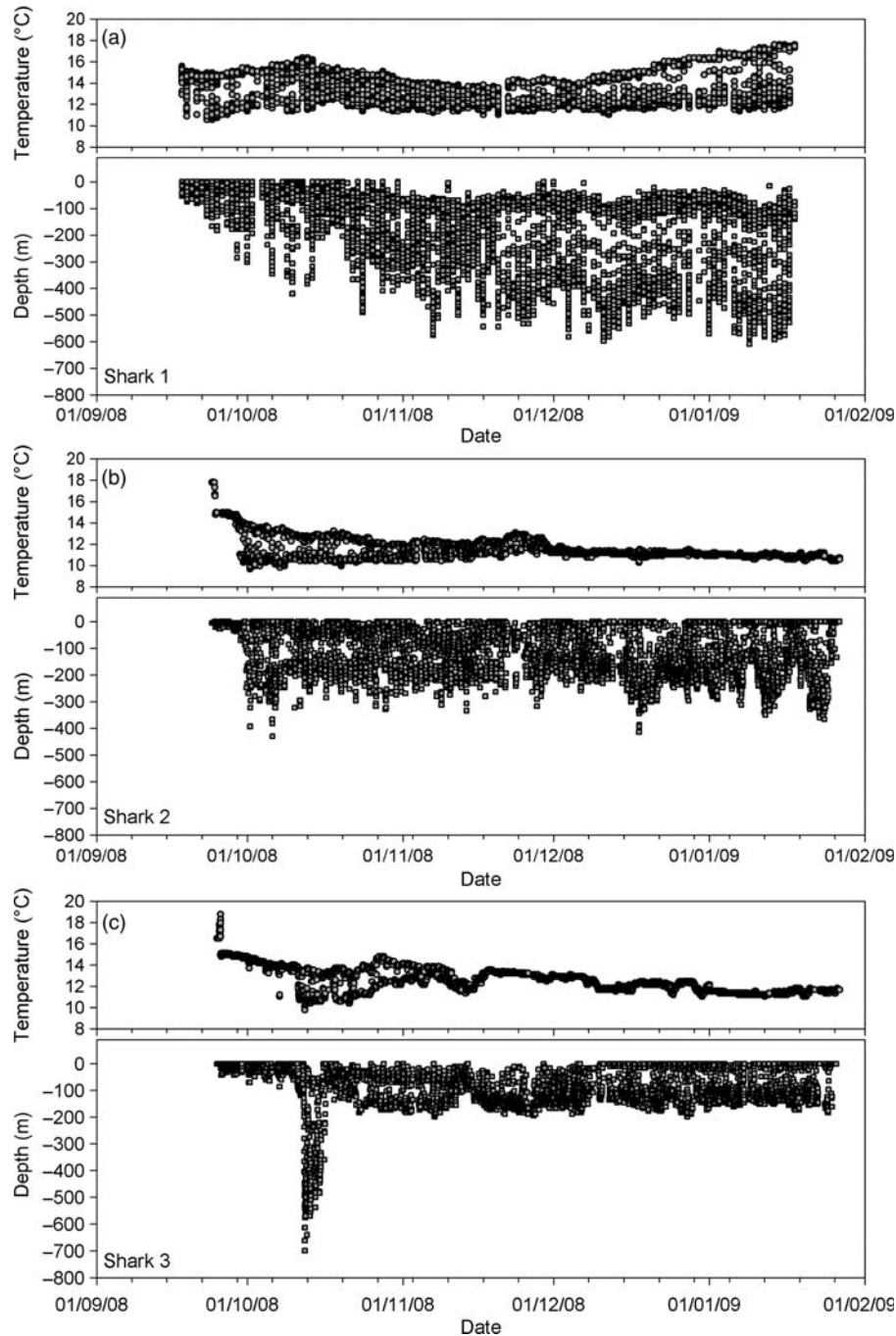


Figure 3. Temperature (top) and depth (bottom) data collected by three PTT-tagged porbeagles at 15-min resolution between 20 September 2008 and 26 January 2009: (a) shark 1; (b) shark 2; and (c) shark 3.

areas during autumn and winter, and that some may also undertake larger-scale movements through more-oceanic waters to regions farther south. Two of the sharks tagged in this study occupied regions mainly close to the shelf break around western Ireland and the Bay of Biscay for prolonged periods, moving not too far away from the tagging locations. This trend is in general accord with the results of other studies on porbeagles in the region (Stevens, 1976, 1990; Pade *et al.*, 2009) and could be a function of high localized food availability. For example, Atlantic mackerel (*Scomber scombrus*) is a known prey species of porbeagles (Stevens,

1973), and they are often very abundant in these regions (Molloy, 2004, 2006), possibly as a function of the enhanced primary and secondary production that is characteristic of such on-shelf/shelf-break regions (Cushing, 1990; Sims and Quayle, 1998). Other work has shown too that species such as bluefin tuna (*Thunnus thynnus*) are common in similar areas around the west coast of Ireland and the Bay of Biscay, possibly also as a consequence of increased food availability (Stokesbury *et al.*, 2007; Cosgrove *et al.*, 2008). Our shark 1 migrated a long distance rapidly, ending ~500 km off the west coast of Morocco coast after the

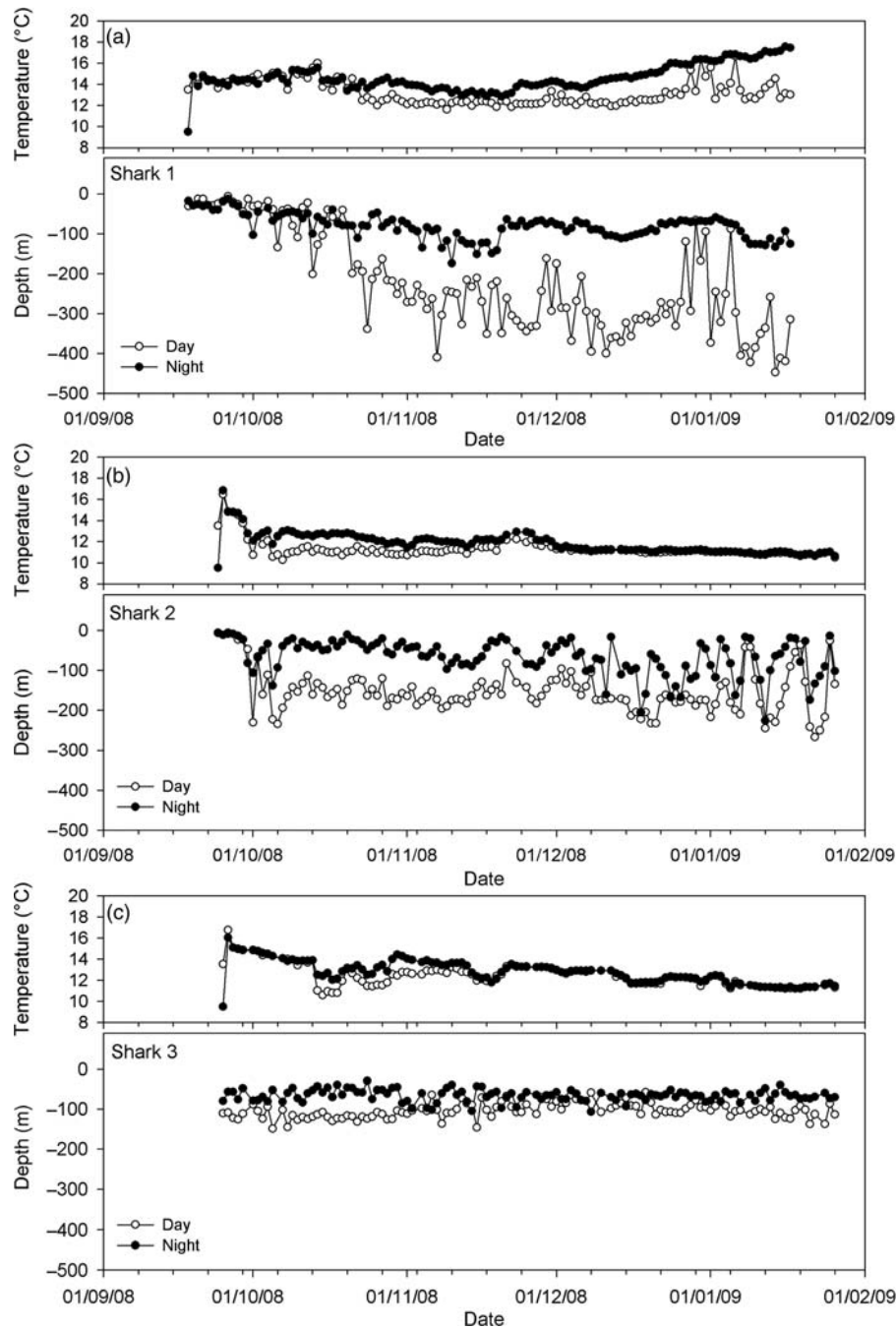


Figure 4. Mean temperature (top) and depth (bottom) by day (07:00–18:59) and night (19:00–06:59) from (a) shark 1, (b) shark 2, and (c) shark 3.

122 days. Other studies have shown that porbeagles may undertake large-scale migrations in the Northeast Atlantic, for instance, one shark marked around Ireland was recaptured off Norway after 13 years (Stevens, 1990), but this is the first time such a rapid migration has been observed directly. The results of this study suggest the importance for assessment and management to consider the linkages between statistical areas 27 (ICES Area) and 34 (Central Eastern Atlantic Area, CECAF). Currently, porbeagles are assessed separately in each of these regions.

Studies in the Northwest Atlantic have indicated that porbeagles are often common in shallower, on-shelf waters during

spring and summer, before moving into deeper water during winter (Campana *et al.*, 2008). Pade *et al.* (2009) suggested that long-distance migrations by porbeagles away from the UK shelf to off-shelf waters around Ireland might be a seasonal phenomenon, with porbeagles migrating north to cooler water in winter to exploit food resources not taken by ectothermic predators such as blue sharks (*Prionace glauca*) when they migrate to warmer water in the south. Those authors suggested that the endothermic porbeagle shark has a physiological advantage at higher latitudes, allowing them to exploit prey resources that become seasonally unavailable to ectothermic predators. The

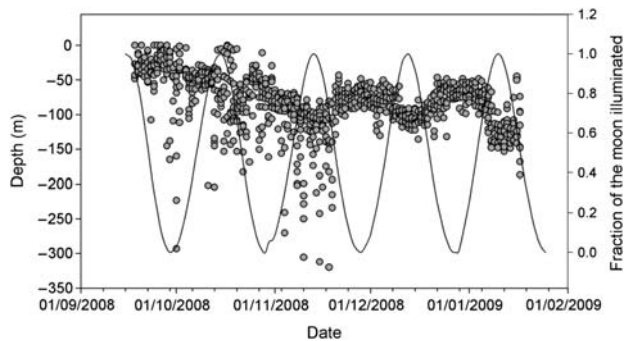


Figure 5. Night-time (19:00–06:59) depth distribution of shark 1 in relation to the observed lunar cycle. The depth data (grey circles) are at a resolution of one hour, and the lunar cycle (line) is expressed as the fraction of the moon illuminated at midnight per day.

results of our study support the idea that porbeagles may undertake long-distance migrations to deeper water during winter, but suggest that migrations are not necessarily north to cooler regions. Two of the sharks we tracked moved away from Ireland in a southerly direction, with one moving to warmer water. Why porbeagles exhibit such extensive migrations is unclear, although it is most probably linked to searching for better feeding environments or searching for mates (Weng *et al.*, 2005). More data are required to shed light on the distribution and seasonal migratory behaviour of porbeagles in the eastern Atlantic.

Our results suggest that porbeagle populations around Ireland, the UK, northwest Africa, and the Mediterranean Sea are potentially connected and that there may be regular mixing between these locations. It is apparent that porbeagles traverse and occupy regions that are fished intensively by pelagic tuna and billfish fisheries during their migrations. ICCAT (2009) identify the region traversed by the most wide-ranging of our study specimens as very important for bluefin tuna, swordfish (*Xiphias gladius*), and albacore tuna (*Thunnus alalunga*) catches. Clearly, more information on the interactions of porbeagles and these fisheries is required. Also, the Bay of Biscay is a region targeted intensively by the French pelagic shark fishery (ICES, 2008). Current international management boundaries and fishing zones appear somewhat arbitrary for such a broad-scale migratory species, a fact that needs to be taken into account during stock-assessment planning and when devising robust ecosystem-based management strategies. Our results support those of Pade *et al.* (2009) that indicate that porbeagles should be considered for protected status listing on the Convention for the Conservation of Migratory Species of Wild Animals (Bonn Convention).

The results of our study indicate distinct differences in vertical movement and diving behaviour of porbeagles that, to a large extent, relates to the regional habitat in which they are found. For example, it appears that porbeagles often occupy the upper surface layers when situated close to the shelf break, but position themselves deeper in the water column and seldom move to the surface during long-distance, horizontal migrations through oceanic waters. A similar trend was observed for the salmon shark (*Lamna ditropis*) in the eastern North Pacific (Weng *et al.*, 2005). The salmon shark has a Subarctic to subtropical niche, ranging from 2 to 24°C, and it seldom comes to the surface when migrating through increasingly warm waters towards the subtropics. Also, it often remains submerged below the thermocline for prolonged periods in warmer regions, and it has been

suggested that this might arise from physiological constraints. However, the temperature range experienced by the porbeagles in this study was not as great as that of the salmon shark, and the reasons for avoiding the surface layers when migrating through oceanic waters are not clear from our data. Other lamnid sharks, such as white sharks (*Carcharodon carcharias*), experience wide temperature ranges (c. 4–26°C), and it has been suggested that endothermic physiology is a key factor in determining the range expansion of these sharks (Boustany *et al.*, 2002). The sharks tracked in our study appeared to occupy a relatively narrow range of temperatures (c. 9–17°C) compared with that of other lamnid sharks, although the observed range is of a similar order to that experienced by ectothermic sharks. The sharks we tagged were much smaller than those tagged in other studies, which might account for the more limited thermal range observed. However, they were also only tracked for a relatively short period and perhaps they inhabited warmer/colder climates outside our window of observation. Owing to their endothermic physiology, we hypothesize that porbeagles in the Northeast Atlantic have a temperature range similar to that of other lamnid sharks, and that continued tagging of the species with archival pop-up tags will cast new light on the limits of their distributional range.

There was distinct evidence of day–night differences in vertical distribution for each shark. During late autumn and winter, each shark was deeper in the water column by day than by night, and these results broadly support earlier findings from studies of porbeagles around the UK and Ireland (Pade *et al.*, 2009). Differences between daylight and night-time distribution could be a response to changes in vertical distribution of planktivorous fish that feed on diel vertically migrating zooplankton (Carey and Scharlod, 1990; Sims *et al.*, 2005; Pade *et al.*, 2009). In general, the sharks we tagged resided and dived deeper than those tagged in similar regions during summer (e.g. maximum dives in this study 700 m vs. 552 m in the study of Pade *et al.*, 2009). This may be indicative of a seasonal deepening in depth distribution that may also be related to the seasonal distribution of planktivorous fish and zooplankton. For example, studies have shown a distinct seasonal (winter) deepening of deep scattering layers (DSLs) that typically comprise zooplankton and nekton (Anderson *et al.*, 2005; Saunders *et al.*, 2007). Porbeagles may therefore have to dive deeper in winter to exploit these food resources. One of the sharks tagged in our study exhibited a nocturnal vertical distribution that was associated closely with the lunar cycle. To our knowledge, this is the first time such behaviour has been observed for the porbeagle, but correlations between lunar phase and swimming depth have been demonstrated for several other fish species and pelagic sharks. For example, swimming depths can be notably deeper around the full moon for bluefin tuna (Wilson *et al.*, 2004), swordfish (Carey and Robinson, 1981), school sharks (*Galeorhinus galeus*; West and Stevens, 2001), and whale sharks (*Rhincodon typus*; Graham *et al.*, 2006). Moreover, analyses of commercial fisheries and recreational angler catch per unit effort have revealed a strong relationship between lunar phase and catch rates of certain shark species, catches tending to peak over the period from the new moon to the first quarter-moon when the sharks are generally positioned higher in the water column (Lowry *et al.*, 2007). These studies generally hypothesize that changes in the vertical distribution of the studied species reflect shifts in the distribution of prey associated with the DSL in response to increased lunar illumination. Organisms inhabiting the DSL, such as squid, myctophids, and bathylagid fish, are important

components of the diet of many higher-level predators and are sensitive to changes in light levels (Anderson *et al.*, 2005), migrating to the surface over the new moon and descending to deeper, darker water during the full moon (Boden and Kampa, 1967; Blaxter, 1974). Such behaviour could be a strategy to maximize energy intake from the more-productive surface waters while reducing the risk of mortality from visual predators (Tarling *et al.*, 2000).

To conclude, our study has revealed that porbeagles may undertake extensive horizontal migrations during winter and that there are connections between porbeagle populations around Ireland and those found farther south. During such long-distance migrations, porbeagles traverse several international fishing zones, and this fact needs to be considered when conducting stock assessments and proposing conservation measures. Archival pop-up tags provide new insight into the spatial ecology of porbeagles in the Northeast Atlantic, where the species is vulnerable to population depletion through sustained fishing activity. Increased data from these platforms will probably be invaluable to resource management and conservation of the species.

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