Journal of Experimental Marine Biology and Ecology 370 (2009) 64–74

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: Area fidelity, wider-scale movements and plasticity in diel depth changes

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ARTICLE INFO

Article history:
Received 9 October 2008
Received in revised form 1 December 2008
Accepted 2 December 2008

Keywords:
Behaviour
Endothermy
Fish
Habitat use
Niche expansion
Spatial ecology
Vertical migration

ABSTRACT

Understanding the habitat preferences of large marine vertebrates has only recently become tractable with the widespread availability of satellite telemetry for monitoring movements and behaviour. For many species with low population abundances, however, little progress has been made in identifying space use patterns. The endothermic porbeagle shark, *Lamna nasus*, has declined in the North Atlantic due to severe fishing pressure, with little evidence of recovery. One potential factor exacerbating population decline is area fidelity to coastal waters where fisheries are intensive. We tested for short-term area fidelity by attaching pop-up satellite-linked archival transmitters to four porbeagles in summer 2007, resulting in 175 days total tracking time covering an estimated 10,256 km distance. Throughout July and August the sharks occupied localised areas (8,602 – 90,153 km^2) within the Celtic Sea, between the south-west UK, south-west Wales and southern Ireland. Only one shark was tracked into the autumn, when it moved into deep water off the continental shelf, then north towards colder latitudes. Sharks occupied a broad vertical depth range (0 – 552 m) and water temperatures (9° - 19 °C). Dives were made frequently from the surface to near the seabed in shelf areas, however, in shelf edge habitats extended periods of time were spent at depths >300 m. Porbeagles showed considerable plasticity in diel depth changes within and between individuals and as a function of habitat type. In addition to no obvious day-night difference in depth occupation, some sharks showed reverse diel vertical migration (DVM) (dawn ascent – dusk descent) in well-mixed coastal waters whereas normal DVM (dawn descent – dusk ascent) characterised movements into deeper, thermally well-stratified waters. The variable behaviours may reflect the need for different search strategies depending on habitat and prey types encountered. These results show porbeagles are potentially vulnerable to fisheries throughout the summer when they aggregate, and that large scale movement across national boundaries identifies the need for international conservation measures.

1. Introduction

Within the last decade advances in animal-attached electronic tags have allowed scientists unparalleled insights into the behaviour and movement ecology of many elusive marine vertebrate species (seals; Biuw et al., 2007; turtles; Hays et al., 2006; sharks; Sims et al., 2003). Such studies have begun to document not only where these animals move to, but have begun to investigate behavioural processes, such as why particular habitats are selected over others that appear equally available (Sims et al., 2006a,b). Process-based investigations are a natural progression from simple plots of marine vertebrate trajectories, and may contribute to identifying behavioural decision-making criteria associated with habitat selection across diverse taxa (Heithaus et al., 2002; Sims et al., 2008). Knowledge about habitat selection is a necessary prerequisite for predicting movements and distributions with some realism in relation to changing environments (McMahon and Hays, 2006). For example, species in higher latitudes whose movements and migrations are constrained by temperature minima and maxima may trade-off feeding opportunities with thermal tolerances that together can typify changes in seasonal distribution (Hays et al., 2004). Clearly, species with physiological or behavioural adaptations that expand seasonal spatial distributions, or extend temporal occupation of favoured areas beyond that of potential competitors, may help identify why certain behaviour patterns are utilised as environments change. Furthermore, a predictive framework for understanding species spatial dynamics and the consequent

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0022-0981/$ – see front matter © 2008 Published by Elsevier B.V.
doi:10.1016/j.jembe.2008.12.002

population re-distributions will be invaluable in guiding the management and conservation of vulnerable species that often undertake long-distance movements or migrations across political-economic boundaries (Robinson et al., 2008). However, for the majority of large marine vertebrates, data on movements and behaviour in relation to environment has not been collected. This is usually because even though appropriate technology may be available, species may be relatively rare throughout much of their range, and hence difficult to find in sufficient numbers to support tagging studies.

Within lamnid sharks, a family comprising five of the largest predatory, endothermic sharks, satellite tracking and archival tagging technologies have been used to demonstrate niche expansions in white shark, *Carcharodon carcharias* and salmon shark *Lamna ditropis*, not only geographically, but also vertically and thermally (e.g. Boustany et al., 2002; Weng et al., 2005). Salmon sharks for example appear able to remain in high-latitude feeding areas due to physiological adaptations associated not only with endothermy but with maintenance of cardiac muscle performance in cold water, characteristics not present in ectothermic sharks that are potential competitors (Weng et al., 2005). Shortfin mako *Isurus oxyrinchus* have also been the subject of electronic tagging studies (Holts and Bedford, 1993), however there are no similar studies of porbeagle shark *Lamna nasus*. There is a need for archival tagging of this species to determine geographical extent, spatial dynamics and habitat preferences, because this warm-bodied shark (Burne, 1923) may be capable of remaining in high-latitude locations irrespective of season, where it may remain particularly vulnerable to targeted fisheries.

Porbeagle shark grow to over 3 m total length, inhabiting waters between 5 and 20 °C (Campana and Joyce, 2004) in temperate seas of the North and South Atlantic, as well as the Mediterranean and the Baltic seas (Compagno, 2001). Like most pelagic sharks it is particularly prone to over-exploitation by fisheries due to relatively slow growth rates, a late age at sexual maturity (Natanson et al., 2002) and low fecundity (Jensen et al., 2002). It has been cited as a notable example of stock collapse in a chondrichthyan species (Stevens et al., 2000). Porbeagle sharks have been heavily exploited since the 1930s in the North-East Atlantic, principally by countries such as Denmark and Norway. In the late 1950s the north-east porbeagle fishery was apparently depleted, becoming uneconomical and, as a consequence, by the 1960s the principal fishing grounds moved to the North-West Atlantic off the coast of Canada. However, by 1967 the north-west fishery suffered large decreases in catches (Campana et al., 2008). It is estimated that population numbers of mature individuals were reduced to 21-24% by the early 1990s due to unsustainable fishing efforts (DFO, 2005). Despite this, there are no regulated management plans for this species and recent proposals for conservation listing (e.g. Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)) were rejected due to the lack of basic biological data. In particular, very little is known about porbeagle shark spatial ecology, movement and habitat preference to inform conservation. Mark-recapture in the North-West Atlantic since the 1960s has revealed seasonal migration in Canadian waters, with porbeagles captured by fisheries found mainly in northeastern waters during the spring, and more south-westerly in the summer and autumn, with some individuals caught 500-1000 km from their tagging location (Campana et al., 2003). It was concluded that these animals moved short to moderate distances along the continental shelves, and only one individual was observed to move far off the shelf (Francis et al., 2008). Number tag returns from commercial fisheries in the North-East Atlantic reported *L. nasus* recaptures occurring mainly in the same area as they were released off southwest England and northern France, with only one individual being recaptured far to the north (2,370 km straight line distance) (Stevens, 1976, 1990). Indeed, of some 1,850 tags deployed, only one individual is known to have crossed the Atlantic, from Ireland to Canada, traversing some 4,260 km (P. Green, personal communication in Francis et al., 2008) suggesting ocean-basin-scale movements may be rare.

The purpose of the present study therefore was to test, using satellite-linked archival tags (a fishery-independent method of monitoring movements), whether porbeagle sharks exhibit largely localised movements, as suggested from conventional number tagging. Secondly, since tags collect data on swimming depth of sharks and water temperatures experienced it was also possible to describe for the first time the sub-surface behaviour and habitats occupied by porbeagles.

2. Materials and Methods

2.1. Transmitter Tagging

Porbeagle sharks were caught using rod and line with circular hooks to facilitate removal. They were brought on board for body-length measurement and tagging, which lasted no longer than 5 min prior to release. Four porbeagle sharks were fitted with pop-up satellite archival transmitters in July 2007 off the south-west UK (Fig. 1). Shark 1 was tagged with a Mark 4 pop-up archival transmitting tag (PAT4, Wildlife Computers, Redmond, USA), an archival data logger with an Argos-certified satellite transmitter, which collects data on pressure (depth) (maximum depth = 1000 m, accuracy = 0.5 m), temperature (temperature range = -40 °C - 60 °C, accuracy = 0.05 °C) and light level (at 550 nm wavelength). The tag was programmed to detach after 60 days and sampled each parameter every 20 seconds. A further 3 sharks (#2 – 4) were tagged with Mk 10 PAT tags (Wildlife Computers) with pressure (depth), water temperature and ambient light level sampled each second throughout the deployment. All four tags were attached in the dorsal musculature using a 5 cm stainless steel T-bar, with a 25-cm long monofilament (250 lb test) connection to the tag, inserted 10 cm deep at a 45° angle. The PAT Mk10s were programmed to detach 30, 60 or 90 days post-deployment. After detachment, each tag floated to the surface and was geolocated by Argos receivers on NOAA polar-orbiting satellites. Estimated accuracy of these 'pop-up' locations as determined by Argos was 150 – 250 m (Argos location class 2, respectively).

2.2. Track Reconstructions

The movement of each shark was estimated using data recovered from each tag or, for one tag (PAT Mk10), from archival data after it was physically retrieved after being washed ashore. Positions of each shark between attachment and tag pop-up were reconstructed using satellite retrieved or archival data of daily maximal rate-of-change in light intensity to estimate local time of midnight or midday for longitude calculations, and daylength estimation for calculating latitude, both using software provided by the manufacturer (WC-GPE: Global Position Estimator Program suite, www.wildlifecomputers.com) (Sims et al., 2006a). Anomalous longitude estimates resulting from dive-induced shifts in the estimated timings of dawn and dusk from light curves were discarded from the data set. Geolocations > 3° of longitude from the previous longitude estimate were also removed. Latitude along the longitude was then estimated using a purpose-written program in Matlab (MathWorks Inc., MA, USA). Here, latitude was fixed by matching minimum and maximum tag-recorded water temperatures from the shallowest depth bin recorded in each 4-h period to sea surface temperature (SST) values on night-time, 8-day summary Moderate Resolution Imaging Spectroradiometer (MODIS) remote-sensing images. The most parsimonious location was derived by matching individual pixel SSTs within a variable-sized circular area (radius 100 - 500 km) around the previous tag position. If no matches were made within the smallest area, the radius was increased incrementally until matches occurred. Variable-sized areas were used because geolocations were not always determined daily due to gaps in satellite-received data, so travel distances could exceed the estimated 100 km daily maximum. A geographic mean position was

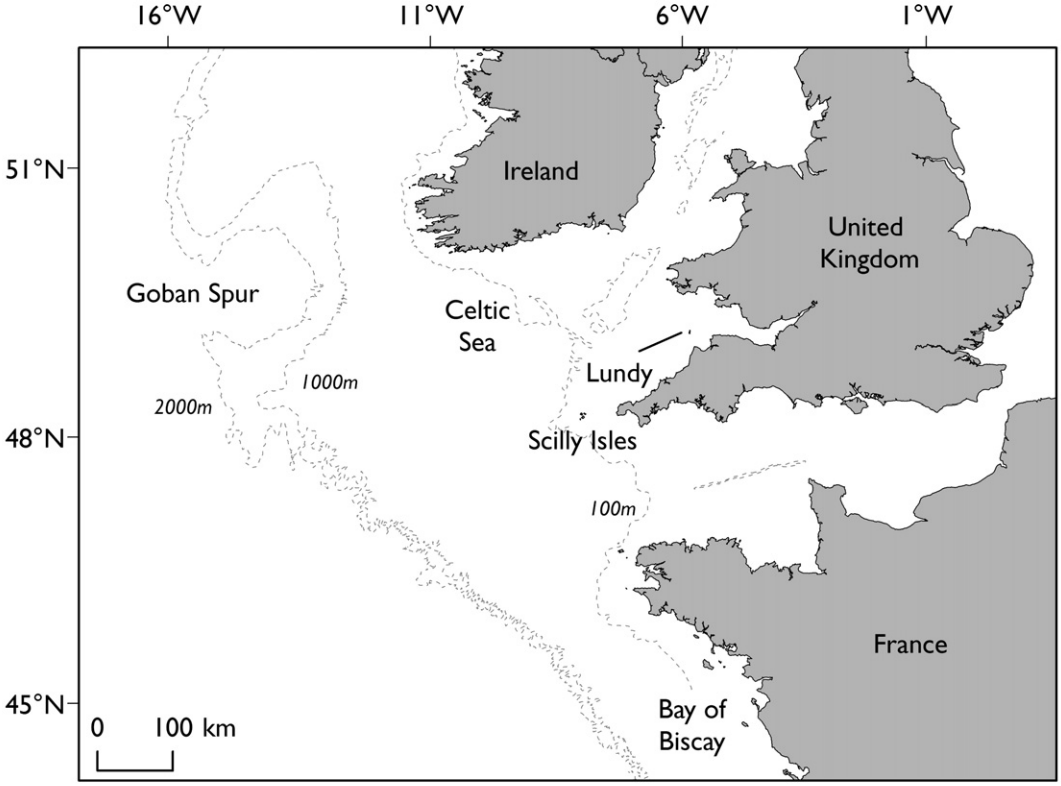

Fig. 1. Map of the study area in the North-East Atlantic with location place names mentioned in the text.

calculated from all possible pixel locations within this area to derive each track position. Maximum dive depth on the day each position was estimated was compared with seabed depths from a digital bathymetric map within each area to filter anomalous positions where the dive depth recorded was greater than seabed depth. Intermediate waypoints were applied to track steps where trajectories between located positions crossed land. The final estimated positions were then analysed point-to-point with a 1 m s^{-1} swim-speed filter (equivalent to 86.4 km per day straight-line travel distance) that is consistent with cruise speeds of other pelagic shark (Sims, 2000). A position separated from an adjacent position by a distance too great to achieve in the speed-filter-imposed time between those positions was shifted to the location along the track where the imposed speed limit provided an acceptable distance. Estimated mean error distance of light/SST geolocation compared with tagging or pop-up locations was 78.0 km ± 21.4 S.D. (range 54.7 – 100.0 km).

2.3. Habitat Area Estimation

The core habitat (space) use of each shark was estimated from α-hull bounding polygons (Burgman and Fox, 2003). Briefly, a Delaunay tessellation from each shark's geolocation pattern was constructed to form a network of triangular polygons. All connections in the triangulation were measured and connections with a length greater than the mean length plus 1.5 standard deviations were excluded. The area of any remaining triangles was then calculated and summed and for the purposes of display (Fig. 2) the remaining triangle edges were dissolved to form a concave polygon for each shark.

3. Results

In total, 3 males and 1 female were tagged, with all four tags reporting data. The tag attached to shark 1 uplinked to Argos satellites but transmitted only a few messages. Inspection of the data indicated the tag detached prematurely from the shark after about 22 days (data after this time were disregarded). The tag attached to shark 2 released and transmitted data to satellites on time, however because the tag popped up within 3 km of the shore, it was quickly blown ashore and messages were not received thereafter. However, this tag was physically recovered and a full archival dataset for the 30-day deployment was downloaded. The tag attached to shark 3 collected data for 34 days but a constant depth was recorded for the remaining 26 days prior to release. The fourth tag (shark 4) popped up and transmitted on schedule after 90 days. In total, porbeagle shark movements and behaviour were tracked for 175 days, covering an estimated total distance of 10,256 km from a total of 88 geolocations. The relatively large errors associated with light-level based geolocations make accurate identification of actual distances travelled hard to attain (Bradshaw et al., 2007). The estimated errors of light-level geolocations determined for porbeagles was between 50 and 100 km. However, even given these errors, the distances between tagging and pop-up locations were between 38 and 397 km for sharks 1 – 3, and 596 km for shark 4 (Table 1), indicating the distances over which they moved in 22 – 90 d were relatively small.

3.1. Horizontal Movements

From estimated light-level/SST geolocations it appears shark 1 left the general tagging area off the north coast of the southwest peninsula of the UK during the first 10 days, heading south to the western English Channel and the European continental shelf edge and undertaking dives to over 400 m depth (Figs. 1 and 2a). This was the only individual to head south towards the shelf edge during the first 30 days after tagging and, as such, the space use estimate was high relative to the 22 day track time (42,753 km^2; Fig. 2a). For much of July and August sharks 2 – 4 remained within a relatively localised area of the Celtic Sea; broadly an area between the south-west UK and south-west Wales and southern Ireland (bounded by co-ordinates 49.0 – 52.3° N and 4.0 – 8.0°W) (Fig. 2b–d). Shark 2 was estimated to have

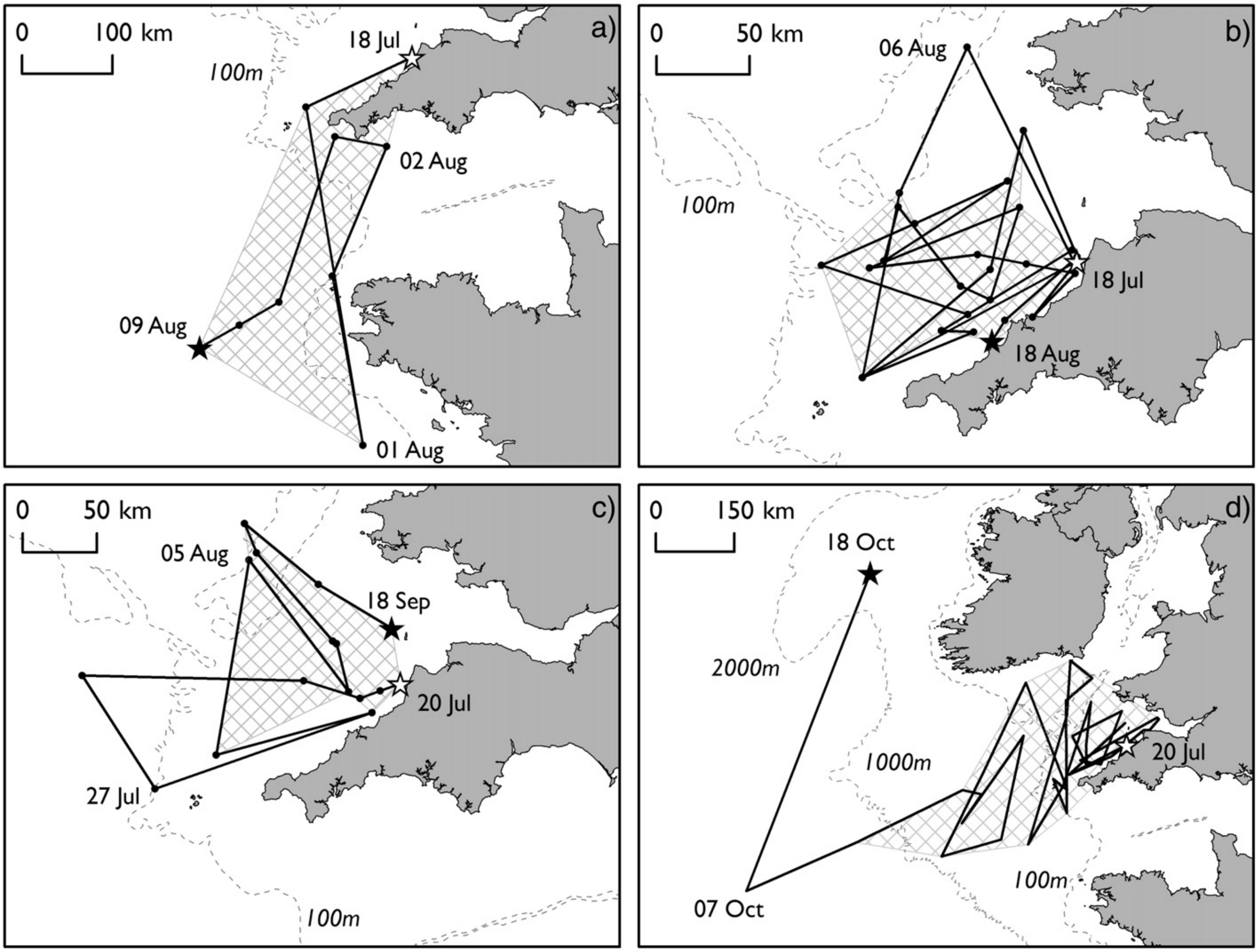

Fig. 2. Movement and core areas occupied by four porbeagle sharks, *L. nasus*, tagged with PSAT tags. (a) Shark 1 (male); (b) shark 2 (male); (c) shark 3 (female); (d) shark 4 (male). Open star symbol indicates tagging location, closed denotes tag pop-up location. Small black circles represent estimated position at indicated date. Hatched areas denote α-hull concave bounding polygons that estimate core habitat areas used by individual sharks. Core areas: Shark 1, 42753 km^2; shark 2, 8602 km^2; shark 3, 9961 km^2; shark 4, 90153 km^2.

used the smallest geographical area of all sharks tracked (8,602 km^2; Fig. 2b) with most geolocations being associated with the inshore coastal features of north Cornwall. Indeed, the tag popped up <5 km from shore after 30 days attachment time (Fig. 2b). The movements of shark 3 differed from shark 2; more geolocations were fixed offshore for this individual, with an apparent movement west from the tagging area within 7 days of tag attachment, with a return movement into shallower water at the beginning of August, before a second movement into deeper water prior to the shark moving close to a nearshore island off north Cornwall where the tag popped up (Fig. 2c). However, the space use estimate was only slightly greater (9,961 km^2) than that of shark 2 because most geolocations were inshore. Shark 4 was the only shark tracked past the month of August (Fig. 2d). During July and August the distribution pattern of geolocations was similar to sharks 2 and 3, with inshore and offshore movements evident (Fig. 2d). However, during early September estimated geolocations occurred consistently further south and west, with several locations in the vicinity of the continental shelf edge resulting in a much larger core space use estimate of 90,153 km^2 compared with all other sharks. By early October, shark 4 was located over deep water south of the shelf edge. Eleven days later the tag popped up and was geolocated by Argos satellites about 650 km north in the region of the Goban Spur on the shelf edge, some 150 km west of Ireland. (Fig. 2d). This indicates a transition for shark 4 from relatively localised movements in the summer to longer range movements at the beginning of autumn.

3.2. Vertical movements and water temperature

Overall, sharks 1 – 4 demonstrated a wide vertical distribution occupying depths from the surface to 552 m, and a water temperature

Table 1
Summary data of the four *L. nasus* tagged with pop-up satellite-linked archival tags off south-west UK

Shark	ID	Sex	Fork Length (m)	Location Tagged	Tagging Date	Pop-up Date	Distance between tagging and tag pop-up (km)	Days at liberty	Pop-up Latitude (°N)	Pop-up Longitude (°W)
1	60587	Male	1.80	Cornwall	18/07/07	13/08/07	397	22	49 18.43	07 52.57
2	40394	Male	1.85	Cornwall	20/07/07	18/08/07	63	30	50 26.05	05 08.46
3	40395	Female	1.60	Cornwall	20/07/07	22/08/07	38	34	51 12.52	04 49.10
4	40396	Male	1.80	Cornwall	20/07/07	18/10/07	596	90	52 44.29	12 44.14

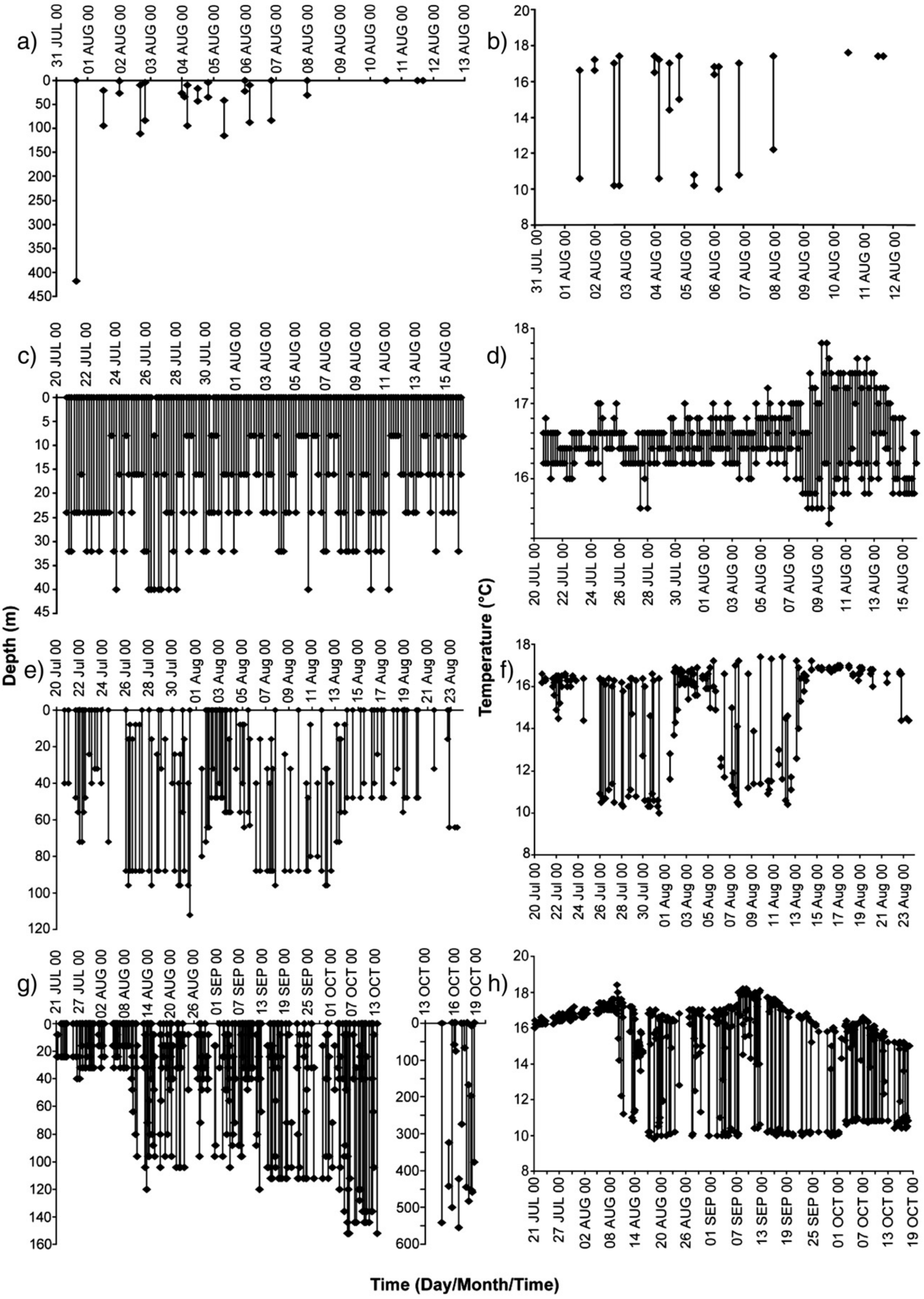

Fig. 3. Minimum-maximum depths and water temperatures occupied by four tagged *L. nasus*. Black lines show the range of temperatures and depths that each shark experienced on each day data was available. Shark 1: a, b; shark 2: c, d; shark 3: e, f; shark 4: g, h.

range from 9.8 to 18.5 °C. Maximum depth for sharks 1 – 4 were 416, 40, 112 and 552 m respectively, and largely reflected the sea bottom depths of the shelf/shelf-edge habitats they occupied. When occupying shelf waters the four *L. nasus* tracked appeared to utilise much of the water column available to them (Fig. 3). Diving behaviour often extended from the surface to the maximum depth available in waters <120 m, and dives often commenced from the surface (Fig. 3a,c,e,g). Shark 2, that remained principally inshore, showed consistent movements from the surface to depths between 8 and 40 m in each consecutive 4-hour period for the 30-day tag deployment time, with only two periods during which it did not approach the surface (Fig. 3c). Water temperatures experienced by shark 2 varied little, between only about 16 and 17 °C in the first 3 weeks post tagging, whereas a much wider range in the final week (15.3 – 17.8 °C) indicated dives through more strongly stratified waters (Fig. 3d). Shark 3 showed similar vertically extensive diving behaviour in shallow water (<50 m), but during the two periods of time when it occupied deeper waters of the Celtic Sea (<120 m) in late July and early August, its behaviour was different (Figs. 2c and 3e). Although in each 4 h period movements between the surface and the maximum depth occurred, there were also times during both offshore intervals when the shark remained at depth (between about 30 and 90 m) for an entire 4 hour period, and sometimes even between consecutive periods (Fig. 3e). During diving in offshore habitats the range of water temperatures occupied was between 9 and 18 °C, which reflected at least some vertical movements through strongly stratified waters compared with further inshore (Fig. 3f). When it remained at depth in offshore waters of the Celtic Sea, shark 3 was often below the thermocline (Fig. 5f).

Sharks 1 and 4 were the only ones tagged that made dives below 120 m (Fig. 3a–g). These deep dives were consistent with horizontal movements away from the continental shelf edge (>200 m depth) (Fig. 2a,d). Shark 4 showed a progressive movement from shallower inshore areas near the coast (<40 m) in July and early August to waters down to 120 m deep further west in the Celtic Sea until late September (Fig. 3g). When inshore, shark 4 ranged from the surface to depth (20–30 m) during each consecutive 4-h period, whereas when offshore dives from the surface to the deepest depth (over 100 m) were less frequent. As with shark 3, when in deeper waters shark 4 often remained at depth during a 4 h period, however, over a 24 h period, movements between the surface and maximum depth were common (Fig. 3g). Off shelf and shelf edge areas were occupied in October where dives reached a maximum of 552 m. On several occasions movements ranged from the

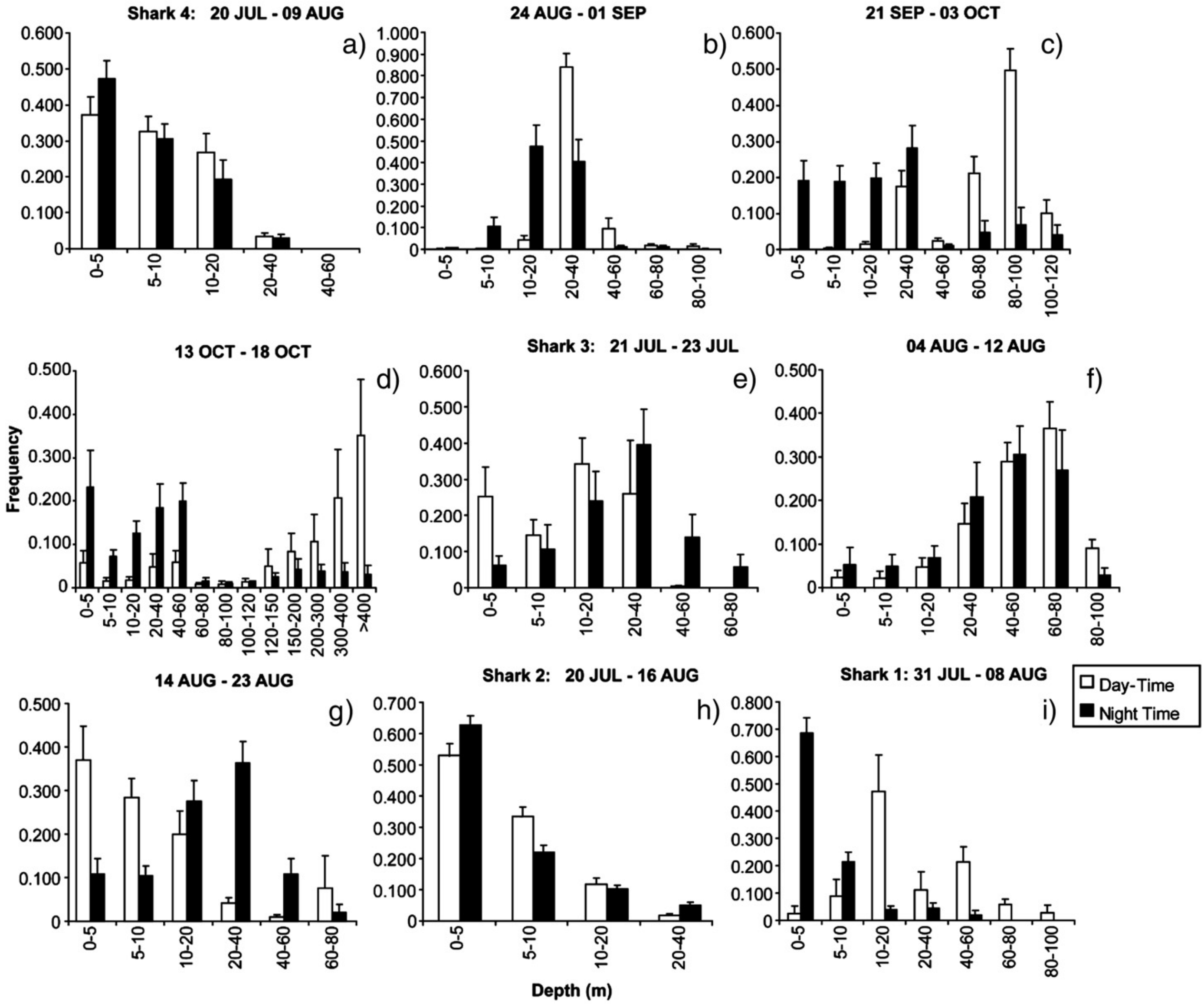

Fig. 4. Depth distributions of four *L. nasus* showing diel changes in vertical movement. Mean frequency (proportion) of time at depth (±S.E.) was determined using all 4-h sampling periods received from satellites within day (08:00 – 20:00 h) (white bars) and night (20:00 – 08:00 h) (black bars) phases.

surface to 500 m in a 4 h period, although on two occasions the entire 4-h time period was spent at depths between 325 and 440 m, and 425 and 552 m, respectively (Fig. 3g). Water temperatures experienced by shark 4 varied little inshore (16.0–17.6 °C), but were indicative of vertical movements through the thermocline in deeper Celtic Sea and off-shelf habitats, where they ranged from 9.8 to 18.2 °C (Fig. 3h).

Despite fewer data being available for shark 1, the results were consistent with the general patterns found for the other sharks tagged. For example, vertical movements from the surface to >400 m were recorded within a 4 h period when the shark was geolocated off the continental shelf, while in shallow waters shelf-associated dives occurred from surface or near surface waters to between 90 and 120 m depth (Fig. 3a). As with sharks 3 and 4, water temperatures occupied during surface-100 m dives in offshore waters of the continental shelf ranged from 10 to nearly 18 °C (Fig. 3b).

3.3. Diel depth changes

The diel vertical movements of tagged porbeagle sharks indicated both intra- and inter-individual differences, both within and between areas occupied. Within the same habitat, similar as well as different diel depth changes were evident. For example, between 20 July and 9 August when in shallow (<40 m depth) coastal habitat, shark 4 spent the highest proportion of time in surface waters (0–5 m) during both day (37%) and night (47%), with the least amount of time spent between 20 and 40 m (<4%) (Fig. 4a). The same pattern of surface occurrence was also shown by shark 2 in coastal waters between 20 July and 16 August (Fig. 4h). However, between the 21 and 23 July the vertical movements of shark 3 were different. More time during daytime was spent near the surface (0–5 m) and at 10 – 20 m depths, whereas during nighttime nearly 60% of time was spent deeper at 20 – 40 m and at depths between 60 and 80 m (Fig. 4e). Profiles of water temperature at depth indicate that the water column in the shallow coastal areas occupied by sharks 2 – 4 was relatively isothermal, characteristic of well mixed, tidally influenced waters (Fig. 5a,e,h).

Shark movements into deeper waters of the Celtic Sea between late August and early October were characterised by a different pattern of diel movements. Between 24 August and 1 September shark 4 spent over 80% of time during the day at 20 – 40 m depth but ascended into shallower depths at night (Fig. 4b). This pattern changed further,

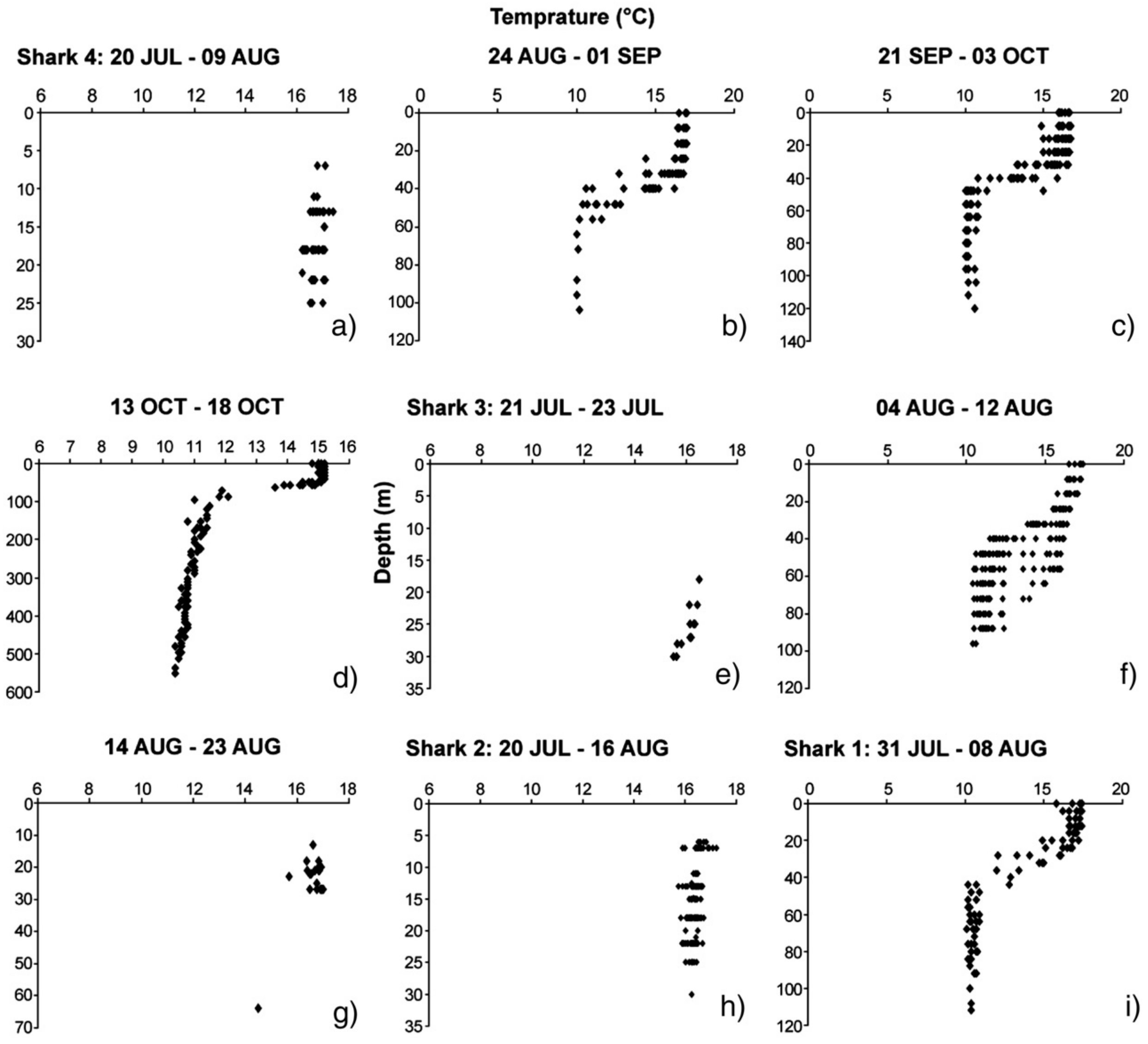

Fig. 5. Water temperature-at-depth profiles for corresponding the depth distributions shown in Fig. 4. Porbeagles dived through isothermal water as well as through pronounced thermoclines. Sharks 2, 3 and 4 occupied water with similar thermal depth profiles in shallow water where temperatures fluctuated little (16°-18 °C) early in the study period (a,e,h). In stratified water sharks undertook diel vertical migration, often encountering temperature changes of more than 5 °C (b,c,d,i). Shark 3 also undertook diel vertical migration, however this was not concentrated around the thermocline (e,g).

however, as the shark moved into deeper water (down to 120 m) to a bimodal distribution of time at depth, with depths below 60 m occupied for 80% of the daylight hours, whereas during the night nearly 90% of time was spent above 40 m (Fig. 4c). The areas occupied by shark 4 between late August and early October were strongly stratified vertically, with the thermocline depth at about 40 m (Fig. 5b,c). The depth preferences of shark 4 were therefore associated with the thermocline depth in water <100 m deep, but in water <120 m deep most time was spent below the thermocline in daytime and above it during night time. This general diel pattern broadly continued when shark 4 moved to shelf edge and off-shelf habitats, however there were some important differences. At night between 13 and 18 October, about 80% of time was spent above 60 m, whereas during the day 70% of time was spent below 120 m, and with more than 35% of time below 400 m (Fig. 4d). This indicates that the thermocline zone itself (between 50 – 100 m) was generally not occupied, rather the warm stratified layer above (~15 °C) during the night, and the colder layers below (10 – 11 °C) during the day (Figs. 4d and 5d).

A similar pattern of surface water occupation during the night (90% of time less than 10 m) and deeper during the day (>10 m) was recorded for shark 1 in waters of the Celtic Sea <100 m depth (Fig. 4i). In contrast to shark 4, this did not appear to be clearly associated with the thermocline depth of 20 – 40 m (Fig. 5i).

The diel pattern seen for sharks 1 and 4 was not observed for shark 3 however, even though it occupied the same general area of the Celtic Sea. Between 4 and 12 August shark 3 showed no clear difference in time spent at depth during day and night, even though a thermally stratified water column was evident in at least some of the locations occupied, with a thermocline depths at 30 – 40 m (Fig. 5f). This lack of diel differences in depth preference shifted when shark 3 moved into water <100 m deep further north near Lundy Island (Fig. 2c). Between 14 and 23 August, over 65% of time was spent shallower than 10 m during the day compared with during the night when about 65% of time was spent below 10 m (Fig. 4g). Although a diel pattern was apparent (daytime shallow, night time deep), it was the reverse of that seen for sharks 1 and 4 (daytime deep, night time shallow), and more similar to the pattern shown when shark 3 was in coastal waters off north Cornwall (Fig. 4e).

4. Discussion

To our knowledge this is the first study to track the horizontal and vertical movements of the endothermic porbeagle shark, *Lamna nasus*, with electronic tags. The results of tagging four porbeagles with satellite-linked archival transmitters indicated that: (1) during summer months they show some fidelity to coastal and shelf habitats with estimated core habitat use ranging from 8,602 to 90,153 km^2; (2) towards late summer and early autumn a long-distance movement to shelf edge and off-shelf areas was apparent for the single shark we tracked across these seasons; (3) behavioural plasticity in diel depth preferences was evident both within and between individuals and as a function of habitat depth. The study also demonstrated that porbeagle sharks move through the water column on a very regular basis, but also often spend long periods of time near the surface, especially at night in some areas. In off-shelf habitat this species is also capable of deep dives to at least 552 m, where they may remain for many hours.

4.1. Horizontal and Vertical Movements

A principal aim of this study was to test whether porbeagle sharks in the north-east Atlantic remain associated with relatively localised areas for appreciable lengths of time. The motivation for this investigation was to better understand the space use of *L. nasus* with respect to its conservation given that large declines in population have been recorded in the Atlantic as a consequence of fishing (Campana et al., 2008). A contributing factor to such declines may be the propensity of porbeagles to aggregate for seasonal feeding opportunities in coastal areas where they become readily available to fisheries. Even though in the present study only four *L. nasus* were tagged, it was apparent that three sharks remained in a localised area of the North Cornwall coast and Celtic Sea for at least a month during summer. Although the light-level/SST geolocation method cannot resolve fine-scale horizontal movements (for discussion see Sims et al., 2006a), data indicated movements into deeper water of the Celtic Sea in addition to coastal occupancy. The one shark tracked past one month exhibited a gradual movement into deeper water prior to a relatively rapid, long-distance movement ending up 150 km west of Ireland after 90 days. The results broadly support earlier findings from mark-recapture tagging. Stevens (1990) marked 26 porbeagle shark in the English Channel between 1972 and 1980. Among the eight recaptures made during 1975–1986, three sharks were recaptured in the same area they were released either in the same year or up to several years later, two were recaptured in the Bay of Biscay in winter and early spring between 0.75 and 3.0 years later, while one shark was recaptured 13 years later in northern Norway, some 2,000 km away (Stevens, 1990). In the North-West Atlantic, porbeagles are believed to be present in the shallower waters of the shelf during the spring and summer, before heading into deeper water during the winter (Campana et al., 2002), a pattern consistent with our 3-month tracking of a porbeagle in the North-East Atlantic.

The purpose of localised aggregations of porbeagle shark in shallow coastal waters is not known but most likely relate to feeding opportunities. It is not uncommon to find otherwise pelagic species on the continental shelf. Albacore tuna (*Thunnus alalunga*), salmon shark (*L. ditropis*) and mako shark (*Isurus oxyrinchus*) utilise rich, productive coastal waters in the summer to feed (Beamish et al., 2005; Stevens, 2008; Weng et al., 2005). In this study porbeagles were captured for tagging off north Cornwall where three fish remained for at least a month. This area is characterised by persistent tidally induced thermal fronts (Sims et al., 2000; Sims et al., 2006a) which aggregate zooplankton patches that are attended by schooling fish such as Atlantic mackerel, *Scomber scombrus* (Sims and Quayle, 1998) (see Section 4.2 for more detail on fronts). *S. scombrus* is a predominant prey type of porbeagle shark in the North-East Atlantic (Stevens, 1973) and particularly large mackerel schools are present annually during mid to late summer inshore off the north coast of the UK south-west peninsula; these are also predated by huge aggregations of diving seabirds, often comprising up to 8,000 individuals (Darlaston, 2003). Therefore, it is likely that porbeagle sharks also aggregate and remain in this locale due to the high seasonal availability of energy-rich fish prey. Electronic tag records showed very regular vertical movement through the water column to the seabed depth on a daily basis, with some longer-term patterns evident (see Section 4.2), behaviour most likely related to porbeagles undertaking extensive foraging searches of the water column during coastal movements. Interestingly, data from the Canadian long-line porbeagle fishery showed that *L. nasus* has litte affinity with fronts in the fall, suggesting that the species only seek out these fronts in spring and summer months (Campana and Joyce, 2004). The application of archival tags that measure stomach temperature in the endothermic porbeagle (where drops in temperature occur after ingestion of cold-bodied fish prey) may shed further light on the interaction between movements and feeding success (Austin et al., 2006; Bestley et al., 2008).

Taken together with this study, the movement data for porbeagle in the North-East Atlantic overall indicates fidelity to particular areas such as the Celtic Sea and English Channel. In addition, long-distance movements away from such areas, that may be seasonal in occurrence, appear characteristic of porbeagle spatial ecology observed elsewhere. Longer term deployments of tags with pop-up times in winter will determine whether the northward movement we observed in autumn was likely part of a seasonal migration of North-East Atlantic porbeagles. At mid to high latitudes in the North-West and North-

East Atlantic large ectothermic marine vertebrates such as basking shark (Sims et al., 2003; Skomal et al., 2004) and leatherback turtle (Hays et al., 2006; James et al., 2005; McMahon and Hays, 2006), generally move southward as seas start to cool in early autumn. Northward movements around the same time by the porbeagle shark tagged in this study may illustrate how physiological endothermy is advantageous at higher latitudes for allowing exploitation of prey resources that become seasonally unavailable to ectothermic predators such as the blue shark *Prionace glauca* (Weng et al., 2005), that also feed on mackerel in the Celtic Sea and English Channel (Stevens, 1973) and appear to make southerly migrations to warmer waters in autumn and winter (N. Queiroz, D.W. Sims, unpublished data). In the North-East Atlantic, high concentrations of mackerel eggs are located on the Celtic Sea shelf-edge indicating adult spawning aggregations during summer, extending into late summer (Coombs and Mitchell, 1981; Coombs et al., 1990). However, adult mackerel are also known to over-winter in deep waters of the continental shelf and along shelf edges (Studholme et al., 1999) so it is possible that porbeagles disperse into deeper water in northern regions in autumn and winter to track seasonal distributions of fish prey. The vertical movement data for shark 3 and 4 in our study showed very regular deep diving continued when sharks moved into deeper water, with some very deep dives to over 550 m by shark 4 off the shelf edge. This demonstrates that regardless of habitat type occupied, a consistent behaviour of porbeagle shark is to undertake vertical searches regularly, and on at least a 4-h time scale. This is an effective strategy for detecting clues to prey location because olfactory trails spread horizontally in the ocean due to current shear between different density layers (Carey and Scharold, 1990), so moving vertically enables the greatest chance of detecting trails. Such regular patterns of vertical movement have been observed in other large sharks including blue, tiger (*Galeocerdo cuvier*), and the endothermic salmon shark, so this appears a general characteristic of large pelagic shark behaviour (for review see Sims, in press). Endothermic sharks may have an energetic advantage over ectotherms in being able to remain at colder depths for longer. Our results support this idea of vertical as well as horizontal habitat expansion for endotherms because shark 4 was recorded to have remained at depths between 325 and 552 m and temperatures down to ~10.5 °C for up to 4 hours.

It is possible that the spatially limited movements by tagged porbeagles reflect not only feeding opportunities but are linked to searching for mates. Since we tagged mature males and an immature female, and mature and pregnant females have been captured off south-west England (Caunter, 1961), this possibility cannot be discounted. Generally little is known about the distribution of sexually mature porbeagles in UK waters but it may be important as a feeding, breeding and parturition area for porbeagle.

4.2. Diel depth changes

Changes in diel use of vertical habitats was a striking feature of the current study both within and between individual sharks. The within-individual differences were most closely related to changes in habitat use by each shark and were characterised by changes in seabed depth. On the European continental shelf, thermal structuring of the water column is strongly dependent on the relationship between tidal stream strength and water depth (Pingree, 1978). In shallow waters where tidal streams are strong, the water column is well mixed vertically, whereas in deeper water tide has less influence and the water column stabilises resulting in vertical thermal stratification (Le Fèvre, 1986). The boundaries between deeper, well stratified and shallow, well-mixed waters are transitional or frontal zones where the thermocline outcrops at the surface; these are associated with high zooplankton and pelagic fish abundance (Sims and Quayle, 1998; Sims et al., 2005). For sharks 2 and 4 in well-mixed coastal waters (<60 m deep) there were no apparent diel differences in depth occupancy, whereas shark 3 in water <80 m depth remained predominantly in surface waters in daytime and >20 m depth at night. In contrast, when shark 4 moved into thermally well-stratified deeper waters (<100 m deep) most time during the day was spent at the thermocline depth (20 – 40 m) with a partial shift above it at night. In deeper shelf water (to 120 m depth) this pattern changed, with daytime spent below the well defined thermocline (gradient of 5 °C between 30 and 40 m) and night time above it. In shelf-edge and off-shelf habitats, this pattern was even stronger, with very little time spent at the thermocline depths (4 °C change between 50 and 100 m) but considerable time below it during the day and above it at night.

These diel depth patterns are all consistent with those recorded for the large plankton-feeding basking shark (*Cetorhinus maximus*) (Sims et al., 2005) and may point to at least some commonalities in responses. This is reasonable to assume since the schooling fish prey of porbeagle sharks (mackerel, herring *Clupea harengus*) also feed on zooplankton, so diel depth changes of porbeagle prey may be similar. The pattern shown by shark 3 in well-mixed coastal waters was consistent with a reverse diel vertical migration (rDVM) pattern (dusk descent – dawn ascent) observed for basking shark foraging on zooplankton in thermal fronts (Sims et al., 2005). In transitional coastal waters zooplankon often aggregate in surface waters during the day, which may influence schooling fish distribution. In deeper, well-stratified waters of the Celtic Sea and shelf edge, porbeagles undertook normal DVM (nDVM) (dusk ascent – dawn descent) presumably in response to vertically migrating fish prey like herring (Huse and Korneliussen, 2000). Interestingly, basking sharks also shift diving pattern to nDVM in well-stratified habitats since zooplankton there undertake predominantly nDVM (Hays, 2003; Sims et al., 2005). Similarly, diel vertical movements have also been observed in other sharks (Holts and Bedford, 1993; Sepulveda et al., 2004), tuna (Lutcavage et al., 2000; Musyl et al., 2003), billfish (Gunn et al., 2003) and turtles (Hays et al., 2004). Our observations of diel depth changes by porbeagle sharks indicate considerable plasticity in individual movements across coastal, shelf and shelf-edge habitats that probably reflect the changing distributions and availability of prey resources. Coastal waters of the continental shelf represent important feeding grounds for porbeagle shark seasonally. Analysis of porbeagle stomach contents from Canadian waters indicate pelagic fish and cephalopods dominate diets in spring when sharks are further offshore on the Scotian shelf, whereas in autumn the amount of demersal fish in diets increases with movements into shallow waters of the Grand Banks and the Gulf of St. Lawrence (Joyce et al., 2002). The presence of different prey types in porbeagle stomach contents (Stevens, 1973) may reflect the need for different search behaviour and/or habitat use by sharks in locations or at times when specific prey types are available. The apparently variable diet of porbeagles within and between different habitats may explain this study's results of inter-individual differences and similarities in diel depth changes and shifts in vertical pattern according to broader habitat changes.

4.3. Conservation implications

The sharks tagged in the current study comprised three males and one female. The single female (shark 3), stayed in the same coastal and offshore areas of the Celtic Sea as the two males that also remained (sharks 2 and 4). This indicates the region is occupied by both sexes during the summer months. All three males tagged were sexually mature, although the female was most likely immature (Jensen et al., 2002). Thus the areas occupied in the Celtic Sea are probably utilised by adult males and sub-adult females, but with a bias towards males as a previous study also indicates for this study area (Ellis and Shackley, 1995). Although segregation by sex and age is common among sharks and other vertebrates, it is possible that sex-biased exploitation may occur for porbeagle shark in European waters and may exacerbate declines already observed (Wearmouth and Sims, 2008). In this regard, our results in particular identify that porbeagle sharks exhibit area site fidelity (bounded by co-ordinates 49.0 – 52.3° N and 4.0 – 8.0°W) for at least part of the summer in coastal and shelf waters where fisheries are intensive (Witt and Godley, 2007), including targeted longlining for pelagic shark. This apparent aggregative behaviour by *L. nasus* may be seen to enhance this species' risk of capture in the absence of catch controls in the European area. Given that declines of porbeagle of up to 90% of their historical biomass have been suggested in the North-East Atlantic (Stevens et al., 2006), identifying aggregation areas occupied seasonally by this species will be important in the context of marine protected areas (MPAs). Satellite tags have the potential to measure mortality of individuals directly (Hays et al., 2003; Graves and Horodysky, 2008) which may provide fisheries independent catch rates and locations of porbeagles in the future. Furthermore, the large scale movement of shark 4 over an estimated distance of nearly 6,000 km provides clear evidence that this species crosses national political boundaries, perhaps seasonally. From September to October 2007 shark 4 crossed from the UK fishing zone into International waters (i.e. not within the 200 nautical mile zones of UK, France or Ireland), before moving into the Republic of Ireland fishing zone. Therefore, our results indicate porbeagle shark should be considered for protected status listing on the Convention for the Conservation of Migratory Species of Wild Animals (CMS) (Bonn Convention).

Acknowledgements

This research was facilitated through the European Tracking of Predators in the Atlantic (EUTOPIA) programme in the European Census of Marine Life (EuroCoML). The authors thank R. Peirce, K. Bennett, and the 2007 field season participants for facilitating tagging. NGP was supported by a University of Aberdeen Scholarship and PADI Aware provided additional funding. NQ was funded by Fundação para a Ciência e a Tecnologia (FCT) grant SFRH/BD/21354/2005. DWS and a part of this research was supported through the Marine Biological Association of the UK (MBA) component of the Natural Environment Research Council (NERC) Oceans 2025 Strategic Research Programme (Theme 6 Science for Sustainable Marine Resources). DWS was also supported by an MBA Senior Research Fellowship. **[SS]**

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