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Transatlantic migration and deep mid-ocean diving by basking shark

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Despite being the second largest fish, basking sharks (*Cetorhinus maximus*) have been assumed to remain in discrete populations. Their known distribution encompasses temperate continental shelf areas, yet until now there has been no evidence for migration across oceans or between hemispheres. Here we present results on the tracks and behaviour of two basking sharks tagged off the British Isles, one of which released its tag off Newfoundland, Canada. During the shark's transit of the North Atlantic, she travelled a horizontal distance of 9589 km and reached a record depth of 1264 m. This result provides the first evidence for a link between European and American populations and indicates that basking sharks make use of deep-water habitats beyond the shelf edge.

Keywords: conservation; habitat; satellite tag; foraging; diel pattern; behaviour

1. INTRODUCTION

While basking shark numbers in Europe may, following protection, recover from previous targeted exploitation, populations elsewhere continue to be heavily depleted for the Southeast Asian shark fin trade (Harelde *et al.* 2007). Of great concern is that knowledge of the species' biology remains incomplete, with considerable uncertainty over their annual migration patterns.

Until the 1990s, it was suggested that the sharks might pass the winter in deep water beyond the continental shelf edge (Parker & Boeseman 1954). More recent findings suggest that basking sharks principally migrate north to south along the continental shelf of Europe (Sims *et al.* 2005*a*; eight tags), and separately along the east coast of North America (Skomal *et al.* 2004; Skomal 2005; three tags). None of these 11 sharks moved away from shelf areas into the deep ocean. Here, however, we provide the first conclusive evidence for basking shark use of the deep mid-ocean.

2. MATERIAL AND METHODS

Two basking sharks were tagged with MK10 pop-up archival transmitting (PAT) tags (Wildlife Computers, Redmond, USA) off the southwest Isle of Man, under licence from the Department of Agriculture, Fisheries and Forestry (DAFF), Isle of Man. Each tag was attached via a short nylon leader to a dart at the base of the dorsal fin, and was able to measure water temperature from −40 to 60°C (±0.05°C) and depth to more than 1500 m (0–1000±0.05 m, 1000–1500±0.1 m), as well as light levels (as irradiance in W cm^{-2} at 550 nm wavelength). Data were recorded as frequency histograms in 12 hour time periods to provide day and night series within the UTM time zone, stored in 14 linear bins ranging from less than 1 to more than 1000 m in depth and from 1–3°C to greater than 15°C in temperature. A depth protection device was fitted to the tether that would release the tag at depths in excess of 1800 m. The length of the sharks was measured against the markers established on the boat when alongside the shark for tagging.

Following tag detachment from the shark (set for 100 days), data were transmitted to Argos receivers on NOAA satellites. Geolocation positions were determined by the WC-GPE program (Wildlife Computers) using light levels at dawn and dusk. Resulting locations were excluded if movement of greater than 1° latitude or longitude per day occurred or if the distances of travel between locations that might be considered excessive, requiring swimming speeds of over 5.5 and 4.5 km h^{-1} for sharks A and B, respectively. Coastal latitude estimations were refined (after Sims 1999) using sea surface temperature (SST) data from advanced very high resolution radiometer (AVHRR) images with remote-sensing data analysis service (RSDAS) along the longitude. Remaining locations and subsequent tracks were plotted using MAPTOOL (www.seaturtle.org). Sensor data were extracted for analysis using WC-AMP program (Wildlife Computers). Potential upwelling zones were inferred from geostrophic current analysis (www.seaturtle.org) and phytoplankton concentrations from AVHRR images (RSDAS).

3. RESULTS

Two basking sharks (A and B) were tagged with PAT tags on 21 June 2007 and in the same vicinity, off the Isle of Man (table 1). The larger shark (A) moved southwards within the Irish Sea before turning west and travelling into the Atlantic Ocean (figure 1). She was in water at a depth of less than 500 m until 5 July 2007, but subsequently moved through waters in a depth of more than 4500 m. On 2 August 2007, she reached an area west of the mid-Atlantic ridge, where she remained for 9 days, before moving further northwest to a region east of the Newfoundland shelf edge, where she circulated for a further 32 days until her tag was released. Her track represents a horizontal distance of 9589 km, almost three times further than the previous longest record (3421 km; Sims *et al.* 2003) for this species, taking her nearly as far from the point of tagging as a white shark that covered 11 000 km on the South Africa to Australia leg of a return migration (Bonfil *et al.* 2005).

Shark A's vertical movements also exceeded any previously published movements from a depth sensor tagged shark of any species. For the first five days after tagging, she remained at a relatively constant and shallow depth (80 m or less), which became much greater (to 200 m or less) in the following 10 days. On leaving the continental shelf, she made numerous deep dives, to a record maximum of 1264 m, whereas the previous maximum reported being between 750 and 1000 m (Sims *et al.* 2003). During this period, she showed a very strong diel pattern, her mean depth at night was fluctuating between 200 and 300 m, while that by day decreased gradually from 800 to 400 m (figure 2*a*). It should be noted that due to the westward track of the shark and consequent change in time zones the distinction of day and night records becomes inaccurate by a

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Table 1. Date and location of tag deployment and pop-up. (Note that only shark A was sexed with certainty.)

shark	A	B
date and location tag deployed	21 Jun 2007 54.3° N 4.75° W SW Isle of Man	21 Jun 2007 54.3° N 4.75° W SW Isle of Man
date and location of tag pop-up	10 Sep 2007 54.28° N 45.23° W off Newfoundland, Canada	31 Jul 2007 55.61° N 4.70° W Firth of Clyde, Scotland
estimated total length (m) and sex	8.0 female	6.5 unknown
distance travelled (km)	9588.9	1806.5
days tagged	82	41

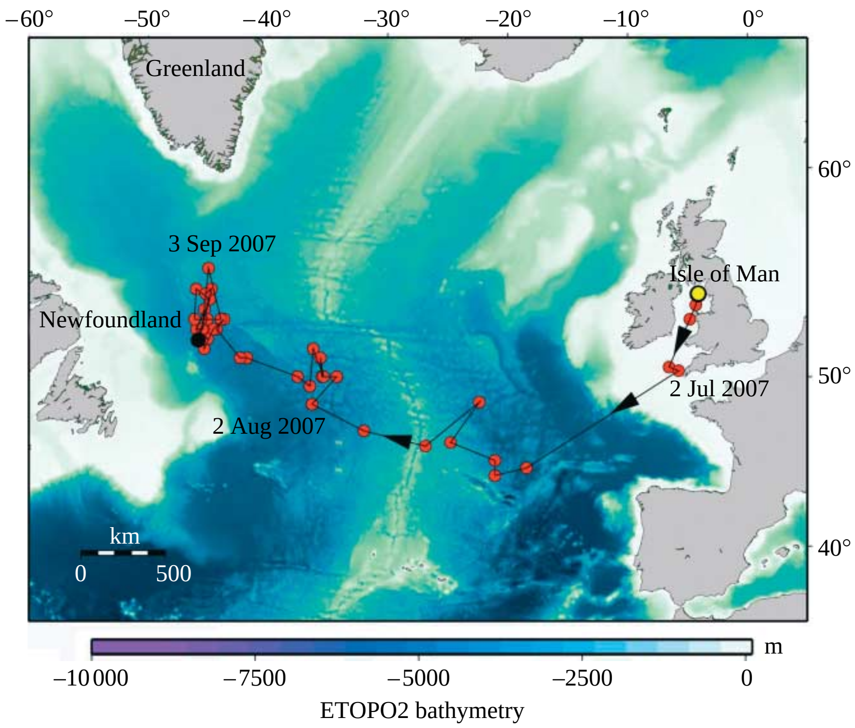

Figure 1. Track of basking shark A superimposed on chart showing seabed bathymetry. Yellow circle, site of tag deployment; black circle, site of tag pop-off and red circles, successive geolocations. The abscissa represents latitude and the ordinate longitude.

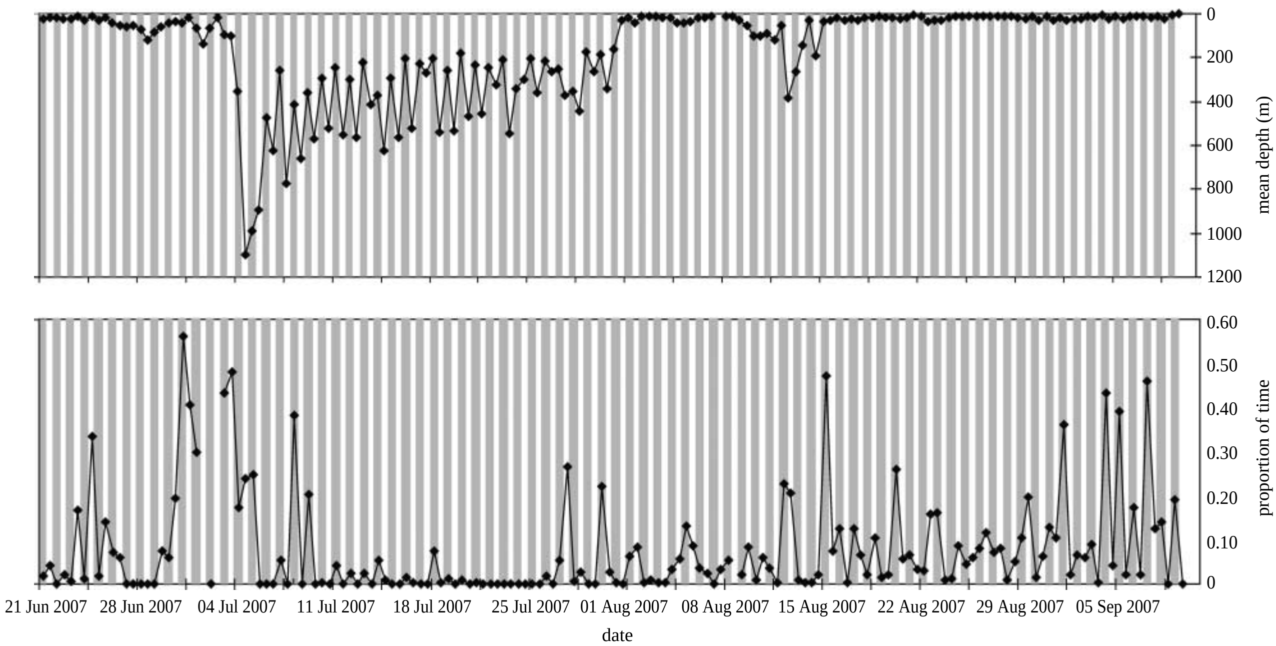

Figure 2. (*a*) Mean depth (m) and (*b*) proportion of time at surface (0–1 m deep) of basking shark A for 12 hour periods over days. White columns, daytime (05.00–16.59) and grey columns, night-time (17.00–04.59).

factor of approximately 20%. By contrast, the shark remained near the surface (figure 2*b*) for the last 40 days, with mean depth of 30 m or less even though she was in very deep water.

A very different behaviour was shown by shark B (table 1) who travelled north, remaining in continental shelf waters at a depth of 200 m or less, showing much less vertical (maximum depth of less than 80 m) and horizontal movements and conforming to the recent view of basking shark annual migration.

4. DISCUSSION

The two sharks in this study were tagged in the same area and close in time (table 1), but followed very different migratory paths. Previous observations with PAT tags (Sims *et al.* 2003; Skomal 2005) have indicated that basking sharks tend to follow individual paths rather than travelling as a group or along regular routes, and restrict themselves to continental shelf and shelf-edge habitats. However, shark A travelled directly across the Atlantic, through waters in a depth of more than 4500 m, and diving to a record depth of 1264 m. Such a record was foreshadowed by the data from New Zealand, where deep-water trawl fisheries caught occasional basking sharks down to depths of 904 m (Francis & Duffy 2002). Furthermore, the squalene oil concentrated in basking shark liver is characteristic of shark species exploiting deep-water habitats (Karnovsky *et al.* 1948).

The difference in behaviour might be related to difference in size as shark A was larger than both shark B and those tagged by Sims *et al.* (2005*a*), and was probably mature. The putative basking sharks courtship behaviour has been observed not only off Nova Scotia (Harvey-Clark *et al.* 1999) but also off Britain (Sims *et al.* 2000).

Alternatively the long-distance movement of shark A may reflect large-scale foraging. Bonnet *et al.* (2005) have shown an abundance of a preferred prey species, *Calanus finmarchicus* (Sims & Merrett 1997), near the Labrador Coast towards which shark A migrated. Further, satellite imagery from the period (see §2) indicates high productivity through putative upwelling and high abundance of phytoplankton in the western Atlantic regions, where shark A remained for periods of time.

The diel fluctuations in depth shown by both sharks have been demonstrated previously in basking sharks (Sims *et al.* 2005*b*) and a similar species (whale sharks; Rowat & Gore 2007), but in no case were they on the scale shown by shark A after leaving the continental shelf. The diel segregation of activities was not accurate in the later periods due to the increasingly westward movement of the shark resulting in an error of 2.7 hours over the entire course of her 82-day journey. Her diving, however, was not simply a function of seabed depth, since dive depth did not show a significant relationship with actual ocean depth (GLM: $F_{1,32}=2.57$, $p=0.1$). On occasion, shark A spent over 12 hours per day at depths of 800–1000 m or more, strongly suggesting that she was finding or searching for food at these depths, as mesopelagic copepods occur at such depths (Mauchline 1995). Furthermore, the semi-regular pattern of daytime dives to gradually reducing depths is suggestive of systematic foraging behaviour. This appears to support the hypothesis that these dives are to search for horizontally dispersed food-related chemosensory cues (Sims *et al.* 2003; Rowat & Gore 2007).

The likelihood that transoceanic migration is a normal feature of basking shark biology, even if shown by only a minority of adults, is strengthened by recent demonstrations of similar long-distance migrations in other large shark species. Individual whale sharks migrate across the Indian Ocean (Rowat & Gore 2007) and some white sharks between both South Africa and Australia (Bonfil *et al.* 2005) and California and Hawaii (Boustany *et al.* 2002). Such long-distance migrations have implications for the population genetics of each species. Although basking shark populations had appeared to be separated by intervening ocean basins and tropical waters, Hoelzel *et al.* (2006) found low genetic diversity ($\pi=0.0013$) in the Atlantic with no significant difference in genotypes between Atlantic and Pacific Ocean basins. Shark A has indicated how female-mediated gene flow may occur across ocean basins and supports the findings of low diversity of genetic structure and consequent lack of identifiable populations.

This conclusion has significant implications for the species' conservation, especially given an estimate of an effective population size of only 8200 individuals globally (Hoelzel *et al.* 2006) and its IUCN status as Vulnerable (Fowler 2008). Despite protective legislation, the numbers in the northeast Atlantic may show only limited recovery if mature adults are exposed to exploitation in other oceanic regions.

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Bonfil, R., Meÿer, M., Scholl, M. C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D. & Paterson, M. 2005 Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* **310**, 100–103. (doi:10.1126/science.1114898)

Bonnet, D. *et al.* 2005 An overview of *Calanus helgolandicus* ecology in European waters. *Prog. Oceanogr.* **65**, 1–53. (doi:10.1016/j.pocean.2005.02.002)

Boustany, A. M., Davis, S. F., Pyle, P., Anderson, S. D., Le Boeuf, B. & Block, B. A. 2002 Satellite tagging: expanded niche for white sharks. *Nature* **415**, 35–36. (doi:10.1038/415035b)

Fowler, S. L. 2008 *Cetorhinus maximus*. In *2007 IUCN Red List of Threatened Species*. (www.iucnredlist.org)

Francis, M. P. & Duffy, C. 2002 Distribution, seasonal abundance and bycatch composition of basking sharks *Cetorhinus maximus* in New Zealand, with observations on their winter habitat. *Mar. Biol.* **140**, 831–842. (doi:10.1007/s00227-001-0744-y)

Harelde, N. R. *et al.* 2007 *European shark fisheries: a preliminary investigation into fisheries, conversion factors, trade products, markets and management measures*. European Elasmobranch Association.

Harvey-Clark, C. J., Stobo, W. T., Helle, E. & Mattson, M. 1999 Putative mating behaviour in basking sharks off the Nova Scotia coast. *Copeia* **3**, 780–782. (doi:10.2307/1447614)

Hoelzel, A. R., Shivji, M. S., Magnussen, J. & Francis, M. P. 2006 Low worldwide genetic diversity in the basking shark (*Cetorhinus maximus*). *Biol. Lett.* **2**, 639–642. (doi:10.1098/rsbl.2006.0513)

Karnovsky, M. L., Rapson, W. S., Schwartz, H. M., Black, M. & Van Rensburg, N. J. 1948 South African fish products, Part XXVII. The composition of the liver oils of the basking shark (*Cetorhinus maximus*, Gunner) and the spiny shark (*Echinorus spinosus*, Gmelin). *J. Soc. Chem. Ind.* (*Lond.*) **67**, 104–107.

Mauchline, J. 1995 Bathymetric adaptations of life history patterns of congeneric species (*Euchaeta* Calenoida) in a 2000 m water column. *ICES J. Mar. Sci.* **52**, 511–516. (doi:10.1016/1054-3139(95)80064-6)

Parker, H. W. & Boeseman, M. 1954 The basking shark (*Cetorhinus maximus*) in winter. *Proc. Zool. Soc. Lond.* **124**, 185–194.

Rowat, D. & Gore, M. 2007 Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. *Fish. Res.* **84**, 32–40. (doi:10.1016/j.fishres.2006.11.009)

Sims, D. W. 1999 Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? *Proc. R. Soc. B* **266**, 1437–1443. (doi:10.1098/rspb.1999.0798)

Sims, D. W. & Merrett, D. A. 1997 Determination of zooplankton characteristics in the presence of surface feeding basking sharks *Cetorhinus maximus*. *Mar. Ecol. Prog. Ser.* **158**, 297–302. (doi:10.3354/meps158297)

Sims, D. W., Southall, E. J., Quayle, V. A. & Fox, A. M. 2000 Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B* **267**, 1897–1904. (doi:10.1098/rspb.2000.1227)

Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C. & Metcalfe, J. D. 2003 Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Mar. Ecol. Prog. Ser.* **248**, 187–196. (doi:10.3354/meps248187)

Sims, D. W., Southall, E. J., Metcalfe, J. D. & Pawson, M. G. 2005*a* Basking shark population assessment. Final report for Global wildlife Division of Defra Tender CR 0247.

Sims, D. W., Southall, E. J., Tarling, G. A. & Metcalfe, J. D. 2005*b* Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J. Anim. Ecol.* **74**, 755–761. (doi:10.1111/j.1365-2656.2005.00971.x)

Skomal, G. 2005 Basking shark tagging update. *DMF News*, fourth quarter 2004–first quarter 2005, 4.

Skomal, G. B., Wood, G. & Caloyianis, N. 2004 Archival tagging of a basking shark, *Cetorhinus maximus*, in the western North Atlantic. *J. Mar. Biol. Assoc. UK* **84**, 795–799. (doi:10.1017/S0025315404009968h)