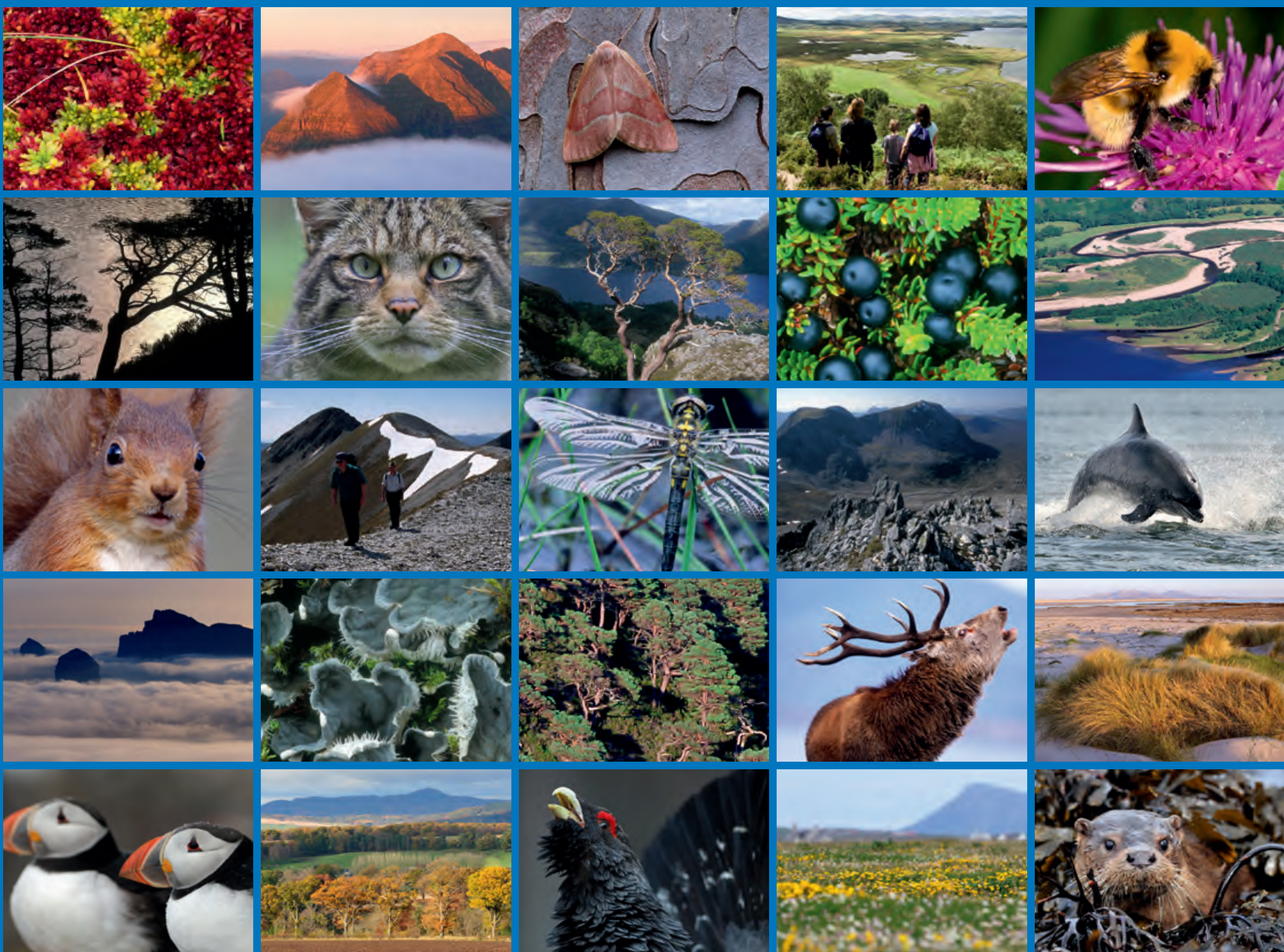
Scottish Natural Heritage
Commissioned Report No. 908

Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement, distribution and behaviour using satellite telemetry



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COMMISSIONED REPORT

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Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement, distribution and behaviour using satellite telemetry

Final Report

For further information on this report please contact:

Dr Suzanne Henderson
Scottish Natural Heritage
Great Glen House
INVERNESS
IV3 8NW
Telephone: 01463 725238
E-mail: suzanne.henderson@snh.gov.uk

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COMMISSIONED REPORT

Summary

Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement, distribution and behaviour using satellite telemetry

Final Report

Commissioned Report No: 908
Project No: 15078
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Keywords

Basking shark; satellite tagging; seasonal fidelity; Sea of the Hebrides.

Background

The areas around Hyskeir, Coll and Tiree have been identified as "hotspots" for basking sharks from 20 years of public sightings record. The area from Skye to Mull, on the west coast of Scotland, has also been recently identified as a Marine Protected Area (MPA) search location as part of the Scottish MPA Project. Large numbers of basking sharks are seasonally sighted foraging and engaging in putative social behaviours, such as breaching and in courtship-like aggregations in this area. These observations highlights that the area may be important for key elements of basking shark life history ecology. To gain detailed insights in to the distribution, habitat-use, movements and behaviours in these areas, Scottish Natural Heritage (SNH) and the University of Exeter (UoE) initiated a research project to attach satellite tags to basking sharks in the summer months of 2012, 2013 and 2014. This report provides analyses, interpretation and comment on data resulting from three years of tag deployments, with particular focus upon basking shark movements and depth use within the Sea of the Hebrides MPA proposal.

Main findings

- Satellite tagged basking sharks demonstrated high levels of intra- and inter-annual site fidelity to waters around Coll, Tiree and Hyskeir during summer (July to September).

- Basking sharks occupy shallow coastal waters during summer months, predominantly using surface waters, but move to deeper waters from autumn onwards.

- The Irish and Celtic Seas represent an important migration corridor for basking sharks moving between the Sea of the Hebrides, the Isle of Man and southwest England.

- Tagged basking sharks disperse widely in the autumn, moving to the west of Ireland, the Bay of Biscay, Iberian Peninsula and North Africa. Some sharks however remain relatively close to Scotland throughout the winter.

- Evidence of diel vertical migration (DVM), reverse DVM and yo-yo diving behaviour, suggest basking sharks exhibit a high degree of plasticity when adapting to local conditions.

For further information on this project contact:
Dr Suzanne Henderson, Scottish Natural Heritage, Great Glen House, Leachkin Road, Inverness IV3 8NW.
Tel: 01463 725238 or suzanne.henderson@snh.gov.uk
For further information on the SNH Research & Technical Support Programme contact:
Knowledge & Information Unit, Scottish Natural Heritage, Great Glen House, Inverness, IV3 8NW.
Tel: 01463 725000 or research@snh.gov.uk

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Acknowledgements

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We are most thankful to Jackie and Graham Hall of Manx Wildlife Trust (Manx Basking Shark Watch) who manufactured the satellite tag application equipment. They provided expert knowledge on the behaviour of basking sharks in an open and collegiate manner. Their support and encouragement throughout the project has been considerable. Jackie and Graham Hall have also provided access to basking shark satellite tracking data gathered in 2013 from tags deployed in the waters of the Isle of Man. The inclusion of their data in this report supported the consideration of connectivity between the waters of the northern Irish Sea and the west coast of Scotland.

We extend our since thanks to the skippers and crew of the *Sula Crion* and *Bold Ranger*, of Sealife Surveys, Tobermory. Their unfaltering professionalism made this project possible, particularly in the often challenging conditions of working with wild animals at sea.

1. INTRODUCTION

The basking shark (*Cetorhinus maximus*) is the world's second largest fish species. It has a circumglobal distribution and can undertake extensive trans-ocean basin migrations (Gore *et al.* 2008; Skomal *et al.* 2009); although the relative frequency and purpose of these migrations is unknown. This species is an obligate ram-feeding zooplanktivore. Basking sharks are slow to mature and have low fecundity, which has made the species slow to recover from wide scale historical exploitation by fisheries for its oil, meat and leather (Kunzlik 1988). Seasonally abundant aggregations of basking sharks form in temperate continental shelf waters of the Atlantic, Pacific and Indian Oceans for feeding and presumed reproduction. Basking shark size (body length) at first reproduction is thought to be between 5-7m, approximately 12 to 16 years of age for males, and 8-10m, approximately 16-20 years of age for females, with maximum lengths of approximately 10m (circa 50 years of age; reviewed by (Sims 2008).

Population size for the basking shark in the north-east Atlantic is unknown, with tracking efforts to date (Sims *et al.* 2003; Stéphan *et al.* 2011) demonstrating short-term movements (months) along the European continental shelf. The capacity for basking sharks to undertake transatlantic and transequatorial movement does, however, exist (i.e. thousands of kilometres; (Gore *et al.* 2008; Skomal *et al.* 2009). Limited genetic studies have been unable to robustly describe the structuring of the north-east Atlantic population (Noble *et al.* 2006), although genetic diversity is thought to be low globally (Hoelzel *et al.* 2006). Anthropogenic activity in the north-east Atlantic is increasing (Halpern *et al.* 2008), including large vessel traffic and marine renewable energy installations (Witt, *et al.* 2012a). There is, therefore, a growing need to better understand the spatial and temporal components of basking shark distribution, abundance and behaviour to inform marine spatial planning activities. Since the introduction of the Marine (Scotland) Act in 2010, there has been an increased focus on the spatial management of the marine environment, for example, through the development of Scotland's National Marine Plan and selection of Nature Conservation Marine Protected Areas (MPAs). One specific measure under consideration is the Sea of the Hebrides MPA proposal - identified for minke whale (*Balaenoptera acutorostrata*) and basking sharks as part of the Scottish Marine Protected Area project. The Sea of the Hebrides MPA proposal was identified in 2014 (SNH, 2014), and Scottish Ministers are currently considering whether and when a public consultation should be undertaken.

This report presents the findings from the Basking Shark Satellite Tagging Project, a partnership between Scottish Natural Heritage (SNH) and the University of Exeter (UoE). The project has attached a variety of satellite transmitting tags to basking sharks in the Sea of the Hebrides to improve the understanding of basking shark movement, behaviour and habitat use. Efforts have focused on four areas for satellite tag attachments: areas to the south and west of Tiree, at Gunna Sound (between the islands of Coll and Tiree), Cairns of Coll (north-east of Coll) and at Hyskeir (Fig. 1). These areas are known basking shark hotspots within the UK (Speedie *et al.* 2009; Witt *et al.* 2012b). Data gathered by the satellite tracking project has contributed to an assessment of whether spatial protection may be an appropriate conservation strategy for basking sharks and if so, what the scale and location of any potential protected area might be (SNH, 2014).

The results of the satellite tag deployments help to address the following questions:

- How do basking sharks use the waters around Hyskeir, Coll, Gunna Sound and Tiree?
- How long do basking sharks remain within the Sea of the Hebrides?
- Are there any areas that are used to a greater extent than others?
- To what extent do tagged basking sharks use areas outside the Sea of the Hebrides MPA proposal?

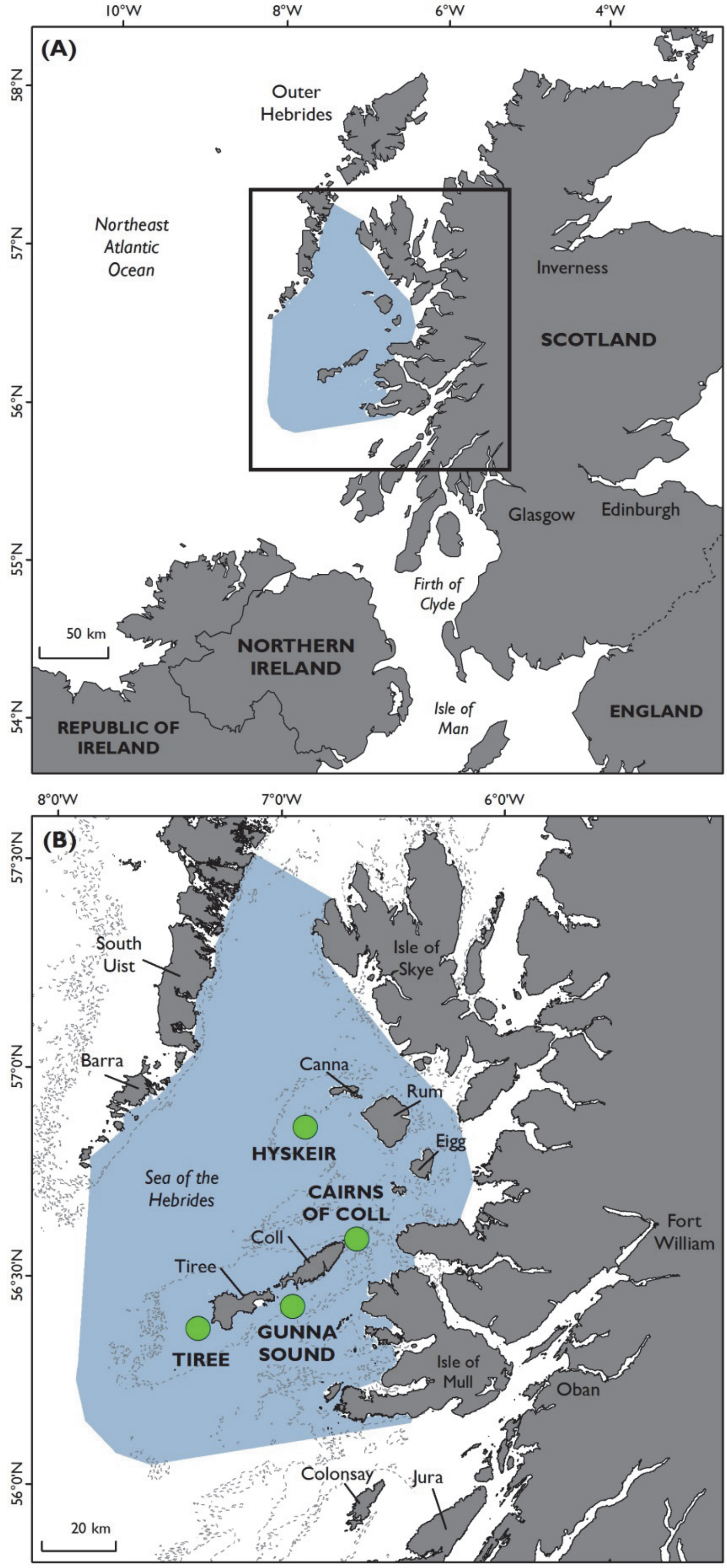


Figure 1. Basking shark satellite tracking project. *(A) Study location; west coast of Scotland showing the Sea of the Hebrides MPA proposal (blue polygon) and (B) Satellite tag deployment areas (Hyskeir, Cairns of Coll, Gunna Sound and Tiree; green filled circles). 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

2. METHODS

2.1 Study area

The deployment of satellite tags to basking sharks was undertaken in the Sea of the Hebrides on the west coast of Scotland (Fig. 1). Boat-based surveys providing effort-corrected estimates of basking shark density have shown that this area supports appreciable numbers of basking sharks throughout summer months (July to September; (Speedie *et al.* 2009). Satellite tags were therefore deployed at locations with high (relative) values of effort-corrected sightings data (Fig. 1B). Data collected from satellite tags, occurring both within and outside the study area, are considered in this report, but particular attention is given to data occurring within the Sea of the Hebrides MPA proposal. Efforts were made each year to visit the same locations for tag deployment (i.e. Tiree, Gunna Sound and Hyskeir); however, actual tag deployment locations were dictated by the presence of basking sharks, boat facilities and prevailing weather conditions.

2.2 Satellite tracking system, Fastloc^{TM} and light geolocation

2.2.1 Argos System

The Argos System is a satellite-based tracking system that was established to collect data from fixed and mobile platforms (e.g. ocean buoys, ships and other monitored platforms). The Argos System uses seven Polar Orbiting Environmental Satellites (POES) operated by a consortium of international bodies, including the US Government's National Aeronautical and Space Agency (NASA) and National Oceanographic and Atmospheric Administration (NOAA), as well as the European Organisation for the Exploitation of Meteorological Satellites (EUMETSAT), and Satellite with Argos and AltiKa (SARAL). The Argos System uses the principles of the Doppler Effect to locate platforms, while also collecting data.

The Argos System has been used to track a wide variety of animal taxa on land and at sea. The Argos System can only locate marine animals and their associated platforms (tags) when they are at the sea surface as transmissions travel poorly through water and cannot penetrate the water surface. When tags detect they are at the sea surface they transmit identification messages every 45 seconds, which are collected by the Argos System during each satellite overpass. A satellite overpass at 55° latitude (approximate latitude for Scotland) is, on average, 15-min. in duration. The more transmissions received by a satellite from a tag during an overpass, the more accurate the resulting location of the tag will be. As such, animals can be located more frequently and accurately when tags spend extended periods of time at the sea surface, for example when animals might be engaged in surface feeding or resting.

The quality of each location derived by the Argos System (http://www.argos-system.org/manual/3-location/34_location_classes.htm) is assigned to one of a series of seven location classes, with a class 3 location having the highest accuracy (typically within 250m of true location), class 2 locations having the second highest accuracy (typically within 500m of true location) and class 1 locations with low accuracy (typically within 1km from true location). The remaining four location classes (i.e. A. B, Z and 0) are considered auxiliary and lack an associated estimate of location accuracy. Satellite tracking of marine vertebrates, which spend more time below the sea surface than on it, typically leads to a high proportion of auxiliary locations, which often results in a high proportion of data being rejected due to low levels of accuracy. Simultaneous collection of Argos and GPS data from the FastlocTM system has suggested that many auxiliary positions may be accurate to within 1km (Witt *et al.* 2010). The current best practice is to retain all locations classes, with the exception of class 0 and class Z locations, but then to apply strict quality control, for example using speed and turning angle filtering, eliminating implausible locations (Witt *et al.* 2010).

2.2.2 Fastloc^{TM} GPS

The Global Positioning Satellite (GPS) network consists of at least 24 Navstar satellites orbiting the Earth. Estimates of location on the sea surface, or on land, can be determined by using a land-based receiver able to collect information from the GPS network. In order to establish a GPS-derived location, GPS receivers typically require at least several minutes to acquire Ephemeris and Almanac data from the satellite system, which describe the relative positions and timing schedules of the satellites making up the GPS network, thus allowing a receiver to calculate its relative position with high accuracy. However, given the need for animal tracking devices to capture highly accurate location data at much shorter intervals, the FastlocTM system was developed, permitting capture of potential locations in only tens of milliseconds. GPS technology integrated into satellite tags therefore represents a significant progression towards generating high accuracy locations (Hazel 2009; Sims *et al.* 2009; Costa *et al.* 2010; Witt *et al.* 2010). FastlocTM, like the Argos System, has several limitations and an understanding of these is essential before interpreting data; for example, 1) the accuracy of a FastlocTM location (i.e. how far the estimated location is from the actual location), is influenced by the number of visible GPS satellites when the tag is at the surface. Estimates of location derived from three or less satellites are of low accuracy and are typically discarded. 2) Acquisition of FastlocTM data requires considerable power resources; animal-borne satellite tags fitted with FastlocTM therefore typically have short deployment times (several months), which can be extended by programming tags to only collect data at a comparatively low frequency (i.e. one FastlocTM position a day). 3) FastlocTM performs best when the receiver is floating level with the sea surface with no water splash as the GPS signal is easily attenuated by water.

2.2.3 Light geolocation

Data on ambient light levels collected by some animal-borne satellite tags can be used to estimate the location of study animals while they are below the sea surface and at liberty, this process is termed light geolocation (Hill 1994; Hill and Braun 2001). This is a low-resolution tracking method, accurate to within several tens of kilometres of the true location of the study animal. The method is common to fisheries research and is used on species that spend little or no time at the sea surface, such as large tuna (Block *et al.* 2005) and billfish (Evans *et al.* 2011). Light geolocation makes use of the fact that day length varies predictably with latitude, and that local noon (when the sun is at its highest point) varies with longitude. Latitude can be estimated by calculating day length (the time elapsed between dawn and dusk) and comparing it against the calendar year for a given longitude, providing several solutions. In order to solve which might be most likely, these estimates are further reduced using a range of plausibility checks, such as the distance between subsequent and current locations and the depth of the study animal each day with respect to information on surrounding seabed depths.

Light geolocation performs best in polar regions (where changes in day length between days are more marked than in equatorial regions) and in periods of time furthest from solstices (Hill 1994; Hill and Braun 2001). In addition, other issues may hinder how well the tag can record light levels (e.g. turbidity from suspended organic material in coastal regions), animal depth (deeper waters having less light penetration), sensor accuracy and precision, tag positioning on the study animal and the behaviour of the study animal at differing times of the day (e.g. crepuscular behaviour, where animals are more active during dawn and dusk).

A variety of analytical techniques are available to reconstruct the likely movements of study animals from archived light data. Three techniques were evaluated for this project, these included 1) using proprietary software from the satellite tag manufacturer (Wildlife Computers Global Position Estimator), 2), an open source software package working within the R statistical environment that is often used for determining the movements of tuna and billfishes (Nielsen and Sibert 2007), and 3) an approach developed by CLS Argos. The latter technique was adopted for this project as the estimated error for each location appeared well constrained and the analytical process adopts more recent advances in state-space modelling techniques. The technique provides a daily estimate of the most likely locations, which are then constrained by a selection of environmental data (e.g. sea surface temperature and depth data), allowing a putative track to be constructed. The track is then smoothed further using the tag release and tag detachment locations (which are known with certainty) to influence the reconstructed movement track.

2.3 Description of satellite tags

2.3.1 SPOT

An early variant of a real-time Argos tracking device was first attached to a basking shark in 1984 (for 17 days (Priede 1984; Priede and Miller 2009)), the technology has advanced considerably since this time. Smart Position and Temperature tags (SPOT; Fig. 2A) communicating with the Argos System were used in this project to provide information on the horizontal movements of basking sharks. SPOT tags can make approximately 65,000 transmissions. The spatial accuracy of locations varies from approx. 350 to 1000m. Some locations are not accompanied by an estimate of their accuracy but may still be useful. The reliability of SPOT tags permits their wide scale deployment across multiple individuals. The basking shark satellite tracking project described here deployed SPOT tags in 2012 (N=8) and 2013 (N=15).

2.3.2 PAT-F

Pop-up Archival Transmitting with FastlocTM tags (PAT-F; Fig. 2B) communicating with the Argos System were used to collect information on depth use behaviour, GPS locations in the coastal zone and the longer-range spatial movements using light geolocation. PAT-F tags collected data on the ambient environment at 10-sec. intervals, including data on water temperature in 12 temperature classes (-4-0, 0-4, 4-6, 6-8, 8-10, 10-12, 12-14, 14-16, 16-18, 18-20, 20-22, >22°C), light levels and depth. Information on depth use, including estimates of the percentage of time spent in 12 depth classes (surface to 1m, 1-5m, 5-10m, 10-25m, 25-50m, 50-75m, 75-100m, 100-250m, 250-500m, 500-750m, 750-1000m and >1000m), were created from sampled data every 4-hours. These summary data were subsequently transmitted to overpassing satellites once the tag had detached from the study animal. PAT-F tags deployed in 2012 (N=12) were programmed to detach from study animals 280 days following deployment.

2.3.3 MiniPAT

Mini Pop-up Archival Transmitting tags (MiniPAT; Fig. 2C) are designed for deployment over extended periods of time (many months to years). These tags collected data on the ambient environment at 15-sec. intervals, including data on water temperature, light levels and depth (like PAT-F tags). Summary data are archived on the tag and summarised at 24-hour intervals and subsequently transmitted to overpassing satellites once the tag has detached from the study animal. MiniPAT tags deployed in 2013 (N=12) were programmed to follow either of two deployment schedules; 280 days (N=9) or 365 days (N=3) attachment periods.

2.3.4 SPLASH-F

SPLASH-F tags (Fig. 2D-E) transmitted to the Argos System in real-time (in the same way as SPOT tags), and also collected data on the ambient environment at 10-sec. intervals, including data on water temperature in 12 temperature classes (-4-0, 0-4, 4-6, 6-8, 8-10, 10-12, 12-14, 14-16, 16-18, 18-20, 20-22, >22°C), light levels, pressure (depth) and GPS locations (in the same way as PAT-F tags). Information on depth use, including estimates of the percentage of time spent in 12 depth classes (surface to 1m, 1-5m, 5-10m, 10-25m, 25-50m, 50-75m, 75-100m, 100-250m, 250-500m, 500-750m, 750-1000m and >1000m), were created from sampled data every 4-hours. These summary data were transmitted to overpassing satellites during the period when tags were attached and also after tags had detached from the study animal. SPLASH-F (version 1) tags deployed in 2013 (N=4) were programmed to detach from study animals 45 days after deployment due to the prototype nature of the tags. SPLASH-F (version 2) tags deployed in 2014 (N=10) were programmed to detach on 1st May 2015 (N=8) and 1st of July 2015 (N=2).

All models of satellite tags used in the basking shark satellite tracking project were hydrodynamic in form, hence minimising drag. Biofouling of tags during deployment can increase drag and the likelihood that a tag may fail to transmit when it is at the sea surface; as such, tags were coated in anti-fouling paint. These approaches help to minimise impact on the study animal while attempting to maximise satellite tag retention. Although many satellite tags transmit summarised data following detachment, if tags can be physically recovered a more detailed time series of data can be downloaded from the memory of the tag.

Figure 2. Satellite tags. *Models of satellite tags used for satellite tracking basking sharks (A-E; source: Wildlife Computers). Photograph of satellite tags on 1cm graticule (F).*

2.3.5 Tether system

The preferred method of satellite tag attachment was one with the least degree of interaction with the study animal. Tags were attached quickly and in a manner that exposed the tag to the sea surface, particularly important for tags that transmit to the Argos Systems and/or collect GPS locations. Satellite tags were attached to the shark via a dart using a tether, the length of which varied between deployments.

Satellite tags were designed to be buoyant and the tether enabled the tag to reach the sea surface to allow transmissions to the Argos System and to collect GPS data. The dart was inserted into the cartilage-muscle interface region at the base of the dorsal fin using an extendable darting pole. Tethers consisted of nylon-coated braided stainless steel wire or plastic monofilament of high breaking strain (approx. 900lbs or 400kg), covered with heat shrinkable tubing, a swivel and a mechanical depth-release device (Wildlife Computers; RD1800). This device released the tag by severing the tether at 1800m depth to prevent damage from high pressure. As a safety mechanism, tether assemblies were configured to break away if a significant force was applied (e.g. in entanglement with fishing nets, pot lines or other submerged objects).

2.3.6 Deployment of satellite tags

Sea Life Surveys provided boat services in 2012, 2013 and 2014. A Mitchell 35 (9.5m length; Sula Crion) and a Nelson 42 workboat (12.7m length; Bold Ranger) were used as tagging platforms. At each of the four tagging locations (Fig. 1B), basking sharks were first observed at distance so to identify candidate animals for tagging. Suitable animals were those that appeared to be in good health (with no obvious external signs of serious and/or recent injury), and were engaged in feeding at the surface. Sharks often spent large proportions of the time at the surface, thus they could be confidently followed for several minutes to carry out the following protocol:

1. The survey vessel was prepared for an encounter with a candidate shark, by manoeuvring the vessel towards the animal at ‘dead slow’ speed.
2. A pole mounted camera was used to inspect the pelvic area of each shark to determine sex (Fig. 3A). It was not possible to sex all sharks that were tagged as some moved deeper into the water column and/or some of the images collected were inconclusive.
3. The shark was darted using a titanium metal dart inserted into the base of the dorsal fin on the right side of the animal using a darting pole (Fig. 3 B-C).
4. A genetic sample was taken by using a sponge pad or cotton cloth mounted on a pole; this was swabbed over the skin of the shark (Fig. 3B). The sponge pad or cotton cloth was stored in absolute alcohol for genetic analysis by the University of Aberdeen.
5. The length of the shark was estimated using the known length of the survey vessel as a reference.

The location of each tagging event was recorded using a hand-held GPS receiver (Garmin). Each tagging event was accompanied by vertical plankton trawl from the sea bed to the sea surface, using a 250μm gauge net with a 300mm opening. Plankton were stored in Borax buffered formaldehyde. The vertical structure of the water column was recorded using a Conductivity-Temperature-Density (CTD) instrument (XR-420 or Concerto; RBR Ltd).

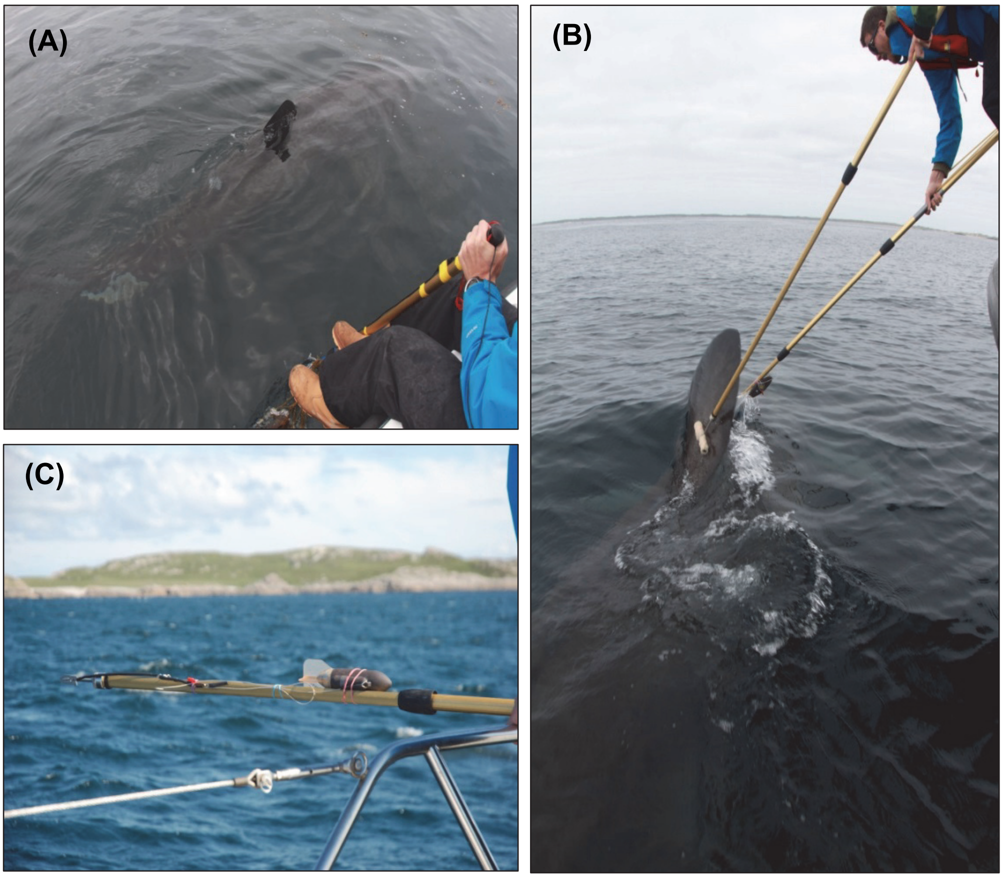


Figure 3. Field techniques. *(A) Use of pole mounted camera to determine sex of basking sharks, (B) genetic swab pole and darting pole being used simultaneously, and (C) darting pole with satellite tag and tether prepared for use.*

2.4 Estimating tag detachment dates

Satellite tracking of each basking shark reached completion when the tag detached from the study animal, either at a pre-determined date or earlier if tag attachment failed. In general, when a satellite tag detaches from a study animal, it will float on the surface generating many high quality locations. These data are unusual for tags still attached to wild animals, as it does not reflect their natural behaviour, and as such provides a useful indicator on the likely status of the tag. Determining whether a tag had detached differed among the tag types used.

2.4.1 SPOT

These tags (Fig. 2A and Fig. 4) were permitted to make 250 transmissions a day to overpassing satellites. The transmission counter on the tag reset at 00:00 UTC each day. A tag could transmit every 45 sec. (when not submerged). A tag was therefore likely to have detached when all available transmissions had been made within the first few hours of each day. The spatial quality of the location estimates also increases once the tag has detached from the animal, suggesting the tag is permanently afloat on the sea surface.

2.4.2 PAT-F, SPLASH-F and MiniPAT

These tags support diagnostic capabilities that report the date and depth at which the tag detaches from the study animal, be it at a pre-determined date or following premature detachment.

Figure 4. Towed satellite tag. *A basking shark towing a SPOT satellite tag (grey object floating on the surface in the foreground of the picture; Credit: Laurie Campbell/SNH).*

2.5 Data analysis

2.5.1 Reconstructing movements

In 2012 and 2013, SPOT tags provided the main source of basking shark location data via the Argos System. A range of filters were applied to these Argos location data to remove implausible estimates (Witt *et al.* 2010). Only locations with location accuracy classes of 3, 2, 1, A and B were used. The locations were filtered using a maximum plausible rate of travel of 15km.h-1. A turning angle filter was also applied, this filter removed locations necessitating turning angles of ≤10°. In 2014, SPLASH-F tags providing GPS locations were selected over Argos locations as the number of GPS locations for each individual were more numerous than resulting Argos locations.

Longer-range movements of sharks fitted with PAT-F, MiniPAT and SPLASH-F (version 2) tags were also determined by light geolocation. This technique provides a single daily estimate of location. Light geolocation was undertaken by Argos CLS using a proprietary technique.

2.5.2 Estimating areas of relative importance

Argos and GPS location data gathered from SPOT (2012-2013) and SPLASH-F (2014) tags were analysed to ascertain whether tracked animals showed preference for particular areas within the study region (i.e. to identify areas with high relative importance). Three methods were used to estimate areas of relative importance; minimum convex polygon, grid-based point counting, and kernel density estimation (Worton 1989). Locations received from each shark were first filtered to a single location for each day to minimise the influence of pseudo-replication and auto-correlation. Locations collected between July and end-September were used. This period represents the time between tag deployment and the end of summer surfacing behaviour on the west coast of Scotland.

Minimum convex polygon: A two dimensional delineation of the region that tracked basking sharks utilised.

Grid enumeration: A grid-based counting approach (Witt *et al.* 2008), using a grid of approx. 25km2; this grid was used to sum spatially coincident location data.

Kernel density estimation: A two dimensional smoothing algorithm was applied to location data to highlight areas that were most densely occupied by study animals. The relative density of sharks was calculated at intervals on a grid of cells ($1km^2$). Basking shark location data were first projected from their native geographic coordinate system (World Geodetic System 1984) to a European Equidistant coordinate system. The kernel process smoothed the location data at a resolution of 5km. The method resulted in an estimate of density that incorporated areas containing known densities (i.e. a region containing the 25% most densely aggregated data, and further regions containing, 26 to 50%, 51 to 75% and 76 to 90% of data).

2.5.3 Environmental data

The distribution of basking shark locations (Argos and GPS) were contextualised using a range of physical data describing the marine environment; including, bathymetry (© SeaZone Solutions, 2013, Licence O1035263) and the seabed substratum (http://jncc.defra.gov.uk/EUSeaMap). Data on tidal speed were obtained from the Polpred CS20 coastal model made available by the National Oceanography Centre under licence to the University of Exeter (approx. 2km pixel resolution; Licence 24249, http://noc.ac.uk/tag/polpred). Tidal data were extracted at 4-hour intervals and spatially averaged. Environmental values coincident to basking shark (Argos and GPS) locations were extracted from these described products.

2.5.4 Persistence model

Data on modelled habitat persistence of basking sharks were obtained (Paxton *et al.* 2014). These data were based on multi-annual visual transect data incorporated in to a statistical modelling process. To summarise, to identify regions of persistent (relatively) high density, prediction surfaces were generated for each summer 2001 – 2012. Cells within the surfaces with a predicted relative density higher than the mean predicted relative density for the Scottish territorial waters were marked as 1, cells lower than the average marked as 0. Thus a persistence-certainty score could be developed (on a scale of 0 to 6000). This persistence-certainty score combined the probability of a cell having a value greater than average density in the summer as well as the uncertainty associated with the estimated year-specific density. Basking shark tracking locations were then interpreted with respect to this persistence model.

2.5.5 Fastloc™

GPS locations were received from PAT-F and SPLASH-F tags enabled with Fastloc™. Locations derived using three or fewer GPS satellites were discarded due to a high degree of spatial error. GPS locations were mapped and compared to Argos locations for the same individuals. In addition, to create an understanding of basking shark vertical habitat use within the study area, data summarising depth use (on a 4-hour interval) were associated with GPS locations. Depth data were only used for this mapping exercise when they were accompanied by contemporaneous GPS locations.

2.5.6 Depth use time series

Depth use behaviour gathered by MiniPAT, PAT-F and SPLASH-F tags was examined on both short- and longer time scales (July to end-September and complete tracking durations, respectively). Where satellite tags were physically recovered then data direct from these tags were preferred to the summary form received via the Argos System. Time series data on daily maximum depths were created for each shark. Depth use data were also analysed to examine the proportion of time basking sharks spent within predefined depth zones. These data were examined for the summer period July to end-September and for the whole year, including the winter period when satellite tagged sharks undertook migrations away from the Sea of the Hebrides.

2.5.7 Temperature data

Data on encountered temperature (recorded at 10-sec. or 15-sec. intervals depending on satellite tag model) were obtained from physically recovered tags (PAT-F, MiniPAT and SPLASH-F). For each individual the mean monthly temperature experienced was calculated. Data were integrated across individuals to determine the thermal range of encountered water temperature throughout basking shark tracking periods.

2.5.8 Public engagement

Satellite tracking data were hosted at www.wildlifetracking.org for public viewing. This website provides a near real-time overview of the movements of basking sharks fitted with SPOT tags. The data shown on the website are subject to strict quality control. Expert interpretation of satellite data is required and as such maps displayed on www.wildlifetracking.org do not constitute publication. To enhance wider participation with the public, SNH undertook a media campaign to allow members of the public to suggest names for each of the SPOT tagged sharks and these can be viewed on the SNH website[1]. Public interest in the satellite tracking project was demonstrated by the approx. 135,000 visits to the www.wildlifetracking.org project page over the lifetime of the project. Nearly 500 people subscribed to daily updates on the locations of tagged basking sharks. The University of Exeter held an informal talk and discussion evening at the Tobermory visitor centre to engage the local community and visitors in the work being carried out.

2.5.9 Species licensing

The attachment of satellite transmitters to vertebrate species is regulated by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence: PPL 30/2975). Ethical review of this project was undertaken by the University of Exeter Ethical Review Group (for Home Office Licensing) and by the University of Exeter College of Life and Environmental Science Ethical Review Committee. Activities also required licensing under the Wildlife and Countryside Act 1981 (as amended) Scotland (Licence(s): 13904, 13937 and 13971).

[1] http://www.snh.gov.uk/about-scotlands-nature/species/fish/sea-fish/shark-tagging-project/

3. RESULTS

3.1 Satellite tag deployments

Sixty-one satellite tags of four types were deployed by the basking shark satellite tracking project during July and August of 2012 (N=20), 2013 (N=31) and 2014 (N=10). All satellite tags were deployed within the Sea of the Hebrides (Fig. 1B). Satellite tags were attached to 21 female, 13 male and 27 basking sharks of unknown sex. Tagged sharks ranged from 4m to 9m in total length. Basking sharks in the size range 5-6m (N=26) were most frequently tagged.

3.1.1 Deployments in 2012

Eight SPOT tags and 12 PAT-F tags were deployed across three sites in the Sea of the Hebrides during July and August 2012 (Table 1). SPOT tags remained attached to basking sharks for 108±101 days (mean ± SD; 19 to 322d). Nine of 12 PAT-F tags yielded useful datasets over a mean deployment duration of 114±92 days (mean ± SD; 19 to 280 days range). Eight of 12 PAT-F tags detached from their study animal and transmitted archived data. Four PAT-F tags did not transmit following their programmed release date, but one was found by a member of the public within the Firth of Clyde during summer 2013 and usable data were recovered (119842). Two PAT-F tags (119843 and 119845) that transmitted data following premature detachment were found by members of the public on Scottish and Irish beaches in early summer 2013.

Table 1. Operational history of satellite tags deployed in 2012. *Tags ordered by tag type and transmission duration. Tag physically retrieved (*).Tag failed to transmit (X). Tag transmitting from within Sea of Hebrides MPA proposal (dark grey); tag operational (light grey). Tag detached during indicated month or transmissions permanently ceased (D). Light geolocation tag (cross hatched); accurate geolocation against MPA with high confidence not possible.*

Tag ID	Tag type	Sex	Length *m*	2012						2013					
				J	A	S	O	N	D	J	F	M	A	M	J
*120500	SPOT	M	6-7		D										
119855	SPOT	U	6-7		D										
120497	SPOT	F	4-5		D										
*119856	SPOT	M	5-6				D								
120496	SPOT	F	5-6				D								
120498	SPOT	F	5-6					D							
120499	SPOT	M	7-8						D						
119854	SPOT	U	4-5											D	
119850	PAT-F	F	8-9		D										
119848	PAT-F	U	5-6		D										
*119851	PAT-F	U	5-6		D										
119852	PAT-F	F	6-7					D							
119843	PAT-F	M	7-8						D						
119846	PAT-F	F	6-7							D					
*119845	PAT-F	M	4-5								D				
*119853	PAT-F	M	6-7											D	
*119842 (X)	PAT-F	F	4-5	Failed to transmit; tag physically retrieved – data obtained											
119844 (X)	PAT-F	M	8-9	Failed to transmit											
119847 (X)	PAT-F	F	5-6	Failed to transmit											
119849 (X)	PAT-F	F	7-8	Failed to transmit											

3.1.2 Deployments in 2013

Fifteen SPOT, four SPLASH-F (version 1) and 12 MiniPAT tags were deployed at two sites (Gunna Sound and Tiree) in the Sea of the Hebrides during July and August 2013 (Table 2). No tags were deployed at Hyskeir in 2013, although three days of search for basking sharks were conducted at the site. SPOT tags provided location data throughout the summer period, transmissions ceased in late September and October 2013. Tags recommenced transmissions in the following spring (2014). Two of four SPLASH-F tags remained attached for 45 days as programmed. One tag (129432) prematurely released after 34 days and one tag (129431) failed to release as programmed. Ten MiniPAT tags transmitted data; five tags remained attached for the programmed operational period, the remaining five detaching prematurely. Of 31 satellite tags deployed in 2013, 10 were retrieved.

Table 2. Operational history of satellite tags deployed in 2013. *Tags ordered by tag type and transmission duration. Tag physically retrieved (*). Tag failed to transmit (X). Tag transmitting from within Sea of Hebrides MPA proposal (dark grey); tag operational (light grey). Tag detached during indicated month or transmissions permanently ceased (D)**.** Light geolocation tag (cross hatched); accurate geolocation against MPA with high confidence not possible.*

Tag ID	Tag type	Sex	Length *m*	2013						2014								
				J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
129432	SPLASH-F (v1)	U	5-6		D													
*129431	SPLASH-F (v1)	F	7-8		D													
*129433	SPLASH-F (v1)	M	7-8		D													
*129434	SPLASH-F (v1)	U	5-6			D												
*129447	SPOT	U	4-5			D												
*129435	SPOT	F	5-6			D												
129438	SPOT	M	5-6			D												
129446	SPOT	U	5-6			D												
129443	SPOT	F	6-7				D											
129450	SPOT	F	5-6								D							
129441	SPOT	M	5-6									D						
129445	SPOT	U	7-8											D				
129444	SPOT	U	7-8													D		
129437	SPOT	U	5-6														D	
*129448	SPOT	U	5-6														D	
129449	SPOT	U	5-6														D	
129439	SPOT	U	6-7															D
129436	SPOT	U	5-6															D
129440	SPOT	F	4-5															D
*131890	MiniPAT	U	5-6				D											
*129453	MiniPAT	U	4-5					D										
129451	MiniPAT	U	5-6							D								
129459	MiniPAT	U	4-5							D								
129457	MiniPAT	U	7-8								D							
*129454 (X)	MiniPAT	F	5-6										D					
*129456	MiniPAT	F	5-6										D					
129455	MiniPAT	F	5-6										D					
129442	MiniPAT	U	4-5											D				
129452	MiniPAT	F	5-6											D				
129458	MiniPAT	U	4-5											D				
131891 (X)	MiniPAT	U	5-6	Failed to transmit														

3.1.3 Deployments in 2014

Ten SPLASH-F tags (version 2) were deployed in the area of the Cairns of Coll and to the north of Coll during 2014 (Table 3). No tags remained attached for their programmed operational period, although two tags (137654, 137651) remained attached until early April 2015. Two tags (137647, 137651) failed to transmit data at the programmed release date, but did transmit during the period these sharks where in the Sea of the Hebrides. Four tags were physically retrieved, three by the University of Exeter and one by Scottish Natural Heritage. One tag (137647) failed to create GPS locations. Argos data received from SPLASH-F tags during the July to end-September period were limited (N=305 filtered locations) in comparison to GPS (N=462 filtered locations), and as such GPS data were used for all subsequent analysis.

Table 3. Operational history of satellite tags deployed in 2014. *Tags ordered by transmission duration. Tag physically retrieved (*).Failed to detach and transmit (T). Tag transmitting from within Sea of Hebrides MPA proposal (dark grey); tag operational (light grey). Tag detached during indicated month or transmissions permanently ceased (D). Light geolocation tag (cross hatched); accurate geolocation against MPA with high confidence not possible.*

Tag ID	Tag type	Sex	Length *m*	2014						2015						
				J	A	S	O	N	D	J	F	M	A	M	J	J
137647 (T)	SPLASH-F (v2)	M	5-6		D											
*137646	SPLASH-F (v2)	M	6-7		D											
*137653	SPLASH-F (v2)	M	7-8			D										
137648	SPLASH-F (v2)	F	6-7			D										
137645	SPLASH-F (v2)	U	7-8				D									
137650	SPLASH-F (v2)	F	7-8					D								
137652	SPLASH-F (v2)	U	6-7					D								
*137649	SPLASH-F (v2)	U	6-7						D							
*137654	SPLASH-F (v2)	U	7-8										D			
137651 (T)	SPLASH-F (v2)	F	5-6										D			

3.2 Summer movements of basking sharks (July to end-September)

Argos and GPS location data collected by the basking shark satellite tracking project reveal this species is likely present throughout much of the southern extent of the Sea of the Hebrides MPA proposal during the summer (Fig. 5). Recorded patterns of basking shark distribution varied in each year due to the tagging locations and number of tags deployed; however, gathered data indicate that the tagged basking sharks concentrated in the areas around Tiree and Coll but also demonstrated dispersal throughout the region (Fig. 5).

Satellite tracking revealed a wide range of movement behaviours, with some individuals remaining close to their tagging locations for extended periods of time (months; Fig. 5A-B and Annex 1) and others dispersing further, yet remaining within the area of the proposed Sea of the Hebrides MPA (Fig. 6C and Annex 1). Some tracked individuals moved to neighbouring islands of Mull, Colonsay, Jura and Isla (Fig. 6D and Annex 1), while other sharks undertook extended forays to the northern coast of the Republic of Ireland and Northern Ireland, with some individuals subsequently returning to the area of Coll and Tiree (Fig. 6E-F and Annex 1).

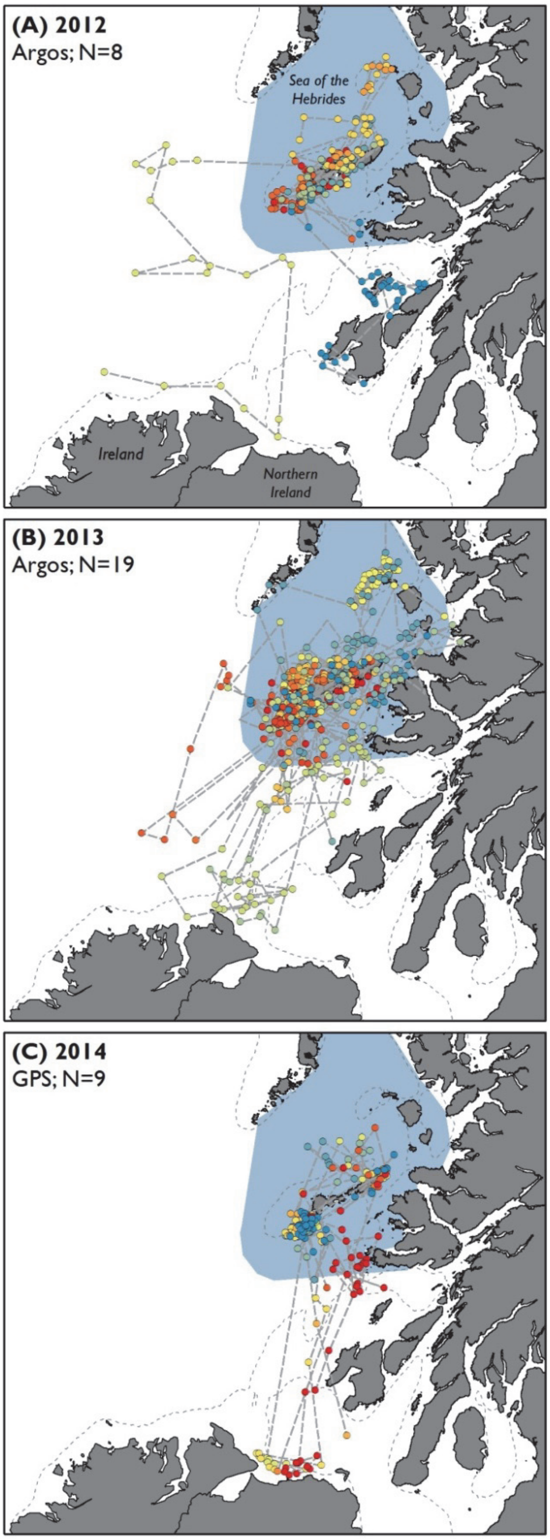


Figure 5. Overview of summer movements of basking sharks tracked using SPOT and SPLASH-F tags. *Movements of basking sharks fitted with SPOT tags (Argos locations; 2012 and 2013) and SPLASH-F (GPS locations; 2014) tags for the period July to end-September. Number of individuals (N). Each colour represents a dataset from a single tracked individual. Showing single highest quality daily Argos locations for tracked individuals (SPOT; 2012 and 2013), and randomly selected single daily GPS locations for tracked individuals (GPS; 2014). Sea of the Hebrides MPA proposal (blue polygon). 50m depth contour (grey broken line; GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.*

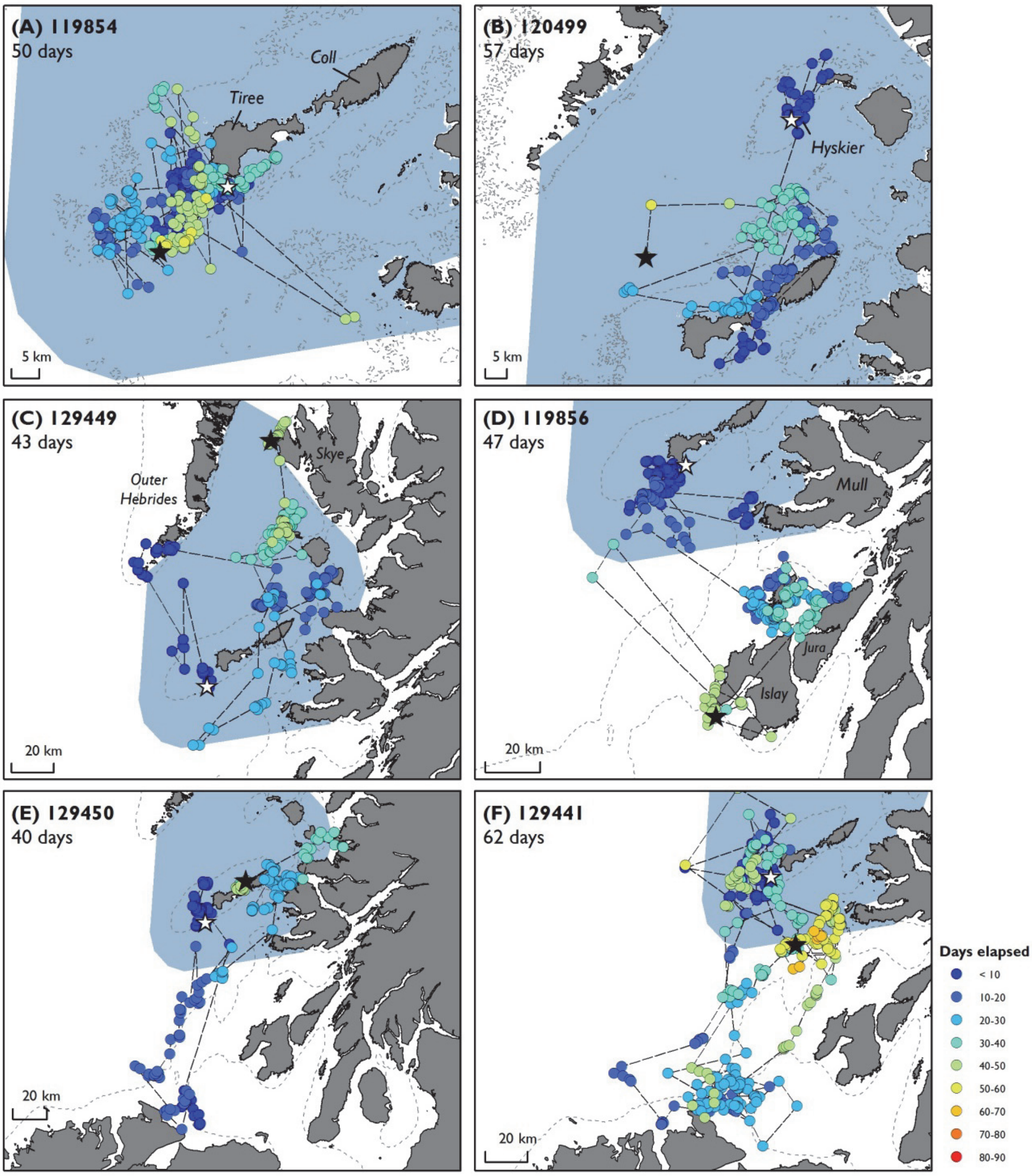


Figure 6. Movements of basking sharks tracked with SPOT tags. *Selected examples of movement behaviour demonstrated using all available Argos locations post-filtering - providing multiple locations per day. Attachment locations (white stars), tag detachment locations (black stars). (A,B) remaining close to the tagging locations of Coll, Tiree and Hyskeir, (C) movement away from Tiree to outer Hebrides and Skye, (D) movement from tagging area to the islands of Islay and Jura, and (E,F) longer-range movements away from and returning to the Sea of the Hebrides. Dashed lines join consecutive locations but do not infer straight line movement. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263 and GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.*

3.2.1 Areas of high relative importance

Areas of high relative importance were assessed using basking shark tracking data (Argos and GPS locations) gathered between July and end-September in 2012, 2013 and 2014. It should be cautioned that tag deployment locations have varied each year due to logistical constraints, identifying areas where basking sharks are present, and due to weather conditions for safe operation at sea. As such, resulting areas of high relative importance are likely biased to the locations of satellite tag deployments. Annual minimum convex polygons highlight that while tagged basking sharks concentrated around the islands of Coll and Tiree, they also dispersed widely throughout the southern extent of the Sea of Hebrides MPA proposal; to the south and east of the Outer Hebrides (including South Uist and Barra) and to the north of Ireland (Fig. 7A; 2012-2014). Two areas; one to the south and west of Tiree and the other, Gunna Sound, identified by grid enumeration and kernel density estimation, are annually persistent areas of high relative importance for basking sharks (Fig. 7B-C; 2012-2014). Sharks tagged at these locations, and at the others tagging locations largely converge on these areas, either remaining throughout summer tracking or returning on variable schedules.

Grid enumeration and kernel density estimation also identified less dense areas of basking shark location data away from these core areas. These occurred to the west of Mull and along the southern boundary of the Sea of the Hebrides MPA proposal. Less dense aggregations of location data also occurred near the islands of Rum and Eigg.

3.2.2 Environmental features and habitat model

Single daily highest quality Argos locations (2012 and 2013; SPOT tags) and randomly selected single daily GPS locations (2014) from satellite tracked basking sharks were contextualised with information on the physical environment (Fig. 8), and with data on extant boat-based surveys, modelled basking shark persistence and public sightings data (Fig. 9).

Basking sharks were associated with shallow (relative) waters (Table 4 and Fig. 8A), with waters overlaying rock and reef seabed substratum (Table 4 and Fig. 8B), and waters of low to moderate (relative) tidal speeds (Table 4 and Fig. 8C).

Basking sharks locations largely occurred within areas of modelled high (relative) persistence (Table 4; Fig. 9B). This habitat model was produced independently of satellite tracking data (Paxton *et al.* 2014) and is in part based on boat-based survey data (Fig. 9A) and so a spatial comparison of tracking data and the model yields a useful corroboration of both datasets. The comparison also highlights areas of modelled high persistence that were not occupied by satellite tracked basking sharks, such as west of the Outer Hebrides, and this highlights the need for further research in these areas.

3.2.3 Plankton

Vertical plankton trawls were conducted at the location of basking shark tagging events and throughout the wider operating region. These trawls were undertaken to help improve knowledge regarding the plankton community upon which basking sharks were feeding at the time of tagging. SNH funded the analysis of a subset of these samples for zooplankton species abundance and diversity. The results of these analyses will feature in a further report.

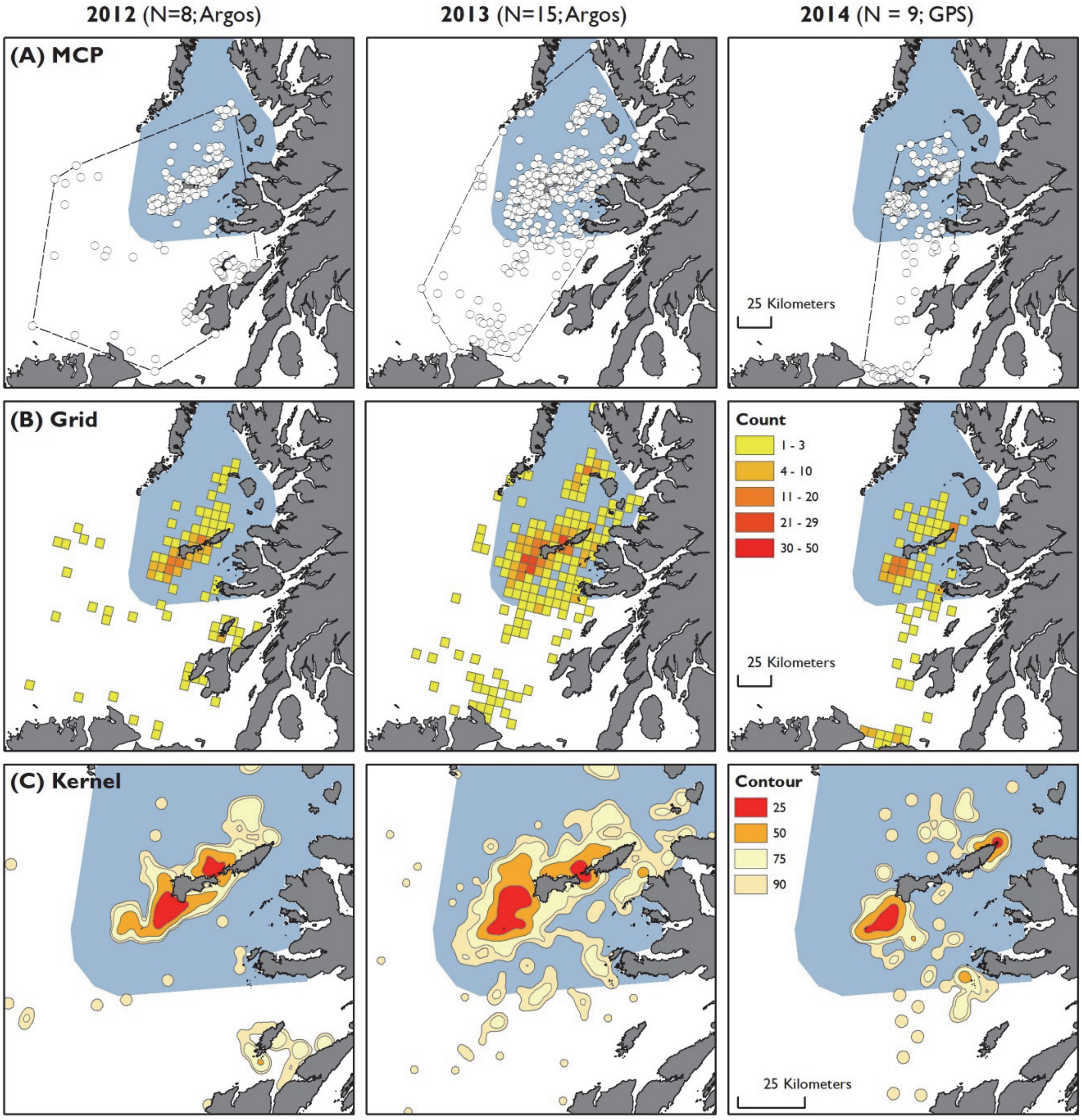


Figure 7. Identifying areas of relative importance. *Areas of relative importance for the period July to end-September (2012 to 2014) estimated using (A) Minimum Convex Polygon (MCP), (B) Grid; Point density enumeration and (C) Kernel. In 2012 and 2013 locations (white circles) are daily highest quality Argos locations from basking shark tagged with SPOT. In 2014, locations (white circles) are randomly selected single daily locations from SPLASH-F tags. Sea of the Hebrides MPA proposal (blue polygon), Contains Ordnance Survey data © Crown copyright and database right 2013.*

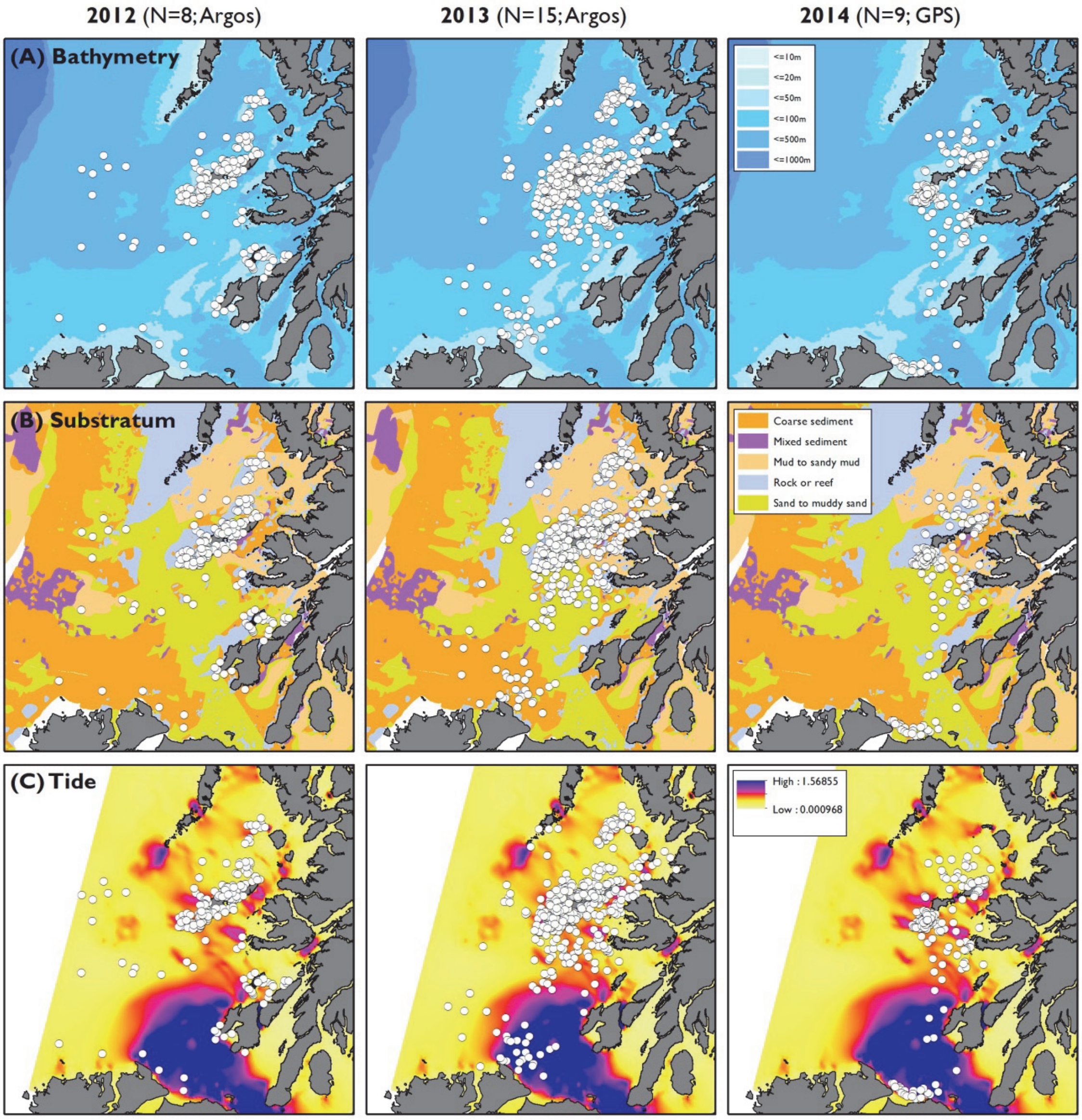


Figure 8. Basking sharks and their environment. *Distribution of daily highest quality Argos satellite locations from tagged basking sharks (SPOT and SPLASH-F tags; white circles; n = 873; July to end-September 2012-2014) with respect to (A) bathymetry [m] (B) substratum and (C) tide [Polpred; m^{-s}]. Contains Ordnance Survey data © Crown copyright and database right 2013. Bathymetry © SeaZone Solutions, 2013, Licence O1035263.*

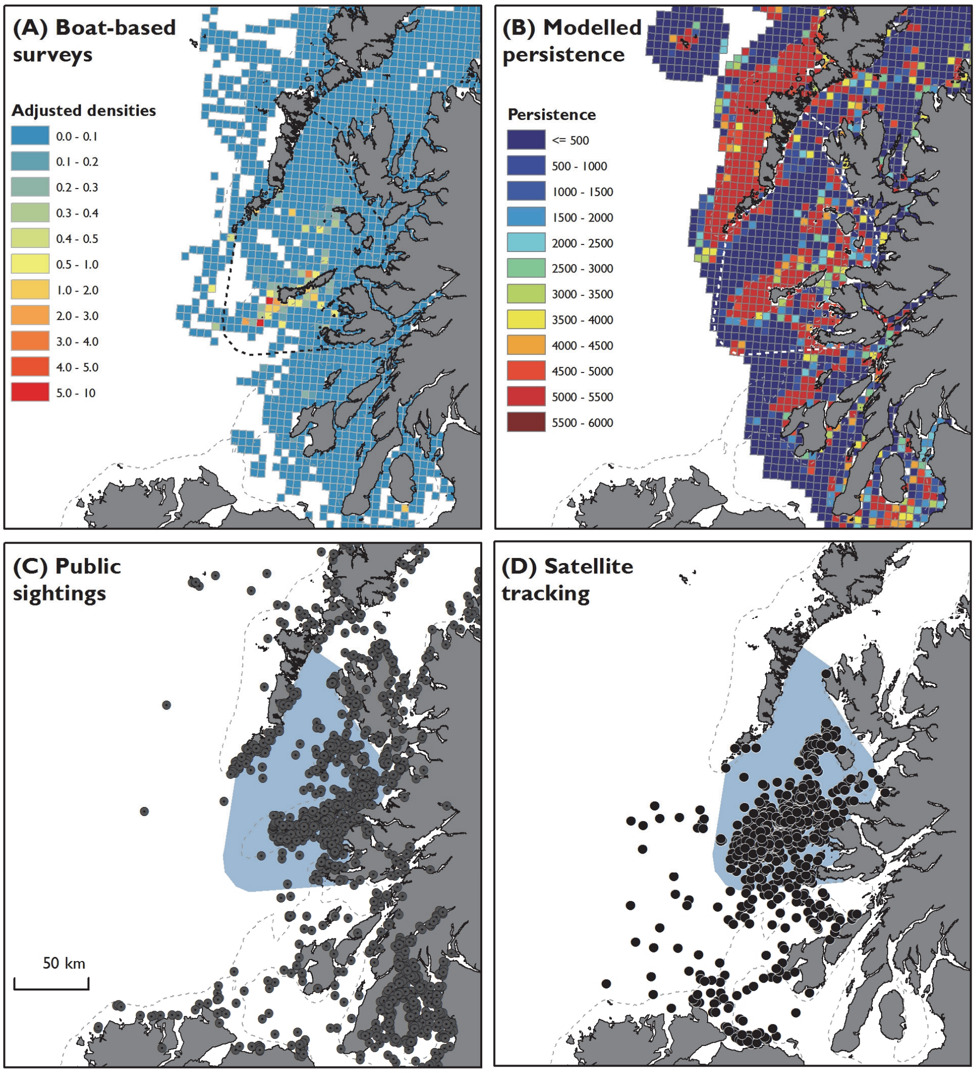


Figure 9. Distribution of basking sharks from multiple techniques. *Distribution of basking shark occurrence with respect to (A) adjusted sightings from boat based surveys (Speedie et al. 2009) (B) modelled distribution of basking shark persistence based on visual transect sightings and predictive habitat suitability model* (Paxton et al. 2014) *(C) effort corrected public sightings (Witt et al. 2012a) and (D) best daily locations for (July to end-September 2012-2014) from satellite tracking. 50m depth contour (grey broken line; GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.*

***Table 4. Basking sharks, the MPA proposal and their environment**. Percentage of Argos and GPS locations occurring within the Sea of the Hebrides MPA proposal. Summary of environmental variables sampled at the location of highest quality Argos locations (one per day per animal) for basking sharks tracked with SPOT tags (2012 and 2013) and randomly selected GPS locations (one per day per animal) for basking sharks tracked with SPLASH-F tags (2014) for the period July to end-September.*

Year *(Method)*	**N sharks** (n loc.)	**MPA** % within proposal	**Bathymetry** *(GEBCO, m)* *Mean*±1SD (range)	**Substratum** % of locations coincident to substratum type	**Tide** *(m.s^{-1})* *Mean*±1SD (range)	**Persistence model** *Mean*±1SD (range)
2012 (Argos)	8 (240)	78	42 ± 37 (0 - 194)	Mud to sandy mud; 4%	0.23 ± 0.13 (0.03 – 1.2)	4040 ± 941 (2404 – 4757)
				Sand to muddy sand; 12%		
				Coarse sediment; 14%		
				Rock and reef; 70%		
2013 (Argos)	19 (674)	89	45 ± 29 (0 - 176)	Mud to sandy mud; 4%	0.26 ± 0.13 (0.03 – 0.95)	3993 ± 641 (3049 – 5466)
				Sand to muddy sand; 14%		
				Coarse sediment; 18%		
				Rock and reef; 64%		
2014 (GPS)	9 (198)	80	55 ± 30 (0 - 193)	Mud to sandy mud; 6%	0.3 ± 0.17 (0.08 – 1.15)	3427 ± 806 (1963 – 5045)
				Sand to muddy sand; 28%		
				Coarse sediment; 12%		
				Rock and reef; 54%		

3.2.4 Fastloc^{TM} and Argos

Satellite tags enabled with Fastloc^{TM} were used to build further understanding on the distribution of basking sharks in the Sea of the Hebrides. GPS tags are approximately three times the purchase cost of SPOT tags; as such, GPS tags each year represented only a subset of all satellite tags deployed (with the exception of 2014). PAT-F and SPLASH-F tags performed with variable efficiency, with tags deployed in 2014 (SPLASH-F version 2) performing better (creating more GPS locations), on the whole, than those in 2012 and 2013. Patterns of movement and distribution for each individual from the two independent geolocation techniques (Fastloc^{TM} and Argos) largely resulted in the same areas of occupation, but GPS provided some finer level of insight into movement (Fig. 10 and Annex 1). Most GPS locations were received during the summer in each year (July to end-September) which, along with Argos location data, highlighted the surface-orientated behaviour of basking sharks during this period. The capability of Fastloc^{TM} tags to generate GPS locations over short intervals at the sea surface (a few milliseconds) was highlighted by a basking shark (137653) that moved to the north coast of Northern Ireland, however, Argos transmissions were not received from the tag during this time (Fig. 10).

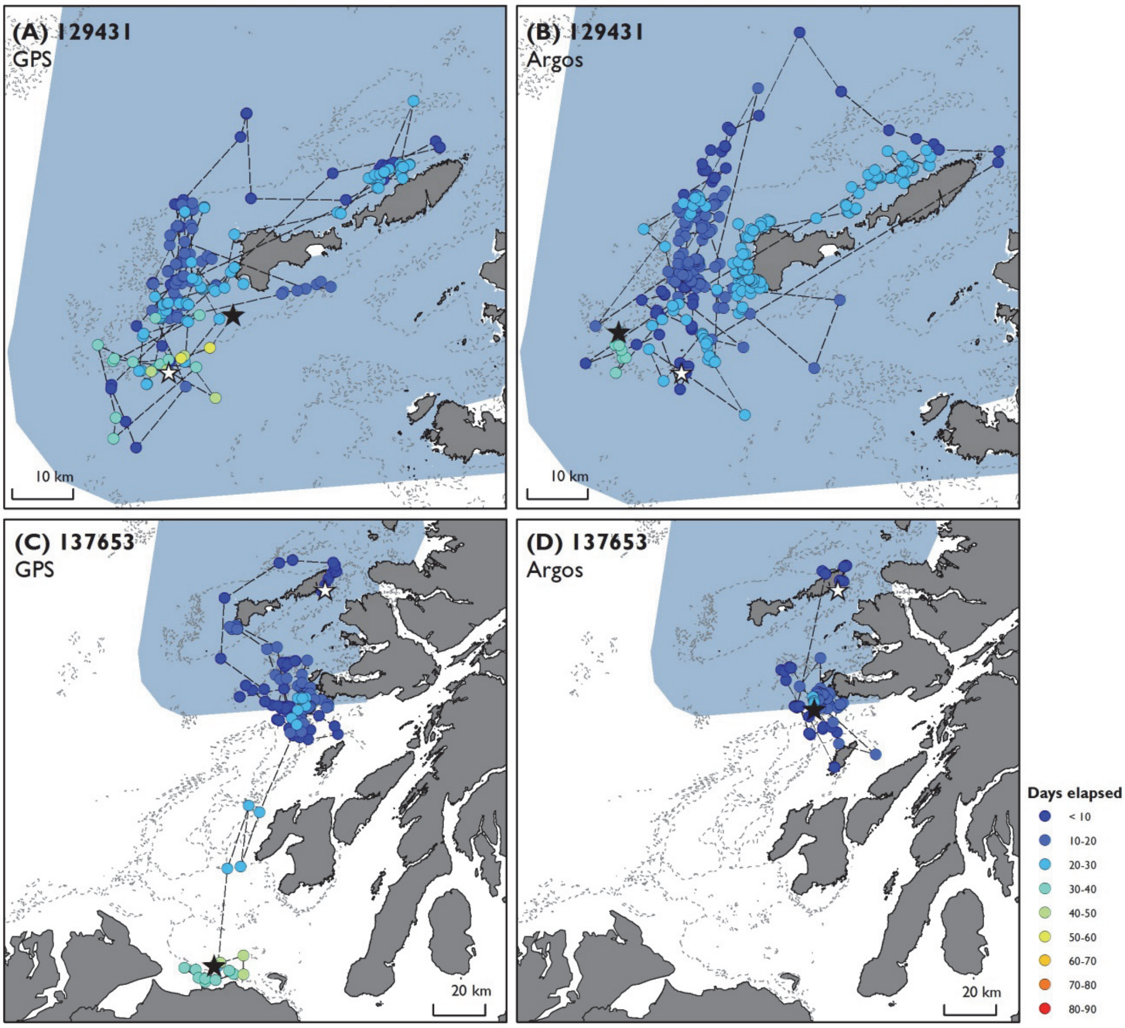


Figure 10. Fastloc™ GPS and contemporaneous Argos locations for basking sharks form SPLASH-F tags. *Example movements from two sharks revealed by GPS-enabled satellite tags with contemporaneous Argos locations. Attachment locations (white stars), tag detachment locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

3.3 PAT-F, MiniPAT and SPLASH-F tag detachment locations

Satellite tags with programmable release dates (PAT-F, MiniPAT and SPLASH-F) detached and transmitted either on programmed release dates (N=6) or following detection of premature detachment (N=20). Tags detached from their study animals in the northern Irish Sea, Celtic Sea and to the north and west of Ireland. Tag detachment locations, occurring from November onwards in each year (N=17), suggest movement of basking sharks away from the Sea of the Hebrides following their summer occupancy in the region (Fig. 11).

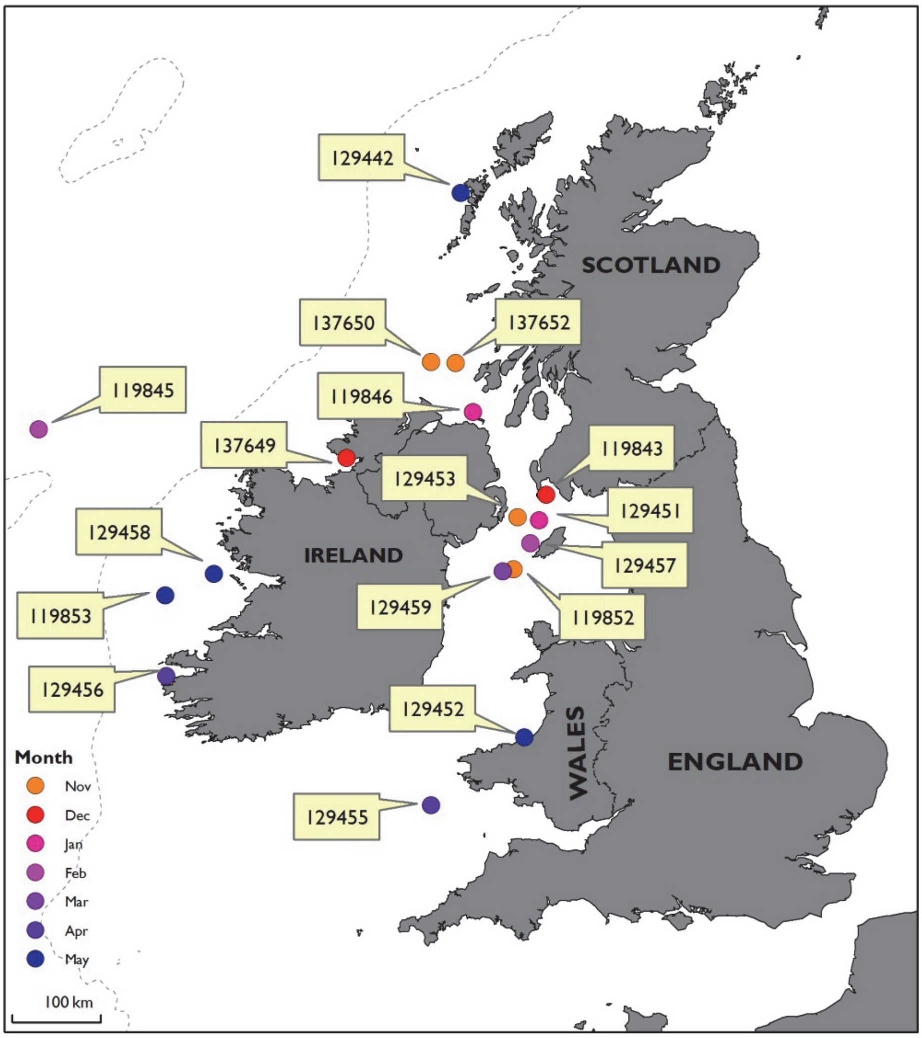


Figure 11. Tag (pop-off) detachment locations for PAT-F, MiniPAT and SPLASH-F tags. *Locations of tag detachment (pop-off). Locations coloured by month of tag detachment (November to May). Satellite tags detaching between July and October in year of tag deployment not shown. 200m depth contour (grey broken line; source: GEBCO).*

3.4 Long-distance movements revealed by Argos

SPOT tags deployed on two basking sharks (119854, 120498) revealed insights into long-distance migration (Fig. 12). Basking sharks travelled south-west for approximately 3300km and 3400km respectively (minimum straight-line along-track distance) through the Economic Exclusive Zones of Ireland, Spain (Canary Islands) and Portugal (mainland and Madeira) to the coast of North Africa. These tags eventually detached in Madeira and the Canary Islands, 322 days and 132 days following deployment in the Sea of the Hebrides (Fig. 12). A further basking shark (137651) tagged with SPLASH-F in 2014 also undertook long-distance movement from Scotland towards the north coast of Africa over the winter period, this tag began transmitting in April 2015 from east of Madeira.

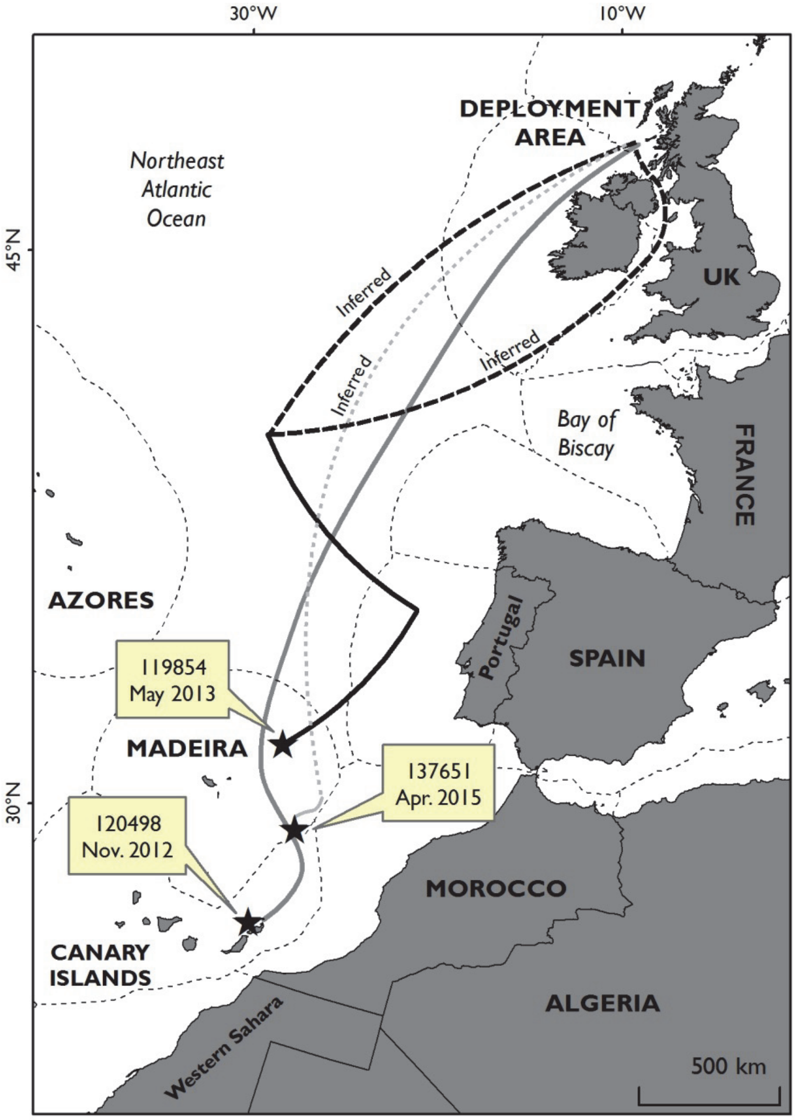


Figure 12. Long-range movements of basking sharks from Scotland revealed by Argos satellite tracking*. Two SPOT-tagged basking sharks in 2012 (119854, 120498) and one SPLASH-F tagged shark in 2014 (137651). Exclusive Economic Zone boundaries (black dashed lines). Tag ID and month of tag detachment indicated.*

3.5 Spring-time movements revealed by SPOT tags

Nine basking sharks fitted with SPOT tags in summer 2013 retained their tags throughout the autumn and winter period and into the subsequent spring of 2014. These tags did not provide location data during autumn and winter as the sharks were deeper in the water column and away from the surface. SPOT tags initially ceased transmissions between September and December 2013 before recommencing transmission in late February, March and April of 2014, from the Bay of Biscay, west of Ireland, the Celtic Sea and from southern Ireland (Fig. 13 and Annex 1). Seven of nine sharks that re-appeared in spring 2014 made northerly movements progressing towards Scotland, although some tags ceased transmitting along western shores of Ireland (Annex 1).

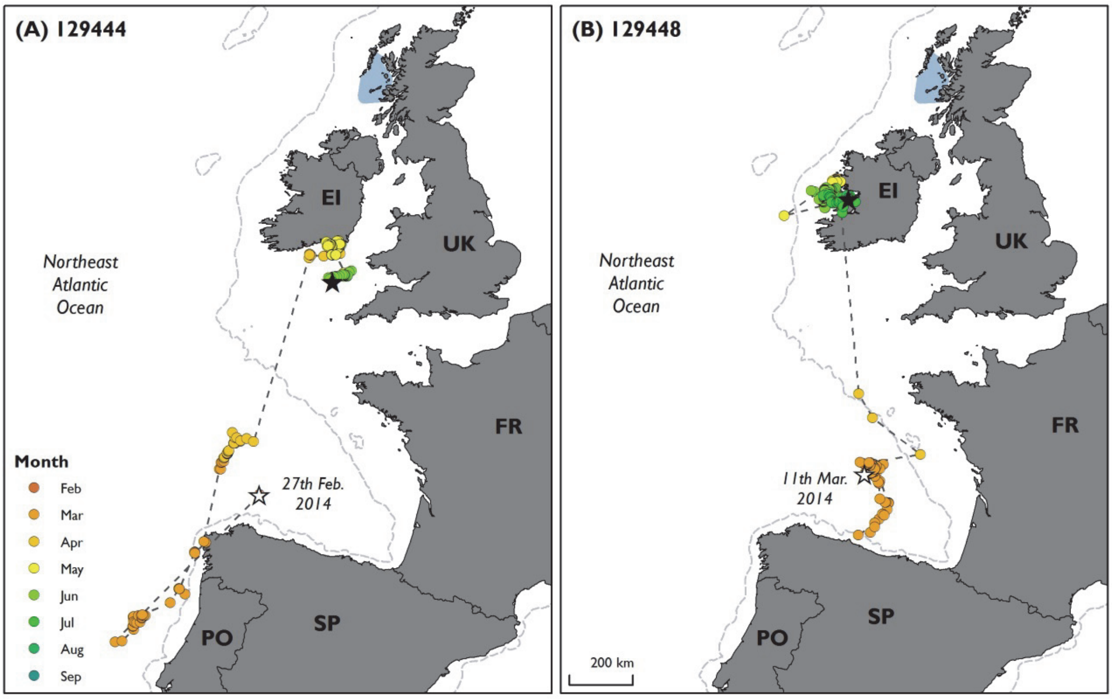


Figure 13. Spring-time surfacing and northward movement made by basking sharks. *Examples of spring-time (2014) re-surfacing events (white stars) and subsequent spring-summer movements for two basking sharks tagged in the summer of 2013. No transmissions received during winter period (2013/2014). Positions coloured by month of occurrence. Final locations (black stars).Tag ID indicated for each figure part. Dashed lines join consecutive locations but do not infer straight line movement (grey broken line). Sea of the Hebrides MPA proposal (blue polygon). Contains Ordnance Survey data © Crown copyright and database right 2013. 200m bathymetric contour (grey narrow-dashed line; source: GEBCO).*

3.6 Inter-annual fidelity to Scotland revealed by SPOT

Four tagged basking sharks returned to waters of the Western Isles of Scotland in the year following tag attachment (2013-14; N=2 and 2014-15; N=2). Two examples include, one shark (129439) tagged in 2013, where transmissions ceased in late August. The tag recommenced transmissions eight months later (April 2014) from nearshore southern Ireland. Transmissions ceased again before recommencing and relocating the shark to the south and west of Barra in August 2014, the tag then remained operational until mid-September of that year. The footprint of this shark while in coastal waters of Scotland in 2013 (14 days tracking) was somewhat smaller than in 2014 (48 days tracking; Fig. 14A). A second shark (129449) departed surface waters of Scotland in mid-September in 2013, re-surfaced eight months later in the Bay of Biscay during April 2014 then intermittently transmitted from the Celtic Sea, West of Ireland while making a northerly migration before returning to the Sea of the Hebrides in late July of 2014. The sea area used by this basking shark in 2013 (44 days tracking) was somewhat larger than in 2014 (32 days tracking; Fig. 14B).

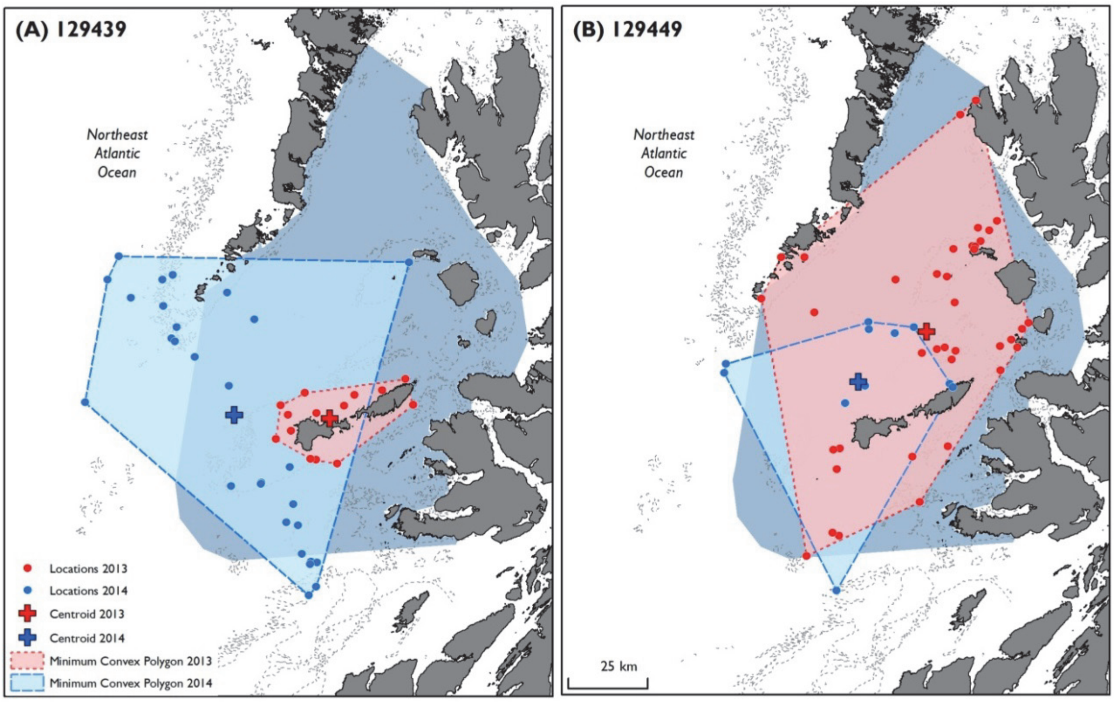


Figure 14. *Inter-annual site fidelity. Example distribution of two sharks demonstrating inter-annual site fidelity to Sea of the Hebrides MPA proposal. Single highest quality Argos locations per day (red and blue circles for 2013 and 2014 respectively). Minimum convex polygons for data gathered in 2013 and 2014 (red and blue polygons respectively), geographic mean centroid of Argos locations for 2013 and 2014 (red and blue crosses respectively). Tag ID indicated for each figure part. Dashed lines join consecutive locations but do not infer straight line movement (grey broken line). Sea of the Hebrides MPA proposal (blue polygon). 50m bathymetry (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

3.7 Movements of basking sharks reconstructed from light geolocation

Light geolocation datasets were collected by PAT-F, MiniPAT and SPLASH-F tags. Light geolocation data are best used to describe broader-scale movements of migrating animals. Of the gathered datasets, 12 were greater than 170 days in length (i.e. light geolocation data extended past December of the year in which tags were deployed). This limitation was applied to ensure overwintering behaviour could be determined with greater confidence. Basking sharks tagged with these archival tags for the majority undertook one of two dispersal strategies following summer residency in the Sea of the Hebrides:

Semi- or complete circumnavigation of Ireland opting to travel either through the north-east Atlantic or through the Celtic and Irish Seas with periods of focused presence to the south or west of Ireland either on the continental shelf or slope (N=10; Fig. 15A and Annex 1). Detailed examples of movement include one shark that departed waters to the west of the Outer Hebrides and headed south-west into the north-east Atlantic then circumnavigated Ireland, passing through the Irish Sea in a northerly direction in December 2013 (119845; Fig. 15A). This individual spent the winter months in areas where water depth exceeded 200m to the west of the UK and Ireland; the tag detached in February 2014. A second basking shark departed the Sea of the Hebrides, moved southwards through the Irish Sea (119853; Fig. 15B), to spend much of the winter in sea areas (approx. depth of shark 150-200m) to west of the UK western approaches and then headed northwards along the western coast of Ireland before the tag released in May 2014. This shark undertook deep diving events in March and April to approx. 900-1000m depth.

Longer range movements moving through the Bay of Biscay and beyond to the west of the Iberian Peninsula (N=2; Fig. 15C and Annex 1). An example shark adopting this behaviour departed the Sea of the Hebrides and headed into the north-east Atlantic to waters adjacent to Portugal and North Africa approximately equidistant between the Straits of Gibraltar and Madeira (129458; Fig. 15C). The shark reached this southerly extent of the migration in February 2014 before returning to coastal waters of Ireland in April and May 2014 at which point the tag detached. Depth data received from this tag were infrequent; however, data that were received for the February period indicated this shark was at depths of approx. 200-500m during this southernmost part of the migration.

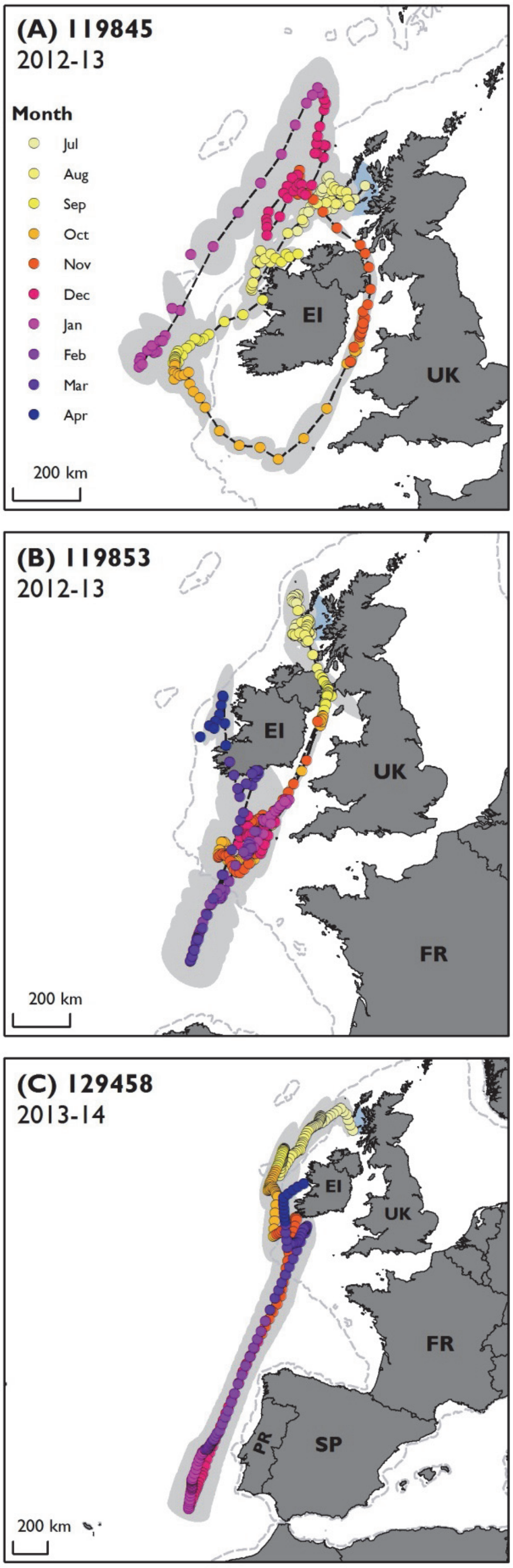


Figure 15. Basking shark movements revealed by light geolocation. *Light geolocation estimates of basking shark movement. Colour of location indicates progressing month of tracking. Grey polygons surrounding estimated locations represent spatial error for each location. Year range of tracking indicated for each individual. 200m bathymetric contour (grey dashed line; source: GEBCO).*

3.8 Basking shark depth distribution in the coastal zone

Data gathered by SPLASH-F tags allow basking shark depth use in the Sea of Hebrides to be spatially mapped using contemporaneous GPS locations. This was achieved using 4-hour summarised estimates of depth use from nine basking sharks during the period July to end-September 2014. Mean percentage of time spent at 0-10m depth was mapped for periods of day (08:00h to 20:00h; Fig. 16A) and night (20:00h to 08:00h; Fig. 16B). During daylight hours sharks spent much of their time near to the surface across their range. By night the pattern reversed with comparatively little time spent near the surface, with some notable exceptions to the north of Coll and to the west of Mull.

The above process was repeated using all available time-at-depth histogram data from PAT-F and SPLASH-T tags across all study years (2012, 2013 and 2014). Throughout the study area, during July to end-September, there was a tendency for tagged basking sharks to spend a greater proportion of their time near the surface (0-10m depth) during the hours of daylight (Fig. 17).

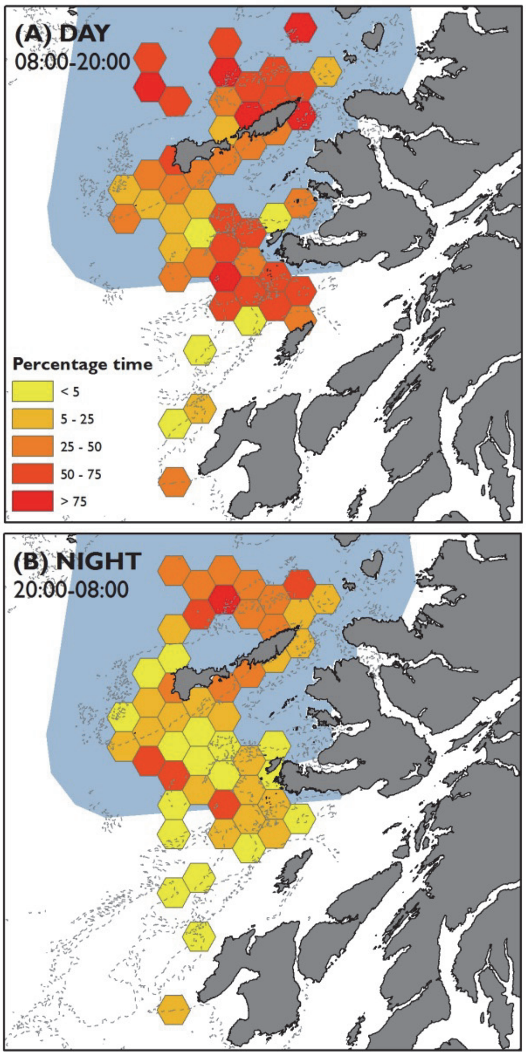


Figure 16. Percentage of time spent near surface (0-10m) by day and night. *Mapped depth use behaviour of basking sharks tagged in 2014 with SPLASH-F tags (N=9). Colour scale depicts percentage time spent between the sea surface and 10m depth, determined from 4-hour histogram data on depth use in specified depth classes. 50m bathymetry (grey dashed contour; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

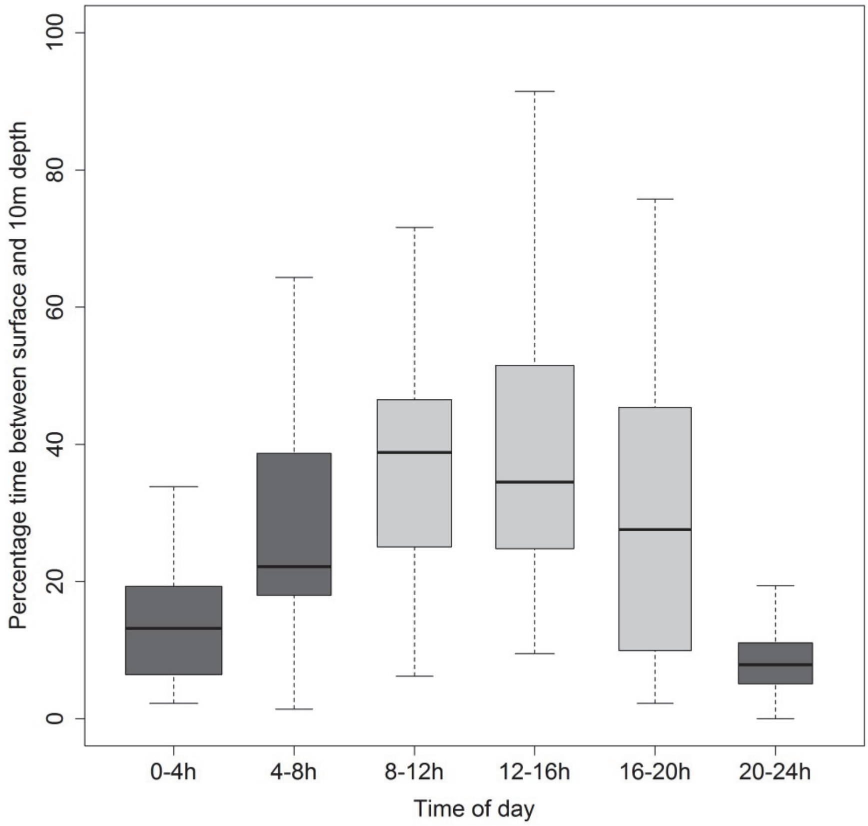


Figure 17. Basking shark depth-use by time of day. *Percentage time spent between the surface and 10m depth for the period July to September 2012 to 2014 summarised at 4-hour intervals (N=32 sharks). Night time (20:00 to 08:00; dark grey boxes), day time (08:00 to 20:00; light grey boxes). Each vertical box displays the distribution of mean percentage time spent within each time block from each shark. Bold horizontal line (median), upper and lower extent of each box (hinges) represent the 25th and 75th percentiles respectively. Dashed vertical lines extending from hinges indicate the range of observed values to approximately the 2.5th to 97.5th percentiles.*

3.8.1 Time-series depth use in the coastal zone

SPLASH-F tags attached to basking sharks were programmed to record depth data at 15-sec. intervals, which were subsequently summarised at 5-min. frequency to mean depths (and range) for transmission via the Argos System (Fig. 18). These data were temporally linked to Argos locations to reveal the approximate geographic locations of depth use. For one individual (129433), this technique revealed a range of depth use behaviour, from periods of near-surface activity (Fig. 18, regions 1, 2 and 4) to intermittent periods of deep-water habitat use (Fig. 18, region 3) occurring to the west of Eigg and Rum.

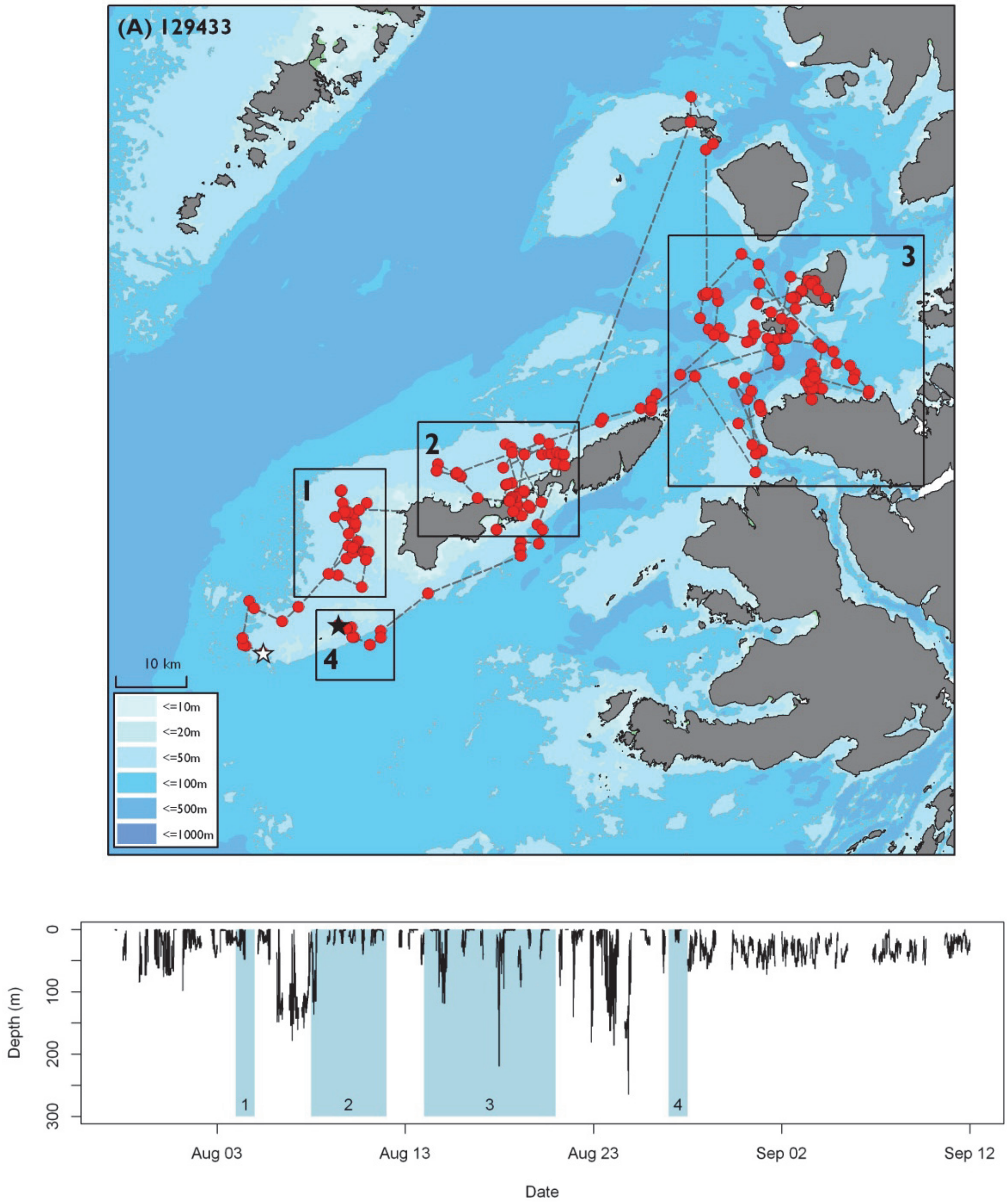


Figure 18. Basking shark depth use from SPLASH-F tags in 2013. *Locations of basking sharks tracked with a SPLASH-F tag (red circles; upper panel). First location received following tagging (white star), final location received (black star). Average depths recorded at 5-min. intervals (lower panel). Numbered regions in map correspond to periods of depth use similarly labelled in the lower panel. Background shading shows bathymetry (© SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

3.8.2 High resolution depth use from physically recovered tags

Four PAT-F tags from 2012, four MiniPAT tags from 2013 and four SPLASH-F tags from 2014 were recovered and data downloaded from the tags. Depth use data for a representative 10 day period during summer residency in the Sea of the Hebrides highlights a variety of behaviours including diurnal and crepuscular movements, deeper water habitat use and prolonged periods of near-surface behaviour (Fig. 19 and Annex 2). These sharks showed evidence of reverse diurnal vertical migration (DVM), whereby an animal moves towards surface waters during the day, returning to deeper waters at night, although showing repeated patterns of bouts of 'yo-yo' dives (Holland *et al.* 1992) during the hours around dusk and dawn.

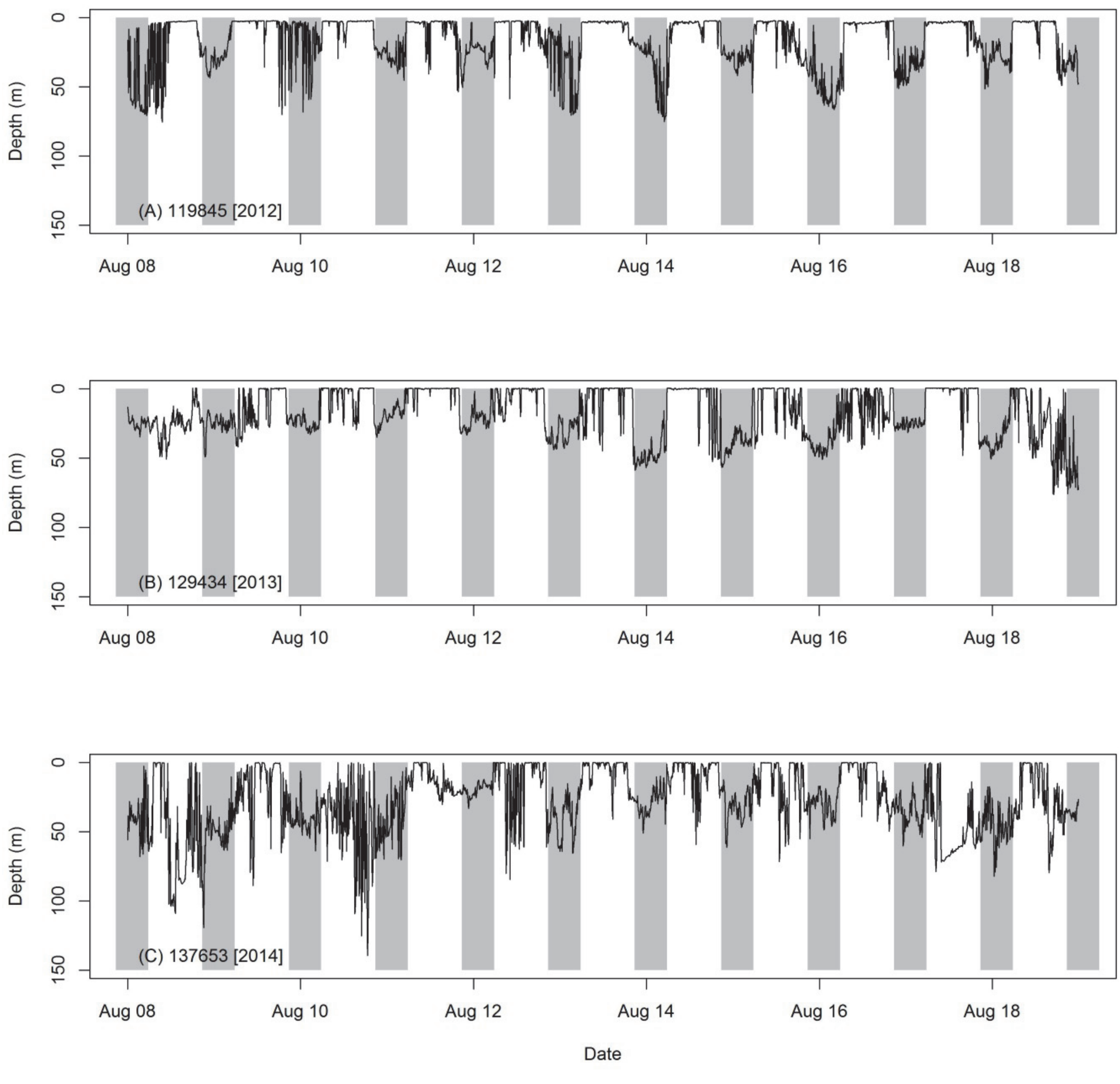


Figure 19. Basking shark depth-use time series from recovered satellite tags. *Example depth-use behaviour from three sharks for arbitrary 10 day period in 2013 (A), 2013 (B), and 2014 (C). Mean depth reported at 5 min. intervals. Grey vertical filled bars indicate periods between sunset and sunrise (approx. 9-hour duration, starting at 9pm BST daily) for the period.*

3.8.3 Basking shark depth distribution

Time-at-depth histogram data (4-hr frequency) were gathered from all archival tags (PAT-F, MiniPAT and SPLASH-F) for complete deployment periods and averaged on a daily basis for each individual. Basking sharks most frequently occupied depths of between 25 and 50m (Fig. 20). When occupying near surface waters (top 10m) basking sharks spent more time in the top 1m of the water column. Relatively little time was spent at great depths >500m (Fig. 20), highlighting that these sharks are predominantly a species of the epipelagic zone.

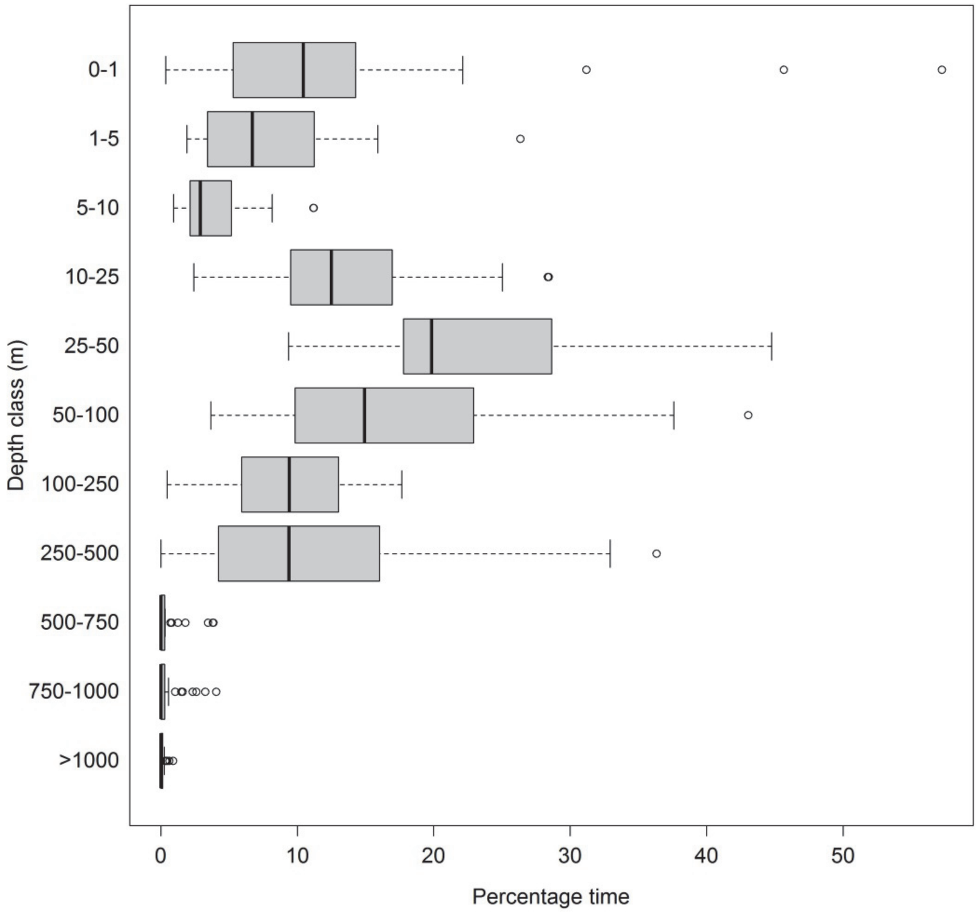


Figure 20. Depth utilization behaviour. *Basking shark depth use (mean percentage time spent in depth class across individuals) from depth-recording satellite tags deployed from 2012-2014 using complete time-series (N=33 tags).*

3.8.4 Maximum depth use

Twenty sharks fitted with archival tags (PAT-F, MiniPAT and SPLASH-F) transmitted data for longer than 100 days each, allowing a reconstruction of depth use behaviour across seasons. Received data indicate a pattern of predominantly shallow depth use (<250m depth) with intermittent excursions to deeper water. Periods of deep water use (>1000m) were observed in seven basking sharks (Fig. 21 and Annex 2). These events occurred off the European continental shelf (Fig. 22). Depth use data also indicate the start of offshore movement in mid-September to early October with marked changes in depth use (i.e. basking sharks moving deeper into the water column as they progress away from the Sea of the Hebrides (Fig. 21 and Annex 2).

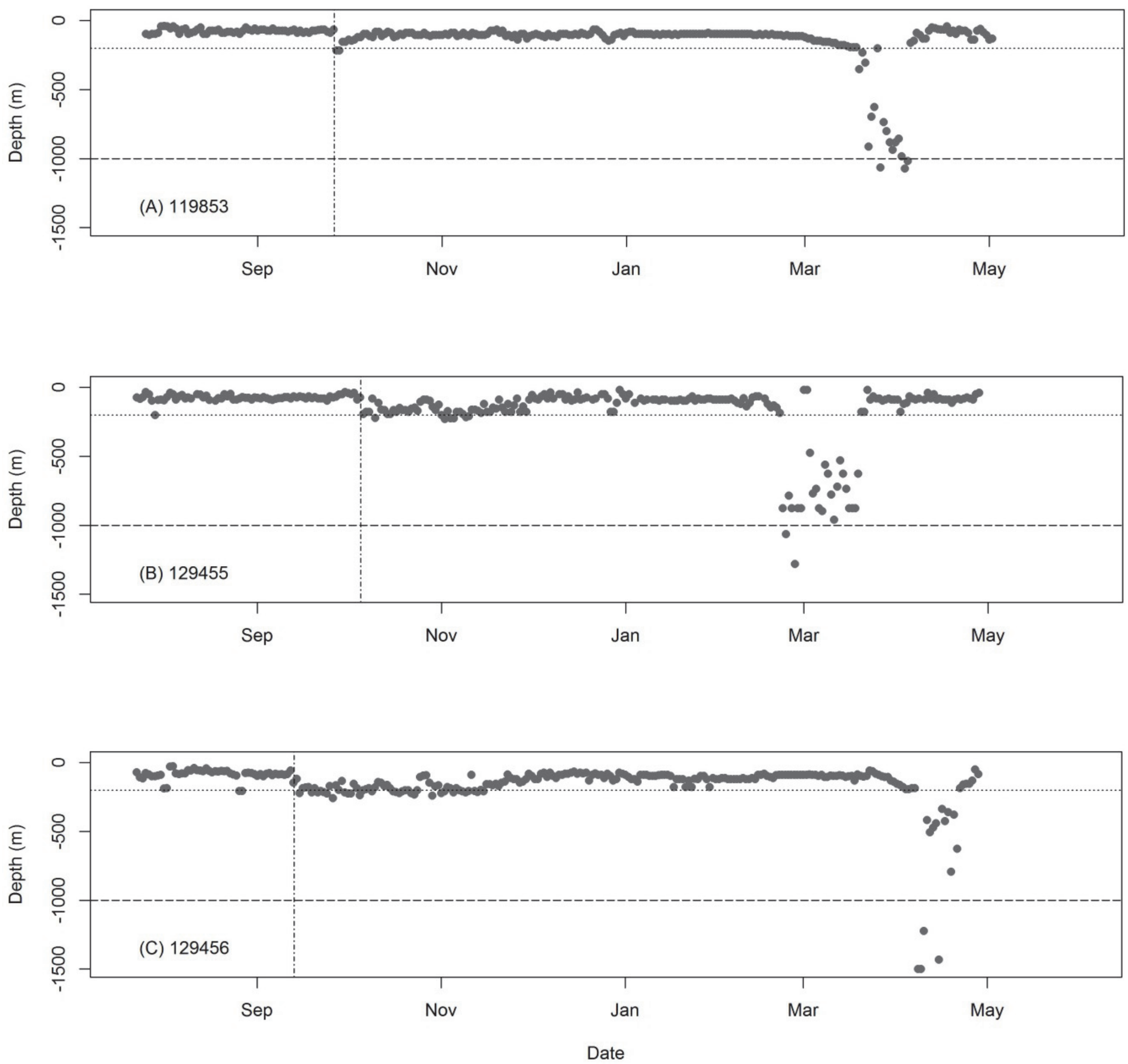


***Figure 21**. **Maximum daily depths for seasonally deep-diving sharks**. Maximum depths (filled circles) from three arbitrary sharks occupying deep waters (>1000m depth) during winter and early spring. Day of change in depth behaviour (broken vertical dot-dash line; A: 26^{td} Sept. 2012; B: 5^{th} Oct. 2013, and C: 13^{th} Sept. 2013). Depth of continental shelf (200 m; short dotted horizontal line), 1000m depth (long-dash horizontal line).*

3.8.5 Geographic locations of deep water utilisation

The geographic locations of deep water use were determined by matching depth use data with light geolocation estimates (Fig. 22). Deep water events were largely restricted to the west of the Bay of Biscay, although this pattern was not exclusive; for example, deep water usage occurred to the west of the Outer Hebrides and to the west of Portugal.

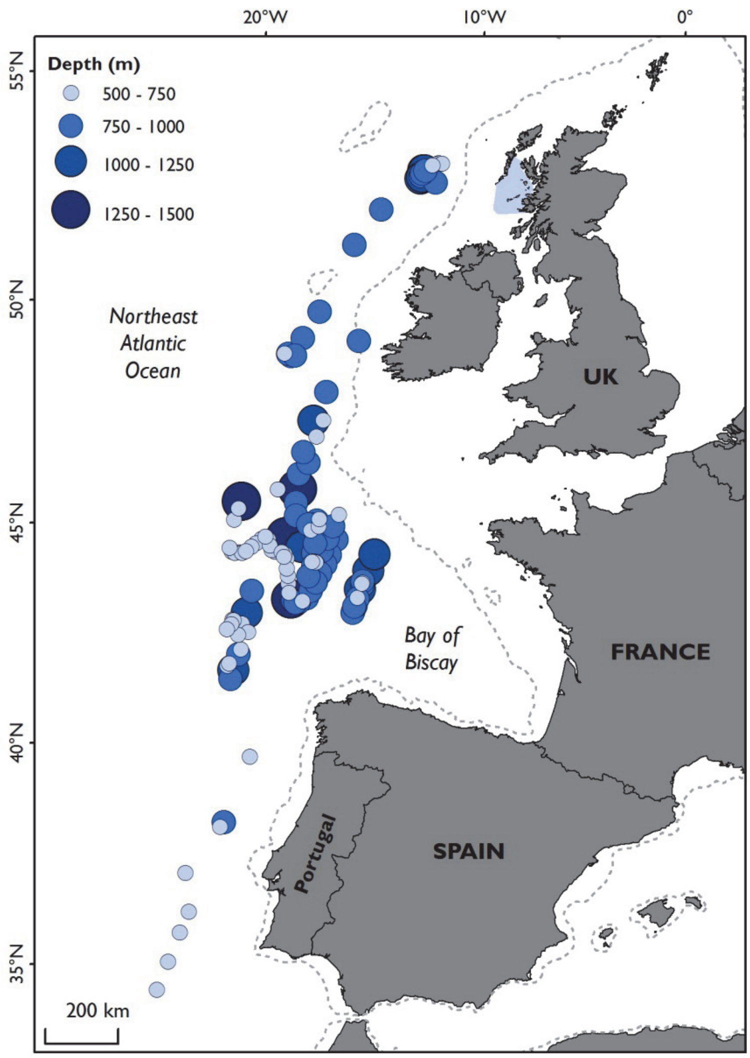


Figure 22. Geographic locations of deep water usage. *Events where daily maximum depth use exceed 500m, locations determined from light geolocation estimates (N=8 sharks; N=126 events). 200m bathymetric contour (grey dashed line; source: GEBCO).*

3.9 Encountered water temperature

Archival tags (PAT-F, MiniPAT and SPLASH-F) gathered data on water temperature encountered by tagged basking sharks. These data were expressed by month (mean value per month) for each individual. Coolest waters were encountered by basking sharks in April. Warmest waters were encountered during the summer months of July, August and September (Fig. 23).

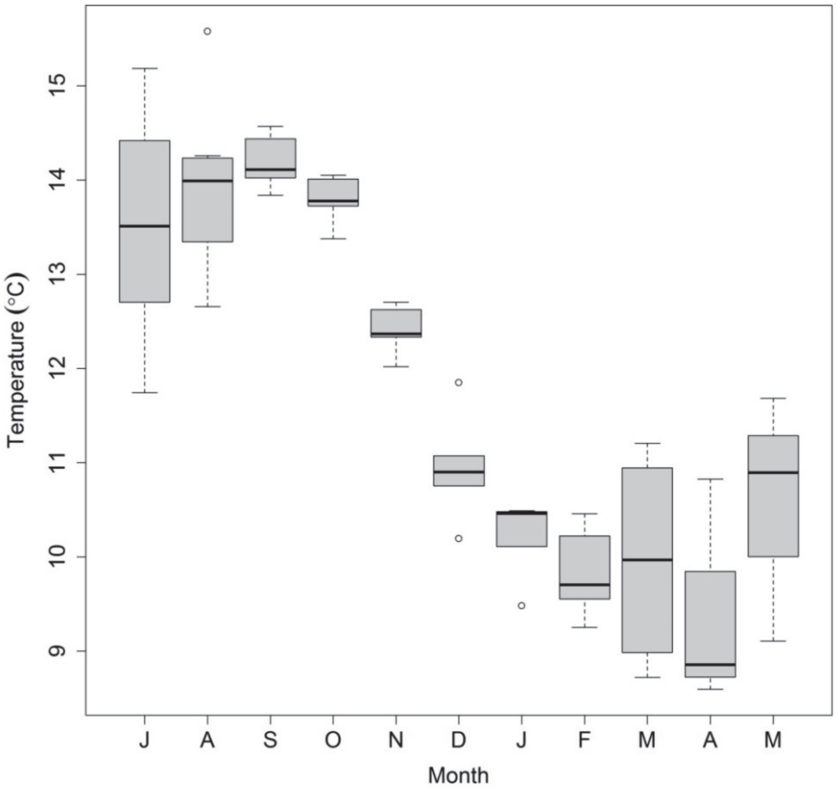


Figure 23. Monthly distribution of water temperature encountered by basking sharks. *Each vertical box displays the distribution of monthly water temperature encountered by sharks (from physically recovered tags, N=12). Bold horizontal line (median), upper and lower extent of each box (hinges) represent the 25th and 75th percentiles respectively. Dashed vertical lines extending from hinges indicate the range of observed values to approximately the 2.5th to 97.5th percentiles. Open circles represent outliers-values occurring outside the 2.5th and 97.5th percentiles of data distribution.*

4. DISCUSSION

4.1 Overview

The deployment of multiple satellite tagging technologies has provided detailed insight into the spatio-temporal movements and depth use behaviour of basking sharks in the Sea of the Hebrides and the north-east Atlantic Ocean. This study is the first, to the authors' knowledge, to deploy this combination of tag technology. Furthermore, the study is the first to spatially link Argos and GPS location data with information on depth use in sharks. As such, the study provides unique insight into both vertical and horizontal movements in an iconic species of conservation concern.

4.2 Basking shark movements

Basking sharks satellite tracked in this study spent a large proportion of their time in the Sea of the Hebrides, particularly in summer months (July to end-September). The results of the tagging highlight seasonal residence to coastal regions. Previous efforts to track this species, with tags deployed in the southern English Channel (N=3), the Clyde Sea (N=2) and the Isle of Man (N=10), have shown movements of sharks into the waters around Scotland's west coast in summer months (Sims *et al.* 2003; Gore *et al.* 2008; Stéphan *et al.* 2011). However, with the exception of recent tag deployments in the Isle of Man, none have demonstrated seasonal residency to coastal regions on a near daily basis with such high spatial accuracy.

Many sharks tracked in this study headed south into waters of the Celtic and Irish Seas and to the west of Ireland, and several individuals moved as far south as the northern African coast. Movements within the north-east Atlantic Ocean have been described from earlier tracking studies (Sims *et al.* 2003; Gore *et al.* 2008) and when considered together, data from available tracking studies and from this project highlight the importance of coastal and offshore waters to the west of the UK and Ireland. It would seem that regular seasonal migrations throughout these waters are commonplace. Data suggest there may be a general trend of southerly migration from Scottish waters after summer, with at least some individuals returning each year. However, there is little evidence to show significant northerly migration, despite basking sharks being present in Norway, see (Compagno 2001).

4.3 Key areas of basking shark occurrence and MPAs

Protecting highly mobile species, such as the basking shark, is inherently difficult due to the large geographic areas they inhabit. Identifying areas where species may aggregate for aspects of life history ecology may provide a useful and tractable focus for conservation activities. Several documented examples exist of MPAs benefitting free-ranging species (Worm *et al.* 2003; Koldewey *et al.* 2010), including cetaceans, pinnipeds, sea otters, sea birds, sharks, cephalopods, and fish (Hooker and Gerber 2004). Waters off the west coast of Scotland have been identified as basking shark ‘hotspots’ from analysis of public sightings and boat-based surveys and may therefore represent candidate areas for protection (Speedie *et al.* 2009; Marine Science Scotland 2012; Witt *et al.* 2012; Scottish Natural Heritage 2014).

Gathered location and depth data from basking sharks in the coastal zone of Scotland provide an important contribution to the evidence-base in relation to the spatial scale of MPAs and the contribution that they make to the conservation of basking sharks. The MPA proposal offers a potentially suitable candidate measure to help conserve sharks as the species is both geographically focused in the summer, but also predominantly near-surface and hence spatio-temporal management of human activities seems tractable. Protection of highly migratory species throughout their entire range is likely not feasible but MPAs can be used to protect areas of high relative importance or areas supporting key stages of life history ecology, such as breeding or foraging grounds (Lauck *et al.* 1998; Hooker and Gerber 2004); such a conservation goal could be achieved by the Sea of the Hebrides MPA proposal.

Location data collected from satellite tagged basking sharks lend support to the existence of ‘hotspots’, or areas of high relative importance, which persist through the months of July to end-September each year. Key hot spot areas identified remained broadly within the Sea of the Hebrides MPA proposal, with smaller more frequently occupied areas identified across multiple years. Some individuals utilised more than one of these smaller areas during the summer, and displayed occasional movements to the edges of the MPA proposal boundary (and further; to coastal areas of Northern Ireland) before returning. Satellite tags were, for the majority, deployed when numbers of sightings increased in the summer, as such some bias is likely to exist in describing the year-round whereabouts of sharks. However, without comprehensive knowledge of basking shark distribution and abundance throughout their range it is difficult to contextualise the hotspots and their risk profile at the regional (i.e. north-east Atlantic Ocean) and global level.

4.4 Seasonal and annual site fidelity

The term site fidelity is used to describe the repeated use of a location through time (Chapman *et al.* 2005; DeAngelis *et al.* 2008). Site fidelity has been observed in a range of shark species, including; white sharks (C*archarodon carcharias;* (Anderson *et al.* 2011)), tiger sharks (G*aleocerdo cuvier;* (Heithaus 2001))*,* Caribbean reef shark (*Carcharhinus perezi*, (Bond *et al.* 2012)) and spot-tail sharks (*Carcharhinus sorrah;* (Knip *et al.* 2012)). The factors influencing site fidelity are likely to include environmental conditions, such as prey availability (Speed *et al.* 2010), and potentially access to mating opportunities and other key life history functions.

Site fidelity was observed in satellite tracked basking sharks, where individual sharks demonstrated persistent use of the coastal zone during summer months; however, the degree of fidelity observed differed considerably. Some basking sharks undertook forays outside the boundaries of the proposed Sea of the Hebrides MPA, but returning to core areas, while others showed greater fidelity from the outset, remaining within the core areas for periods of up to several weeks. The drivers of site fidelity in basking sharks in Scotland may be associated with the availability of prey (given observed foraging behaviour), and/or factors such as the propensity for adults to aggregate, conceivably with the purpose of finding a mate (given observed behaviour suggestive of courtship).

The project also showed annual site fidelity. Tags deployed in 2013 and 2014 ceased transmission in late summer, but recommenced transmissions the following spring in the Bay of Biscay and to the west of Portugal. Northward movements were then recorded. A single individual recommenced transmissions in early summer to the west of Barra having not transmitted for several months. A further individual, tagged in 2014, returned to the tagging site in early summer 2015 (137654). Describing annual fidelity with satellite telemetry provides further evidence that basking sharks can return year-on-year to the Sea of the Hebrides, although the relative frequency of this behaviour can only be robustly assessed with continued satellite tag deployments or the use of acoustic tags that have longer retention times and are somewhat cheaper. Acoustic tags require the installation of an acoustic receiving network, such as that being established for skate in the Argyll on the west coast of Scotland. Putative locations for acoustic receivers for basking sharks could include Gunna Sound – where mooring infrastructure already exists. The description of site fidelity in Scotland in this report concurs with a similar pattern demonstrated in south-west England, where a female shark was identified via photographic identification of the dorsal fin, several years later (Sims *et al.* 2000).

4.5 Environmental drivers

Knowledge of predictable environmental features may also help in describing potential boundaries for MPAs. For example, in this study, basking sharks occurred in shallow waters over rocky substratum, with low to moderate (relative) tidal speeds. Assuming their preference remains constant, or that monitoring can highlight if preferences change, these factors could be utilised in the identification of MPA boundaries (Hyrenbach *et al.* 2000; Baum *et al.* 2003). This approach has been suggested elsewhere for other species of sharks. For example, (Worm *et al.* 2003) found shark biodiversity hotspots are often associated with prominent habitat features such as reefs, shelf breaks, or seamounts and often coincided with zooplankton and coral reef hotspots.

Some studies have documented feeding aggregations of basking sharks near frontal activity (Sims, D.W. & Quayle 1998) while other studies have explained variation in basking shark numbers with present and lagged sea surface temperature, which could act as a proxy for prey abundance (Sims *et al.* 1997; Sims, D.W. & Quayle 1998; Cotton *et al.* 2005). Some studies have also suggested that lower thermal limits may drive basking shark migration (e.g. Skomal *et al.*, (2004) suggesting that basking sharks departed north-west Atlantic water in response to temperature falling below 12.7°C . Basking sharks satellite tracked in this project largely commenced southward migration away from the Sea of the Hebrides in October, although substantial variations exist. During this period mean daily encountered water temperatures were approximately 13-14°C.

Statistical habitat modelling techniques have been successfully applied to large mobile marine vertebrate species, using datasets collected from boat-based observations (Paxton *et al.* 2014) and from individual-based satellite telemetry data (Pikesley *et al.* 2013; Siders *et al.* 2013). This project compared satellite location data with a modelled map of basking shark persistence; and for the majority, found tagged basking sharks occupied regions of moderate to high persistence. The satellite location data identified regions where tracked sharks did not go, but which were of modelled high persistence, highlighting the need for further work in these geographic areas, in particular to the west of the Outer Hebrides.

4.6 Medium and long-range movements

Recording longer distance movements was a key objective for the project and migrations were observed spanning waters of multiple European geopolitical zones.

The movement of four basking sharks to Madeira and the Canary Islands was documented, the most southerly tracking of basking sharks in the north-east Atlantic Ocean. These movements were determined by two satellite tag technologies employing different geolocation techniques (Argos locations and light geolocation). Similar southerly movement has been described elsewhere in the western Atlantic, where 18 basking sharks were tracked with pop-up archival tags off the coast of Cape Cod, USA (Skomal *et al.* 2009). Six of these sharks moved into sub-tropical and tropical waters, as far south as Brazil, representing the first documented movement of basking sharks into tropical latitudes. It is therefore evident that basking sharks have the capacity to undertake ocean basin wide movements.

Multiple individuals in the present study travelled south to the Celtic and Irish Seas where tags ceased transmission. Basking sharks were also shown to travel northwards from the Irish Sea (Isle of Man) towards Scottish waters (Fig. 24, N=3; Manx Basking Shark Watch), with one individual moving into the proposed Sea of the Hebrides MPA. Movement of basking sharks both into and away from the Sea of the Hebrides MPA proposal suggest a strong connectivity between the Irish Sea and waters to the west of Scotland. The northern channel of the Irish Sea facilitates movement between these two regions (waters to the west of Scotland and the Irish Sea), potentially exhibiting evidence of a migratory corridor. Furthermore, basking sharks also appear to move into the Sea of the Hebrides MPA proposal in spring and summer from waters west of Ireland.

Light geolocation data gathered by MiniPAT, PAT-F and SPLASH-F tags provided information on migration across seasons. Gathered data suggest basking sharks likely depart coastal waters of Scotland in October and November. Basking sharks disperse either into the north-east Atlantic Ocean or through the Irish Sea in to the Celtic Sea and Bay of Biscay (as also observed with SPOT tags and from the release locations of prematurely detaching archival tags). During the winter basking sharks occupy a range of habitats in the north-east Atlantic Ocean, but appear not to undergo extensive westerly movement, although this has been observed elsewhere (Gore *et al.* 2008). We observed some northward movement in tagged sharks, but the distances involved where not appreciable, although one shark travelled to an area south and west of the Faroe Islands. Some individuals appear to focus their overwintering distribution to discrete regions, spending several months in relatively constrained geographic regions (e.g. within the Celtic Sea, to the west or Ireland, remaining within the Bay of Biscay), whereas other individuals appear to cover greater areas. Given such extensive winter movements, yet with some geographic focus to the north-east Atlantic Ocean and in particular to the west of Ireland, it seems multi-national cooperation will be essential for a positive conservation outcome for the basking shark. The Convention on Migratory Species (CMS or Bonn Convention) will no doubt be essential in ensuring that a shared responsibility is adopted by all relevant nations.

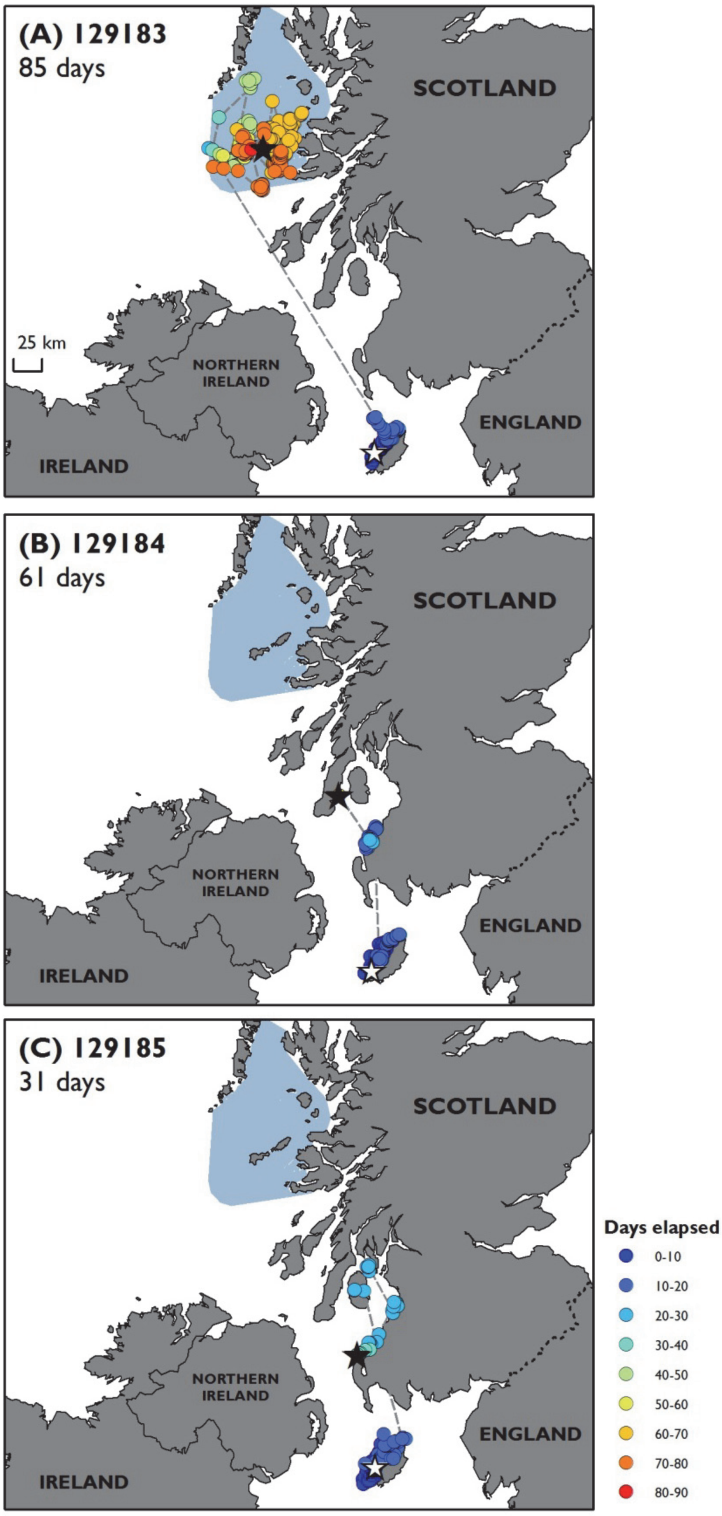


Figure 24. Movements of basking sharks tracked with SPOT tags in 2012 from the Isle of Man (data from the Manx Basking shark Watch 2013; courtesy of Jackie Hall and Graham Hall). *Satellite-derived locations from basking sharks tagged in coastal waters of the Isle of Man. Shark tag ID and attachment duration indicated for each figure part. Dashed lines join consecutive locations but do not infer straight line movement. Sea of the Hebrides MPA proposal (blue polygon).*

4.7 Depth use

Tagged basking sharks were recorded making repeated oscillatory vertical movement between the surface and deeper waters, termed 'yo-yo dives' (Holland *et al.* 1992). This behaviour is relatively ubiquitous and has been recorded in a wide range of shark species including, whale sharks (*Rhincodon typus,* (Brunnschweiler *et al.* 2009), basking sharks (Sims *et al.* 2005; Shepard *et al.* 2006), white sharks (Klimley *et al.* 2002; Domeier and Nasby-Lucas 2008), scalloped hammerhead sharks (*Sphyrna lewini,* (Jorgensen *et al.* 2009)) and tiger sharks (Nakamura *et al.* 2011). These behaviours are generally attributed to foraging, however, it is also possible that they are involved in thermoregulation or aid energy conservation (Holland *et al.* 1992; Klimley *et al.* 2002).

Diel vertical migration (DVM), the process of migrating vertically on a daily basis has been described for the planktivorous megamouth shark (*Megachasma pelagios;* (Nelson *et al.* 1997), whale sharks (Wilson *et al.* 2005; Graham *et al.* 2006) and basking sharks (Sims *et al.* 2005)). Migration may be towards the surface during the night time (DVM), or towards the surface during the daytime (reverse DVM) and both patterns have been observed in whale sharks (Rowat *et al.* 2006) and basking sharks (Shepard *et al.* 2006). Both strategies may be used, allowing sharks to capitalise upon their heterogeneous environment. Depth use data collected in the present study suggest that basking sharks, when within areas of the Sea of the Hebrides MPA proposal, exhibit both DVM and reverse DVM behaviour, most likely adopting a strategy appropriate to the water column they encounter. Changes in depth use behaviour likely occur as the sharks move from shallow areas of frontal activity to deeper, more stratified, waters (Sims *et al.* 2005). Further, while in the coastal zone basing sharks predominantly occupied near-surface waters, potentially increasing the opportunity for interaction between sharks and boats. Data describing how basking sharks utilise the water column within areas of high relative importance could contribute to discussions regarding management options for the conservation of basking sharks as well as being useful in contributing to the estimation of shark numbers present in key areas from surface sightings data.

The greatest depth previously recorded for any basking shark was 1,264m (Gore *et al.* 2008), which superseded the previously recorded 904m (Francis, M., Duffy 2002), with (Sims *et al.* 2003) also recording a basking shark occupying waters between 750 and 1000m depth. During the present study, several sharks were recorded at depths greater than 1,000m, adding to this body of knowledge. The greatest depths observed in this project (>1000m depth) typically occurred during the winter and early spring and were widely spread, occurring off the continental shelf to the west of Ireland, to the west of the Celtic Sea and Western Approaches and within the Bay of Biscay. Irrespective of these exceptional deep depth use events, gathered depth data indicates basking sharks predominantly occupy the epipelagic zone, but have the capacity to undertake extensive vertical movements over short periods of time (days).

4.8 Anecdotal observations

4.8.1 Sexual or ontogenetic segregation

Segregation of foraging aggregations by body size or sex has been widely described in shark species (Klimley 1987; Wearmouth and Sims 2008), however, no evidence was found of this during field work, although collecting robust data that would provide insight on these topics was not our primary aim. Both sexes and a range of body sizes (4-5 to 8-9m) were observed in foraging aggregations, no sharks 3m or less in body length were observed. It has been suggested that although juveniles are observed in the same feeding aggregation as adults juveniles may forage later in the season (Sims, D. W., and Merrett 1997).

4.8.2 Courtship behaviour

During fieldwork a range of basking shark behaviour was observed, most intriguing were; nose-to-tail following, lateral approaches and breaching. These behaviours have previously been attributed to courtship display (Nova Scotia, (Harvey-Clark *et al.* 1999), Gulf of Maine (Wilson 2004). A longer term study of such behaviour (between 1995 and 1999) linked these with seasonally persistent fronts (Sims 2000). This led the author to hypothesise that the south-west UK may represent an annual breeding area for basking sharks, although mating itself has yet to be observed. It seems possible that the areas around Coll and Tiree in the Sea of the Hebrides could also host courtship and breeding. Comparatively little is known about the breeding systems of shark species in the wild and the information that does exist has come mainly from animals held in captivity (Pratt and Carrier 2001), thus it is difficult to confidently assign the underlying reason for the behaviours observed. Group related social behaviour has been reported regularly within areas of the proposed Sea of the Hebrides MPA (Speedie *et al.* 2009). Breeding is essential to the conservation of the species, and the behaviours preceding breeding can be important in the breeding success. Spatially safeguarding the habitats where courtship-like activities occur will likely convey benefits for the basking shark.

4.9 Knowledge gaps and challenges

4.9.1 Satellite tags and attachment methods

This study made use of emerging and established tracking technologies with tag attachment methods previously only used on manta rays (Graham *et al.* 2012) and whales sharks (Eckert *et al.* 2002). Use of novel technologies and methods can have unexpected outcomes, but the opportunity to gather otherwise unobtainable data represents an important step in furthering the knowledge base of the species. Some problems were encountered predominantly with PAT-F tags. These devices had a higher than expected premature detachment rate, four of 12 tags failed to transmit data and a lower than expected number of GPS locations were received. Nonetheless, the tags recorded a basking shark moving into the Clyde Sea, demonstrating connectivity between the Sea of the Hebrides and this region. The problems associated with PAT-F tags were likely associated to insufficient tag buoyancy and prohibitively fast basking shark movement, which appears to have prevented the tags from surfacing, and thus reduced the opportunity to gather GPS location data. Biofouling and insufficient buoyancy may be responsible for why data were never received from four tags, although one tag was subsequently found. SPLASH-F tags also suffered from buoyancy issues resulting in fewer Argos locations than anticipated. However, buoyancy was sufficient to gather GPS locations – the primary role of these tags. Further enhancements to the tag design or tether optimisation may help to improve rates of communication with the Argos System.

Future tracking work should aim to deploy devices that remain attached for longer durations (years) to investigate questions regarding multi-year site fidelity. Such deployments are now possible with emerging technology and battery capacity; however, the problem of tag retention remains and many projects have comparatively short durations (<1 year). Multi-year assessments of movement will become increasingly important as marine managers move towards the assessment of cumulative threat over extended periods.

Fieldwork for this project demonstrated that it is challenging to re-sight individual sharks and it is thus challenging to monitor the success of different attachment methods. As such improvements to tag attachment methods are generally slow for a wide range of animal taxa (Hazen *et al.* 2012). The present study attempted to reduce such impacts by working with Manx Basking Shark Watch to share information about best tag attachment practice.

4.9.2 Behaviour

It is not immediately apparent if the environmental conditions in which tracked basking sharks were observed represent the absolute range of environmental preference (i.e. upper and lower bounds of thermal tolerance) or whether environmental conditions might influence subsequent behaviour, such as decisions on long-distance migration or choosing when and where to breed. It is highly likely that this is the case, but to date no data exist to support such an observation. Behaviour in the coastal zone may be influenced by environmental conditions far from Scotland (e.g. conditions at other geographic areas key to the life cycle may exert an effect on time spent in Scotland or whether sharks forego coastal foraging and remain offshore in years when energetic investment to travel might be otherwise invested). Behaviour in the coastal zone may therefore represent a response to a combination of a number of factors dictated far from Scotland (e.g. reproductive and nutritional state.)

Understanding the causative reasons behind observed behaviour may assist in designing management plans for species of conservation concern. For example, high resolution movement and physiological data, gathered by multichannel biotelemetry loggers, would help to interpret the function of the depth use patterns observed in the present study. While it has been shown that it is likely that shallow depth use might be consistent with foraging, it is not clear why basking sharks may relatively quickly move to much greater depths (several hundred metres). The possibility that it represents deeper foraging, predation avoidance, competitive exclusion and/or temporary resting, has been previously hypothesised for this species (Parker and Boeseman 1954), but remains to be empirically demonstrated.

5. CONCLUSIONS

a) The basking shark satellite tracking project successfully collected data from an unprecedented range of tag types fitted to basking sharks, providing novel insights into horizontal and vertical space use behaviour, including the first spatial linkage between GPS and depth use data for sharks.

b) Gathered data confirm that basking sharks remain predominantly within coastal waters of the UK between July and late September, showing seasonal site fidelity within the Sea of the Hebrides MPA proposal. Basking shark behaviours, previously attributed to courtship display, were also observed in these areas of persistent use.

c) After the summer months, October onwards, basking sharks spend more time at greater depth, with a number of basking sharks moving in a southerly direction and further afield. The Irish Sea and waters to the north of Ireland represents an important migratory corridor.

d) An appreciable number of sharks tagged with light geolocation tags occupied winter habitats to the west of Ireland and the Celtic Sea and these regions are worthy of further investigation.

e) Basking sharks can occupy depths >1,000m but are, for the majority, a species of the epipelagic zone. In coastal areas they occupy shallow waters and use of these habitats likely increases the possibility of negative interaction with humans (e.g. propeller strike or entanglement in gear, repeated disturbance etc.).

f) This study sampled a subset of the available population; as such, it is difficult to fully describe the proportion of the population that adopt differing movement strategies, especially with respect to long-range movements. Nonetheless, the sample size is appreciable and appropriate inferences may be made if adequately caveated.

g) Future efforts to gather data necessary to assist in developing management options for basking sharks within the MPA should focus on understanding the propensity of annual site fidelity. This would aid in the estimation of cumulative risk over years (potentially using acoustic tags) and help understand individual level behavioural responses to human activities, and could make use of emerging high-frequency movement loggers and aerial videography of basking shark behaviour in experimental conditions.

h) Comparison of satellite tracking data gathered in this project with modelled areas of high persistence for basking sharks reveals a paucity of tracking data associated with a high persistence region to the west of the Outer Hebrides. This is intriguing and outlines a need for work in this region. Insight from this area could be achieved rather quickly using lower-cost SPOT tags and digital aerial photography.

i) Open and collegiate sharing of knowledge is important to be able to observe large-scale trends in order to see connectivity between sub-populations and monitor fluxes in these populations. This form of cooperation will be critical to achieving a positive conservation outcome for the species.

6. REFERENCES

Anderson, S.D., Chapple, T.K., Jorgensen, S.J., Klimley, A.P., Block, B.A. 2011. Long-term individual identification and site fidelity of white sharks, *Carcharodon carcharias*, off California using dorsal fins. *Marine Biology*, 158(6), 1233–1237, available: http://link.springer.com/10.1007/s00227-011-1643-5.

Baum, J.K., Myers, R. A, Kehler, D.G., Worm, B., Harley, S.J., Doherty, P. A 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science (New York, N.Y.)*, 299(5605), 389–92, available: http://www.ncbi.nlm.nih.gov/pubmed/12532016 [accessed 28 Oct 2012].

Block, B.A., Teo, S.L.H., Walli, A., Stokesbury, M.J.H., Farwell, C.J., Weng, K.C., Dewar, H., Williams, T.D. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature*, 434, 1121–1127.

Bond, M., Babcock, E., Pikitch, E., Abercrombie, D., Lamb, N., Chapman, D. 2012. Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier reef. *PLoS ONE*, 7(3), 1–14.

Brunnschweiler, J.M., Baensch, H., Pierce, S.J., Sims, D.W. 2009. Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. *Journal of fish biology*, 74(3), 706–14, available: http://www.ncbi.nlm.nih.gov/pubmed/20735591 [accessed 9 Nov 2012].

Chapman, D.D., Pikitch, E.K., Babcock, E., Shivji, M.S. 2005. Marine Reserve Design and Evaluation Using Automated Acoustic Telemetry: A Case-study Involving Coral Reef-associated Sharks in the Mesoamerican Caribbean. *Marine Technology Society Journal*, 39(1), 42–55.

Compagno, L.J. V. 2001. *FAO Species Catalogue for Fisheries Purposes: Sharks of the World - an Annotated and Illustrated Catalogue of Shark Species Known to Date.* Food and Agriculture Administration of the United Nations.

Costa, D.P., Robinson, P.W., Arnould, J.P.Y., Harrison, A.-L., Simmons, S.E., Hassrick, J.L., Hoskins, A.J., Kirkman, S.P., Oosthuizen, H., Villegas-Amtmann, S., Crocker, D.E. 2010. Accuracy of ARGOS Locations of Pinnipeds at-Sea Estimated Using Fastloc GPS. *PLos ONE*, 5(1), e8677.

Cotton, P.A., Sims, D.W., Fanshawe, S.A.M., Chadwick, M. 2005. The effects of climate variability on zooplankton and basking shark (*Cetorhinus maximus*) relative abundance off southwest Britain. *Fisheries Oceanography*, 14(2), 151–155.

DeAngelis, B.M., McCandless, C.T., Kohler, N.E., Recksiek, C.W., Skomal, G.B. 2008. First characterization of shark nursery habitat in the United States Virgin Islands: Evidence of habitat partitioning by two shark species. *Marine Ecology Progress Series*, 358, 257–271.

Domeier, M.L., Nasby-Lucas, N. 2008. Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Marine Ecology Progress Series*, 370, 221–237.

Eckert, S.A., Dolar, L.L., Kooyman, G.L., Perrin, W., Rahman, R.A. 2002. Movements of whale sharks (*Rhincodon typhus*) in South-east Asian waters as determined by satellite telemetry. *Journal of Zoology*, 257, 111–115.

Evans, K., Baer, H., Bryant, E., Holland, M., Rupley, T., Wilcox, C. 2011. Resolving estimation of movement in a vertically migrating pelagic fish: Does GPS provide a solution? *Journal of Experimental Marine Biology and Ecology*, 398(1-2), 9–17.

Francis, M., Duffy, C. 2002. Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. *Marine Biology*, 140(4), 831–842, available: http://www.springerlink.com/openurl.asp?genre=article&id=doi:10.1007/s00227-001-0744-y [accessed 5 Nov 2012].

Gore, M. A, Rowat, D., Hall, J., Gell, F.R., Ormond, R.F. 2008. Transatlantic migration and deep mid-ocean diving by basking shark. *Biology letters*, 4(4), 395–8, available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2610142&tool=pmcentrez&rendertype=abstract [accessed 29 Oct 2012].

Graham, R.T., Roberts, C.M., Smart, J.C. 2006. Diving behaviour of whale sharks in relation to a predictable food pulse. *Journal of the Royal Society, Interface*, 3(6), 109–116.

Graham, R.T., Witt, M.J., Castellanos, D.W., Remolina, F., Maxwell, S., Godley, B.J., Hawkes, L. A. 2012. Satellite tracking of manta rays highlights challenges to their conservation. *PloS one*, 7(5), e36834, available: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3349638/?tool=pmcentrez [accessed 27 October 2012].

Halpern, B.S., Walbridge, S., Selkoe, K. A, Kappel, C. V, Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R. 2008. A global map of human impact on marine ecosystems. *Science (New York, N.Y.)*, 319 (5865), 948–52.

Harvey-Clark, C.J., Stobo, W.T., Helle, E., Mattson, M. 1999. Putative Mating Behavior in Basking Sharks off the Nova Scotia Coast. *Copeia*, 1999(3), 780–782.

Hazel, J. 2009. Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. *Journal of Experimental Marine Biology and Ecology*, 374(1), 58–68.

Hazen, E., Maxwell, S., Bailey, H., Bograd, S., Hamann, M., Gaspar, P., Godley, B., Shillinger, G. 2012. Ontogeny in marine tagging and tracking science: technologies and data gaps. *Marine Ecology Progress Series*, 457, 221–240, available: http://www.int-res.com/abstracts/meps/v457/p221-240/ [accessed 3 Nov 2012].

Heithaus, M.R. 2001. The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: Sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes*, 61(1), 25–36.

Hill, R. 1994. Theory of geolocation by light levels. In: LeBoeuf, B.J. and Laws, R.M., eds., *Elephant Seals: Population Ecology, Behaviour and Physiology*, University of California Press: Berkeley, CA, 227–236.

Hill, R.D., Braun, M.J. 2001. Geolocation by light level - the next step: latitude. In: Sibert, J.R., ed., *Electronic Tagging and Tracking in Marine Fisheries*, Kluwer Academic Publishers, 315–330.

Hoelzel, A R., Shivji, M.S., Magnussen, J., Francis, M.P. 2006. Low worldwide genetic diversity in the basking shark (*Cetorhinus maximus*). *Biology letters*, 2(4), 639–42, available:http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1833978&tool=pmcentrez&rendertype=abstract [accessed 5 Nov 2012].

Holland, K.N., Brill, R.W., Chang, R.K., Sibert, J.R., Fournier, D. A. 1992. Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature*, 358(6385), 410–412.

Hooker, S.K., Gerber, L.R. 2004. Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna. *BioScience*, 54(1), 27, available: http://bioscience.oxfordjournals.org/content/54/1/27.abstract.

Hyrenbach, K.D., Forney, K.A., Dayton, P.K. .2000. Marine protected areas and ocean basin management. 458(April), 437–458.

Jorgensen, S.J., Klimley, A. P., Muhlia-Melo, A. F. 2009. Scalloped hammerhead shark *Sphyrna lewini*, utilizes deep-water, hypoxic zone in the gulf of California. *Journal of Fish Biology*, 74(7), 1682–1687.

Klimley, A. P. .1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes*, 18(1), 27–40.

Klimley, P. A., Beavers, S.C., Curtis, T.H., Jorgensen, S.J. 2002. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*, 63(2), 117–135.

Knip, D.M., Heupel, M.R., Simpfendorfer, C. A. 2012. To roam or to home: site fidelity in a tropical coastal shark', *Marine Biology*, 159(8), 1647–1657, available: http://www.springerlink.com/index/10.1007/s00227-012-1950-5 [accessed 29 Oct 2012].

Koldewey, H.J., Curnick, D., Harding, S., Harrison, L.R., Gollock, M. 2010. Potential benefits to fisheries and biodiversity of the Chagos Archipelago/British Indian Ocean Territory as a no-take marine reserve. *Marine Pollution Bulletin*, 60(11), 1906–1915.

Kunzlik, P. 1988. The Basking Shark. Department of Agriculture and Fisheries for Scotland, Aberdeen, UK.

Lauck, T., Clark, C.W., Mangel, M., Munro, G.R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications*, 8(1), 72–78.

Marine Science Scotland. 2012. *Marine Protected Areas and Basking Sharks: Position Paper Position Paper for the 4th MPA Workshop, 14-15 March 2012,* available: www.gov.scot/Resource/0038/00389463.doc.

Nakamura, I., Watanabe, Y.Y., Papastamatiou, Y.P., Sato, K., Meyer, C.G. 2011. Yo-yo vertical movements suggest a foraging strategy for tiger sharks *Galeocerdo cuvier*. *Marine Ecology Progress Series*, 424, 237–246.

Nelson, D.R., McKibben, J.N., Strong, W.R., Lowe, C.G., Sisneros, J.A., Schroeder, D.M., Lavenberg, R.J. 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes*, 49(4), 389–399.

Nielsen, A., Sibert, J.R. 2007. State–space model for light-based tracking of marine animals. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(8), 1055–1068.

Noble, L.R., Jones, C.S., Sarginson, J., Metcalfe, J.D., Sims, D.W., Pawson, M.G. 2006. Conservation Genetics of Basking Sharks. *Final Report for Defra Tender CR 0288*.

Parker, H.W., Boeseman, M. 1954. The basking shark (*Cetorhinus maximus*) in winter. *Proceedings of the Zoological Society of London*, 124, 185–194.

Paxton, C.G.M., Scott-Hayward, L.A.S., Rexstad, E. 2014. Statistical Approaches to Aid the Identification of Marine Protected Areas for Minke Whale, Risso's Dolphin, White-Beaked Dolphin and Basking Shark*. Scottish Natural Heritage Commissioned Report No. 594.*

Pikesley, S.K., Maxwell, S.M., Pendoley, K., Costa, D.P., Coyne, M.S., Formia, A., Godley, B.J., Klein, W., Makanga-Bahouna, J., Maruca, S., Ngouessono, S., Parnell, R.J., Pemo-Makaya, E., Witt, M.J. 2013. On the front line: integrated habitat mapping for olive ridley sea turtles in the southeast Atlantic. *Diversity and Distributions*, 19(12), 1518–1530.

Pratt, H.L., Carrier, J.C. 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes*, 60(1-3), 157–188.

Priede, I.G. 1984. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing. *Fisheries Research*, 2(1964), 201–216.

Priede, I.G., Miller, P.I. 2009. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing II: New analysis reveals orientation to a thermal front. *Fisheries Research*, 95(2-3), 370–372, available: http://linkinghub.elsevier.com/retrieve/pii/S0165783608003202 [accessed 19 November 2012].

Rowat, D., Meekan, M.G., Engelhardt, U., Pardigon, B., Vely, M. 2006. Aggregations of juvenile whale sharks (*Rhincodon typus*) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes*, 80(4), 465–472, available: http://www.springerlink.com/index/10.1007/s10641-006-9148-7 [accessed 29 October 2012].

Scottish Natural Heritage. 2014. Further advice to Scottish Government on selection of Nature Conservation Marine Protected Areas for the development of the Scottish MPA network. *Scottish Natural Heritage Commissioned Report* No. 780', 16 pp, available: http://www.snh.org.uk/pdfs/publications/commissioned_reports/780.pdf [accessed 15 December 2015].

Shepard, E.L.C., Ahmed, M.Z., Southall, E.J., Witt, M.J., Metcalfe, J.D., Sims, D.W. 2006. Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology Progress Series*, 328, 205–213.

Siders, Z.A., Westgate, A.J., Johnston, D.W., Murison, L.D., Koopman, H.N. 2013. Seasonal Variation in the Spatial Distribution of Basking Sharks (*Cetorhinus maximus*) in the Lower Bay of Fundy, Canada. *PLos ONE*, 8(12), e82074.

Sims, D., Southall, E., Richardson, A., Reid, P., JD, M. 2003. Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series*, 248, 187–196.

Sims, D.W. 2000. Filter-feeding and cruising swimming speeds of basking sharks compared with optimal models: they filter-feed slower than predicted for their size. *Journal of Experimental Marine Biology and Ecology*, 249(1), 65–76.

Sims, D.W. 2008. Sieving a living: a review of the biology, ecology and conservation status of the plankton-feeding basking shark *Cetorhinus maximus*. *Advances in marine biology*, 54(08), 171–220.

Sims, D.W., Fox, A.M., Merrett, D.A. 1997. Basking shark occurrence off south-west England in relation to zooplankton abundance. *Journal of Fish Biology*, 51(2), 436–440.

Sims, D.W., Queiroz, N., Humphries, N.E., Lima, F.P., Hays, G.C. 2009. Long-Term GPS Tracking of Ocean Sunfish *Mola mola* offers a New Direction in Fish Monitoring. *PLos ONE*, 4(10), e7351.

Sims, D.W., Southall, E.J., Tarling, G.A., Metcalfe, J.D. 2005. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology*, 74(4), 755–761.

Sims, D.W., Speedie, C.D., Fox, A.M. 2000. Movements and growth of a female basking shark re-sighted after a three year period. *Journal of the Marine Biological Association of the United Kingdom*, 80(6), 1141–1142.

Sims, D. W., and Merrett, D.A. 1997. Determination of zooplankton characteristics in the presence of surface feeding basking sharks *Cetorhinus maximus*. 158, 297–302.

Sims, D.W. & Quayle, V. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature*, 393, 460-464.

Skomal, G.B., Wood, G., Caloyianis, N. 2004. Archival tagging of a basking shark, *Cetorhinus maximus*, in the western North Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 84(4), 795–799.

Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K.W., Thorrold, S.R. 2009. Transequatorial migrations by basking sharks in the western Atlantic Ocean. *Current Biology,* 19(12), 1019–22, available: http://www.ncbi.nlm.nih.gov/pubmed/19427211 [accessed 29 October 2012].

Speed, C.W., Field, I.C., Meekan, M.G., Bradshaw, C.J.A. 2010. Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series*, 408, 275–293.

Speedie, C.D., Johnson, L.A., Witt, M.J. 2009. Basking Shark Hotspots on the West Coast of Scotland : Key sites , threats and implications for conservation. *Scottish Natural Heritage Commissioned Report* 339.

Stéphan, E., Gadenne, H., Jung, A. 2011. Satellite Tracking of Basking Sharks in the North-East Atlantic Ocean. *Non-governmental Organization for the Study and Conservation of Elasmobranchs,* available: http://www.asso-apecs.org/Resultats-et-rapport-final-Fevrier.html [accessed 15 December 2015]

Wearmouth, V.J., Sims, D.W. 2008. Sexual segregation in marine fish, reptiles, birds and mammals behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology*, 54(08), 107–70, available: http://www.ncbi.nlm.nih.gov/pubmed/18929064 [accessed 3 December 2012].

Wilson, S.G. 2004. Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. *Fisheries Oceanography*, 13(4), 283–286.

Wilson, S.G., Polovina, J.J., Stewart, B.S., Meekan, M.G. 2005. Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology*, 148(5), 1157–1166, available: http://www.springerlink.com/index/10.1007/s00227-005-0153-8 [accessed 29 October 2012].

Witt, M.J., Åkesson, S., Broderick, A.C., Coyne, M.S., Ellick, J., Formia, A., Hays, G.C., Luschi, P., Stroud, S., Godley, B.J. 2010. Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. *Animal Behaviour*, 80(3), 571–581, available: http://linkinghub.elsevier.com/retrieve/pii/S0003347210002113.

Witt, M.J., Broderick, A.C., Coyne, M.S., Formia, A., Ngouessono, S., Parnell, R.J., Sounguet, G., Godley, B.J. 2008. Satellite tracking highlights difficulties in the design of effective protected areas for Critically Endangered leatherback turtles *Dermochelys coriacea* during the inter-nesting period. *Oryx*, 42(02), 296–300, available: http://www.journals.cambridge.org/abstract_S0030605308006947 [accessed 20 November 2012].

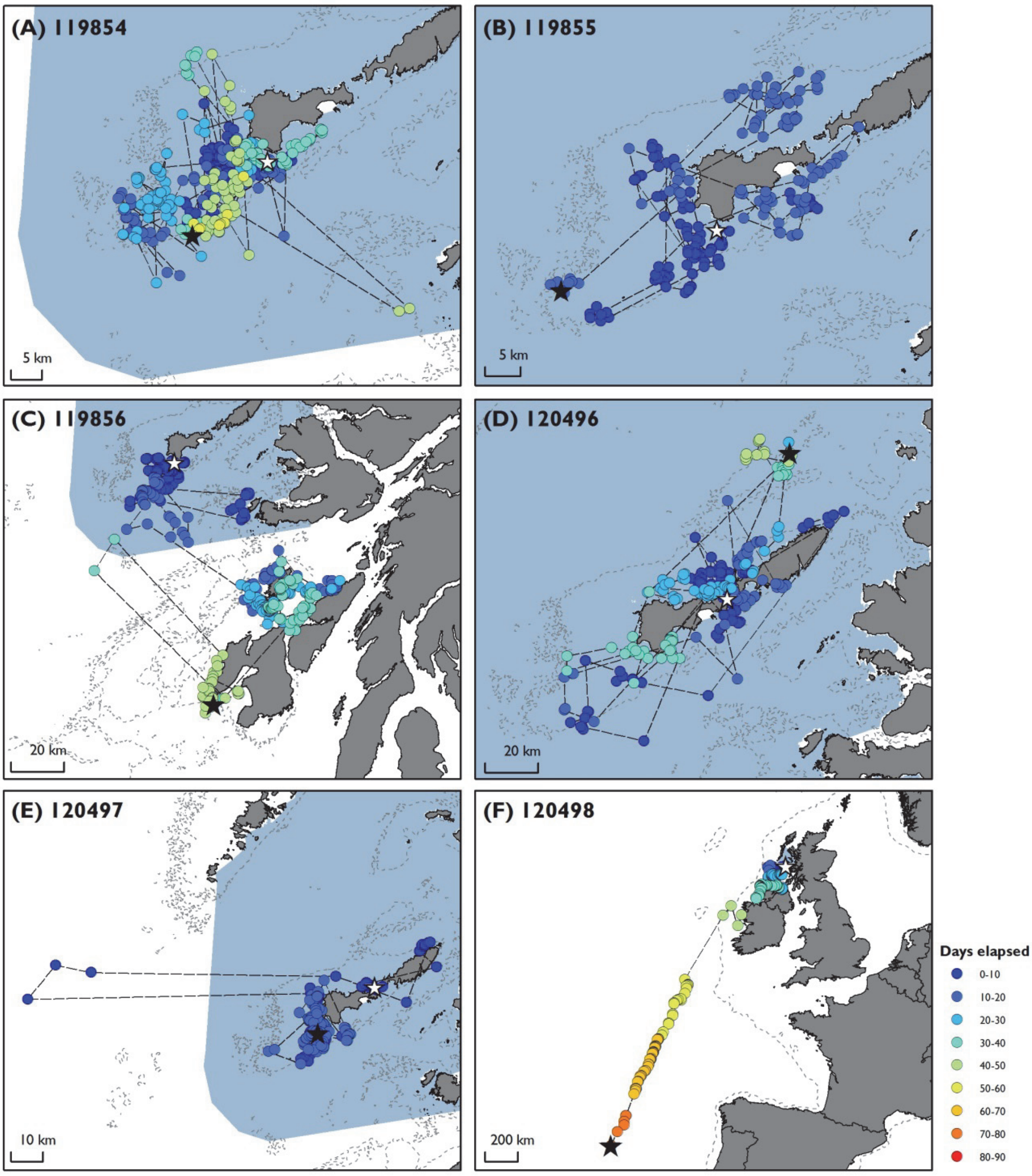
Witt, M.J., Hardy, T., Johnson, L., McClellan, C.M., Pikesley, S.K., Ranger, S., Richardson, P.B., Solandt, J.-L., Speedie, C., Williams, R., Godley, B.J. 2012a. Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters. *Marine Ecology Progress Series*, 459, 121–134.

Witt, M.J., Sheehan, E. V, Bearhop, S., Broderick, A.C., Conley, D.C., Cotterell, S.P., Crow, E., Grecian, W.J., Halsband-Lenk, C., Hodgson, D.J., Hosegood, P., Inger, R., Miller, P.I., Sims, D.W., Thompson, R.C., Vanstaen, K., Votier, S.C., Attrill, M.J., Godley, B.J. 2012b. Assessing wave energy effects on biodiversity: the Wave Hub experience. *Philosophical Transactions of the Royal Society A*, 370, 502–509.

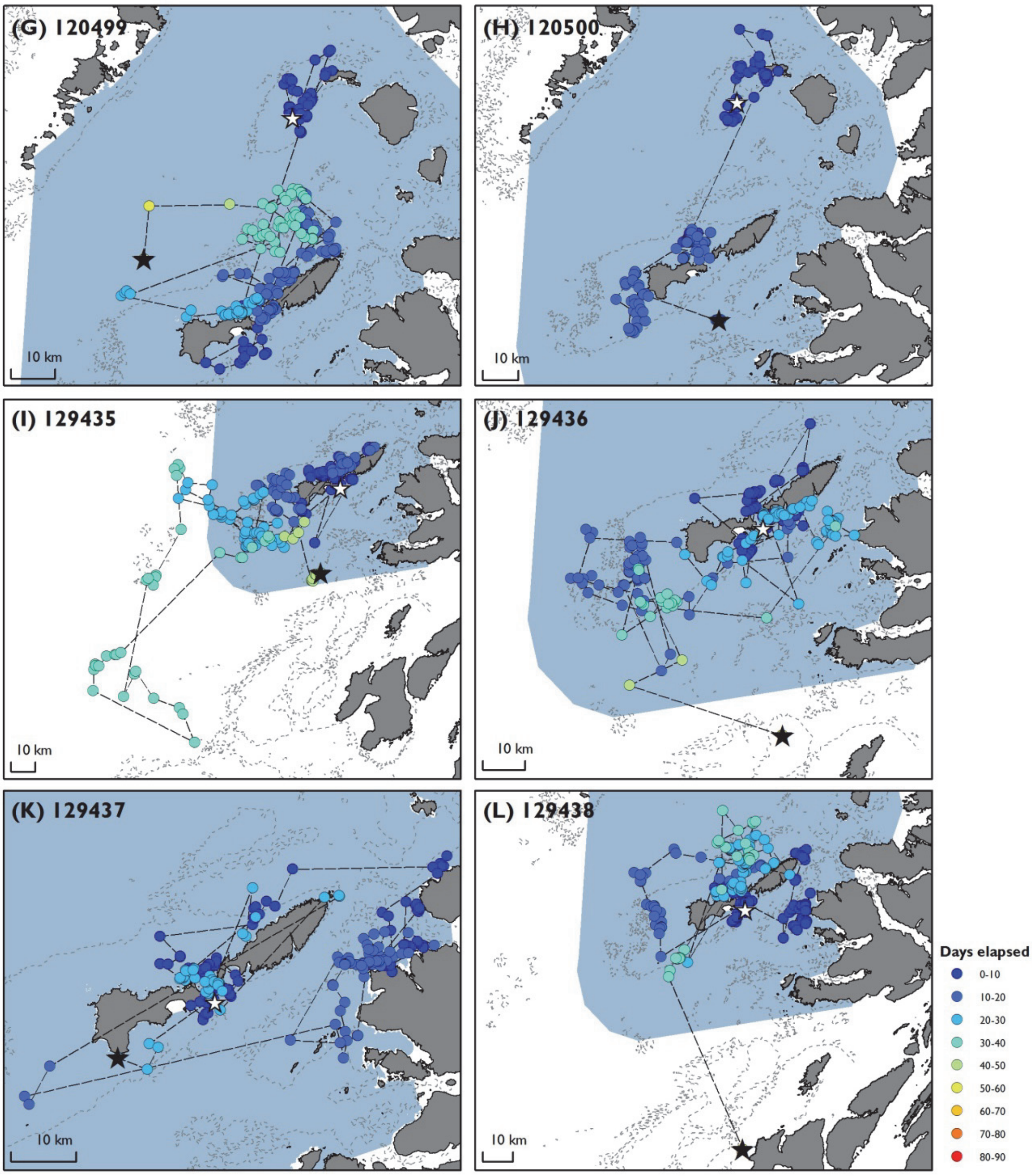
Worm, B., Lotze, H.K., Myers, R. A. 2003. Predator diversity hotspots in the blue ocean. *Proceedings of the National Academy of Sciences of the United States of America*, 100(17), 9884–8, available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=187874&tool=pmcentrez&rendertype=abstract.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164–168.

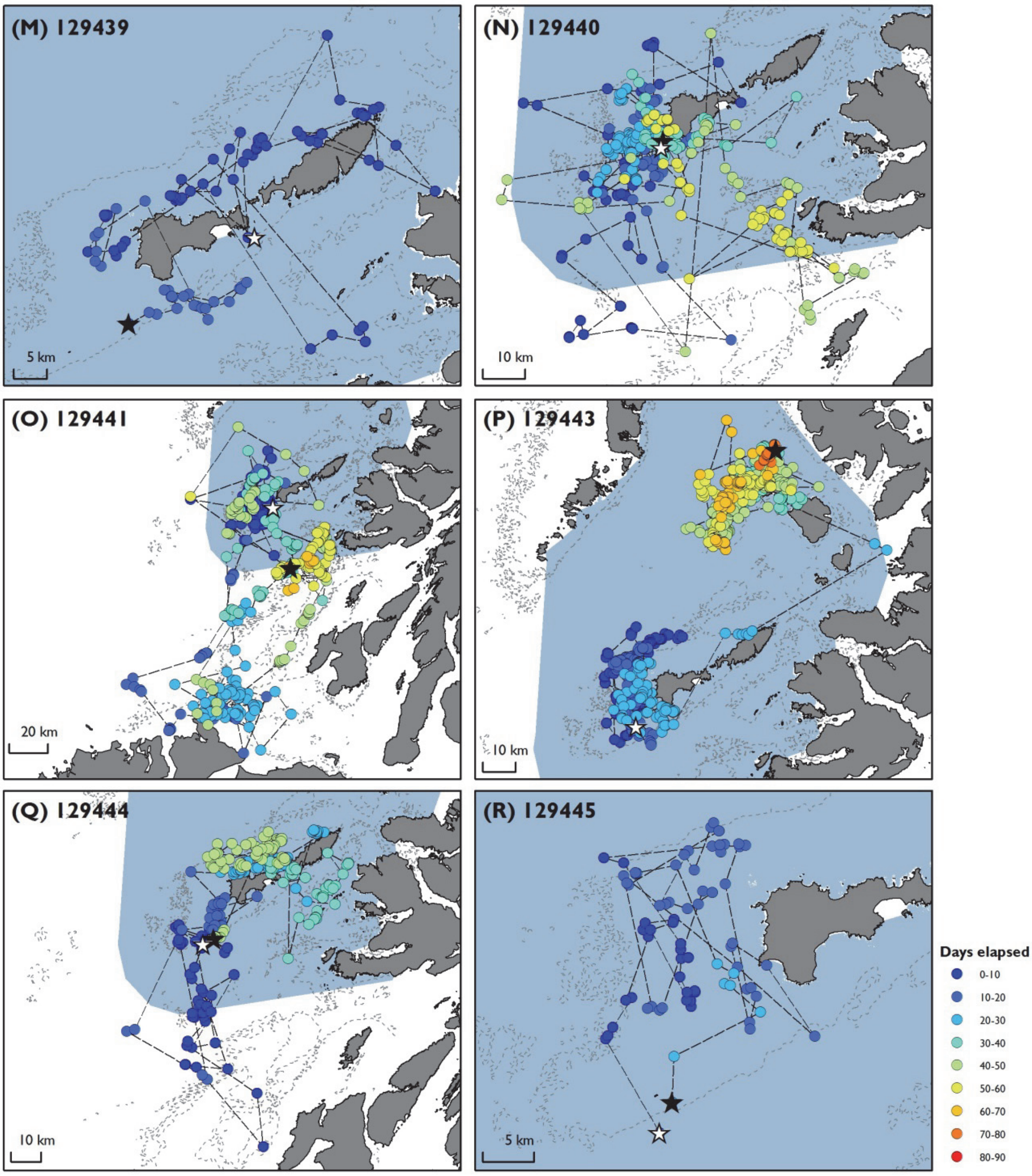
ANNEX 1: SPATIAL MOVEMENTS



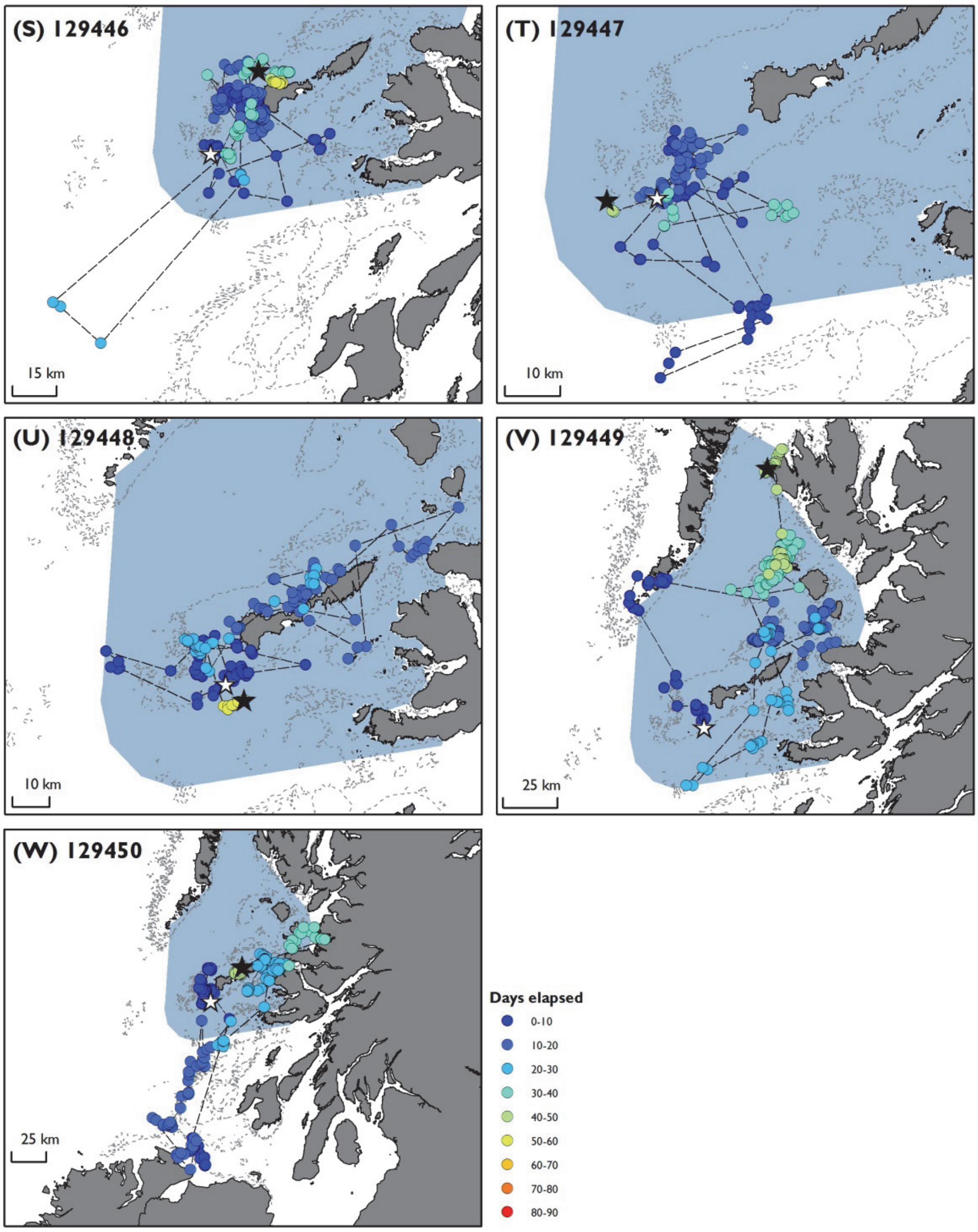
Supplemental Figure 1. Movements of basking sharks tracked with SPOT tags. *All sharks movement behaviour (Argos locations). Figure parts ordered by ascending tag number. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



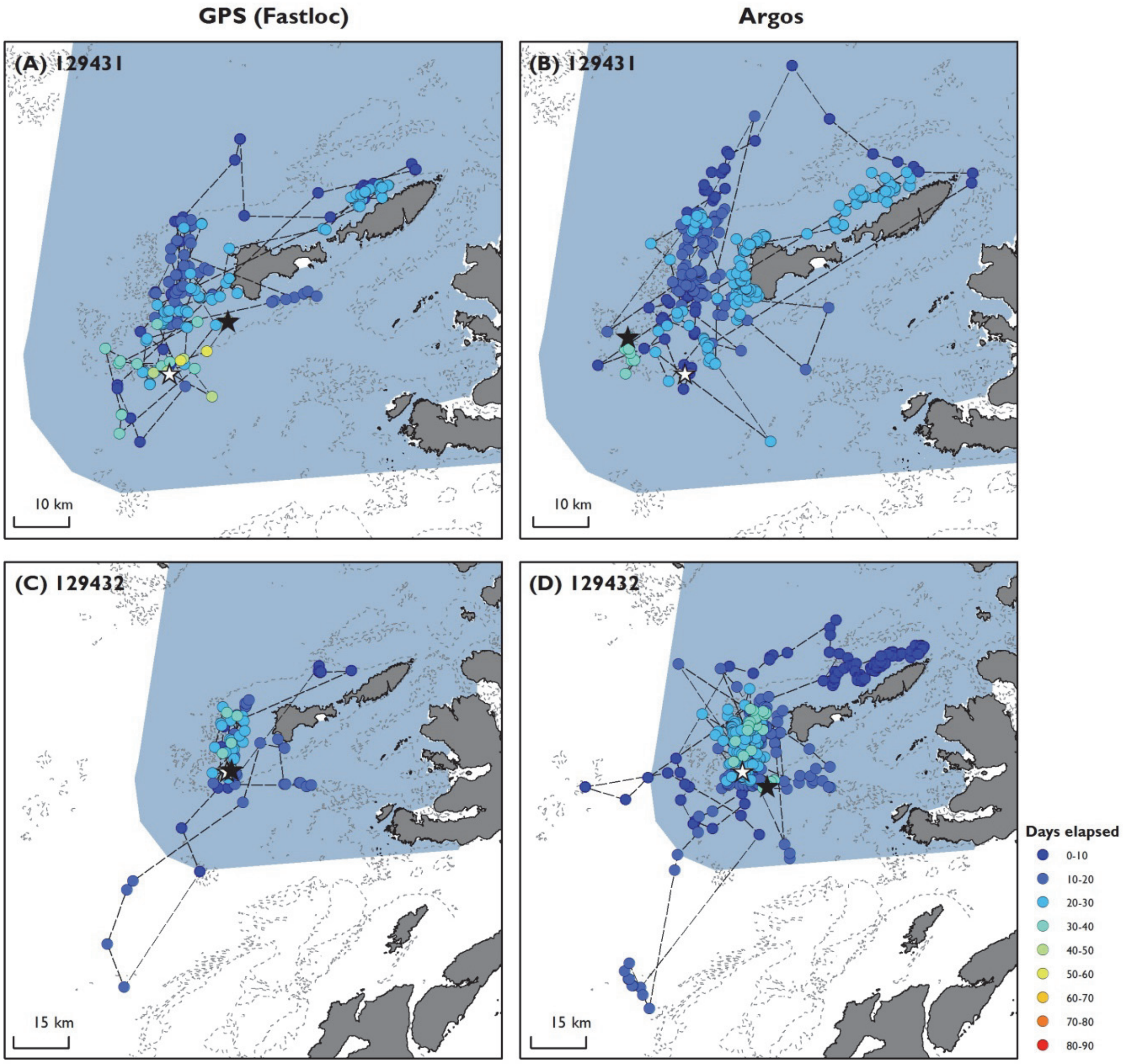
Supplemental Figure 1 cont. Movements of basking sharks tracked with SPOT tags. *All sharks movement behaviour (Argos locations). Figure parts ordered by ascending tag number. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, License O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



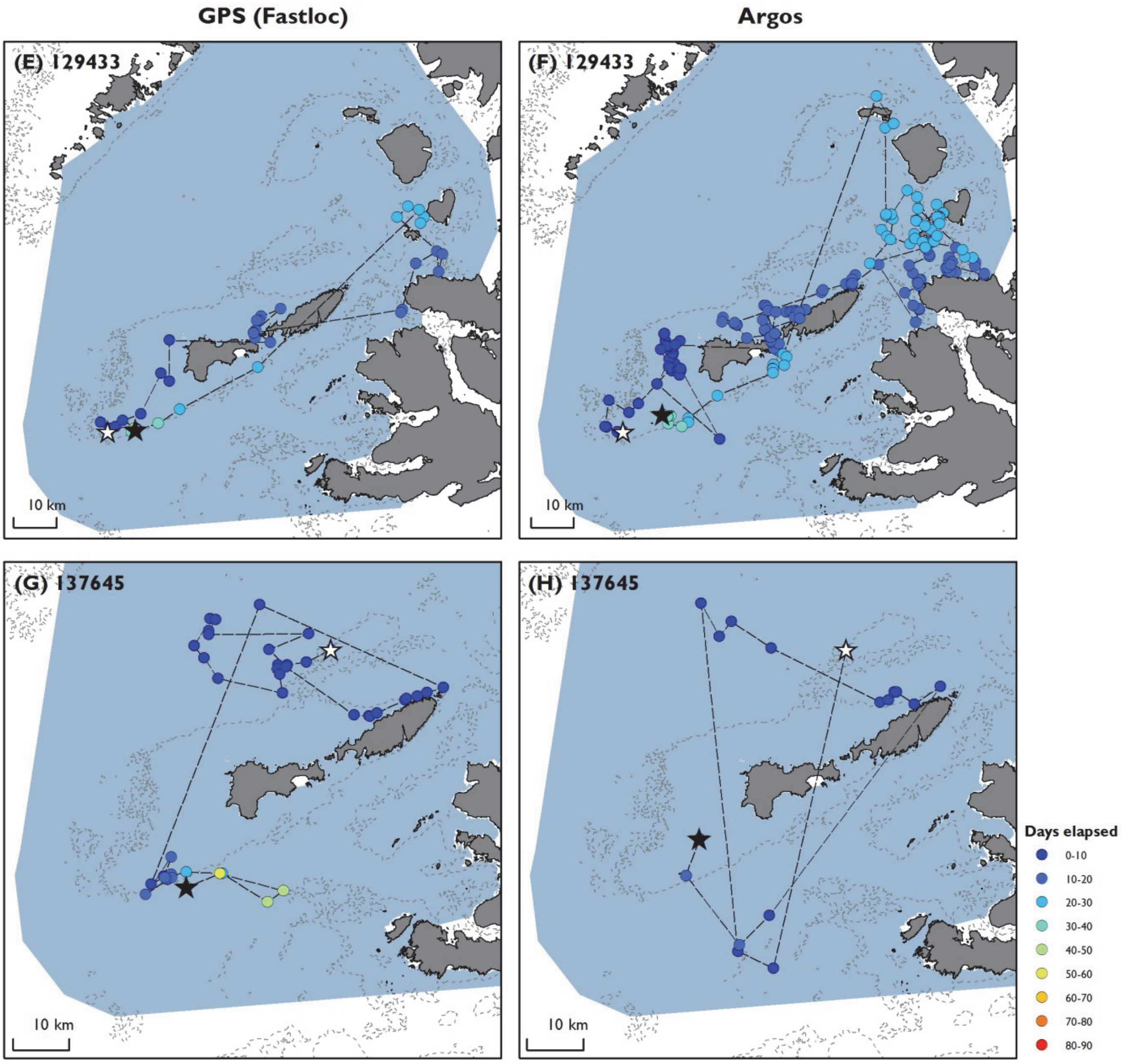
Supplemental Figure 1 cont. Movements of basking sharks tracked with SPOT tags. *All sharks movement behaviour (Argos locations). Figure parts ordered by ascending tag number. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



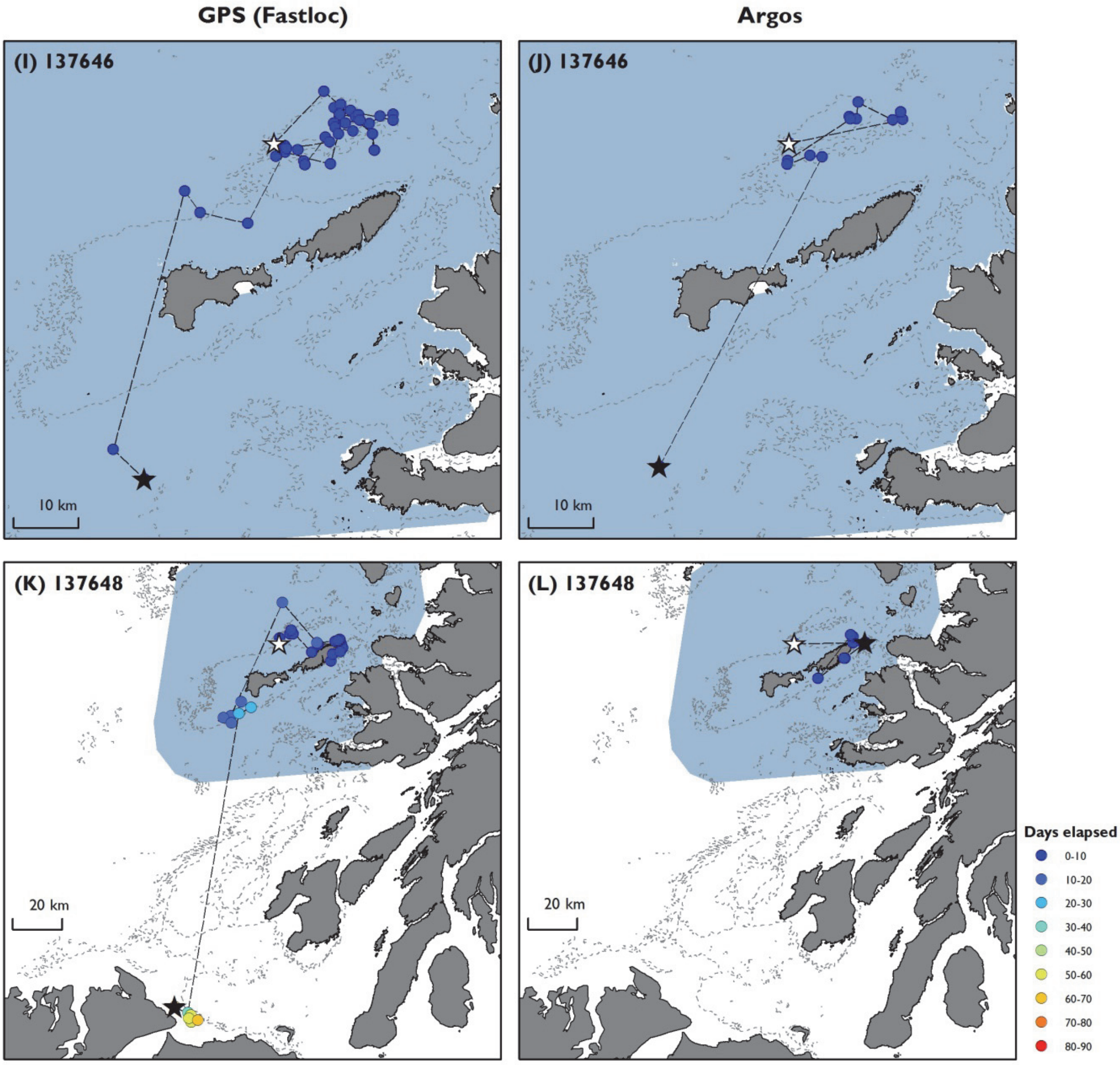
Supplemental Figure 1 cont. Movements of basking sharks tracked with SPOT tags. *All sharks movement behaviour (Argos locations). Figure parts ordered by ascending tag number. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, License O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



***Supplemental Figure 2. Fastloc™ GPS and contemporaneous Argos locations for basking sharks tracked with SPLASH-F tags**. Movements of sharks revealed by GPS-enabled satellite tags with contemporaneous Argos locations. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Tag ID indicated for each figure part. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



Supplemental Figure 2 cont. Fastloc™ GPS and contemporaneous Argos locations for basking sharks tracked with SPLASH-F tags*. Movements of two sharks revealed by GPS-enabled satellite tags with contemporaneous Argos locations. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Tag ID indicated for each figure part. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



Supplemental Figure 2 cont. Fastloc™ GPS and contemporaneous Argos locations for basking sharks tracked with SPLASH-F tags*. Movements of sharks revealed by GPS-enabled satellite tags with contemporaneous Argos locations. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Tag ID indicated for each figure part. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013*

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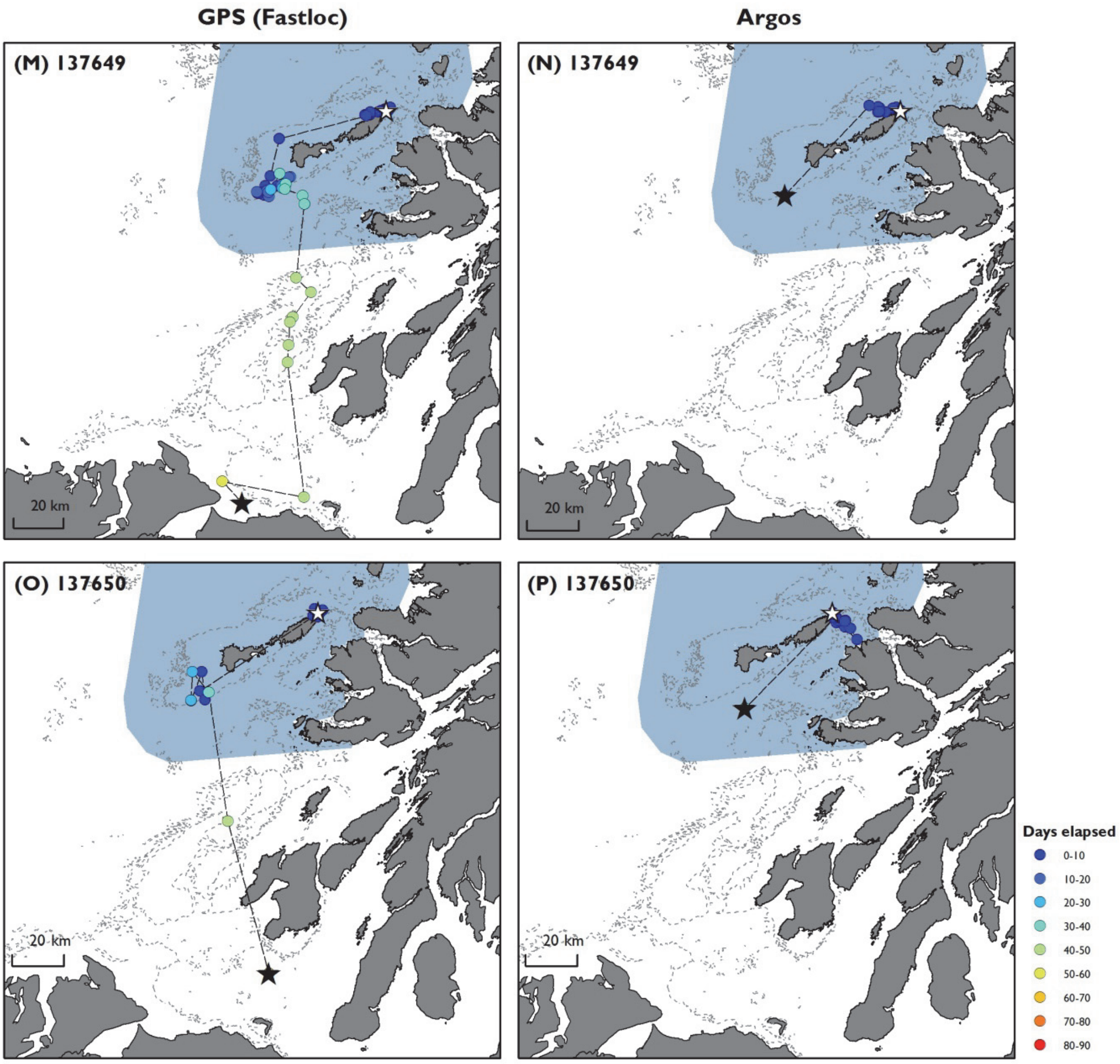
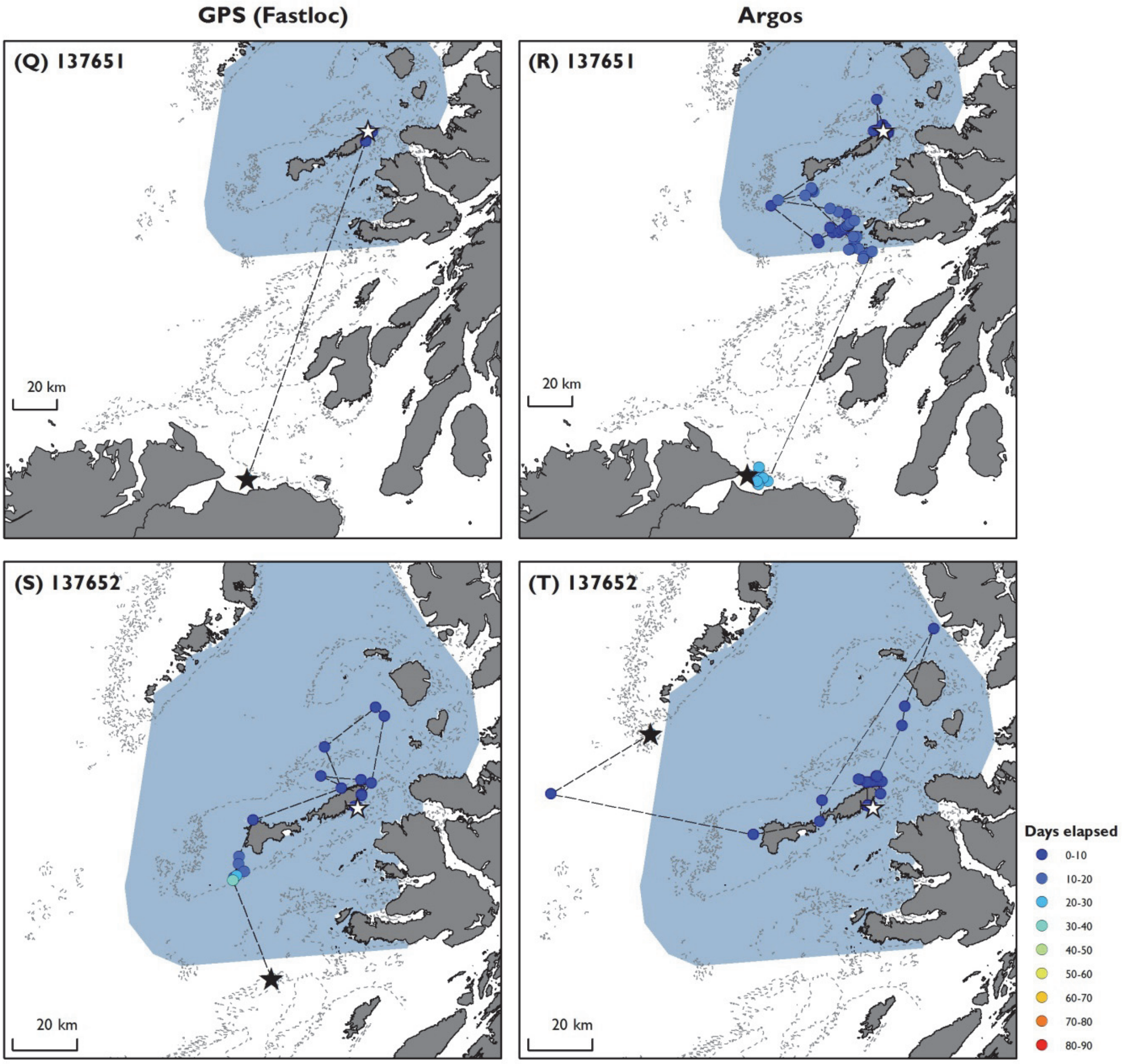
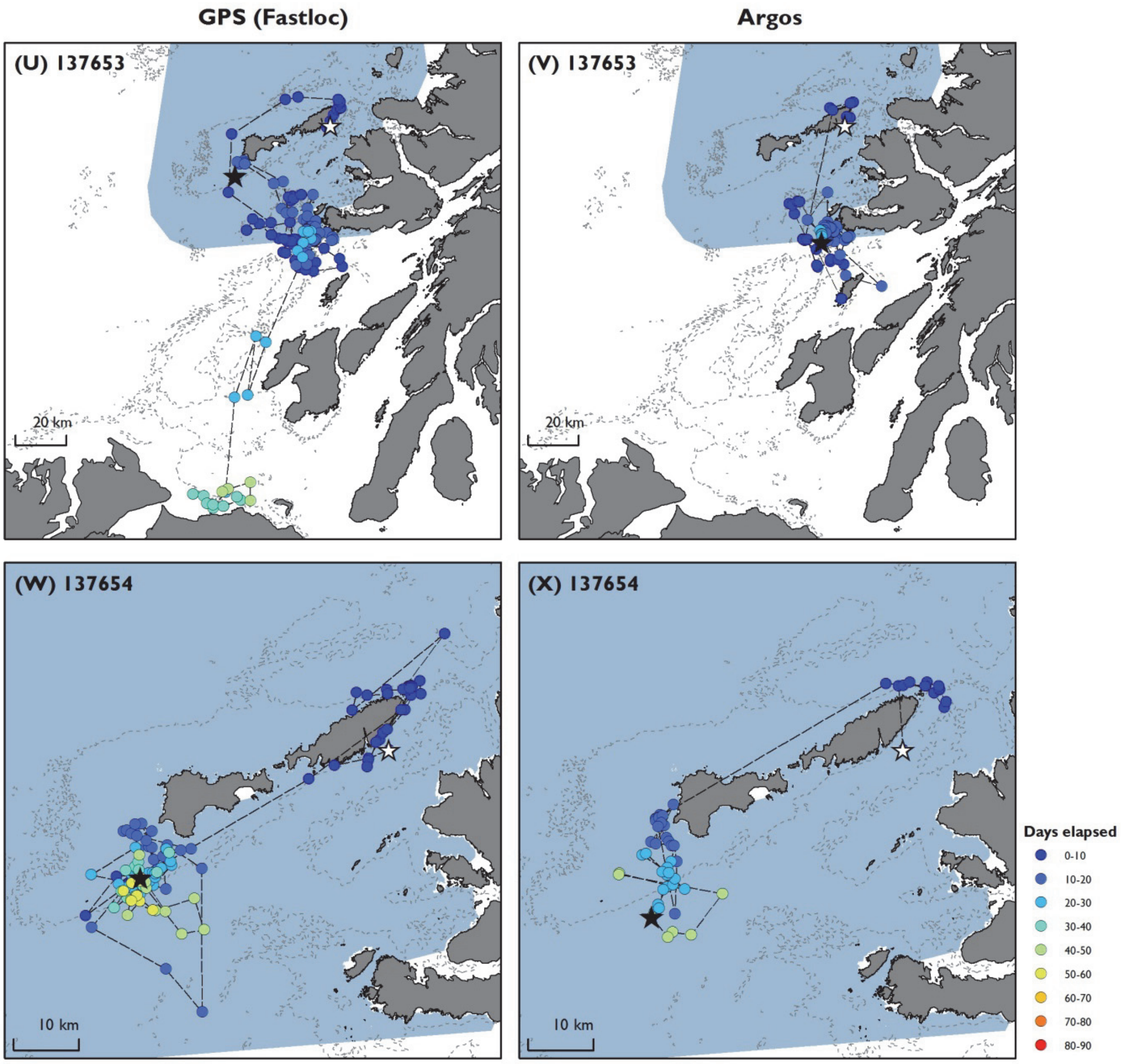


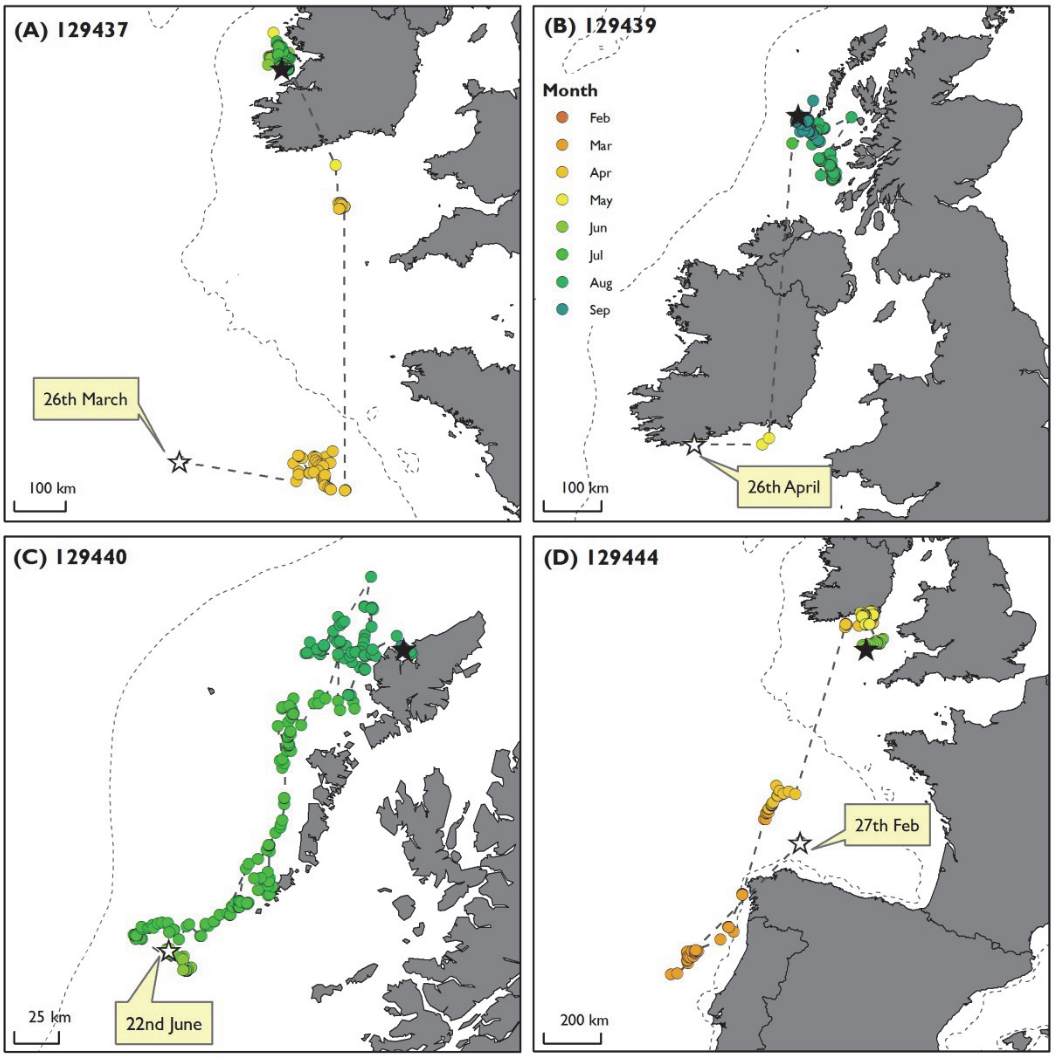
Supplemental Figure 2 cont. Fastloc™ GPS and contemporaneous Argos locations for basking sharks tracked with SPLASH-F tags*. Movements of sharks revealed by GPS-enabled satellite tags with contemporaneous Argos locations. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Tag ID indicated for each figure part. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



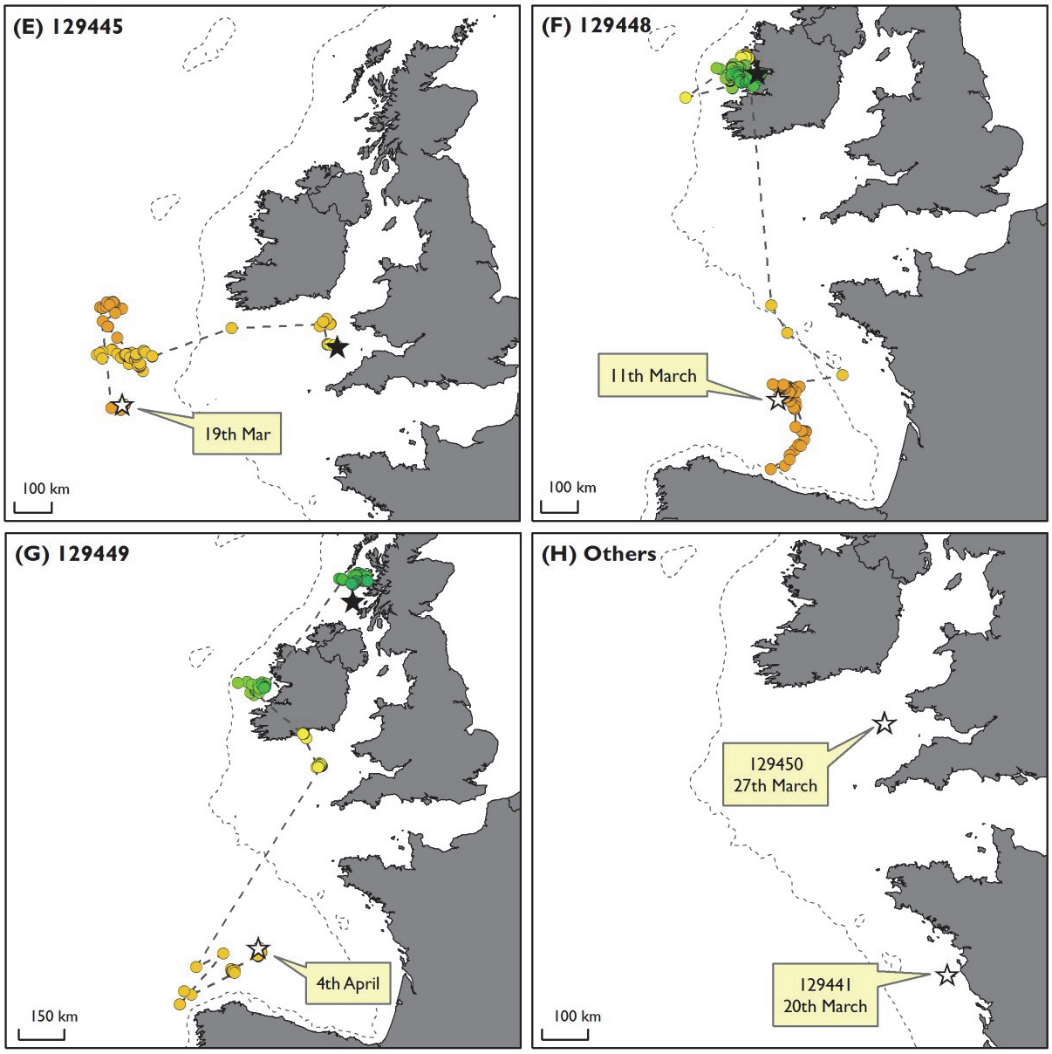
Supplemental Figure 2 cont. Fastloc™ GPS and contemporaneous Argos locations for basking sharks tracked with SPLASH-F tags. *Movements of sharks revealed by GPS-enabled satellite tags with contemporaneous Argos locations. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Tag ID indicated for each figure part. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, License O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



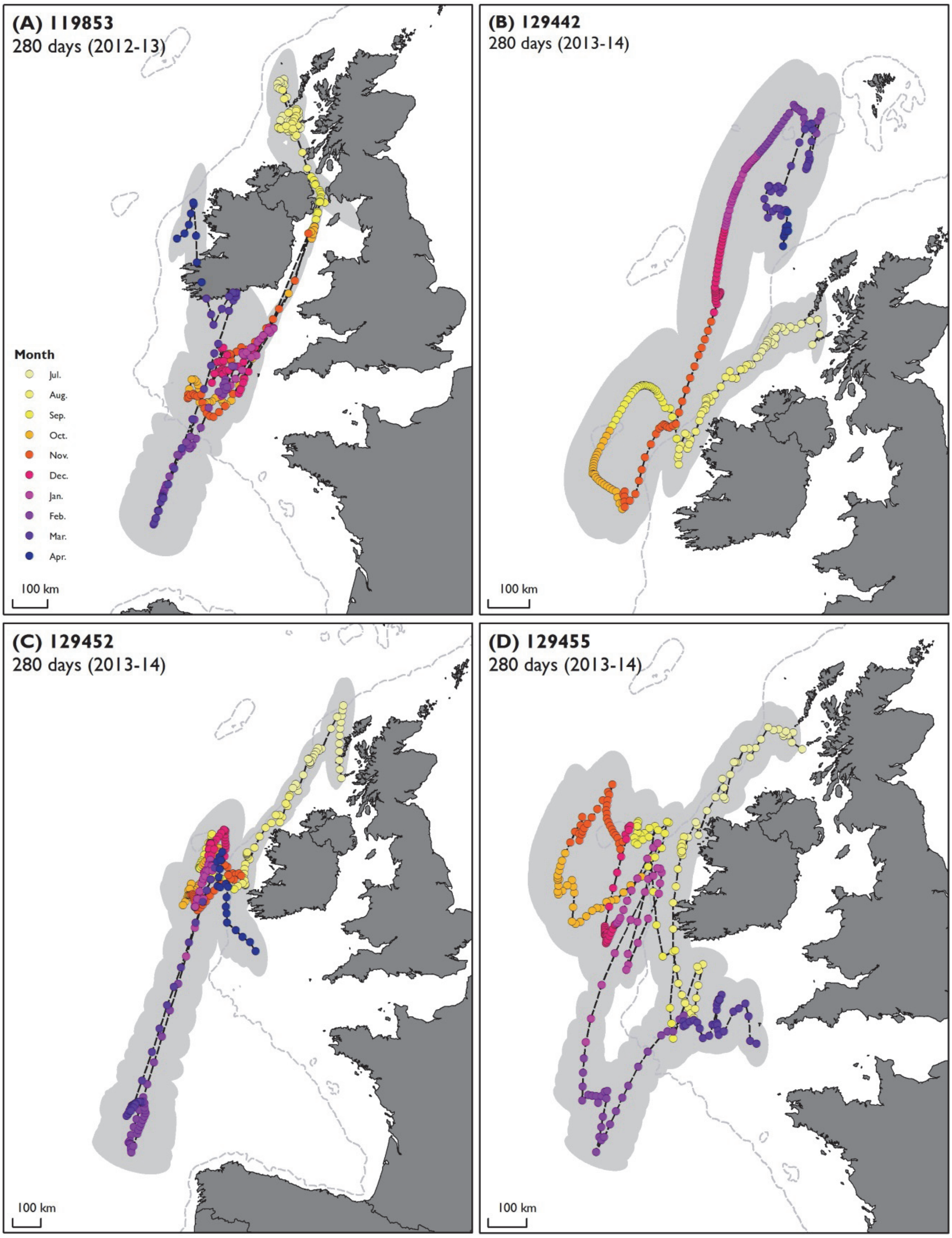
Supplemental Figure 2 cont. Fastloc™ GPS and contemporaneous Argos locations for basking sharks tracked with SPLASH-F tags*. Movements of sharks revealed by GPS-enabled satellite tags with contemporaneous Argos locations. Attachment locations (white stars), final locations (black stars). Dashed lines join consecutive locations but do not infer straight line movement. Tag ID indicated for each figure part. Sea of the Hebrides MPA proposal (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, License O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*



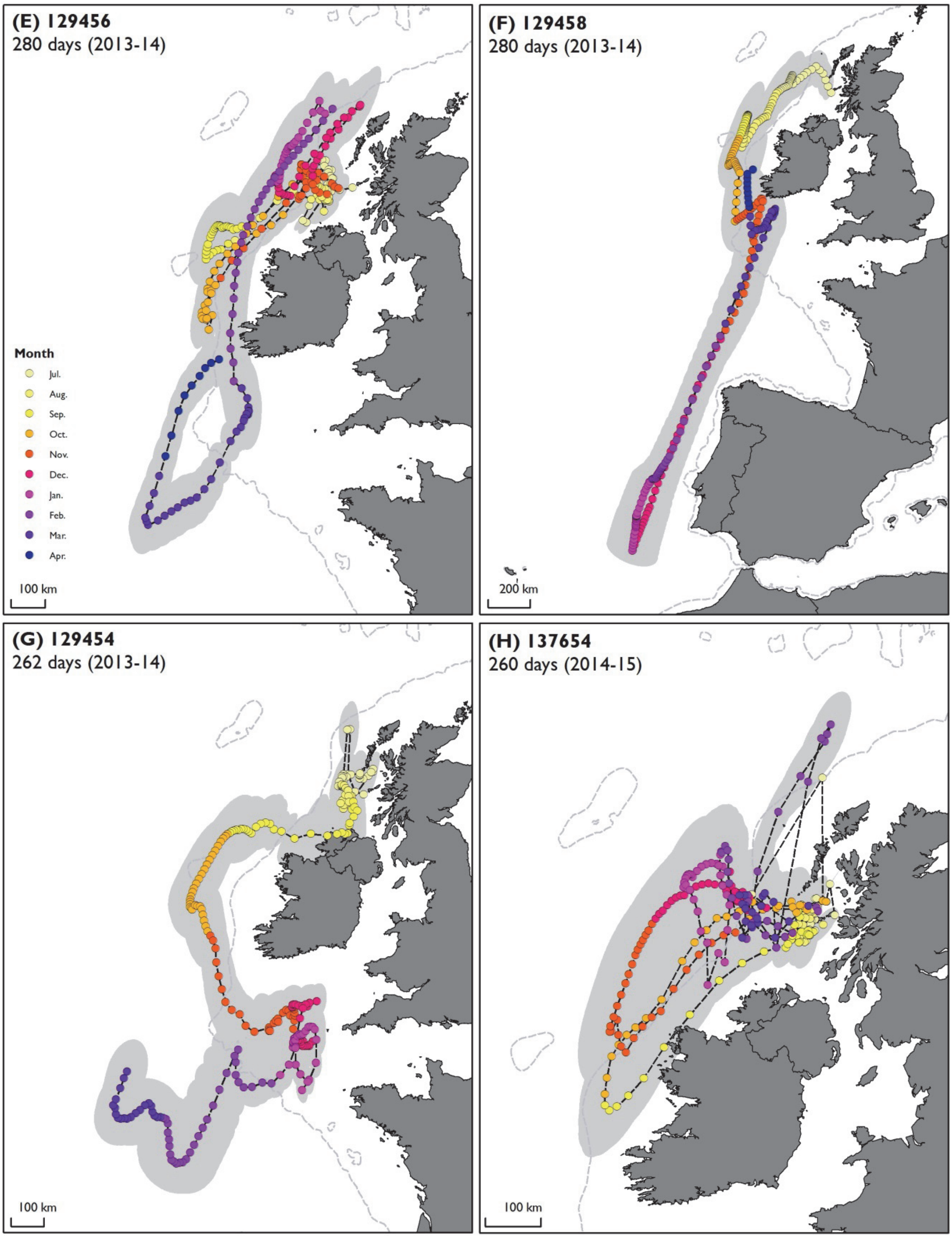
Supplemental Figure 3. Spring surfacing and northward movement made by basking sharks. *All surfacing events of basking sharks in 2014 (white stars). Sharks tagged in Scotland in summer 2013. Positions coloured by month of occurrence. Final locations (black stars). Tag ID indicated for each figure part. Figure parts ordered by ascending tag number. Dashed lines join consecutive locations but do not infer straight line movement (grey broken line). 200m bathymetric contour (grey narrow-dashed line; source: GEBCO).*



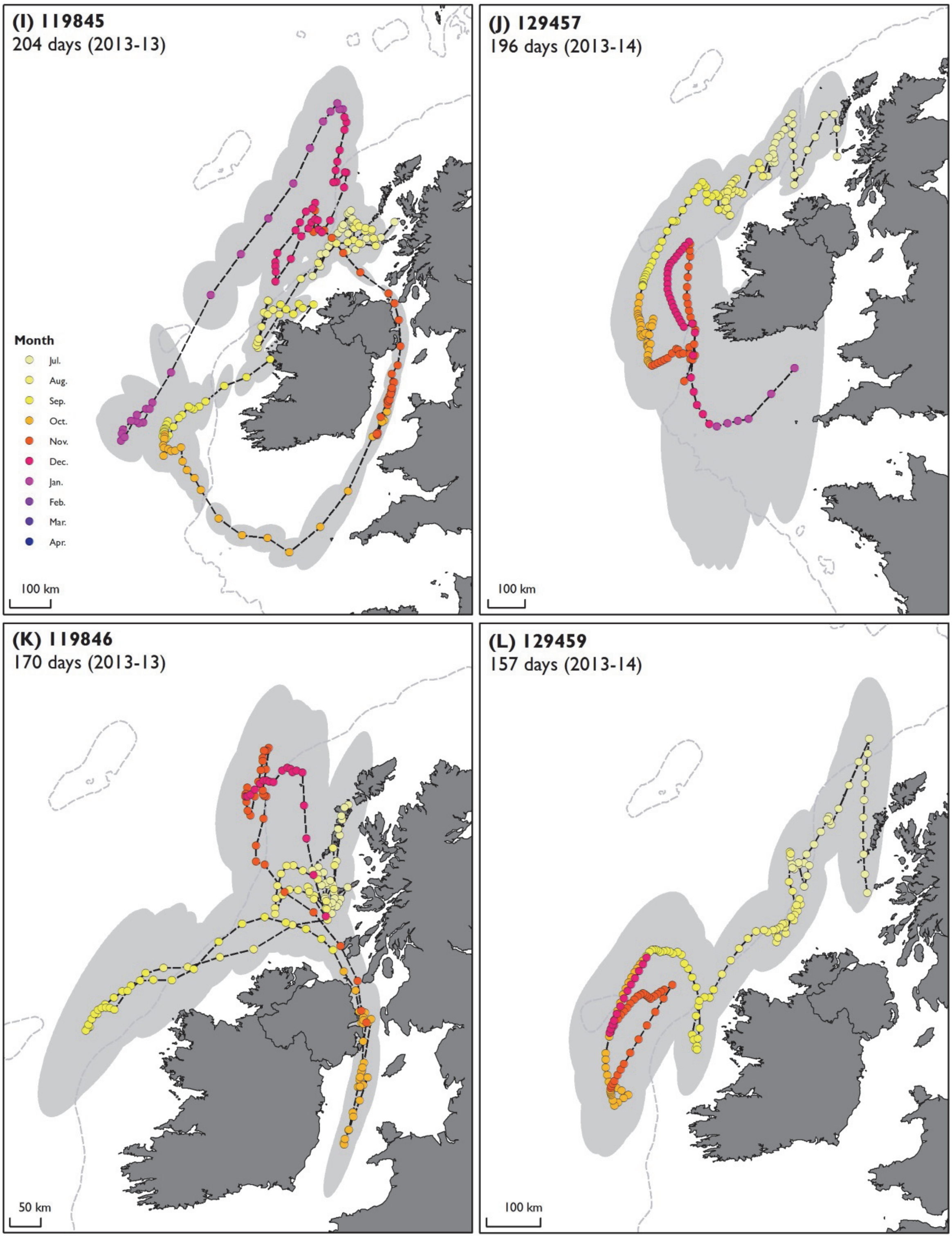
Supplemental Figure 3 cont. Spring surfacing and northward movement made by basking sharks. *All surfacing events of basking sharks in 2014 (white stars). Sharks tagged in Scotland in summer 2013. Positions coloured by month of occurrence. Final locations (black stars). Tag ID indicated for each figure part. Figure parts ordered by ascending tag number. Dashed lines join consecutive locations but do not infer straight line movement (grey broken line). 200m bathymetric contour (grey narrow-dashed line; source: GEBCO).*



Supplemental Figure 4. Basking shark movements revealed by light geolocation. *Light geolocation estimates of basking shark movement. Colour of location indicates progressing month of tracking. Tag ID indicated for each figure part. Figure parts sorted by tracking duration (descending). Grey polygons surrounding estimated locations represent spatial error for each location. 200m bathymetric contour (grey dashed line; source: GEBCO).*

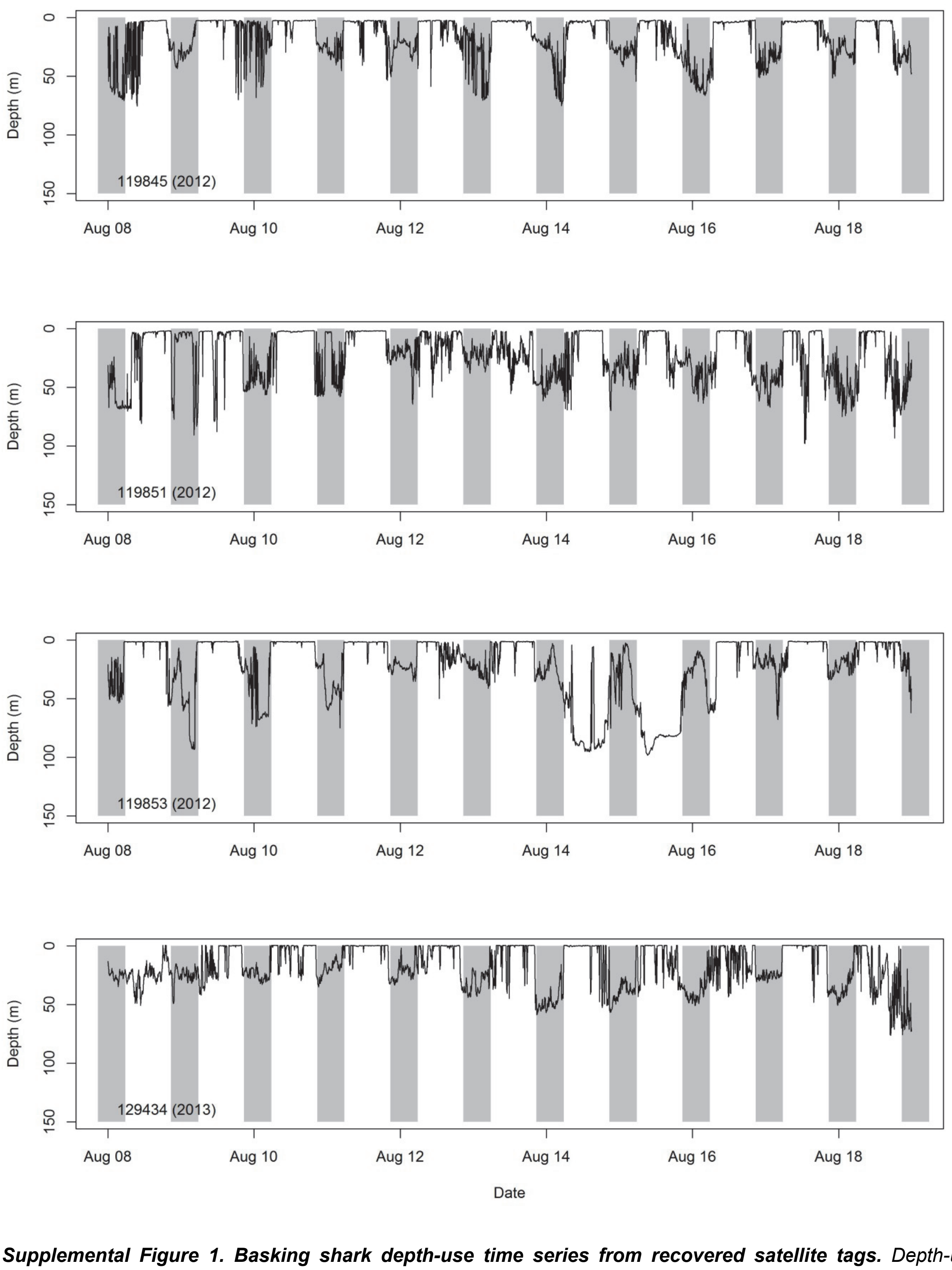


Supplemental Figure 4 cont. Basking shark movements revealed by light geolocation. *Light geolocation estimates of basking shark movement. Colour of location indicates progressing month of tracking. Tag ID indicated for each figure part. Figure parts sorted by tracking duration (ascending). Grey polygons surrounding estimated locations represent spatial error for each location. 200m bathymetric contour (grey dashed line; source: GEBCO).*

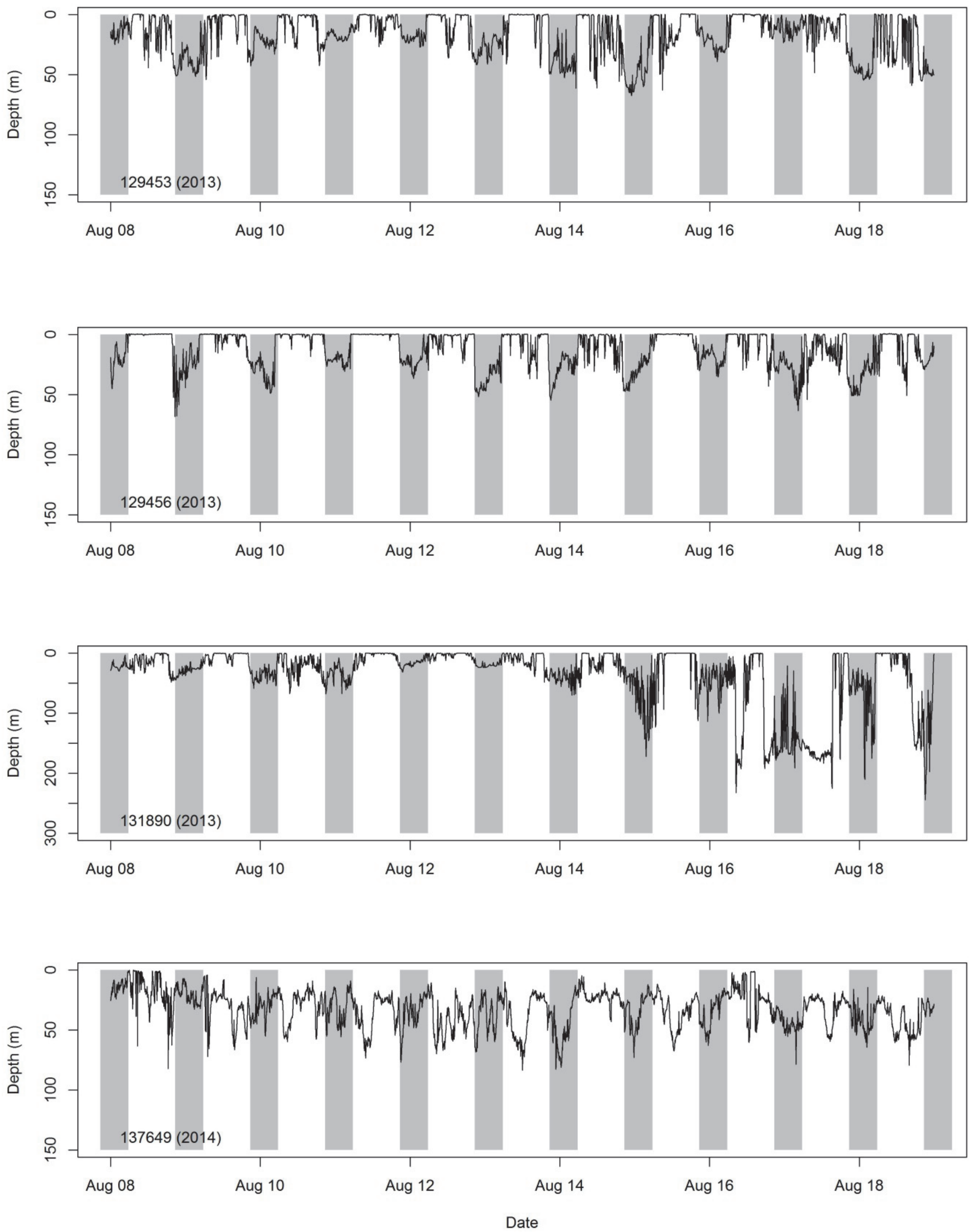


Supplemental Figure 4 cont. Basking shark movements revealed by light geolocation*. Light geolocation estimates of basking shark movement. Colour of location indicates progressing month of tracking. Tag ID indicated for each figure part. Figure parts sorted by tracking duration (descending). Grey polygons surrounding estimated locations represent spatial error for each location. 200m bathymetric contour (grey dashed line; source: GEBCO).*

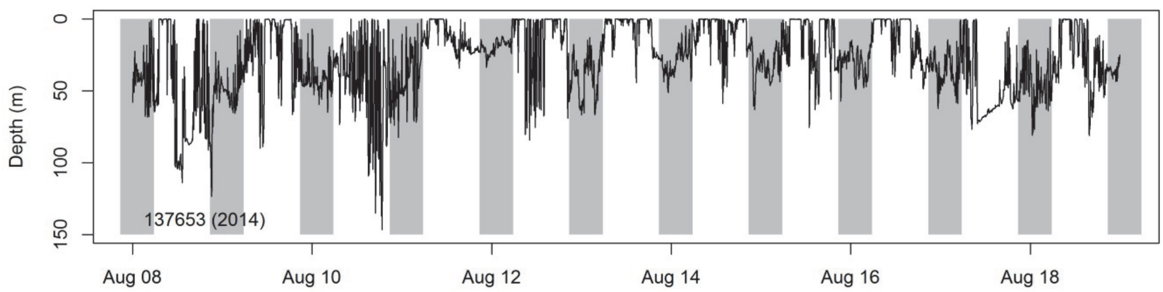
ANNEX 2: DEPTH USE

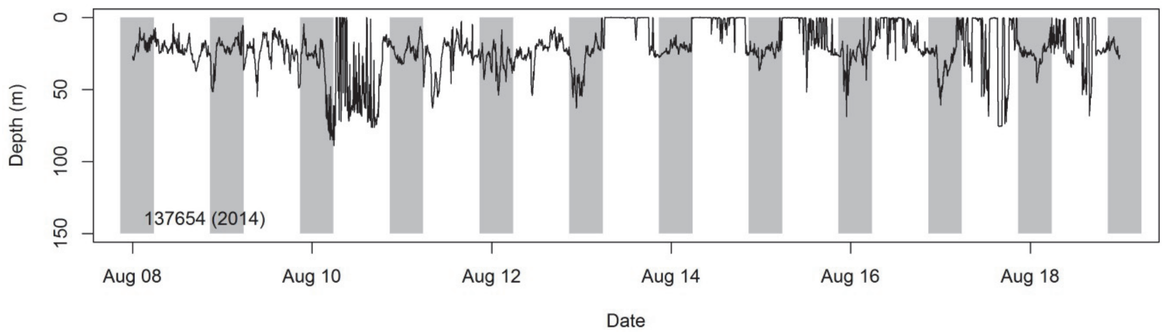


Supplemental Figure 1. Basking shark depth-use time series from recovered satellite tags. *Depth-use behaviour for arbitrary 10 day period in 2012, 2013 and 2014. Mean depth reported at 5 min. intervals. Grey vertical filled bars indicate periods between sunset and sunrise (approx. 9-hour duration, starting at 9pm BST daily) for the period. Figure parts ordered by tag ID number (ascending). Y-axis depth limits for tag 131890 differ from remaining figure parts. Tags 119842 and 137646 were not operational during the 10 day period and are not displayed.*

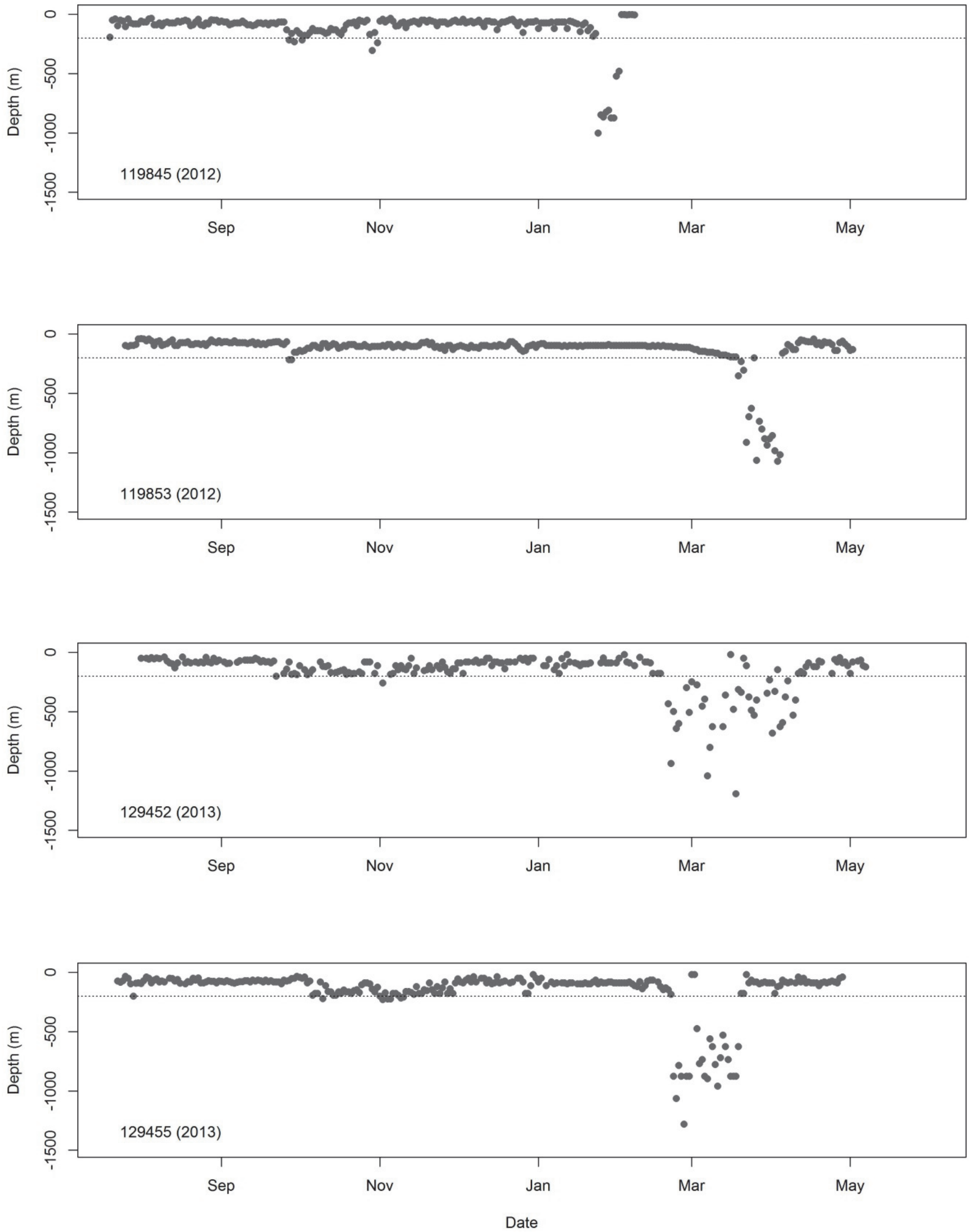


Supplemental Figure 1 cont. Basking shark depth-use time series from recovered satellite tags. *Depth-use behaviour for arbitrary 10 day period in 2012, 2013 and 2014. Mean depth reported at 5 min. intervals. Grey vertical filled bars indicate periods between sunset and sunrise (approx. 9-hour duration, starting at 9pm BST daily) for the period. Figure parts ordered by tag ID number (ascending). Y-axis depth limits for tag 131890 differ from remaining figure parts. Tags 119842 and 137646 were not operational during the 10 day period and are not displayed.*

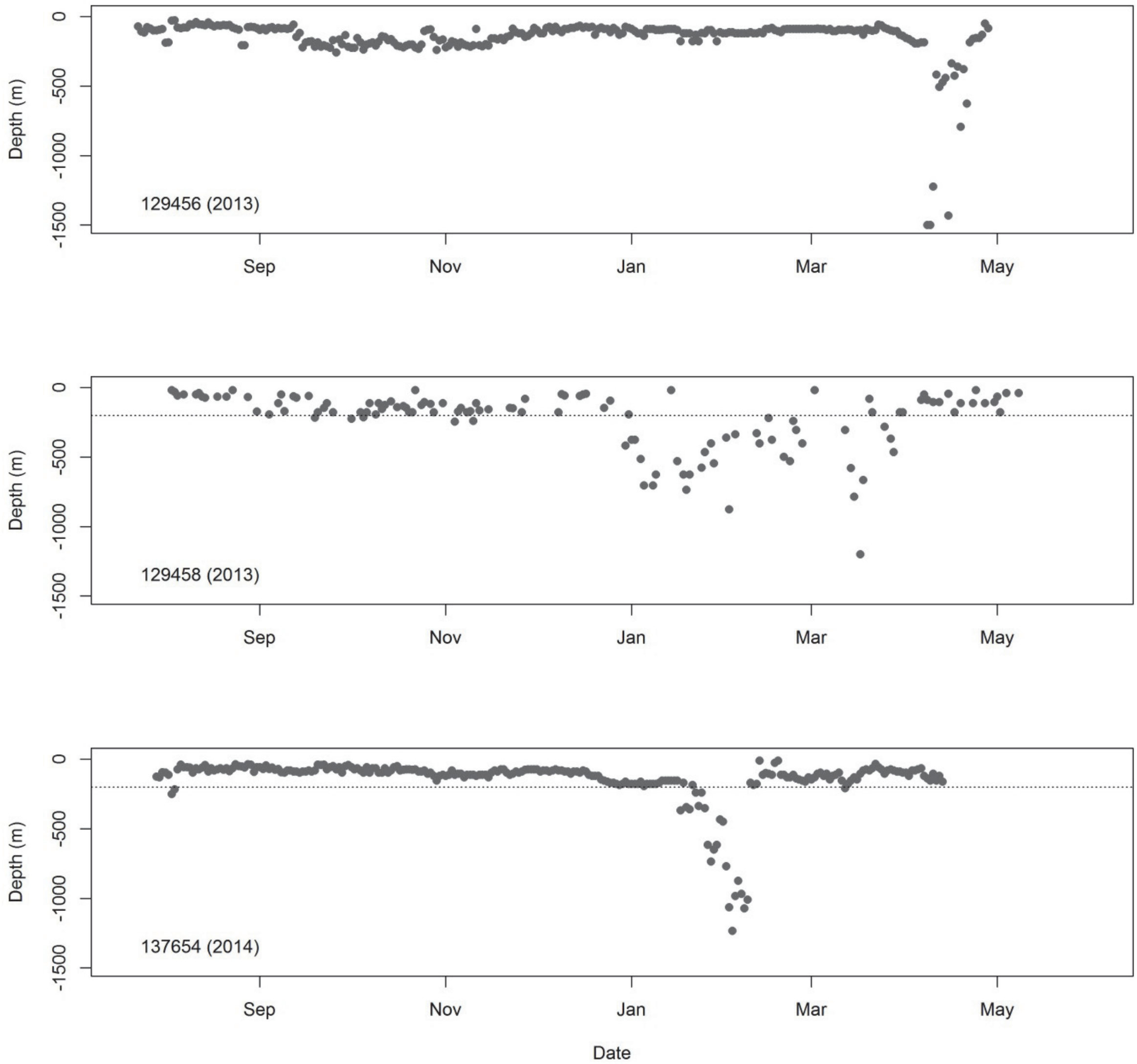




Supplemental Figure 1 cont. Basking shark depth-use time series from recovered satellite tags. *Depth-use behaviour for arbitrary 10 day period in 2012, 2013 and 2014. Mean depth reported at 5 min. intervals. Grey vertical filled bars indicate periods between sunset and sunrise (approx. 9-hour duration, starting at 9pm BST daily) for the period. Figure parts ordered by tag ID number (ascending). Y-axis depth limits for tag 131890 differ from remaining figure parts. Tags 119842 and 137646 were not operational during the 10 day period and are not displayed.*



Supplemental Figure 2 cont. Maximum daily depths for seasonally deep-diving sharks*. Maximum depths (filled circles) for sharks occupying deep waters (>1000m depth) during winter and early spring. Figure parts ordered by tag ID number (ascending). Indicative depth of continental shelf (200 m; broken horizontal line).*



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Policy and Advice Directorate, Great Glen House,
Leachkin Road, Inverness IV3 8NW
T: 01463 725000

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