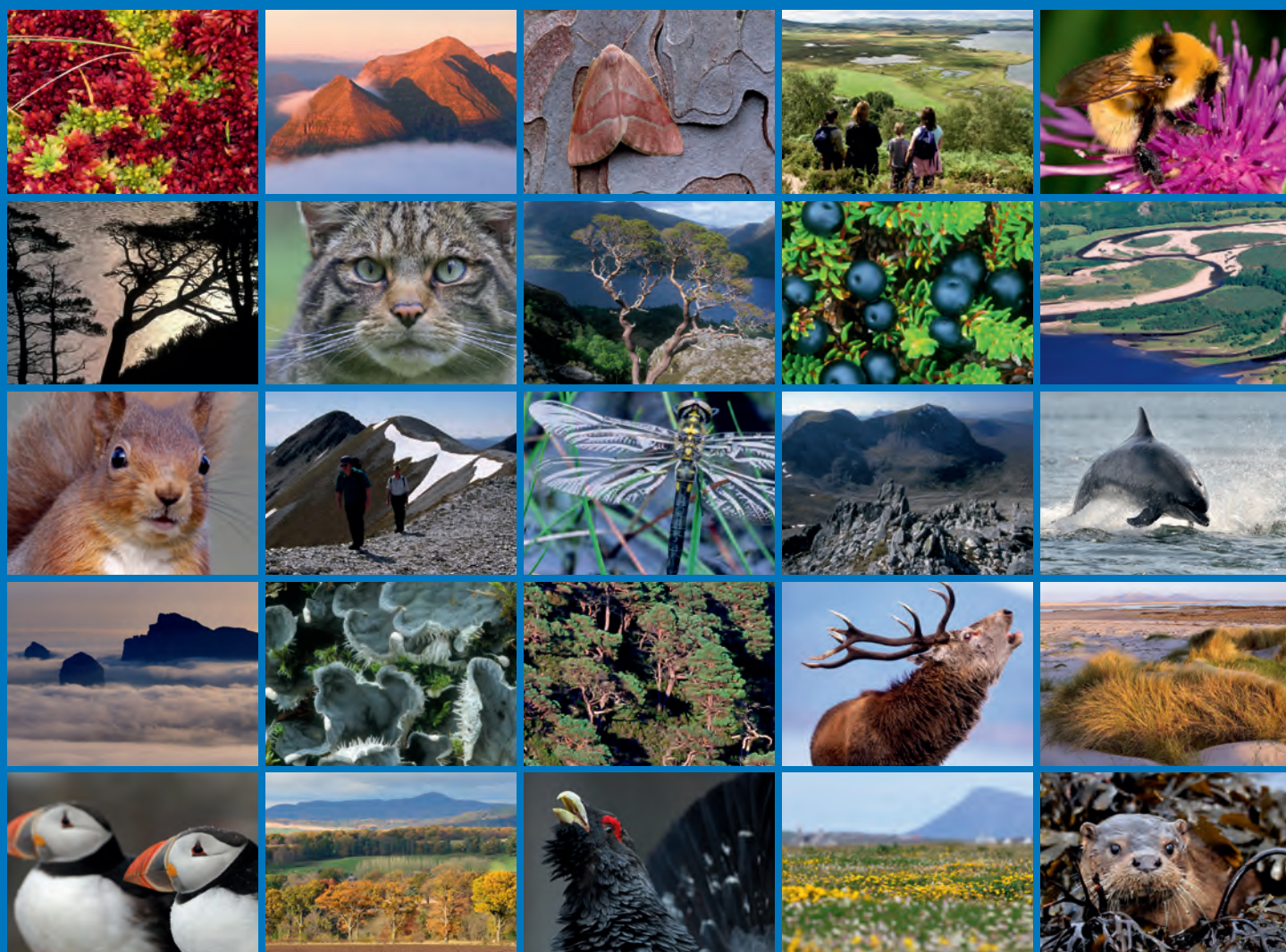


Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement and distribution using satellite telemetry (Interim report November 2013)





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COMMISSIONED REPORT

Commissioned Report No. 700

**Basking shark satellite tagging project: insights
into basking shark (*Cetorhinus maximus*)
movement and distribution using satellite
telemetry (Interim report November 2013)**

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COMMISSIONED REPORT

Summary

Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement and distribution using satellite telemetry (Interim report November 2013)

Commissioned Report No.: 700
Project no: 14082
Contractor: University of Exeter
Year of publication: 2013

Background

The areas around Coll, Tiree, Hyskeir and Canna have been identified as “hotspots” for basking sharks (*Cetorhinus maximus*) from 20 years of public sightings records (Witt *et al.*, 2012). 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 social activities, such as breaching and courtship-like behaviour within the Inner Hebrides. This evidence highlights that the area may be important for key life cycle stages of basking sharks. To gain detailed insights into the distribution, habitat-use, movements and behaviour of basking sharks in the Inner Hebrides, Scottish Natural Heritage (SNH) & the University of Exeter initiated a research project to attach satellite tags to basking sharks in the summers of 2012 and 2013. This report provides an overview of these data collected by satellite tags deployed on basking sharks in 2012. Further information can also be found within the post-fieldwork report (Witt *et al.*, 2013).

Main findings

- Some broad patterns of behaviour were recorded although substantial individual variation was observed and therefore interpretation is presented with caution:
 - six of the eight sharks tagged with SPOTs (that function as real-time satellite transmitters) were found within the Sea of the Hebrides for several months following tag attachment, showing a degree of site fidelity.
 - several areas of high relative density of sharks were highlighted from initial analysis.
 - two individuals were tracked migrating southwards over 3,000km to Madeira and the Canary Islands.
 - basking shark depth-use was successfully spatially linked to mapped locations with GPS accuracy.
 - depth-use behaviour with respect to time of day suggests diel vertical migration, at least within the coastal zone.
 - two sharks attained maximum depths of 1,000m, which indicated movement off the European continental shelf.

- Results have increased our understanding of basking behaviour in Scottish waters and further analysis of data from tags deployed in 2013 will add confidence by increasing the sample size, and will enable an investigation of shark behaviour across two years.

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We extend our sincere thanks to the skippers and crew of the Sula Crion, 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

This report provides an overview of data collected by satellite transmitting tags that were attached to basking sharks at three locations in the Sea of the Hebrides between July and August 2012. Two types of satellite tags were deployed, SPOT (Smart Position Only Tag), which provided near-real time location data on tagged sharks when they were at the sea surface; and PAT-Fs (Pop-up Archival Transmitting tag with Fastloc™ GPS; *Global Positioning System*), whose primary function was to gather data on shark depth-use behaviour, as well as information on temperature and ambient light levels. PAT-F tags also gathered estimates of location when sharks were at the sea surface using an integrated GPS receiver.

This combination of tag types allowed for a synthetic overview of the coastal and offshore movements of basking sharks in Scottish waters. SPOTs provided short to medium term data (weeks to months) on movements predominantly in the coastal zone. PAT-F tags provided information on behaviour relating to depth-use. Opportunistic collection of GPS locations by PAT-F tags further enabled mapping of basking shark depth-use behaviour.

Individual movements of basking sharks tracked with SPOTs in 2012 were described in Witt *et al.*, (2013). This report builds on those findings, in particular, highlighting basking shark site fidelity and depth-use.

The results provide initial insight into some key aspects of basking shark behaviour:

- the duration of time that basking sharks remain in the Sea of the Hebrides;
- identification of key areas of basking shark occurrence;
- description of depth-use behaviour of basking sharks.

The results contained within this interim report are based on 21 satellite-tagged basking sharks, 17 of which provided data. As yet, a detailed understanding of the size of the basking shark population does not exist and therefore it is not possible to reliably estimate what proportion of the population the results represent. A second season of satellite tag deployments on basking sharks, which began in July 2013, will further elucidate the behaviour of basking sharks detailed in this report.

2. METHODS

2.1 Argos System

The Argos System is a satellite-based tracking system (www.argos-system.org) that was established to collect data from fixed and mobile platforms, e.g. ocean buoys, ships and other monitored platforms, worldwide. The Argos System uses seven Polar Orbiting Environmental Satellites (POES). Argos receivers are based on four satellites 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). Two Argos receivers are also hosted on satellites METOP-A and METOP-B operated by the European Organisation for the Exploitation of Meteorological Satellites (EUMETSAT). The most recent Argos receiver is based on SARAL (Satellite with Argos and AltiKa); this being a cooperative partnership between the Indian Space Research Organisation (ISRO) and Centre National d'Études Spatiales (CNES) France. The Argos System uses the physical principles of the Doppler Effect (the change in perceived frequency of a wavelength as an observer moves towards or away from an emitting source) to locate platforms and collect data.

The Argos System has now been used to track a wide variety of animal taxa worldwide both on land and at sea. However, the Argos System can only locate marine animals when they are at the sea surface, i.e. when the satellite tag is exposed to air, since tag transmissions travel poorly through water. Tags continuously transmit identification messages, 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-minutes in duration. The more messages received by the satellite 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 the tag spends long periods of time at the sea surface, for example when surface feeding.

The quality of each location collected and processed by the Argos System is assigned one of a series of seven 'location classes', with a class 3 location having the highest accuracy (within 350m of true location), class 2 locations the second highest accuracy (within 500m of true location) and class 1 locations the lowest (>1km from true location). The remaining four location classes are considered 'auxiliary' locations and normally lack an associated estimate of location accuracy, which has led to the rejection of auxiliary location classes in Argos tracking analyses. However, satellite tracking of marine vertebrates, which are more often below the sea surface than on it, typically leads to a high proportion of auxiliary locations, resulting in a high proportion of data being rejected. Simultaneous collection of Argos and GPS data on animals has suggested that auxiliary positions may be accurate to within 1km (Witt *et al.*, 2010) and therefore current analysis typically retains all location classes, but with strict quality control (for example using speed and turning angle filtering), eliminating many implausible locations (Witt *et al.*, 2010).

2.2 Tether system

Satellite tags cannot at present be directly attached to basking sharks, e.g. using glue, harnesses or clamps, because it is not possible to detain sharks for sufficient time to make such attachments. Tags must thus be attached quickly, preferably remotely and in a manner that exposes the tag to the sea surface. Current best practice is to attach tags to the shark via a dart, attached to a tether varying in length, on the end of which is the satellite tag. Towed satellite tags are designed to be buoyant and the tether enables the tags to reach the sea surface if the study animal is sufficiently close, permitting transmissions to the Argos System. The dart is typically inserted into the tough musculature next to the dorsal fin using an extendable darting pole. Tethers used in the present study consisted of nylon-coated braided stainless steel wire, a swivel and a depth-release device (Wildlife Computers;

RD1800). This device releases the tag (severs the tether) at 1800m depth to prevent damage from the huge ambient pressure at depths greater than 2000m.

Tether lengths were customised for each shark according to their body size, so that tethers were sufficiently short so as not to make contact with the caudal fin but sufficiently long to reach the sea surface. Tether assemblies were configured to break away if significant force were applied, e.g. in entanglement with fishing nets, pot lines or submerged objects.

2.3 Study area

The main study area for the deployment of satellite transmitters was the Inner Hebrides on the west coast of Scotland. Boat-based surveys providing effort-corrected estimates of basking shark density have shown that this geographical area receives appreciable numbers of sharks throughout summer months (SNH, 2012; Speedie *et al.*, 2009). Satellite tags were therefore deployed on basking sharks at three locations within the area of the Inner Hebrides with the highest rates of effort-corrected sightings: Tiree, Gunna Sound and Hyskeir (Figure 1).

Data collected from satellite tags, occurring both within and outwith the main study area, are considered in this report, but particular attention is given to data occurring within two smaller areas; the Skye to Mull Marine Protected Area (MPA) search location and the proposed Argyll Array. These are two areas where a greater understanding of basking shark movement and distribution and their use of these areas will be of immediate benefit:

- The Skye to Mull MPA search location is an area identified through the Scottish Marine Protected Areas Project for basking sharks and minke whales. Data collected from this satellite-tracking project will feed into the further assessment against the MPA Selection Guidelines (Marine Scotland, 2011) to help determine whether spatial protection will benefit basking sharks in Scotland.
- The proposed Argyll Array is an area that Scottish Power Renewables hold exclusive rights to pursue the feasibility of the development of an offshore wind farm. A Marine Licence is required before development can take place, and the interaction with basking sharks is one of the environmental issues that will require consideration in the licence process.

2.3.1 Deployment of tags and sample collection

A total of nine SPOTs and twelve PAT-F tags were deployed in 2012 and the results are presented and discussed in this interim report. A further twenty-seven tags were deployed in 2013; fifteen SPOTs and twelve miniPATs and these results will be analysed and discussed in the final report. Deployments in 2013 also included the SPLASH-F tag, which is the successor to the PAT-F tag, and results from these tags will also be included in the final report.

DNA samples were taken from tagged sharks, in the form of external skin slime using a cotton cloth mounted on a pole, to facilitate genetics work being undertaken by the University of Aberdeen.

In addition, vertical zooplankton samples were taken at all tagging locations in 2012 and 2013; additional zooplankton samples were also collected within the study area during fieldwork in 2013. These samples are still to be analysed.

The attachment of satellite transmitters was regulated by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (ASPA Project Licence: PPL

30/2975). Activities also required licensing under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971).

A full description of the 2012 field-work methodology and tagging technology can be found within Witt *et al.*, 2013.

2.4 SPOT

To the authors' knowledge, the present study is the first to use SPOT-tagging technology on basking sharks. While an early variant of a real-time Argos tracking device was attached to a basking shark in 1984 (for 17 days (Priede, 1984; Priede & Miller, 2009)), the technology has advanced considerably since this time. For example, SPOTs can currently make 65,000 transmissions to the Argos System (each location being derived from at least four transmissions), allowing for insights into movement of basking sharks over many months, with an accuracy of up to 350m.

In this report, SPOT location data were filtered prior to mapping, to remove low quality and implausible locations (Witt *et al.*, 2010). To avoid pseudo-replication, multiple daily estimates of location for each basking shark were resolved to one best daily location. Location data from SPOTs were also displayed on the Wildlife Tracking website (www.wildlifetracking.org) to allow the public to participate in the project by following the movements of sharks in near-real time. Data presented on www.wildlifetracking.org were filtered to provide easy-to-view maps, whereas location data presented in this report have been more thoroughly filtered to facilitate statistical analysis.

The first 28 days of satellite tracking represented a period when all but two SPOTs transmitted continuously, thereby providing the greatest sample size for further analysis of shark movement and site residency in the coastal zone.

Basking shark movements were contextualised with their habitat, including bathymetry (source: EDINA Marine Digimap and GEBCO), seabed type (source: JNCC SeaMap), mean averaged ultra-high resolution 1km² sea surface temperature (source: Global High Resolution Sea Surface Temperature Multiscale Ultrahigh Resolution L4 daily product) and mean averaged tidal speed (source: Polpred; NOC Liverpool; under licence to the University of Exeter).

2.4.1 Estimating areas of relative importance (site fidelity)

Location data gathered from SPOTs (n = 8 sharks) were analysed to ascertain whether tracked basking sharks showed preference for particular areas in the Sea of the Hebrides, i.e. to identify areas with high or low relative basking shark density. Locations received from each shark were first filtered to a single, most accurate location for each day to avoid pseudo-replication, this approach is particularly important to limit the potential for biased estimates of density. Only locations collected within the first 28 days of tracking were initially used; a period, when all individuals could contribute near equal number of locations to the analysis. Analysis of site fidelity was also undertaken for a longer period (July to September) although this used data from only four sharks. Two methods were used to estimate areas of relative importance; kernel density estimation (Worton, 1989) and a simple grid-based point counting approach (Maxwell *et al.*, 2011).

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 comprising cells of 0.01° (latitude and longitude), and this process smoothed the data at a resolution of 0.05° (approx. to 5km). Kernel density estimation (or KDE) created a smoothed estimate of density that incorporated

areas containing specified densities, e.g. a region containing the 25% most densely aggregated data, and further regions containing, 25 to 50%, 50 to 75% and 75 to 90% of data by their density.

Grid-based point counting: A non-statistical grid-based counting approach was also adopted (Maxwell *et al.*, 2011); this used an underlying grid of 0.01° (latitude and longitude) to create grid cells of approximately 1km². This grid was then used to sum spatially coincident best daily location data.

2.5 PAT-F tags

PAT-F tags collected data on the ambient environment at 10-second intervals, including data on water temperature, light levels, pressure (depth) and battery voltage. These data were archived on the tag, along with Fastloc™ GPS data (see below), and data were summarised at 4-hour intervals. For example, depth-use data, including estimates of the percentage of time spent at 12 depth classes, i.e. 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 the data every 4-hours. These summary data were subsequently transmitted to over-passing satellites once the tag had detached from the study animal. PAT-F tags were programmed to detach from study animals 280 days after deployment so that the maximum amount of data could be gathered without compromising the ability of the tag to transmit after detachment. Although tags remotely transmit data, if they can be recovered a more detailed time-series of data can be downloaded from the tag's physical memory along with Fastloc™ GPS locations (see below).

Depth-use by tagged basking sharks with respect to time of day was analysed for the first 28 days of tagging for each individual. We imposed this 28 day limit to minimise the potential for using data collected outwith coastal areas of Scotland. Collected location data suggests that movement away from coastal areas during this period was infrequent. Depth-use data, for periods when tagged sharks were more likely to have moved away from coastal areas (October onwards), were examined separately.

In addition to collecting data on depth-use, PAT-F tags also collected location data using an integrated GPS receiver (locations of approximately 100m accuracy). In order to establish a GPS location, devices require at least several minutes to download 'Ephemeris' and 'Almanac' data, which describe the relative positions and timing schedules of the satellites making up the GPS network, thus allowing the device to calculate its relative position with high accuracy. However, given the need for animal tracking devices to capture accurate location data at much shorter intervals, the GPS Fastloc™ system was developed, permitting for capture of locations in only tens of milliseconds. Fastloc™ GPS technology integrated into satellite tags therefore represents a significant progression towards creating high accuracy locations (Hazel, 2009; Sims *et al.*, 2009; Costa *et al.*, 2010; Witt *et al.*, 2010). PAT-F tags were programmed to obtain a single GPS location at 4-hour intervals.

Fastloc™ GPS technology has several limitations and an understanding of these is essential before interpreting resulting GPS data; for example, 1) the accuracy of a GPS position, i.e. how far the estimated position is from the actual position, is determined by the number of GPS satellites in the sky above the tag when the tag is at the surface. Estimates of location derived from three or less satellite are of low accuracy and were discarded. 2) Acquisition of GPS data using Fastloc™ technology requires considerable power resources, as such tags fitted with Fastloc™ GPS typically have short deployment times (several months), which can be extended by programming tags to only collect GPS data at a comparatively low frequency, i.e. one position a day cf. Argos - anytime the tag is at the surface and three or more Argos enabled satellites are available. 3) Fastloc™ performs best when the hardware

(receiver dome) is floating level at the sea surface with no water splash as the GPS signal is easily attenuated by water.

2.5.1 Mapping depth-use behaviour

To facilitate an understanding of basking shark depth-use across the study area, depth-use data were extracted every time a Fastloc™ GPS location was simultaneously gathered. Data were summarised, including, maximum depth, modal depth (the most frequent depth) and depth range.

2.5.2 Light geolocation

PAT-F tags also collected information on ambient light intensity. These data can be used to estimate the location of study animals while below the sea surface using a process called light geolocation (Hill, 1994; Hill & 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 particularly for species that spend little or no time at the sea surface, such as large tuna (Block *et al.*, 2005). 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 predictably with longitude, when compared with a reference noon at Greenwich Mean Time (GMT). Longitude is normally solved before latitude as follows: the tag records the time at which light level was greatest in a given day and compares it to noon GMT. If, for example, the greatest light levels were 2 hour 30 min after noon at GMT, the study animal must be west of the prime meridian. In order to calculate how far west, we use the fact that each hour difference between local noon and GMT is equivalent 15° longitude. In the above example, the study animal would have been approximately 37.5° west of GMT (Equation 1: $15 \times 2.5 = 37.5^\circ \text{ W}$). Latitude can then 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. The estimates of latitude and longitude are then combined to provide a potential location for the study animal.

Light geolocation performs best in polar regions (where changes in day length between days are more exaggerated than in equatorial regions) and in periods of time away from solstices (Hill 1994, Hill & Braun 2001), where variation in day length with latitude is smaller. In addition, other issues may hinder how well the tag can record light levels, e.g. turbidity from suspended organic material, 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. Several methods are available to improve estimates of location derived from light geolocation, in particular by comparing temperature recorded by the tag (should the animal come to the surface) with sea surface temperature data (Teo *et al.*, 2004; Lam *et al.*, 2008; Pade *et al.*, 2009).

As it has a low spatial resolution, light geolocation is most useful when reconstructing the movements of tagged animals over hundreds to thousands of kilometres and less useful for describing localised movements. Light levels in the present study were collected at 10-second intervals by the tags and will be used to derive estimates of latitude and longitude in this way in the final report.

3. RESULTS

3.1 Overview

Nine SPOTs and twelve PAT-F tags (Table 1) were deployed across three sites (Gunnel Sound, West of Tiree and Hyskeir) in the Sea of the Hebrides during July-August 2012 (Figure 1). One SPOT suffered an electronic failure on deployment and was excluded from further analysis. SPOTs remained attached to basking sharks for 108 ± 101 days (mean \pm SD; 19 to 322 days range). One SPOT (119856) was found by a member of the public in Machrihanish Bay, Kintyre on June 22nd 2013. This device had tracked the movements of Caerban (Table 1) from July to October 2012.

Nine of the twelve PAT-F tags yielded useful datasets over a mean duration of 114 ± 92 days (mean \pm SD; 19 to 280 days range). Seven of the 12 PAT-F tags successfully detached from their study animal and transmitted archived data, but prior to their scheduled detachment dates. An eighth tag detached on the programmed date of release (280 days following deployment; PAT-F 119853). The remaining four PAT-F tags did not transmit on their programmed release date, however, one was found by a member of the public within the Firth of Clyde during summer 2013 (PAT-F 119842); the tag had been operational for 37 days. Two PAT-F tags, which successfully transmitted data following detachment, were also found by members of the public on Scottish and Irish beaches in early summer 2013 (PAT-F tags 119843 and 119845) and data have subsequently been obtained directly from the tag.

Table 1. Operational periods of SPOTs and PAT-F tags deployed on basking sharks in July-August 2012. Ordered by tag type and transmission duration. Legend: Tag transmitting (Argos or GPS) from within the MPA search location (dark grey), tag transmitting (Argos or GPS) from outside the MPA search location (light grey). Tag operational but no locations received (hatched). * Tag physically retrieved. **D** - Tag detached from shark during indicated month (for PAT-F tags either prematurely or through programmed release; for SPOT following receipt of high quality locations for several consecutive days, indicating tag no longer attached to study animal). Tag 120499: Last received location in December 2012, but these did not indicate tag detachment, no transmissions received since this date. Tag 119845: no GPS locations received, but tag deployed within MPA search location.

Tag ID	Tag Type	Name	Status	Duration (d)	2012						2013							
					J	A	S	O	N	D	J	F	M	A	M	J		
I20500	SPOT	Fionnalgh	Detached	19		D												
I19855	SPOT	Solas	Detached	20		D												
I20497	SPOT	Marna	Detached	20		D												
*I19856	SPOT	Caerban	Detached	96														
I20496	SPOT	Gill	Detached	100														
I20498	SPOT	Cailleach	Detached	135														
I20499	SPOT	Roy	Ceased	158														
I19854	SPOT	Elgol	Detached	322														D
I19850	PAT-F		Early release	19		D												
I19848	PAT-F		Early release	20		D												
*I19842	PAT-F		Early release	37		D												
I19851	PAT-F		Early release	45		D												
I19852	PAT-F		Early release	111														
I19843	PAT-F		Early release	140														
I19846	PAT-F		Early release	170														
*I19845	PAT-F		Early release	204														
*I19853	PAT-F		Released	280														
I19844	PAT-F		No data															
I19847	PAT-F		No data															
I19849	PAT-F		No data															

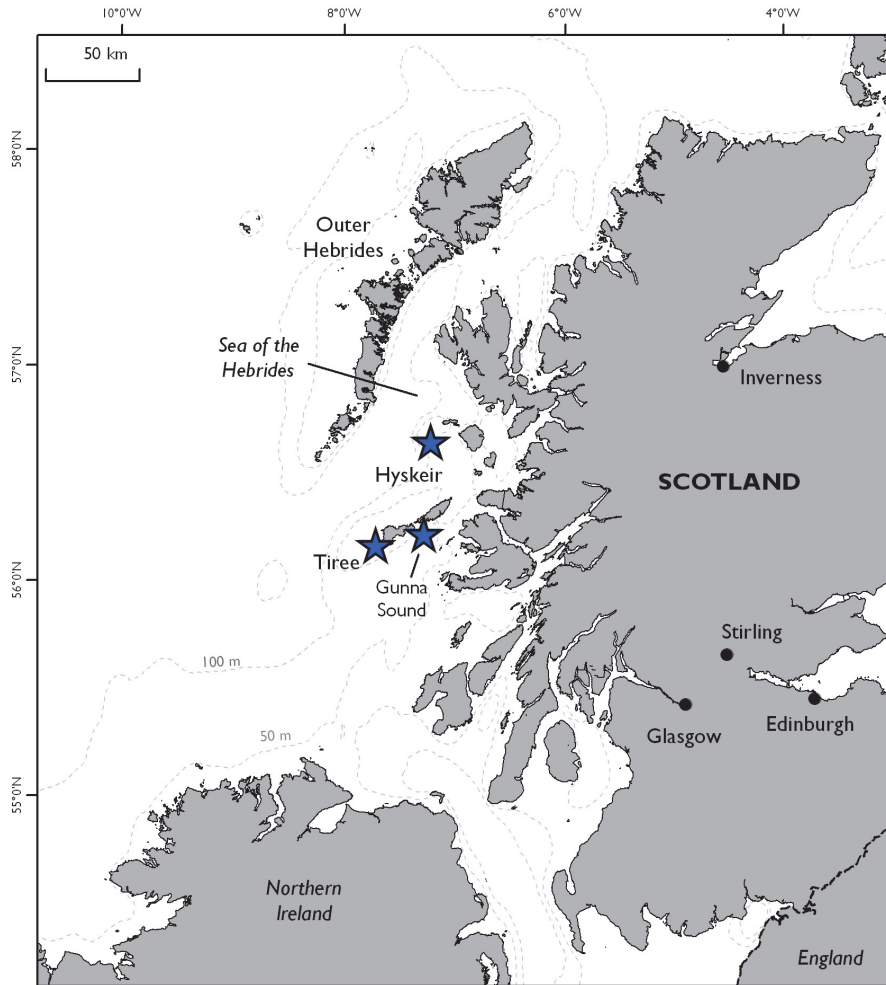


Figure 1. West of Scotland and deployment sites (Gunna Sound, Hyskeir and southwest of Tiree; blue filled stars) for basking shark satellite tags in July-August 2012. 50m and 100m depth contours; labelled grey broken lines (source GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.

3.2 Basking shark movements in the Sea of the Hebrides

To describe basking shark association with environment features, we used SPOT data from the first 28 days of tracking; a period when all but two tags functioned continuously. Basking sharks moved between headlands, shelves, drop-offs and regions of open water (Fig. 2A; Fig. 3). Initial assessment of these movements with a selection of environmental data allow for a preliminary description of habitats occupied. For example basking sharks appeared to be associated with:

- waters typically less than 100m deep (Fig. 2A; range 2 to 194m, median 25m; excludes those locations with low spatial precision that occurred on land),
- waters overlaying rock or reef seabed habitat types (Fig. 2B; 78% of locations occurring on rock and reef habitats),
- sea surface temperature (Fig. 2C; 12.4 to 13.3°C; median 12.6°C)
- mean tidal speed (Fig. 2D; 0.03 to 0.66m^s).

CREEM (The Centre for Research into Ecological and Environmental Modelling; University of St Andrews) are currently using statistical approaches to predict areas of importance for

basking sharks using visual sightings from effort-corrected boat surveys combined with data on environmental features, and the work will be published separately.

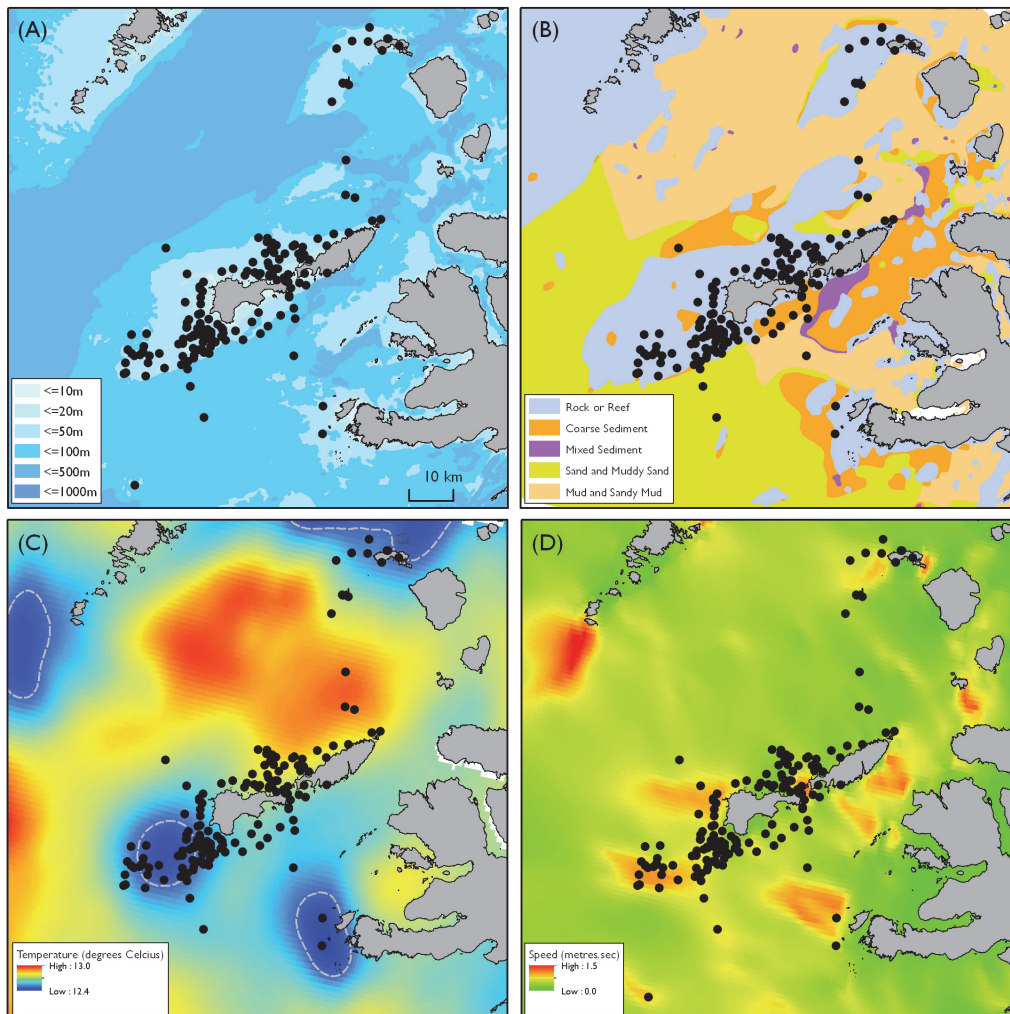


Figure 2. Satellite tracking of basking sharks. Maps show the highest quality location per day for eight basking sharks tagged with SPOT for up to 28 days of initial tracking data (black dots; $n = 177$ locations, repeated for all plots) upon (A) seabed depth, (B) seabed bottom type, (C) sea surface temperature - mean average for a 28 day period from the 17th of July to the 11th of August with contours of constant temperature (12.5°C ; grey broken lines), and (D) mean tidal speed from Polpred CS_20 model for the same 28 day period. Contains Ordnance Survey data © Crown copyright and database right 2013.

Basking sharks tracked for the first 28 days after tag attachment either remained in close proximity to their tagging sites of Tiree and Gunna Sound ($n = 4$ basking sharks; Fig. 3 A, B, D and E), moved from the tagging area in Hyskeir towards the vicinity of Coll and Tiree ($n = 2$ basking sharks; Fig. 3 G and H), moved to other Hebridean Islands ($n = 1$; Fig. 3 C) or to offshore deeper water ($n = 1$; Fig. 3 F).

Analysis over the first four months of tracking (July to October 2012), using data from five basking sharks (SPOTs: 119854, 119856, 120496, 120497 and 120499), which contributed similar numbers of locations, revealed further patterns of movement including longer-range dispersal and movement southwards along the western coast of Scotland (Fig. 4 B and C).

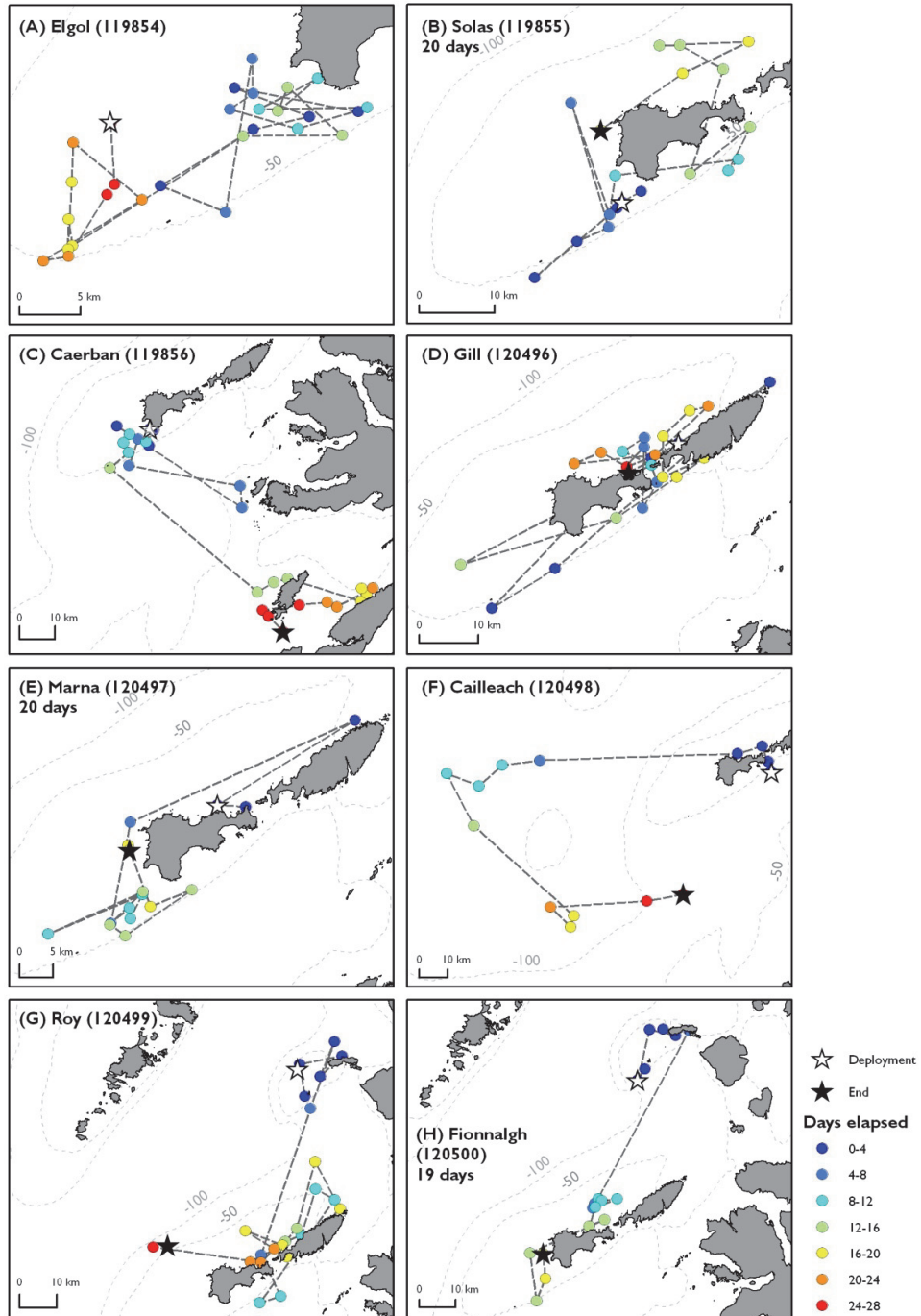


Figure 3. Movements of basking sharks tracked with SPOT. Satellite tracking data from eight basking sharks fitted with SPOT for the first 28 days of tracking. Inferred tracks are shown as lines between consecutive locations; grey long broken lines. Three basking sharks tracked for less than 28 days (B, E and H). 50m and 100m depth contours (labelled grey broken lines; source GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.

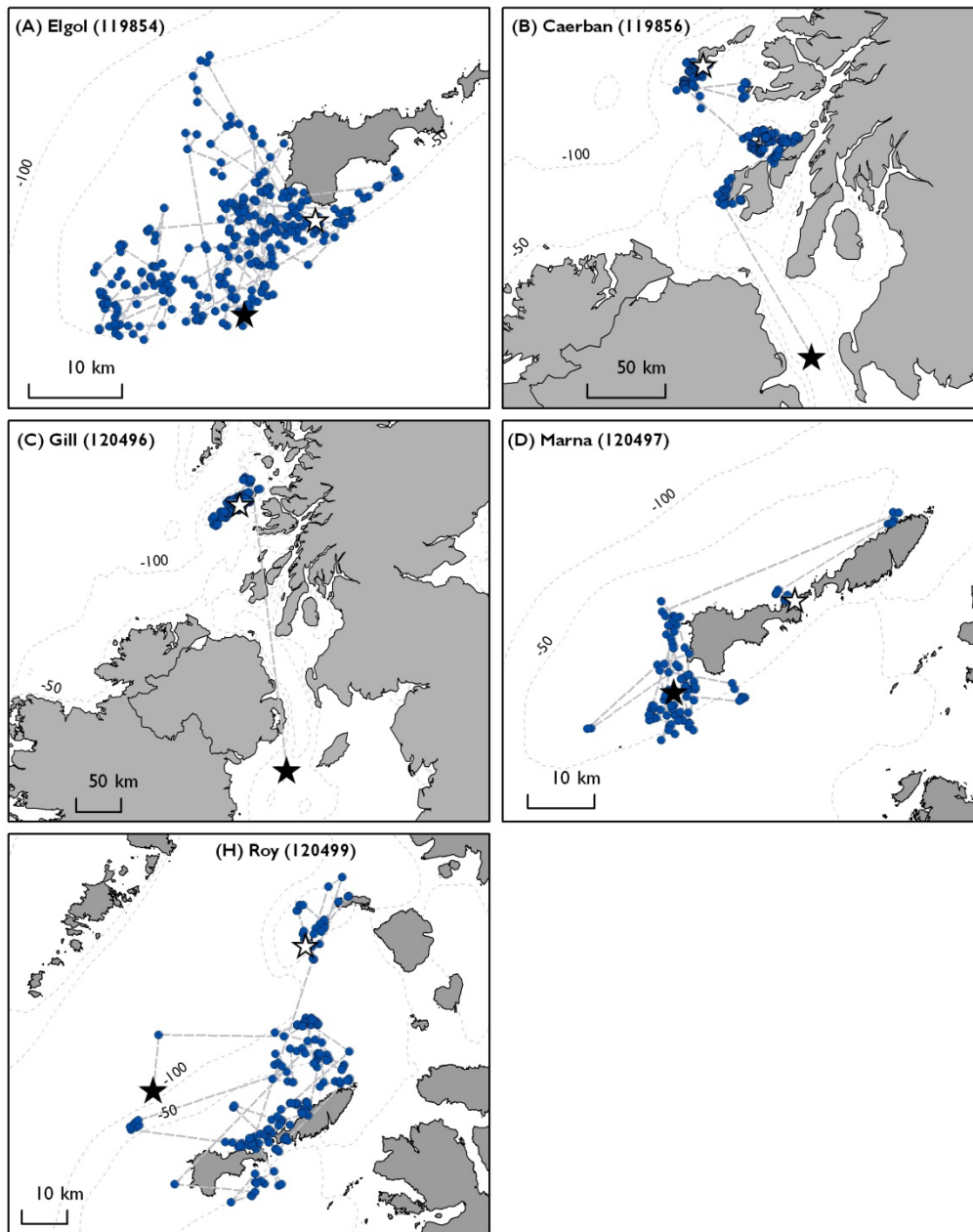


Figure 4. Movements of basking sharks tracked with SPOT. Satellite tracking data from five sharks fitted with SPOT for the period July to October. Inferred tracks are shown as lines between consecutive locations; grey long broken lines. 50m and 100m depth contour (grey short broken lines; source GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013. Start and end positions are shown as in Figure 3.

3.3 Areas of high relative importance for basking sharks in the Sea of the Hebrides

Basking shark movements determined from SPOTs were quantified with respect to the spatial extents of the Skye to Mull MPA search location and the proposed Argyll Array. During the first four weeks of tracking (28 days), basking sharks spent $83.7 \pm 28.3\%$ of days within the extents of the MPA search location (mean estimate from eight individuals) and $25.4 \pm 23.9\%$ of days within the proposed Argyll Array (mean estimate from eight individuals).

Location data from SPOTs were also used to identify areas of high relative importance for satellite-tagged basking sharks (Fig. 5; Table 1). Several core areas, which circumscribe 25% of the most aggregated location data, were evident from the analysis. These areas generally occurred southwest of Tiree and between Coll and Tiree in the region of Gunna Sound (Fig. 5 A and B). A simple grid cell count enumeration technique similarly highlighted the importance of these areas (Fig. 5 C and D; core areas with 25% of the most aggregated location data (shaded red) containing more than 10% of all locations (n = 185 locations in total). Areas of high relative abundance identified using both techniques occurred within the Skye to Mull Marine Protected Area search location and the proposed Argyll Array.

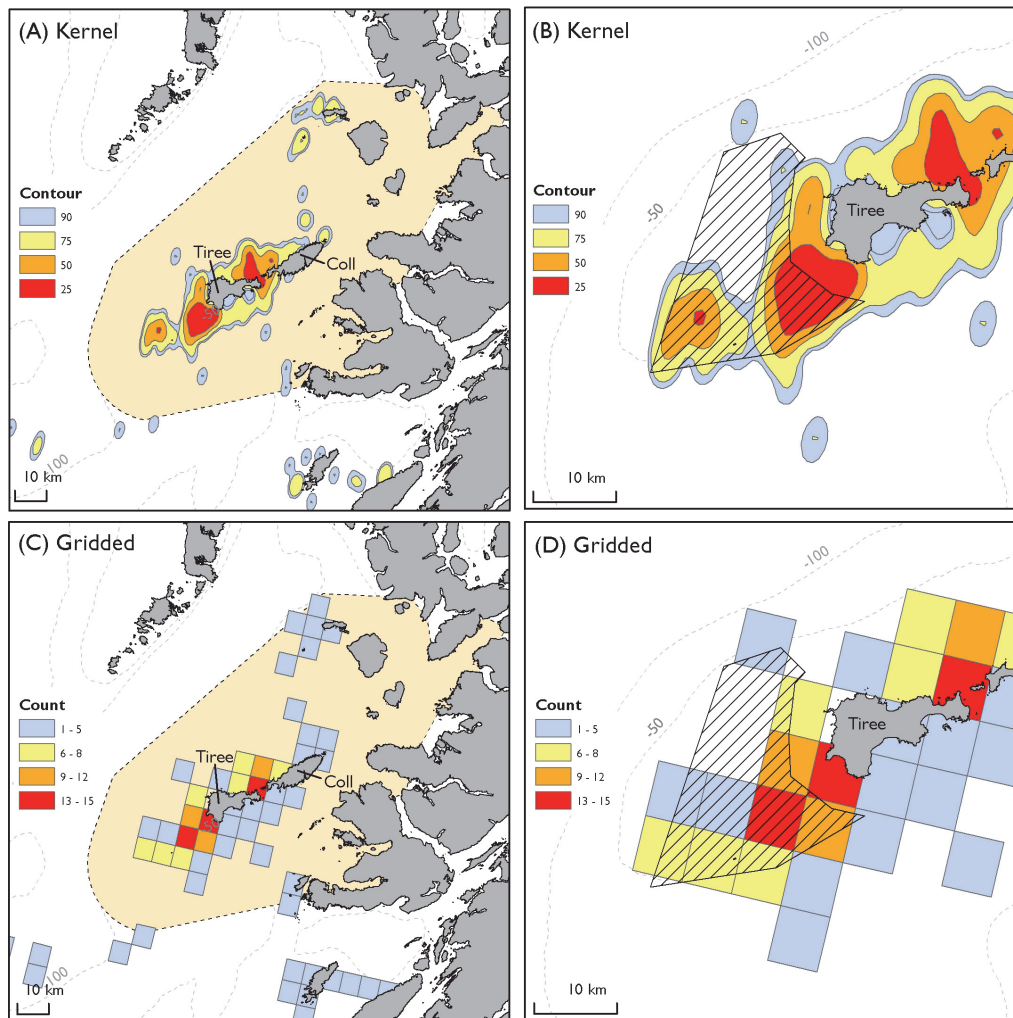


Figure 5. Identifying areas of high relative importance. Density estimation techniques applied to the first 28 days of satellite tracking data from SPOT-tagged basking sharks (n = 8), using single daily highest quality locations for each basking shark (total locations n = 177). (A) Density estimated using quartic density kernel, displaying regions of density circumscribing the upper 25th, 25-50th, 50-75th and 75-90th most aggregated data, with respect to the Skye to Mull MPA search location (beige filled polygon) and (B) with respect to the proposed Argyll Array (hatched polygon). (C) Density estimation using a simple grid cell point counting technique with respect to the Skye to Mull MPA search location and (D) with respect to the proposed Argyll Array (D). 50 m and 100 m depth contour (labelled grey broken line; source GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.

This procedure was repeated using location data from four basking sharks (SPOTs: 119854, 119856, 120496 and 120499) who's SPOTs functioned throughout the first four months of tracking (July to October), and remained in waters to the west of Scotland (Fig. 6). The core areas identified in this subsequent analysis broadly remained within the MPA search location, however, smaller and less dense areas of aggregated location data occurred outwith the bounds of this area, such as off the Isles of Jura, Colonsay and Islay (Fig. 6).

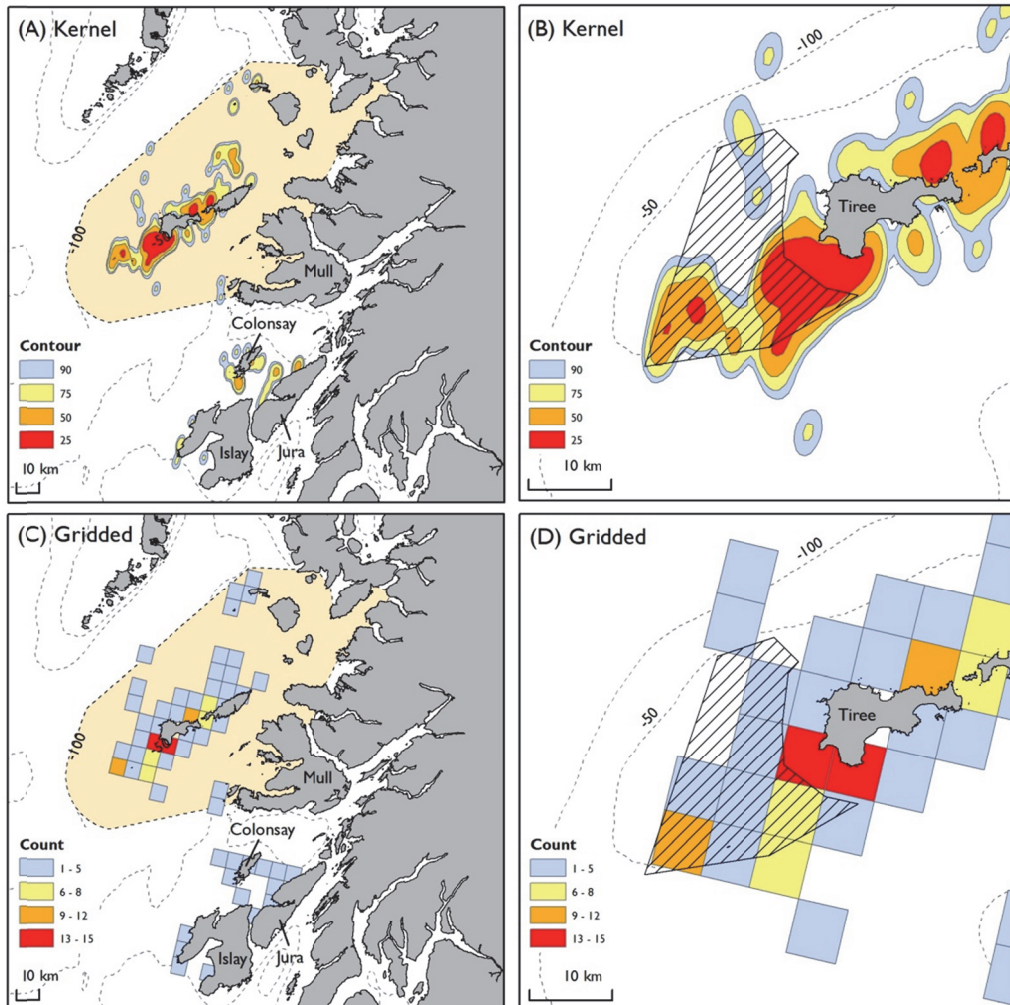


Figure 6. Identifying areas of high relative importance. Density estimation techniques applied to satellite tracking data from four SPOT-tagged basking sharks received between July and October, using single daily highest quality locations for each shark (Tag IDs: 119854, 119856, 120496 and 120499, which provided the most continuous data in the coastal zone: total locations $n = 819$). (A) Density estimated using quartic density kernel, displaying regions of density circumscribing the upper 25th, 25-50th, 50-75th and 75-90th most aggregated data, with respect to the Skye to Mull MPA search location (beige filled polygon) and (B) with respect to the proposed Argyll Array (hatched polygon). (C) Density estimation using a simple grid cell point counting technique with respect to the Skye to Mull MPA search location and (D) with respect to the proposed Argyll Array (D). 50m and 100m depth contour (labelled broken grey line; source GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.

3.4 Long-range movements of basking sharks

SPOTs on two basking sharks functioned for sufficient time to reveal insights into long-distance migration. Basking sharks travelled south-west for approximately 3300km and

3400km (minimum along-track distance) through Spanish and Portuguese national waters to the coast of North Africa (Fig. 7). The tags eventually ceased transmission in Madeira and the Canary Islands, 322 days and 132 days later. These represent the first detailed tracks of basking sharks moving long distances from summer foraging grounds to putative overwintering grounds at more southerly latitudes.

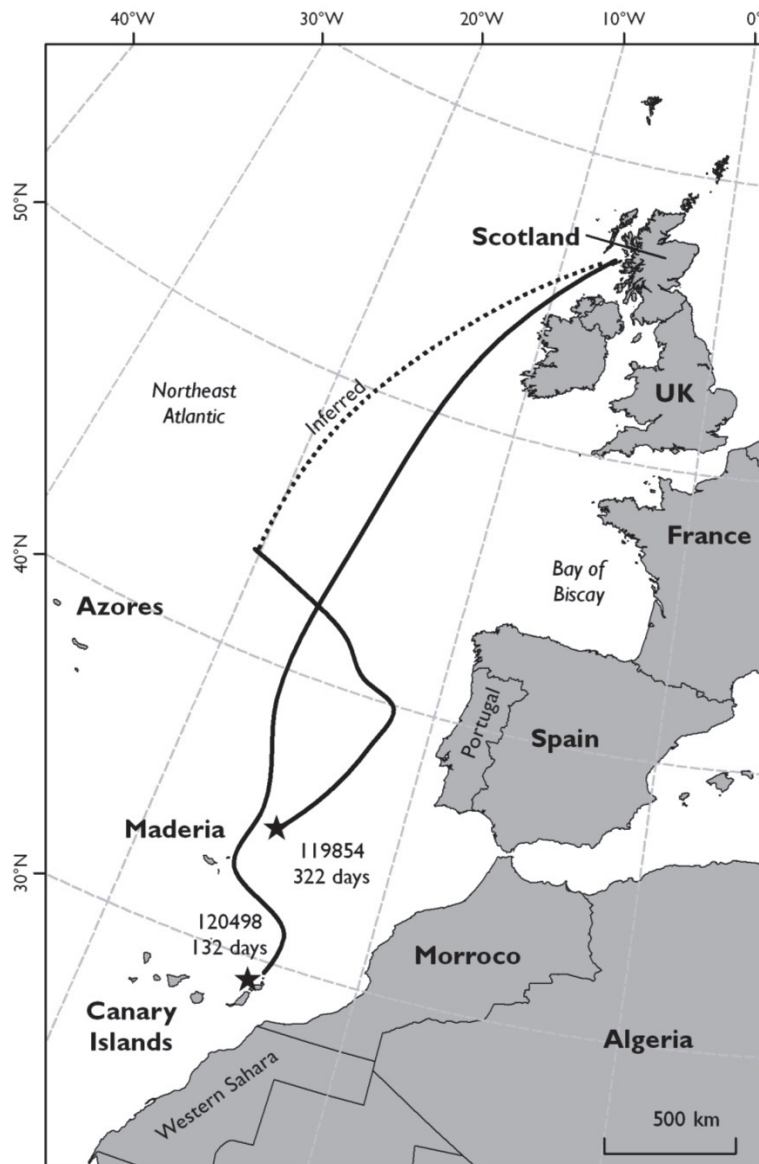


Figure 7. Long-range movements of two basking sharks (Tag IDs: 119854 and 120498) from Scotland identified from SPOTs. Tracking duration (days) indicated next to tag ID.

3.5 PAT-F tag overview

Twelve PAT-F tags were deployed on basking sharks during summer 2012 and eight of these successfully transmitted archived data following programmed ($n = 1$) or early ($n = 7$) detachment (Fig. 8; Table 1). All PAT-F tags were programmed to detach after a 280-day deployment, however, two released 19 days following deployment (cause unknown). Immediately following detachment, PAT-F tags were located in the Sea of the Hebrides ($n = 3$; attachment durations less than two months), in the northern Irish Sea ($n = 3$; attachment

durations between four and six months) and west of Ireland (n = 2; attachment durations approx. seven and nine months). Two of these eight PAT-F tags (Tag IDs: 119853 and 119845), were found by members of the public during the summer of 2013 (Table 1); both were discovered on western shores of Ireland. These tags detached some miles offshore to the west of Ireland four to five months prior to them being discovered.

A ninth PAT-F tag (Tag ID: 119842; Table 1) was found by a member of the public on the 1st of June 2013 close to Portavadie, Loch Fyne; Argyll (Fig. 8; green filled circle). This tag had failed to transmit but had successfully stored all depth and location data, which were subsequently downloaded. The tag functioned from deployment on the 20th of July 2012 through to the 26th of August 2012 (n = 37 days data). The cause of failure was linked to water ingress, which the manufacturer believes is likely due to physical damage. Ten months had elapsed between the tag apparently ceasing to store data and it subsequently being found. The final GPS location from the tag was collected on the 4th of August 2012 within the Firth of Clyde, south-east of the Isle of Arran. The remaining three PAT-F tags failed to transmit any data (Table 1).

Estimates of location based on light-level recordings will require further filtering and full analysis before migratory routes can be determined; these routes are likely to feature in the final project report.

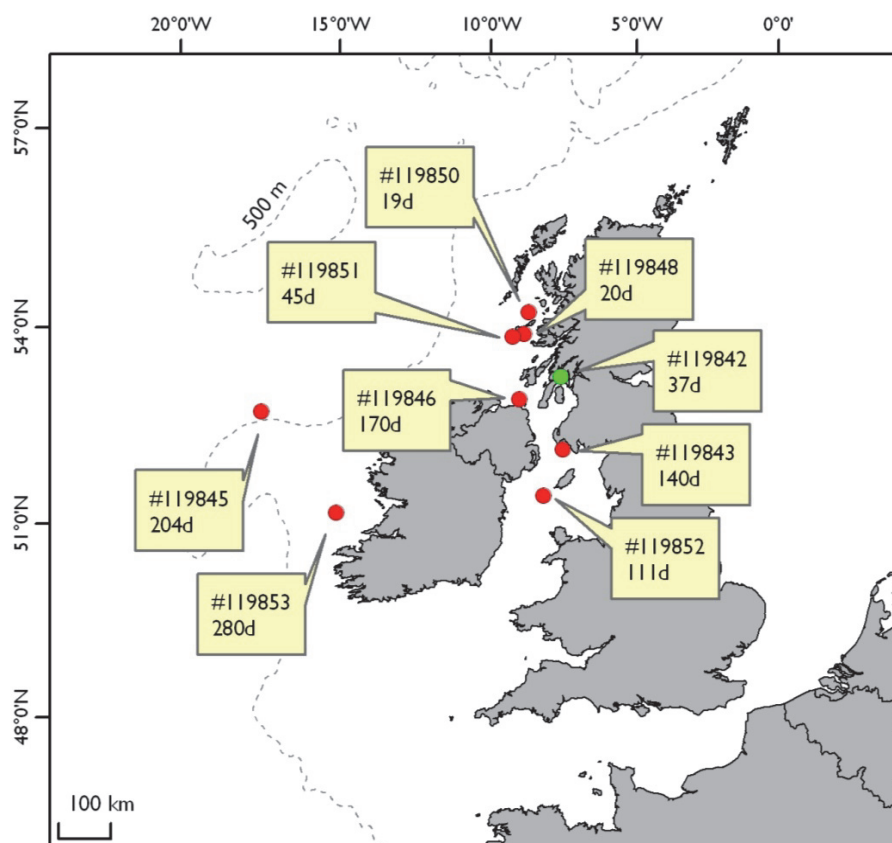


Figure 8. PAT-F detachment locations and the location of a retrieved PAT-F tag that did not transmit. Pop-off locations of eight PAT-F tags (red filled circles); retrieval location of PAT-F (Tag ID: 119842; green filled circle). Attachment durations (days) detailed with tag ID. 500m depth contour (labelled broken grey line; source GEBCO).

3.6 PAT-F tag and Fastloc™ GPS locations

The majority ($n = 55$) of Fastloc™ locations ($n = 71$) were recorded while basking sharks occupied coastal waters of western Scotland, including the Sea of the Hebrides and the Firth of Clyde (Fig. 9). PAT-F tags provided 8 ± 9 (mean \pm SD) Fastloc™ GPS locations for each shark over the total deployment (range 1 to 30 locations). Four PAT-F tags provided seven or more GPS location estimates over the study period (Tag IDs: 119842; $n = 8$, 119846; $n = 13$, 119851; $n = 7$ and 119853; $n = 30$) (Fig. 9). The remaining tags ($n = 5$) provided between one and four GPS locations (Fig. 10). Most GPS locations were obtained between July and September 2012 ($n = 55$ locations, $n = 9$ sharks), with the exception of data received from PAT-F 119853, which continued to collect GPS data until March 2013 (Fig. 9D). This tag detached as programmed on the 2nd of May 2013; two months after the final GPS location was received.

GPS locations collected by PAT-F tags occurred infrequently through time, preventing a more robust assessment of the duration that these sharks spent within the spatial extents of the Skye to Mull MPA search location and the proposed Argyll Array. However, of all positions received in the period from deployment till the end of September ($n = 55$), 81.8% of locations ($n = 45$) occurred within the MPA search location. Locations occurring outside the MPA search location occurred to the south-west of Mull, in the Firth of Clyde and in northern Irish Sea, and occurred, for the majority, from October onwards.

Fewer Fastloc™ GPS locations were received than anticipated, particularly in comparison to the number of locations created by SPOTs. This may have been due to insufficient buoyancy of the PAT-F tag, reducing the amount of time that the tag could acquire GPS signals.

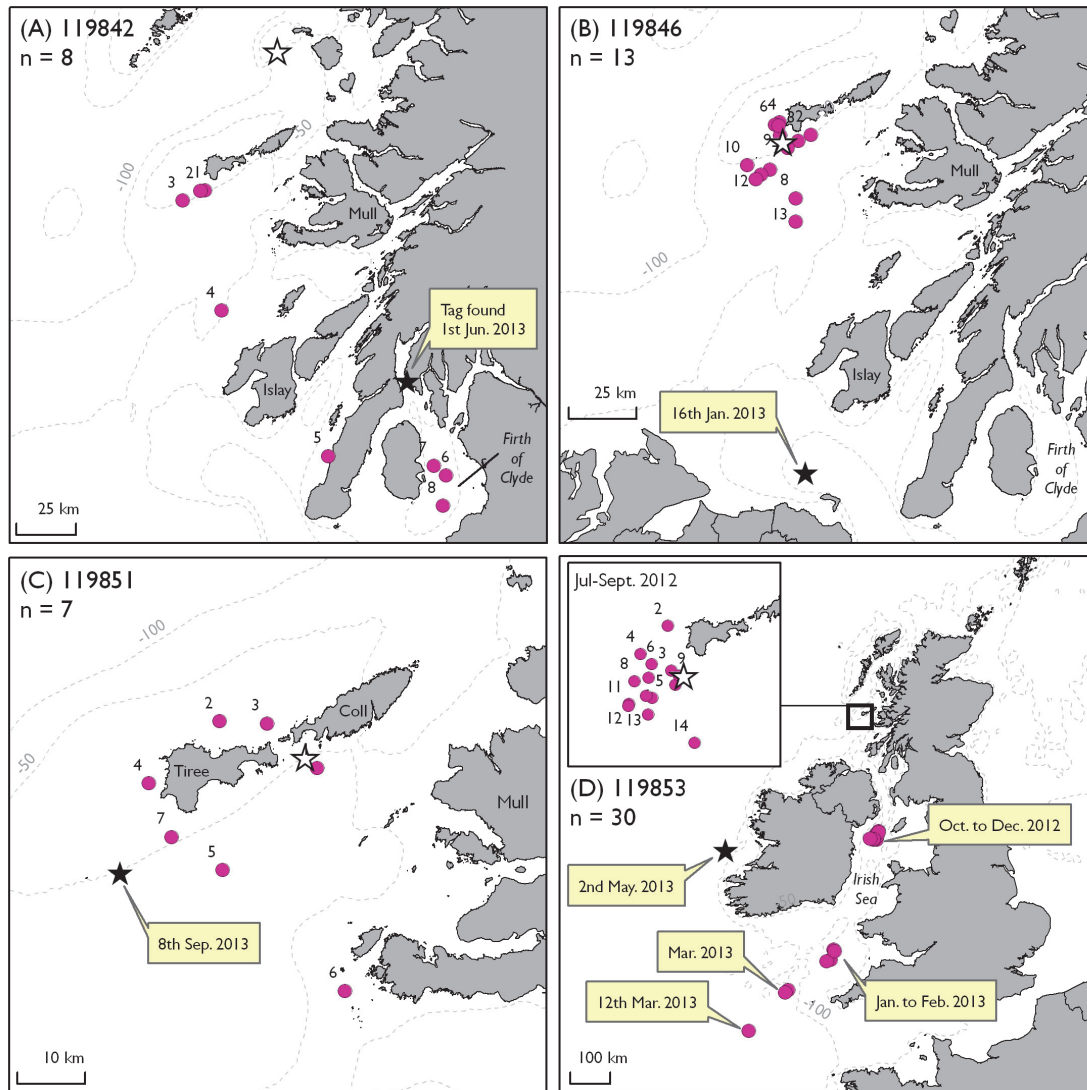


Figure 9. GPS locations of basking sharks. GPS locations gathered for basking sharks (Tag IDs: 119842, 119846, 119851 and 119853) tagged with PAT-F tags. PAT-F tag attachment locations (empty stars), PAT-F tag pop-off locations derived from first received Argos location following detachment (filled stars). GPS locations are sequentially numbered in time order of occurrence. Number of locations given with each tag ID. 50m and 100m depth contour (labelled broken grey lines; source GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.

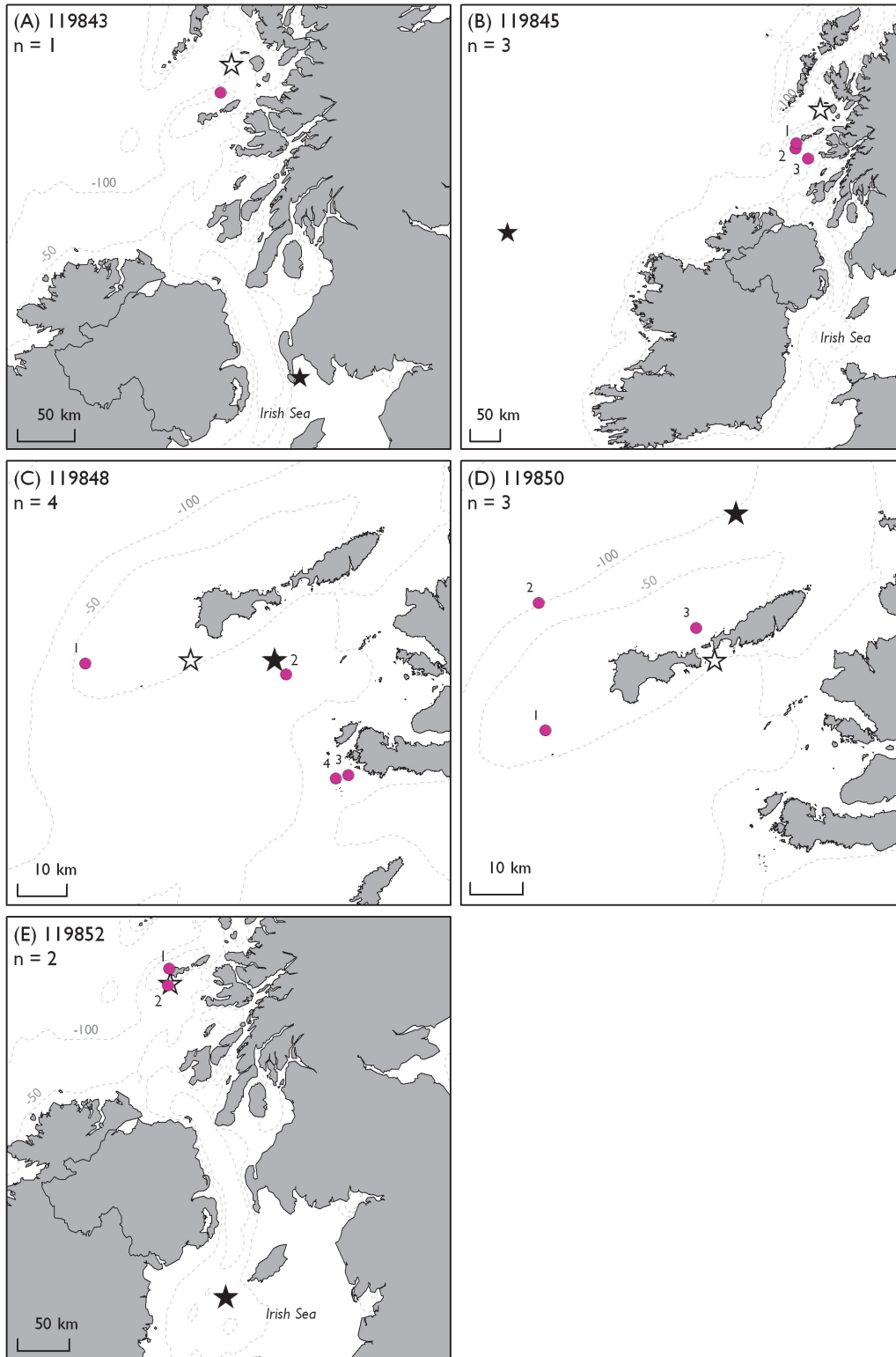


Figure 10. GPS locations of basking sharks. GPS locations gathered for sharks with PAT-F tags producing four or less locations for each shark (Tag IDs: 119843, 119845, 119848, 119850 and 119853). PAT-F tag attachment locations (empty stars), PAT-F tag pop-off locations derived from first received Argos location following detachment (filled stars). Number of locations with tag ID. 50m and 100m depth contours (labelled broken grey lines; source GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.

3.7 PAT-F tags and mapped depth-use behaviour

Using data from PAT-F tags, it was possible to map the GPS locations of basking sharks and associate these to contemporaneous data on depth-use. This was achieved using thirty-eight 4-hour summarised estimates of depth-use from six basking sharks (Figs. 11 and 12). These are the first spatially linked depth-use data for basking sharks to the authors' knowledge.

Data suggested that sharks were likely occupying sea bed depths for at least some part of each 4-hour depth-use period as maximum depths recorded on the tags were well matched to concurrent charted seabed depth (Fig. 11). Analysis of modal depth-use (Fig. 12; the most frequent depth class occupied) provide tentative insight into why the areas around Coll and Tiree appear to support appreciable sightings of basking sharks (Speedie *et al.*, 2009; Witt *et al.*, 2012). In these areas, there is a high occurrence of near-sea surface use, with the modal depth-use being predominantly 1-5m (Fig. 12). However, this should be cautiously interpreted as the temporal scales of Fastloc™ GPS locations (gathered within a few milliseconds) and depth-use data (summarised over a temporally coincident 4-hour period) are clearly very different, such that sharks may have moved away from the area in which the GPS location was collected. The approach may also show bias, particularly for modal depth, where we have mapped those 4-hour summary periods containing a GPS location, which by their nature require at least some time near the surface (to gather the GPS location).

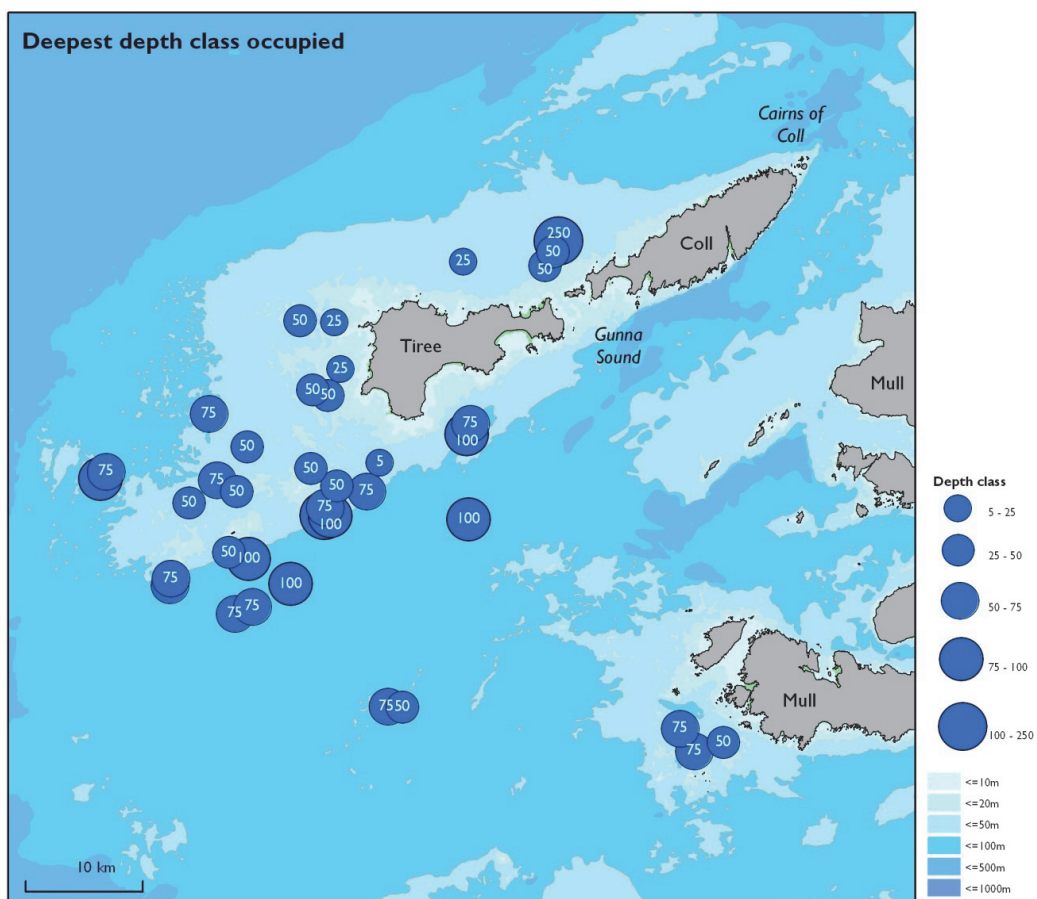


Figure 11. Depth-use with a geographical context. Deepest depth class occupied at given locations from data recorded by PAT-F tags from July to September 2012 ($n = 38$ locations from six basking sharks) mapped using temporally coincident GPS locations. Numbers in blue circles represent the maximum depth for that 4-hour summary. Bathymetry (source Digimap Marine). Contains Ordnance Survey data © Crown copyright and database right 2013.

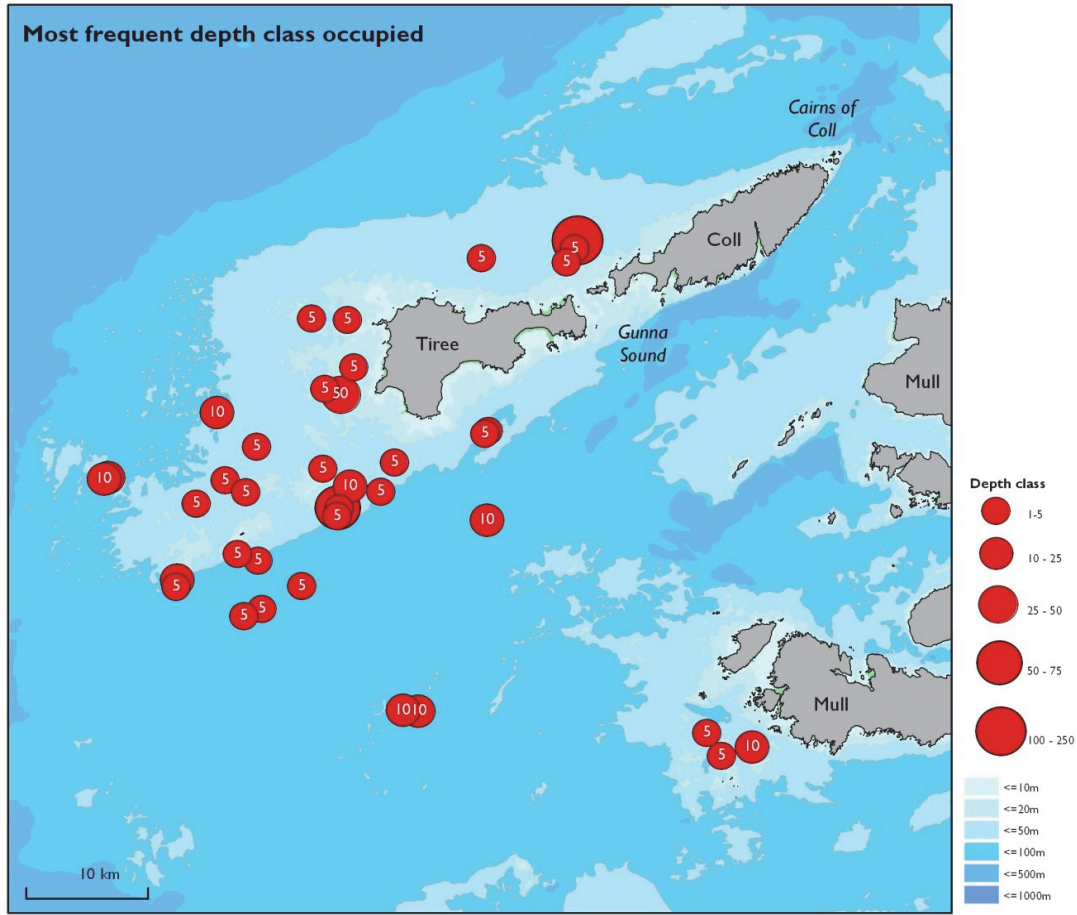


Figure 12. Depth-use with a geographical context. Most frequent depth class occupied at given locations from data recorded by PAT-F tags from July to September 2012 ($n = 38$ locations from six basking sharks) mapped using temporally coincident GPS locations. Numbers in red circles represent the modal depth for that 4-hour summary. Bathymetry (source Digimap Marine). Contains Ordnance Survey data © Crown copyright and database right 2013.

3.8 Depth-use by basking sharks

Analysis of depth-use data without respect to location, i.e. depth-use data that are not spatio-temporally coincident to collection of an Argos or GPS location, permits further insight into basking sharks' depth preference. Four sharks with PAT-F tags that collected data for the longest periods appeared to make use of a range of depths from 1 to 5m, up to a maximum depth-use of 1,000m or more (Fig. 13). Depth-use histograms (Fig. 13) suggest bimodality in depth selection, with the majority of peaks within the 1m class and within classes between 25 to 100m depth; although one shark spent most of its time within the 100 to 250m depth class (Fig. 13 D). Near-surface depth-use, along with behavioural observations during fieldwork (unpublished) and previously published data (Speedie *et al.*, 2009) is suggestive of surface foraging. It is not possible with the present dataset to infer what behaviours take place at the 25 to 100m depth categories.

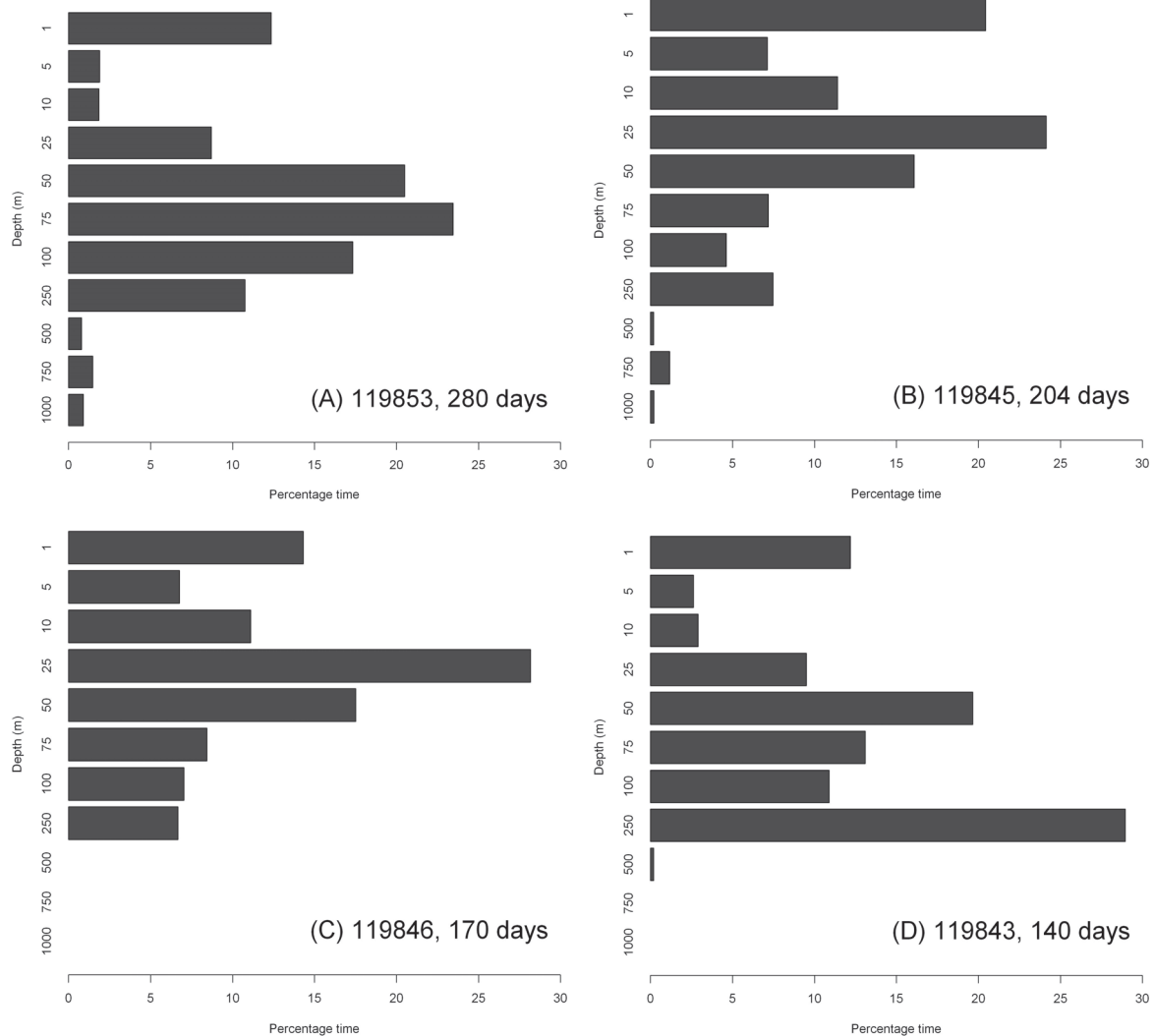


Figure 13. Percentage of time spent in depth categories. Depth-use from PAT-F tags deployments for four tags with the longest attachment durations. Number of days data are indicated alongside tag ID. The maximum depth of each depth class is given on Y-axis.

3.9 Depth-use with time of day in the coastal zone

Depth-use behaviour with respect to time of day in near-surface waters (<10 m depth) was analysed using data from the first 28 days of tracking. Interim analysis suggests that basking sharks ($n = 9$) were more likely to be near the surface (<10m depth) at night than during the day (Fig. 14; $n = 132$ 4-hour data summaries; 15 ± 6 summaries from each shark [range 3 to 18 summaries per study animal]). Basking sharks tagged with PAT-F tags spent $33 \pm 13\%$ of time (grand mean across individuals) between the surface and 10m depth between 20:00h and 04:00h (GMT) as compared to $9.5 \pm 4.5 \%$ of time (in depths of 10m and less) between 12:00h and 16:00h (GMT).

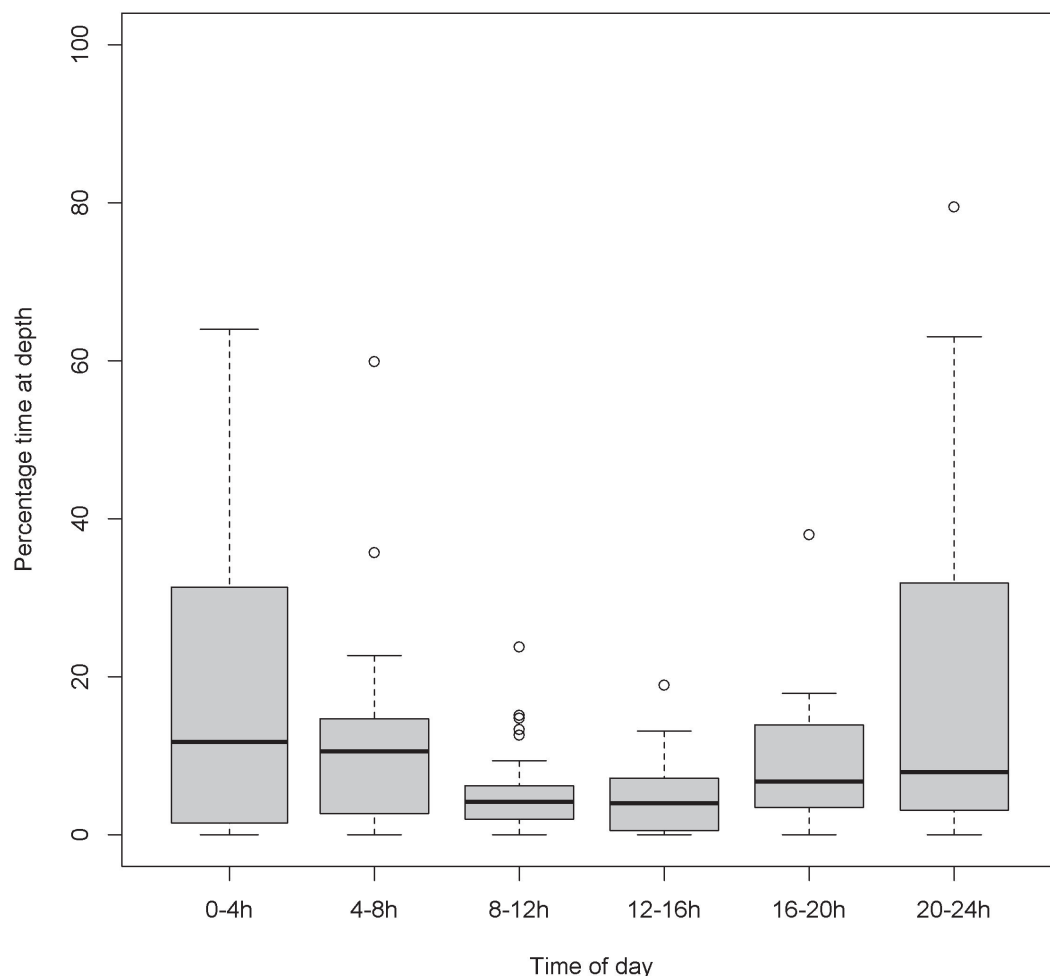


Figure 14. Basking shark depth-use behaviour with time of day within the Inner Hebrides. Percentage time spent between the surface and 10 m depth within the first 28 days of PAT-F tag deployments ($n = 9$ basking sharks) summarised at 4-hour intervals. Each vertical box represents the range of values observed from received data (25th and 75th percentiles) for the relevant time period. The bold horizontal line represents the median value for each vertical box. Dashed vertical lines extending from the top and bottom of the boxes (the hinges) indicate the range of values in the distribution to the 2.5th to 97.5th percentiles. Open circles represent outliers; these are values occurring outside the 2.5th and 97.5th percentiles of data distribution.

3.10 Longer-term patterns of depth-use

PAT-F tags from four basking sharks transmitted data series with durations of more than 100 days (Fig. 15), allowing the reconstruction of detailed time-series of depth-use. Data showed a pattern of depth-use predominantly <250m with intermittent periods of deep-water occupation (> 750m depth) (Fig. 15). Two sharks (Tag IDs: 119845 and 119853) attained maximum depths of 1000m (24th of January 2013) and 1073 m (3rd of April 2013) respectively. These deeper water events can only have occurred off the European continental shelf. Estimates of location from light-levels are currently being analysed and will hopefully be used to map the general geographic area of wintertime movements and will feature in the final report. Depth-use data indicate the potential for offshore movement, or movement to deeper waters, between late September and early October; at this time, four basking shark's depth-use extended to approximately 250m, having previously exhibited depth-use generally <150m (Fig. 15 A-C and E). Depth-use behaviour from sharks with shorter tag attachment periods (a few days to a few months) showed depth-use predominantly <100m, suggesting movements might be constrained to the continental shelf (Fig. 16).

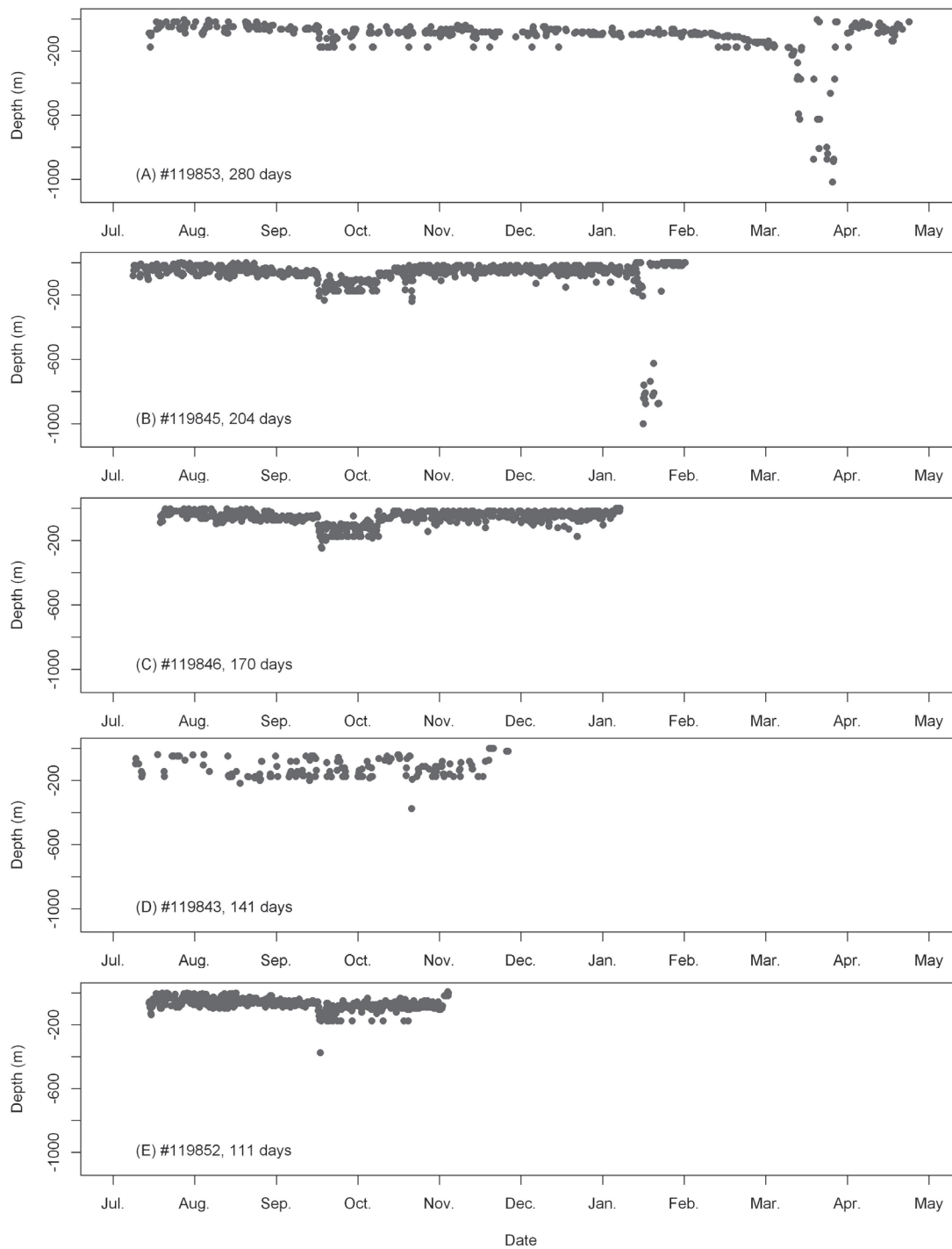


Figure 15. Maximum depths recorded at 4-hour intervals. Maximum depths (filled circles) from 4-hour summary intervals [non-contiguous] from five of the longest depth-use time series collected by PAT-F tags. Tags sorted by decreasing attachment duration.

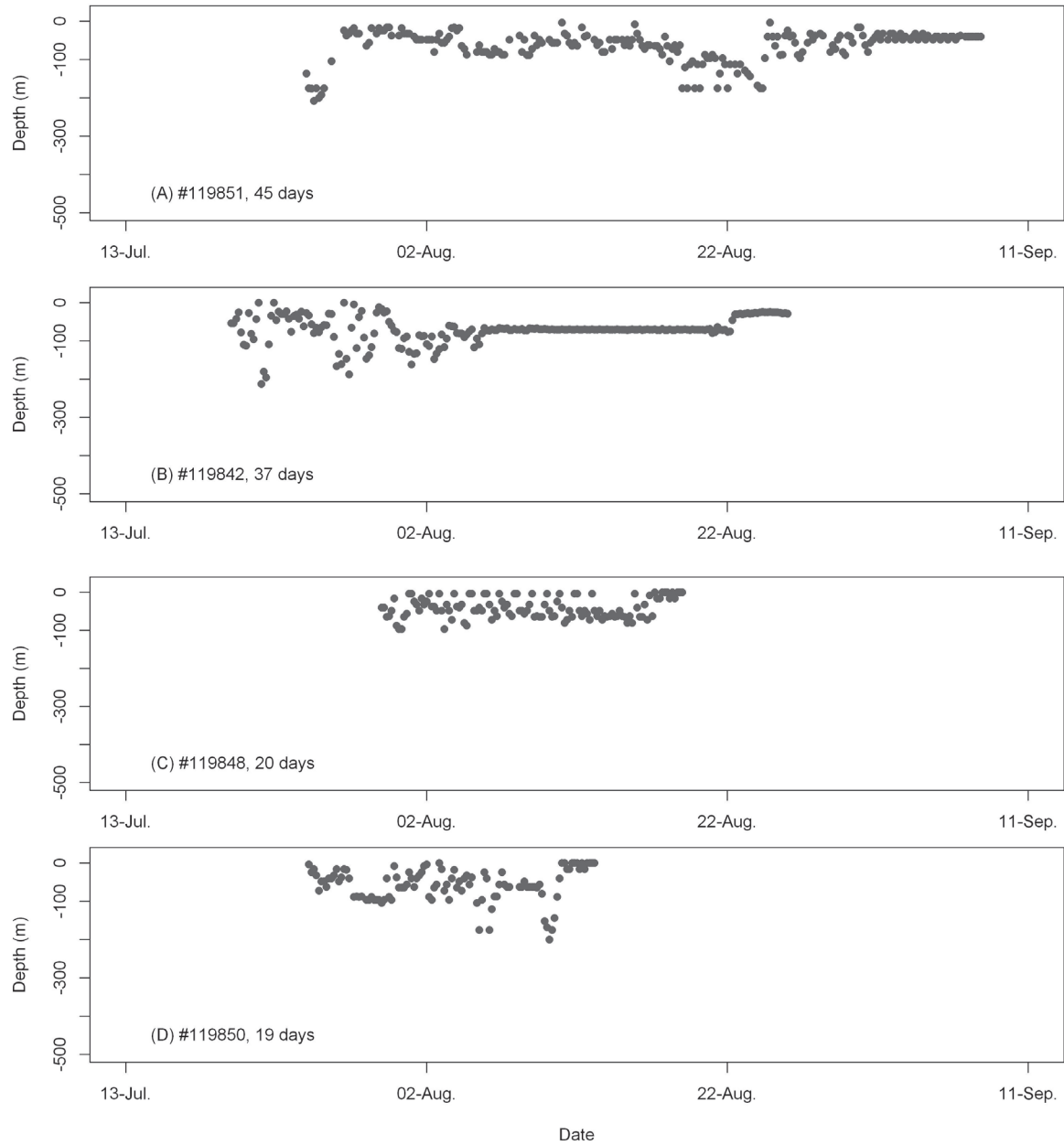


Figure 16. Maximum depths recorded at 4-hour intervals. Maximum depths (filled circles) from 4-hour summary intervals [non-contiguous] collected by PAT-F tags. Tags sorted by decreasing attachment duration. Data from tag 119842 (B) after early August require further investigation.

4. DISCUSSION

4.1 Overview

The combined deployment of SPOT and PAT-F tags has provided detailed insights into the spatial and temporal movements and depth-use behaviour of basking sharks occupying the coastal regions of the Sea of the Hebrides and beyond. The present study is the first, to the authors' knowledge, to deploy both tag types on basking sharks within a single season and has thus permitted for insight into basking shark behaviour. In particular, the present study is the first to spatially link, GPS and depth-use data for basking sharks. Satellite tracking of large marine vertebrates is particularly challenging, from a number of perspectives; including cost, logistics, operating conditions, technology and technical expertise. The successes of the project to date are far from trivial and represent an exceptional effort on behalf of all involved parties.

4.2 Basking shark movements

4.2.1 *The Sea of the Hebrides*

Most satellite-tagged (SPOT) basking sharks were to be found within the Sea of the Hebrides for several months following tag attachment, although two individuals moved away from the area soon after tags had been deployed. Basking sharks tagged with PAT-F tags remained within the MPA search location between Mull and Skye during the summer months (at least July to September), although two individuals moved further south. Location data from PAT-F tags and SPOTs, and depth data from PAT-F tags, indicate the start of offshore movements in at least some individuals occurs around September and October. Data from the satellite-tracking project are generally supportive of previous sightings-based work (Witt *et al.*, 2012) and boat-based transect surveys (Speedie *et al.*, 2009)

4.2.2 *Site fidelity*

SPOT location data highlighted some level of site fidelity (or residency), which in the context of this report entails remaining faithful or resident to an area over an extended period of time, e.g. weeks to months. Residency of individual basking sharks at sites around Coll and Tiree, and to a lesser extent Gunna Sound, appeared to be on the order of several months, but with marked individual variation, e.g. some basking sharks tracked with SPOTs departed the area only a few days following tag attachment. PAT-F tag detachment locations for basking sharks with shorter tracking durations (a few weeks to a few months) suggest these individuals did not range particularly far from their tagging location either (tens to a few hundred kilometres maximum) and that they likely move offshore during autumn and winter.

4.2.3 *Key areas of basking shark occurrence*

SPOT location data indicated several areas of high relative density, most significantly the area to the west of Tiree and in Gunna Sound, which appears to be a regional hotspot for basking shark occurrence. The relative importance of the region is, however, likely to vary year-on-year due to the environmental effects on copepod plankton distribution and abundance, the main prey type of basking sharks (Matthews & Parker, 1950; Sims 2008). Smaller areas of higher density occurred along shores of other islands of western Scotland, although these typically represented only single sharks that exhibited prolonged residency to such locations. It should be noted that the present dataset does not inform on inter-annual space use, individually or across the population. Estimating regions of high relative density in this report is restricted to a small number of animals, representing a small proportion of the number of sharks that visit western Scotland each year (unknown pop. estimate), as such, we caution about generalising from the findings in the report.

4.2.4 Long-distance migrations

Two individuals tagged with SPOT in 2012 were tracked migrating southwards to Madeira and the Canary Islands, the first time to the authors' knowledge that such a detailed route has been described.

4.2.5 Knowledge gaps

1. It is not clear what biotic and abiotic factors influence apparent residency of basking sharks to Scottish waters and how future change, e.g. climate change or changes in fisheries practices, might impact their distribution. Satellite-tagging projects provide an important avenue for a more detailed examination of environmental preference and results from tags deployed in 2012 have enabled a simple first description of environmental preference. Detailed predictive habitat modelling for basking sharks would be advantageous from a wildlife management perspective and is best achieved using multi-year tracking datasets.
2. As yet, a robust understanding of the spatial and temporal scale of residency of basking sharks to Scottish waters does not exist, although efforts in 2012 provide a valuable first insight for basking sharks tagged within the Sea of the Hebrides.
3. Owing to limited tracking durations, it is not possible to ascertain whether the majority of tagged basking sharks would have made long-distance migrations south to the Canaries and Madeira as were seen for two individuals. Current data cannot inform what the function of the migration might be (for example, reproduction) and how often it might occur. Future tracking work should aim to deploy devices for longer durations to investigate these important questions.

4.3 Basking shark depth-use

4.3.1 Diel vertical behaviour in coastal waters

Depth-use data collected by PAT-F tags suggest that basking sharks, occurring within the footprint of the MPA search location between Mull and Skye exhibit diel vertical behaviour: being typically deeper than 10m during the day and shallower than 10m at night. Any consistent depth preferences displayed by basking sharks could be significant in interpreting boat-based survey sightings and in understanding the possible interactions between basking sharks and other marine users.

4.3.2 Depth-use: surface and 1000m depth

Data highlighting the modal depths used by basking sharks in coastal waters around Coll and Tiree support the observed high incidence of surface feeding in these regions, which may be why public sightings are so numerous in the area (Witt *et al.*, 2012). Over the longer-term (months), PAT-F tag depth data suggest basking sharks predominantly occupy the upper 250m of the water column, but have the capacity to undertake extensive vertical movements to 1,000m depth.

4.3.3 Knowledge gaps

1. Without higher resolution movement and physiological data (for example, accelerometry and body temperature) it is not possible to interpret further what function the depth-use behaviour observed in the present study might play.
2. For example, while it is highly likely that very shallow depth-use is consistent with observed foraging patterns for this species, it is not clear whether use of much greater depths (several hundred metres to over one thousand metres depth) represents a different foraging pattern, predation avoidance, competitive exclusion, temporary resting,

or even hibernation, as has been previously hypothesised for this species (Parker & Boeseman, 1954).

5. LIMITATIONS

The basking shark satellite-tracking project in 2012 successfully collected an unprecedented volume of SPOT-derived location data (several thousand locations) but less location data from PAT-F tags than had been expected. The low number of locations from the majority of PAT-F tags may have been due to a combination of insufficient tag buoyancy and prohibitively fast basking shark movement, both of which most likely led to the tags surfacing less frequently, and thus having reduced opportunity to gather GPS data. Attachment durations for most tags were shorter than expected, which may have occurred for several reasons. For example, short tethers (10s of centimetres) are typically used for conventional PAT tags, as the tags do not require access to the sea surface. In these situations deployments can regularly exceed 200 days (Stéphan *et al.*, 2011). PAT-F tags in the present study, however, used embedded GPS technology and as such tags required longer tethers, permitting access to the sea surface to collect locations. Longer tethers might be expected to have increased risk of entanglement (for example with fisheries gear), which may prematurely detach tags, reducing attachment durations. Other reasons for premature tag detachment may include bio-fouling, boat strike or dart rejection by the shark, but without more detailed information it is not possible to ascertain fate for individual sharks. It is extremely challenging to re-sight individual sharks (without the use of radio tracking technology) and to monitor the success of different attachment methods, meaning that improvements to tag attachment technology are generally slow for a wide range of animal taxa (Hazen *et al.*, 2012). The present study has attempted to ameliorate such impacts by liaising with the Isle of Man Basking Shark Tracking Project to share information about best tag attachment practice and the project also has a working relationship with the tag manufacturer (Wildlife Computers; Washington, US) facilitating feedback into future, and more successful, tag design.

When interpreting data from this report we caution that tagging studies are methodologically biased to only describing animal behaviour at sites where tags are deployed. Deployments of tracking technologies on basking sharks elsewhere may thus demonstrate other, novel behaviours. This is a perennial challenge for animal tagging studies and is not easy to overcome although is significantly reduced through increased sample size and number of deployment locations. Tagging efforts for this project were concentrated on areas where large numbers of basking sharks could be located so as to increase the likelihood of successfully deploying equipment. Deploying tags in areas of low shark density would have led to prohibitively expensive boat-charters and increased costs associated with staff-time.

6. CONCLUSIONS & FURTHER WORK

The results of satellite tracking have progressed our understanding of basking shark movement and distribution in the Sea of the Hebrides and some broad patterns of behaviour have emerged, including diel vertical migration, and spatial residency, but still substantial individual variation exists. Further tagging efforts in 2013 will increase the sample size of the project and will hopefully provide initial insights into inter-annual variation in behaviour.

The final report of the project due in March 2014 will provide additional insight on several fronts, notably:

- 1) Detailed analysis of depth-use behaviour across all individuals fitted with PAT-F tags.
- 2) Analysis of light-based geolocation data to identify geographic regions associated with post-summer seasonal movements.
- 3) Integration of GPS location datasets gathered from PAT-F tags (in 2012) and SPLASH-F (in 2013) to further develop site fidelity assessment. Initial data from SPLASH-F shows them to have performed exceptionally well; particularly in terms of the volume GPS locations produced and consequently the improved capacity to map depth-use behaviour.
- 4) Merging of SPOT data collected from 2012 ($n = 8$) with those collected in 2013 ($n = 15$), thereby providing an inter-annual assessment of sites of high relative abundance.
- 5) Analysis of depth data from SPLASH-F, four of which were deployed in 2013.
- 6) Zooplankton sample analysis to indicate the abundance and species of zooplankton in the areas sharks were tagged during 2012 and more widely in the study area from samples in 2013.
- 7) More advanced descriptions of basking shark associations with environmental parameters, i.e. seabed types, temperatures, tides etc.

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