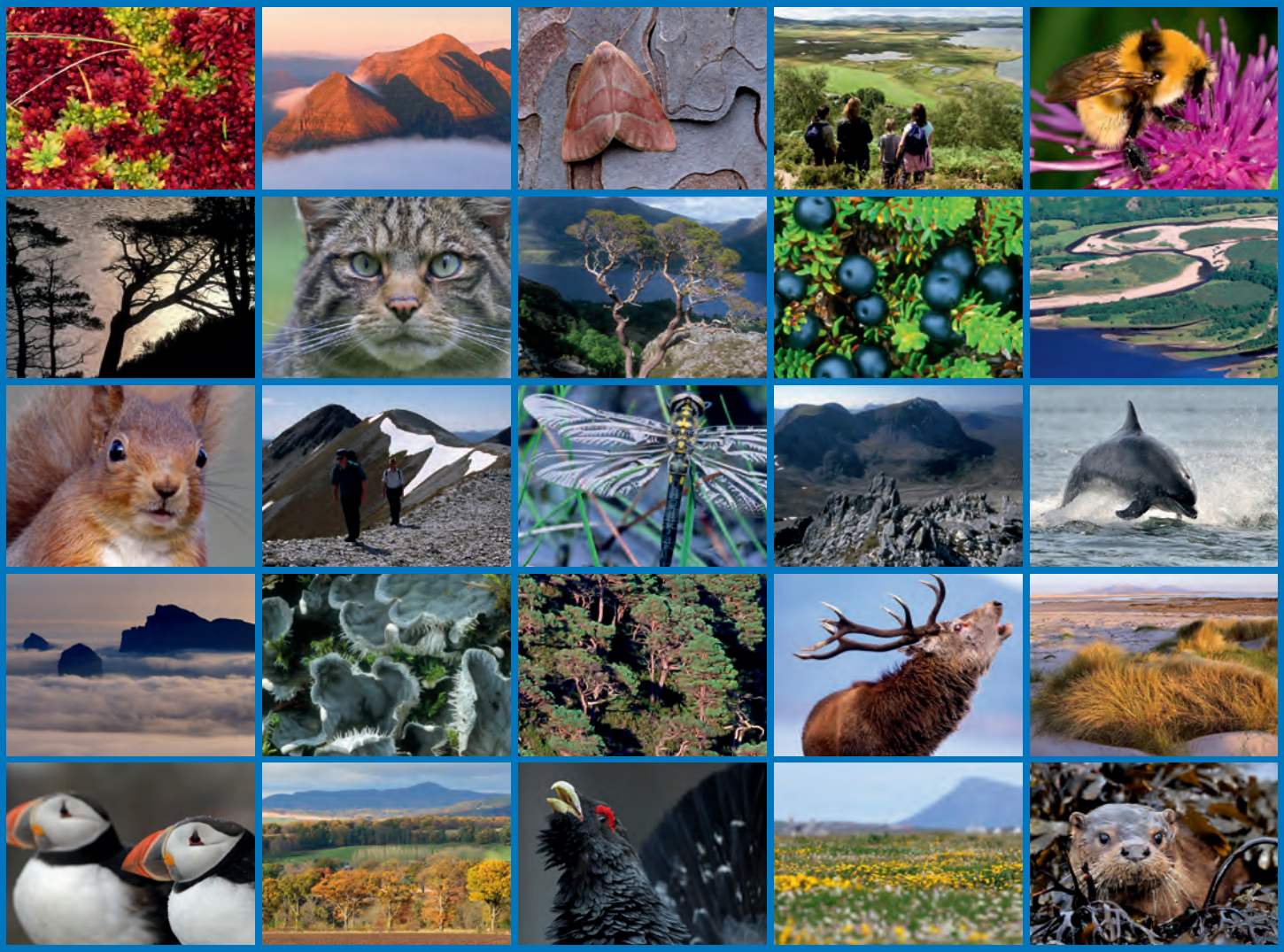
Scottish Natural Heritage
Commissioned Report No. 752

Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement, distribution and behaviour using satellite telemetry (Phase 1, July 2014)



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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 (Phase 1, July 2014)

For further information on this report please contact:

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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 (Phase 1, July 2014)

Commissioned Report No. 752
Project No: 14082
Contractor: University of Exeter
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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 (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 perceived social behaviours, such as breaching and in courtship-like aggregations in this area. This evidence highlights that the area may be important for key life cycle stages of basking sharks. 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 and 2013. This report provides analyses, interpretation and comment on data resulting from two years of tag deployments, with particular focus upon basking shark movements within the Sea of the Hebrides and the Skye to Mull MPA search location. These data enhance the evidence-base upon which decisions may be made in relation to the spatial scale of the search location and the contribution that any site may make to the conservation of basking sharks.

Main findings

- Satellite tagged basking sharks demonstrated high levels of site fidelity to waters around Coll, Tiree and Hyskeir during summer months (July to September) of 2012 and 2013.
- Approximately 85% of basking shark locations occurred within the Skye to Mull MPA search location, likely signifying an area of high importance to basking sharks.
- Basking sharks occupy shallow coastal waters during summer months, predominantly using surface waters, but move to deeper waters from autumn onwards.
- Interpretation and conclusions presented in this report are based on initial analyses of collected data, with some aspects of analysis focusing on data collected over short periods of tracking.
- 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 south-west England.

- 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.

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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.

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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 function of these migrations is unknown. This species is an obligate ram-feeding zooplanktivore. The species is slow to mature and has low fecundity, which has made the species slow to recover from 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 (reviewed by Sims (2008)), 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).

Population size estimates for the basking shark in the north-east Atlantic are unknown, with tracking efforts to date (Sims *et al.* 2003, Stéphan *et al.* 2011) demonstrating short-term movements (months) on the north-east Atlantic continental shelf but as yet no detailed description of broad-scale movements for multiple individuals, or repeatability of annual cycles, exists. The capacity for basking sharks to undertake transatlantic and transequatorial movement does however exist (thousands of kilometres; (Gore *et al.* 2008, Skomal *et al.* 2009)). Limited genetic studies have been unable to confidently 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.* 2012), and therefore there is a growing need to better understand the spatial and temporal components of basking shark distribution, abundance and behaviour to better 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 currently under assessment is the Skye to Mull search location - identified for basking sharks and minke whale (*Balaenoptera acutorostrata*) as part of the Scottish Marine Protected Area (MPA) project (Marine Scotland 2011). The Skye to Mull search location was identified in 2012, however further assessment is continuing in light of the results of this report (and other research), and the boundary is likely to change in the advice Scottish Natural Heritage (SNH) give to Marine Scotland in 2014. The 2012 Skye to Mull search location boundary has been used within this study as the assessment work is not completed.

Here we report on 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 refine our understanding of shark movement, behaviour and habitat use. Efforts have focused on three areas for tag attachments; areas to the south and west of Tiree, at Gunna Sound (between the islands of Coll and Tiree) and at Hyskeir (Fig. 1). These areas are known basking shark 'hotspots' within the UK (Speedie *et al.* 2009, Witt *et al.* 2012).

Data gathered by the project contribute 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 protective area might be.

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

- How do basking sharks use the waters around Hyskeir, in Gunna Sound and off south-west of Tiree?
- How long do basking sharks remain in the area?

- Are there any areas that are used to a greater extent than others?
- To what extent do tagged basking sharks use areas outside the MPA search location?

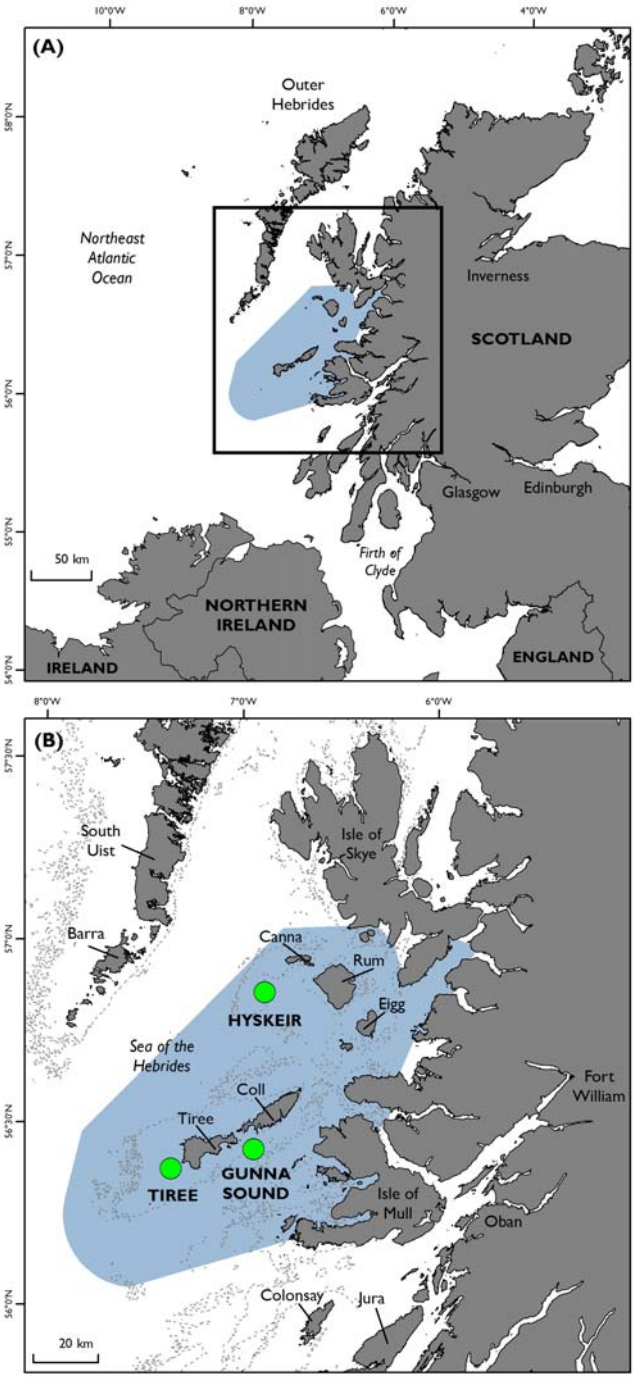

Figure 1. *(A) Study location; west coast of Scotland, showing Skye to Mull MPA search location (blue polygon) in the Sea of the Hebrides and (B) Satellite tag deployment areas in 2012 and 2013 (Hyskeir, Gunna Sound and Tiree; green circles). 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

2. METHODS

2.1 Study area

The deployment of satellite transmitters to basking sharks was undertaken in the Sea of the Hebrides on the west coast of Scotland (Fig. 1A). Boat-based surveys providing effort-corrected estimates of basking shark density have shown that this area has appreciable numbers of sharks throughout summer months (July to September) (Speedie *et al.* 2009). Satellite tags were therefore deployed on basking sharks at three locations, Hyskeir, Gunna Sound and Tiree (north to south) (Fig. 1B); these locations having the highest values of effort-corrected sightings of basking sharks.

Data collected from satellite tags, occurring both within and outwith the study area, are considered in this report, but particular attention is given to data occurring within the Skye to Mull MPA search location.

2.2 Satellite tracking system and light geolocation

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); 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 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. When tags detect they are at the sea surface they 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-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 attached 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 is assigned to 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 having the second highest accuracy (within 500m of true location) and class 1 locations with the lowest accuracy (>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 traditional Argos-based tracking analyses. 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 from the Fastloc™ system has suggested that auxiliary positions may be accurate to within 1km (Witt *et al.* 2010). The current best practice is to retain all locations classes, but then to apply strict quality control, for example using speed and turning angle filtering, eliminating many implausible locations (Witt *et al.* 2010).

Fastloc™ 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 Fastloc™ system was developed, permitting for capture of 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).

Fastloc™, like Argos, has several limitations and an understanding of these is essential before interpreting data; for example, 1) the accuracy of a Fastloc™ location, i.e. how far the estimated location is from the actual location, is determined 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 Fastloc™ data requires considerable power resources; tags fitted with Fastloc™ 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 Fastloc™ position a day. 3) Fastloc™ 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.

Light geolocation

Data on ambient light levels collected by some satellite tags used in the project can be used to estimate the location of study animals while they are below the sea surface, this process is termed 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 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. These 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 marked than in equatorial regions) and in periods of time furthest from solstices (Hill 1994, Hill & 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. 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). Received light level data are currently being analysed and resulting analyses will be shared in the Phase II report.

2.3 Description of satellite tags

SPOT

Smart Position or 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 used in the project can make approximately 65,000 transmissions to the Argos System (locations being derived from at least four or more transmissions). The spatial accuracy of locations varies from 350 to 1000m. Some locations are not accompanied by an estimate of their accuracy. The reliability of these tags permits their wide scale deployment across multiple individuals. 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.

PAT-F

Pop-up Archival Transmitting with Fastloc^{TM} tags (PAT-F; Fig. 2B) communicating with the Argos System were used in this project to collect information on depth use behaviour and the spatial movements of basking sharks using light geolocation and Fastloc^{TM}. PAT-F tags collected data on the ambient environment at 10-sec. intervals, including data on water temperature at 12 temperature bins (-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 pressure (depth). Information on depth use, including estimates of the percentage of time spent at 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 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 collected data after detachment.

SPLASH-F

SPLASH-F tags (Fig. 2C) 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 at 12 temperature bins (-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 Fastloc^{TM} locations (in the same way as PAT-F tags). Information on depth use, including estimates of the percentage of time spent at 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 over-passing satellites during the period while the tag was attached and also after the tag had detached from the study animal. These tags were also programmed to generate continuous time series information on depth use and encountered water temperature at 5-min. intervals. These data were compressed for transmission via the Argos System. SPLASH-F tags were programmed to detach from study animals 45 days after deployment due to battery constraints and the prototype nature of the tags.

MiniPAT

Mini Pop-up Archival Transmitting tags (MiniPAT; Fig. 2D) 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 pressure (depth). Summary data are archived on the tag and summarised at 24-hour intervals and subsequently transmitted to over-passing satellites once the tag had detached from the study animal. MiniPAT tags were programmed to follow either of two deployment schedules; 280-day or 365-day attachment periods. These tags were also programmed to generate information on depth and water temperature at 15-min. intervals. These time series data were optimally

compressed for transmission via the Argos System and represent a relatively new development in data compression and transmission techniques for satellite tags.

All models of satellite tags (Fig. 2) are hydrodynamic in form, 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 prior to deployment. These approaches also help to minimise impact on the study animal while attempting to maximise satellite tag retention. Although tags, i.e. PAT-F, SPLASH-F and MiniPAT, transmit archived data following detachment, if they can be recovered a more detailed time series of data can be downloaded from the tag's physical memory.

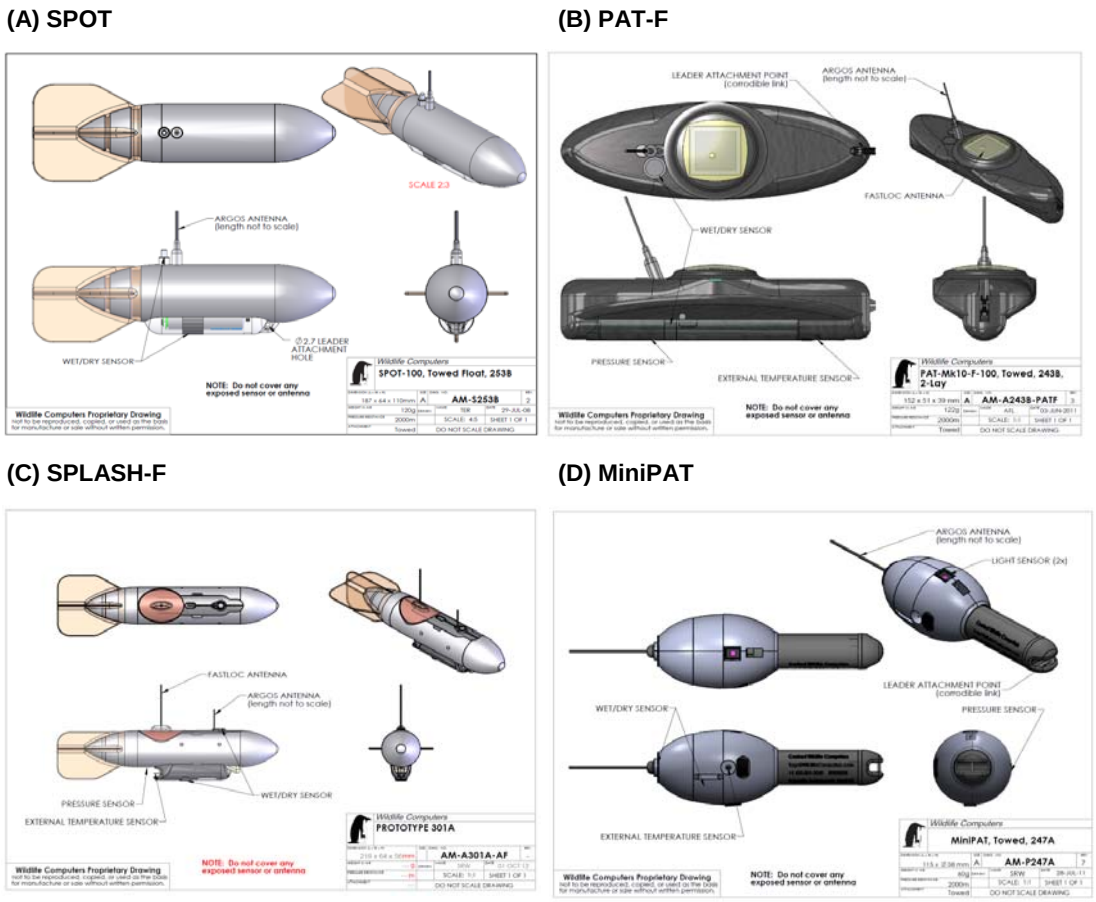

Figure 2. *Animal-borne satellite tag technologies (Images: Wildlife Computers).*

2.4 Tether system

The preferred method of tag attachment is one with the least degree of interaction with the sharks. Tags must thus be attached quickly, preferably remotely and in a manner that exposes the tag to the sea surface, particularly for tags that transmit in real-time to the Argos Systems and/or collect Fastloc^{TM} locations. Current best practice is to attach satellite tags to the shark via a dart using a tether of varying length.

Satellite tags are designed to be buoyant and the tether enables the tags to reach the sea surface to allow transmissions to the Argos System. The dart is typically inserted into the cartilaginous 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 (~900lbs; approx. 400kg), covered with heat shrinkable tubing, a swivel and a depth-release device (Wildlife Computers; RD1800). This device releases the tag by severing the tether at 1800m depth to prevent damage from the high ambient pressure. As a safety mechanism, tether assemblies were configured to break away if significant force were applied, e.g. in entanglement with fishing nets, pot lines or submerged objects.

2.5 Deployment of satellite tags

Sealife Surveys provided boat services in 2012 and 2013. 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 three tagging locations (Fig. 1B), sharks were first observed at distance so to identify candidate animals for tagging. Suitable animals appeared to be in good health (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:

a) The survey vessel was prepared for an encounter with a candidate shark, by manoeuvring the vessel towards the animal at ‘dead slow’ speed.

b) 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.

c) The shark was darted using a titanium metal dart inserted into the base of the dorsal fin using a darting pole (Fig. 3 B,C).

d) 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.

e) The length of the shark was estimated using the known length of the survey vessel as a guide.

f) The location of each tagging event was collected using a hand-held GPS receiver. Each tagging event was accompanied by vertical plankton trawl from the seabed 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 instrument.

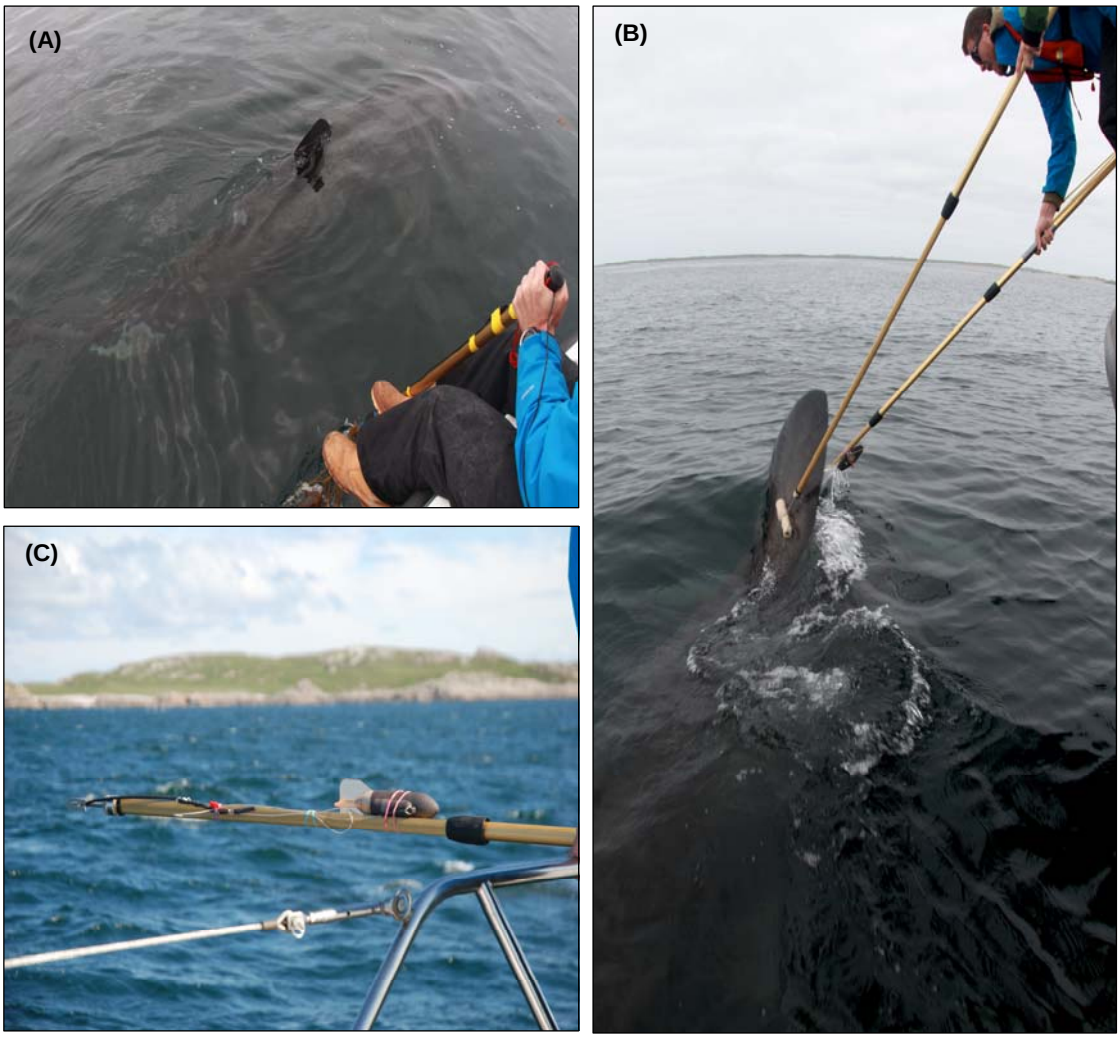

Figure 3*. Use of pole mounted camera to determine sex of satellite tagged basking sharks (A), genetic swab pole and darting pole being used simultaneously (B) and darting pole with satellite tag and tether prepared for use (C).*

2.6 Estimating tag detachment dates

The tracking period for each shark reached completion when the tag detached from the study animal, either at a pre-programmed 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. This type of data would be 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 for the tag types:

SPOT

These tags were permitted to send 250 transmissions a day to over-passing satellites. The transmission counter on the tag resets at 00:00 UTC each day. A tag can transmit every 45 sec. (when not submerged). A tag is therefore likely to have detached when all available transmissions have 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.

PAT-F, SPLASH-F and MiniPAT

These tags support diagnostic capabilities that record the date and depth at which the tag detaches from the shark. PAT-F and MiniPAT tags do not transmit to the Argos System until they have detached. If transmissions are received from the tag during the programmed attachment period then it is assumed that the tag is no longer attached to the study animal.

2.7 Data management

Data received from all satellite tag types were available on a rolling 10-day server at www.argos-system.org. These data were downloaded on a daily basis and subject to validation and filtering procedures. Data are also held on www.wildlifetracking.org servers as a precautionary measure.

2.8 Data analysis

Reconstructing movements

SPOT tags provided the main source of basking shark location data. A range of filters were applied to these location data to remove implausible estimates (Witt *et al.* 2010)**.** Only locations with location accuracy classes of 3, 2, 1, and A were used. The locations were filtered using the maximum rate of travel of 15km.h^{-1}. A turning angle filter was also applied, this filter removed locations necessitating turning angles of ≤10°. Movements of sharks determined by light geolocation (from PAT-F and MiniPAT tags) will be available in the Phase II report.

Estimating areas of relative importance

Location data gathered from SPOT tags were analysed to ascertain whether tracked basking sharks showed preference for particular areas within the study area, 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, most accurate location for each day to avoid pseudo-replication. Locations collected within the first 28 days of tracking were initially used; a period, when all individuals could contribute near equal number of locations. The analysis was repeated using data for a longer period, representing the time between tag deployment and the apparent end of summertime surfacing behaviour on the west coast (July to September).

Minimum convex polygon: Two dimensional delineation of the total area that tracked sharks utilised during this period.

Grid-based point counting: A grid-based counting approach (Witt *et al.* 2008), using a grid of 25km^2. This grid was used to sum spatially coincident best daily 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). This process smoothed the data at a resolution of 5km. The method resulted in an estimate of density that incorporated areas containing specified densities, i.e. 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.

Environmental data

The distribution of basking shark locations from SPOT tag were contextualised using a range of biophysical data describing the marine environment; including, bathymetry (© SeaZone Solutions, 2013, Licence O1035263) and seabed substratum (EUSeaMap, http://jncc.defra.gov.uk/EUSeaMap). Daily sea surface temperature (SST) data were obtained from the Global High Resolution Sea Surface Temperature project (1km^2 resolution, http://www.ghrsst.org). An average daily SST map was derived for the first 28 days of tracking in both 2012 and 2013. 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 for the first 28 days of basking shark tracking in both 2012 and 2013. Monthly Chlorophyll-*a* concentration data were obtained from the Goddard Space Flight Centre (4km pixel resolution, L3m product; http://oceancolor.gsfc.nasa.gov). Data on thermal horizontal fronts were obtained from the Defra project '*Marine Protected Areas – gathering/developing and accessing the data for the planning of a network of Marine Conservation Zones - MB0102'* (Report No. 20, (Miller *et al.* 2010)). Environmental values coincident to locations gathered by SPOT tags were extracted from the above described products. These locations represented the highest quality location data received in each day, for each individual, in both 2012 and 2013. Where multiple locations of the highest quality were received in the day we used the first to occur.

Fastloc^{TM} locations from PAT-F and SPLASH-F tags

Fastloc^{TM} locations were received from PAT-F and SPLASH-F tags. Locations derived using three or fewer GPS satellites were discarded due to a high degree of spatial error. Locations gathered by Fastloc^{TM} enabled tags were subsequently mapped. Data collected by SPLASH-F tags were also subjected to kernel density estimation. The number of Fastloc^{TM} locations produced by PAT-F tags in 2012 was insufficient for kernel density estimation to be performed.

Fastloc^{TM} locations and depth use

To create an understanding of basking shark depth use within the study area, data summarising depth use (on a 4-hour interval) were associated to geographic locations provided by PAT-F (in 2012) and SPLASH-F tags (in 2013).

Argos locations and depth use

Depth use was further examined using data collected by SPLASH-F tags in 2013. These tags provided a non-contiguous time series of mean depth at 5-min. intervals, which when aligned with Argos location data enable a spatial overview of the approximate location of dive behaviour.

Depth use and time of day

Depth use with respect to time of day was analysed from the first 28 days of data collected from each shark fitted with a PAT-F tags in 2012. We imposed this 28 day limit to minimise the potential for including depth data collected outwith coastal areas of Scotland.

Zooplankton analysis

Analysis of zooplankton samples will be included within the Phase II report.

2.9 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, but given that expert interpretation of satellite data are always required, the 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 satellite tagged sharks and these can be viewed on the SNH website[1]. The University of Exeter posted updates and information via Twitter and uploaded video clips and photos to www.Flickr.com during the fieldwork period to allow the public to engage with the project. To date (Jan 31st 2014), 438 people have subscribed to daily updates on the locations of tagged basking sharks and 98,140 views of the satellite tracking website have been made.

2.10 Species licensing

The attachment of satellite transmitters was regulated by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence: PPL 30/2975). Witt, Godley, Hawkes and Doherty were individually licensed to undertake tag attachment and genetic sampling (Personal Licence(s): PIL 30/9990, PIL 40/9630 and PIL 30/9991 respectively). Ethical review of the 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) (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

Deployments in 2012

Nine SPOT tags and 12 PAT-F tags (Table 1) were deployed across three sites in the Sea of the Hebrides during July and August 2012 (Fig. 1). One SPOT tag suffered an electronic failure on deployment and was excluded from further analysis. SPOT tags remained attached to basking sharks for 108 ± 101 days (mean ± SD; 19 to 322 range). One SPOT tag (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 12 PAT-F tags yielded useful datasets over a mean deployment duration of 114 ± 92 days (mean ± SD; 19 to 280 days range). Seven of 12 PAT-F tags detached from their study animal and transmitted archived data, but earlier than their scheduled detachment dates. An eighth tag detached on the programmed date of release (119853). 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 (119842); the tag had been operational for 37 days. Two PAT-F tags (119843 and 119845), which successfully transmitted data following detachment, were found by members of the public on Scottish and Irish beaches in early summer 2013; data were downloaded directly from the tags.

Deployments in 2013

Fifteen SPOT, four SPLASH-F and 12 MiniPAT tags (Table 2) were deployed at two sites (Gunna Sound and Tiree) in the Sea of the Hebrides during July and August 2013 (Fig. 1). No tags were deployed at Hyskeir in 2013, although three days of search for basking sharks were conducted at the site.

SPOT tags remained operational for 144 ± 63 days (mean ± SD; 41 to 197 range). Ten SPOT tags likely remain attached to their study animals (Jan. 31st 2014). Although transmissions have ceased, data received in late September and October in 2013 before tags stopped regular transmission, did not indicate tag detachment. One SPOT tag (129447) was found on the north coast of Tiree and returned by a member of the public.

Two of four SPLASH-F tags remained attached for 45 days as programmed. One tag (129432) prematurely released after 34 days. One tag (129431) failed to release as programmed from the study animal. One SPLASH-F tag (129434) failed to record Fastloc™ locations.

Three MiniPAT tags (129451, 129453 and 131890; as of Jan. 31st 2014) prematurely detached, two of which have been physically retrieved (129453, 131890), allowing direct download of data. One MiniPAT tag (129451) transmitted for only two days following attachment, providing a fragmented and unusable dataset.

Table 1. Operational periods of SPOT and PAT-F tags deployed on basking sharks in 2012. *Tags ordered by tag type and transmission duration. Tag physically retrieved (*). Tag transmitting locations from within the Skye to Mull MPA search location (dark grey). Tag transmitting locations from outside the MPA search location (light grey). Tag operational but no locations received (hatched). Tag detached from shark during indicated month (D). Transmissions ended within indicated month, but tag still believed to be attached (C). Month of programmed detachment for archival PAT-F tags (P; pop-off).*

Type	Tag ID	Sex	Length (m)	Status	Duration (d)	2012						2013					
						J	A	S	O	N	D	J	F	M	A	M	J
SPOT	120500	M	6-7	Detached	19		D										
	119855	U	6-7	Detached	20		D										
	120497	F	4-5	Detached	20		D										
	*119856	M	5-6	Detached	96				D								
	120496	F	5-6	Detached	100				D								
	120498	F	5-6	Detached	135					D							
	120499	M	7-8	Ceased	158						C						
	119854	U	4-5	Detached	322											D	
PAT-F	119850	F	8-9	Early release	19		D									P	
	119848	U	5-6	Early release	20		D									P	
	*119842	F	4-5	Early release	37		D								P		
	*119851	U	5-6	Early release	45		D									P	
	119852	F	6-7	Early release	111					D						P	
	119843	M	7-8	Early release	140						D				P		
	119846	F	6-7	Early release	170							D				P	
	*119845	M	4-5	Early release	204								D		P		
	*119853	M	6-7	Released	280											D	
	119844	M	8-9	No data	No data										P		
	119847	F	5-6	No data	No data											P	
	119849	F	7-8	No data	No data											P	

Table 2. Operational periods of SPLASH-F, SPOT and MiniPAT tags deployed on basking sharks in 2013. *Tags ordered by tag type and transmission duration. Tag physically retrieved (*). Tag transmitting locations from within the Skye to Mull MPA search location (dark grey. Tag transmitting locations from outside the MPA search location (light grey). Tag operational (active) but no locations received (hatched). Tag detached from shark during indicated month (D). Transmissions ended within indicated month, but tag still believed to be attached (C). Month of programmed detachment for archival MiniPAT tags (P; pop-off).Tag remains active (A).*

Type	Tag ID	Sex	Length (m)	Status	Duration (d)	2013						2014					
						J	A	S	O	N	D	J	F	M	A	M	J
SPLASH-F	129432	U	5-6	No release	34												
	129431	F	7-8	Detached	45			D									
	129433	M	7-8	Detached	45			D									
	*129434	U	5-6	Detached	45			D									
SPOT	*129447	U	4-5	Detached	41			D									
	129435	F	5-6	Detached	43			D									
	129438	M	5-6	Detached	55			D									
	129446	U	5-6	Detached	58			D									
	129443	F	6-7	Detached	87				D								
	129439	U	6-7	Attached	178		C										
	129436	U	5-6	Attached	178				C								
	129437	U	5-6	Attached	178			C									
	129448	U	5-6	Attached	186			C									
	129449	U	5-6	Attached	186			C									
	129450	F	5-6	Attached	186			C									
	129444	U	7-8	Attached	194			C									
	129445	U	7-8	Attached	194		C										
	129440	F	4-5	Attached	197						C						
	129441	M	5-6	Attached	197			C									
MiniPAT	*131890	U	5-6	Detached	64				D								
	*129453	U	4-5	Detached	121					D							
	129451	U	5-6	Detached	153							D				P	
	129442	U	4-5	Attached	184							A				P	
	129452	F	5-6	Attached	184							A				P	
	129458	U	4-5	Attached	184							A				P	
	129459	U	4-5	Attached	184							A				P	
	131891	U	5-6	Attached	184							A					P
	129454	F	5-6	Attached	193							A			P		
	129455	F	5-6	Attached	193							A			P		
	129456	F	5-6	Attached	193							A			P		
	129457	U	7-8	Attached	193							A					P

3.2 Basking shark movements in the Sea of the Hebrides

Initial movements following tagging (2012)

Basking sharks (N = 8) tracked for the first 28 days in 2012 either remained in close proximity to their tagging sites (N = 4; Fig. 4 A-D), moved from the tagging area in Hyskeir towards the vicinity of Coll and Tiree (N = 2; Fig. 4 E,F), moved to other Hebridean Islands, including Mull and Jura (N = 1; Fig. 4G), or moved to offshore deep water before heading south towards the north coast of Ireland (N = 1; Fig. 4H).

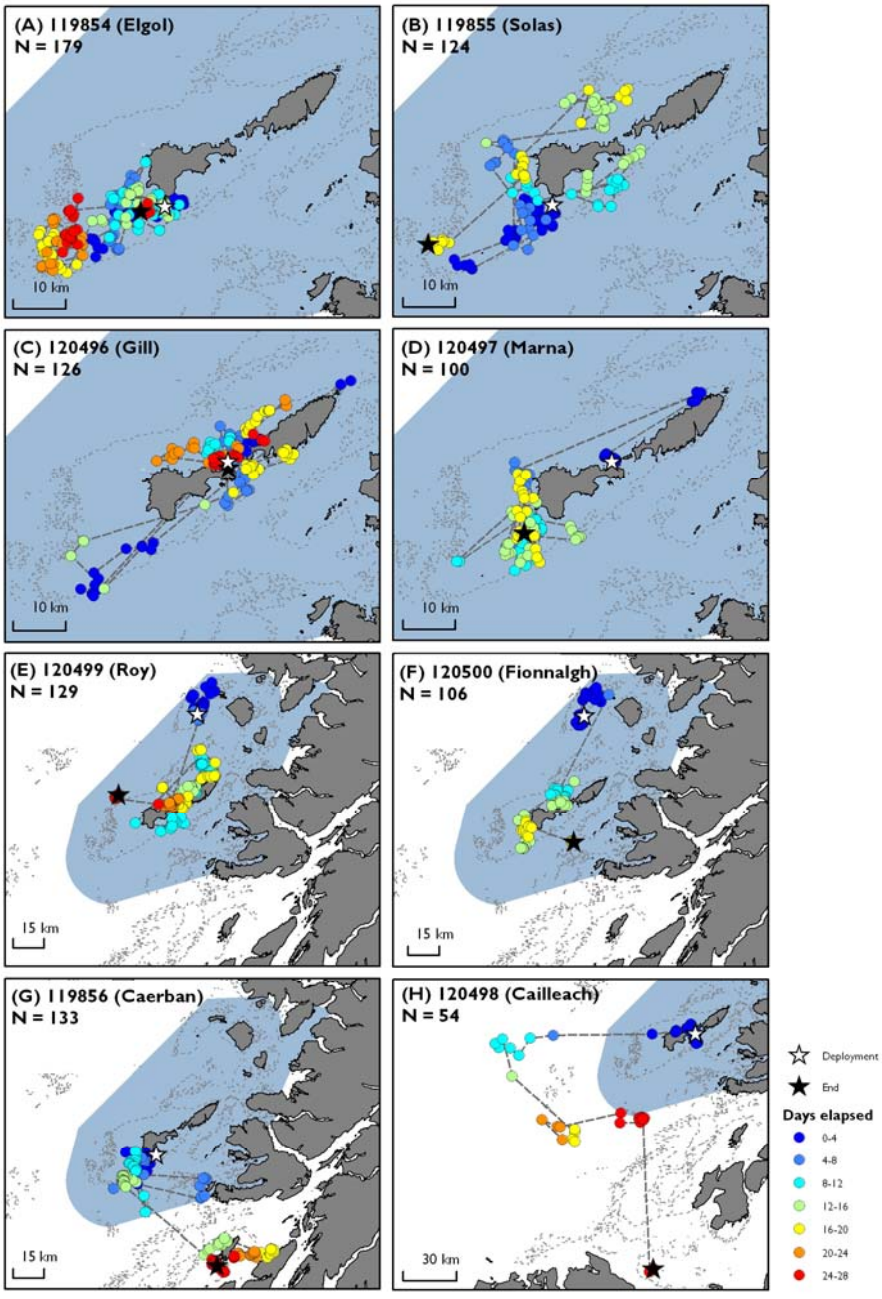

Figure 4. Movements of basking sharks tracked with SPOT tags in 2012. *Satellite tracking data from basking sharks for the first 28 days of tracking. Shark tag ID, name and total number of filtered locations indicated for each figure part. Note three basking sharks were tracked for less than 28 days (B, D and F) and figure parts to differing scales. Dashed lines join consecutive locations but do not infer straight line movement. Skye to Mull MPA search location (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

Initial movements following tagging (2013)

Basking sharks (N = 15) tracked for the first 28 days in 2013 either remained within the extents of the Skye to Mull MPA search location (N = 8; Fig. 5 A-H), undertook short-range movements outside the boundaries of the MPA search location (N = 4; Fig. 5 I-L) or undertook wider range movements either heading south to coastal waters of Ireland (N = 2; Fig. 5 M,N) or to the southern reaches of the Outer Hebrides (N = 1; Fig. 5O), prior to returning to the area of the MPA search location.

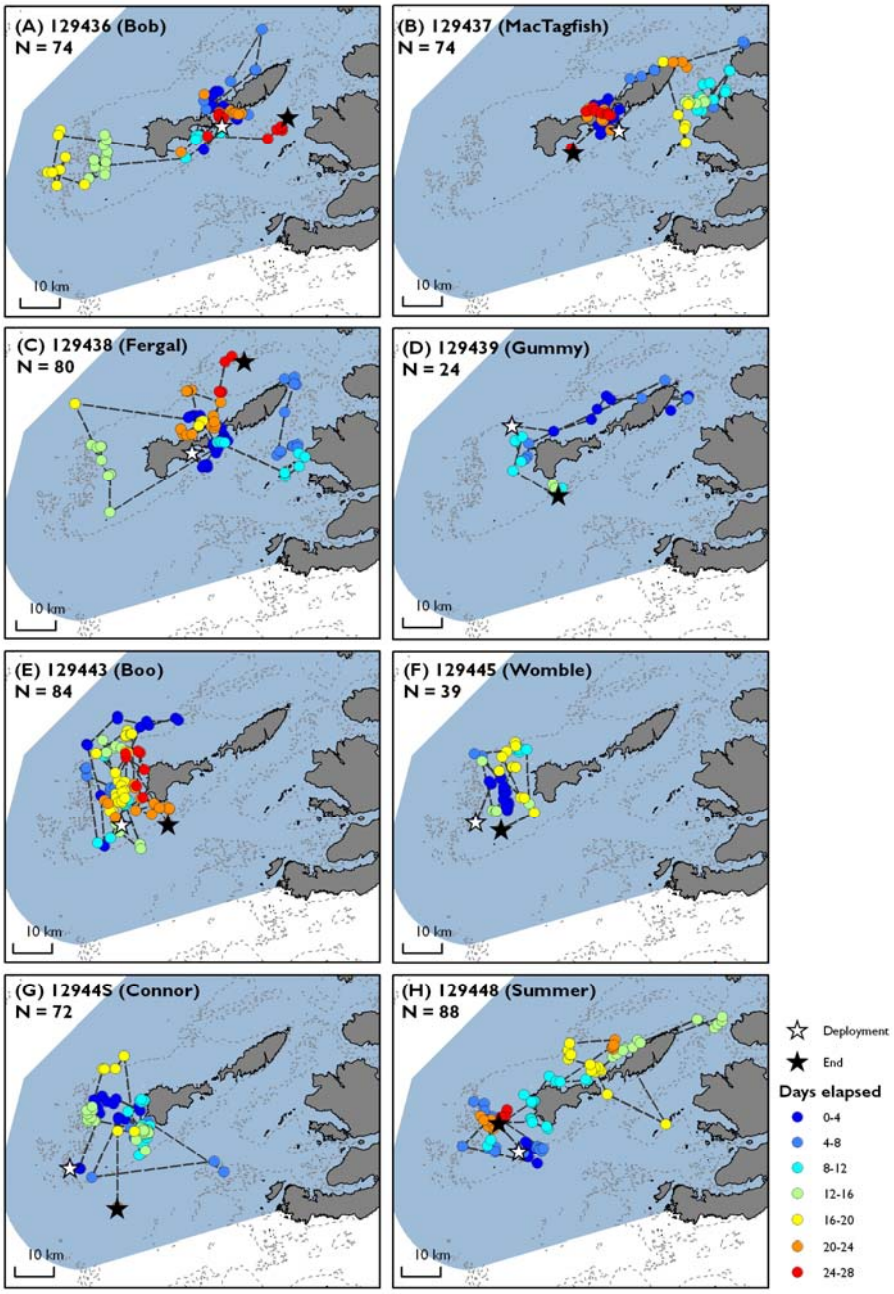

Figure 5. Movements of basking sharks tracked with SPOT tags in 2013. *Satellite tracking data from basking sharks for the first 28 days of tracking. Shark tag ID, name and total number of filtered locations indicated for each figure part. Note figure parts to differing scales. Dashed lines join consecutive locations but do not infer straight line movement. Skye to Mull MPA search location (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

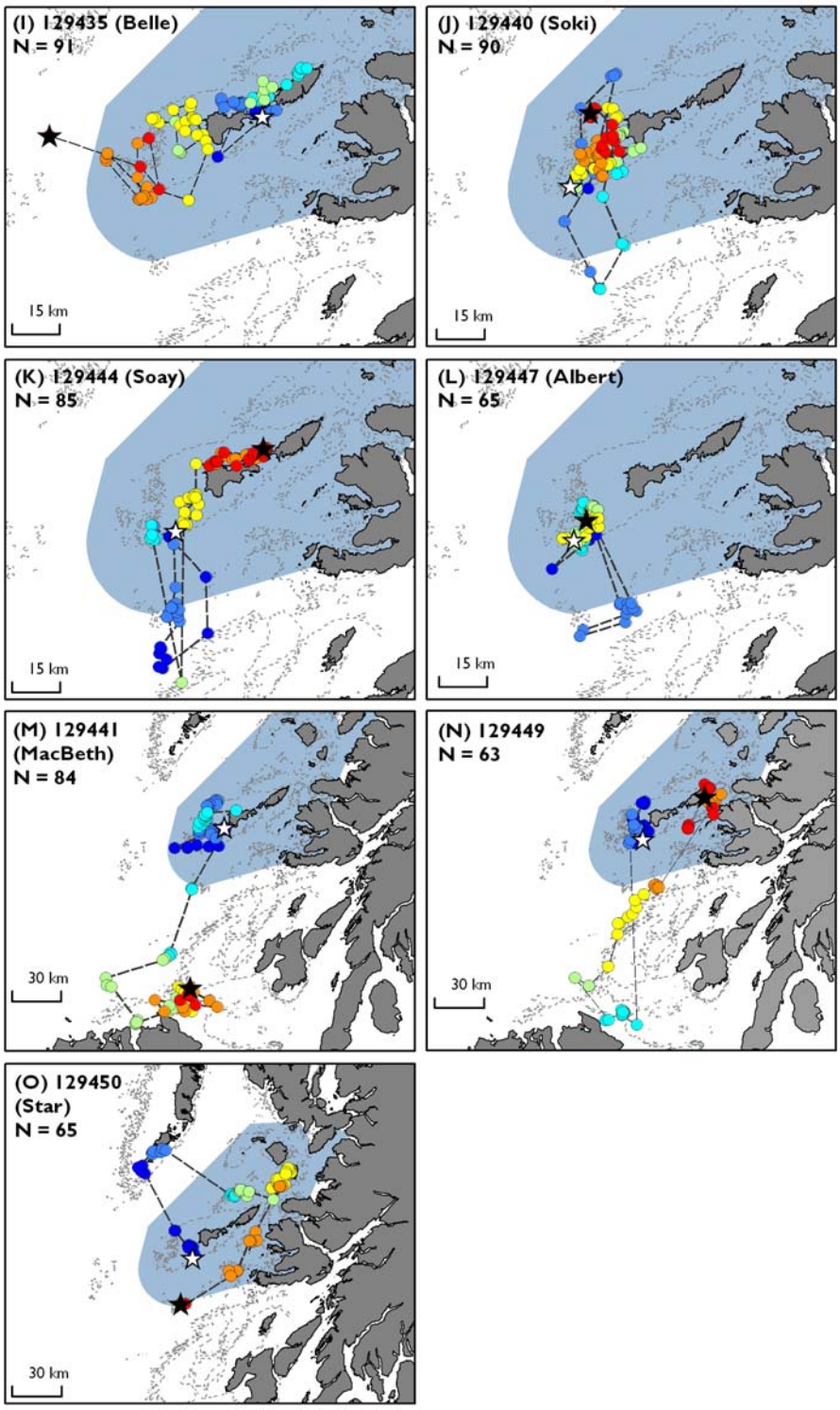

Figure 5 Continued. Movements of basking sharks tracked with SPOT tags in 2013.

3.3 Summertime movements of basking sharks (July to September)

Movements between July and September (2012)

Mapping movements of basking sharks beyond the first 28 days of tracking (N = 5) revealed that the majority of sharks remained within the area of Coll and Tiree (Fig. 6 A-D and Fig. S1 A). One individual undertook longer-range movement along the west coast of Scotland, to the islands of Jura and Colonsay (Fig. 6E).

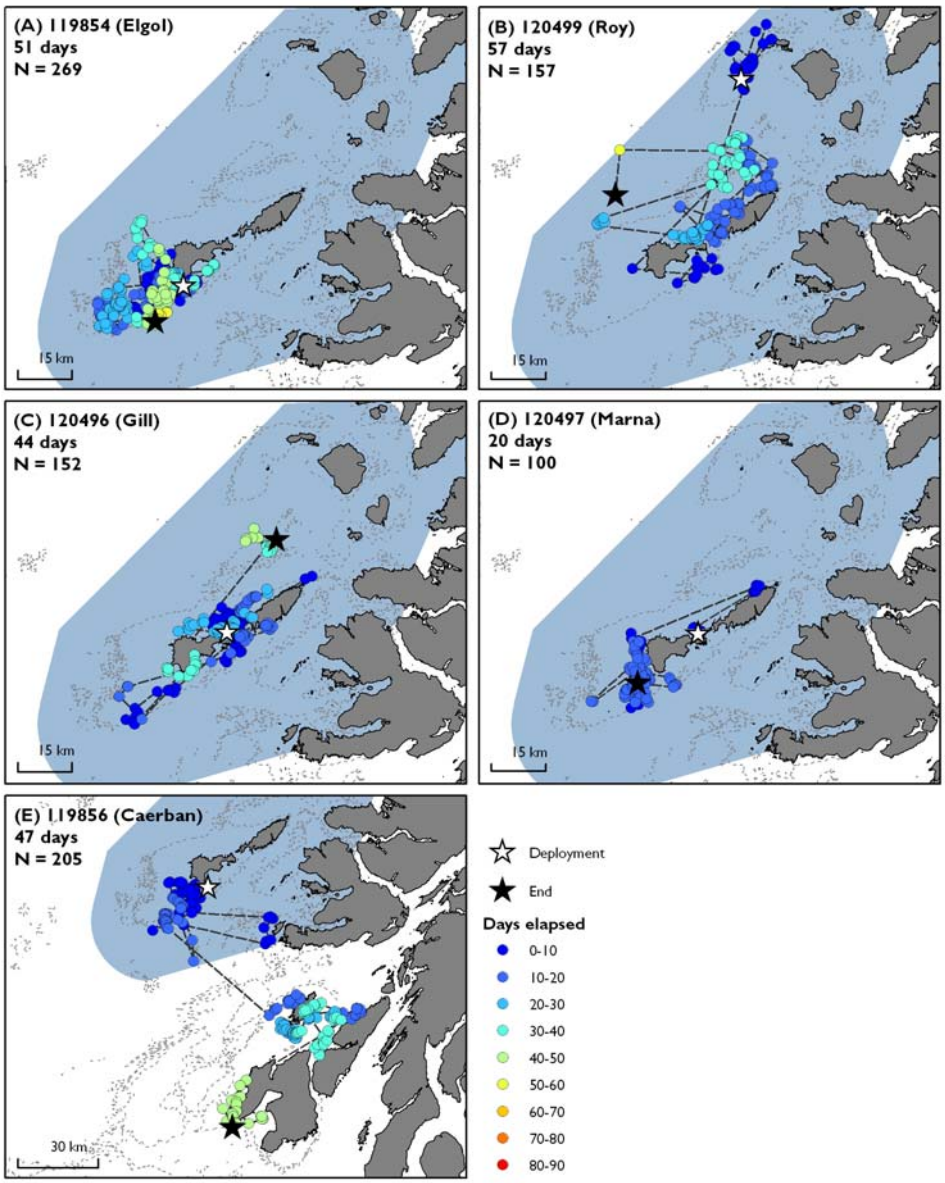

Figure 6. Summertime movements of basking sharks tracked with SPOT tags in 2012. *Satellite tracking data from basking sharks satellite tracked between July and September. Shark tag ID, name (if applicable), tracking duration and total number of filtered locations indicated for each figure part. Note figure parts to differing scales. Dashed lines join consecutive locations but do not infer straight line movement. Skye to Mull MPA search location (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

Movements between July and September (2013)

Movements made by basking sharks tagged with SPOT tags in 2013 (N = 10), whose tracks extended past 28 days, appeared more wide ranging than those observed in 2012, which may in part be due to the longer tag retention times (mean 108 ± 101 days in 2012 versus mean 114 ± 63 days in 2013) and due to the larger sample size (Fig. 7 and Fig. S1 B). Several sharks made short-range movements away from the MPA search location to other areas along the west coast of Scotland only to return to the MPA search location some days later (N = 4; Fig. 7 G-J).

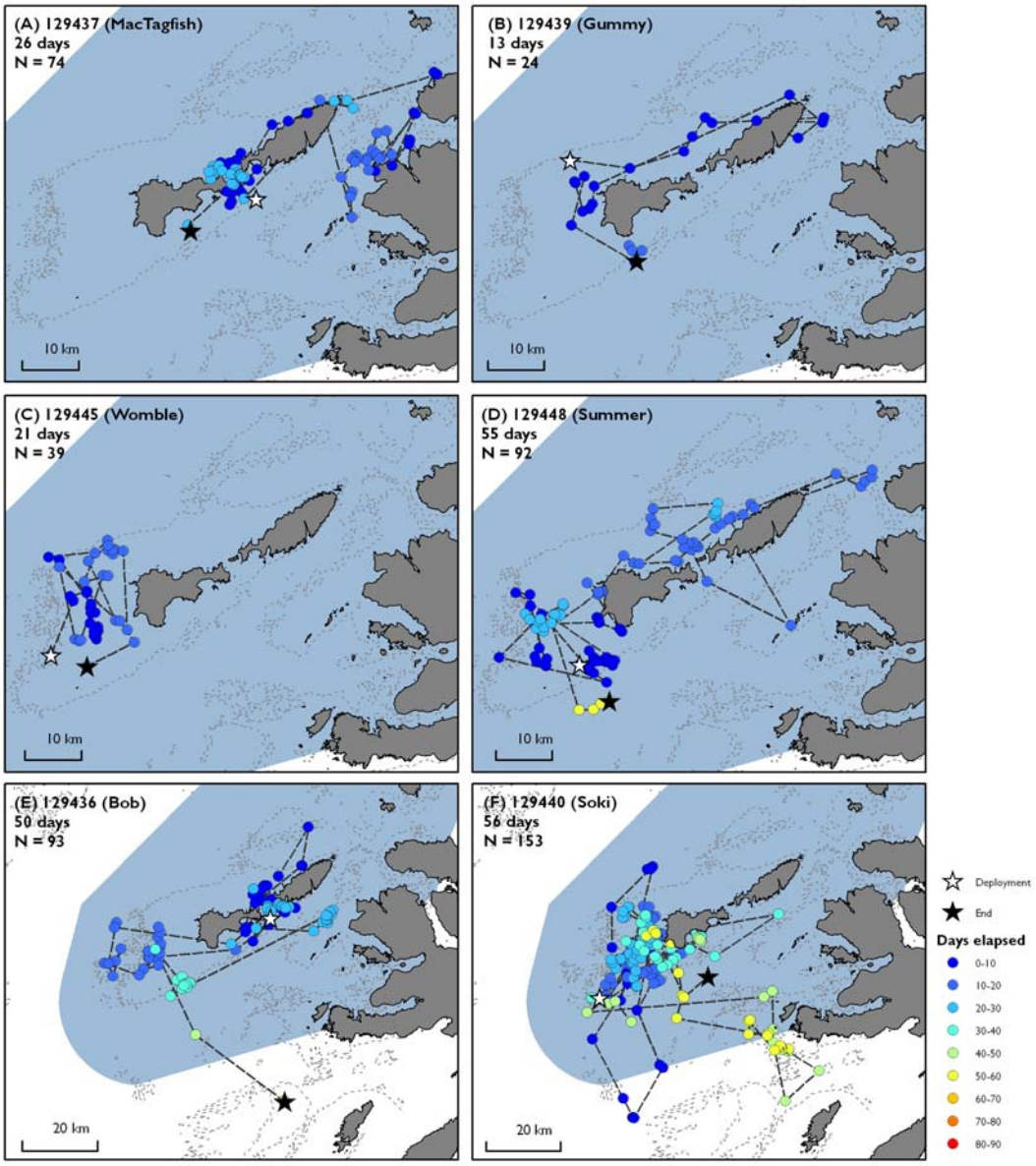

Figure 7. Summertime movements of basking sharks tracked with SPOT tags in 2013. *Satellite tracking data from basking sharks satellite tracked between July and September. Shark tag ID, name (if applicable), tracking duration and total number of filtered locations indicated for each figure part. Note figure parts to differing scales. Dashed lines join consecutive locations but do not infer straight line movement. Skye to Mull MPA search location (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

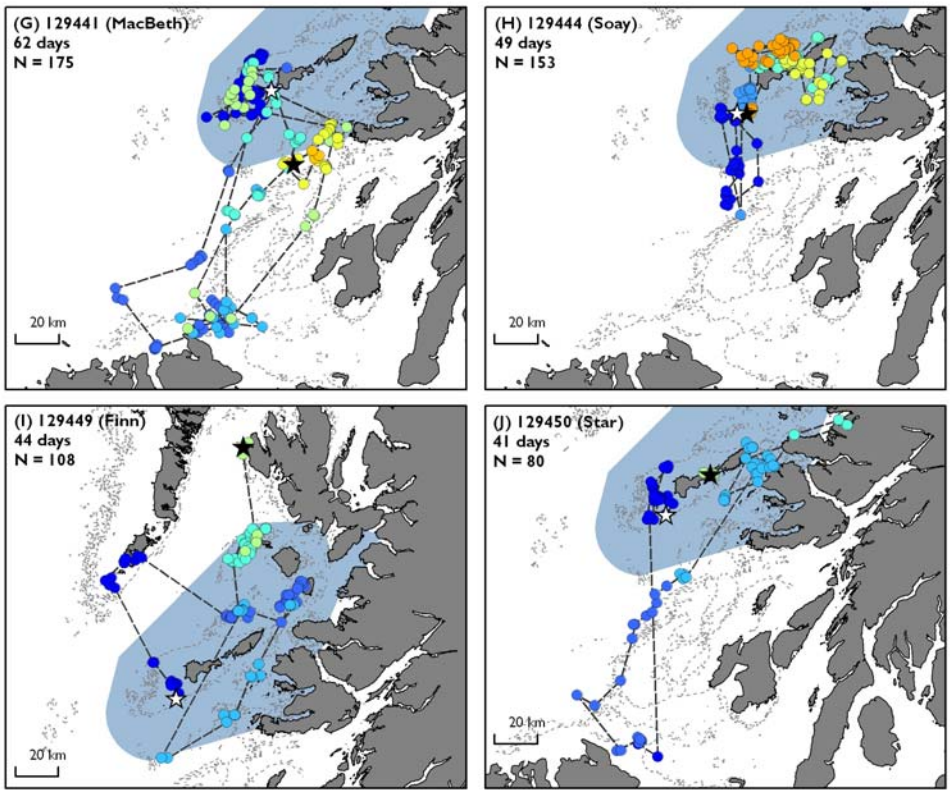

Figure 7 Continued. Summertime movements of basking sharks tracked with SPOT tags in 2013.

3.4 Areas of high relative importance within the Sea of the Hebrides

Skye to Mull MPA search location

Basking shark locations obtained from SPOT tags were quantified with respect to the spatial extents of the Skye to Mull MPA search location. In 2012, during the first 28 days of tracking, tagged sharks spent 83 ± 28% of their time (range 27-100%) within the MPA search location. During the period July to September in 2012 tagged sharks spent 78 ± 35% of their time (range 10-100%) within the extents of the Skye to Mull MPA search location (Table S1). In 2013, tagged sharks spent 89 ± 17% (range 46-100%) and 88 ± 15% (range 48-100%) of their time within the Skye to Mull MPA search location for the first 28 days of tracking and for the period July to September respectively (Table S1).

Areas of high relative importance (first 28 days of tracking)

Basking shark location data from the first 28 days of tracking (from SPOT tags) were used to identify areas of high relative importance. This period was chosen as it represented the longest initial period over which all tags operated successfully in both 2012 and 2013. Minimum Convex Polygons (MCP; Fig. 8 A,B) were fitted to location data to delineate the maximum potential area that tracked sharks utilised during this period. The resulting area spanned the Skye to Mull MPA search location and as far south as the north coast of Ireland, most notably during 2013 (Fig. 8B). Grid point enumeration (Grid; Fig. 8 C,D) highlighted the west of Tiree and Gunna Sound as areas most frequently used by basking sharks. Kernel density estimation (Kernel; Fig. 8 E,F) was used to identify core areas of utilisation (25% of the most aggregated location data; shaded red). These broadly matched with regions of highest density obtained from grid point estimation.

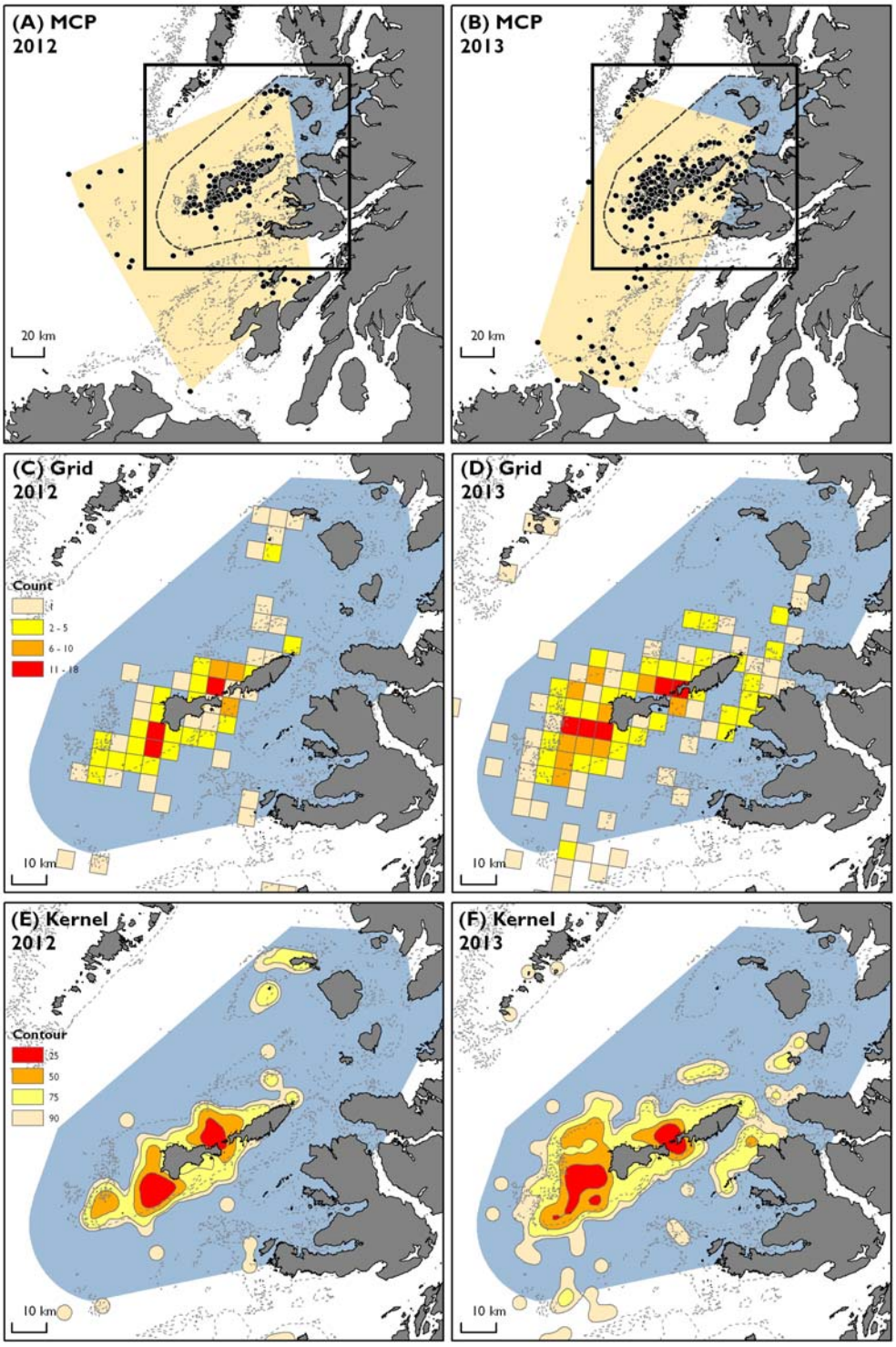

Figure 8. Identifying areas of high relative importance in the first 28 days of tracking. *Areas of relative importance, estimated using: i) Minimum Convex Polygon (MCP; A,B), ii) Grid; Point density enumeration (C,D) and iii) Kernel; density estimation (E,F) for SPOT-tagged basking sharks in 2012 (A, C and E) and 2013 (B, D and F) using daily highest quality location from individual basking sharks. Spatial extents of figure parts C-F (black empty polygon) shown in figure parts A and B. Skye to Mull MPA search location (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

Areas of high relative importance (July to September)

Using data from July to September (Fig. 9), a period when the majority of location data were collected in each year, the core areas identified broadly remained within the MPA search location. The MCP areas for movements made by basking sharks were 16,700km^2 and 20,000km^2 for 2012 and 2013 respectively (Fig. 9 A,B). Movements made by a shark to the west of Skye in 2013 extended the respective MCP to a more northerly latitude than recorded in 2012. Movements were also observed from the tagging area to easterly shores of the Outer Hebrides in 2013, further extending the range of movement.

Kernel density estimation identified smaller and less dense areas of aggregated location data outside the boundaries of the immediate tag deployment areas in 2013 (Fig. 9 E,F). These regions occurred to the west of Mull and along the southern boundary of the MPA search location. Less dense aggregations of location data also occurred near the islands of Rum and Eigg. Efforts were made to tag sharks at Hyskeir in 2013 but no tags were deployed as sharks were not encountered. Nonetheless, sharks moved to this area and to the north of Canna from the tagging locations of Tiree and Gunna.

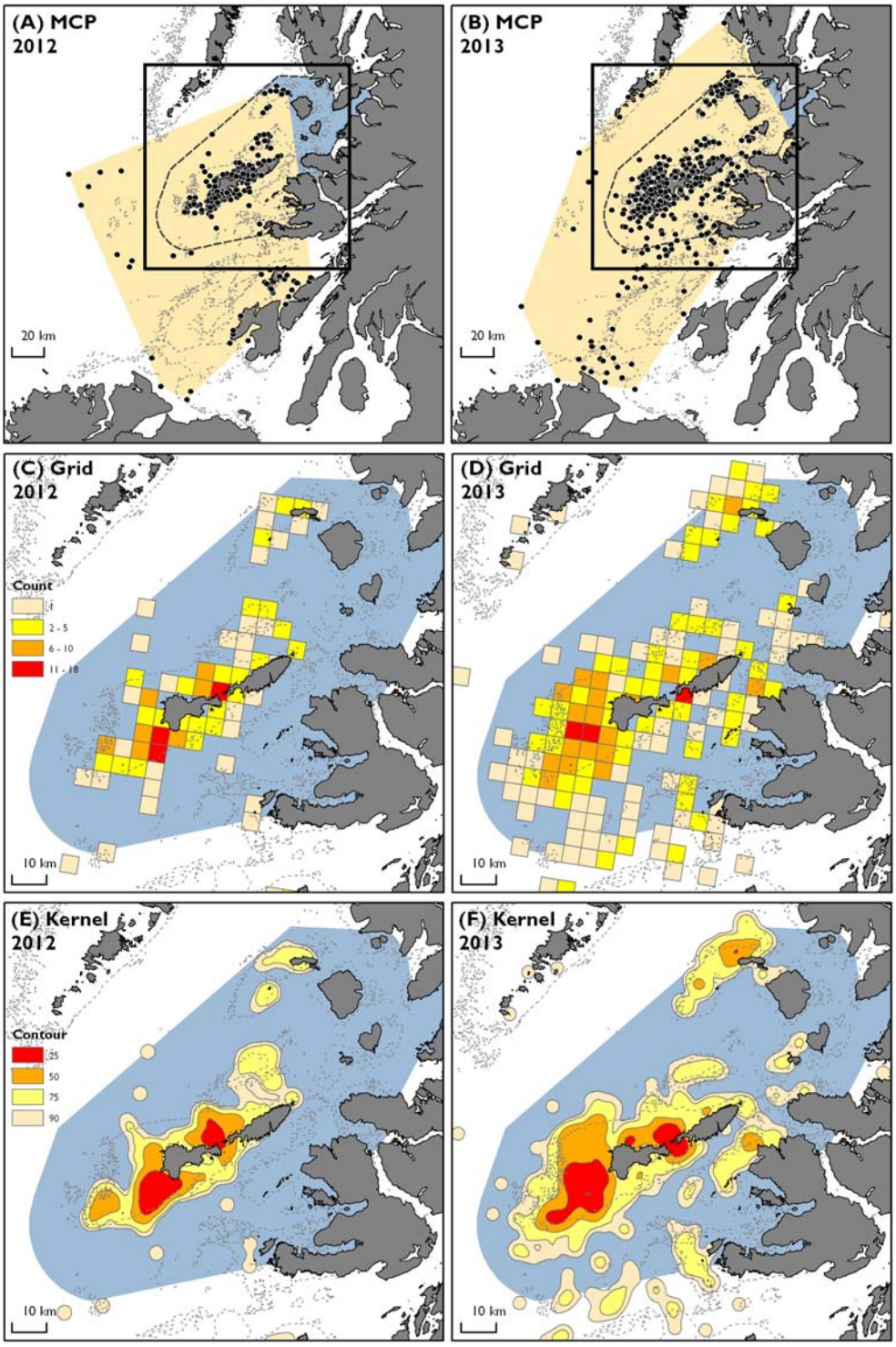

Figure 9. Identifying areas of high relative importance (July to September). *Areas of relative importance, estimated using: i) Minimum Convex Polygon (MCP; A,B), ii) Grid; Point density enumeration (C,D) and iii) Kernel; Quartic density estimation (E,F) for SPOT-tagged basking sharks in 2012 (A, C and E) and 2013 (B, D and F) using daily highest quality location from individual basking sharks. Spatial extents of figure parts C-F (black empty polygon) shown in figure parts A and B. Skye to Mull MPA search location (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

Spatial distribution across years

To investigate consistency in space use across years we combined estimates of location density created for the period July to September for 2012 and 2013, i.e. Fig. 9 C, D. The mean proportion of total density within each grid cell was calculated to inform on areas more frequently occupied throughout 2012 and 2013, represented as grid cells with higher relative proportion (Fig. 10). This procedure highlighted three regions of high relative density; one to the south and west of Tiree, a second at Gunna Sound and a third to the north-west of Canna.

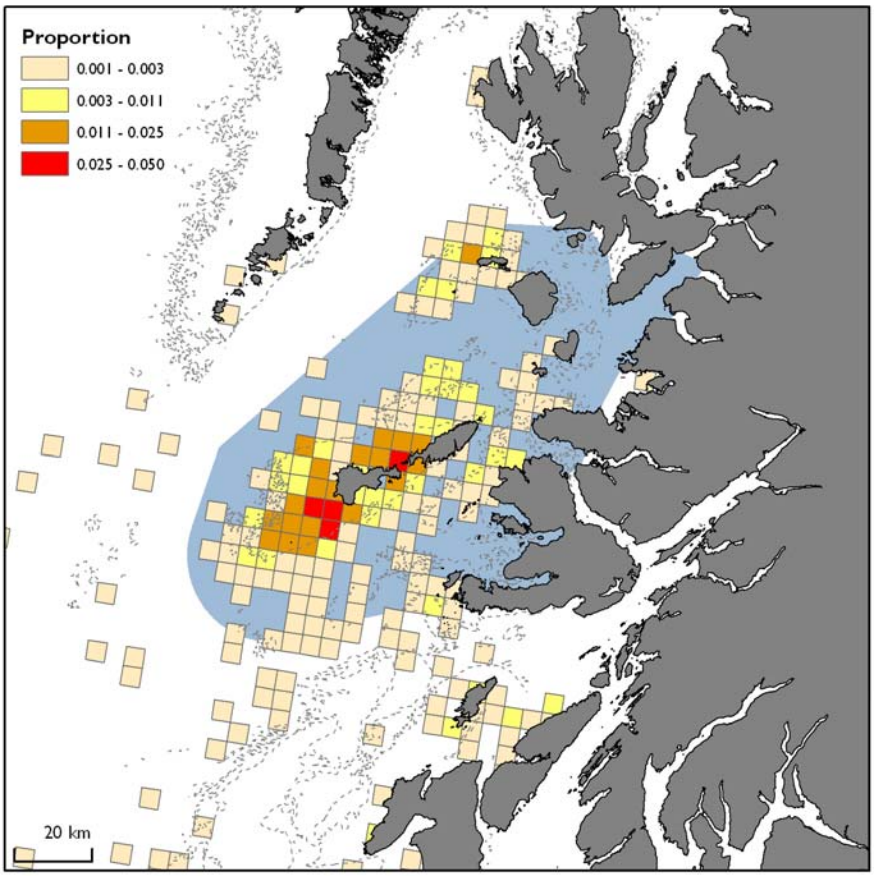

Figure 10. Identifying areas of high relative importance across years. *Mean average count as proportions in grid cells across 2012 and 2013 (July to September). Skye to Mull MPA search location (blue polygon), 50m depth contour (grey broken line; (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

3.5 Environmental features

To describe basking shark association with environment features we used SPOT tag location data from the first 28 days of satellite tracking in 2012 and 2013. Basking sharks moved between headlands, shelves, drop-offs and regions of open water. Analysis of these movements showed that basking sharks associated with shallow waters (grand mean 39 metres depth; Table 3, Fig. 11 A,B) and with waters overlaying mainly rocky or reef seabed substrata (Table 3,Fig. 11 C,D; 69% of 490 locations occurring over rock and reef habitats). Basking sharks encountered waters with a mean temperature of 13.9˚C (Table 3, Fig. 12 A,B) and with moderate tidal speeds (0.3m^{-s}; Fig. 11 C,D). Individuals were generally located in waters with chlorophyll-*a* concentration of 1.2 $mg.m^{-2}$ (Table 3, Fig. 12 E,F) and where fronts persisted for 26.2% of the time (Table 3, Fig. 13 A,B).

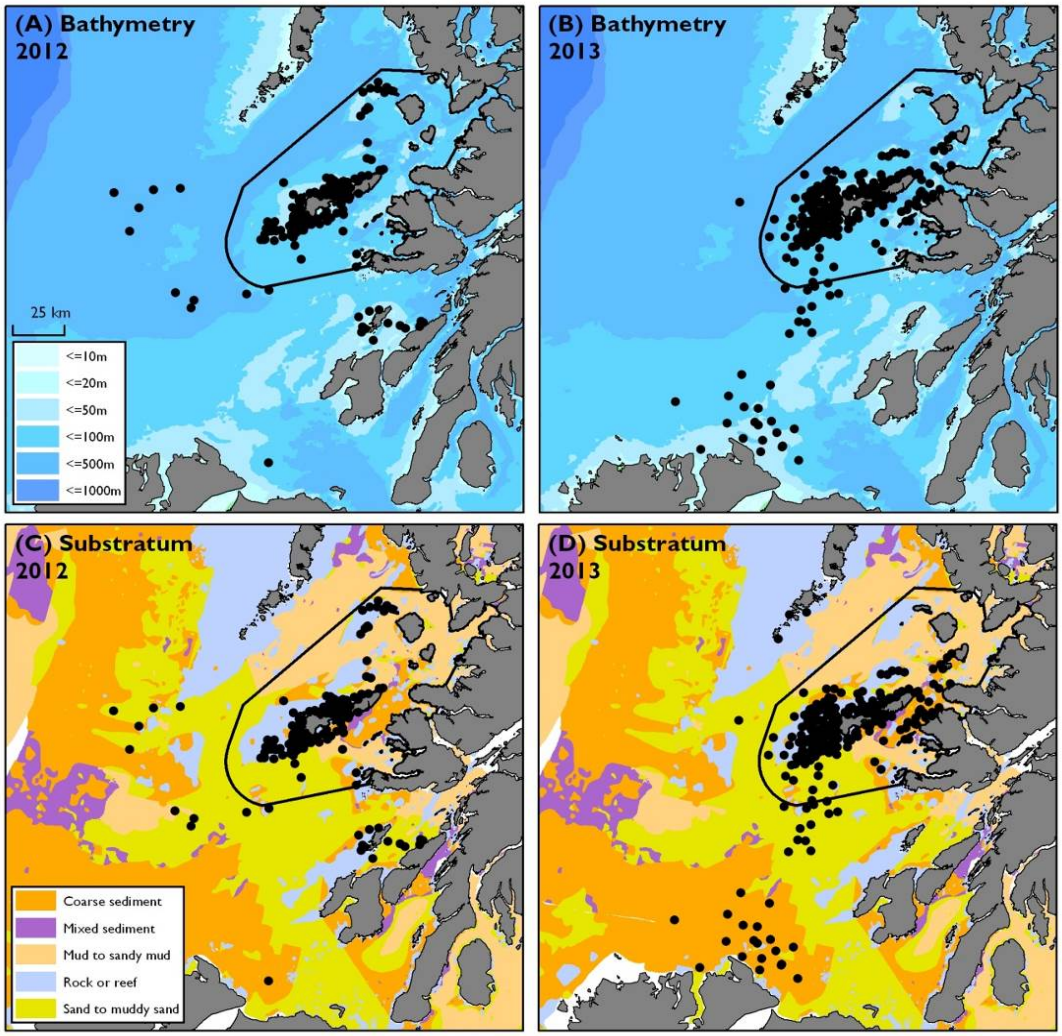

Figure 11. Basking sharks and their environment. *First 28 days of satellite tracking locations from individual basking sharks (black circles) in 2012 (A and C; N = 8 sharks; N = 177 locations) and 2013 (B and D; N = 15 sharks; N = 313 locations) with respect to bathymetry (m; A,B) and seabed substratum (C,D). In the first 28 days of tracking sharks are predominantly located in waters less the 50m deep (A,B) and over rock or reef substratum (C,D). Contains Ordnance Survey data © Crown copyright and database right 2013. Bathymetry © SeaZone Solutions, 2013, Licence O1035263.*

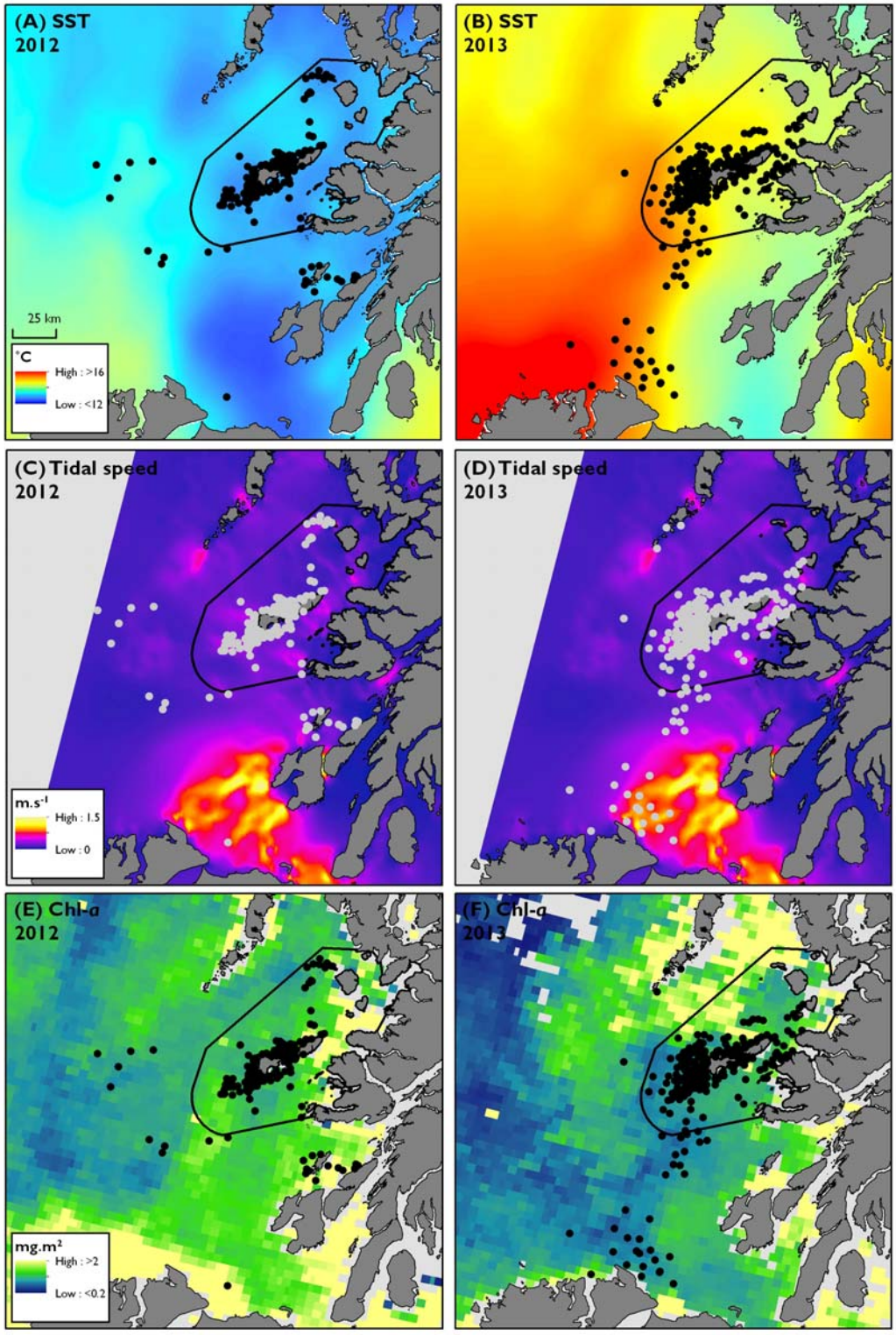

Figure 12. Basking sharks and their environment. *First 28 days of satellite tracking locations from individual basking sharks (A, B, E, F black circles and C, D grey circles) in 2012 (A, C and E, N = 8 sharks; N = 177 locations) and in 2013 (B, D and F, N = 15 sharks; N = 313 locations) with respect to sea surface temperature (SST; °C) and tidal speed (m.s^{-1}). Mean average of daily data from 13th July to 11th August 2012 (A,C), mean average of daily data from 19th July to 3rd September 2013 (B,D). Chlorophyll-a concentration (mg.m^{-2}, mean average of daily data for July 2012 (E) and August 2013 (F). Waters around the tagging areas were considerably warmer in 2013 than in 2012 (A,B) (mean temperature, 13.0˚C in 2012 and 14.7˚C in 2013). Contains Ordnance Survey data © Crown copyright and database right 2013.*

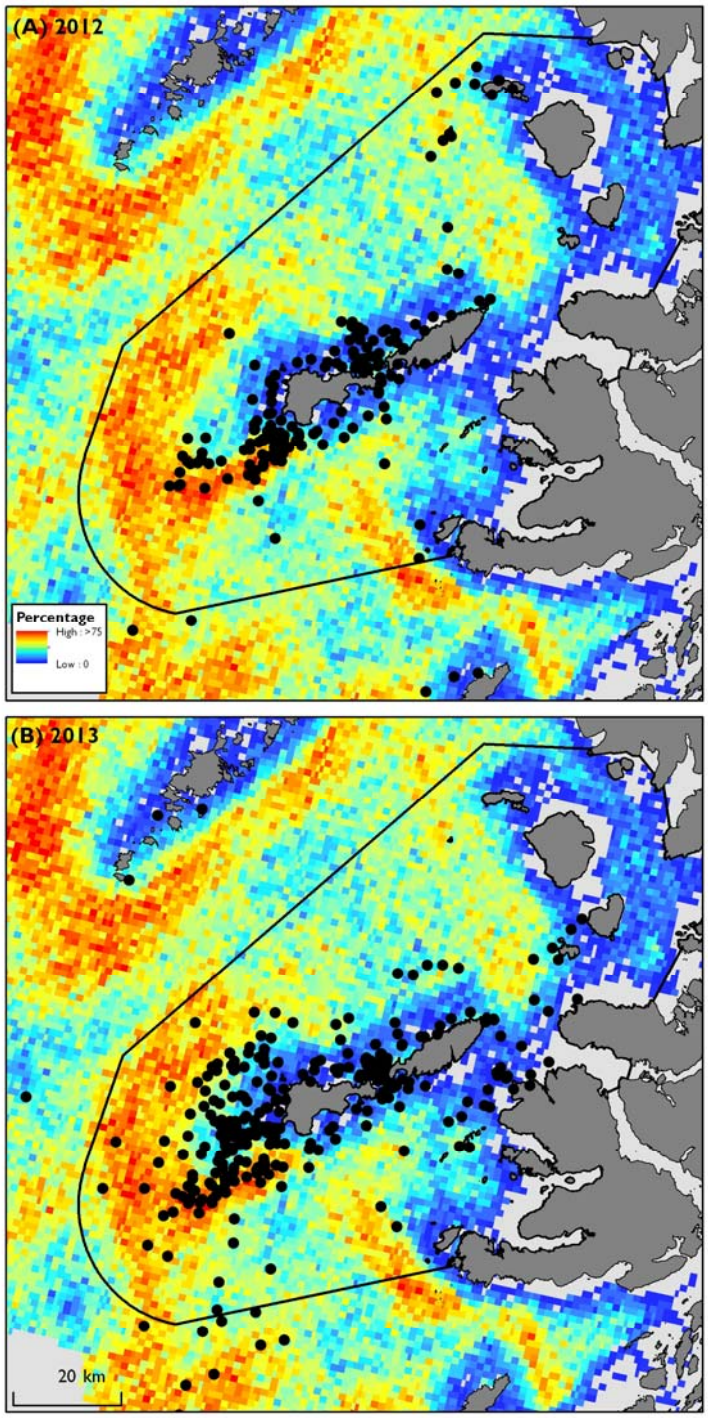

Figure 13. Basking sharks and fronts. *Locations of basking sharks in the first 28 days of tracking (black circles) in 2012 (A) and 2013 (B) with respect to persistent fronts. Background image indicates persistence of horizontal surface thermal fronts (data from Defra MB0102 Project (Report No. 20, Miller* et al. *2010). Skye to Mull MPA search location (black empty polygon). Contains Ordnance Survey data © Crown copyright and database right 2013.*

Table 3. Basking sharks and their environment. Summary of environmental variables sampled at the daily highest quality location for individual basking sharks satellite tracked with SPOT tags for the first 28 days of tracking in 2012 and 2013 and percentage of locations occurring within Skye to Mull MPA search location.

Year	N Individ. (N Loc.)	Substratum	Bathymetry	SST	Tidal speed	Chl-*a*	Fronts
		% of locations coincident to substratum type	Mean ± SD (min.-max.) *metres*	Mean ± SD (min.-max.) *°C*	Mean ± SD (min.-max.) *$m.s^{-1}$*	Mean ± SD (min.-max.) *$mg.m^{-2}$*	Mean ± SD (min.-max.) *percentage*
2012	8 (177)	Rock and reef; 73% Coarse sediment; 12% Sand to muddy sand; 10% Other; 5%	39 ± 35 (0 - 194)	12.9 ± 0.2 (12.8 - 13.4)	0.2 ± 0.1 (0.03 - 0.66)	1.3 ± 0.34 (0.85 - 3.53)	25.7 ± 21 (0 - 79)
2013	15 (313)	Rock and reef; 65% Coarse sediment; 21% Sand to muddy sand; 10% Other; 4%	39 ± 24.8 (0 - 146)	14.8 ± 0.3 (14.3 - 16.0)	0.3 ± 0.15 (0.06 - 1.0)	1.0 ± 0.25 (0.58 - 2.87)	26.7 ± 22 (46 - 100)
Mean of means		Rock and reef; 69% Coarse sediment; 16% Sand to muddy sand; 10% Other; 5%	39	13.9	0.3	1.2	26.2

3.6 Fastloc™ locations

PAT-F (2012)

The majority of Fastloc™ locations from PAT-F tags (N = 55 of 65) were recorded while basking sharks occupied coastal waters off western Scotland, including the Sea of the Hebrides and the Firth of Clyde. Four PAT-F tags provided seven or more Fastloc™ locations during the study period (Fig. 14). Remaining tags (N = 5) provided between one and four Fastloc™ locations (Fig. S2). Most locations were obtained between July and September 2012 (N = 55 locations, N = 9 sharks), with the exception of data received from a PAT-F tag (119853) that collected Fastloc™ location data through to March 2013 (Fig. 14E). This tag detached as programmed on May 2nd 2013, two months after the final Fastloc™ location was received.

Fastloc™ 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 extent of the Skye to Mull MPA search location. Nonetheless, the majority of locations (81.8%; N = 45 of 55) 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.

Fewer Fastloc™ locations were received than anticipated, particularly in comparison to the number of locations created by SPOT tags. 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.

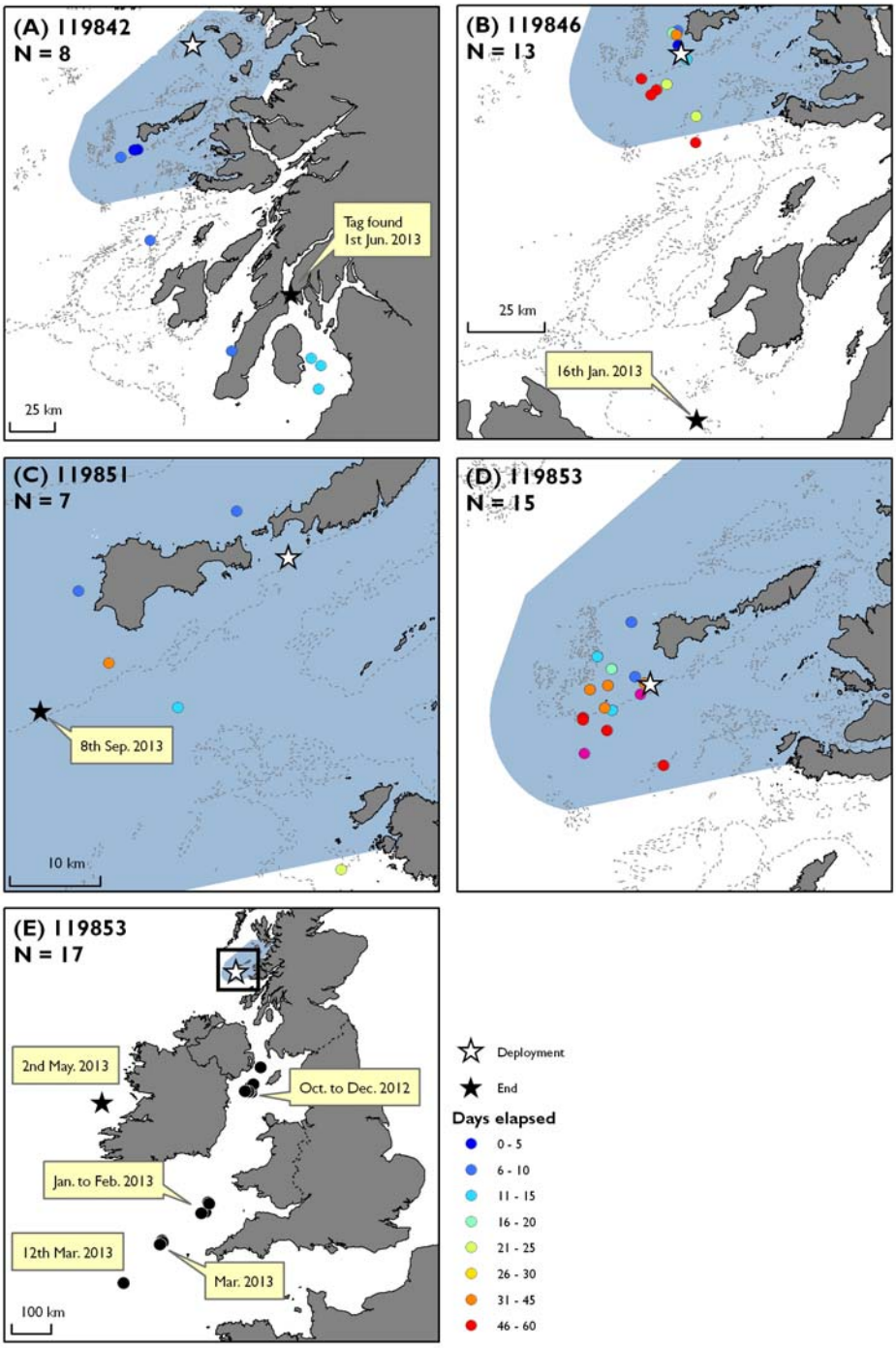

Figure 14. Fastloc™ locations of four PAT-F tagged basking sharks in 2012*. PAT-F tag attachment locations (white stars), PAT-F tag pop-off locations (black stars). Insufficient locations were transmitted to estimate density, see also Fig. S2 for locations from tags collecting four or less Fastloc™ locations. Locations from tag 119853 are displayed across two figure parts (D: locations in the area of the Skye to Mull search locations and E: locations from southward migration through the Irish and Celtic Seas (with positions in E shown as black circles). Number of successfully derived locations given with tag ID. Skye to Mull MPA search location (blue polygon). 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

SPLASH-F (2013)

Three SPLASH-F tags successfully gathered Fastloc™ locations in 2013; one tag (129434) failed to record Fastloc™ data. The majority of locations were within the boundaries of the Skye to Mull MPA search location (N = 273 of 279, Fig. 15 A, C and E). Fastloc™ location data were analysed using kernel density estimation (Fig. 15 B, D and F). Results complement the findings from Argos locations by highlighting areas west of Tiree and within Gunna Sound as regions supporting individual residency by sharks over periods of multiple days. The analysis also highlighted habitat use by a single individual along the northern edge of Coll (Fig. 15B).

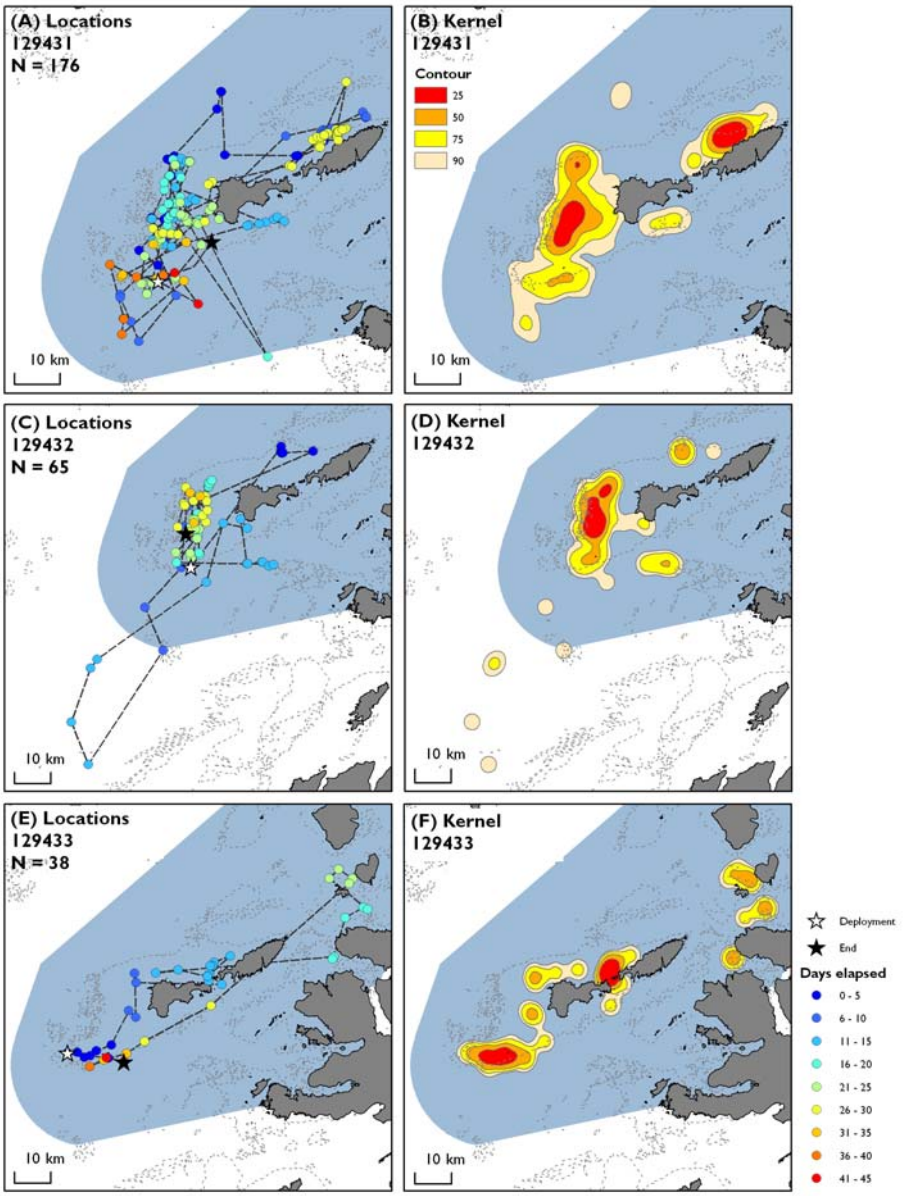

Figure 15. Fastloc™ locations of three SPLASH-F tagged basking sharks in 2013*. GPS locations (A, C and E), and resulting density (B, D and F) estimated using quartic density estimation. Attachment location (white star), SPLASH-F tag pop-off locations derived from first received Argos location following detachment (black star). Shark tag ID, name (if applicable), tracking duration and total number of filtered locations indicated for each figure part. Note figure parts to differing scales. Dashed lines join consecutive locations but do not infer straight line movement. Skye to Mull MPA search location shown (blue polygon), 50m depth contour (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

3.7 PAT-F and MiniPAT tag detachment locations

Twelve PAT-F tags were deployed on basking sharks during summer 2012 and eight successfully transmitted data following programmed (N = 1) or early (N = 7) detachment (Fig. 16; Table 1). All PAT-F tags were programmed to detach after a 280-day deployment, however, two released after 19 days (cause unknown). Twelve MiniPAT tags were deployed in 2013. Three tags have prematurely detached (as of Jan. 31st 2013).

Detachment locations of PAT-F and MiniPAT tags were located in the Sea of the Hebrides (N = 3; attachment duration less than 2 months), to the north of Northern Ireland (N = 2; attachment durations approx. 2 and 7 months), in the northern Irish Sea (N = 4; attachment durations between four and six months) and west of Ireland (N = 2; attachment durations approx. seven and nine months).

Two of eight PAT-F tags (119853, 119845) deployed in 2012, were found by members of the public during the summer of 2013 (Table 1); both were discovered on western shores of Ireland. A ninth PAT-F tag (119842; Table 1) was found by a member of the public in June 2013 close to Portavadie, Loch Fyne; Argyll (Fig. 16; green circle). This tag had failed to transmit but had archived depth, temperature and Fastloc™ location data. The tag functioned and collected data from deployment for 37 days (until Aug. 26th 2012). The cause of failure was linked to water ingress due to physical damage. Ten months elapsed between the tag ceasing to operate and it being found. The final Fastloc™ location from the tag was collected on Aug. 4th 2012 within the Firth of Clyde, south-east of the Isle of Arran. The remaining three PAT-F tags failed to transmit data (Table 1).

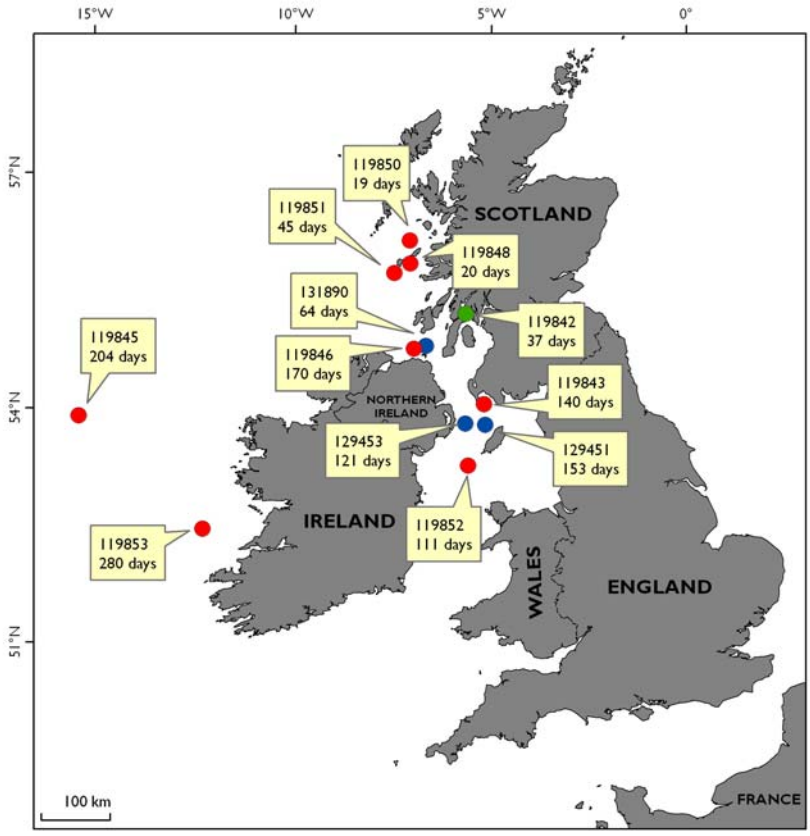

Figure 16. PAT-F and MiniPAT satellite tag detachment locations*. Pop-off locations of PAT-F tags (red circles; N = 8), MiniPAT tags (blue circles; N = 3) and retrieval location of a non-transmitting PAT-F tag (green circle, N = 1). Attachment durations given with tag ID.*

3.8 Long and medium-range movements

SPOT tags deployed on two basking sharks in 2012 (119854, 120498) revealed insights into long-distance migration (Fig. 17A). Basking sharks travelled southwest for approximately 3300km and 3400km respectively (minimum along-track distance) through the Economic Exclusive Zones of Spain (Canary Islands) and Portugal (mainland and Madeira) to the coast of North Africa. The tags eventually detached in Madeira and the Canary Islands, 322 days and 132 days following deployment.

Three SPOT tags (119856, 120496 and 120499) and two PAT-F tags (119845, 119853) deployed in 2012 and one SPOT tag (129440) deployed in 2013 highlighted basking shark movements into the Irish and Celtic Seas away from Scottish coastal waters (Fig. 17B).

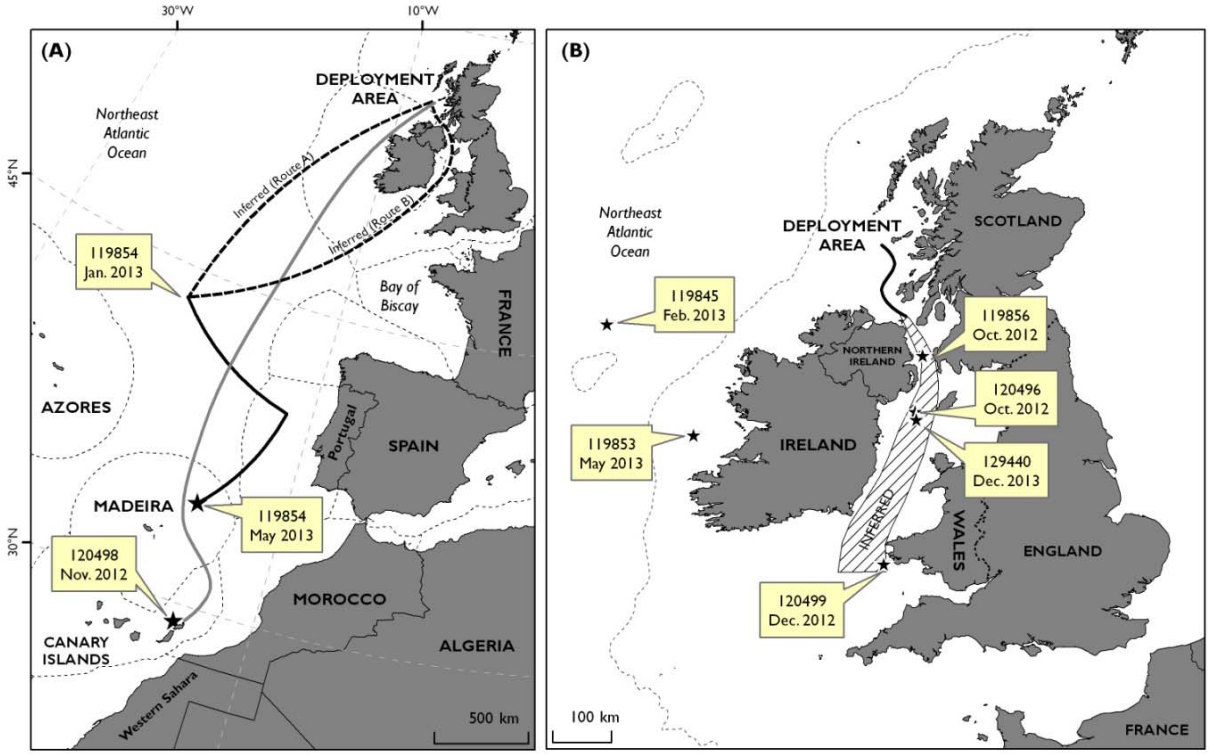

Figure 17. Long and medium-range movements of basking sharks from Scotland*. (A) Two SPOT-tagged basking sharks in 2012 (119854, 120498). (B) Boundaries of Exclusive Economic Zones (black dashed line). Three SPOT (119856, 129496 and 129499) and two PAT-F (119845, 119853) tagged basking sharks in 2012 and one SPOT (129440) tagged basking shark in 2013 moving in to the Irish and Celtic seas from the Sea of the Hebrides. Hatched region (B) identifies an inferred movement corridor stretching from Scotland to the Celtic Sea. Month of tag detachment indicated with tag ID. 200m depth contour (grey broken line; (grey broken line; © SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013*

3.9 Linking depth use with spatial movements

Using data from PAT-F and SPLASH-F tags it was possible to map the Fastloc™ locations of basking sharks and associate these to contemporaneous data on depth use. This was achieved using 4-hour summarised estimates of depth use from six basking sharks in 2012 (Fig. 18A; Fig. 19A) and from three basking sharks in 2013 (Fig. 18 B-D; Fig. 19 B-D).

Data suggested that sharks were likely occupying the seabed for at least some part of each 4-hour period as maximum depths recorded on the tags matched charted seabed depth (Fig. 18). Analysis of modal depth use (Fig. 19; the most frequent depth class occupied) provide tentative insight into why the areas around Coll and Tiree 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 being predominantly 1-5m (Fig. 19). This finding should be interpreted cautiously as the temporal scales of Fastloc™ locations (gathered within a few milliseconds) and depth use data (summarised over a temporally coincident 4-hour period) are clearly different, such that sharks may have moved away from the area in which the Fastloc™ location was collected.

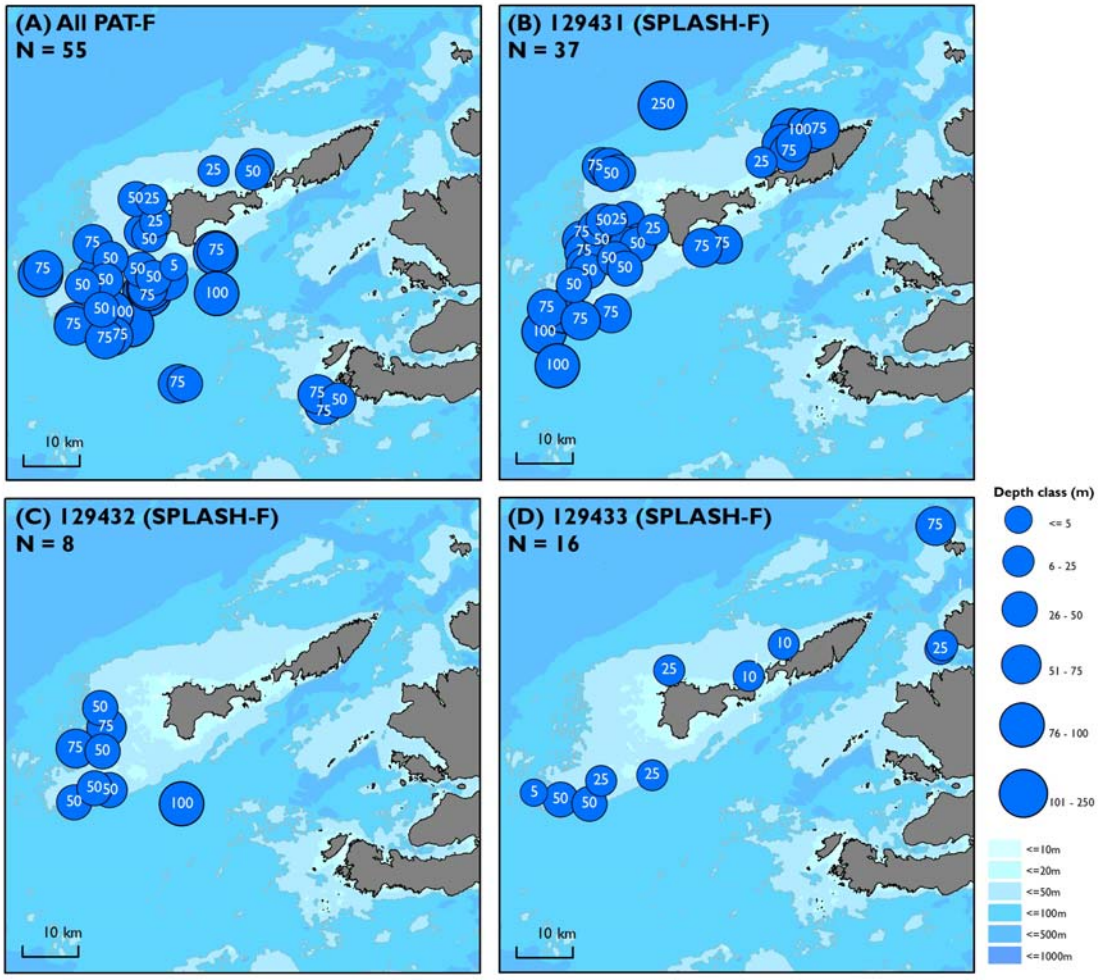

Figure 18. Three dimensional space use from PAT-F (2012; N = 6) and SPLASH-F tags (2013; N = 3). *Maximum depth recorded during dives where a temporally coincident Fastloc™ location was available. Circle size indicates dive depth (deeper dives represented by larger circles). Maximum depth value indicated in circle in white text. Background shading shows bathymetry (© SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

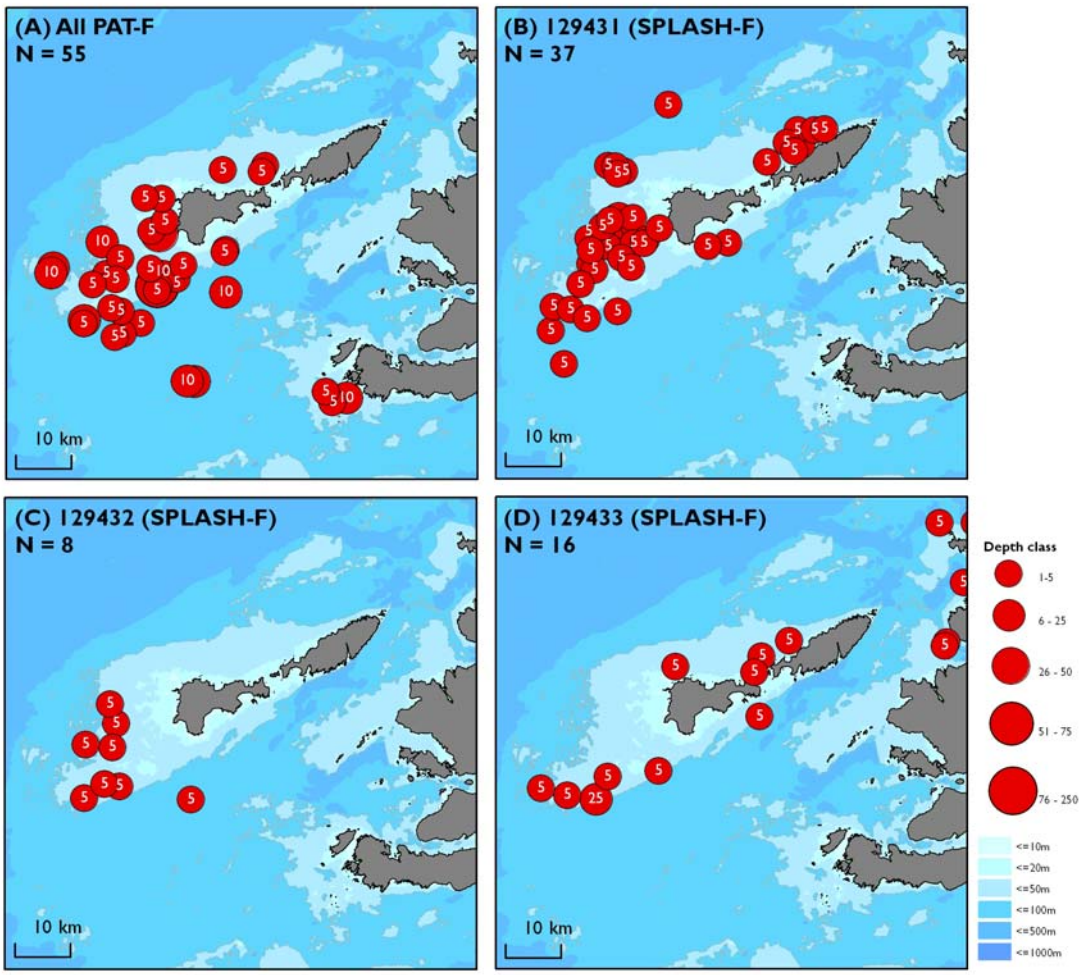

Figure 19. Three dimensional space use from PAT-F (2012; N = 6) and SPLASH-F tags (2013; N = 3). *Most frequent depth class occupied during dives where a temporally coincident Fastloc™ location was available. Circle size indicates depth class (deeper dives represented by larger circles). Most frequent depth class indicated in circle in white text. Background shading shows bathymetry (© SeaZone Solutions, 2013, Licence O1035263). Contains Ordnance Survey data © Crown copyright and database right 2013.*

High resolution depth use

Two SPLASH-F tags 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. 20). These data were temporally linked to Argos locations to reveal the approximate geographic locations of depth use. Transmitted time series data, recorded at comparatively high frequencies i.e. <1-hour, are a relatively novel development in satellite tracking studies and provide an interesting insight into vertical movements that are closely linked to their geographic location. For one individual, this technique revealed a range of depth use behaviour, from periods of predominantly surface or near-surface activity (Fig. 20A, Regions 1, 2 and 4) to intermittent periods of deep water habitat use (Fig. 20A, Region 3) occurring to the west of Eigg and Rum. Initial horizontal movements to the west of Tiree by a second individual were more widespread, occupying a range of depths between the surface and approx. 150m, followed by a period of more focused residency in the area of Hyskeir (Fig. 20B, Region 3).

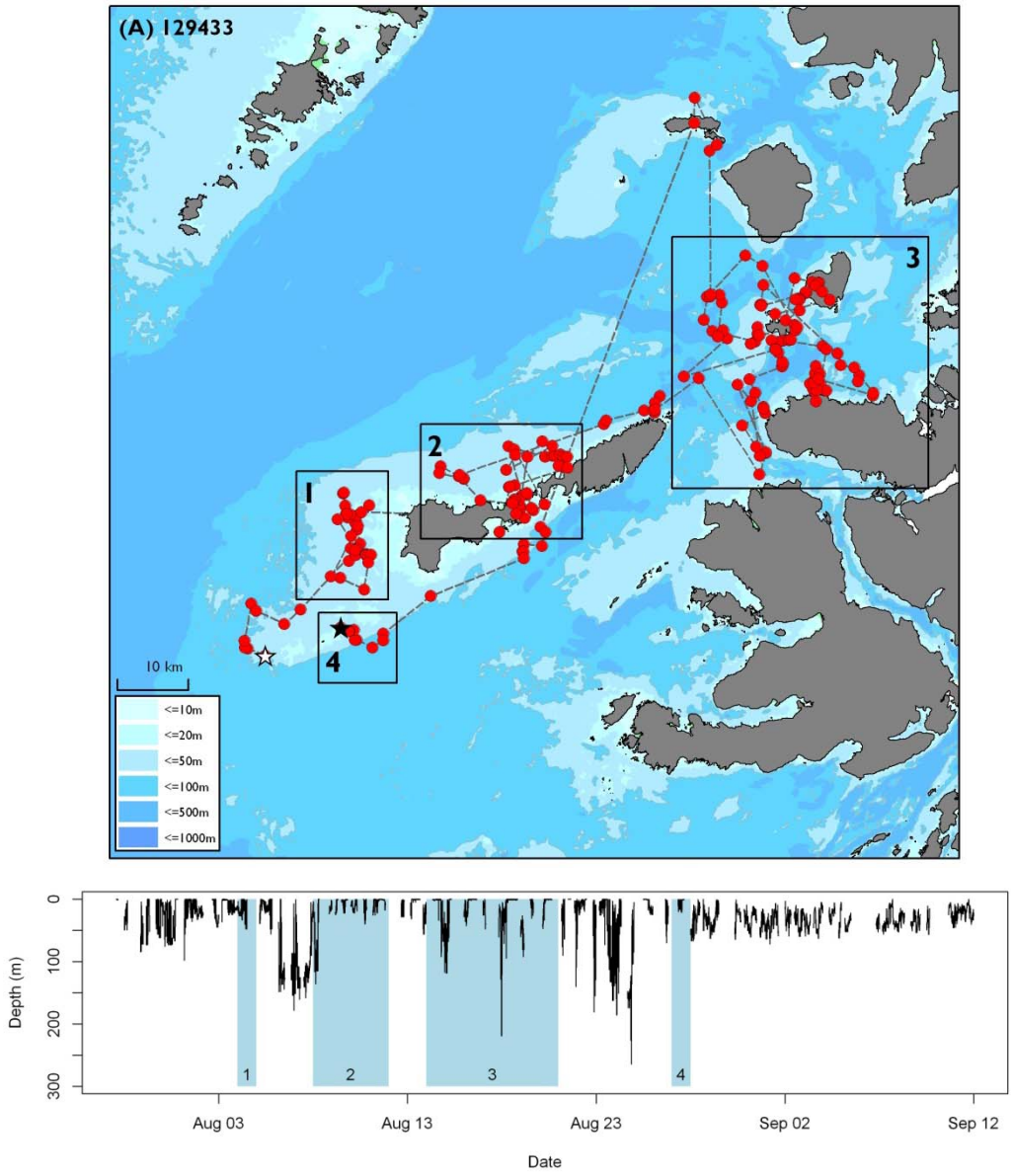

Figure 20. Basking shark depth use from SPLASH-F tags in 2013. *Locations of basking sharks tracked with a SPLASH-F tag (red circles; upper panel). First location received following tagging (white star), final location received (black star). Average depths recorded at 5-min. intervals (lower panel). 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).

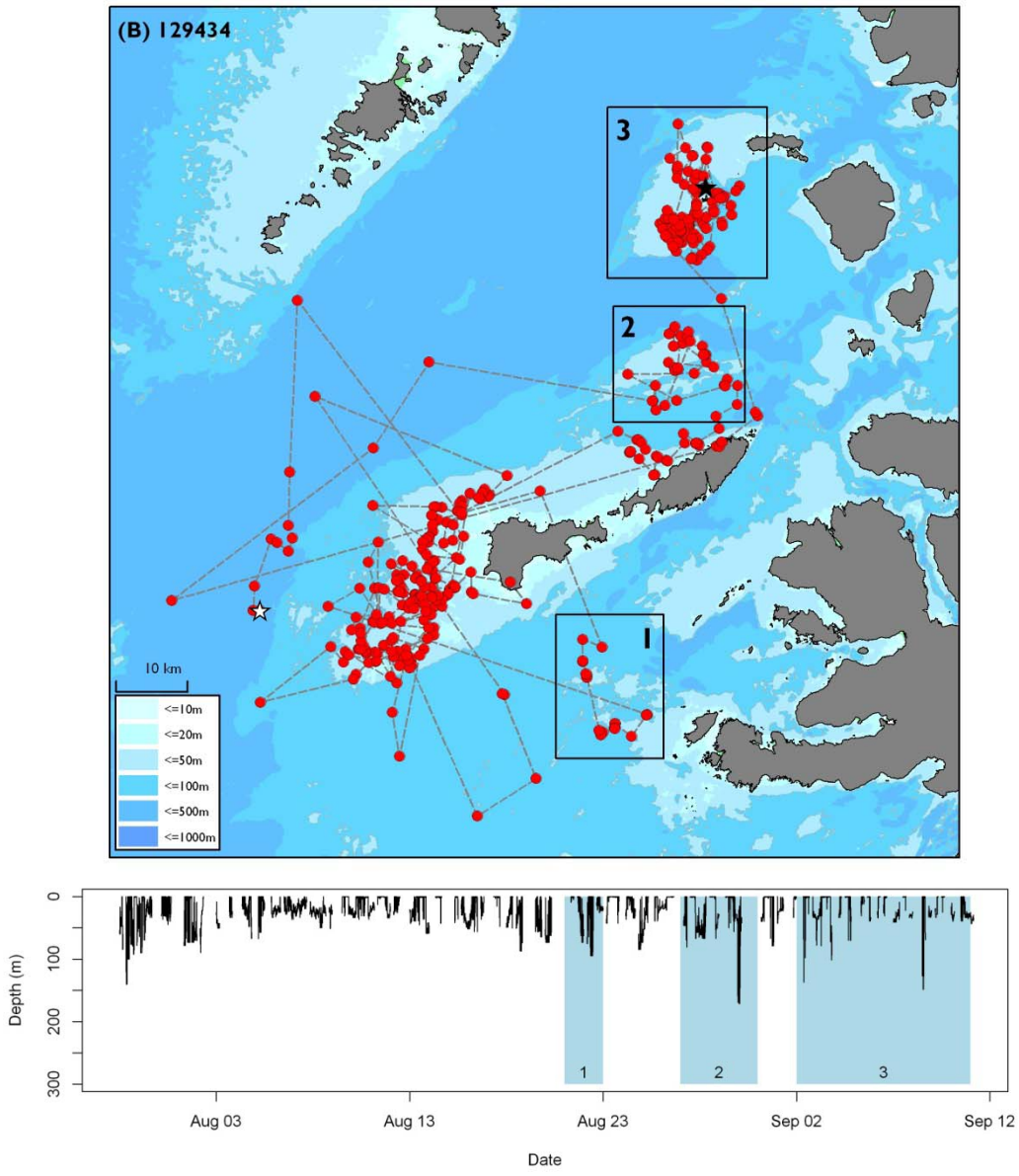

Figure 20 Continued. Basking shark depth use from SPLASH-F tags in 2013.

3.10 Depth use by time of day

The percentage of time spent between the surface and 10m depth (near-surface waters) for each day was determined at 4-hour intervals using data collected during the first 28 days of basking sharks tracking by PAT-F tags in 2012 (N = 9).

For the night-time periods, 00:00 to 04:00h and 20:00 to 04:00h, tagged basking sharks spent 11.8% and 8.0% of time (medians) in near-surface waters respectively. For the day-time periods, 04:00 to 08:00h, 08:00-12:00h, 12:00h to 16:00h and 16:00 to 20:00h, tagged basking sharks spent 10.6%, 4.2%, 4.0%, 6.8% of time (medians) in near surface waters respectively. Individual behaviour in the time spent in near-surface waters was more variable during night time periods (Figure 21).

Data recorded by MiniPAT tags deployed in 2013 operated on 24-hour interval summaries (a constraint of tag hardware), and as such could not be integrated with data collected by PAT-F in 2012.

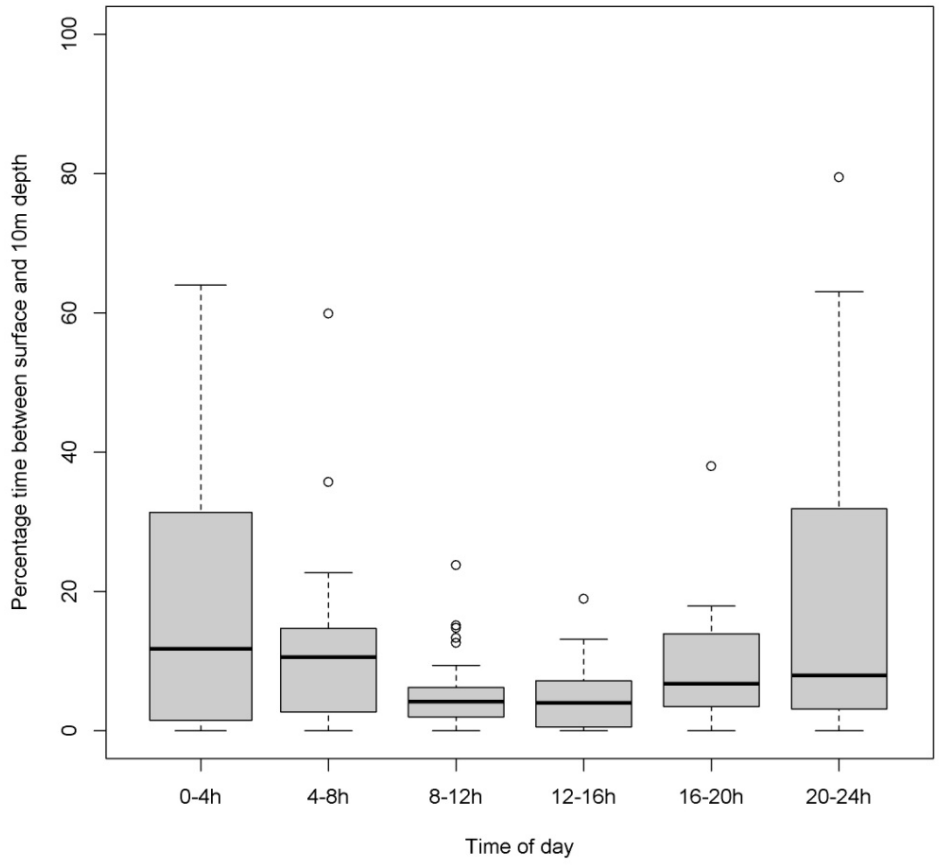

Figure 21. Basking shark depth use with time of day in the Sea of the Hebrides in 2012. *Percentage time spent between the surface and 10m depth within the first 28 days of PAT-F tag deployments (N = 9 basking sharks) summarised at 4-hour intervals. Each box represents the range of values observed from received data for the relevant time period. The bold horizontal line represents the median value for each vertical box, upper and lower extent of each box represents the 25th and 75th percentiles respectively. Dashed vertical lines extending from the top and bottom of the boxes indicate the range of values in the distribution to approximately 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.*

3.11 High resolution depth use from physically recovered tags

Four PAT-F tags from 2012 (Fig. 22 A-D) and two MiniPAT tags from 2013 (Fig. 22 E,F) were recovered and data were physically downloaded. These data, for at least the first 28 days of deployment, highlight a variety of depth use behaviour including diurnal movements, deep water habitat use and prolonged periods of near-surface behaviour. In some instances, sharks cover their minimum and maximum depth use over periods less than 24 hours. The depth use behaviour of one individual, in the second half of tag deployment, is unusual in comparison to other collected data; little vertical movement of the tag occurs with a tidally-induced oscillation apparent for a two week period before the tag failed (Fig. 22A). This tag was eventually recovered in Loch Fyne.

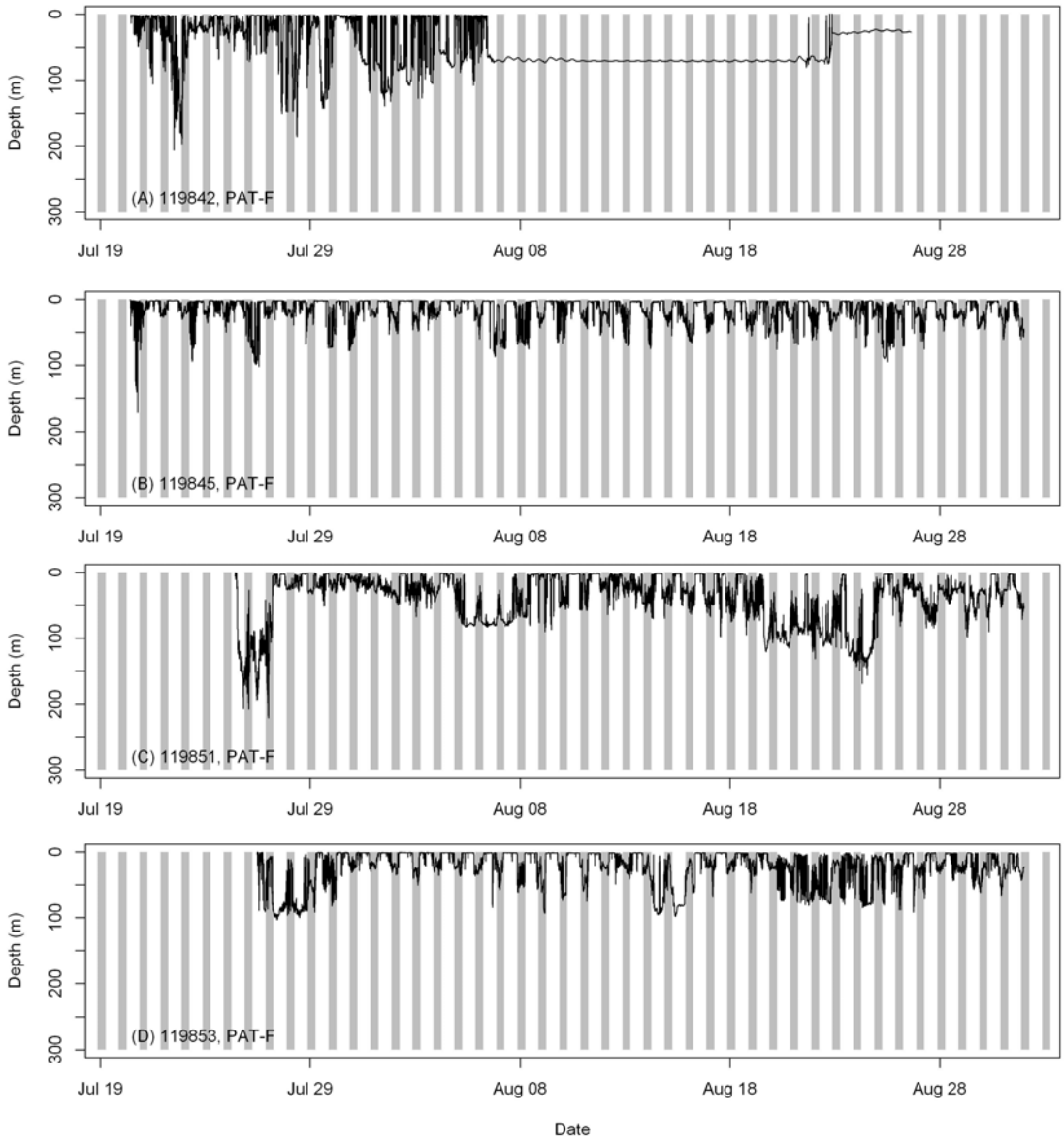

Figure 22. Basking shark depth use time series from physically recovered PAT-F, SPLASH-F and MiniPAT tags. *Depth recorded at a10-second frequency and summarised at 5 min. intervals from physically recovered tags. All figures plots displayed for period between 19th July and 28th August (N = 40 days). Grey bars indicate period between mean civil sunset and mean sunrise (9-hours duration, starting at 9pm daily) for the period.*

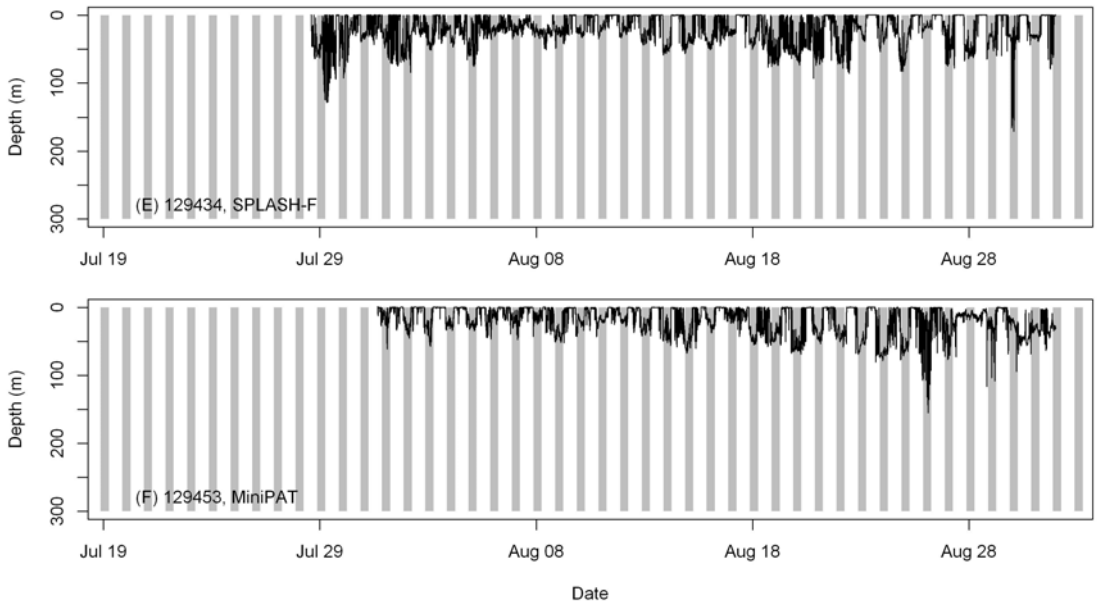

Figure 22. Continued. Basking shark depth use time series from physically recovered PAT-F, SPLASH-F and MiniPAT tags.

3.12 Long-term patterns of depth-use

Proportion of time spent at depth

Analysis of depth use data provided insight into basking shark depth preference. PAT-F tags (N = 4, deployed in 2012) and MiniPAT tags (N = 2; prematurely released in 2013) indicated use of a range of depths by basking sharks up to a maximum of 1,000m or more (Fig. 23). Depth use histograms (Fig. 23) suggest bimodality in depth selection, with a considerable proportion of time spent in near-surface waters (1-5m), followed by a separate mode occurring at depth, typically between the 25-100m depth classes (although two sharks spent approx. 25-30% of time within the 250 to 500m depth class; Fig. 23 D,E). The predominance of near-surface depth use in the months following deployment, when sharks are largely in the Sea of the Hebrides, along with behavioural observations during fieldwork and previously published data (Speedie *et al.* 2009), suggests this behaviour may be associated with near-surface foraging.

Maximum depth use

Five sharks fitted with PAT-F tags transmitted data that had been collected for 100+ days (Fig. 24), allowing a reconstruction of longer-term depth use. Data show a pattern of predominantly shallow depth use (<250m depth) with intermittent excursions to more than >750m depth (Fig. 24). Two sharks (119845, 119853) were recorded at maximum depths of 1000m and 1073m (April and January 2013 respectively). These deeper water events can only have occurred off the European continental shelf where seabed depths are 1,000m and greater. Depth use data indicate the potential for offshore movement between late September and early October with five shark's depth use increasing from <150m to over 250m depth (Fig. 24 A-C and E). Change in maximum depth use was most apparent on Sep. 30th 2012; a day when behaviour appears to change across individuals, moving from shallow to deeper water behaviour.

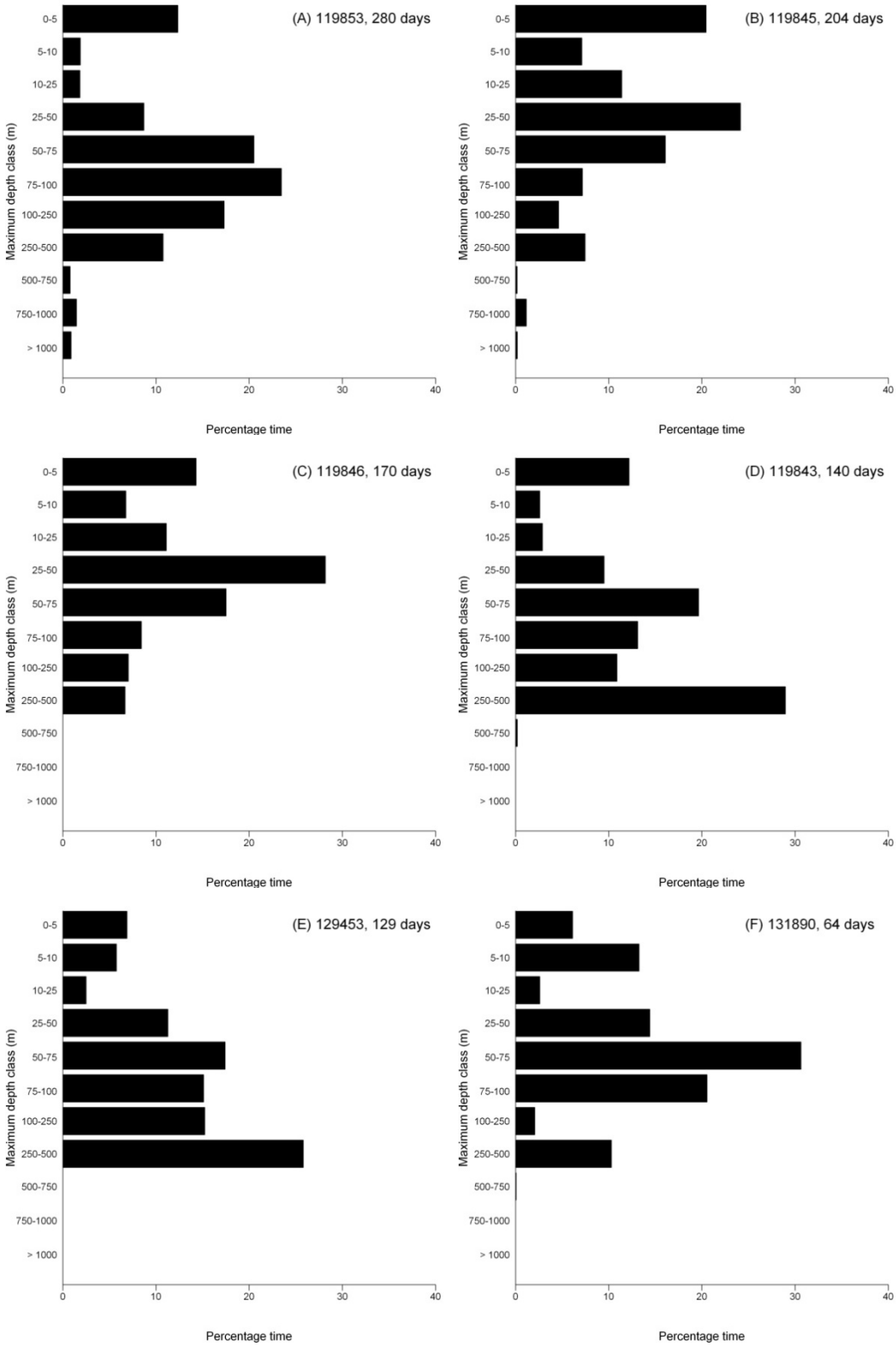

Figure 23. Histograms of time spent in depth classes. *Basking shark depth use from PAT-F (2012; A-D) and MiniPAT tags (2013; E-F). The six tags with the longest attachment durations are shown. Number of days data are indicated with tag ID.*

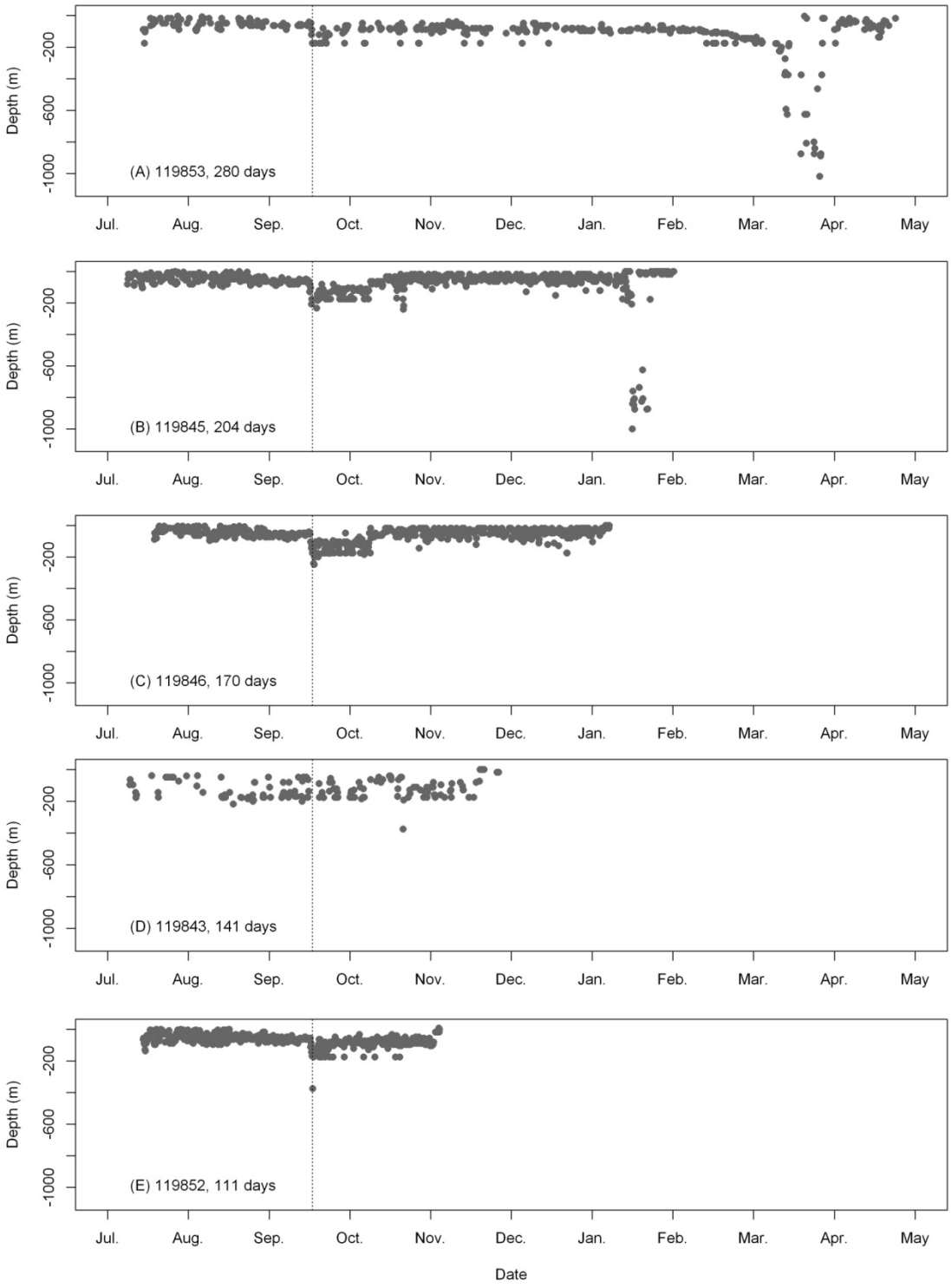

Figure 24. ***Maximum depths recorded at 4-hour intervals***. *Maximum depths (filled circles) from 4-hour summary intervals [non-contiguous] from five of the longest depth use time series collected by PAT-F tags in 2012. Tags sorted by decreasing attachment duration. Vertical dashed line indicates the 30th of September 2012 where depth-use behaviour appears to change across individuals. The majority of dives were to less than 200m and deeper dives (more than 500m) tend to occur mid-winter to spring. See also Figure S3 for dive data from PAT-F tags with deployments 20 days or less.*

3.13 Depth use and temperature from transmitted time series data

MiniPAT were programmed to gather continuous time series style data (10-min. intervals) on depth use and ambient temperature and transmit to over-passing satellites upon tag detachment (Fig. 25); this is a comparatively novel development in archival and transmitting satellite tag technology. Data of this type were received from two prematurely detached MiniPAT tags deployed in 2013. Transmitted time series data from the remaining MiniPAT tags (programmed to detach in spring 2014) will be more thoroughly analysed in subsequent reports. Preliminary oversight of received data show that encountered water temperature ranged from 9.4 to 15.2˚C and 9.7 to 15.3˚C for sharks instrumented with tags 129453 (Fig. 25A) and 131890 (Fig. 25B) respectively.

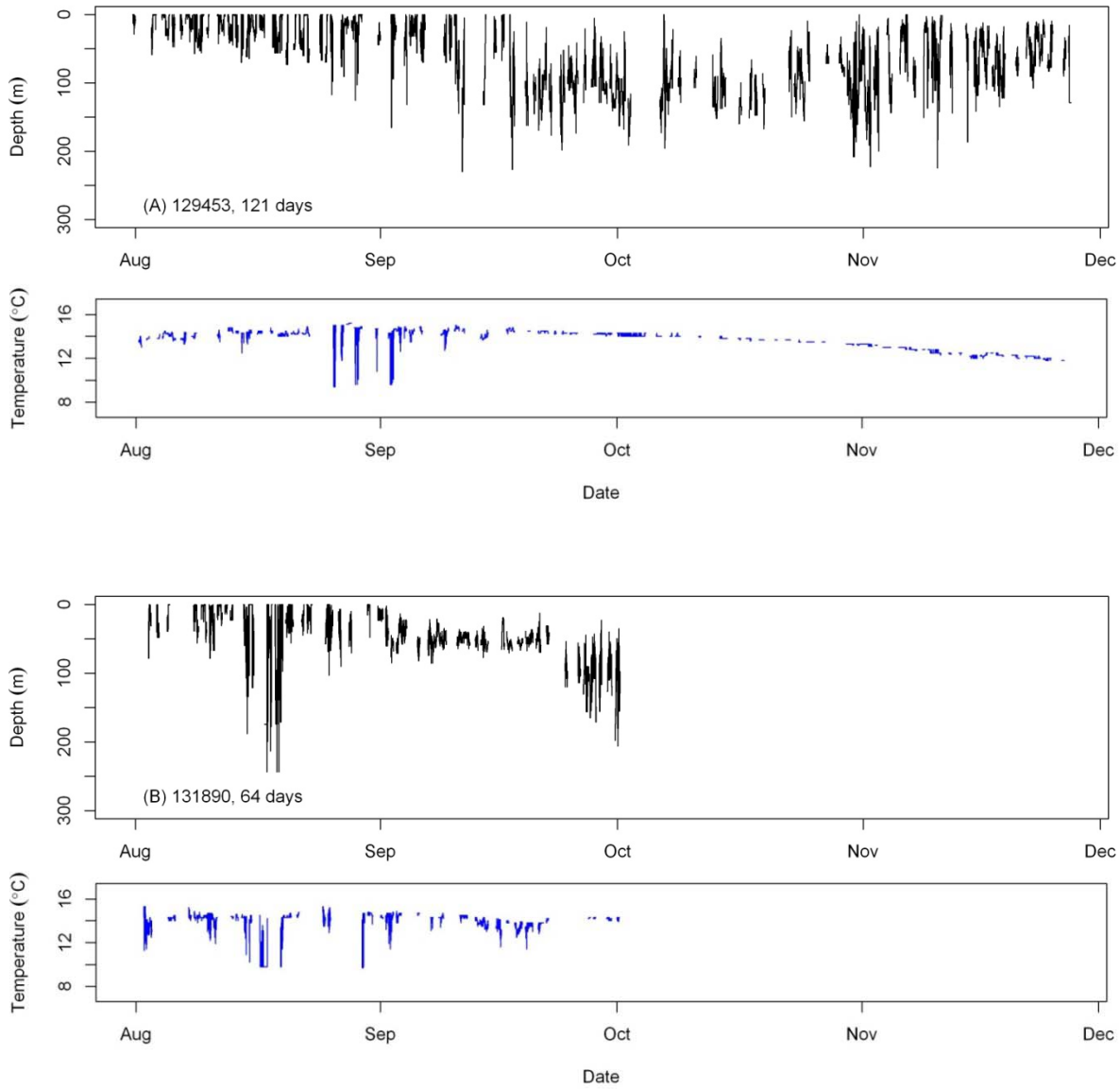

Figure 25. Basking shark depth utilisation and ambient environmental temperature time-series from MiniPAT in 2013. *Mean depths (upper panels; black line) and mean temperatures (lower panels; blue line) calculated at ten-minute intervals [non-contiguous] from two prematurely detached MiniPAT tags. Tags sorted by decreasing attachment duration.*

3.14 Time at temperature

PAT-F tags summarised the time study animals spent within defined temperature ranges (2˚C ranges from 0 to 28˚C; Fig. 26). Four sharks experienced water temperatures between 10 and 18°C, with two sharks experiencing temperature below 10°C (Fig. 26 A,B). Time at temperature histograms indicate the vast majority of time was spent in water temperatures between 12 and 16°C.

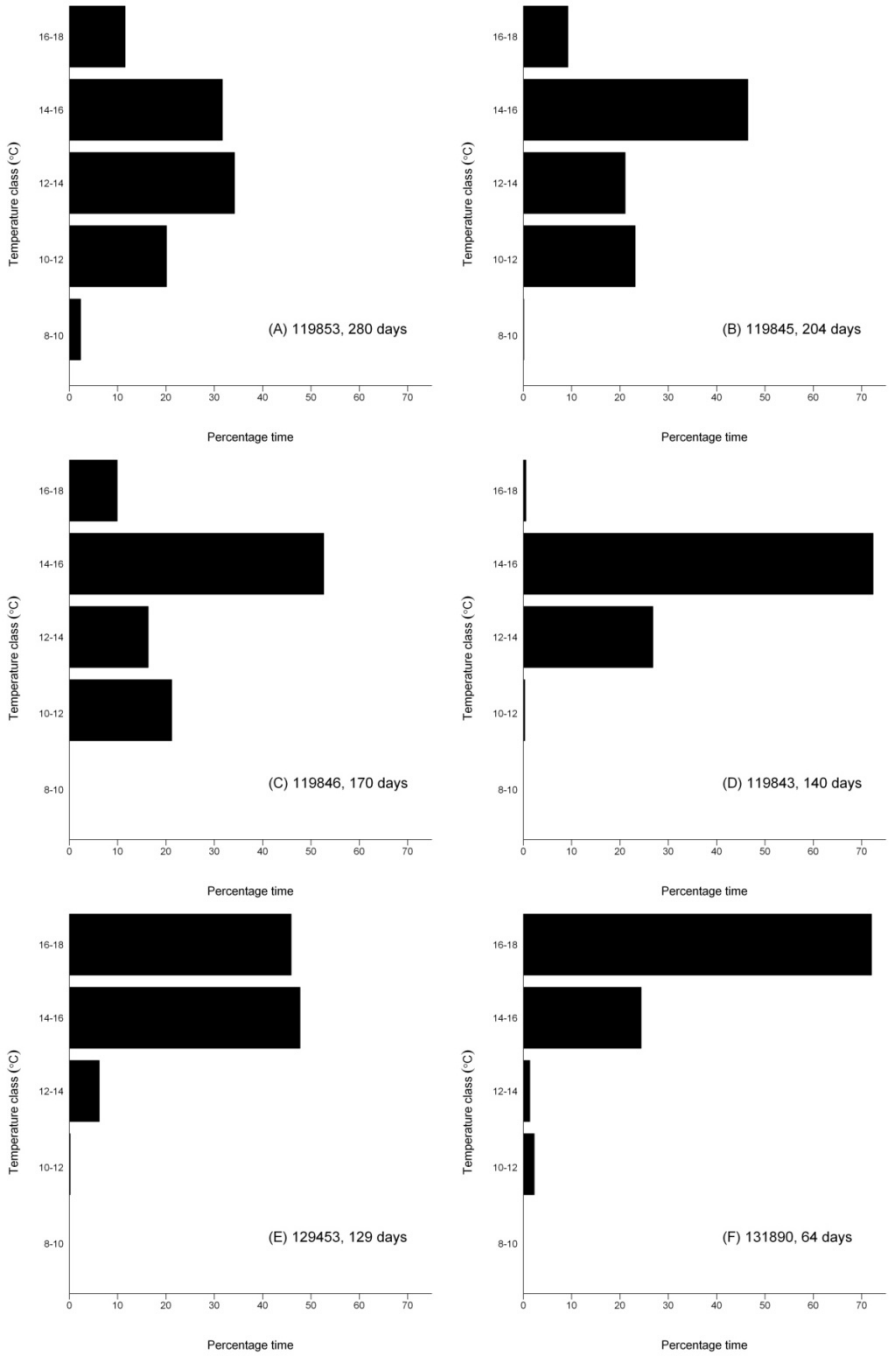

Figure 26. Histograms of time spent in temperature classes. *Water temperature encountered by basking sharks tracked by PAT-F (2012; A-D) and MiniPAT tags (2013; E-F); the six tags with the longest attachment durations. Number of days data are indicated with tag ID.*

4. DISCUSSION

4.1 Overview

The deployment of a wide range of 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 beyond. This study is the first, to the authors' knowledge, to deploy this combination of tag types. 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 September). The results of the tagging show seasonal residence over a period of two years to coastal regions. Previous efforts to track this species, with tags deployed in the southern English Channel, the Clyde Sea and the Isle of Man, 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.

Several sharks tracked in this study headed south into the Celtic and Irish Seas, and two individuals moved as far south as the northern African coast; movements that were recorded from early autumn onwards (approx. October). Movements within the north-east Atlantic, such as these, have been described from earlier tracking studies (Sims *et al.* 2003, Gore *et al.* 2008). When considered together, data from tracking studies suggest the importance of coastal waters to the west of the UK and Ireland. It would seem regular seasonal migrations of varying distance and depths throughout these coastal and offshore waters are commonplace. Evidence suggests there may be a general trend of southerly migration from Scottish waters after summer, although it is still to be elucidated if the same sharks return north again and repeat migrations annually. However, there has been no evidence to show more northerly migration than the Sea of the Hebrides (only one shark moved to northern Skye in this current study), despite basking sharks being present in Norway (see Compagno (2001)).

4.3 Key areas of basking shark occurrence and MPAs

Location data collected from satellite tagged basking sharks lend support to the existence of the hotspots, in that areas emerge that are used persistently through the months July to September. Key areas identified remained broadly within the MPA search location, with three smaller more frequently occupied areas identified. Some individuals utilised more than one of these smaller areas during the summer, and displayed occasional movements to the edges of the MPA search location boundary (and further) before returning back again. Without comprehensive knowledge of basking shark distribution and abundance throughout their range it is difficult to contextualise these hotspots at the regional (north-east Atlantic) and global level.

Protecting highly mobile species, such as basking sharks, is inherently difficult due to the large 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 & Gerber 2004). Waters off the west coast of Scotland have been identified as basking shark ‘hotspots’ from analysis of public sightings (Witt *et al.* 2012) and boat-based surveys (Speedie *et al.* 2009) and may therefore represent candidate areas for protection.

The area of the Skye to Mull MPA search location encompassed 86% of locations gathered within the first 28 days of tracking and 83% of locations over summer months (July to September). These data provide an important contribution to the evidence-base in relation to the spatial scale of the search location and the contribution that it may make to the conservation of basking sharks. 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 (Clark 1996, Lauck *et al.* 1998, Hooker & Gerber 2004). We highlight that such a conservation goal could be achieved in the Sea of the Hebrides.

Seasonal 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.

We observed such site fidelity in satellite tracked basking sharks in both 2012 and 2013, where individual sharks demonstrated persistent use of the coastal zone during summer months; however, the degree of fidelity observed differed considerably. Some undertook forays outside the boundaries of the Skye to Mull MPA search location returning relatively quickly to core areas, while others showed heightened 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).

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 (mean 39m) over rocky substratum, with relatively warm surface temperatures (mean 13.9˚C) and low to moderate tidal speeds (mean 0.3m.s^{-1}). Assuming their preference remains constant, or that monitoring can highlight if preferences change, these factors could be utilised in the designation 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.

The extent to which environmental features are correlative versus predictive for basking shark presence is difficult to determine. Some studies have documented feeding aggregations of basking sharks near frontal activity (Sims & Quayle 1998, Sims 2008) 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 & Merrett 1997, Sims & 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) suggested that basking sharks departed north-west Atlantic water in response to temperature falling below 12.7°C.

Emerging 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).

4.4 Medium and long-range movements

Recording longer distance movements was a key objective for the project. Following the summer period of site fidelity, we observed migrations spanning waters of multiple European nations and geopolitical zones.

We documented the movement of two basking sharks to Madeira and the Canary Islands, the most southerly tracking of a basking shark in the north-east Atlantic. 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 capability to undertake ocean basin wide movements.

Six individuals in the present study travelled south to the Celtic and Irish Seas where tags ceased transmission. It is unclear whether these 'end' locations represented the final destination of these sharks annual cycle of movement or whether these sharks may have continued to more southerly latitudes or out into the north-east Atlantic. Basking sharks have also been shown to travel northwards from the Isle of Man towards Scottish waters (Fig. 27, N = 3), with one individual moving into the extent of the Skye to Mull MPA search location. These data were collected by Manx Basking Shark Watch in the summer of 2013 using towed SPOT tags.

Movement of basking sharks into and away from the Skye to Mull MPA search location (this study and findings from Fig. 27) along with tag release locations from PAT-F and MiniPAT tags suggests a strong connectivity between the Irish Sea and waters to the west of Scotland. The northern channel of the Irish Sea appears to facilitate movement between these two regions (waters to the west of Scotland and the Irish Sea), potentially exhibiting evidence of a migratory corridor.

These patterns of movement suggest 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.

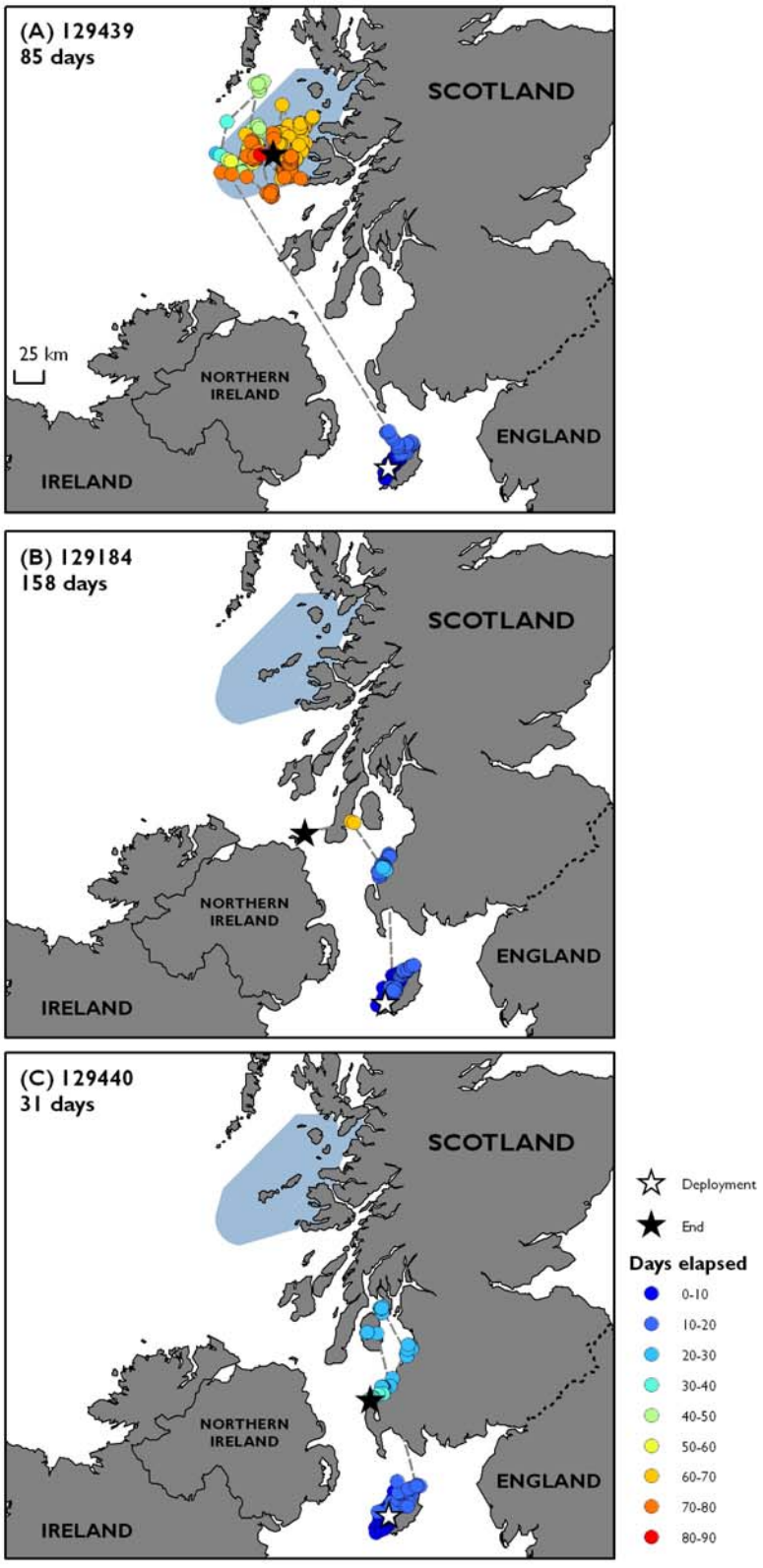

Figure 27. Movements of basking sharks tracked with SPOT tags in 2012 from the Isle of Man. *Satellite-derived locations from basking sharks tagged in the water surrounding the Isle of Man. Shark tag ID, name (if applicable) and attachment duration indicated for each figure part. Note one basking shark (A) transmits from within the Skye to Mull search location. Dashed lines join consecutive locations but do not infer straight line movement. Skye to Mull MPA search location (blue polygon). Contains Ordnance Survey data © Crown copyright and database right 2013.*

4.5 Basking shark depth utilisation

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 (*Rhincodon typus,* Brunnschweiler *et al.* (2009), basking (Sims *et al.* 2005, Shepard *et al.* 2006), white (Klimley *et al.* 2002, Domeier & Nasby-Lucas 2008), scalloped hammerhead (*Sphyrna lewini,* Jorgensen *et al.* (2009)) and tiger (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).

The deepest depth previously recorded for any basking shark was 1,264 m (Gore *et al.* 2008), which superseded the 904m recorded by Francis & Duffy in 2002 (Francis & Duffy 2002), with Sims *et al.* (2003) also recording a basking shark occupying waters between 750 and 1000 m depth. During the present study, two sharks were recorded at 1,000 m and 1,073 m respectively, adding to this body of knowledge. Over the longer-term (months), depth data suggest basking sharks predominantly occupy the upper 250 m of the water column, but have the capacity to undertake extensive vertical movements.

Gathered data indicate that modal (most frequent) depths occupied by basking sharks in coastal waters to the west of Scotland, in particular around Coll and Tiree, are predominantly shallow, which may help to explain the high proportion of public sightings in the region (Witt *et al.* 2012). Nonetheless, depth data also highlight the considerable variability in behaviour.

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 Sims *et al.* (2005), 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 Skye to Mull MPA search location, 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). The data describing how basking sharks utilise the water column within key areas can contribute to discussions over the conservation of basking sharks e.g. providing a 3 dimensional picture of where most sharks are within the water column and when; as well as being useful in contributing to the estimation of shark numbers present in key areas from surface sightings data.

4.6 Anecdotal observations

Sexual or ontogenetic segregation

Segregation of foraging aggregations by body size or sex has been widely described in shark species (Klimley 1987, Wearmouth & Sims 2008), however, we found no evidence 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. It has been suggested that although juveniles are observed in the same feeding aggregation as adults (Berrow & Heardman 1994, Sims & Merrett 1997) juveniles may forage later in the season (Sims & Merrett 1997), i.e. that some temporal segregation may exist, which may have been a factor in low observation incidences of juveniles during this study.

Courtship behaviour

During fieldwork we observed a range of basking shark behaviour, 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 *et al.* 2000). This led Sims *et al*. (2000) to hypothesise that the southwest UK may represent an annual breeding area for basking sharks, although mating itself has yet to be observed (Sims *et al.* 2000). 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 captivity (Pratt & Carrier 2001), thus it is difficult to confidently assign the underlying reason for the behaviours we observed. Group related social behaviour has been reported regularly within areas of the Skye to Mull MPA search location (Speedie *et al.* 2009). Breeding is essential to the conservation of the species, and the behaviours preceding breeding can be important in breeding success. Spatially safeguarding the habitats where courtship-like activities occur will likely convey benefits for the basking shark, including on the west coast of Scotland.

4.7 Knowledge gaps and challenges

Satellite tags and attachment methods

This study made use of both 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. Problems were encountered predominantly with PAT-F tags. These devices had a higher than expected premature detachment rate, three tags failed to transmit data and we received a lower than expected number of Fastloc^{TM} locations. Nonetheless, the tags recorded a basking shark moving into the Clyde Sea, demonstrating connectivity between the Sea of the Hebrides and this region, one tag recorded the near circumnavigation of Ireland by a basking shark over a nine month period and other tags recorded deep diving events off the European Continental Shelf. 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 for sufficient durations, and thus reduced the opportunity to gather Fastloc^{TM} location data. Biofouling and insufficient buoyancy may be responsible for why data were never received from three tags.

Owing to relatively limited tracking durations in 2012, it is not possible to ascertain whether the majority of tagged basking sharks would have made longer-distance migrations (as was seen for two individuals). Data from tagging efforts in 2013 are still being received and so it is difficult to conclude on the frequency of this behaviour at this time. Future tracking work should aim to deploy devices that remain attached for longer durations to investigate these important questions. Multi-year deployments are now possible with emerging technology and battery capacity; however, the problem of tag retention remains and many projects have comparatively short durations. However, many of the SPOT tags (N = 10) and MiniPAT tags (N = 8) deployed in 2013 appear to be attached to their study animals (as of Jan. 31st 2014) and so the potential remains to describe year-round movements.

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 liaising with Manx Basking

Shark Watch to share information about best tag attachment practice, including optimising tether lengths and materials.

Behaviour

It is not immediately apparent if the environmental conditions in which we observed tracked basking sharks are representative of their absolute preference or whether environmental conditions can act as drivers of key events, 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 and represent a response to a combination of a number of factors, 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 we have shown 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 & Boeseman 1954), but remains to be empirically demonstrated.

5. CONCLUSIONS

a) The present study successfully collected data from an unprecedented range of tag types on 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) Interpretation and conclusions presented in this report are based on initial analyses of collected data, with some aspects of analysis focusing on data collected over short periods of tracking (first 28 days; determined largely by shorter tracking durations in 2012). This approach has enabled between year comparisons, particularly with respect to space-use in the waters of the Inner Hebrides.

c) Data confirm that sharks remain predominantly within coastal waters between July and late September, showing seasonal site fidelity within the Skye to Mull MPA search location. Basking shark behaviours, previously attributed to courtship display, were also observed in these areas of persistent usage.

d) After the summer months, October onwards, sharks then spend more time at greater depth, with all sharks for which location data is available, moving in a southerly direction likely further afield. It seems plausible that the Irish Sea represents an important migratory corridor, although at least one shark utilised the west coast of Ireland in its migration south.

e) Basking sharks can occur down to 1,000m depth, but in coastal areas make surprisingly shallow dives. Use of shallow waters in the coastal zone likely increases the chances of positive and negative interaction between sharks and humans e.g. increased likelihood of people seeing and enjoying watching basking sharks but also potentially greater risks of propeller strike.

f) The use of high spatial resolution Fastloc^{TM} tags has helped to confirm the utility and application of less costly SPOT tags, which provided the majority of basking shark location data in the project.

g) Further techniques, including multi-channel bio-logging units, acoustic arrays and tri-axial accelerometry may help to further investigate the strategies and behaviours exhibited by basking sharks and potentially address the knowledge gaps highlighted in this report.

h) Data demonstrate the importance e.g. key areas of high usage, seasonal site fidelity, and reputed courtship behaviour, of waters off the west coast of Scotland and, in particular, the waters of the Skye to Mull MPA search location for basking sharks. When interfacing public sightings, predictive habitat modelling and satellite telemetry, it becomes clear that the west of Scotland is likely a stronghold for the species in the north-east Atlantic.

i) As this study sampled only a subset of the available population, it is difficult to fully describe the proportion of the population that adopt differing movement strategies (horizontal and vertical), especially with respect to long-range movements.

j) Open and collegiate sharing of knowledge is important to be able to see 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.

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7. SUPPLEMENTARY MATERIALS

Table S1. Basking sharks and the Skye to Mull MPA search location. Percentage of locations occurring within Skye to Mull MPA search location during the first 28 days of tracking for each individual and over the summertime period (July to September) when tags were actively transmitting.

2012			
Tag ID	**Type**	**First 28d**	**Summer**
119854	SPOT	100	100
119855	SPOT	100	100
*119856	SPOT	52	34
120496	SPOT	96	94
120497	SPOT	94	94
120498	SPOT	27	10
120499	SPOT	100	100
120500	SPOT	95	95
Mean		83	78
SD		28	35
Min		27	10
Max		100	100

2013			
Tag ID	**Type**	**First 28d**	**Summer**
129435	SPOT	96	83
129436	SPOT	96	94
129437	SPOT	95	95
129438	SPOT	100	97
129439	SPOT	100	100
129440	SPOT	96	90
129441	SPOT	46	48
129443	SPOT	100	95
129444	SPOT	82	90
129445	SPOT	100	100
129446	SPOT	100	93
*129447	SPOT	87	89
129448	SPOT	100	100
129449	SPOT	80	81
129450	SPOT	57	59
Mean		89	88
SD		17	15
Min		46	48
Max		100	100

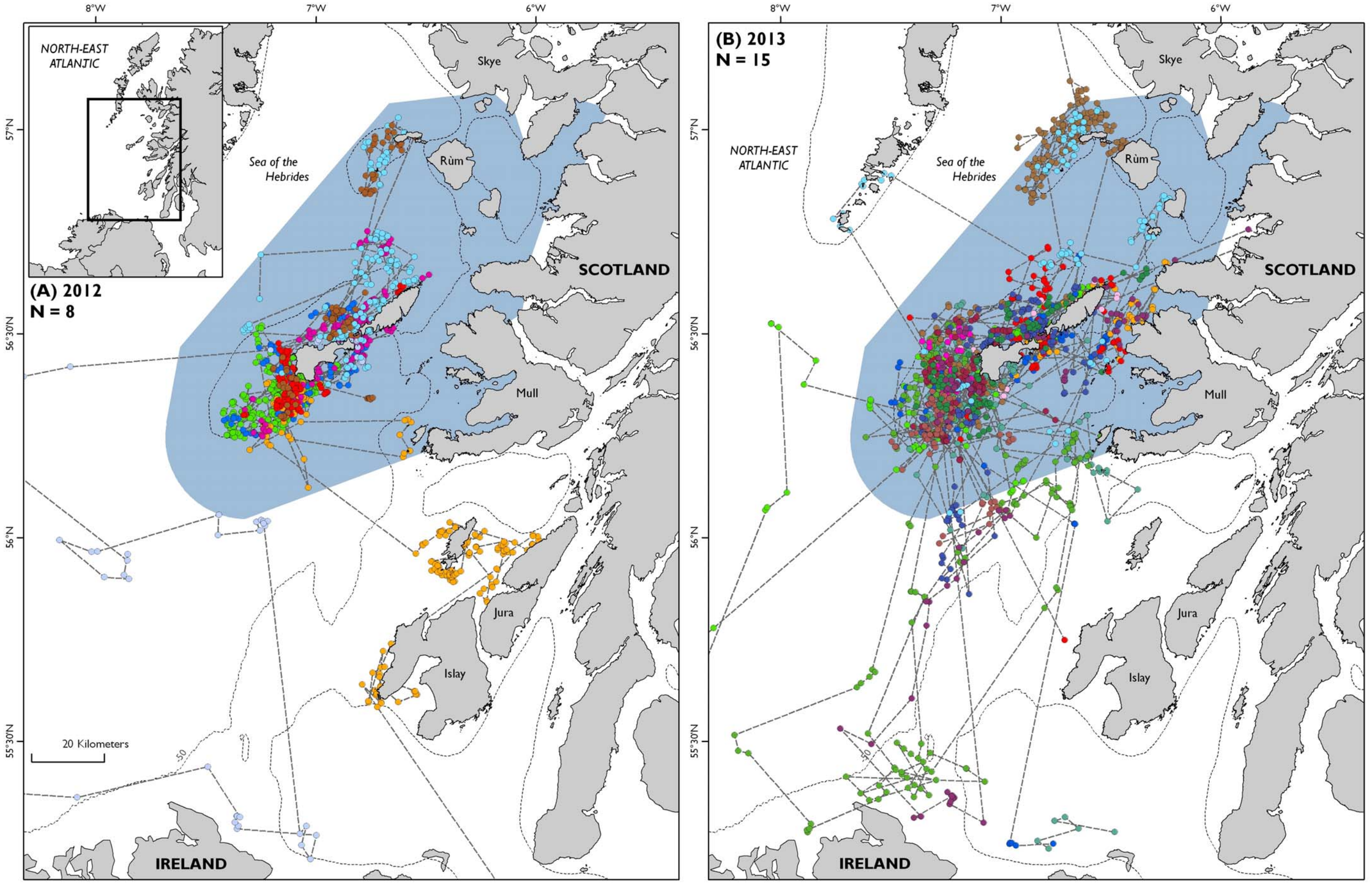

Figure S1. Satellite tracking locations of basking sharks gathered in the Sea of the Hebrides from SPOT tags during (A) 2012 and (B) 2013. *Individual shark locations represented by single colour points, dashed line joins consecutive locations. Skye to Mull MPA search location (blue polygon). Contains Ordnance Survey data © Crown copyright and database right 2013.*

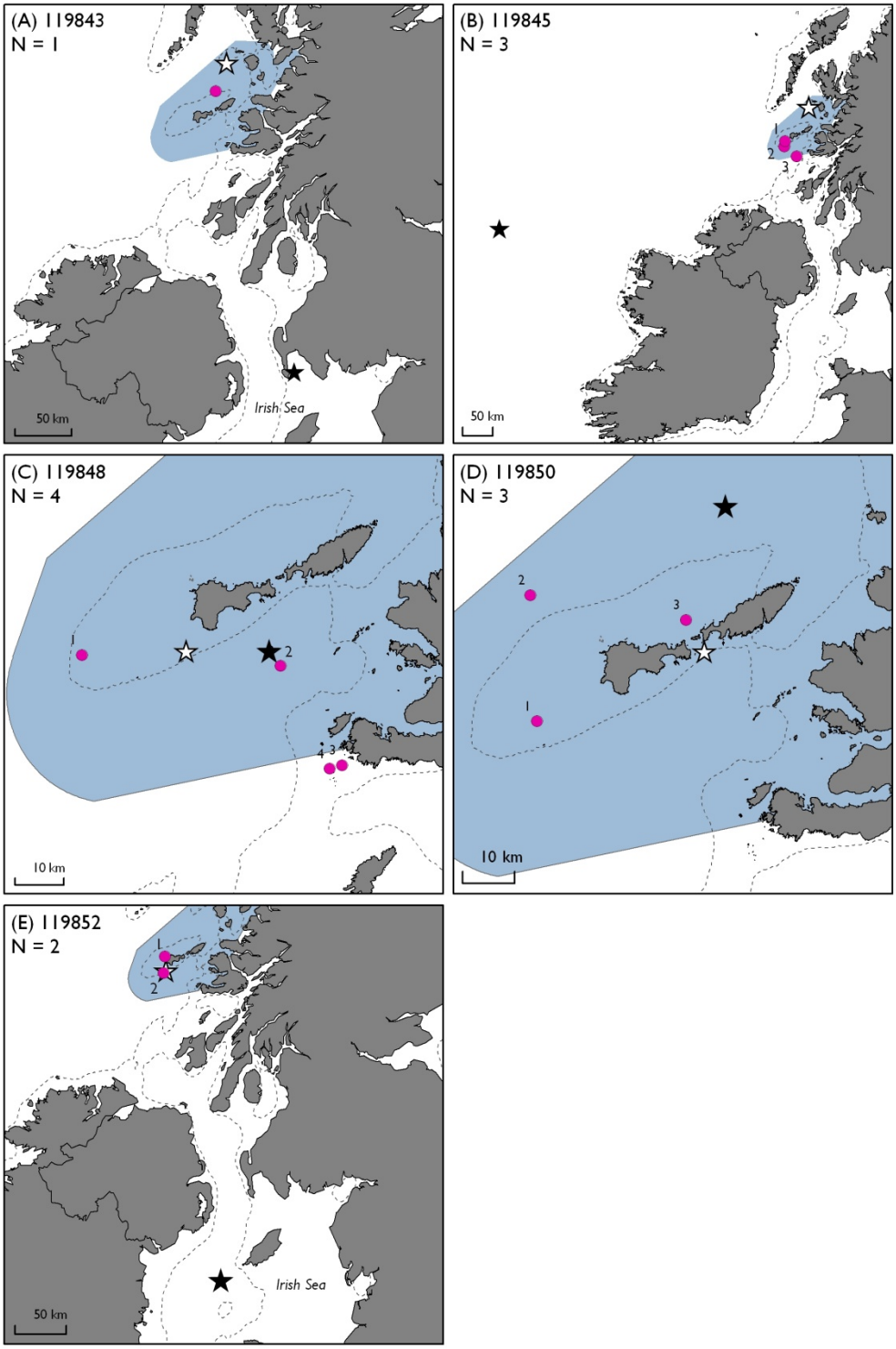

Figure S2. GPS locations of basking sharks from PAT-F tags in 2012*. GPS locations gathered from tags producing 4 or less. GPS locations sequentially numbered in order of occurrence. PAT-F tag attachment locations (empty stars), PAT-F tag pop-off locations (filled stars). Number of locations given with tag ID. Skye to Mull MPA search location shown (blue polygon). 50m depth contour (broken grey line; GEBCO). Contains Ordnance Survey data © Crown copyright and database right 2013.*

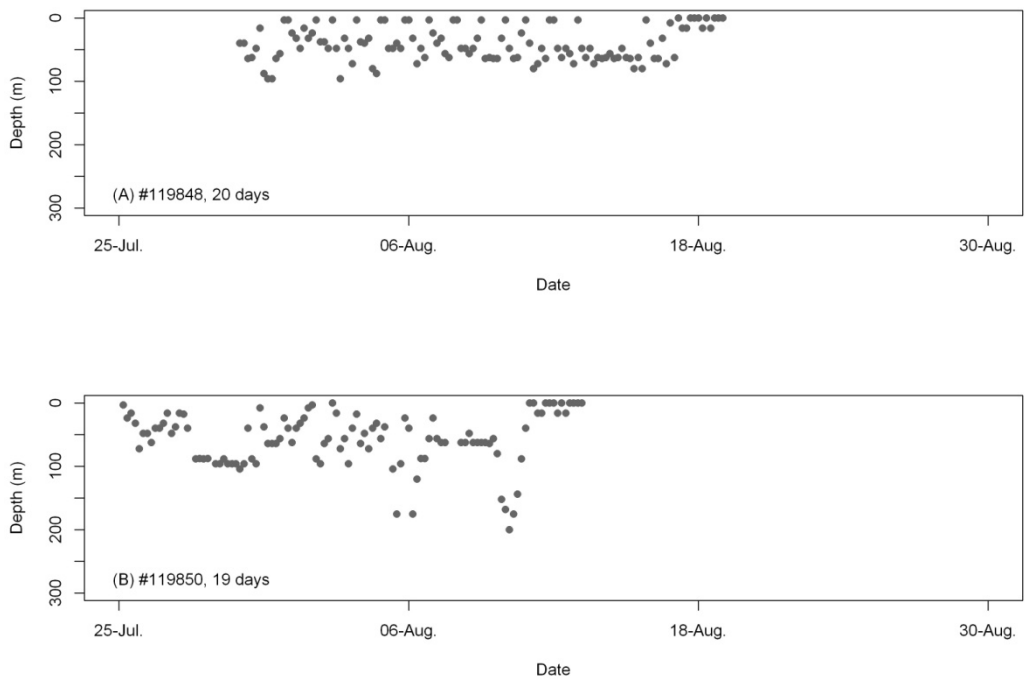

Figure S3. Maximum depths recorded at 4-hour intervals*. Maximum depths (filled circles) from 4-hour summary intervals [non-contiguous] collected by PAT-F tags.*

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