

Basking shark movement ecology in the north-east Atlantic



Submitted by

Philip David Doherty

To the University of Exeter as a thesis for the degree of

Doctor of Philosophy in Biological Sciences

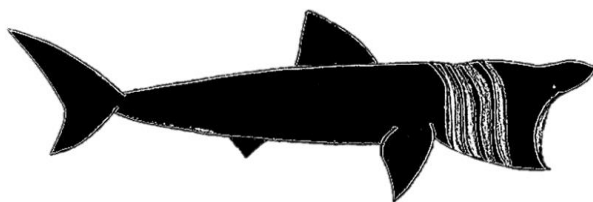
March 2017

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

A handwritten signature in blue ink, which appears to read "Philip Doherty". The signature is stylized and cursive.

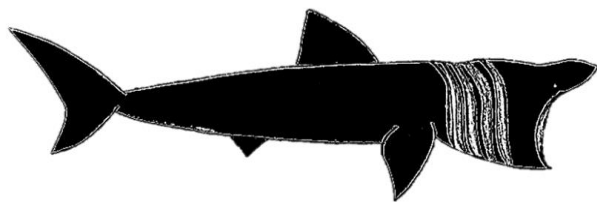
.....
Philip D. Doherty



Abstract

Large marine vertebrate species can exhibit vast movements, both horizontally and vertically, which challenges our ability to observe their behaviours at extended time-scales. There is a growing need to understand the intra- and inter-annual movements of mobile marine species of conservation concern in order to develop effective management strategies. The basking shark (*Cetorhinus maximus*) is the world's second largest fish species, however, a comprehensive understanding of this species' ecology, biology and spatial behaviour in the north-east Atlantic is currently lacking. This thesis seeks to investigate the movement ecology of basking sharks using a suite of technologies to integrate biologging, biotelemetry, remotely sensed data, and ecological modelling techniques.

I use satellite telemetry data from basking sharks tracked in 2012, 2013 and 2014 to quantify movements in coastal waters off the west coast of Scotland within the Sea of the Hebrides proposed MPA. Sharks exhibited seasonal residency to the proposed MPA, with three long-term tracked basking sharks demonstrating inter-annual site fidelity, returning to the same coastal waters in the year following tag deployment (**Chapter 2**). I reveal that sharks tracked into winter months exhibit one of three migration strategies spanning nine geo-political zones and the High Seas, demonstrating the need for multi-national cooperation in the management of this species across its range (**Chapter 3**). I examine the vertical space-use of basking sharks to improve an understanding of the processes that influence movements in all dimensions. Basking sharks exhibit seasonality in depth-use, conduct deep dives to over 1000 m, and alter their depth-use behaviour in order to remain within thermal niche of between 8 and 16 °C (**Chapter 4**). Finally, I combine contemporaneous data recorded by deployed satellite tags with remotely sensed environmental data to employ novel ecological modelling techniques to predict suitable habitat for basking sharks throughout the Atlantic Ocean (**Chapter 5**).



Acknowledgements

People often talk of that one special teacher or mentor that inspired a passion for a subject or were instrumental in furthering your career. I have been extremely lucky to have two of these, my supervisors, Matt and Brendan. You two form the perfect combination of meticulous attention to detail, and the ability to cut straight to it, see the big picture and put it all into context. I have learned so much from the two of you and I am sincerely grateful for all your help and advice. Thank you for the opportunity, it's been a blast.

To the two best men I know, my brother Steve, and my dad; you are, and have always been extremely encouraging, and have not once flinched at helping and supporting me follow this slightly absurd dream of researching sharks. I can't thank you enough.

This project has been a massive collaborative effort, and a special thanks to: Scottish Natural Heritage (SNH), the crew of Sea Life Survey, especially Jimbo, you guys made the fieldwork really easy and an absolute joy, and to all my co-authors for invaluable insight into the nuances of animal tracking, amazing knowledge of the technology, tagging methods, and study sites. This really would have not been possible without all your help.

The University of Exeter Penryn Campus is an amazing place to work. The academics, post-grads, techs, support staff and students (all too numerous to name) make it what it is and I have loved my time here. Special shout out to the Marine Verts group, it has been great learning from and alongside all of you and for providing light relief when most need, it really is an awesome group.

Thanks to the "Winch" crew for reminding me that there is more to life than science and the residents of 289 Longfield (plus Faye, Jenny and Dom) for lots of adventures and laughs; loads of great memories.

To the Thompson family (including Merrick's and Davies'), you have always shown great enthusiasm in my work and encouraged me and Faye to pursue our dreams. Thank you for your support and welcoming me into the family.

Finally, to Faye, thank you for going on this journey with me. Both of us doing our PhDs at the same time is probably a good test of our nerves, but we did it. You have been so supportive and patient along the way and have always managed to make me smile, which I know, is not always the easiest thing to do, so thank you for everything you do.

Table of contents

Abstract	3
Acknowledgements	5
List of tables	10
List of figures	11
Author’s declaration	12
Publications	13
Definitions	15
Chapter 1: General introduction	17
Movement ecology	19
Conservation status of chondrichthyans.....	22
The basking shark.....	23
Threats and conservation actions	25
Device attachment effects	27
Study area	29
Thesis aims and outline.....	32
Chapter 2: Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed marine protected area	33
Abstract	35
Introduction	36
Methods.....	38
Results	41
Discussion.....	48

Chapter 3: Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic.....	54
Abstract	57
Introduction	58
Results	61
Discussion.....	69
Methods.....	75
Chapter 4: Vertical behaviour of basking sharks reveals seasonal depth-use, extreme diving events, and behavioural thermoregulation.....	79
Abstract	81
Introduction	82
Methods.....	84
Results	87
Discussion.....	97
Chapter 5: Pan-oceanic niche modelling for an elusive marine vertebrate: Basking sharks in the Atlantic.....	103
Abstract	105
Introduction	106
Methods.....	109
Results	115
Discussion.....	123
Chapter 6: General discussion.....	130
Overview	133
Basking shark movement ecology.....	133
Conservation	135
Limitations.....	135
Future research areas	137
Concluding remarks.....	139

References	141
Appendices	173
Appendix A	175
Appendix B	183
Appendix C	195
Appendix D	197
Appendix E.....	207
Appendix F.....	215

List of tables

Chapter 1

Table 1. National and international regulations and protection measures for basking sharks.....	27
---	----

Chapter 2

Table 1. Space-use within proposed MPA boundaries.....	44
--	----

List of figures

Chapter 1

Figure 1. Study area.....	31
---------------------------	----

Chapter 2

Figure 1. Movement of tracked basking sharks in summer months.....	42
Figure 2. Identifying areas of relative importance.....	45
Figure 3. Inter-annual site fidelity.....	47

Chapter 3

Figure 1. Minimum latitude observed for satellite-tracked basking sharks	63
Figure 2. Overall post-summer distribution.....	64
Figure 3. Grid density enumeration identifying areas of relative importance	66
Figure 4. Plots showing minimum monthly latitudes occupied	67
Figure 5. Proportion of daily maximum depths for associated migration strategy	68

Chapter 4

Figure 1. Depth distribution by time of day for each season.....	88
Figure 2. Time spent at varying depths.....	90
Figure 3. Grid density enumeration of minimum and maximum depths	91
Figure 4. Basking shark winter depth-use time-series data.....	92
Figure 5. Basking shark depth-use time series data.....	94
Figure 6. Temperature by month experienced by tracked basking sharks.....	95
Figure 7. Time spent in waters above 10 m following a dive.....	95

Chapter 5

Figure 1. Locations of satellite tracked basking sharks.....	116
Figure 2. Winter depth use (October – March).....	117
Figure 3. Summer EENM model predictions of suitable surface habitat	119
Figure 4. Summer EENM model predictions of suitable habitat in the north-east Atlantic	120
Figure 5. Winter EENM prediction of suitable habitat.....	122
Figure 6. Correlation plots validating HYCOM temperature-at-depth data layers.....	123

Author's declaration

All chapters presented in this thesis were written by Philip D. Doherty under the supervision of Dr Matthew J. Witt and Professor Brendan J. Godley who provided guidance throughout. Additional comments were provided by Dr Lucy A. Hawkes and Dr Stephen K. Pikesley for Chapter 5 and from all co-authors on the publications listed.

All satellite tag attachment procedures were approved by and carried out in accordance with the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (issuing Project Licence 30/2975), under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971), and internally through the University of Exeter's animal welfare and ethics review board (AWERB).

The research in this thesis was funded by Scottish Natural Heritage (SNH), with Dr Matthew J. Witt as Primary Investigator (PI). Philip D. Doherty was supported by a Natural Environment research Council (NERC) PhD studentship NEL/L501669/1.

All photographs used in this thesis have associated credit within the image and are used with consent of the owner.

Publications

At the time of submission the following two chapters have been published as they appear here:

Chapter 2: Published in Biological Conservation

Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed marine protected area

Doherty, P.D.^{1,2}, Baxter, J.M.³, Godley, B.J.^{1,2}, Graham, R.T.⁴, Hall, G.⁵, Hall, J.⁵, Hawkes, L.A.², Henderson, S.M.⁶, Johnson, L.⁷, Speedie, C.⁷, & Witt, M.J.^{1,2*}

¹Environment and Sustainability Institute, University of Exeter, Penryn Campus, Cornwall, TR10 9FE, UK.

²Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall, TR10 9FE, UK.

³Scottish Natural Heritage, Silvan House, 231 Corstorphine Road, Edinburgh, EH12 7AT, UK.

⁴MarAlliance, PO Box 283, San Pedro, Ambergris Caye, Belize.

⁵Manx Basking Shark Watch, Glen Chass Farmhouse, Glen Chass, Port St Mary, Isle of Man, IM9 5PJ.

⁶Scottish Natural Heritage, Great Glen House, Inverness, Scotland, IV3 8NW, UK.

⁷Wave Action, 3 Beacon Cottages, Falmouth, TR11 2LZ, UK.

Chapter 3: Published in Scientific Reports

Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic

Doherty, P.D.^{1,2}, Baxter, J.M.³, Gell, F.R.⁴, Godley, B.J.^{1,2}, Graham, R.T.⁵, Hall, G.⁶, Hall, J.⁶, Hawkes, L.A.², Henderson, S.M.⁷, Johnson, L.⁸, Speedie, C.⁸, & Witt, M.J.^{1, 2*}

¹Environment & Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK.

²Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK.

³Scottish Natural Heritage, Silvan House, 231 Corstorphine Road, Edinburgh, EH12 7AT, UK.

⁴Department of Environment, Food and Agriculture, Thie Sileau Whallian, Foxdale Road, St John's, Isle of Man, IM4 3AS.

⁵MarAlliance, PO Box 283, San Pedro, Ambergris Caye, Belize.

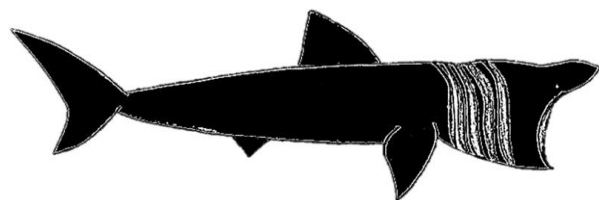
⁶Manx Basking Shark Watch, Glen Chass Farmhouse, Port St Mary, Isle of Man, IM9 5PJ.

⁷Scottish Natural Heritage, Great Glen House, Inverness, Scotland, IV3 8NW, UK.

⁸Wave Action, 3 Beacon Cottages, Falmouth, TR11 2LZ, UK.

Definitions

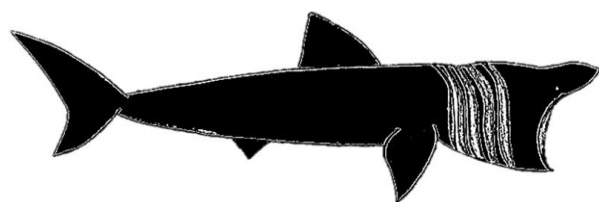
ACC	Antarctic Circumpolar Current
AUC	Area Under the Curve
AWERB	Animal Welfare and Ethics Review Board
BAP	Biodiversity Action Plan
BRT	Boosted Regression Tree
CFP	Common Fisheries Policy
Chl-a	Chlorophyll α
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CLS	Collecte Localisation Satellites
CMS	Convention of Migratory Species
DVM	Diel Vertical Migration
EENM	Ensemble Ecological Niche Model
EEZ	Exclusive Economic Zone
ENM	Ecological Niche Model
GAM	Generalised Additive Model
GLM	Generalised Linear Model
GLMM	General Linear Mixed-effect Model
GME	Geospatial Modelling Environment
GPS	Global Positioning System
HMM	Hidden Markov Model
HYCOM	Hybrid Coordinate Ocean Model
IQR	Inter-Quartile Range
IUCN	International Union for Conservation of Nature
KAPPA	Cohen's Kappa (Heidke skill score)
KDE	Kernel Density Estimation
LoCoH	Local Convex Hull
MCP	Minimum Convex Polygon
MPA	Marine Protected Area
PAT	Pop-off Archival Tag
PTT	Platform Transmitter Terminal
PVC	Percentage Volume Contour
rDVM	Reverse Diel Vertical Migration
RICC	Relative Importance of the Contribution to the model Coefficients
ROC	Receiver Operating Characteristic
SD	Standard Deviation
SE	Standard Error
SIED	Single Image Edge Detection
SPOT	Smart Position or Temperature
SR	Success Ratio
SST	Sea Surface Temperature
STAT	Satellite Tracking and Analysis Tool
T-LoCoH	Time Local Convex Hull
TSS	True Skill Statistic
UD	Utilisation Distribution



Chapter 1: General introduction



Credit: Matthew J. Witt



Movement ecology

The fact that most aquatic organisms from microscopic bacteria to the largest species on the planet move, facilitates many ecological processes (Hussey *et al.* 2015). Movement ecology applies the study of animal movement to understand drivers, physiology, and the environment such as seasonal migration, dispersal, and foraging (Hays *et al.* 2016). To observe these patterns, biologging is employed, whereby miniaturised tags are attached to the subject animal, which can relay physical and biological data, known as biotelemetry (Hooker *et al.* 2007; Hays *et al.* 2016). Biologging technologies have become more readily available and applicable to more species relatively recently (last two decades), and continue to advance rapidly.

Animal-attached tags are being applied to an increasingly wide range of animals from king prawns (*Penaeus (Melicertus) plebejus*; (Taylor & Ko 2011)) to blue whales (*Balaenoptera musculus*; (Irvine *et al.* 2014)). In the marine environment, where it is almost impossible to directly observe individual animals over extended periods, the attachment of archival data loggers and/or data relay devices is important for monitoring animal behaviour beneath the sea surface. An understanding of such behaviour is in turn important for the assessment and understanding of the role these animals play within the wider biophysical systems in which they operate and for an appreciation of their sensitivity to environmental change. As a science, bio-logging lies at the interface between scientific enquiry and technological feasibility (Hooker *et al.* 2007).

A justification for many tracking studies is that knowledge of the movements of animals might help inform conservation management (Cooke 2008; Costa, Breed & Robinson 2012). However, incorporation of movement data into conservation strategies remains underutilised (Jeffers & Godley 2016). Tracking data can potentially help designate the location, size, and timing of conservation zones and test their efficacy. Movement data can also aid stock assessments, identification of stock boundaries for species of

conservation concern, ecosystem-based management, and management of highly migratory species (Hays *et al.* 2016).

Prey distributions can dictate where animals move and behaviours indicative of prey encounter have been observed (Womble *et al.* 2014; Goldbogen *et al.* 2015). Diel Vertical Migration (DVM) patterns of prey movement have been shown to influence depth-use in predators, however, species potentially vary their behaviour across habitat types supporting different prey distributions (Humphries *et al.* 2010). Large marine megavertebrates can act as ecosystem regulators, either through predation or grazing (top-down; (Atwood *et al.* 2015)) or linking surface waters to the deep ocean (bottom-up; (Thorrold *et al.* 2014)). Key to understanding these ecological roles are analyses of spatiotemporal patterns of abundance and behaviours, which are driven by movement decisions. Fixed and fluctuating abiotic environmental variables (e.g. bathymetry and temperature respectively) can strongly influence movement patterns (Curtis *et al.* 2014; Sequeira *et al.* 2014).

Many species undertake long-distance migrations (thousands of kilometres) to utilise resources in different habitats varying on spatial and temporal scales (Werry *et al.* 2014) providing conditions favourable for different life-history events (Block *et al.* 2011). Maximum migration distances generally scale with body size, and also vary with taxa and mode of locomotion and are thought to be constrained by energy stores and metabolism along with the cost of movement (Hein, Hou & Gillooly 2012; Jacoby *et al.* 2015). Information about an animal's geographic location can be achieved via a range of methods: manual active tracking, estimated using light levels from archived data onboard tags, or calculated in near real-time using the Argos satellite system. The advent of Global positioning system (GPS) tags can also provide near-real time and archived locations, and the recent development of fast acquisition GPS fixes (Fastloc™) can provide accurate location estimates for animals only appearing at the surface for short periods of time.

Placing movement in context with a species environment aids the interpretation of behavioural data and provides information on what features of the environment are important to animals, how they locate these features, and what happens when these features form and breakdown (Hooker *et al.* 2007). The level of information obtained from satellite tracking of animals and therefore inferences made likely changes as sample size increases. For example, tracking one individual can reveal the extent of movement in very limited detail, tracking several individuals can begin to reveal individual variability, while tracking many tens of individuals can reveal population level behaviours (Fossette *et al.* 2014).

Human activities are impacting the global marine environment, with the majority of maritime ecosystems around the world negatively affected by various drivers of ecological change (Halpern *et al.* 2008). Interactions with anthropogenic threats can alter the movements, behaviour, and survival of large marine fauna (Ellenberg, Mattern & Seddon 2013; New *et al.* 2014). Therefore, the description of movement patterns can provide data essential for the identification and mitigation of potential impacts. The description of movement patterns in places and at times when marine megafauna are exposed to potential threats from anthropogenic activities is a key objective for research that seeks to optimise strategies for the management, and conservation (Sequeira *et al.* 2014). Coastal zones and continental shelf waters have been predicted to have high cumulative impacts from anthropogenic activity (Halpern *et al.* 2008). Impacts from fisheries (Worm *et al.* 2009; Jackson 2010) and climate change (Gattuso *et al.* 2015; Sydeman *et al.* 2015) have been identified as key stressors.

To successfully implement conservation policy in order to mitigate against anthropogenic induced threats, and their associated impacts on marine species, requires knowledge and understanding of the spatial ecology of species, particularly when species are highly migratory (Costa *et al.* 2012). Investigating movement patterns of species within high-use areas, such as foraging grounds or along migratory corridors, may provide new insights into the spatial and temporal use of key habitats and help identify potential hotspots. This

increased understanding can assist the decision process of designating protection (Heupel & Simpfendorfer 2005; Meyer, Holland & Papastamatiou 2007). However, effective design, implementation and regulation of protection for mobile marine species can be challenging; especially when the species perform wide-ranging movements in the pelagic realm of the ocean (Lauck *et al.* 1998; Hooker & Gerber 2004).

Conservation status of chondrichthyans

There is increasing evidence that over millennia human impacts have permanently altered terrestrial biodiversity, in particular vertebrates (Hoffmann *et al.* 2010), with increasing concern for marine biodiversity, particularly when considering the vast increase in activity in this realm (Jackson 2010). Overfishing and habitat degradation have had profound impact on marine ecosystems and species (Lotze *et al.* 2006), in particular sharks and rays (Stevens 2000; Ferretti *et al.* 2010; Dulvy *et al.* 2014).

Chondrichthyans (sharks, rays, and chimeras) are part of one of the most ecologically diverse vertebrate groups, arising over 420 million years ago (Compagno 1990). They are some of the slowest maturing and slowest reproducing of all vertebrate groups, exhibiting the longest gestation periods and some of the highest levels of maternal investment in the animal kingdom (Cortés 2000). The extreme life histories of many chondrichthyans result in very low population growth rates, placing them at increased sensitivity to elevated fishing mortality (Cortés 2002).

Approximately 25% of all chondrichthyans species are threatened with extinction, with large-bodied, shallow-water species at greatest risk (Dulvy *et al.* 2014). Chondrichthyan extinction risk is substantially higher than for most other vertebrates, with only one-third of species are considered safe along with population depletion having occurred throughout the world's ice-free waters (Dulvy *et al.* 2014).

The basking shark

The basking shark (*Cetorhinus maximus*) is a very large, filter-feeding, cold-water pelagic species of shark. It is the only member of the family *Cetorhinidae*, can reach up to lengths of 12 m, weighing approximately 4 tonnes, and is the world's second largest fish species. The global status of the basking shark is assessed as Vulnerable, with the north-east Atlantic stocks, which have been subject to target fisheries, assessed as Endangered (Fowler 2005). Basking sharks have a circumglobal distribution occurring in temperate and boreal oceans and can undertake extensive trans-ocean basin migrations (Gore et al. 2008; Skomal et al. 2009); although the relative frequency and purpose of these migrations is unknown.

The reproductive biology is likely similar to that of other lamnoid sharks (Kunzlik 1988), exhibiting embryonic ovophagy, with the mother providing infertile eggs for the embryos to feed upon. Estimates for gestation range between 12 to 36 months with a resting period of at least a year between litters (Parker & Stott 1965). Males become sexually mature at a length of 5-7 m, age estimated at 12-16 years old. Females are mature at 8.1-9.8 m and perhaps 16-20 years old (Compagno 1984).

Basking sharks have five gill slits encircling each side of the head. Within these gill slits are the gill lamellae that enable respiration by the exchange of oxygen with seawater, and the gill rakers; comb-like structures arranged in a single row along each gill arch. When the mouth is open, two rows of gill rakers extend across each gill slit gap and filter out zooplankton prey from the continuous flow of seawater produced by ram-filter feeding (Matthews & Parker 1950; Kunzlik 1988; Sims 2008). The liver of basking sharks is huge, containing high concentrations of squalene oil, and can comprise up to 25% of its body weight (Kunzlik 1988).

In the North Atlantic, basking sharks occur between Atlantic and Arctic waters (including the Gulf of Maine, south of Iceland and off the North Cape of Norway and Russia) to the Mediterranean Sea and south to Senegal and Florida (Fowler 2005). In the South Atlantic basking sharks occur off South Africa, Brazil to Ecuador, South Australia and New Zealand (Compagno 1984). Basking sharks have largely only been recorded from coastal areas; however this unlikely represents their entire habitat as distribution throughout the entire epipelagic zone of ocean basins is possible (Sims 2008). However sightings data away from coasts are lacking, suggesting either sharks are not present in these areas or they are away from sight at depth (Southall *et al.* 2005).

Segregation by sex and/or body size is common in shark species (Klimley 1987; Wearmouth & Sims 2008; Mucientes *et al.* 2009), however there is no compelling evidence to suggest this occurs in basking sharks. Individuals from both sexes and of all sizes have been observed foraging in the same areas during the summer (Berrow & Heardman 1994), yet there is a paucity in observations of occurrence away from coastal areas and throughout the annual cycle, with a female bias in catches from directed fisheries (Kunzlik 1988).

Basking sharks are obligate ram-filter feeders, unlike the other two planktivorous sharks, the megamouth shark (*Megachasma pelagios*) and the whale shark (*Rhincodon typus*) that exhibit gulp or suction feeding (Clark & Nelson 1997; Nakaya, Matsumoto & Suda 2008), feeding predominantly calanoid copepod species (Matthews & Parker 1950).

Very little is known about mating and breeding in basking sharks, with no observations recorded. A range of behaviours have been observed in basking sharks, such as nose-to-tail following, lateral approaches, and breaching and are often attributed to courtship displays (Harvey-Clark *et al.* 1999; Wilson 2004). Comparatively little is known about the breeding systems of shark species in the wild with most information originating from captive observations (Pratt & Carrier 2001), thus it is difficult to confidently assign the underlying reason for the behaviours observed.

Limited genetic studies have been unable to robustly describe the structuring of the north-east Atlantic population (Noble *et al.* 2006), although genetic diversity is thought to be low globally (Hoelzel *et al.* 2006). Population sizes for basking sharks is largely unknown, with a global estimate of effective population size (N_e ; number of individuals contributing offspring to the next generation) of 8,200 individuals (Hoelzel *et al.* 2006). Regional estimates have been made in the north-west Atlantic based on aerial surveys of 6,512 individuals (CI: 4,040-11,886) (Westgate *et al.* 2014). In the Sea of the Hebrides regional estimates of 201-985 individuals were calculated based on photo identification and mark-recapture techniques (Gore *et al.* 2016).

Tracking efforts in the north-east Atlantic to date have tracked basking sharks for up to 245 days, demonstrating movements within and along the European continental shelf (Sims *et al.* 2003; Stéphan, Gadenne & Jung 2011), with one observation of trans-Atlantic movement (Gore *et al.* 2008). These studies however have been limited by sample size, with the majority of movements confined to the continental shelf. With growing concern regarding the rate of decline of global shark populations (Dulvy *et al.* 2014), the importance of defining the extent and connectivity of mobile species populations has increased (Heupel *et al.* 2015).

Threats and conservation actions

Basking sharks have been exploited for their meat, fins, skin, and liver (containing the sought after squalene oil) for several centuries by targeted fisheries most notably occurring in the north-east Atlantic (Kunzlik 1988). Between the mid-1940s and the mid-1980s directed fisheries from Norway, Scotland and Ireland landed 77,204 individual basking sharks either using entanglement in nets or harpoons (Myklevoll 1946; Kunzlik 1988). More recently, Norway landed 14,263 tonnes of basking shark liver, which was calculated to approximate to >28,000 individual basking sharks between 1989 and 1997 (Sims 2008). Most basking shark fisheries showed a level of collapse after initial high yields and therefore basking sharks are considered to be extremely vulnerable to overfishing (Compagno 1984).

Incidental catch is still of concern for basking sharks, with estimates of approximately 77-120 sharks are taken annually in the bottom gill-net fishery in the Celtic Sea (Berrow 1994), and basking sharks commonly appear as by-catch in trawl and set net fisheries in New Zealand (Francis & Duffy 2002).

Sources of disturbances in the marine realm include increasing boat traffic, marine engineering, naval activities, and energy extraction. The potential impacts of these have not yet been described for basking sharks, but may reduce reproductive success (Kelly, Glegg & Speedie 2004). Plastic debris discarded at sea can lead to entanglement in marine vertebrates (Nelms *et al.* 2016). Plastic entanglement can lead to abrasions, damage to fins, and impacts on body formation (Wegner & Cartamil 2012). Ingestion of plastics can lead to transport of bioaccumulating and toxic substances and physical damage to gills (Fossi *et al.* 2014).

Basking sharks are strictly protected under national and international treaties, including being listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and Appendices I and II in the Convention of Migratory Species (CMS; Table 1) requiring international trade to be monitored.

Table 1. National and international regulations and protection measures for basking sharks.

Regulation	Year	Region
Wildlife & Countryside Act	1981	UK
Manx Wildlife Act	1990	Isle of Man
Biodiversity Action Plan (BAP) priority species	1997	UK
Countryside Rights of Way Act	2000	UK
CITES (Appendix II)	2003	Global
CMS (Appendix I & II)	2005	Global
European Common Fisheries Policy (EU CFP)	2007	Europe
OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic: OSPAR List of Threatened and/or Declining Species and Habitats	2008	Europe
Marine & Coastal Access Act	2009	UK
Marine (Scotland) Act	2010	Scotland
Marine Act (Northern Ireland)	2013	Northern Ireland

Device attachment effects

With the continued use of animal-borne technology to monitor wildlife there is a need to understand and reduce any adverse effects to the animals. This includes less stressful capture techniques, reduced handling time, and consideration of instrument drag and retention time (Jones *et al.* 2013). There are technical challenges to quantifying risks associated with capturing and attachment of devices due to the absence of “true” controls, which hamper our ability to determine what components of the animal’s biology is most affected (Hays *et al.* 2016).

The process of attaching instruments to animals can potentially lead to physiological consequences. In sharks, the dorsal musculature is widely accepted as the most suitable region for tag application due to tough placoid scales that cover a region of thick muscle fibres, cartilage, and pterygiophores (Hammerschlag, Gallagher & Lazarre 2011). This area therefore was the target region for placement of our tags in an attempt to reduce the footprint of the tag and minimise physical damage to the individual. Tags are often directly attached to the dorsal fins of sharks, which involves capture of the individual and creating holes within the fin to facilitate bolting the technology directly to the fin. This

may result in tissue degradation and infection (Hammerschlag *et al.* 2011). However, Jewell *et al.* (2011) found that eight of eleven white sharks (*Carcharodon carcharias*) re-sighted after tagging with dorsally mounted tags showing evidence of healing with likely no long lasting damage for tags attached for between 12 and 24 months. Attachment durations in this study were below this threshold, with tag footprint greatly reduced by using towed tags attached only by titanium dart, and absence of capture and handling.

Some of the most common problems with external tags are tissue damage, tag loss and decreased swimming capacity. Disadvantages of external tagging include; the tag interfering with the body shape of the fish and increasing drag; reducing swimming performance; biofouling of tag; the tag being visible potentially increasing predation risk. Basking sharks are very large bodied animals (smallest animal tagged in this study was 4 m total length) and therefore we feel the effects of tags weighing <200g would pose minimal impact on the swimming performance. All tags were coated in anti-foul to reduce growth occurring on surfaces. Tags were grey in colour, reducing contrast between the shark and the tag, likely reducing any impact of predation on the tag or individual, with basking sharks having few (if any) natural predators.

Chin, Mourier & Rummer (2015) showed high capacity for wound healing in blacktip reef sharks (*Charcharhinus melanopterus*) following a variety of injuries such as umbilical scars, bite wounds, and boat strikes. This study suggests that individual survival may depend more on handling practices and physiological stress rather than the extent of physical injury. We feel techniques deployed in our study greatly reduce effects from handling and physiological strain on the sharks, with the explicit aim of reducing risk of long-lasting effects and optimising ability to observe “true” movements. However, there is still a general paucity of empirical studies on the long-term impacts of electronic tags on sharks, partly because animals with tags are rarely re-encountered.

Study area

The Sea of the Hebrides is an island-studded region of complex bathymetry on the UK continental shelf, west of the Scottish mainland south of the Isle of Skye (Fig. 1; (Howe *et al.* 2012)). The areas around the islands of Hyskeir, Coll and Tiree have been identified as “hotspots” for basking sharks from 20 years of public sightings record (Witt *et al.* 2012) and from effort-corrected boat-based survey estimates in the summer (Speedie, Johnson & Witt 2009), with large numbers of basking sharks are seasonally sighted forming summer aggregations in this area, suggesting the area may be important for key life-history events of basking sharks.

The UK Marine and Coastal Access Act (2009) and the Marine (Scotland) Act (2010) include powers for Scottish Ministers to designate Marine Protected Areas (MPAs). There has been an increased focus on the spatial management of the marine environment in Scotland and as such, the Scotland's National Marine Plan and selection of Nature Conservation Marine Protected Areas has been formed. One specific measure is the proposed 10,325 km² Sea of the Hebrides MPA, between the Isles of Skye, Mull, and the Outer Hebrides (Scottish Natural Heritage 2014). This area has been identified as having a high abundance of minke whale (*Balaenoptera acutorostrata*) and basking shark occurrence (Speedie *et al.* 2009; Witt *et al.* 2012) and was thus proposed as a potential site for MPA designation.

There is a UK Biodiversity Action Plan for the basking shark, now taken forward by the Scottish Government as part of the Scottish Biodiversity Strategy to protect biodiversity for both for the species itself, but also because of the benefits the environment provides to the economy and the public. Part of the project is to develop an evidence base to inform on expanding designation of Scotland's seas in nature conservation MPAs. The UK Marine and Coastal Access Act (2009) and the Marine (Scotland) Act (2010) include powers for Scottish Ministers to designate Marine Protected Areas (MPAs), with the Marine (Scotland) Act providing a framework to help balance competing demands on

Scotland's seas. It introduces a duty to protect and enhance the marine environment, partly through improved marine nature and historic conservation with new powers to protect and manage areas of importance for marine wildlife, habitats and historic monuments. One specific measure is the proposed 10,325 km² Sea of the Hebrides MPA, between the Isles of Skye, Mull, and the Outer Hebrides (Scottish Natural Heritage 2014). This area contains a high level of biodiversity, in particular repeated sightings of minke whales and basking sharks. Scottish Natural Heritage (SNH) were tasked with gaining evidence of basking shark space-use in the Sea of the Hebrides with focus on the area proposed an MPA, particularly during the summer months, when peak sightings of basking sharks at the surface occur (Witt *et al.* 2012). This led to collaboration with the University of Exeter, funded by SNH to deploy satellite tags in multiple summer seasons to analyse basking shark movements in the area. This project is a prime example of using public funds to support evidence driven, impactful science that will likely inform policy.

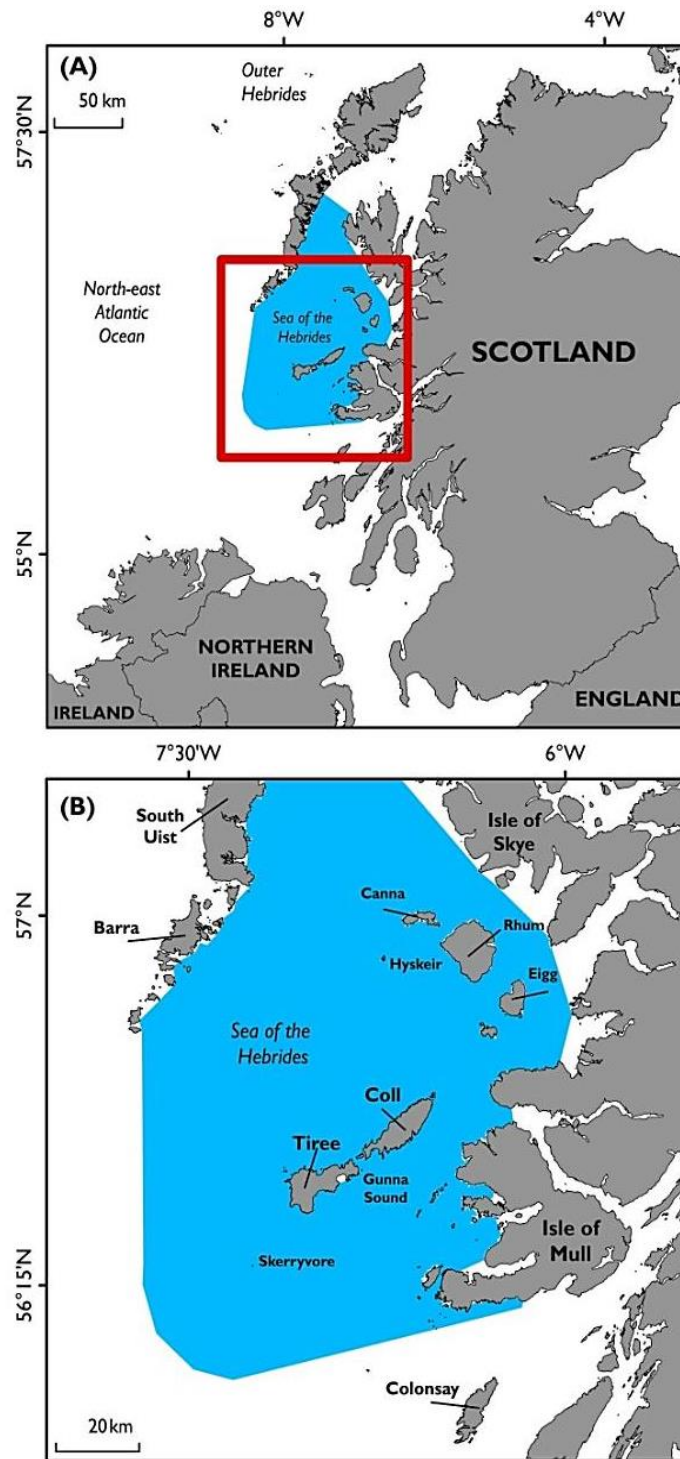


Figure 1. Study area. (A) Study location; west coast of Scotland showing the Sea of the Hebrides proposed MPA (blue polygon) and (B) Sea of the Hebrides proposed MPA (blue polygon), the location of satellite tag attachment to basking sharks between 2012 and 2014.

Thesis aims and outline

In this thesis, I investigate the movement ecology of basking sharks in the north-east Atlantic Ocean using biologging and biotelemetry techniques. Specifically, the thesis aims to (i) explore the surface space-use in a summer foraging site in the Sea of the Hebrides, (ii) describe the long-term, wide-ranging winter migration behaviours, (iii) quantify vertical space-use and encountered temperature range at depth, and (iv) use contemporaneous tag data to inform Ensemble Ecological Niche Modelling (EENM) techniques to predict areas of suitable habitat.

Chapter 2 describes the surface space-use of basking sharks in a summer foraging site in the Sea of the Hebrides, West Scotland. This chapter reveals areas of inter- and intra-annual density and evaluates the potential efficacy of the area as a proposed MPA.

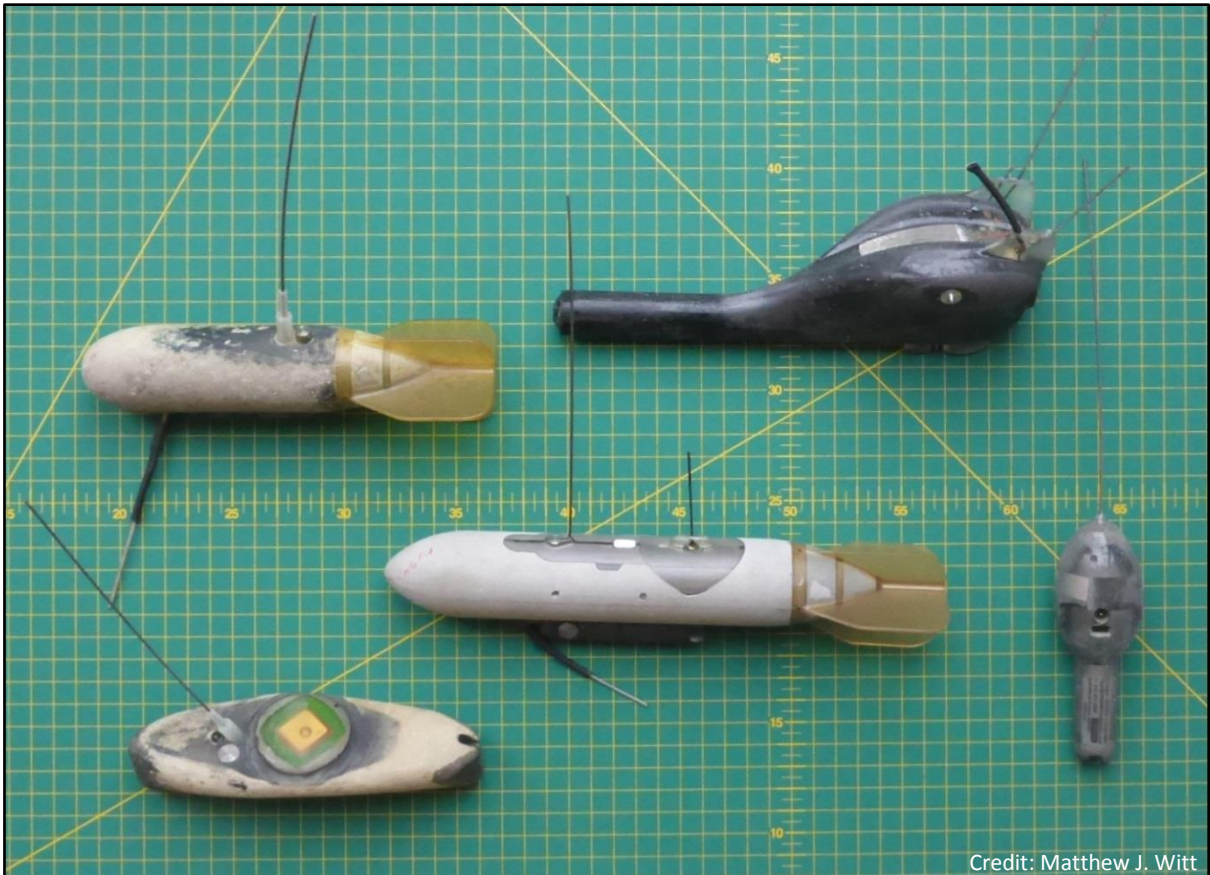
Chapter 3 investigates broad-range movements away from the summer foraging site, in the Sea of Hebrides to provide the largest assessment of basking shark over-wintering behaviour of basking sharks in the north-east Atlantic to date.

Chapter 4 quantifies basking shark vertical space-use and temperatures encountered at depth. This chapter also investigates the seasonality of vertical behaviour and the factors potentially influencing these behaviours.

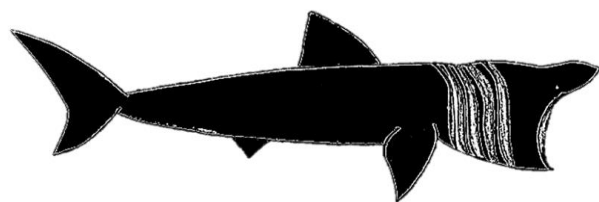
Chapter 5 utilises contemporaneous satellite tag data gathered across the four year satellite tagging programme (2012-2015) to inform Ensemble Ecological Niche Modelling (EENM) techniques to predict areas of suitable habitat. This chapter, as far as I am aware is the first to apply an EENM approach to approximate 3D systems in sharks.

Chapter 6 provides a synthesis and a general evaluation of the findings of this thesis.

Chapter 2: Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed marine protected area



Credit: Matthew J. Witt



Abstract

There is a growing need to understand the inter-annual movements of mobile marine species of conservation concern to inform the design and placement of Marine Protected Areas (MPAs) to maximise their conservation potential. We use satellite telemetry data from 36 basking sharks (*Cetorhinus maximus*) tracked in 2012, 2013 and 2014 (cumulative total: 1,598 days; median: 44 days; range: 10-87 days) to quantify movements in coastal waters off the west coast of Scotland within the Sea of the Hebrides proposed MPA. Sharks exhibited seasonal residency to the proposed MPA, with a mean of 84% of filtered best daily locations occurring within its boundaries (2012 = 80%, 2013 = 90% and 2014 = 74%). Three long-term tracked basking sharks demonstrated inter-annual site fidelity, returning to the same coastal waters in the year following tag deployment, with two returning to within the boundaries of the proposed MPA. These data likely suggest the area experiences favourable conditions and/or resources for basking sharks across years and, if designated, coupled with appropriate management, could afford protection during summer months.

Introduction

With global declines in many marine fish populations and habitats (Watson & Pauly 2001; Baum *et al.* 2003; Lotze *et al.* 2006) the use of Marine Protected Areas (MPAs) has become increasingly popular as a management tool to prevent further population decline, promote recovery and improve biodiversity conservation (Halpern & Warner 2002; Wood *et al.* 2008). Studies have suggested that large, mobile species, with wide-ranging movements may benefit from MPAs, e.g. teleost fish (Farmer & Ault 2011), turtles (Scott *et al.* 2012), whales (O'Brien & Whitehead 2013), as well as sharks (Claudet *et al.* 2009; Barnett *et al.* 2011), depending on protective measures applied to these areas.

In particular, there is growing concern regarding the rate of decline of global shark populations due to overfishing (Dulvy *et al.* 2014). The proportion of time individuals spend within MPA boundaries will affect the degree to which these animals could be protected, should adequate management measures also be in place. This protection is likely to vary with species, life stage, sex, size, body condition and food availability (Speed *et al.* 2010; Escalle *et al.* 2015). Designing MPA boundaries and management measures to be effective for mobile species requires detailed knowledge of the species' biology, movements and habitat use (Grüss *et al.* 2011; Chin *et al.* 2016). Establishing MPAs in areas that mobile species use consistently (e.g. areas of key life-history events) may offer some protection at a population level (Heupel & Simpfendorfer 2005; Meyer *et al.* 2007), and protection will therefore depend on the degree of overlap between core activity areas and the area of protection (Knip, Heupel & Simpfendorfer 2012a).

Basking sharks were historically exploited in the north-east Atlantic for their meat, fins and large liver containing desired squalene oil; with directed fisheries from Norway, Scotland and Ireland. These fisheries landed 77,204 individuals between 1946 and 1986 (Kunzlik 1988), leading to depletion in local stocks (Parker & Stott 1965). Basking sharks are listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Appendices I and II in the Convention of Migratory

Species (CMS; Table A1), and are listed as 'Vulnerable' globally by the International Union for Conservation of Nature (IUCN Red List), and 'Endangered' in the north-east Atlantic (Fowler 2005). The Marine (Scotland) Act (2010) and the UK Marine and Coastal Access Act (2009) include powers for Scottish Ministers to designate MPAs in the seas around Scotland, one of which is the proposed 10,325 km² Sea of the Hebrides MPA, between the Isles of Skye, Mull and Outer Hebrides (Scottish Natural Heritage 2014). This area has been highlighted as a key area for surface sightings of basking sharks (Speedie *et al.* 2009; Witt *et al.* 2012) between July and August each year, and for minke whales (*Balaenoptera acutorostrata*) and was thus proposed for designation as a MPA (Scottish Natural Heritage 2014).

In an attempt to increase protective measures for marine environments and to satisfy international conventions, many MPAs have been implemented opportunistically without prior knowledge of how they may contribute to biodiversity conservation (Roberts 2000). Assessment of the efficacy of a MPA is important in order to maximise its conservation potential (McNeill 1994), otherwise there is a possibility of tokenism if placed arbitrarily (Ashe, Noren & Williams 2010). We used satellite tags in order to (1) describe the seasonal (summer months) space-use of coastal waters off the west coast of Scotland by basking sharks, (2) describe areas of inter- and intra-annual density and (3) evaluate the use of the Sea of the Hebrides proposed MPA and establish the amount of time sharks spent inside the proposed MPA thus quantify the potential importance of this area to basking sharks.

Methods

Tag attachment and specification

Sixty-two satellite tags, communicating with the Argos System, were attached to basking sharks off the west coast of Scotland during July and August in 2012, 2013 and 2014. Basking sharks were approached by boat from behind to avoid the line of sight of the shark and to minimise disturbance. On approach to the shark, the individual was, where possible, sexed using a pole mounted camera and total body length was estimated based on comparison to the total length of the boat (10 metres). Satellite tags were deployed using a titanium M-style dart (Wildlife Computers, Redmond, California, USA) inserted into the sub-dermal layer at the base of the first dorsal fin with a modified pole spear and attached via a tether consisting of heat-shrink covered stainless steel flexible cable, a swivel and monofilament line attached to the tag. Four models of satellite tags were deployed to gather a variety of information on the movements and distribution of tagged animals. Thirty-six satellite tags were used in this analysis; Smart Position or Temperature tags (SPOT; n = 23, Wildlife Computers, Redmond, California, USA) and SPLASH-F tags (n = 13, Wildlife Computers, Redmond, California, USA) and transmitted data in real-time while attached to study animals. Both tag models provided Argos Doppler-based estimates of location (termed Argos locations) during shark surfacing events. SPLASH-F tags also contained Fastloc™ GPS technology, providing GPS locations in addition to collecting light, temperature and depth data. Both, Argos and GPS locations were used for analysis of summer movement patterns and seasonal site fidelity. Remaining tags that transmitted data (n = 24) were Pop-up Archival tags fitted with Fastloc™ GPS technology (PAT-F; n = 12) and MiniPAT (n = 12; Wildlife Computers, Redmond, California, USA). These tags used to gather information on longer-range movements of basking sharks away from the west coast of Scotland using the principles of light geolocation (Doherty *et al.* 2017a).

Location data processing

Analysis focused on coastal movement within the summer months; therefore, data were confined to 90 days (approx. mid July-mid October) following tag deployment and prior to

the departure of sharks from the region. Data from satellite tags transmitting in the year following tag attachment were examined to ascertain inter-annual site fidelity. Argos location data from SPOT tags were subject to filtering, retaining location classes 1 (accurate to 500-1,500m), 2 (accurate to 250-500m), 3 (accurate to <250m), 'A' (three messages received but no accuracy estimation) and 'B' (one or two messages received but no accuracy estimation) (Witt *et al.* 2010). GPS location data from SPLASH-F tags deployed in 2014 were filtered to include only positions with a residual error value of less than 30 and where five or more satellites were visible to estimate the location (Shimada *et al.* 2012). GPS locations from SPLASH-F tags in 2014 were favoured over Argos locations from the same tags as the number of GPS locations was more numerous (662 vs. 463 Argos locations; post-filtering) and GPS locations have a greater spatial accuracy (Table A2). A maximum plausible speed filter was applied to both datasets removing locations if speed between two locations exceeded 10 km h^{-1} . These data were later reduced to a single, most accurate best daily location (highest location class as described above for Argos locations and maximum number of visible satellites for GPS locations) to minimise spatial and temporal autocorrelation. All tag data were downloaded from CLS-Argos and archived using the Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005).

Data analysis

We used four techniques to identify core activity areas of residency during the first 90 days post tag attachment. These techniques were; Minimum Convex Polygons (MCP), polygon sampling grid, Time Local Convex Hulls (T-LoCoH) and Kernel Density Estimation (KDE). MCPs create the smallest convex polygon that incorporates all filtered best daily locations. To determine areas of high relative importance, a polygon sampling grid (hexagonal cells; 2 km from each grid cell centroid to its perimeter; cell area 14 km^2) was spatially intersected with filtered best daily locations. The proportion of locations within each grid cell was calculated for each tracked shark; a mean proportion for each cell was then calculated. We used T-LoCoH to construct utilisation distributions by aggregating local MCPs around each point, which were then sorted and progressively merged to form isopleths. Local Convex Hull (LoCoH) methods have been shown to outperform traditional

kernel-smoothing techniques in excluding areas known not to be used (Getz *et al.* 2007). These attributes make LoCoH methods applicable to analyse collective area use of multiple individuals. T-LoCoH offers an advantage over traditional approaches because it further improves the ability to partition area use and study patterns through time (Lyons, Turner & Getz 2013). We applied the k-based method with no time-based weighting, constructing hulls for defined numbers of neighbouring points due to the absence of areas with high density of clustering as well as areas of sparsely distributed points (Lyons *et al.* 2013). We also applied KDE interpolation with barriers as described by Macleod (2014). KDE with barriers uses the shortest distance between points without intersecting a defined barrier, in this case land, allowing the contour of the kernel to change at the edge of the barrier (Sprogis *et al.* 2016). Output cell size was 250 m side length and the bandwidth (search radius) was 5,000 m. The bandwidth is a smoothing value that determines the width of the kernel. Choice of bandwidth method may vary depending on the study goals, sample size and patterns of space use by the study species (Gitzen, Millsaugh & Kernohan 2006), therefore the bandwidth value was selected by iterative visual inspection of outputs and evaluating the results based on extant ecological knowledge of the species.

Individual trajectories of tracked basking sharks were separated into groups based on movements relative to the boundaries of the proposed MPA using k-means cluster analysis (Hartigan & Wong 1979). Individual tracks were initially separated into *High-use* (n = 29) and *Low-use* (n = 7) groups based on time spent within the boundaries of the proposed MPA. To ascertain the use of the proposed MPA, movements of tracked basking sharks the *High-use* group was further split into *Near* (n = 23) and *Far* (n = 6) groups based on their maximum displacement distances from tagging location.

Data analysis was performed in R (R Core Team 2014), with satellite tag location filtering applied using the *adehabitat* packages (Calenge 2006) and T-LoCoH analysis using the *T-LoCoH* package (Lyons *et al.* 2013). All spatial analyses and maps were created using Geospatial Modelling Environment (GME v 0.7.2.1; Beyer 2012) and ESRI ArcMap 10.1.

Results

The movements of 36 basking sharks were analysed comprising eight males, 11 females and 17 of unknown sex. Sharks ranged from four to eight metres in length (4-5 m, n = 4 sharks; 5-6 m, n = 15 sharks; 6-7 m, n = 8 sharks and 7-8 m, n = 9 sharks). Sharks were tracked for a cumulative summer duration of 1,598 days (mid. July-mid. October; median: 44; range: 10-87 days), moved a median minimum along-track straight-line distance of 353 km (Inter-Quartile Range (IQR): 260 km range: 111-1410 km; Table A2) and were displaced a median 63 km (IQR: 71 km; range: 23-167 km) during that time. Following summer movements, 20 of these sharks were tracked departing the region (Doherty *et al.* 2017a).

Tracked basking sharks demonstrated three movement behaviours throughout the summer (Fig. 1; Figs A1-3), which was independent of tracking duration within the period (GLMM; $\chi^2_1 = 2.07$, $p = 0.15$); here, defined as (1) *High-use and near*, where sharks remain close to tagging location around the coastal waters of the Isles of Coll and Tiree within the boundaries of the proposed MPA (n = 23; Fig. 1B), (2) *High-use and far*, where sharks are mobile, using a high proportion of space within the proposed MPA, but away from tagging location, (n = 6; Fig. 1C) or (3) *Low-use*, where sharks leave the boundaries of the proposed MPA (n = 7) either permanently or re-entering at a later date within the same summer season (Fig. 1D).

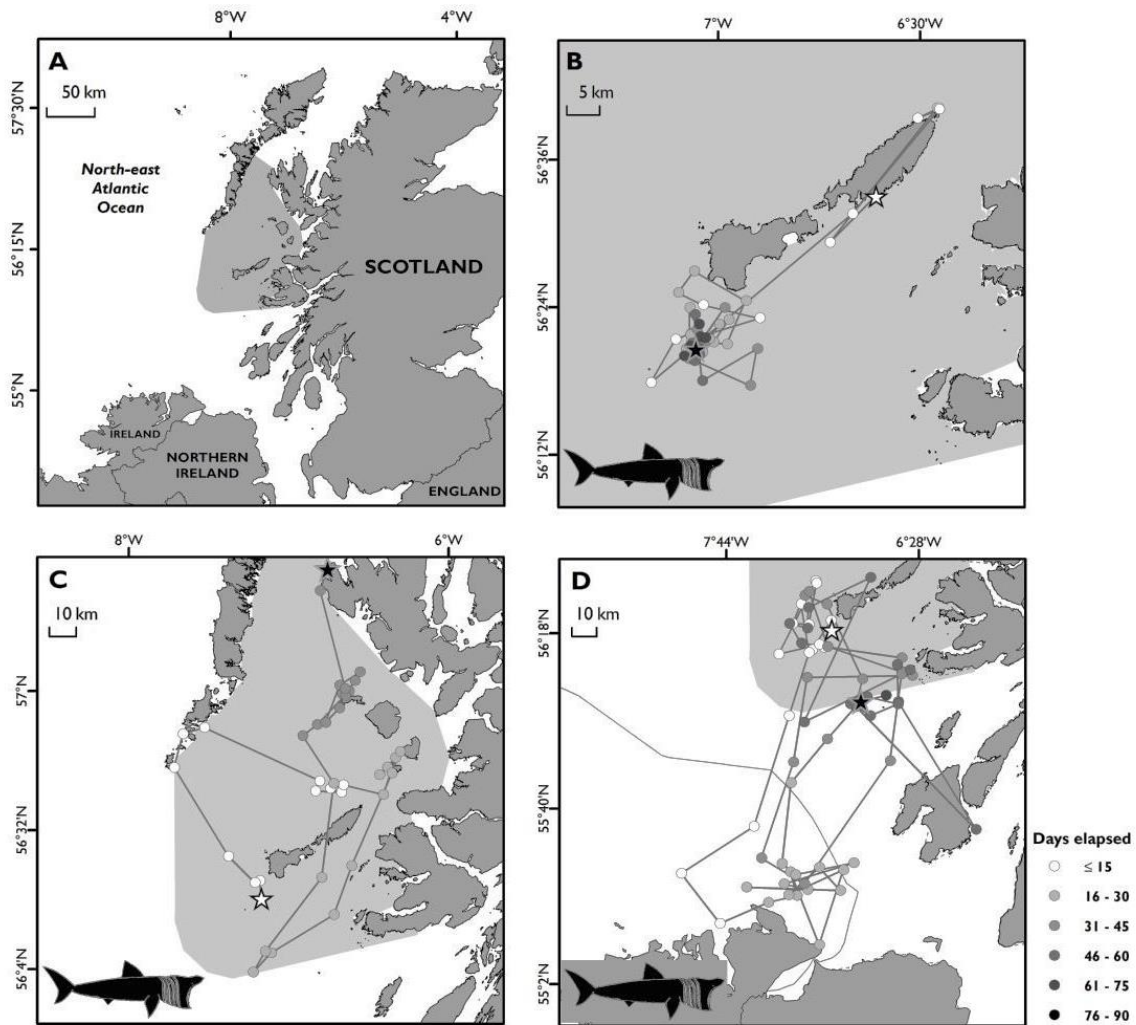


Figure 1. Movement of tracked basking sharks in summer months (2012-2014; mid-July- to mid-October). (A) Study area; west coast of Scotland, showing proposed MPA (grey polygon). Examples of individual tracks that exemplify three modes of movements: (B) *High-use and near*, where sharks remain close to tagging location within the boundaries of the proposed MPA (n = 23), PTT 137654 shown as example; (C) *High-use and far*, where sharks are mobile, using a high proportion of space within the MPA away from tagging location, PTT 129449 shown as example (n = 6); (D) *Low-use*, where sharks leave the boundaries of the proposed MPA PTT 129441 shown as example (n = 7). White stars denote tag deployment, black stars denote track end point for the summer months. Solid line is representative of tracked movement. Economic Exclusive Zone (EEZ) between UK and Ireland (dashed grey line).

Minimum Convex Polygons (MCPs) of tracked basking sharks across years reached from the tagging location and proposed MPA southwards to the coasts of Ireland and Northern Ireland, encompassing the waters off the Isles of Jura and Islay, west of the Outer Hebrides. The boundaries circumscribed areas of 21,182 km² in 2012, 24,532 km² in 2013, and 9,403 km² in 2014. In 2014, Argos and GPS locations were available from SPLASH-F tags, the MCP from Argos locations was 8,641 km² for Argos locations as compared to 9,403 km² for GPS, we chose to use GPS locations in further analysis due to their greater volume, and hence likely improved chance to more accurately describe the occupied MCP in that season. The mean MCP areas of tracked sharks was 2,605 km in 2012, 3,154 km in 2013 and 3,258 km in 2014 (applied to GPS locations compared to 1221 km² for Argos locations) (Table 1; Fig. 2A). The majority of filtered best daily locations (84%) occurred within the boundaries of the proposed MPA across all years (mean value, 2012 = 80%, 2013 = 90% and 2014 = 74%; Table 1, Figs 2A and A1-3). Grid density plots highlighted two common areas of high occupancy; to the south-west of the Isle of Coll, and between the islands of Coll and Tiree, an area known as Gunna Sound (Fig. 2B). These areas were further identified using T-LoCoH and Kernel Density analysis, which show the extent of use of these *hotspots*. The approaches identified other areas to the north, in waters of the Isles of Hyskeir and Canna. Core activity areas were almost entirely encompassed within the proposed MPA boundaries (T-LoCoH 50% isopleth = 91%, KDE 50% contour = 97%).

Table 1. Space-use within proposed MPA boundaries. Shark locations within the proposed MPA boundaries per year, showing size and overlap of activity areas. MCP = Minimum Convex Polygon; MPA = Marine Protected Area; T-LoCoH – Time Local Convex Hull.

	2012	2013	2014
Geolocation method	Argos	Argos	GPS
Number of sharks	8	19	9
Number of best daily filtered locations	235	674	194
MCP area (km²)	21182	24532	9402
Locations in MPA (median; %)	98	95	75
MCP area per shark (mean±SD (range); km²)	2605±3610 (477-11123)	3154±2904 (250-10470)	3258±2344 (552-5984)
25% T-LoCoH isopleth area (km²)	88	190	52
25% T-LoCoH isopleth hull overlap with MPA (%)	100	96	100
25% kernel contour area (km²)	97	181	51
25% kernel overlap with MPA (%)	100	100	100
50% T-LoCoH isopleth area (km²)	296	591	221
50% T-LoCoH isopleth hull overlap with MPA (%)	93	90	91
50% kernel contour area (km²)	309	635	211
50% kernel overlap with MPA (%)	97	100	90
75% T-LoCoH isopleth area (km²)	1372	2282	1106
75% T-LoCoH isopleth hull overlap with MPA (%)	73	94	68
75% kernel contour area (km²)	728	1662	601
75% kernel overlap with MPA (%)	87	100	72
90% T-LoCoH isopleth area (km²)	3502	5344	3077
90% T-LoCoH isopleth hull overlap with MPA (%)	79	89	71
90% kernel contour area (km²)	1294	3088	997
90% kernel overlap with MPA (%)	79	93	69

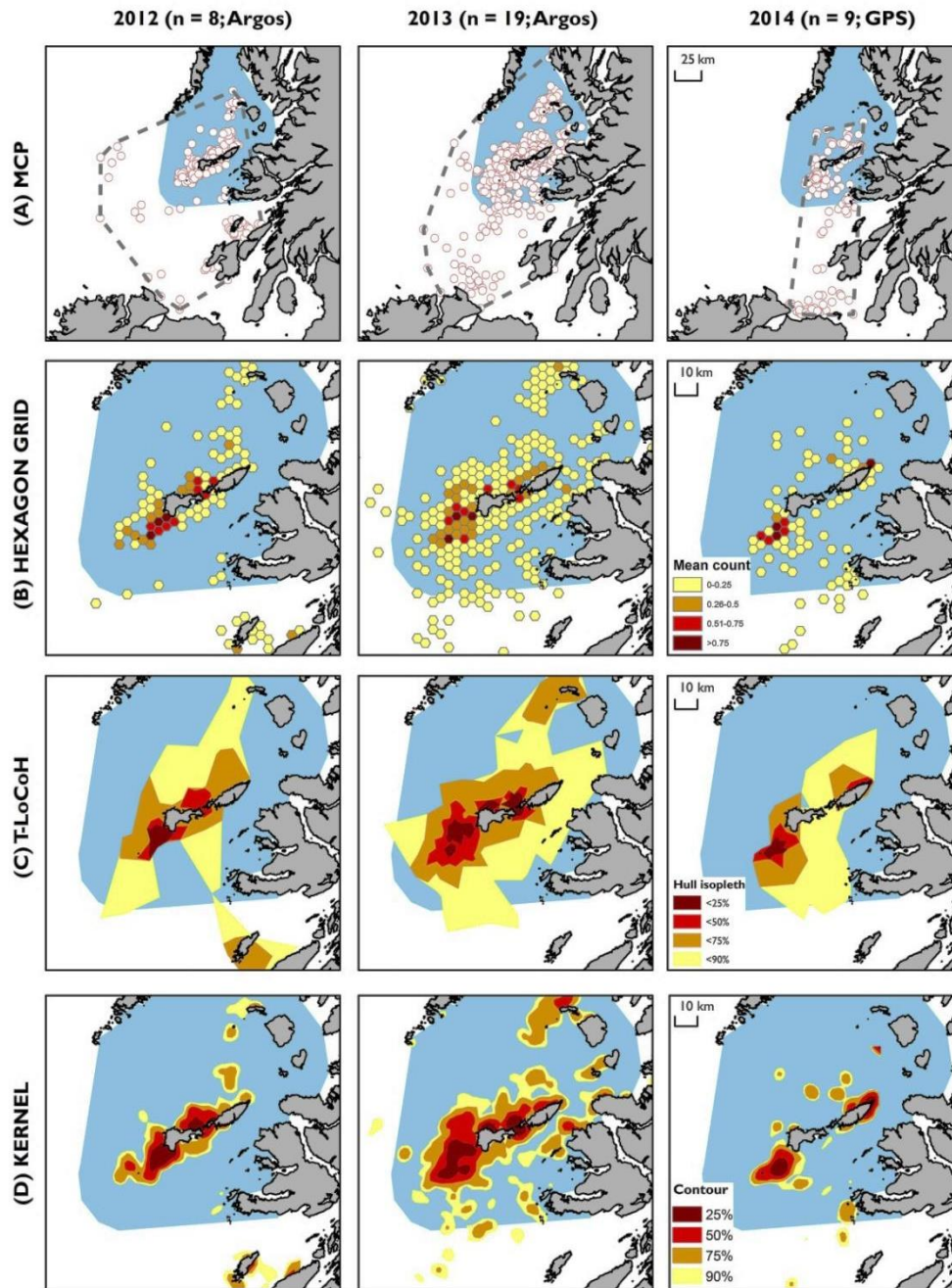


Figure 2. Identifying areas of relative importance. Areas of relative importance for the 90 days post tag attachment during summer months (2012 to 2014; July-October) estimated using (A) Minimum Convex Polygon (MCP), (B) Grid density estimation, (C) Time-Local Convex Hull analysis (T-LoCoH) and (D) Kernel density interpolation with barriers. In 2012 and 2013 locations (white circles) are daily highest quality Argos locations from basking shark tagged with SPOT and SPLASH-F tags. In 2014, locations (white circles) are daily highest quality GPS locations from SPLASH-F tags. Proposed MPA (blue polygon). Extent of figure panels represents area incorporating high activity areas.

Five basking sharks were tracked for longer than a year (>365 days), and three of these sharks returned to the waters off the west coast of Scotland from over-wintering grounds the subsequent summer permitting insights into inter-annual site fidelity. The remaining two sharks were tracked in coastal waters off the west coast of Ireland the subsequent summer. The three returning sharks dispersed 565, 304 and 1,474 km (minimum straight-line distance) from tag attachment location, these distances occurring in April, December and April respectively, and then returning to within 29, 138 and 24 km of the centroid of their core activity area from the first year of tracking respectively (Fig. 3). Two sharks returned to the waters of the proposed MPA in both years (Fig. 3A and C); the third shark was located outside the MPA boundary in the second year of tracking (Fig. 3B, Table A3).

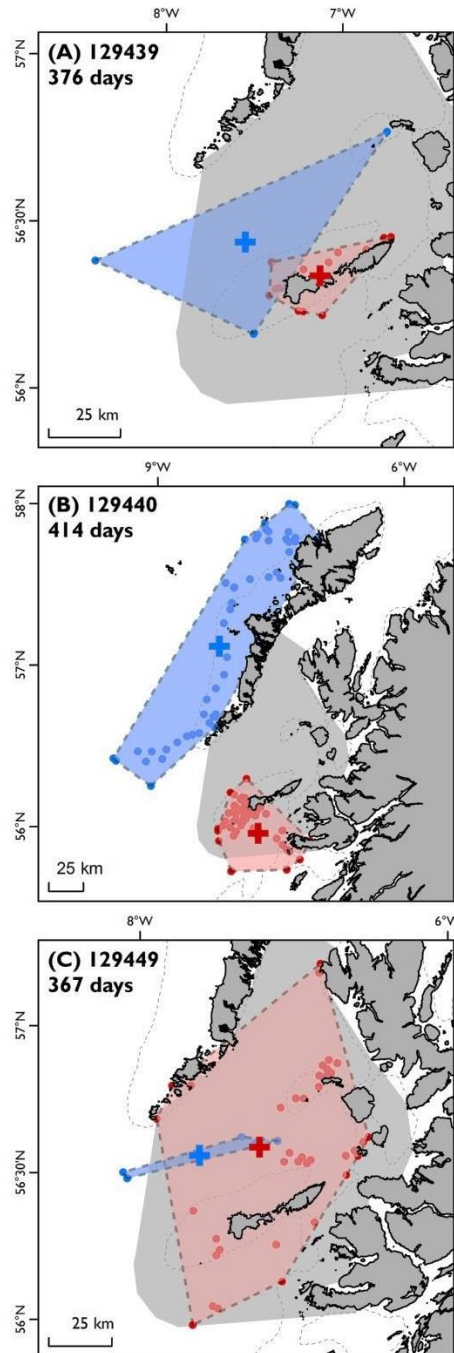


Figure 3. Inter-annual site fidelity. Best daily filtered locations (red and blue circles for 2013 and 2014 respectively) within summer months for three sharks demonstrating inter-annual site fidelity to coastal waters off the west coast of Scotland. Minimum convex polygons (red and blue polygons for 2013 and 2014 respectively), geographic mean centroid of Argos locations (red and blue crosses for 2013 and 2014 respectively). Shark ID and total tag attachment duration indicated for each figure part. Proposed MPA (grey polygon). 50 m bathymetry contour (grey broken line).

Discussion

The need to identify key areas of activity of large marine vertebrates in coastal areas is essential in order to appropriately delineate areas, and their boundaries, where protection measures can be implemented. MPAs can benefit mobile marine species (Worm, Lotze & Myers 2003), including cetaceans, pinnipeds, sea otters, sea birds, sharks, cephalopods, and teleost fish (Hooker & Gerber 2004). Our study showed that satellite tracked basking sharks in the north-east Atlantic exhibited seasonal residency and inter-annual site fidelity during summer months to a proposed MPA. The study area has been recognised as a basking shark aggregation site in the summer months from public sightings data (Southall *et al.* 2005; Witt *et al.* 2012) and boat-based, effort-corrected surveys (Southall *et al.* 2005; Speedie *et al.* 2009) where foraging behaviour can be observed (Matthews & Parker 1950; Berrow & Heardman 1994), but thus far high-resolution tracking data has been lacking.

Near real-time tracking – Argos locations & GPS

The ability to observe fine-scale movements of marine species of conservation concern provides novel insights into horizontal movements that cannot be gained from more traditional boat-based or aerial surveys (Westgate *et al.* 2014). Describing these movements has provided insight into home-ranges, core activity areas and seasonal use of distinct habitats, such as tiger sharks seasonally feeding on fledgling Albatross (*Phoebastria* spp.) at the French Frigate Shoals and subsequent migration once this resource is depleted (Meyer, Papastamatiou & Holland 2010), and large-scale migrations of leatherback turtles (*Dermochelys coriacea*) from Central Africa (Witt *et al.* 2008). More recently, the development of Fastloc™ GPS technology in telemetry allows highly accurate locations to be acquired from very brief (millisecond) surfacing events. This has led to high-resolution coastal water use by reef manta rays (*Manta alfredi*; Braun *et al.* 2014) and whale sharks (*Rhincodon typus*; Berumen *et al.* 2014). Such high resolution data has also permitted the identification of habitat use of the Critically Endangered smalltooth sawfish (*Pristis pectinata*) (Guttridge *et al.* 2015). Here we have revealed diverse, fine-

scale space-use by basking sharks, whereby collectively tracked sharks occupied the same area throughout the summer months, but movements within this area differed at an individual level, which is critical in understanding variation in space-use and habitat preference.

Residency and site fidelity

Residency, where an individual remains in a restricted geographic area for an extended period of time, and site fidelity, the return of an individual to a location where it previously resided after having left for a sustained period of time (Speed *et al.* 2011; Chapman *et al.* 2015) are common in shark species, with most data for reef associated species (see Chapman *et al.* 2015 for review). There is, however, a paucity of information on intra- and inter-annual shared use of an area by multiple basking sharks. Tracked sharks exhibited seasonal summer residency to the coastal waters off the west coast of Scotland. The vast majority of tracked sharks in this analysis (86%; n = 31) showed some degree of residency (>50% locations) to the proposed MPA (Fig. 2). We reveal tracked sharks exhibiting inter-annual site fidelity returning to the coastal waters of West Scotland. Two individuals returned to waters encompassed by the proposed MPA in summer months in the year following tag attachment, returning to within 30 km of the centre of activity from the previous summer, with another shark returning to waters off the west coast of Scotland, 138 km from centre of activity from the previous summer in an area highlighted as having conditions suitable for basking sharks (Fig. 3; Paxton, Scott-Hayward & Rexstad 2014). Until the present study, attachment durations of tags to basking sharks have been insufficient to ascertain information on inter-seasonal migration routes; we present the first description of multiple individuals exhibiting residency and site fidelity in this species.

Other tracking studies have indicated site fidelity and residency occurring in large, migratory sharks (e.g. white (*Carcharodon carcharias*), (Bonfil *et al.* 2005); whale, (Wilson *et al.* 2006); oceanic whitetip (*Charcharhinus longimanus*), (Howey-Jordan *et al.* 2013)), highlighting specific areas of use by these animals that would be suitable for protection

(Kock *et al.* 2013; Howey-Jordan *et al.* 2013; Graham *et al.* 2016). White sharks have been shown to exhibit a high degree of residency and site fidelity, returning to either the central Californian coast (Jorgensen *et al.* 2010) or Guadalupe Island (Domeier & Nasby-Lucas 2008) after migrating to a shared offshore foraging area in the Pacific Ocean. There is potential for a similar pattern of seasonal movement occurring in basking sharks in the north-east Atlantic, whereby the coastal waters off the west coast of Scotland serve as a shared, seasonal foraging site, with basking sharks moving away to separate overwintering areas, as there is evidence for plasticity in dispersal behaviours during winter migrations (Doherty *et al.* 2017a).

MPA use

Protection of highly migratory species throughout their range and life history is likely not feasible but MPAs can be used to protect areas of high relative importance or areas supporting key stages of life history ecology, such as breeding or foraging grounds (Lauck *et al.* 1998; Hooker & Gerber 2004). Establishing management and protection measures for highly mobile species will likely rely on the premise, that if protection of areas encompassing key life history events is achieved, populations may be better sustained (Speed *et al.* 2010). In a summary of evidence for the value of no-take zones for reef shark species, Escalle *et al.* (2015) found 65% of these studies deemed the protection area assessed to be beneficial to sharks, but 35% of studies suggested designated areas were too small based on residency, home-range and space-use; concluding that marine reserves have the potential to benefit sharks, but will be dependent on the amount of time individuals spend within reserve boundaries and the number of life-history stages catered for by the reserve.

Most protected areas are designated with their efficacy tested *post-hoc*, if at all, which may result in the assigned areas and boundaries being unsuitable. This can create a situation where adjustments in boundaries would be needed to provide protection of more appropriate areas, e.g. expansion of protective measures to include U.S territorial waters would effectively protect 100% of core activity areas of highly mobile sharks in the

north-west Atlantic (Graham *et al.* 2016), or a buffer zone of an MPA acting as a year round exclusion zone to industrial trawlers would greatly increase protection of turtles in central Africa (Witt *et al.* 2008). If MPAs are designed with prior knowledge of space-use by species of conservation concern, and designated based on those findings, then they will more likely serve their purpose. In the present study, we have been able to robustly test basking shark space-use of a proposed MPA, prior to designation, in order to evaluate its potential spatial efficacy. We determined a mean of 84% of locations occurred within the boundaries of this proposed MPA across three years of study (Table 1). Core activity areas were robustly tested across multiple analytical techniques, all of which resulted in overlap of these *core* areas (>90%) with the proposed MPA (Fig. 2).

Basking sharks were observed foraging at the surface within the proposed MPA, however, there is potential for this area to provide suitable conditions for other life-history events. Nose-to-tail following and breaching behaviours were also observed in this area; behaviours that have previously been attributed to courtship (Harvey-Clark *et al.* 1999; Sims *et al.* 2000; Wilson 2004), although mating has never been observed. Boat-based transects have also shown the area to have a high level of shark occurrence (mean 1.74 sharks hour⁻¹), where large groups (>10 individuals) can be seen aggregating, with individuals within these large groups displaying courtship-like behaviour (Speedie *et al.* 2009), supporting the notion that this area is a *hotspot* for basking sharks.

Application and MPA management recommendations

MPAs can only be effective if appropriate management and enforcement are employed to reduce threats to species for which they are designated. We have observed basking shark behaviours, often at the surface, occurring within the waters off the west coast of Scotland. The threats to this species are therefore likely to primarily occur from boat strikes (leisure and tourist boats, commercial transportation and fishing vessels) or fisheries activity (entanglement or by-catch). It is often argued that MPAs are too small, often containing a small proportion of a population at any one time (Wilson 2016). However, after testing the space-use of basking sharks in the region, we reveal that high

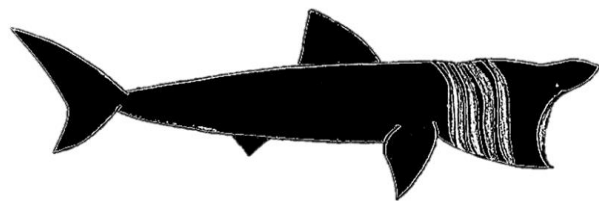
levels of core activity occurred within the boundaries of the MPA. Nevertheless, there is evidence for complementary MPAs to encompass other areas of use observed in satellite tracked basking sharks, most notably off the north-west coast of Ireland, the north coast of Northern Ireland and the waters to the west of the Outer Hebrides. We suggest that the areas of higher relative importance within the proposed MPA boundary should represent zones where vessel speeds are reduced, potentially seasonally between May and October (Speedie *et al.* 2009), fishing gear, in particular bottom set static gear (entanglement) or trawls (bycatch) are regulated and where leisure and tourist boats should adhere to the wildlife-watching best practise guidelines such as, Scottish Marine Wildlife Watching Code (SMWWC; www.marinecode.org) and the Wise Scheme (www.wisescheme.org) when sharing waters with marine wildlife.

Conclusion

Basking sharks are capable of extensive movement (Gore *et al.* 2008; Skomal *et al.* 2009; Doherty *et al.* 2017a), and are an important species of conservation concern in UK coastal waters. Until now there has been a paucity of high-resolution, seasonal information on space-use in basking sharks. The present study provides near real-time tracking of multiple individuals at a shared foraging site in the coastal waters off the west coast of Scotland. We identify core activity areas occurring within the boundaries of the proposed MPA, providing an opportunity for specific management to be implemented within the area. Our work also highlights the repeated seasonal use and inter-annual site fidelity of this area, which may provide suitable conditions for other key life-history events as well as foraging. This study was able to substantiate the importance of the area and assess how basking sharks use the proposed MPA prior to designation, a process not usually afforded to most MPAs.

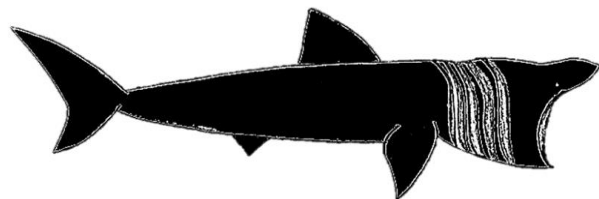
We show high levels of residency within a non-trivial sample size of basking sharks to the proposed MPA in the Sea of the Hebrides. However, we observed variation between individuals resulting in space use outside of these boundaries; towards the north-west coast of Ireland, the north coast of Northern Ireland, and the waters off the western

shores of the Outer Hebrides. These areas may represent other potential strongholds for basking sharks during summer months once scaled up to population level if the tracked sharks here are representative of the population as a whole and are worthy of focus of further studies, potentially to form complimentary MPAs. This tracking study, coupled with sightings data does however suggest that the Sea of the Hebrides, and the area encompassed by the proposed MPA boundaries is a very important area for basking sharks during summer months. Therefore with appropriate legislation and enforcement this proposed MPA will likely be fit for purpose and achieve protection of basking sharks by encompassing key life history events which likely will allow the population to be better sustained.



Chapter 3: Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic





Abstract

Animal migration is ubiquitous in nature with individuals within a population often exhibiting varying movement strategies. The basking shark (*Cetorhinus maximus*) is the world's second largest fish species, however, a comprehensive understanding of their long-term wider-ranging movements in the north-east Atlantic is currently lacking. Seventy satellite tags were deployed on basking sharks over four years (2012-2015) off the west coast of Scotland and the Isle of Man. Data from 28 satellite tags with attachment durations of over 165 days reveal post-summer ranging behaviours. Tagged sharks moved a median minimum straight-line distance of 3,633 km; achieving median displacement of 1057 km from tagging locations. Tagged individuals exhibited one of three migration behaviours: remaining in waters of UK, Ireland and the Faroe Islands; migrating south to the Bay of Biscay or moving further south to waters off the Iberian Peninsula, and North Africa. Sharks used both continental shelf areas and oceanic habitats, primarily in the upper 50-200 m of the water column, spanning nine geo-political zones and the High Seas, demonstrating the need for multi-national cooperation in the management of this species across its range.

Introduction

Animal migration is based upon individuals or groups of individuals attempting to secure optimal environmental conditions and exploit habitats during seasonal changes, and is observed in a wide range of taxa (Dingle 2014). Some individuals within a population often adopt differing migration strategies, which may result from either inter- or intra-individual plasticity with regards to their fidelity to a particular site. The strength of such fidelity can be affected by food availability, reproductive status, competition, predation risk, or body condition (Chapman *et al.* 2015). Describing seasonal and migratory movements in large marine vertebrates can be challenging, largely due to their wide ranging behaviour and the complexities of tracking individuals in water for durations sufficient to observe migratory behaviour (Hammerschlag *et al.* 2011). However, advances in satellite tracking technologies and attachment techniques now allow for repeated observations of movements and insights into intra- and inter-individual variation over extended time-scales (Hussey *et al.* 2015), enhancing our ability to assess life history traits, distribution and extent of range, site fidelity, migratory movements (Block *et al.* 2011; Rosenbaum *et al.* 2014; Hussey *et al.* 2015) and exposure to human threat.

Many sharks undertake migrations and utilise resources in different habitats with residency and fidelity varying at different spatial and temporal scales (Werry *et al.* 2014), with further evidence of behavioural plasticity (Boustany *et al.* 2002; Weng *et al.* 2008; Papastamatiou *et al.* 2013; Lea *et al.* 2015). The basking shark (*Cetorhinus maximus*) is the world's second largest fish species, historically overexploited for its large liver (Kunzlik 1988) resulting in large local population declines leading to recognition by the International Union for Conservation of Nature (IUCN) as Vulnerable globally, and Endangered in the north-east Atlantic (Fowler 2005); with further designations on a range of conservation legislation in the UK and Europe and inclusion under several international conservation treaties (Table B2). The species has a circumglobal distribution and can undertake extensive trans-oceanic basin migrations (Gore *et al.* 2008; Skomal *et al.* 2009); although the relative frequency and function of these migrations is unknown.

Aggregations of basking sharks occur seasonally in temperate continental shelf waters of the Atlantic, Pacific and Indian Oceans to feed, but potentially also for mating and parturition (Sims *et al.* 2000). Population size and structure estimates for the basking shark in the north-east Atlantic are unknown (Sims 2008), although a sub-regional estimate has been conducted (Gore *et al.* 2016). Studies in the region have successfully tracked basking sharks for up to 245 days, showing movements into the open ocean, the waters of the Bay of Biscay (Sims *et al.* 2003; Stéphan *et al.* 2011) and one trans-Atlantic crossing (Gore *et al.* 2008). These studies however have been limited by sample size, with the majority of movements confined to the continental shelf of the north-east Atlantic ($n = 2$; (Gore *et al.* 2008), $n = 7$; (Sims *et al.* 2003, 2006; Shepard *et al.* 2006), $n = 9$; (Stéphan *et al.* 2011)). With growing concern regarding the rate of decline of global shark populations (Dulvy *et al.* 2014), the importance of defining the extent and connectivity of mobile species populations has increased (Heupel *et al.* 2015).

Basking sharks are considered to be vulnerable to interactions with commercial fishing; potentially becoming entangled in set nets, pot lines or caught incidentally in trawls, and is considered as one of the more valued fins within the shark fin trade (Fowler 2005).

Anthropogenic activity in the north-east Atlantic is increasing (Halpern *et al.* 2008), therefore improved knowledge could be instrumental in supporting management decisions (Allen & Singh 2016), including mitigation of putative threats such as fisheries bycatch (Witt *et al.* 2011). Area-based protection measures are often implemented based on the majority of individuals exhibiting repeated behaviours and movement patterns. Behavioural plasticity can result in a range of movement strategies, sometimes resulting in groups of individuals moving away from areas originally designated for their protection (Lea *et al.* 2015). These groups may then remain at heightened risk of mortality. Consequently these behaviours may lead to specific groups (potentially based on sex, ages, reproductive status and condition) being at more risk (Milner-Gulland, Fryell & Sinclair 2011). In this study, long-term movement data gathered from satellite tags attached to basking sharks at known summer 'hotspots' off the west coast of Scotland and

the Isle of Man (Southall *et al.* 2005; Witt *et al.* 2012), were used to examine patterns of individual movement and subsequent post-summer migration strategies. Particular attention is given to over-wintering distributions as least is known of basking shark spatial ecology during this period, hence this represents one of the missing links to a more comprehensive understanding of their life-cycle.

Results

Satellite tracking

Basking sharks satellite tracked into the year following tag deployment ($n = 28$) using real-time tags (SPOT; Wildlife Computers) and light-geolocation archival tags (MiniPAT; Wildlife Computers) provided data for a median 281 days (IQR: 247-349; max. 479), moved a median minimum straight-line distance of 3,633 km (IQR 1987-4,996, range: 469-8,081 km) and were displaced by a median of 1057 km from their respective tagging locations (IQR: 557-1384; range: 264-2,711 km). Sharks tracked using SPOTs collected data for a median 322 days (IQR: 252-375; max. 479), moved a median straight-line distance of 2,280 km (IQR: 1,456-3,375; range: 469-4,310 km) and were displaced by a median of 1057 km from their respective tagging locations (IQR: 374-1560; range: 264-2,711 km). Sharks tracked using MiniPATs collected data for a median 265 days (IQR: 199-280; max. 292), moved a median straight-line distance of 6,050 km (IQR: 4,044-7,029; range: 2,333-8,081 km) and were displaced by a median of 1007 km from their respective tagging locations (IQR: 744-1219; range: 455-2,354 km).

There was no significant interaction effect of sex and estimated body length on the maximum displacement or the minimum latitude recorded by these sharks (GLMM: $\chi^2_2 = 5.64$, $p = 0.06$ and $\chi^2_2 = 5.66$, $p = 0.06$ respectively). There were no significant effects of sex, body length or tag attachment duration on the maximum displacement or the minimum latitude recorded by these sharks (GLMM maximum displacement by sex: $n = 16$, $\chi^2_2 = 1.49$, $p = 0.47$; by body length: $n = 28$, $\chi^2_1 = 0.05$, $p = 0.83$ and by tag attachment duration: $\chi^2_1 = 0.42$, $p = 0.52$. GLMM minimum latitude by sex: $n = 16$, $\chi^2_2 = 0.74$, $p = 0.69$; by body length: $n = 28$, $\chi^2_1 = 0.16$, $p = 0.69$ and by tag attachment duration: $n = 28$, $\chi^2_1 = 0.21$, $p = 0.64$).

Based on archival tag data, post-summer movements (October onwards) indicated basking sharks entered the EEZs of Iceland (<1% of all locations), Faroe Islands (2%), UK (18%), Ireland (51%), France (3%), Spain (4%), Portugal (4%), Madeira (<1%), Morocco (<1%), and

the High Seas (18%; Fig. B1). Areas of relative high importance for the tracked sharks (Fig. 3) include the waters to the west coast of Scotland, the Celtic and Irish Seas and, in particular the areas west of Ireland along the continental shelf break. These areas experienced a relatively high degree of usage by tracked sharks, somewhat indicative of an overwintering ground that links foraging grounds in the waters off the west coast of the UK and Ireland to the destinations adopted by each of the three migration strategies observed (Fig. 3a).

Migration strategies

Basking sharks exhibited wide-ranging post-summer movements, stretching from 33° to 61° N latitude (approx. 3,100 km range) within a longitudinal range (2° to 20° W); along the eastern fringe of the North Atlantic Ocean (Fig. 1 and Fig. B2-4). The general pattern of movement followed a transition to more southerly latitudes from October onwards in each year. These movements varied in distance and duration, with some individuals making short-range movements from the tagging areas and others undertaking longer-range movements (Fig. 2 and Fig. B2-4). Three post-summer migration strategies were identified from archival tags (n = 12); (a) *Celtic Seas* - predominantly remaining in UK and Ireland, with some movement into waters of the Faroe Islands (n = 6; max. displacement range: 455-854 km; one female, one male, four unknown sex), (b) *Bay of Biscay* - movement south to the Bay of Biscay (n = 5; max. displacement range: 1161-1515 km; four females, one male), and (c) *Iberian Peninsula & North Africa* - movement further afield to waters off the west coast of Portugal and North Africa (n = 1; max. displacement: 2,354 km; one unknown sex; Fig. 2 and B4). For Argos Doppler-based geolocation tags (n = 16; three females, six males, seven unknown sex), sharks were displaced by a range of 264-2,711 km.

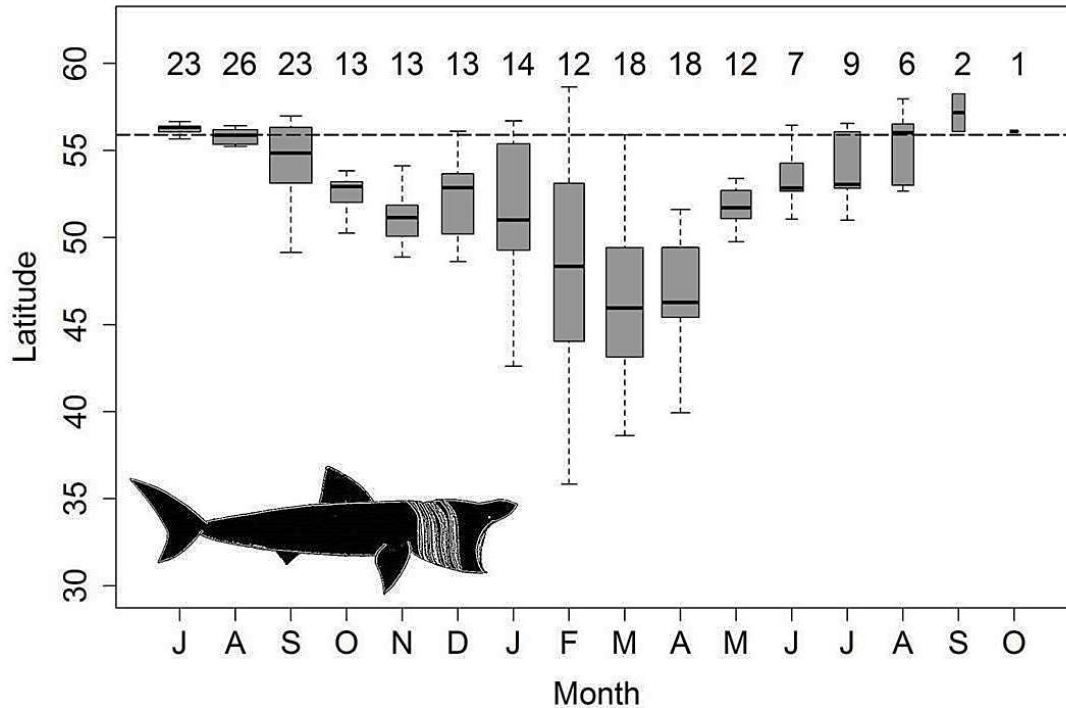


Figure 1. Minimum latitude observed for 28 satellite-tracked basking sharks. Box and whisker plots showing minimum latitudes per shark per month from tag deployment (July onwards). Boxes denote inter-quartile range; horizontal black bar indicates the median (whiskers extend to the 2.5th and 97.5th percentiles). Box width indicates relative data volume of (sample size) for each month; with number of individual sharks contributing to each box shown above corresponding box. Broken line indicates average latitude of tag deployments.

The furthest movement observed was undertaken by a basking shark during a three-month tracking period using a SPOT tag. This individual departed the west of Scotland tagging area in the month following tag application (August 2012), transited to the west of Ireland and the European mainland and arrived in North African waters in November 2012, at which point the tag ceased transmission (Fig. B4F; minimum straight line along-track distance: 3,949 km, straight line displacement from tagging location: 3,088 km).

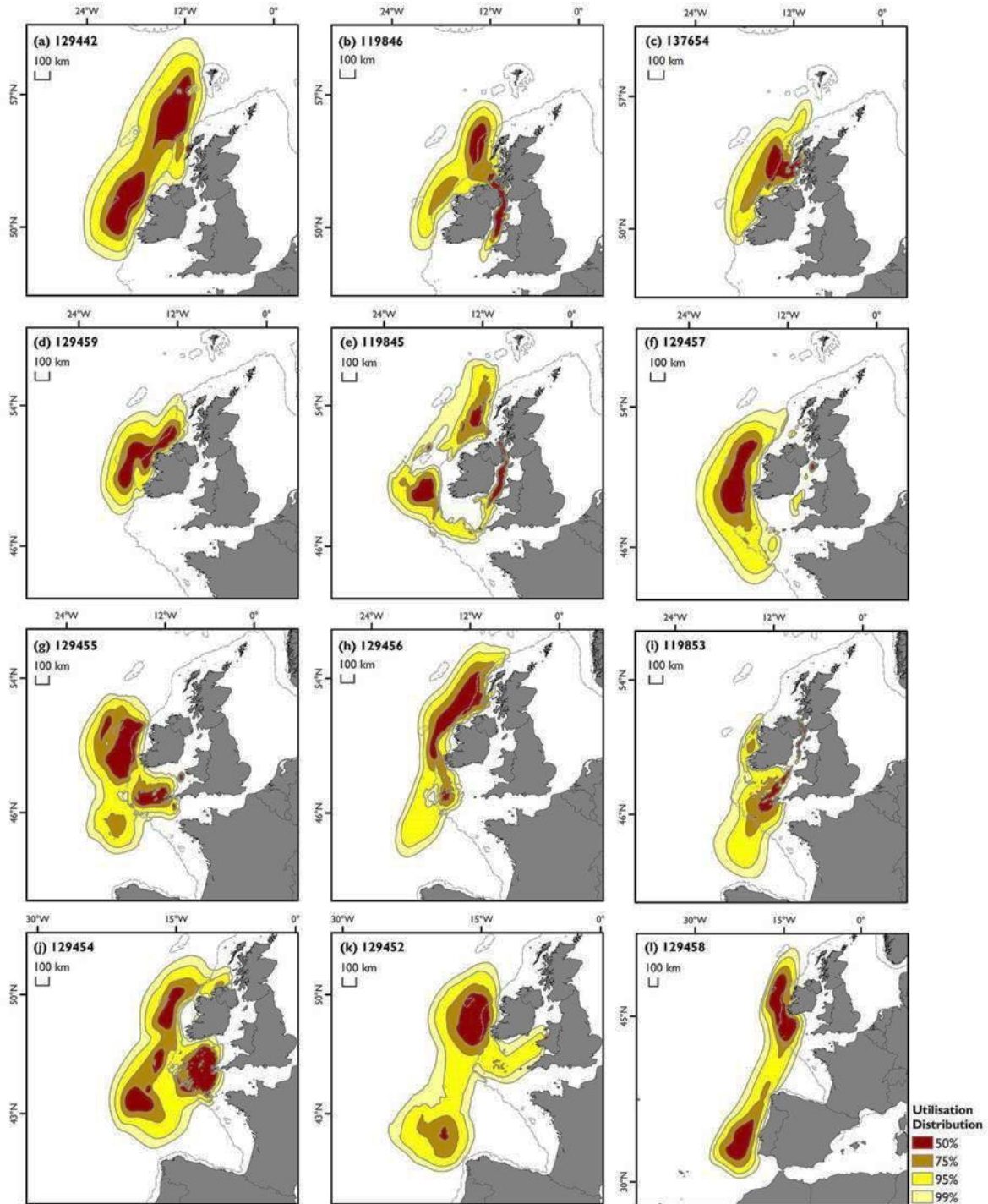


Figure 2. Overall post-summer (October onwards) distribution of individual tracked basking sharks from light-geolocation archival tags ($n = 12$). Normalised Utilisation Distributions (UDs); shaded according to probability of area of space-use. Broken grey line indicates 200 m depth contour (source: <http://www.gebco.net>). Maps created in ESRI ArcGIS version 10.1 using ESRI land shapefiles.

Return migrations

We observed varying degrees of return migration ($n = 15$ tags) in the years following tagging; which can be described as (i) departing the coastal regions of the UK, Isle of Man and Ireland (August to October), and return the following spring/summer (March to June) while remaining within the Exclusive Economic Zone (EEZ) of the UK and Ireland throughout the winter (Fig. 4a and d, $n = 6$; tag numbers: 119846 (Fig. B2B), 129439 (Fig. B2C), 129440 (Fig. B2D), 129442 (Fig. B2E), 129457 (Fig. B2G) and 137654 (Fig. B2I)); (ii) movement outside the EEZ of the UK and Ireland during the winter, but return to the Celtic Seas (Fig. 4b and d, $n = 3$; tag numbers: 129452 (Fig. B3G), 129455 (Fig. B3I) and 129444 (Fig. B4B)); or West Ireland ($n = 5$; tag numbers: 119853 (Fig. B3A), 129437 (Fig. B3B), 129448 (Fig. B3E), 129456 (Fig. B3J), and 129458 (Fig. B4C)) in spring, having undertaken migration strategy b; Bay of Biscay ($n = 6$; tag numbers: 119853 (Fig. B3A), 129437 (Fig. B3B), 129448 (Fig. B3E), 129452 (Fig. B3G), 129455 (Fig. B3I), and 129456 (Fig. B3J)), or migration strategy c; Iberian Peninsula & North Africa (Fig. 4d, $n = 2$; PTT numbers: 129444 (Fig. B4B) and 129458 (Fig. B4C)); or (iii) full return migration, returning to the region of tag attachment (approx. 20 km) after over-wintering outside of UK and Irish waters (Fig 4b, $n = 1$; PTT number 129449 (Fig. B4F). This is the first observation of such return migration in this species.

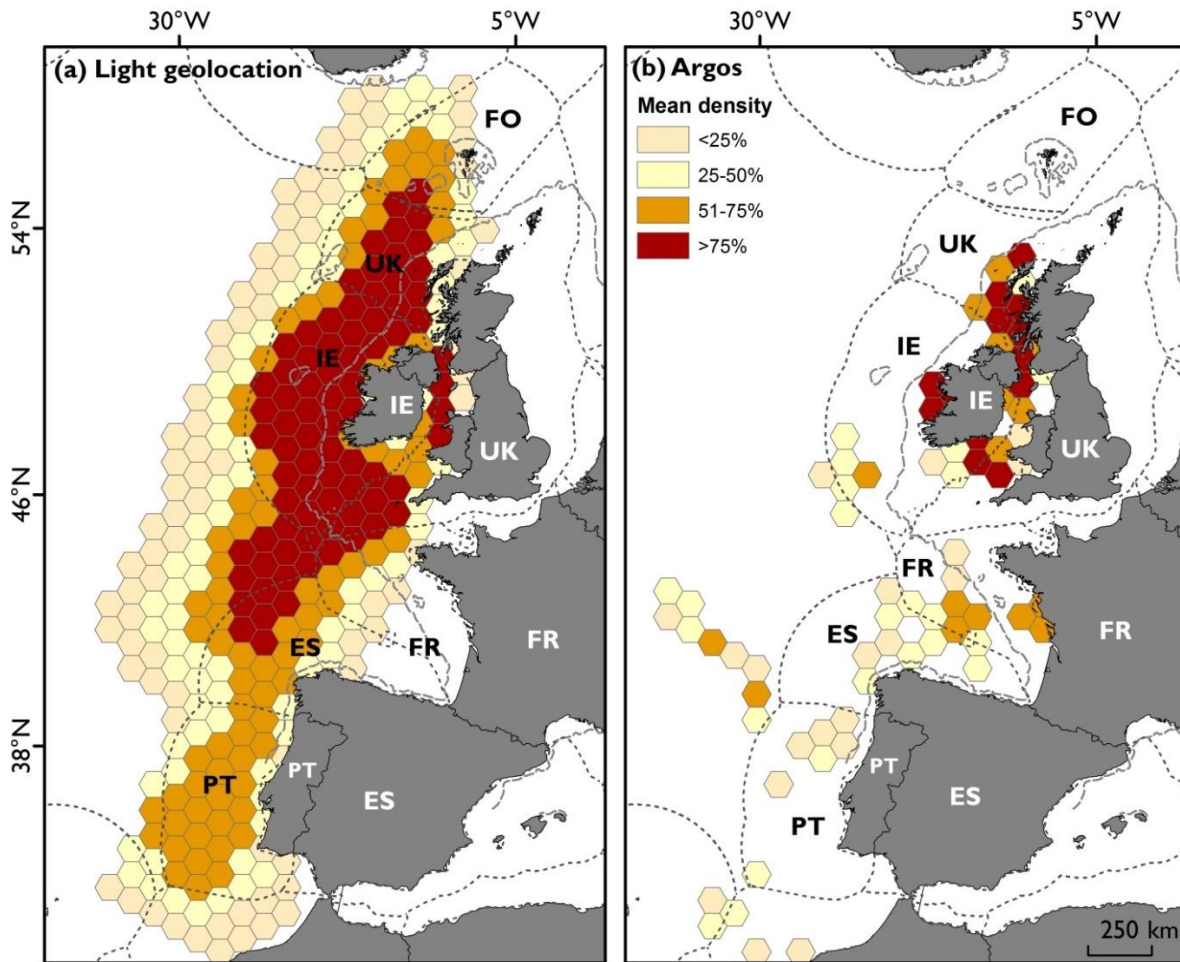


Figure 3. Grid density enumeration identifying areas of relative importance for tracked basking sharks post-summer (October onwards; 2012-2016) for locations derived from light-geolocation archival tags (a; n = 12 tags) and Argos real-time tracking tags (b; n = 16 tags). Mean occurrences from individual basking sharks enumerated on a hexagonal grid (cell edge size: 50 km; cell area: 8,660 km²). Country Economic Exclusive Zones denoted by light grey broken line with associated international two letter codes (white letters=land, black letters=EEZs; FO=Faroe Islands, UK=United Kingdom, IE=Ireland, FR=France, ES=Spain). Broken dark grey line denotes 200m depth contour. Maps created in ESRI ArcGIS version 10.1 (<http://desktop.arcgis.com/en/arcmap>) using ESRI land shapefiles, GEBCO bathymetric contours (<http://www.gebco.net>) and Flanders Marine Institute (VLIZ) Economic Exclusive Zone (EEZ) boundaries (<http://www.marineregions.org>).

Depth-use

For those basking sharks tracked with light-geolocation archival tags, data on depth-use were also available. These data highlighted sharks ($n = 12$) predominantly occupied the epipelagic zone (0-200 m depth; mean 84% of tracking time; Table B5) regardless of migration strategy ((a) *Celtic Seas*: 91%; (b) *Bay of Biscay*: 82%; (c) *Iberian Peninsula & North Africa*: 59%; Fig. 5; Table B5). Individuals exhibiting migration strategy a and b spent the majority of their time in waters 50-200 m deep (80.2% and 78.2% respectively); whereas, individuals exhibiting migration strategy c spent the majority of time in depths between 100 and 500 m (66.2%; Fig. 5; Table B5).

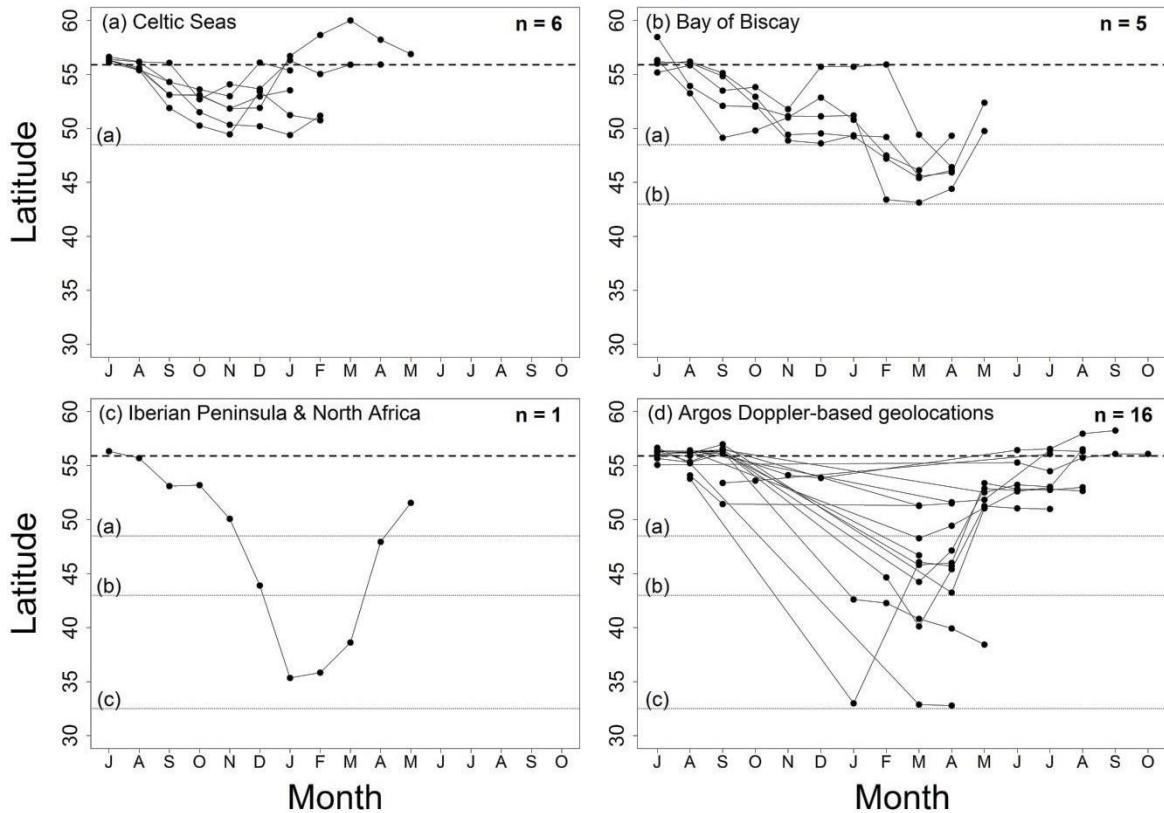


Figure 4. Plots showing minimum monthly latitudes occupied for each tracked shark from tag deployment (July onwards), derived from best daily location estimates from archival tags ($n = 12$) separated by migration strategy (a-c) and all Argos Doppler-based geolocation tracked sharks (d; $n = 16$). Minimum latitude for migration strategies (narrow dashed horizontal and labelled lines). Tag deployment locations (thick dashed horizontal line).

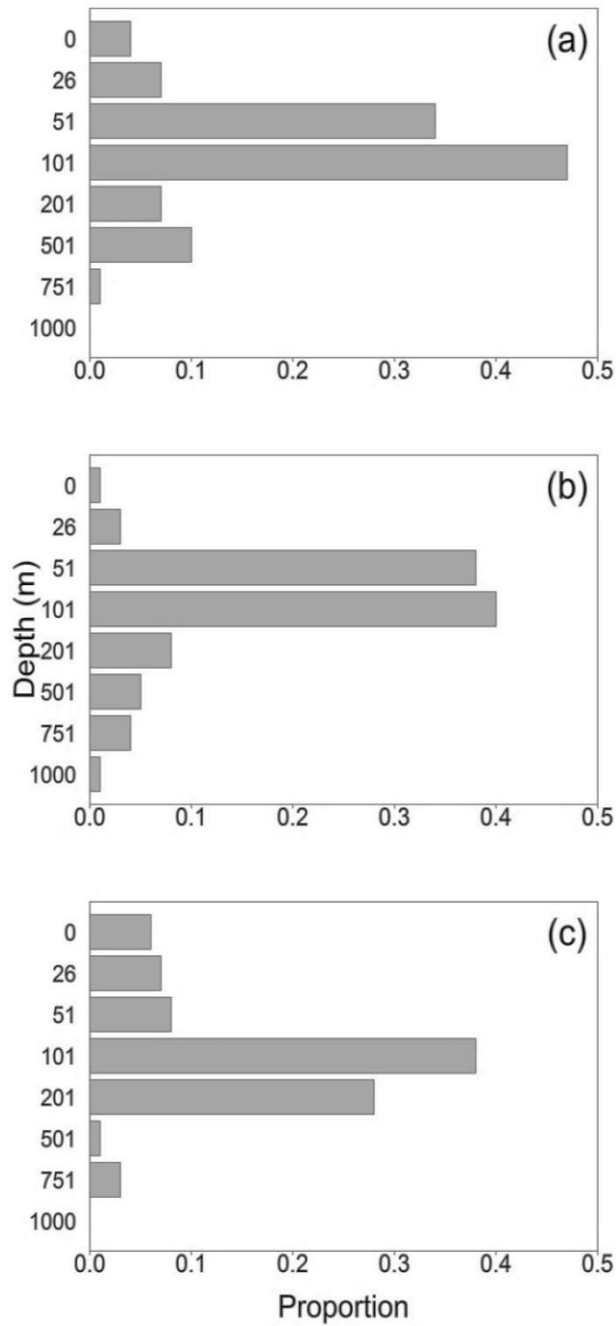


Figure 5. Proportion of daily maximum depths derived from archival tags within eight depth bins for associated migration strategy; (a) Celtic Seas, (b) Bay of Biscay and (c) Iberian Peninsula and North Africa. Depth ranges are represented by the minimum value for each range (0-25 m, 26-50 m, 51-100 m, 101-200 m, 201-500 m, 501-750 m, 751-1000 m, >1000 m).

Discussion

The ability to record intra- and inter-individual variation in the movement and distribution of large marine vertebrates is becoming increasingly possible and provides important information on species space-use (Hart & Hyrenbach 2009; Block *et al.* 2011; Hammerschlag *et al.* 2011; Hussey *et al.* 2015), and has resulted in migration being observed in many taxa (Milner-Gulland *et al.* 2011; Dingle 2014). Our study provides the most detailed investigation of basking shark ranging behaviours in the north-east Atlantic over seasonal timescales to be informed by satellite tracking (Witt *et al.* 2016).

Little is known about basking shark habitat or site preference during the winter as their vertical distribution indicates they spend a large proportion of time away from the surface. Anatomical studies previously suggested that basking sharks hibernate in deep waters around the UK and Ireland during the winter (Matthews & Parker 1950; Parker & Boseman 1954; Matthews 1962). In recent years, however, hibernation seems less likely to occur due to increasing levels of information from electronic tags (Francis & Duffy 2002; Sims *et al.* 2003; Skomal, Wood & Caloyianis 2004). Sims *et al.* (2003)(Sims *et al.* 2003) showed that basking sharks do not lie dormant during the winter months, but show frequent vertical movements throughout the water column with close association to the continental shelf edge, providing evidence that these sharks likely do not *hibernate*. More recent studies have shown that this species makes oceanic scale movements post-summer, travelling towards Newfoundland from the Isle of Man (Gore *et al.* 2008), although this has only been observed in a single individual. Extensive north-south autumn migrations have been observed from basking sharks tagged in coastal waters of north-east United States, with tracked individuals crossing the equator into tropical waters off the coast of Brazil (Skomal *et al.* 2009). It seems increasingly improbable that this species exhibits a sedentary phase during winter months (based on an assessment of movement), and it remains unknown if basking sharks forage during this time, however, there is evidence for diel vertical migration (DVM) occurring away from the surface post-summer (Shepard *et al.* 2006), similar in form to DVM patterns seen in summer months attributed

to associating with the diel vertically migrating *Calanus* sp. layer (Sims *et al.* 2005). There is the potential for basking sharks to subsist on fat reserves in the liver, which has been observed in white sharks (*Carcharodon carcharias*) where these sharks exhibited an increased vertical downward drift rate over the course of long migration movements (>4,000 km), which is indicative of decreased buoyancy caused by the depletion of liver lipid reserves (Del Rave *et al.* 2013). This depletion of lipid reserves has also been noted in historical testimonies from basking shark fishers claiming basking sharks caught earlier in the season had lighter livers (O'Connor 1953).

Historically there have been contrasting opinions on this species' long-term movements and distribution, with suggestions that basking sharks over-winter as a single population off the coast of North Africa returning northwards in the spring (Kunzlik 1988), however, there was a counter argument citing that there was no predictability in first appearance of basking sharks during the spring/summer season from Portugal/Spain northwards as the season progressed (Stott 1982). We show that it is unlikely that all basking sharks adopt a single migration strategy, but more likely behavioural variation occurs within the population, resulting in individuals performing varying movements. It is not yet known whether adopted migration strategy by individuals is annually consistent or changes with body condition, reproductive status, resource availability or other factors.

The primary drivers behind basking shark migrations are still unclear, but may include; searching for foraging grounds, thermoregulation by moving to areas and/or depths of preferred temperature, movement towards mating grounds or natal homing. We show some evidence of this, whereby basking sharks exhibit movement away from the surface during the onset of autumn, likely representing the switch from summer foraging to exhibiting movements towards overwintering grounds. This appears to occur in sharks regardless of migration strategy. Similar patterns have been shown in basking sharks in the north-west Atlantic (Skomal *et al.* 2009) where sharks have moved deeper into the water column during autumn. In another lamnid shark, the Salmon shark (*Lamna ditropis*) there are similar movements, switching to favour deeper waters, however this only occurs

in migrating individuals and not in those over-wintering at depth in relatively close proximity to summer foraging grounds, with high levels of variation in timing of this switch (Weng 2005; Weng *et al.* 2008). Skomal *et al.* (2009) hypothesised that within the north-east Atlantic, stable environmental conditions are mediated by the Gulf Stream, limiting the extent to which basking sharks need to move during winter months to find sufficient food. We find that at least some individuals do undertake large-scale latitudinal movements throughout the winter in the north-east Atlantic, somewhat similar to their results from the north-west Atlantic. We have observed the first evidence of round-trip migrations by individuals leaving UK and Irish waters, over-wintering elsewhere, returning to these coastal waters during the spring and summer. Some tracks ended off North Africa with no evidence of return movements, which may be an artefact of tag attachment duration, with premature tag detachment potentially occurring from biofouling of the tag, predation of the tag by other species or removal of the tag during incidental bycatch. There remains the possibility that sharks could move further south, as has been shown in the north-west Atlantic (Skomal *et al.* 2009). Shark movements were reconstructed for this study using Argos Doppler-based geolocation and light-geolocation; these techniques differ in that Argos Doppler-based geolocation only provides estimates of locations when the tag is at the surface. During the winter, sharks spend proportionally less time at the surface, limiting opportunities to gather information on their location during this period. In contrast, light geolocation can be near-continuous, particularly when integrated with predictive models of animal movement to provide estimates of location when light geolocation alone is unsuccessful. Our assignment of migration strategy likely underestimates the extent of potential movement for sharks tagged with SPOT tags. Nonetheless, all migration strategies (*a* to *c*) were observed independently in the light geolocation data; therefore, broad scale, geographic patterns of movement described here are likely not artefacts of the positioning technology used.

Continued development of tag technology and attachment techniques will allow for multi-year deployments, increasing the ability to quantify individual variability and highlight the likely potential for condition-dependent ranging. Further work is also required to quantify the frequency of newly observed ranging behaviours, whereby individuals adopt a differing behaviour to that of the modal strategy, as these individuals are likely important for maintaining genetic diversity (thought to be low (Hoelzel *et al.* 2006)) and ensure the species has the potential to exploit all areas of the realised or fundamental niche (Kokko & Lopez-Sepulcre 2006; Kokko 2011). Greater knowledge on behavioural plasticity may also help improve predictions on how this large planktivorous species might respond to environmental disturbance and climate change, where fidelity to areas may diminish or strengthen as locations that are regularly used by individuals become less suitable, either for foraging or breeding (Chapman *et al.* 2015). This may be pertinent for basking sharks, as climate change has been suggested to influence the distribution of their preferred prey group (calanoid copepods (Sims, Fox & Merrett 1997; Beaugrand *et al.* 2002)), possibly making some areas less suitable for this species, offering one possible explanation for declines in basking shark sightings within areas of its historical range (Sims & Reid 2002). Highlighting the full range of movements made by a species and partitioning of time within these areas is integral to implementing effective international conservation measures for highly mobile species (Knip, Heupel & Simpfendorfer 2012b; Werry *et al.* 2014).

In this study, satellite tracked basking sharks largely remained within the EEZs of the UK and Ireland; they also appeared to occupy waters of seven other geo-political zones and the High Seas. In a previous study (Southall *et al.* 2006) it was shown that basking sharks spent a higher proportion of their time in the UK EEZ (31%) to that of our study (18%), however, this study showed a much greater use of the France EEZ (22%) than our study (3%) and much less occupancy of the Ireland EEZ (15%) to that shown here (51%). No use of International waters away from the European continental shelf was shown, whereas we observed basking sharks showing appreciable levels of occupancy of the High Seas (18%). This may be due to shorter tag attachment durations of the previous study, resulting in

more data from summer and autumn months. Our study therefore stresses the need for multi-national cooperation in developing a comprehensive conservation strategy for this species, which is still likely recovering from historical exploitation. This is especially apparent during winter months where variation in basking shark behaviour results in multiple geo-political zones being occupied by the population and often away from protected areas. Whilst there are no longer targeted fisheries for basking sharks, by-catch is an area of concern, and research in UK waters (Hetherington *et al.* 2015) has identified incidental catches occurring in fisheries operating off south Ireland in surface and bottom set gill nets (Berrow 1994; Berrow & Heardman 1994), north-west Iberian Peninsula in artisanal gill net fisheries (Valeiras, Lopez & Garcia 2001) and in New Zealand, where basking sharks are a frequent bycatch of trawl and set net fisheries (Francis & Duffy 2002), all with uncertain levels of mortality. The waters to the west of Ireland and the Celtic and Irish Seas are likely important areas for basking sharks, acting as migratory pathways linking foraging areas in the waters off the west coast of Scotland to other areas of importance to basking shark life-history events, which may also include other seasonal foraging or breeding sites. Active fisheries operating within the Irish EEZ, include demersal otter trawling, (approx. 62% of total fishing hours between 2008 and 2012), longliners (15%), gill and trammel nets (7%) and pelagic trawlers (5%) the other most operated gear types (Gerritsen & Lordan 2014). The majority of fishing activity within the Irish EEZ is by foreign vessels (Spanish = 30%, French = 20%, and the UK = 11%), with Irish vessels accounting for 36% of activity with combined landings of over 394,000 tonnes in 2012 (Gerritsen & Lordan 2014). The UK is a signatory to the Convention for Migratory Species with Ireland, France, Portugal, Spain and Morocco; all range states for basking sharks, mandating multi-national cooperation over management of shared activities within ranges of species of conservation concern. An onboard bycatch observer programme may provide a useful tool in which to assess the potential impact of bycatch on basking sharks (Francis & Duffy 2002). This would inform on the extent to which basking sharks are being incidentally caught, and provide baseline information on gear type, effort, and potentially mortality rates within these fisheries from which to form an evidence-based conservation programme.

Satellite tracking has greatly improved our understanding of animal movements. This study further contributes to the growing knowledge of basking shark movements and behaviour, especially for those aspects of movement that have remained elusive, such as during winter months in the north-east Atlantic. We show behavioural variation within the population, with individuals exhibiting one of three migration strategies and the capacity to move from coastal to oceanic habitats. Individuals can undertake movements at an oceanic scale, crossing multiple geo-political zones following periods of residency. Our work has highlighted a potentially important movement corridor along the continental shelf off western Ireland, which may leave a proportion of the population vulnerable for extended periods to trawl and set-net fishery interactions. We did not detect segregation by sex or size in our study, behaviours that are often reported for sharks (Bres 1993; Wearmouth & Sims 2008). There is also the potential for varying combinations of body size and/or sex to influence movement both horizontally and vertically. Larger tiger sharks (*Galeocerdo cuvier*) have been shown to utilise deeper waters, experiencing lower temperatures across both sexes (Afonso & Hazin 2015), with a similar positive correlation shown in mako sharks (*Isurus oxyrinchus*) between body size and maximum depth (Sepulveda *et al.* 2004). However, smaller blue sharks (*Prionace glauca*) have been shown to exhibit deeper diving behaviour (Campana *et al.* 2011). We cannot fully ascertain whether this is occurring in basking sharks, or whether sample size and access to a full range of sizes and sexes in which to tag affected the results seen. The continued development of tag technology, in particular battery life and minimising biofouling, will allow for longer attachment times, which will increase our understanding of the drivers of movement in this species and intra- and inter-individual movement across multiple years, in order to identify key habitats and behaviours and overlap with potential threats. This research can be coupled with other fast-developing techniques such as stable isotopes and genetic analysis to better estimate population sizes and relatedness and to begin to understand foraging strategies, especially during winter months.

Methods

Seventy satellite tags (Smart Position or Temperature tags; SPOT = 32; Pop-up Archival Transmitting with Fastloc™ GPS tags; PAT-F = 12; Mini Pop-up Archival Transmitting tag; Mini-PAT = 12; SPLASH-F = 14; Wildlife Computers, Washington, USA) were attached to basking sharks off the west coast of Scotland (n = 62) and Isle of Man (n = 8) during June, July and August in 2012 (n = 21), 2013 (n = 36), 2014 (n = 10) and 2015 (n = 3) (Witt *et al.* 2016) (for tag programming and deployment see Appendix B). The attachment of satellite transmitters in Scottish coastal waters protocol was approved by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (issuing Project Licence 30/2975). All work was carried out in accordance with the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971) and internally through the University of Exeter's animal welfare and ethics review board (AWERB). Licences to tag sharks in the Isle of Man were issued by the Department of Environment, Food and Agriculture (Isle of Man Government) under the Wildlife Act 1990. Data gathered from 29 sharks (SPOT = 16; PAT-F = 3; MiniPAT = 8; SPLASH-F = 2) were selected for detailed analysis; these sharks were either tracked into at least the January following tag attachment (n = 28; >165 days of tracking; Table B2), or were tracked making long-range movements away from the north-east Atlantic over a shorter period of time (n = 1; Table B2). All tag data were downloaded from CLS-Argos and archived using the Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005). Basking sharks were geolocated during their tracking periods using either standard Argos Doppler-based geolocation when sharks were at the surface (n = 16; SPOT and SPLASH-F tags) or light-based geolocation throughout the tag attachment period (n = 12; PAT-F, MiniPAT and SPLASH-F tags). These data were subsequently processed to single daily tracking locations for each individual. Argos Doppler-based geolocation filtering was achieved using the *adehabitat* package (Calenge 2006).

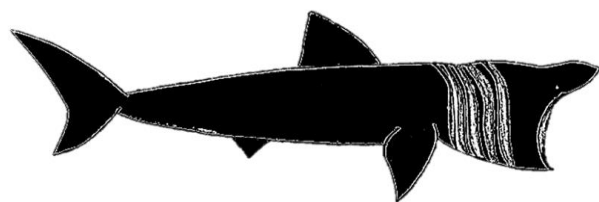
Light geolocation data were obtained from archival tags ($n = 12$, one SPLASH-F tag failed to transmit sufficient light level data for track reconstruction) and analysis of light level data was undertaken by *Collecte Localisation Satellites* (CLS-Argos) (www.argos-system.org). Obtaining daily estimates of location from gathered light data can be challenging for basking sharks as they often spend prolonged periods at depth or exhibit diel vertical migration (DVM), reducing reliability of some light data (Shepard *et al.* 2006). Therefore, to reconstruct the likely movement paths of basking sharks, we used Hidden Markov Models (HMM) implemented as grid filters (Neilson *et al.* 2014) to estimate the daily probability density (or Utilisation Distribution; UD) of the location of tracked animals making use of validated light-based estimates of location to influence the resulting modelled trajectories (Thygesen, Pedersen & Madsen 2009). The HMM used a two-step process, whereby at each sampling time a position prediction step, solving the advection-diffusion equation for the two-dimensional probability of an animal's presence, was implemented (Bias *et al.* 2017). An update step was then performed to combine the predicted probability density using information on latitude, longitude, SST (GHRSSST-OSTIA; <https://www.ghrsst.org/>) and depth (etopo2; <https://www.ngdc.noaa.gov/mgg/global/etopo2.html>) recorded onboard the tag to produce the posterior distribution of the individual (Bias *et al.* 2017). Locations derived from light intensity (obtained using Wildlife Computers GPE2 software) were used as observations. These data were constrained by bathymetry (Thygesen *et al.* 2009), SST and known deployment and pop-off locations. The diffusion coefficient of the HMM model was set to $1000 \text{ km}^2 \text{ d}^{-1}$; the standard deviation of raw light based locations used in the update step was set to 1° longitude and 3.5° latitude and the standard deviation of the difference between recorded and satellite derived SST was set to $0.5 \text{ }^\circ\text{C}$ (Bias *et al.* 2017). The best daily estimate of location for these tags was taken to be the geographic mean of the grid locations weighted by their probability. Once daily UDs were calculated for each tag for the duration of the tag attachment, these were normalised and summed to provide the probability of the animal's presence in the extent of the grid filter for its time at liberty. For each daily distribution probability raster, percentage volume contours (PVC) were calculated to produce density kernels exhibiting likelihood of presence (Fig. 2).

UDs for each shark were created for entire time at liberty post-summer (October onwards). Data from PAT-F, MiniPAT and SPLASH-F tags recording depth ($n = 12$) were used to estimate time spent within pre-determined depth ranges.

To determine areas of high relative importance for tracked basking sharks polygon sampling grids bounded by the maximum limits of observed movement were spatially intersected with filtered tracking locations for Argos Doppler-based geolocation and raster values for light-based geolocation (hexagonal cells; 50 km from grid cell centroid to edge; cell area 8,660 km²). The size of the grid cells was based on the mean error across all light-based geolocation tags (97.68 km). The mean occurrence of daily locations within grid cells was calculated for each individual followed by a spatial mean calculated across all individuals. All spatial analyses and maps were created using Geospatial Modelling Environment (GME v 0.7.2.1) (Beyer 2012) and ESRI ArcMap 10.1.

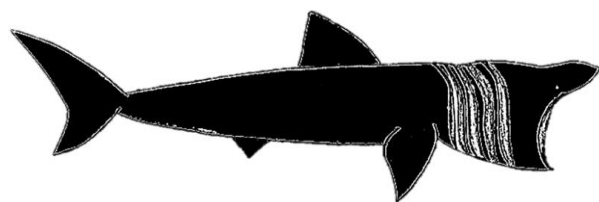
K-means cluster analysis was used to separate individual tracks into migration strategy groups (Hartigan & Wong 1979) based on most southerly latitude observed using best daily locations, which was used as a proxy for putative migration strategy. This analysis was conducted using archival tags only ($n = 12$), as data provided information on the full extent of movement with robust evidence of most southerly latitude reached, followed by return movements North in the spring. All data analyses were performed in R (R Core Team 2014).

To examine the effect of basking shark sex, body length and tag attachment duration on movement we used General Linear Mixed-effect Modelling (GLMMs; lme4 package (Bates *et al.* 2014)). For this analysis the maximal model was fitted with all biologically relevant interactions. The significance of fixed effects were assessed by comparing maximum likelihood ratios of the maximal model to the model without the fixed effect, with non-significant interactions removed to test the main effects (Engqvist 2005).



Chapter 4: Vertical behaviour of basking sharks reveals seasonal depth-use,
extreme diving events, and behavioural thermoregulation





Abstract

Mobile marine species can exhibit vast movements, both horizontally and vertically, which can make developing effective management strategies challenging. Spatial analysis of vertical movements may help improve an understanding of the processes that influence movements. Previous studies in the north-east Atlantic on the vertical space-use of basking sharks described movements mostly within waters of the continental shelf during summer and autumn months, with few records of detailed winter vertical behaviour. We use archival satellite telemetry data from 32 basking sharks (*Cetorhinus maximus*) tracked over four years (2012-2015) providing depth and temperature data for a cumulative 4,489 days (mean 140 ± 97 , range: 10-292 days) in order to describe vertical space-use and thermal niche of basking sharks in the north-east Atlantic. We found basking sharks exhibit seasonality in their depth-use, revealing repeated 'yo-yo' diving behaviour and areas of extreme deep diving to depths greater than 1000 m. We also show the first evidence for behavioural thermoregulation in basking sharks with extended shallow water intervals after movements to depths where temperatures experienced were at the extreme lower boundary of their preferred thermal range during winter months. Describing vertical space-use in different seasons can contribute to knowledge of basking shark movements in order to inform future conservation strategies.

Introduction

Describing seasonal and migratory movements in large marine vertebrates has been challenging, largely due to the complexities of tracking individuals in water for durations sufficient to observe migratory behaviour (Hammerschlag *et al.* 2011). However, advances in satellite tracking technologies and attachment techniques now allow for repeated observations of movements and insights into space-use over extended timescales (Hazen *et al.* 2012; Hussey *et al.* 2015). This enhances our ability to observe life-history events (Block *et al.* 2011; Hussey *et al.* 2015) and also reveal an extraordinary array of behaviours from; ocean basin migrations (Bonfil *et al.* 2005) to individual dive profiles to exceptional depths of over 2,500 m (Schorr *et al.* 2014).

Previous studies in the north-east Atlantic on the vertical space-use of basking sharks have shown these sharks spend the majority of time in shallow surface waters during the summer (Sims *et al.* 2003; Stéphan *et al.* 2011) moving into deeper, mesopelagic waters during winter months (Sims *et al.* 2003; Gore *et al.* 2008; Stéphan *et al.* 2011; Doherty *et al.* 2017a), this has also been described in the north-west Atlantic (Skomal *et al.* 2009). Sims *et al.* (2003) suggested vertical movements were consistent with those associated with foraging, with animals likely feeding year round on zooplankton. These behaviours, however, differed with habitat type; when in deep, stratified waters of the continental shelf-edge basking sharks exhibited normal Diel Vertical Migration (DVM; dusk ascent-dawn descent), but when in shallower, inner-shelf waters basking sharks conducted reverse Diel Vertical Migration (rDVM; dusk descent-dawn ascent) (Sims *et al.* 2005; Stéphan *et al.* 2011). Basking sharks were also shown to switch behaviours to a tidal rhythm when encountering boundaries between thermally stratified, and mixed waters (Shepard *et al.* 2006).

Spatial analysis of vertical movements can help improve understanding of the processes that regulate occupancy of habitats in species where bathymetric constraints vary (Afonso & Hazin 2015). Analysing fine-scale depth data from physically recovered archival satellite

tags can help identify patterns in vertical space-use and gain insight into the underlying factors that influence habitat selection and behaviour (Vaudo *et al.* 2014). We examine the depth and temperature profiles of basking sharks to better understand the function of vertical behaviour and provide insight into the ecology and physiology of this deep-diving elasmobranch.

Using data from a large sample size of archival satellite tags deployed on basking sharks, our aims were to (1) quantify basking shark depth and temperature distributions and depth-use patterns, (2) investigate whether seasonality has an effect on basking shark vertical habitat use, and (3) investigate potential factors that might influence vertical behaviour.

Methods

Tag attachment and specification

Thirty-two archival satellite tags (Pop-up Archival Transmitting with Fastloc™ GPS tags; PAT-F; n = 9, Mini Pop-up Archival Transmitting tag; MiniPAT; n = 10, SPLASH-F; n = 13; Wildlife Computers, Washington, USA) were attached to basking sharks off the west coast of Scotland during July and August in 2012 (n = 9), 2013 (n = 14) and 2014 (n = 9). Satellite tags were attached to 12 females, 6 males and 14 individuals of unknown sex, measuring 4-5 m (n = 6), 5-6 m (n = 10), 6-7 m (n = 7), 7-8 m (n = 8) and 8-9 m (n = 1) estimated total length. These tags were programmed to summarise depth data at four hour intervals use across 12 depth ranges; 0-1 m, 1-5 m, 5-10 m, 10-25 m, 25-50 m, 50-75 m, 75-100 m, 100-250 m, 250-500 m, 500-750 m, 750-1000 m and >1000 m and 12 temperature ranges; 0 °C, 0-4 °C, 4-6 °C, 6-8 °C, 8-10 °C, 10-12 °C, 12-14 °C, 14-16 °C, 16-18 °C, 18-20 °C, 20-22 °C and >22 °C. Satellite-transmitted maximum daily depths of sharks were used to estimate vertical position within the water column during wide-ranging movements throughout winter.

Basking sharks were approached by boat to avoid the line of sight of the shark and to minimise disturbance. On approach to the shark, the individual was, where possible, sexed using a pole mounted camera and total body length was estimated based on comparison to the total length of the boat (10 metres). Satellite tags were deployed using a titanium M-style dart (Wildlife Computers, Redmond, California, USA) inserted into the sub-dermal layer at the base of the first dorsal fin with a modified pole spear and attached via a tether consisting of heat-shrink covered stainless steel flexible cable, a swivel and monofilament line attached to the tag.

The attachment of satellite transmitters in Scottish coastal waters was approved by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and internally through the University of Exeter's Animal Welfare and Ethics Review Board (AWERB). All work was carried out in accordance with the UK HM

Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971).

Location data processing

Light geolocation data were obtained from archival tags with attachment durations greater than 165 days ($n = 12$). One daily location best describing the light level, temperature and depth data recorded onboard the tag was estimated, where possible. Acquiring continuous data can be difficult due to depth behaviour limiting reliability of light data at times (Shepard *et al.* 2006). Grid filters, or Hidden Markov Models (HMM) (Neilson *et al.* 2014) were applied to better estimate the location of individuals between high quality light geolocations (Thygesen *et al.* 2009). This process is split into two steps; (1) a position prediction step. This solves the advection-diffusion equation for the two-dimensional probability of an animal's presence at each sampling location (Bias *et al.* 2017) and (2) an update step, combining the predicted probability density using information on latitude, longitude, SST and depth recorded onboard the tag to produce the posterior distribution of the individual (Bias *et al.* 2017). The mean grid location probability weighted by probability forms the daily location. A modified version of the geolocation method described in Neilson *et al.* (2014) was applied using raw locations derived from light intensity (obtained using Wildlife Computers GPE2 software) as observations. These data are then constrained by bathymetry (Thygesen *et al.* 2009), SST and known deployment and pop-off locations. Constraining parameters of the model were; the diffusion coefficient of the random walk (set to $1000 \text{ km}^2 \text{ d}^{-1}$ as this minimises the SST root mean square deviation), the standard deviation of raw light based locations used in the update step (set to 1° longitude and 3.5° latitude), and the standard deviation of the difference between recorded and satellite derived SST (set to $0.5 \text{ }^\circ\text{C}$) (Bias *et al.* 2017). Analysis of light level data applying HMMs was conducted by *Collecte Localisation Satellites* (CLS-Argos) (www.argos-system.org). Basking sharks tracked for longer than 165 days were separated into two categories; those which remained in UK and Ireland waters during the winter, and those which moved off the continental shelf towards the Bay of

Biscay, Iberian Peninsula and North Africa (based on defined strategies by Doherty *et al.* 2017).

To assess patterns of depth use, 'dives' were categorised as movements into waters greater than 10 m and remaining below that threshold for at least 30 minutes. To investigate thermoregulation during the winter period (October-March) the effect of minimum temperature experienced during a dive on subsequent time spent at less than 10 m was explored using high-resolution time-series data (10-15 second frequency) obtained from archival tags ($n = 6$) during the winter, these tags were physically recovered from across western facing shores of the north-east Atlantic. The duration of each dive event, the minimum temperature experienced, and the subsequent period of time spent shallower than 10 m depth were calculated, with extreme post-dive surface durations removed (>6 hours). These data were used in a General Linear Mixed-effect Model (GLMM; *lme4* package (Bates *et al.* 2014)) with the log of surface duration in minutes as the response variable, minimum temperature as the predictor variable and tag model, shark identification number, and month as random effects. The significance of the fixed effect was assessed by comparing maximum likelihood ratios of the maximal model to the model without the fixed effect. To spatially determine areas of surfacing and deep diving behaviour for tracked basking sharks, polygon sampling grids bounded by the maximum limits of observed movement were spatially intersected with best daily light geolocated tracking locations (hexagonal cells; 50 km from grid cell centroid to perimeter; area 8,660 km²). The area of the grid cells encompassed the mean error across all light-based geolocation location estimates (98 km). The mean minimum and mean maximum depths at daily locations within grid cells was calculated for each individual followed by a spatial mean calculated across all individuals.

Data analysis were performed in R (R Core Team 2014), with satellite tag location filtering applied using the *adehabitat* packages (Calenge 2006). All spatial analyses and maps were created using Geospatial Modelling Environment (GME v 0.7.2.1; Beyer 2012) and ESRI ArcMap 10.1.

Results

General depth-use

Thirty-two archival satellite tags (Table C1. PAT-F; n = 9, MiniPAT; n = 10, SPLASH-F; n = 13) transmitted depth and temperature data over a cumulative 4,489 days (mean 140 ± 97 , range: 10-292 days) providing time-series data and summarised histograms at 4-hour intervals (Table C1). Satellite tracked basking sharks most frequently occupied depths between 25 and 50 m during the summer (median occupancy 47%; Fig. 1A; April-October), but exhibited increased occupancy at the surface (0-1 m) during daylight hours (mean occupancy during daylight hours at the surface 17%, mean occupancy during night-time hours at the surface 8%; Fig. 1A and B). In the winter tracked basking sharks exhibited a deeper range of depth occupancy than during the summer, most frequently between 100 and 250 m during daylight hours (median occupancy 33%; Fig. 1C), but moving into a shallower depth range during the night (median occupancy of 19% between 50 and 75 m; Fig. 1C and D).

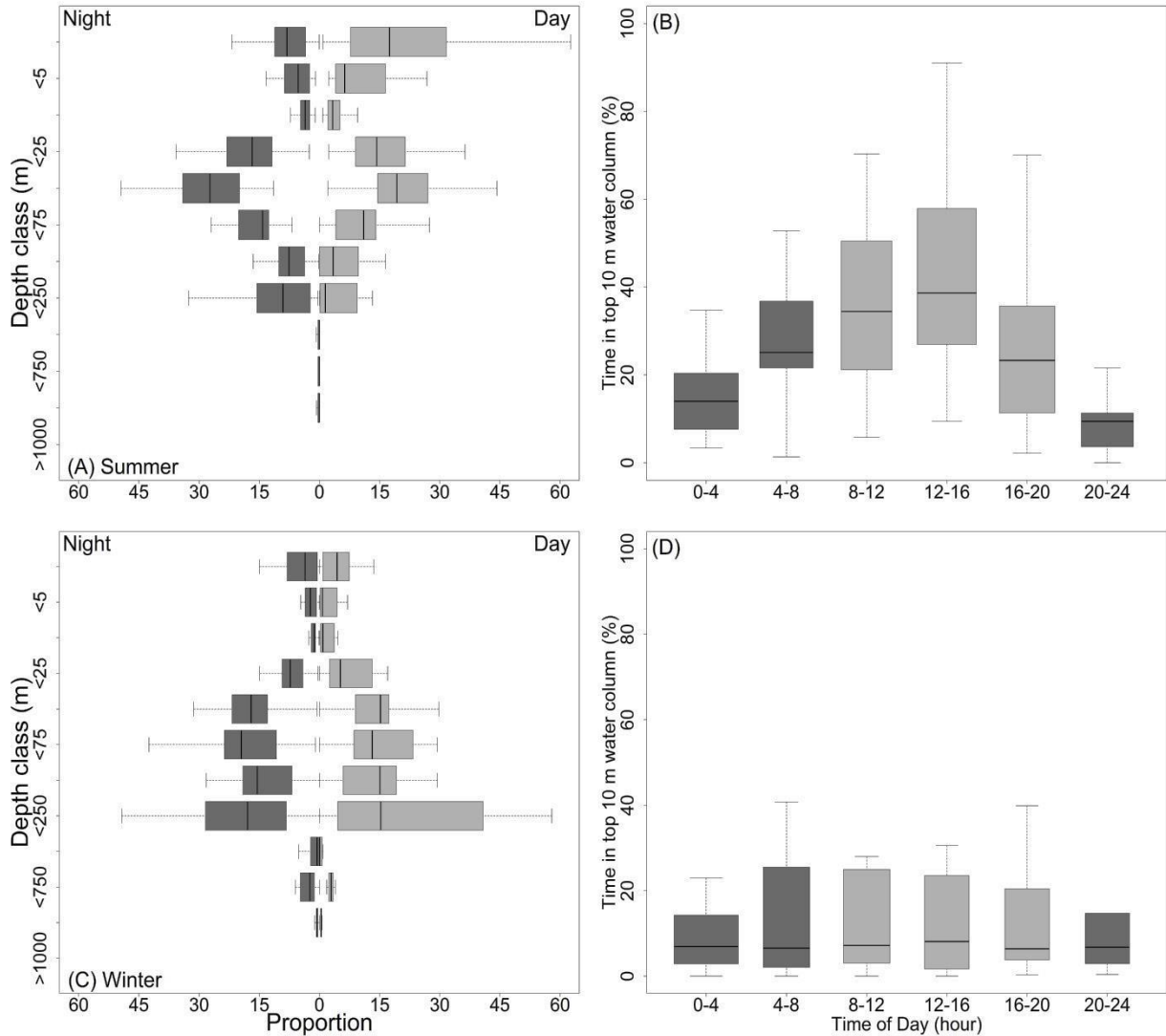


Figure 1. Depth distribution by time of day for each season. Box and whisker plots showing mean proportion of time (summarised at 4-hour intervals) occupying twelve depth-ranges for tracked basking sharks ($n = 32$) during (A) summer (April-October), (B) proportion of time between the surface and 10 m depth during the summer months (April-October), (C) winter months (October-March), and (D) proportion of time between the surface and 10 m depth during the winter months (October-March). Plots are separated into day (08:00-20:00; light grey bars) and night (20:00-08:00; dark grey bars) periods. Boxes denote inter-quartile range; horizontal black bar indicates the median (whiskers extend to the 2.5th and 97.5th percentiles).

Over-wintering depth-use

Twelve archival tags (Table C1. PAT-F; n = 3, Mini-PAT; n = 8, SPLASH-F; n = 1; 5 females, 2 males and 5 individuals of unknown sex, measuring 4-5 m (n = 4), 5-6 m (n = 4), 6-7 m (n = 2), and 7-8 m (n = 2) estimated total length) remained attached to basking sharks for more than 165 days, allowing for insight into over-wintering behaviour (Table C1). Light geolocation data were obtained from these archival tags providing daily estimates of location and minimum and maximum depths. Modal occupancy range for tracked basking sharks was between 50 and 75 m (median occupancy 40%; Fig. 1A Fig. 2A and B). Depth-use occupancy of sharks predominantly remaining in UK and Ireland waters (Fig. 2A) was relatively wide (0-250 m occupancy range: 4-18%) with very little movement into deeper waters (4% combined median occupancy below 250 m). Sharks moving south towards the Bay of Biscay, Iberian Peninsula and North Africa (Fig. 2B) occupied a narrower range of depths (25-250 m occupancy range: 16-21%), but also into greater depth ranges (11% occupancy between 250 and 1000 m).

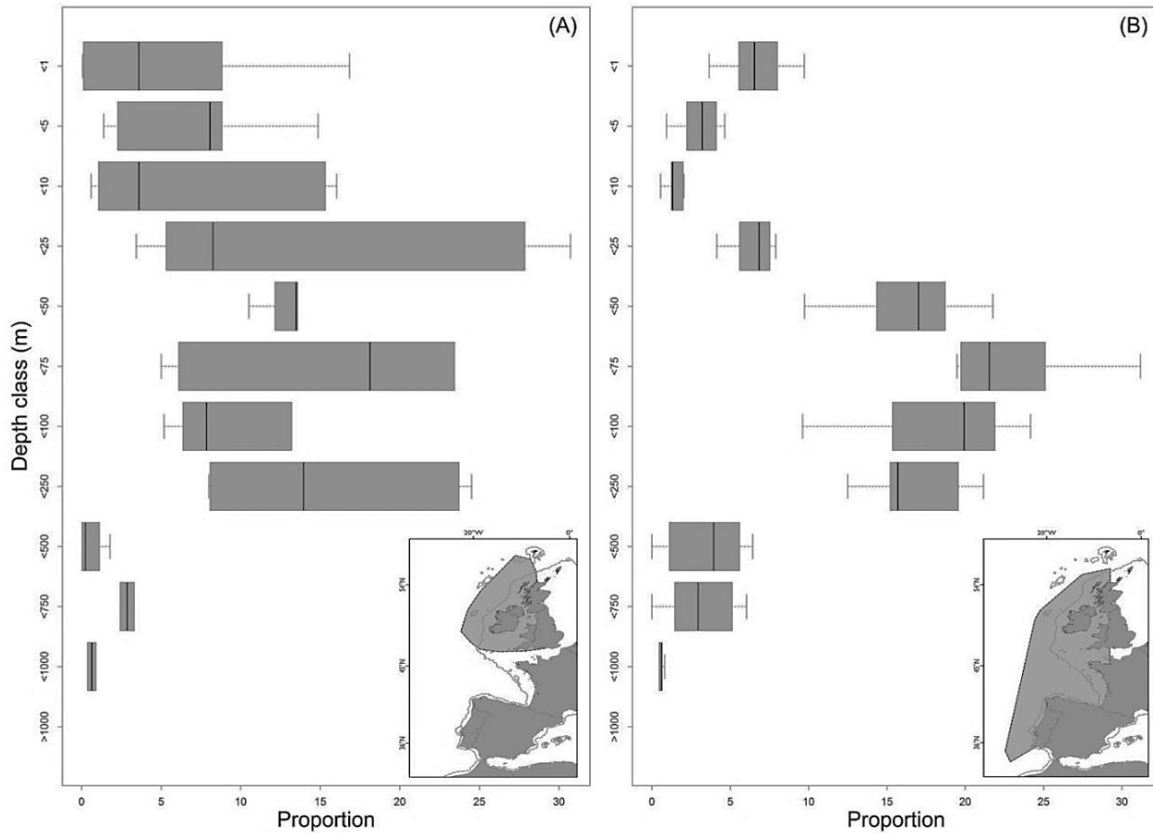


Figure 2. Time spent at varying depths. Box and whisker plots showing mean proportion of time (summarised at 4-hour intervals) occupying twelve depth-ranges for basking sharks tracked for over 165 days during winter months ($n = 12$; October-March). (A) Depth-use of basking sharks exhibiting in the waters of UK and Ireland ($n = 5$) and (B) depth-use of basking sharks in the Bay of Biscay, Iberian Peninsula or North Africa ($n = 7$). Boxes denote inter-quartile range; horizontal black bar indicates the median (whiskers extend to the 2.5th and 97.5th percentiles). Inset maps show areas encompassing defined strategies (shaded grey area), See Doherty *et al.* (2017a) for methods and description of migratory strategies.

Spatially-explicit minimum and maximum depth use by basking sharks reveal an area of deeper diving (>500 m) off the continental shelf, west of the Bay of Biscay, north of the Iberian Peninsula, however, at these locations, sharks also demonstrated use of shallow and surface waters (Fig. 3). Tracked basking sharks depth-use was not directly influenced by bathymetry, with daily maximum depths occurring in waters off the continental shelf shallower than the seafloor (Fig. 3), with dives often remaining within the epipelagic zone in higher latitudes (Fig. 3B).

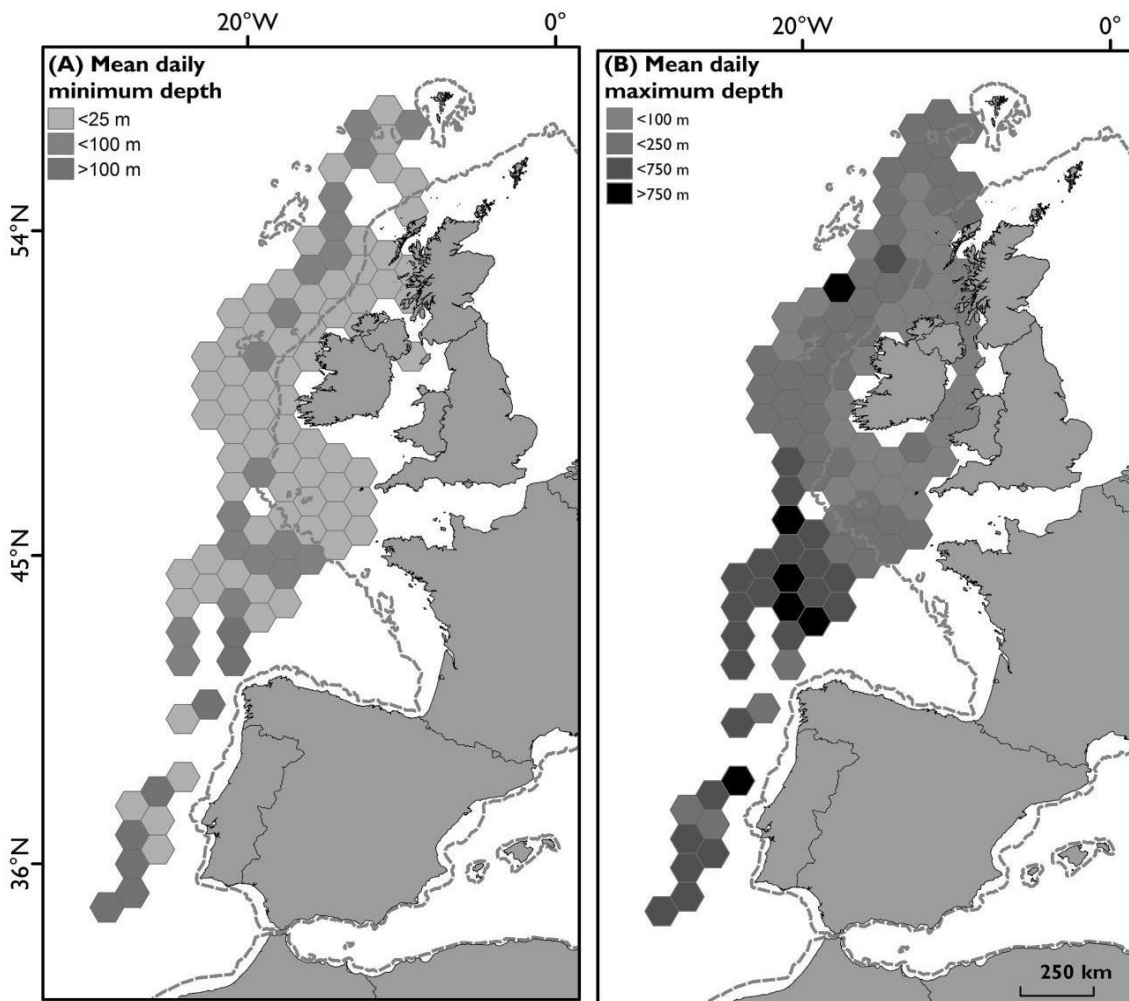


Figure 3. Grid density enumeration of minimum and maximum depths. Mapped mean daily minimum (A) and mean daily maximum (B) depth occurrences on a hexagonal grid (cell edge size: 50 km; cell area: 8,660 km²). Locations derived from modelled light geolocation positions from physically recovered archival tags for basking sharks tracked for over 165 days during winter months (October-March; n = 12). Broken grey line denotes 200 m depth contour.

Individual variation in depth-use

Analysis of depth-use of basking sharks from winter into spring for sharks with extended tracking durations (>165 days; n = 12) revealed extreme deep diving events (>500 m) during late winter-early spring (February-April; Fig. 4). Seven of twelve time-series revealed depth-use greater than 1000 m with two sharks reaching depths of 1500 m (Fig. 4: Table C1).

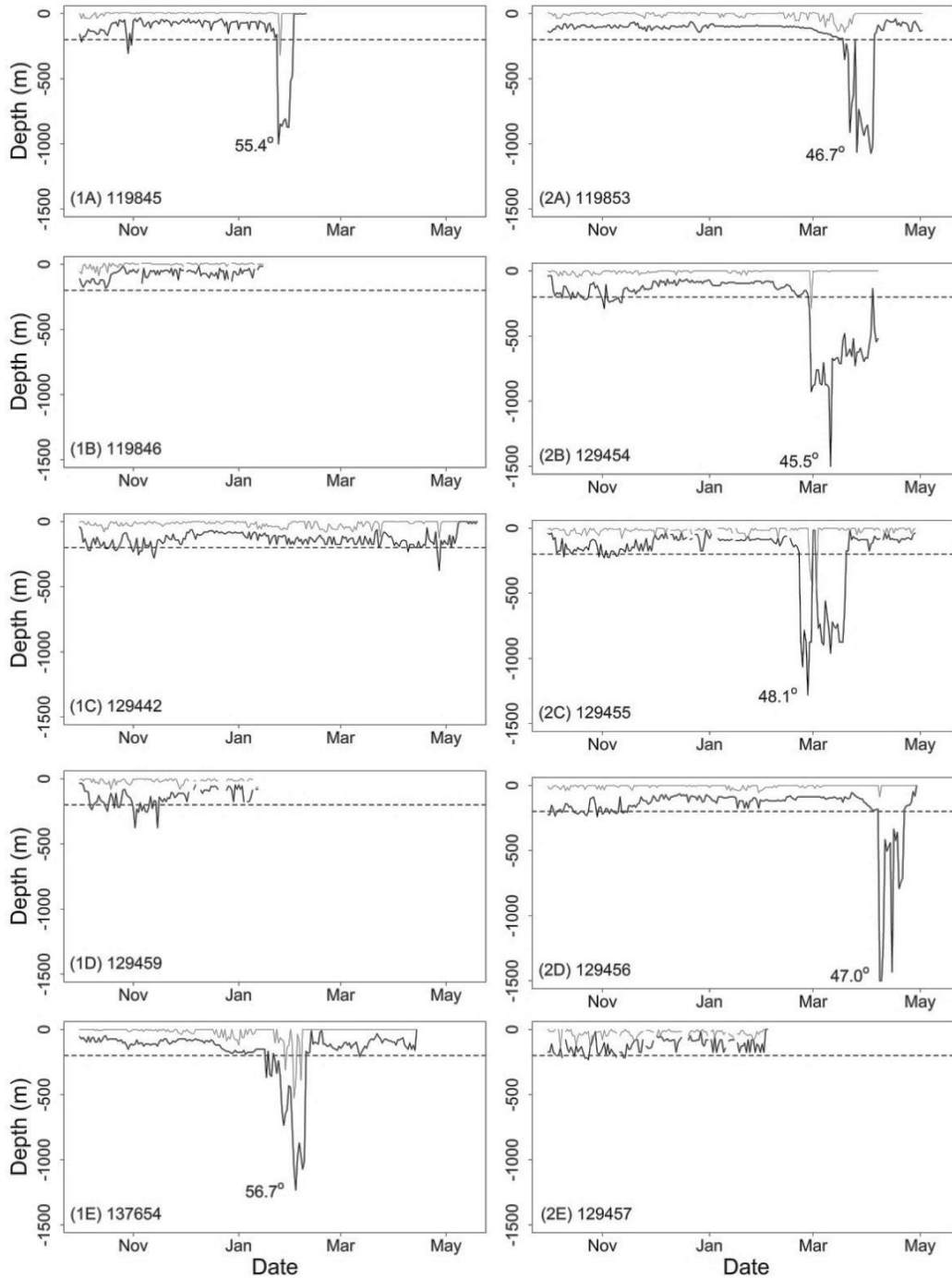


Figure 4. Basking shark winter depth-use time-series data. Daily minimum (grey line) and daily maximum (black line) depths from modelled light geolocation positions from archival tags of basking sharks tracked for over 165 days ($n = 12$). (1A-1E) Sharks remaining within waters of the UK and Ireland (latitude range: $61-45^{\circ}$) and (2A-2E) sharks moving south towards the Bay of Biscay, Iberian Peninsula or North Africa (latitude range: $45-35^{\circ}$). Latitude of greatest maximum daily depth is shown for sharks exhibiting extreme diving events. Tag number shown, dotted line denotes 200 m depth contour.

Twelve archival tags were physically recovered allowing for high-resolution time-series profiles (Table C1; PAT-F; n = 3, MiniPAT; n = 4, SPLASH-F; n = 5; 2 females, 4 males and 6 individuals of unknown sex, measuring 4-5 m (n = 2), 5-6 m (n = 5), 6-7 m (n = 3), and 7-8 m (n = 2) estimated total length). Five of these recovered tags (Table C1. PAT-F; n = 2, MiniPAT; n = 2, SPLASH-F; n = 1; 2 females, 2 males and 1 individual of unknown sex, measuring 4-5 m (n = 1), 5-6 m (n = 2), 6-7 m (n = 1), and 7-8 m (n = 1) estimated total length) remained attached to sharks for greater than 165 days, revealing complete records of depth and temperature encountered by these sharks throughout their movement (Fig. 5). Gathered data indicate a seasonal shift in depth occupancy behaviour from summer to autumn/winter between mid-September and mid-October where tracked sharks exhibited movements deeper, less associated with surface waters and experiencing fewer fluctuations in water temperature (Fig. 5). These detailed time-series data also reveal a conspicuous switch in vertical movements from a relatively uniform use of 50-250 m depths during the winter, to deep, rapid and repeated ‘bounce’ or ‘yo-yo’ dive behaviour from depth to surface waters in the spring (February-April; Fig. 5).

High-resolution time-series data from tags demonstrated basking sharks occupied waters of mean temperature 13 °C (± 1.25 ; range: 5.5-18 °C), and between 8 and 16 °C for a mean 99% (± 3 ; range: 89-100% occupancy). Encountered water temperature decreased with the onset of winter (Fig. 5 and 6). SST showed similar seasonal changes and a comparable temperature range to that experienced by basking sharks at varying depths (Fig. 6; mean of monthly means: 11.8 °C ± 1.7 ; range of monthly means: 10-14 °C). There was a negative relationship between surface duration and minimum temperature experienced during a dive event during the winter (Fig. 7). Surface duration was significantly reduced as the minimum temperature experienced during a dive event increased (GLMM: $\chi^2_1 = 22.39$, $p = <0.001$).

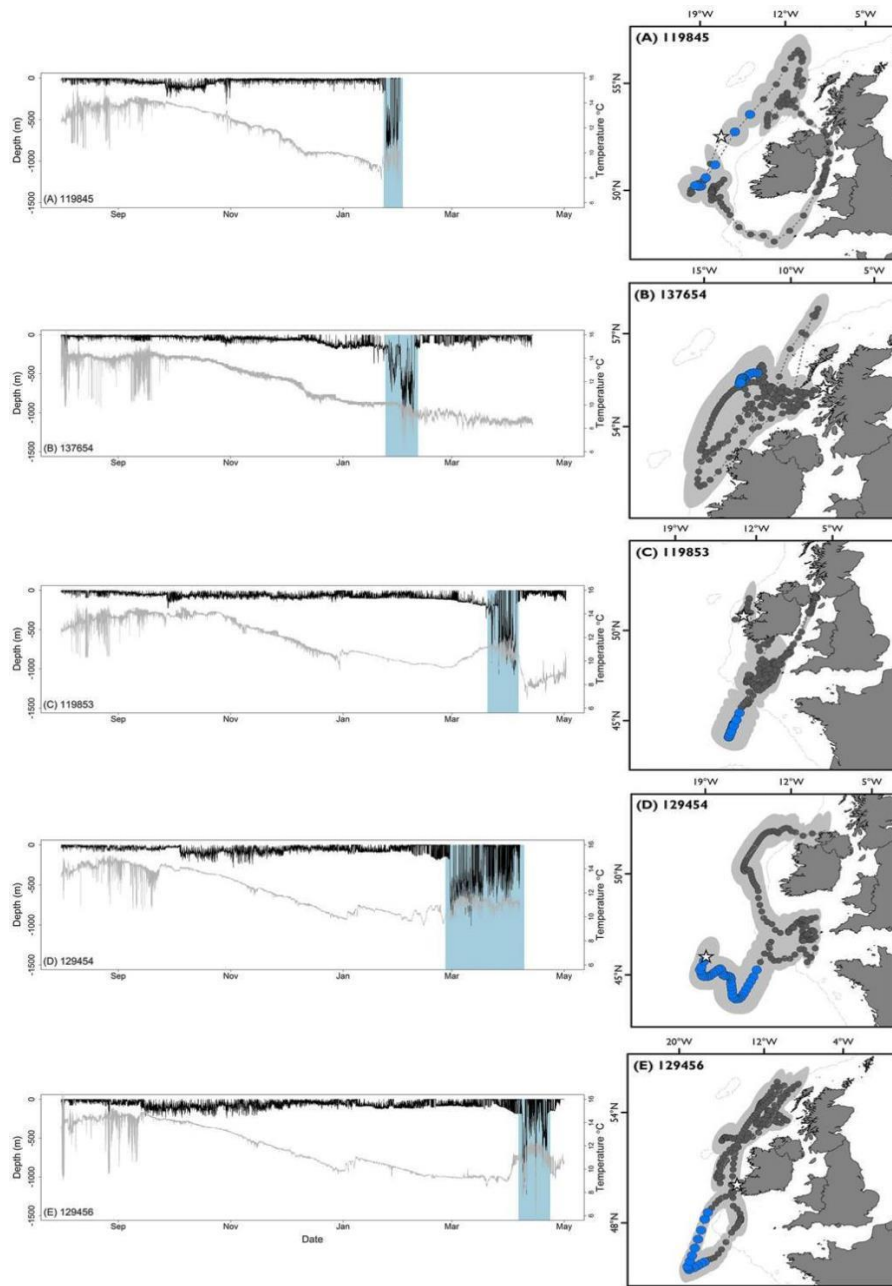


Figure 5. Basking shark depth-use from high-resolution time-series data. Complete depth (black lines), temperature (grey lines) time-series data from physically recovered archival satellite tags for basking sharks tracked for over 165 days (left panels; $n = 5$). Individual movements derived from light geolocation (right panels, $n = 5$), displaying best daily locations (grey circles) with associated error (light grey ellipses), and track end point (white stars). Blue polygons (left panels) correspond to blue circles (right panels) as regions of deep diving behaviour. (A) PAT-F tag depth and temperature recorded at 10-sec. intervals, (B) SPLASH-F tag depth and temperature recorded at 15-sec. intervals, (C) PAT-F tag depth and temperature recorded at 10-sec. intervals, and (D & E) MiniPAT tag depths and temperatures recorded at 15-sec. intervals. Tag numbers shown.

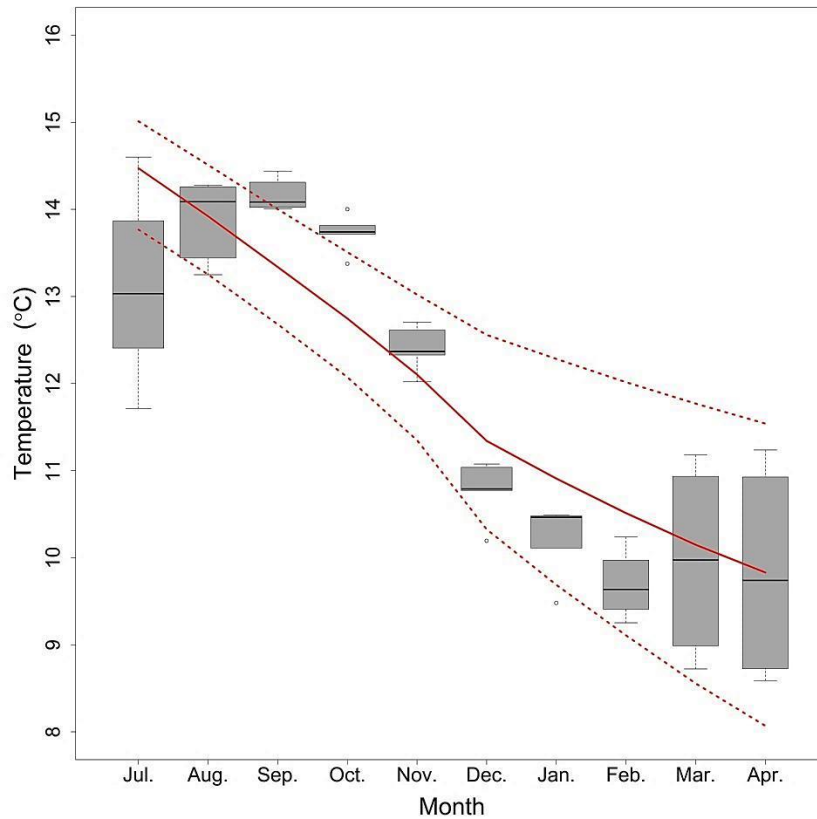


Figure 6. Temperature by month experienced by tracked basking sharks. Box and whisker plots showing mean temperature experienced by tracked basking sharks (time-series data from physically recovered archival tags; $n = 6$) for each month of tracking duration. Boxes denote interquartile range; horizontal black bar indicates the median (whiskers extend to the 2.5th and 97.5th percentiles). Lowest line of mean SST values corresponding to each month (mean; red solid line, \pm SD; dotted red lines). Open circles represent outlier values occurring outside the 2.5th and 97.5th percentiles of data distribution.

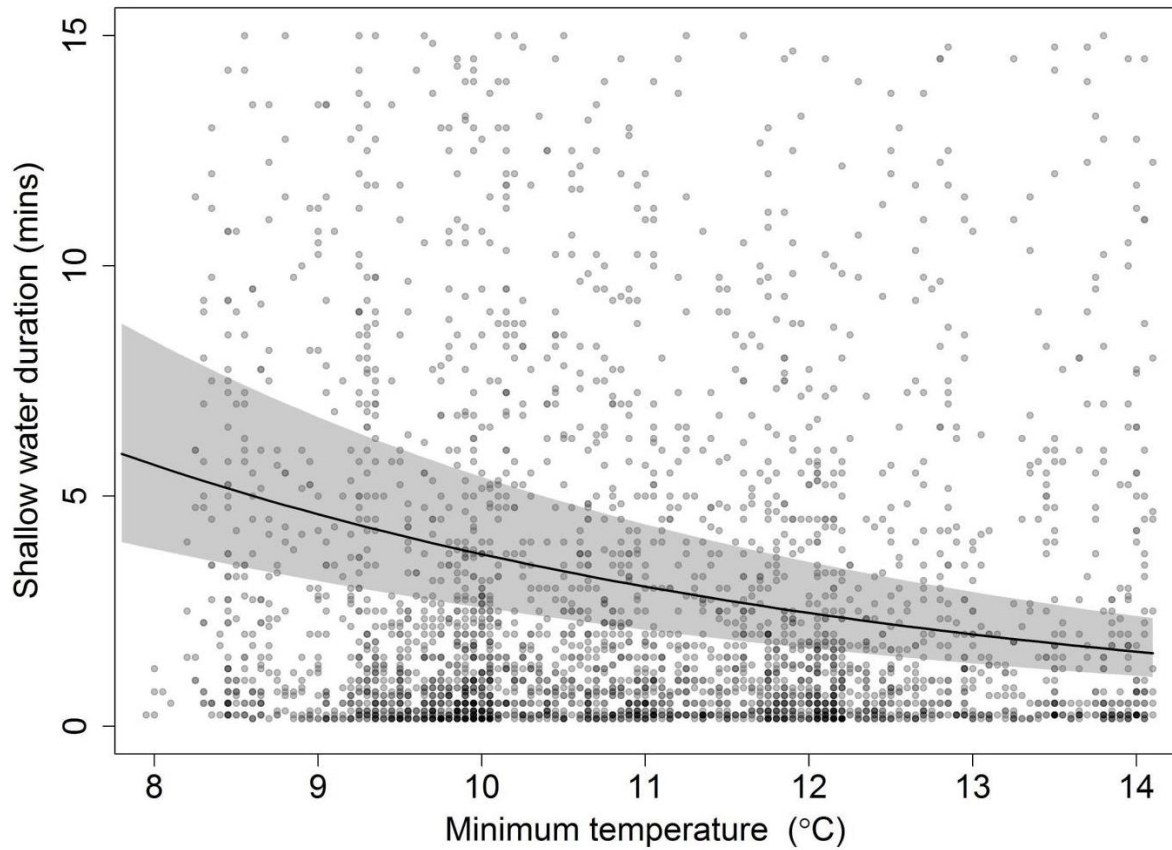


Figure 7. Time spent in waters above 10 m depth following a dive against minimum temperature encountered at depth. Relationship between time spent in shallow waters (<10 m) after a dive event, and the minimum temperature experienced during that dive event for high-resolution time-series data from physically recovered archival tags ($n = 6$) during the winter months (October-March). Solid black line denotes predictions from a GLMM with grey polygon representing Standard Error (SE). Filled circles represent empirical data.

Discussion

The need to identify areas providing suitable conditions for large marine vertebrates to undertake key life-history events, such as foraging, mating, and parturition, is critical to understanding the biology and ecology of species of conservation concern. Marine organisms function within three-dimensions and a number of important factors including; light, pressure, temperature, and oxygen and salinity concentrations vary with depth (Hussey *et al.* 2015). These physical features of the ocean can act as barriers to species movement due to adaptations or limitations of physiology and morphology, however, large marine vertebrates can often occupy many distinct vertical habitats (Hussey *et al.* 2015). Obtaining information on depth use can provide insight into the ecological association between depth and how the conditions at depth might influence their use by marine vertebrates. Our study provides the largest telemetry derived depth-use dataset on basking sharks to date, giving a new view on seasonality and extent of depth occupancy.

We demonstrate seasonality in depth-use by basking sharks in the north-east Atlantic, whereby summer depth-use appears to be associated with surface foraging, whilst winter months are spent at epipelagic to mesopelagic depths, largely away from the surface, with some forays into the bathypelagic zone. Basking sharks are capable of finding dense prey patches, and activity at the surface is likely in relation to these food sources, especially during the day in nearshore waters (Sims *et al.* 2005, 2006). Diel Vertical Migration (DVM), has been described for all three species of planktivorous sharks; megamouth shark (*Megachasma pelagios*; (Nelson *et al.* 1997), whale sharks (Graham, Roberts & Smart 2006; Wilson *et al.* 2006) and basking sharks (Sims *et al.* 2005; Stéphan *et al.* 2011)). Reverse Diel Vertical Migration (rDVM) can also occur with movements switching, and movements towards the surface take place during the day. Both DVM and rDVM have been observed in whale sharks (Rowat *et al.* 2006) and basking sharks (Shepard *et al.* 2006; Stéphan *et al.* 2011), and may be determined by the heterogeneous environmental conditions of the water column they inhabit. Tracked basking sharks in this study

appeared to exhibit rDVM during the summer months, moving shallower during daylight hours when these sharks spent the majority of time within the Sea of the Hebrides (Doherty *et al.* 2017b), switching behaviour to exhibit DVM during the winter months, which is likely due to the sharks moving from shallow, well-mixed areas to deeper, more stratified, waters (Sims *et al.* 2005; Stéphan *et al.* 2011).

Basking sharks modify depth use behaviour during autumn, spending less time associated with the surface, often coinciding with movements towards the continental shelf-edge and offshore (Sims *et al.* 2003; Skomal *et al.* 2004, 2009; Stéphan *et al.* 2011; Doherty *et al.* 2017a). We observe, from high-resolution time-series data, basking sharks making this behavioural change between mid-September and mid-October, corroborating seasonal patterns previously noted (Sims *et al.* 2003; Skomal *et al.* 2009; Stéphan *et al.* 2011), which may represent the breakdown of the summer plankton blooms and the beginning of adopting an over-wintering strategy. Over-wintering migrations can involve broad-scale movements into oceanic waters and has been shown to often be carried out at mesopelagic depths (Gore *et al.* 2008; Skomal *et al.* 2009; Doherty *et al.* 2017a).

Tagged basking sharks were recorded making repeated oscillatory vertical movement between the surface and deeper waters, termed 'yo-yo' dives (Holland *et al.* 1992). This behaviour is relatively ubiquitous and has been recorded in a wide range of shark species including, whale sharks (*Rhincodon typus*, (Brunnschweiler *et al.* 2009), basking sharks (Sims *et al.* 2005; Shepard *et al.* 2006), white sharks (*Carcharodon carcharias*, (Klimley *et al.* 2002; Domeier & Nasby-Lucas 2008), scalloped hammerhead sharks (*Sphyrna lewini*, (Jorgensen, Klimley & Muhlia-Melo 2009)) and tiger sharks (*Galeocerdo cuvier*, (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; Thums *et al.* 2013). We observed these behaviours in late winter-early spring (February-April) where the tracked sharks showed a sudden change in behaviour, carrying out extensive surface to depth movements. These diving behaviours may signify a location (either in space or time) when these sharks begin to actively seek

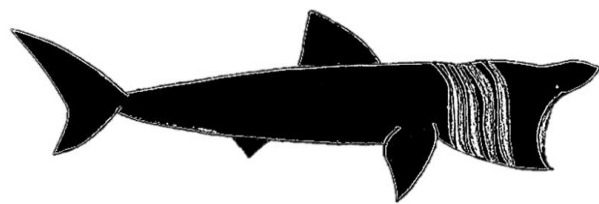
out foraging grounds. Spatially explicit high resolution time-series data shows evidence of some individuals displaying directed movements off the continental shelf before exhibiting repeated oscillatory yo-yo dives for between six and thirteen days before returning to waters of the continental shelf. These movements may be examples of foraging trips, failed foraging trips, or “sampling” of the water column for orientation and/or olfactory cues. This may also represent the beginning of increased activity from a more torpid state during winter months if not actively feeding, or in anticipation of the onset of spring plankton blooms. Olfactory stimuli providing cues for locating food sources are considered to be more extensively distributed horizontally than vertically due to the current shear between water layers of different densities (Carey & Scharold 1990; Klimley *et al.* 2002). Therefore, repeated deep diving behaviour may facilitate sampling of multiple depth layers of the water column for chemical cues over short time period, a behaviour documented for pelagic predatory sharks (Carey & Scharold 1990; Boustany *et al.* 2002) and is likely a common search strategy for both epipelagic planktivores and macropredators (Sims *et al.* 2003).

During the present study, we observe several sharks performing extreme diving events to depths of up to 1500 m. The greatest depth previously recorded for basking sharks was 1264 m (Gore *et al.* 2008), which superseded the previous deepest depth record of 904 m (Francis & Duffy 2002), along with other observations of basking sharks occupying waters between 750 and 1000 m (Sims *et al.* 2003; Skomal *et al.* 2009). The greatest depths observed in this project typically occurred during the winter and early spring, most often occurring off the continental shelf to the west of the Bay of Biscay at the Celtic-Armorica shelf margin. Other planktivorous elasmobranchs have also been shown to perform extreme diving events, such as whale sharks diving to 1928 m (Tyminski *et al.* 2015) and Chilean devil rays (*Mobula tarapacana*) diving to 1896 m suggesting possibility of foraging at depths but also providing an important link between surface foragers and forage species occupying pelagic habitats below the euphotic zone (Thorrold *et al.* 2014).

Tracked basking sharks demonstrated a relatively narrow thermal range, consistently occupying waters between 8 and 16 °C regardless of depth or time of year compared to other wide ranging teleost fish (Atlantic cod (*Gadus morhua*) range: -1.5-20 °C (Righton *et al.* 2010); Atlantic Bluefin tuna (*Thunnus thynnus*) range: 3-31 °C (Block *et al.* 2001)) and sharks (salmon sharks (*Lamna ditropis*) range: 2-24 °C (Weng 2005); mako sharks (*Isurus oxyrinchus*) range: 5-30 °C (Vaudo *et al.* 2016); white sharks range: 5-26 °C (Boustany *et al.* 2002); whale sharks range: 4-25 °C (Afonso & Hazin 2015)). This suggests movements; both horizontally and vertically are linked to the need to maintain a thermal envelope, with many physiological rates and functions (e.g. metabolic rate and reproduction) determined by body temperature (Schlaff, Heupel & Simpfendorfer 2014). Movements to maintain these thermal ranges are possibly due to behavioural thermoregulation, whereby an animal seeks out a thermal niche to maximise vital rates (Sims 2003; Speed *et al.* 2012). Our results suggest behavioural thermoregulation with basking sharks exhibiting intervals in warmer, shallower water, potentially to recover heat loss from time at cooler, deeper waters, as has been shown in several fish species (Carey & Scharold 1990; Holland *et al.* 1992; Klimley *et al.* 2002; Thums *et al.* 2013; Nakamura, Goto & Sato 2015). Our results also suggest conditions may be suitable for basking sharks to occupy surface waters year-round in the north-east Atlantic with sea surface temperature values showing similar seasonal shifts. We observe basking sharks moving into deeper waters in the winter; sea surface temperature ranges suggest surface water temperatures are within the thermal range maintained by basking sharks throughout the year. This may provide evidence for basking sharks feeding on zooplankton in deeper waters during the winter, although we have no direct observations of this. Incorporating new knowledge of vertical space-use into tag programming should be carried out in future research, allowing for depth class assignment to reflect that of what is utilised by basking sharks. Reducing the size of the deeper depth classes may allow for further investigation of timings and proportion of time at more extremes of depth range for these individuals.

Conclusion

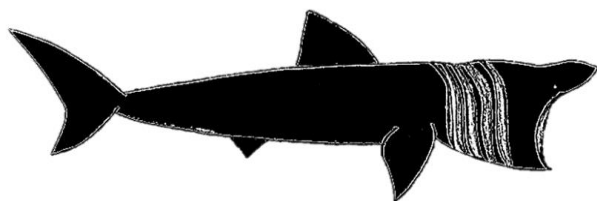
Data describing how basking sharks utilise the water column within areas of high relative importance could contribute to discussions regarding management options for the conservation of basking sharks as well as being useful in contributing to the estimation of shark numbers present in key areas from surface sightings data. We found basking sharks exhibit seasonality in their depth-use, likely reacting to changes in environmental conditions in the habitats and water column ranges they inhabit. Our study demonstrates basking shark space-use into winter months, a period within their annual cycle missing from current knowledge. We display spatially explicit depth-use during this time, revealing areas of extreme deep diving to depths greater than 1000 m. Oscillatory diving behaviour exhibited during late winter and early spring may be an indicator of the beginning of search pattern behaviour in anticipation of upcoming planktonic blooms. We also show the first evidence for behavioural thermoregulation in basking sharks with extended shallow water intervals after movements to depths at the extreme lower boundary of their preferred thermal range during winter months. Combining detailed knowledge of space-use in all dimensions (latitude, longitude, depth and time) for species of conservation concern will best inform on implementation of sustainable conservation and management strategies.



Chapter 5: Pan-oceanic niche modelling for an elusive marine vertebrate:
Basking sharks in the Atlantic



Credit: Rachel T. Graham



Abstract

Understanding the movements and distribution of wide-ranging marine vertebrates is critical to determining important areas of habitat for species of conservation concern and linkages between these areas to inform management strategies. The increased availability and use of satellite telemetry, coupled with remotely sensed environmental data can provide new insights into the spatio-temporal ecology of species and range extent. We used an Ensemble Ecological Niche Modelling (EENM) approach to identify suitable habitats for basking sharks (*Cetorhinus maximus*) using location data from satellite tags deployed in the north-east Atlantic. We developed two models for summer and winter distributions. The *summer* model (April-October) was based on surface location and environmental data whereas the *winter model* (October-March) was developed using HYCOM modelled temperature-at-depth, integrating depth-use knowledge from archival satellite tag data. Sea Surface Temperature (SST) and temperature-at-depth (HYCOM) predicted distribution in *summer* and *winter* models respectively. We reveal migratory pathways that may exist and which likely facilitate movements between eastern and western hemispheres of the Atlantic Ocean. This is the first description of its type for any shark species and reveals key seasonally-important habitat areas and facets of the ecology of this species, which may help inform conservation policy.

Introduction

Describing seasonal and migratory movements in large marine vertebrates can be challenging, largely due to their complexities of tracking individuals for duration and extent of range (Hammerschlag *et al.* 2011). Advances in animal tracking technologies however, allow for longer-term observations of movements and insights into intra- and inter-individual variation (Hazen *et al.* 2012; Hussey *et al.* 2015), enabling assessment of life-history traits, distribution, site fidelity, migratory movements (Block *et al.* 2011; Hussey *et al.* 2015) and exposure to human threat.

The distribution of an organism is a function of its ecological niche, which is the multi-dimensional ecological space comprising all factors that may affect survival (Hutchinson 1959). This *fundamental niche* is where the chances of survival are equal to one in the absence of predators (Hutchinson 1959), however the *realised niche*, which is a more restricted space when accounting for interactions with other individuals and species is more likely to be observed in nature (Peterson 2001). As such, identifying the drivers of a species' distribution might allow their occurrence across a larger land, air or seascape to be estimated. To observe the extents of distribution and highlight areas of suitability, Ecological Niche Models (ENMs) can be applied. ENMs are empirical models connecting field observations to statistically or theoretically derived response environmental surfaces (Guisan & Zimmermann 2000), using species occurrence data, which can comprise of presence, presence-absence, or abundance observations based on random or stratified field sampling (Guisan & Thuiller 2005). The integration of telemetry and remotely sensed environmental data, coupled with ENMs has provided further understanding of spatial and temporal ecology of terrestrial and marine species on both a broad and fine spatial scale (Gschweng *et al.* 2012; Pikesley *et al.* 2015; Scales *et al.* 2015). Increased knowledge on seasonal movements of a species may help inform areas where large numbers of individuals aggregate to undertake important life-history events (Doherty *et al.* 2017b).

Often, only a single modelling framework is applied with its specific biases, reducing the comparability of results and potentially limiting predictive capacity. An alternative is to adopt an Ensemble Ecological Niche Modelling approach (EENM; Araujo & New 2007), which combines the output of multiple algorithms into one predictive surface. Predicting the locations of suitable foraging habitats for wide-ranging pelagic species is non-trivial, given the complex and scale-dependent interactions between oceanographic processes and prey field dynamics, and the diverse aspects of physiology, energetics, reproductive and other constraints that govern foraging behaviour (Scales *et al.* 2015). EENMs can be produced by averaging multiple simulations across more than one set of initial conditions, model classes, parameters, and boundary conditions (Araújo & New 2007). Averaging of several models allows the *signal* of interest to emerge from the *noise* associated with the individual model errors and uncertainties (Araújo & New 2007). EENMs for wide-ranging marine species must reflect the multiple, nested spatial and temporal scales over which animal-environment interactions occur to be accurate and therefore useful in marine spatial planning. Static (e.g. bathymetric depth), dynamic (e.g. Sea Surface Temperature; SST), and oceanographic models (e.g. Hybrid Coordinate Ocean Model; HYCOM) are most often used as dynamic variables within these models (Scales *et al.* 2016).

Large pelagic sharks are highly mobile both horizontally and vertically, leading to wide-scale distributions often crossing multiple geo-political zones (Southall *et al.* 2006; Howey-Jordan *et al.* 2013; Lea *et al.* 2015; Graham *et al.* 2016; Doherty *et al.* 2017a). The extent of these distributions can cause difficulty in attributing suitable habitat conditions necessary to implement management strategies, therefore large scale ENMs may play an important role in pelagic shark ecological and conservation science (Sequeira *et al.* 2012).

In comparison to terrestrial systems, the three-dimensional habitat of the marine realm requires knowledge and application of depth information. One approach is to combine several models applied at different depth ranges to improve the predictions of suitable habitats for pelagic species (Dambach & Rödder 2011).

We use data gathered across a four year satellite tagging programme (2012-2015) using a suite of satellite tag technologies to describe space-use at different stages of annual movements of basking sharks coupled with high-resolution remotely sensed environmental data and a 3D ocean model to; (1) model suitable habitats and likely foraging grounds using EENMs during the summer; and (2) model likely suitable habitat for over-wintering grounds at depths away from the surface.

Methods

Tag attachment and specification

Forty-seven tags (Table D1; Smart Position or Temperature tags; SPOT = 23, Pop-up Archival Transmitting with Fastloc™ GPS tags; PAT-F = 3, Mini Pop-up Archival Transmitting tag; MiniPAT = 8, SPLASH-F = 13; Wildlife Computers, Washington, USA) were attached to basking sharks off the west coast of Scotland during July and August in 2012 (n = 11), 2013 (n = 27) and 2014 (n = 9). Archival tags providing data on temperature and depth were programmed to collect data (summarised at 4 hour intervals) at 12 depth ranges (0-1 m, 1-5 m, 5-10 m, 10-25 m, 25-50 m, 50-75 m, 75-100 m, 100-250 m, 250-500 m, 500-750 m, 750-1000 m and >1000 m) and 12 temperature ranges (0 °C, 0-4 °C, 4-6 °C, 6-8 °C, 8-10 °C, 10-12 °C, 12-14 °C, 14-16 °C, 16-18 °C, 18-20 °C, 20-22 °C, and >22 °C). Maximum daily depths from satellite transmitted data were used to inform on vertical position of tracked basking sharks during broad-scale movements.

Basking sharks were approached by boat and upon approach, where possible sex and body length estimates were made via an underwater pole camera and comparing to boat length (10 m) respectively. Satellite tags were deployed using a titanium M-style dart (Wildlife Computers, Redmond, California, USA) inserted into the sub-dermal layer at the base of the first dorsal fin with a modified pole spear and attached via a tether consisting of heat-shrink covered stainless steel flexible cable, a swivel and monofilament line attached to the tag. Thirty-six satellite tags (SPOT; n = 23, SPLASH-F; n = 13) contributed data to inform on habitat suitability in the boreal summer (April to October; herein *summer model*) and twelve tags (PAT-F; n = 3, MiniPAT; n = 8, SPLASH-F; n = 1) contributed data to inform on habitat suitability in the boreal winter (October to March; herein *winter model*). One SPLASH-F tag remained attached for durations sufficient enough to provide data for both models.

The attachment of satellite transmitters in Scottish coastal waters protocol was approved by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and internally through the University of Exeter's animal welfare and ethics review board (AWERB). All work was conducted in accordance with the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971).

Location data processing

Argos Doppler-based location data from SPOT tags ($n = 23$) were subject to filtering, retaining location classes 3, 2 and 1, A and B (Witt *et al.* 2010). GPS location data from SPLASH-F tags ($n = 13$) were filtered to include only positions with a residual error value of less than 30 and where five or more satellites were used to estimate location (Shimada *et al.* 2012). A maximum plausible speed filter was applied to both datasets removing locations if speed between two locations exceeded 10 km h^{-1} . These data were later reduced to a single, most accurate best daily location (highest location class as described above for Argos locations and maximum number of visible satellites for GPS locations) to minimise spatial and temporal autocorrelation. All tag data were downloaded from CLS-Argos and archived using the Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005).

Light geolocation data were obtained from archival tags ($n = 12$) with attachment durations greater than 165 days. Where possible, one representative location per day best describing light level, temperature and depth-data was recorded onboard the satellite tag. Obtaining continuous daily estimates of location is challenging as basking sharks often spend prolonged periods at depth where the ability to accurately record light levels is reduced or exhibit diel vertical migration (DVM), reducing reliability of some light data received (Shepard *et al.* 2006). Hidden Markov Models (HMM) also known as grid filters (Neilson *et al.* 2014) can be applied in order to estimate the location of individuals between high quality light geolocations (Thygesen *et al.* 2009). A two-step process is

employed; (i) a position prediction step, solving the advection-diffusion equation for the two-dimensional probability of an animal's presence (Bias *et al.* 2017), was applied at each sampling time. (ii) An update step to combine the predicted probability density using information on latitude, longitude, SST and depth recorded onboard the tag to produce the posterior distribution of the individual is performed (Bias *et al.* 2017). The best daily estimate locations of the tag are used as the mean of the grid locations weighted by their probability and used as our best daily locations for analysis. A modified version of the geolocation method described in Neilson *et al.* (2014) was applied using raw locations derived using light intensity as observations (obtained using Wildlife Computers GPE2 software). These data are then constrained by bathymetry (Thygesen *et al.* 2009), SST and known tag deployment and pop-off locations. The parameters applied to constrain the model were; the diffusion coefficient of the random walk (set to $1000 \text{ km}^2 \text{ d}^{-1}$ as this minimises the SST root mean square deviation), the standard deviation of raw light based locations used in the update step (set to 1° longitude and 3.5° latitude), and the standard deviation of the difference between recorded and satellite derived SST (set to 0.5°C ; (Bias *et al.* 2017)). Analysis of light level data and application of HMM was undertaken by *Collecte Localisation Satellites* (CLS-Argos; www.argos-system.org). Average proportions of time for each individual shark tracked into the winter months (>165 days; $n = 12$) at pre-determined depth ranges were used to estimate vertical position during winter migrations.

Habitat modelling

EENMs and a three-dimensional ocean model (HYCOM) were used to identify suitable habitats for basking sharks during distinct seasons, distinguished by behaviour and occupancy at depth. The modelling spatial domain encompassed the Atlantic Ocean (between latitudes 90°N and 90°S , and longitudes between 100°W and 50°E).

Physical and biological environmental data (2012-2015) were prepared using Marine Geospatial Ecological Tools v0.8a64 (Roberts *et al.* 2010). We used monthly averaged Sea Surface Temperature (SST; $^\circ \text{C}$; 4 km resolution, <http://podaac.jpl.nasa.gov>), and monthly

averaged Chlorophyll α concentration (Chl-a; mg/m^{-3} , 4 km resolution, <https://oceancolor.gsfc.nasa.gov>) to generate raster layers of yearly averages for the study period. Daily averaged modelled temperatures at specific depth layers (Hybrid Coordinate Ocean Model; HYCOM, $^{\circ}\text{C}$; 8 km resolution, www.hycom.org), were averaged into monthly, yearly and total study period raster layers. Persistent sea surface temperature frontal activity was created by applying the Cayula and Cornillon single image edge detection (SIED) algorithm (Cayula & Cornillon 1992) to gridded daily averaged SST raster products to create a binary response raster; using a minimum frontal edge detection threshold of 0.5°C (Roberts *et al.* 2010). These daily frontal activity rasters were aggregated into yearly rasters with cumulative totals for daily frontal activity and then averaged into a long-term yearly frontal activity raster with cumulative totals representing persistent SST frontal activity. Bathymetric depth (m; www.gebco.net) were downloaded and used to derive seafloor slope. All data were sampled to the coarsest resolution of the environmental data layers using bilinear interpolation (*summer model* = 4 km, *winter model* = 8 km). A matrix of pair plots were constructed to investigate co-variance within all unique combinations of environmental variables using Spearman's rank tests.

To identify areas of habitat suitability we applied an EENM approach (Araújo & New 2007; Pikesley *et al.* 2015; Scales *et al.* 2015). Within this framework, General linear Models (GLMs), General Additive Models (GAMs) and Boosted Regression Trees (BRTs) were used using the *biomod2* package (Thuiller *et al.* 2016). We used a binary response variable for all models, comprised of values of either *presence* (best daily tracking locations) or *pseudo-absence* (generated locations in the lack of “true” absences to create background data establishing environmental conditions of the area of interest), which were randomly generated from 1000 randomly selected control locations over successive model runs (Barbet-Massin *et al.* 2012). All models were run using 10-fold cross validation, with data randomly split 75/25% for model calibration and model testing, respectively. Model performance was evaluated using five metrics. (1) Area Under (the receiver operating characteristic; ROC) Curve (AUC); a measure of the ability of the forecast to discriminate between events and non-events; (2) Cohen's Kappa (KAPPA) and (3) true skill statistic

(TSS): a measure of accuracy relative to that of random chance; (4) Success Ratio (SR): the fraction of the forecast events that were correctly observed and (5) Accuracy (fraction correct): fraction of forecasts that were correct (Thuiller *et al.* 2009, 2016). All evaluation metrics were scaled to one to compare outputs from different model runs. EENM projected surfaces were combined to form an ensemble projection using an unweighted average across models. This ensemble EENM described the relative suitability of oceanic habitat, scaled between zero and one, where zero represents lowest suitability and one indicates greatest suitability.

The Relative Importance of each environmental variable was calculated via an independent randomisation process, using Pearson's correlation between fitted values and predictions, where each variable under investigation has been randomly permuted (Thuiller *et al.* 2009). If the correlation was high, the variable in question was considered unimportant for the model. A mean Relative Importance of the Contribution to the model Coefficients (RICC) for each environmental variable was calculated over ten model runs (Thuiller *et al.* 2009) by subtracting the mean correlation coefficient from one.

Two models were developed; (1) *summer model* (April to October) based on basking shark surface locations from Argos Doppler-derived location SPOT tags (n = 23) and locations from GPS enabled SPLASH-F tags (n = 13; Fig. 1A, Table D1). The EENM was developed using the environmental variables of SST, Chl-a, bathymetric depth, and persistent surface temperature frontal activity (Fig. D4). This model was also projected for the *austral* summer (September-February) for comparison, with seasonality employed based on southern hemisphere abundance records (Francis & Duffy 2002). (2) A *Winter model* (October to March) was based on basking shark locations at depth from archival light geolocated PAT-F (n = 3), MiniPAT (n = 8) and SPLASH-F (n = 1; Fig. 1B, Table D1) tags from sharks exhibiting over-wintering behaviour (>165 days at liberty). The EENM was developed using the environmental variables of temperature at depth, bathymetry and seafloor slope (Fig. D4). The *winter model* was created by employing a 2.5D approach, averaging individual models (Duffy & Chown 2017), run at increments of temperature-at-

depth HYCOM layers based on occupancy at depth (Fig. 2). Light geolocation positions at associated depths ± 25 m (e.g. 50-100 m depth model incorporated locations at depths between 25 and 125 m) were used as input presence data for each model run. These temperature-at-depth layers were averaged and incorporated in an EENM to approximate a 3D system (Duffy & Chown 2017). To investigate spatial autocorrelation within model residuals we calculated Moran's I coefficients for each of our EENMs (Dormann *et al.* 2007).

To validate HYCOM temperature-at-depth data, we extracted temperature from daily HYCOM depth layers to corresponding point locations and daily utilisation distributions. Spearman's correlation tests were carried out to compare temperatures recorded onboard archival tags and both temperature-at-depth extraction methods .

Data analysis were performed in R (R Core Team 2014), with satellite tag location filtering applied using the *adehabitat* packages (Calenge 2006), environment variable data layer preparation was conducted using the *raster* package (Hijmans 2016) with habitat models executed using the *biomod2* package (Thuiller *et al.* 2016). All spatial analyses and maps were created using ESRI ArcMap 10.3.1 (ESRI; Redmond, California).

Results

Locations from 47 basking sharks satellite tracked from the north-east Atlantic were used as presence locations for EENM analysis (Table D1, Fig. 1). These location data were separated by season to form input presence locations for a *summer model* consisting of Argos and GPS surface locations in the months of April to October (Fig. 1A). A *winter model* was also developed consisting of light geolocated locations ($n = 1925$) in the months of October to March (where sharks most often occupied waters at depths away from the surface; Fig. 1B). Depth-use data from archival tags were used to gather information on occupancy at depth; majority depth use was between 50 m and 250 m (Fig. 2).

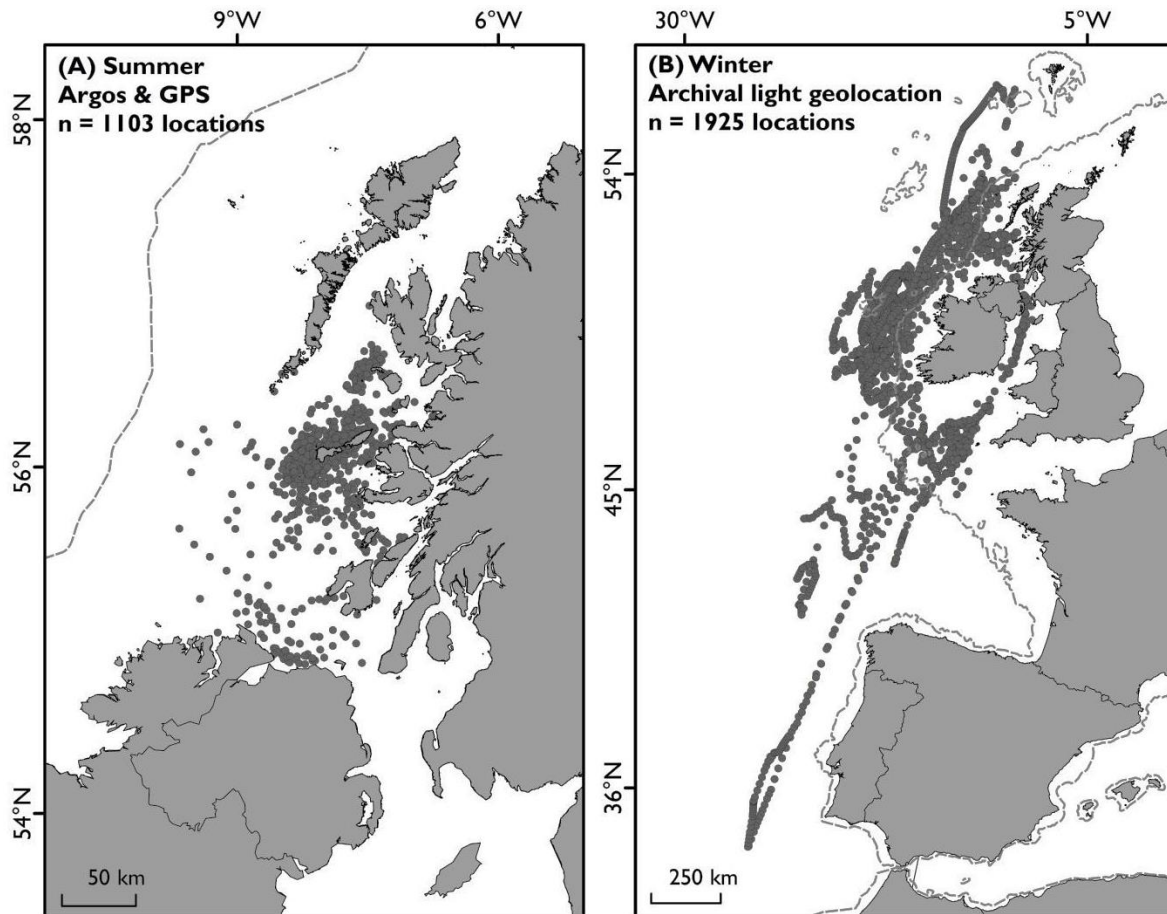


Figure 1. Locations of satellite tracked basking sharks used for summer and winter ecological niche models. (A) Summer; best daily Argos and GPS locations from April to October from SPOT tags ($n = 27$) and FastLoc™ GPS SPLASH-F tags ($n = 9$) and (B) Winter; daily light geolocation estimates from October to March from PAT-F ($n = 3$), MiniPAT ($n = 8$) and SPLASH-F ($n = 1$); using data from sharks transmitting days 165 days). Maps drawn to Geographic Coordinate system: Europe Albers Equal Area Conic.

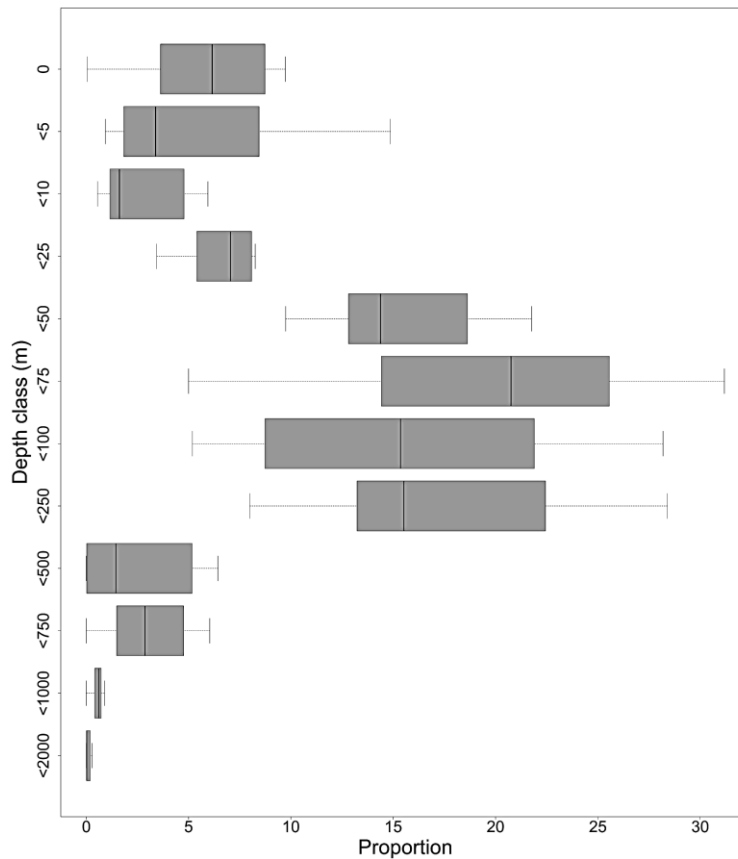


Figure 2. Winter depth use (October – March). Depth class occupancy of satellite tracked basking sharks from the north-east Atlantic exhibiting over-wintering behaviour. Data were used to inform decision making as to which temperature-at-depth layers to be extracted and used as an environmental variable layer for the winter EENM.

Model evaluation

All models (GAM, BRT, and GLM) performed better than random (*summer model* mean \pm SD (range of means): GAM; 0.971 ± 0.016 (0.95-0.988), BRT; 0.979 ± 0.015 (0.961-0.996), GLM; 0.956 ± 0.021 (0.93-0.976); Table D3); *winter model* mean \pm SD (range of means): GAM; 0.970 ± 0.013 (0.914-0.992), BRT; 0.977 ± 0.005 (0.946-0.995), GLM; 0.969 ± 0.017 (0.907-0.994); Table D5) suggesting models predicted habitat suitability concurred with evaluation data (25% of location data). Evaluation scores demonstrated that no one model outperformed the others.

Summer model

Suitable habitat is typically defined by an area with a probability (suitability) greater than 0.5; these areas were largely constrained to coastal regions. In the North Atlantic, areas from the Gulf of Lawrence in Canada south to Massachusetts in the USA (Fig. 3A), and south from the UK and Ireland to northern Africa and east into the North Sea, Scandinavia and the Baltic Sea (Fig. 3B and Fig. 4) exhibited high levels of suitability. In the South Atlantic, the coastal regions of south Brazil, Uruguay and Argentina (Fig. 3C), and the coastal zones of Namibia and South Africa presented as having high levels of suitability for basking sharks (Fig. 3D). Areas further offshore the coasts of Argentina and South Africa were predicted as providing suitable habitat when projected for approximate austral summer conditions (Fig. 3E and F). SST and Chl-a concentration were the most important contributory environmental variables to the *summer* model (Table D4), with mean RICCs of 0.538 (SST) and 0.216 (Chl-a) respectively. Depth and persistent daily SST frontal activity were less important contributory environmental variables (Table D5; RICC: 0.189 and 0.064 respectively). Moran's Global *I* coefficients indicated that there was no spatial autocorrelation within the residuals of the *summer model* ($z = 0.0554$, $p = 0.9558$; Table D2).

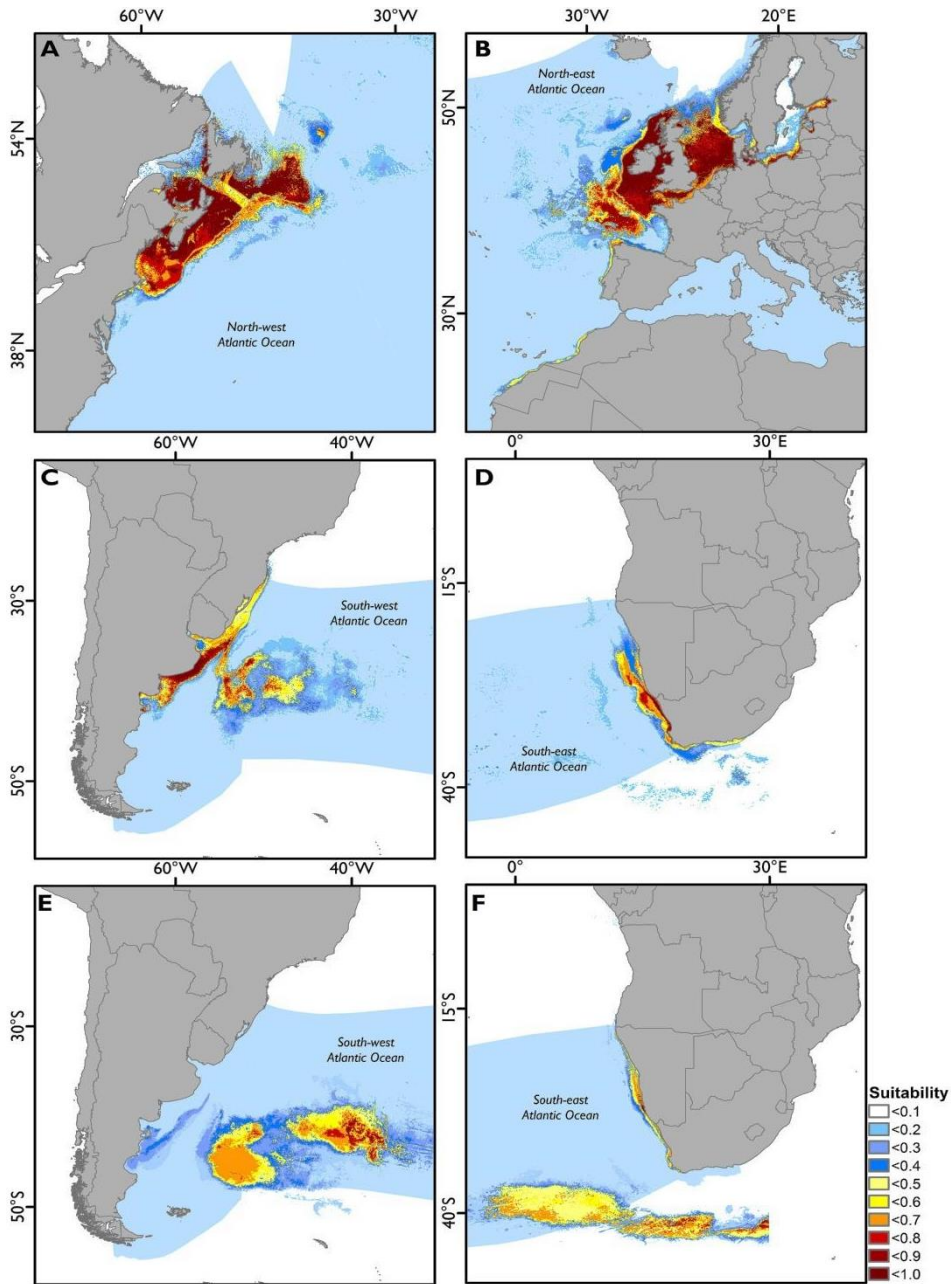


Figure 3. Summer EENM model predictions of suitable surface habitat. EENM utilising Argos and GPS locations for basking sharks at the sea surface, SST, Chl α concentration, persistent surface SST frontal activity and bathymetry data layers (4 km resolution) showing areas of suitable habitat. (A) north-west Atlantic boreal summer (April-October); (B) north-east Atlantic boreal summer (April-October), (C) south-west Atlantic boreal summer (April-October), (D) south-east Atlantic boreal summer (April-October), (E) south-west Atlantic austral summer (September-February), and (F) south-west Atlantic austral summer (September-February). The relative suitability of habitats scaled between 0 and 1; where 1 representing highest suitability. IUCN species distribution (blue polygon). Map plots drawn geographical relevant Albers Equal Area Conic.

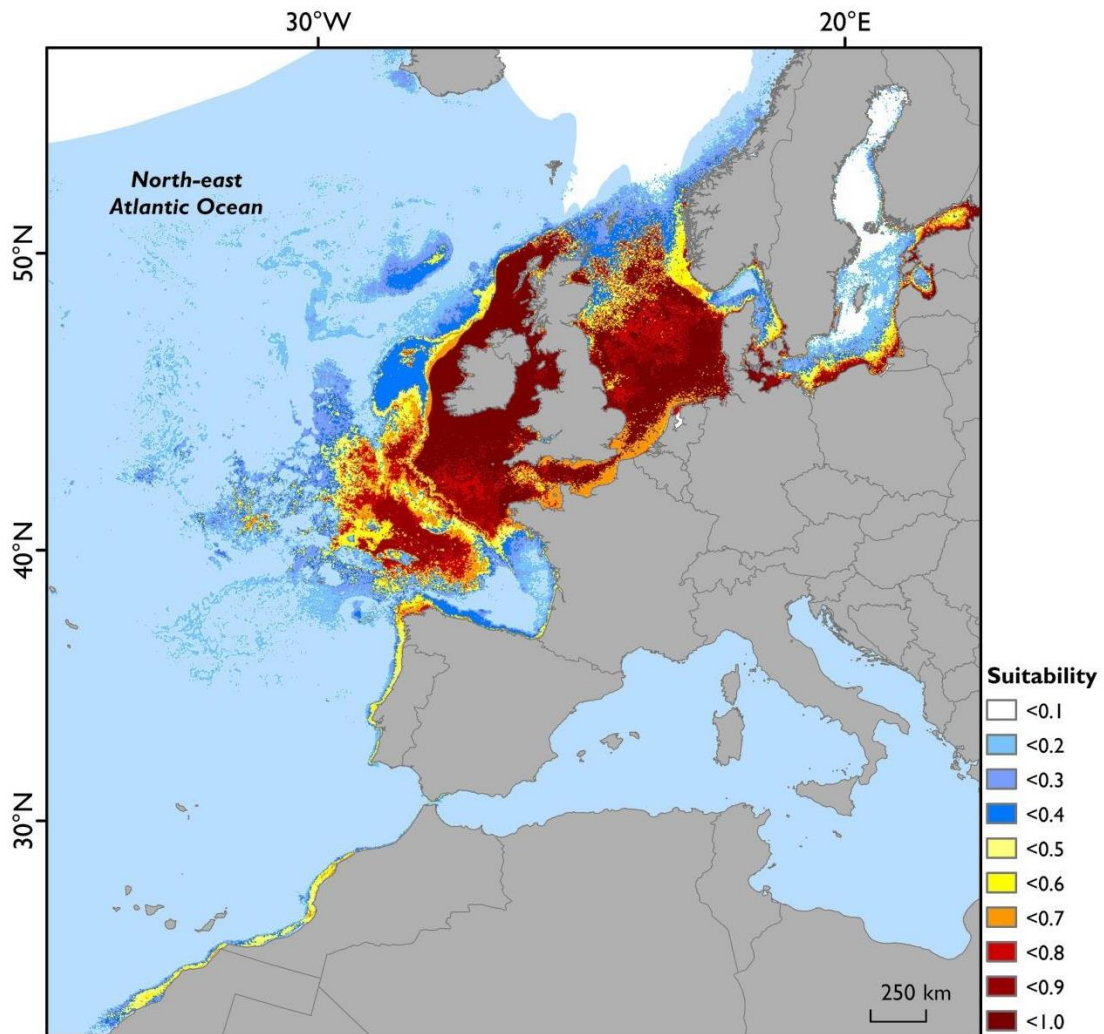


Figure 4. Summer EENM model predictions of suitable surface habitat for the north-east Atlantic. EENM utilising Argos and GPS locations for basking sharks at the sea surface, SST, Chl α concentration, persistent surface SST frontal activity and bathymetry data layers (4 km resolution) showing areas of suitable habitat in the north-east Atlantic summer months (April-October). The relative suitability of habitats scaled between 0 and 1; where 1 representing highest suitability. IUCN basking shark distribution (blue polygon). Map projection: Europe Albers Equal Area Conic.

Winter model

Areas consisting of suitable habitat (>0.5 suitability) in the north-west Atlantic were located off the coast of Massachusetts and Maine (USA), and north towards Nova Scotia (Canada), the north-east Atlantic supported suitable habitat off the UK and Irish coasts, within the Bay of Biscay. In the southern Atlantic Ocean, areas off the coast of Uruguay and Argentina supported high suitability as did coastal regions off South Africa, Namibia, Angola, and some smaller areas off West Africa (Fig. 5). EENMs highlighted areas of suitable habitat that connected eastern and western hemispheres in both the north and south Atlantic, these areas traverse from the Bay of Biscay to Massachusetts, USA and southern South Africa to south Argentina following the Antarctic Circumpolar Current (ACC) respectively (Fig. 5). Temperature-at-depth was the most important contributory environmental variable to the *winter model* (Table D6), with a mean RICC of 0.711. Depth (RICC: 0.274) and slope (RICC: 0.015) were less important contributory environmental variables (Table D6). Moran's Global *I* coefficients indicated that there was no spatial autocorrelation within the residuals of any individual *winter model* (0-10 m model; $z = 0.7173$, $p = 0.4732$; 50-100 m model; $z = 0.1546$, $p = 0.8771$; 150-250 m model; $z = 0.2971$, $p = 0.7664$; Table D2).

Temperature

In the summer, basking shark locations were situated in areas of a mean SST of 12 °C (range: 11-19 °C), with a mean contemporaneous archival tag temperature of 14 °C (range: 6-18 °C). In the winter, sharks were situated in areas with mean temperatures of 11 °C (range: 9-16 °C), with mean contemporaneous archival tag data of 12 °C (range: 7-15 °C). Temperatures derived from HYCOM temperature-at-depth layers showed strong correlation with temperatures corresponding to physically recovered archival tag point location estimates (Fig. 6; $\rho = 0.74-0.98$, $p = <0.001$; $n = 5$ tags) and daily utilisation distributions (Fig. 6; $\rho = 0.61-0.93$, $p = <0.001$; $n = 5$ tags). This suggests telemetry based location data can provide an accurate account for true environmental conditions experienced by the tracked species, and using such data from telemetry devices.

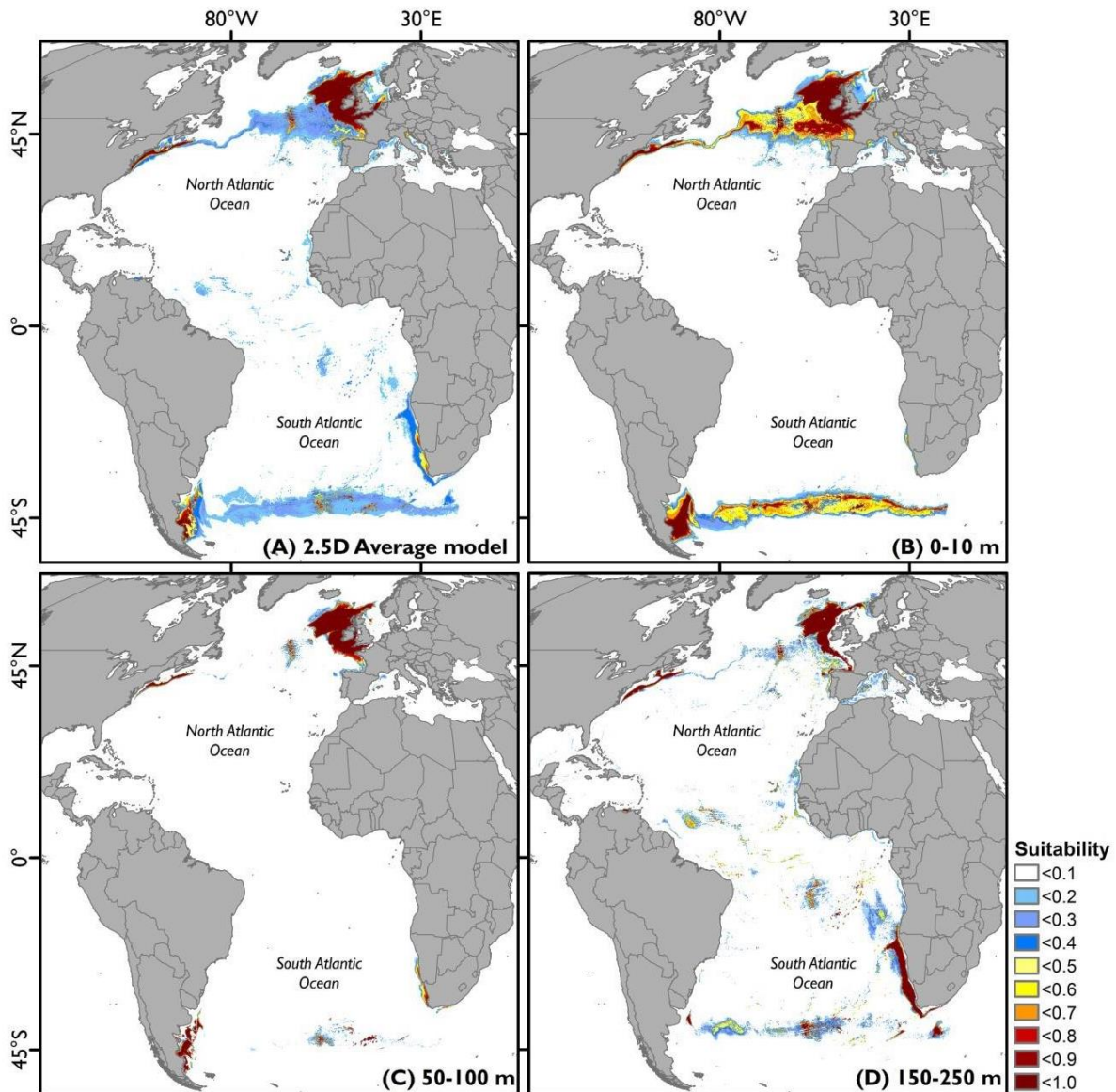


Figure 5. Winter (October – March) EENM prediction of suitable habitat based on temperature at varying depths. EENM utilising light geolocated tag data representing locations from sharks at depth (HYCOM), slope and bathymetry data layers (8 km resolution). Model outputs of suitable habitat at (A) Averaged model output of depth models between 0-250 m, (B) 0-10 m, (C) 50-100 m, and (D) 150-250 m. Atlantic-wide habitat suitability model predicts potential overwintering areas at varying depth ranges based on depth use of satellite tracked basking sharks in the north-east Atlantic (Fig. 2). The relative suitability of habitat is scaled between 0 and 1 with 1 representing the highest suitability. Map drawn to Geographic Coordinate system: Mollweide.

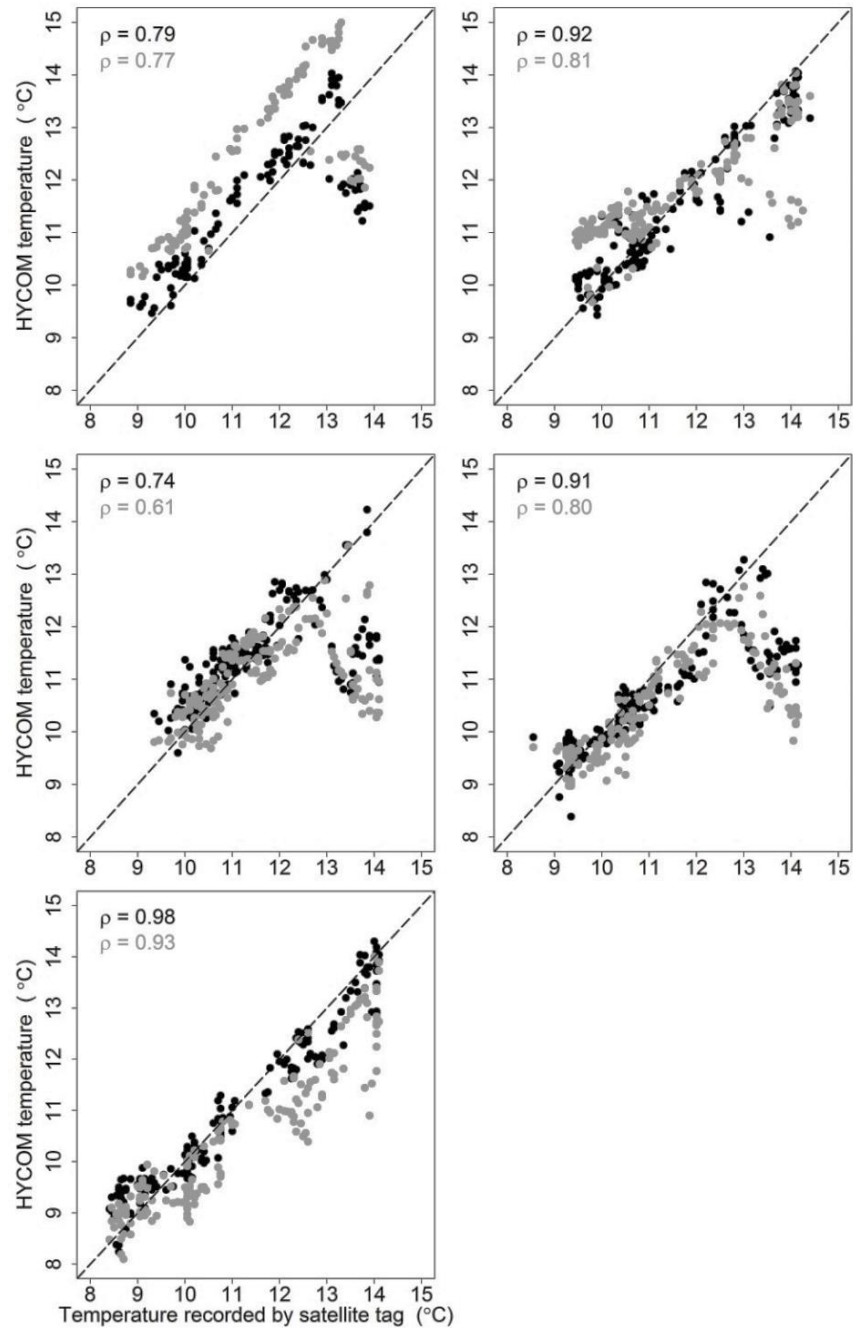


Figure. 6. Correlation plots validating HYCOM temperature-at-depth data layers. Plots of daily HYCOM temperature-at-depth layers extracted to corresponding point locations (black circles) and daily utilisation distributions (grey circles) using time-series data from physically recovered archival tags with attachment durations greater than 165 days ($n = 5$). Dashed line represents a correlation of one. Rho values are shown in corresponding colours to data tested, all correlation tests were significantly different from zero ($p < 0.001$).

Discussion

This is the first time Ensemble Ecological Niche Models (EENMs) have been used to predict areas of suitable habitat for basking sharks over an oceanic scale, and the first to apply three-dimensional oceanographic data based on vertical space-use behaviour to this species.

Basking sharks seasonally aggregate in temperate continental shelf waters to feed and are capable of large, trans-boundary migrations (Gore *et al.* 2008; Skomal *et al.* 2009; Doherty *et al.* 2017a), potentially between areas of seasonal aggregations. However, the whereabouts of basking sharks when absent from these aggregation sites is largely unknown at the population level, with knowledge of the potential oceanographic and biological drivers involved in determining the habitat use lacking. It has been shown that species that undertake large migratory movements appear to be particularly vulnerable to detrimental impacts of climate change (Robinson *et al.* 2008). The magnitude and rate of climate change in higher latitudes is likely to be greatest, with migrants that inhabit these regions relying on highly productive seasonal habitats, such as upwelling, that with climate change, may become less food-rich and predictable in space and time (Robinson *et al.* 2008). Therefore, determining where areas of suitable habitats occur and range of these species is of high concern.

It has been shown that at local scales (<10 km) basking shark distribution is determined by ocean primary productivity (Sims & Merrett 1997; Sims & Quayle 1998; Sims 1999; Siders *et al.* 2013; Miller *et al.* 2015). However, at greater scales (10 – 1000 km), SST and thermal gradients correlate significantly with basking shark distribution (Sims & Quayle 1998; Sims *et al.* 2003; Curtis *et al.* 2014; Miller *et al.* 2015). These observations suggest that for these ectothermic planktivores, prey density likely plays an important role in determining short-term distribution, whereas on a broader scale, long-term movement patterns may be in response to locating regions and depths in order to maintain an optimal thermal habitat

to reduce metabolic and physiological functions (Sims *et al.* 2003; Cotton & Sims 2005; Schlaff *et al.* 2014).

Our *summer model* indicated continental shelf areas to be most suitable for basking sharks between April and October. This model indicated a good fit to areas described from sightings and known distribution both in the north and south Atlantic Ocean, largely occupying continental shelf waters in higher latitude temperate regions (Fowler 2005). SST was the primary statistical significant environmental variable found to influence the distribution of basking sharks during summer months. SST can be related to primary productivity and can indirectly influence shark distribution and movement patterns through availability of preferred prey with areas of positive trophic coupling of chlorophyll and zooplankton biomass at large scales being observed (Irigoien *et al.*, 2004; Ware and Thomson, 2005), resulting in any one area being more suitable than another (Cotton & Sims 2005). Our model therefore is likely predicting areas supporting high suitability for foraging. SST has also been shown to influence movements of planktivorous whale sharks (*Rhincodon typus*; Sequeira *et al.* 2014). Some unexpected areas were highlighted as containing large areas of suitable habitat, most notably in the North Sea between the eastern coast of the UK and waters off the western shores of Denmark. The North Sea and Denmark are historically part of basking shark range; however, sightings in these areas are much less frequent than the waters off the west coast of the UK (Witt *et al.* 2012), with no sharks tracked moving into these areas. This may be a result of historical exploitation removing migration phenotypes from the population (Caro & Sherman 2012), or a reduction and/or regional shift in zooplankton (Provan *et al.* 2009).

Lucifora *et al.* (2015) modelled basking shark occurrences based on sightings, onboard observers and fisheries interactions in the south Atlantic. This study suggested that a combination of Chl-a concentration and SST were the primary drivers of basking shark distribution, highlighting areas off the coasts of Namibia and South Africa in the south-east Atlantic, and Brazil, Uruguay, and Argentina in the south-west Atlantic. These areas were also present in our study and have been shown previously to be areas of high

productivity, supporting marine turtles, seabirds and mammals (Gonzalez-Carman *et al.* 2016). Those models, however, were constrained to continental surface shelf waters, not allowing for prediction beyond these areas, and were limited by few input presence locations.

Our *winter model* suggested temperature-at-depth was the most important factor determining basking shark distribution during this period, when basking sharks most often occupy deeper waters. Basking sharks appear to display a dispersive nature to movements not constrained to moving towards a specific over-wintering area. This dispersive nature of movements within the population does not conform to traditional migration models, however, a potential “exploration-refinement” hypothesis could be suggested describing a reliance on large-scale exploratory movements, which become refined into an individual migratory route and through learning (Guilford *et al.* 2011), but in the absence of multiple year attachment durations for individual basking sharks, route fidelity cannot be described. The model highlights some similar regions to the *summer model*, suggesting some areas could provide suitable habitat and conditions year-round for this species, but at differing depths. The *winter model* also highlights new areas of interest, most notably the Bay of Biscay, Iberian Peninsula and West Africa. These areas show an expansion of the summer habitat to more southerly latitudes for winter months, which correspond with some migratory routes and occupied area observed in satellite tracked basking sharks from the north-east Atlantic (Stéphan *et al.* 2011; Doherty *et al.* 2017a). Areas in the western Mediterranean Sea become apparent as providing suitable habitat in the deeper model runs (150-250 m) during winter months. This area was absent during the *summer model* output, suggesting surface temperatures are too high for basking sharks during the summer, with the potential for basking sharks to be present but at depths away from the surface. Annual mean SST for the Mediterranean Sea has been shown to be approximately 20 °C (Shaltout & Omstedt 2014) and would therefore be at the extreme of basking shark thermal tolerance observed in this study. The *winter model* also identifies two conspicuous corridors running longitudinally across each hemisphere. These areas, one traversing from the Bay of Biscay to north-east America and one south of South Africa

across to Uruguay and Argentina, following the northern boundary of Antarctic Circumpolar Current (ACC) reveal the possible existence of migratory pathways that link eastern and western hemispheres. One satellite tracked basking shark has been shown to make such movements, where this shark travelled at depth from UK territorial waters across the north Atlantic towards Newfoundland, Canada (Gore *et al.* 2008). North to south migratory movements have been observed in basking sharks (Skomal *et al.* 2009; Doherty *et al.* 2017a), but linkages from east to west has been observed only once (Gore *et al.* 2008), potentially doing so along a migratory pathway. Genetic diversity is thought to be low in basking sharks (Hoelzel *et al.* 2006), therefore discovery of these migratory pathways, which may facilitate movements between areas to maintain genetic drift is of ecological and conservation interest.

Applying techniques where locations and depths recorded by satellite tags inform selection of environmental data based on the depth-layers these animals inhabited will likely improve model predictions within the 3D environment (Duffy & Chown 2017).

From our tracking dataset and modelled outputs, movements of basking sharks appear largely determined by maintaining an optimal thermal envelope, however surface waters (<10 m depth) provide suitable thermal conditions based on model output. Basking sharks most often occupy depths away from surface waters during the winter. This potentially suggests other drivers of vertical behaviour, such as foraging at depth. In the absence of zooplankton density-at-depth data, descriptions of these potential drivers are lacking.

One notable absence from our *winter model* output is that of the eastern Caribbean Sea and waters off the northern South American coast were not shown as supporting suitable habitat for basking sharks. There have been observations of basking sharks in these regions (Geelhoed, Janinhoff & Verdaat 2016), and satellite tracking from the USA showing movements into these locations throughout winter months (Skomal *et al.* 2009). Skomal *et al.* (2009) described basking sharks moving into waters off the Bahamas, Puerto Rico, Guyana, and Brazil, but doing so at depths between 200 and 1000 metres, stating that the 5 °C thermocline off the coast of Bahamas was between 750 and 1000 metres but

between 300 and 400 metres depth off the coast of Brazil. These data may reveal that in order to make migratory movements from the north-west Atlantic towards the south-west Atlantic and maintain thermal optimum, these sharks have to do so at much greater depths than seen in the eastern Atlantic. This is supported by the appearance of suitable habitat off the coast of north-east South America in our 150-250 m model output, and a re-emergence of suitable habitat forming potential corridors appearing at these depths. This further substantiates the need to use ecological and behavioural data from telemetry devices to inform models in order to obtain more robust and accurate outputs.

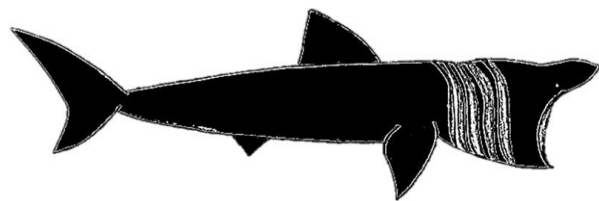
Although some issues with the application of telemetry data to habitat modelling have been identified (Aarts *et al.* 2008), such as environmental data not coinciding with usage data, autocorrelation, cross-correlation of environmental data, and points in space not being equally accessible to individuals. We have taken steps to minimise these limitations through incorporation of a large sample size of location points, with all areas potentially available for occupancy by basking sharks. We used best daily locations as presence data to reduce spatio-temporal autocorrelation and made efforts to test for collinearity and spatial autocorrelation and minimise where necessary. Additionally, the application of EENMs allows us to create a single, averaged model of several algorithms to maximise the strengths of each approach.

We apply the same seasonality for both northern and southern hemispheres within the *summer model* as climatically we don't find support of the *austral* summer representing a mirror setting for the *boreal* summer. Seasonally-explicit incidence rates of basking shark encounters are largely lacking in the southern Atlantic Ocean. This is an area worthy of exploration in order to improve modelling techniques; however, our approach was intended as a robust first account of suitable habitats for basking sharks on an ocean scale in order to describe potential distribution of this species throughout the Atlantic Ocean. In addition, our results largely support and extend extant knowledge of basking shark distribution at many locations in both hemispheres.

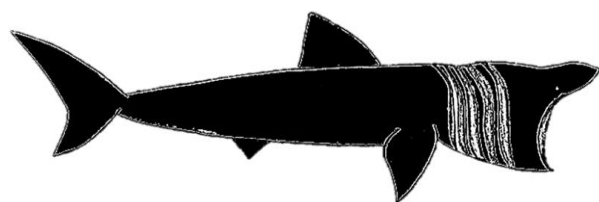
Conclusion

This study enhances our understanding of habitat suitability, likely seasonal distribution, and range extent for basking sharks in the Atlantic Ocean. Environmental factors, in particular SST and temperature at occupied depths were the main drivers for basking shark habitat suitability in summer and winter respectively. Identifying and protecting critical habitats of species of conservation concern is a major application of habitat suitability models for conservation purposes (Guisan *et al.* 2013). A better understanding of the drivers of habitat utilisation is valuable for the management of populations of mobile marine vertebrates, in particular species of conservation concern. An ability to identify and therefore predict the locations of important habitats has relevance for the design of marine protected areas (MPAs) and marine spatial planning (Paxton, Scott-Hayward & Rexstad 2014b; Scales *et al.* 2014; Doherty *et al.* 2017b) and could inform projections of range shifts under future climate scenarios (Miller *et al.* 2015).

We did not observe frontal activity as a significant environmental variable influencing suitable habitat for basking sharks, which has been previously cited as a major component for describing movements in this species (Sims & Merrett 1997; Sims & Quayle 1998; Sims 1999; Siders *et al.* 2013; Miller *et al.* 2015). This may be due to scale, as our environmental data were averaged across seasons, whereas many of these studies demonstrate the importance of these variables at shorter timeframes (days to weeks). Spatial scale of environmental variables may also hinder the ability for the modelling technique to detect fine-scale ephemeral frontal activity. However, we feel that our study demonstrates that at a larger scale and probably more generally, temperature is a major driver in the patterns of distribution of basking sharks as these sharks seek out optimal thermal ranges within the water column depending on season, however more information on prey distribution, especially at depth is needed. We show the utility of telemetry data to inform species distribution models, not only as accurate location (presence) data but as a source of behavioural and ecological data that is essential to describe the animal's movements in space and time in order to fully describe its distribution, particularly at large scales.







Overview

Basking sharks are an important species of conservation concern in UK coastal waters. Until now there has been a paucity of high-resolution, seasonal information on space-use for the species. The basking shark was historically the target of directed fisheries in the north-east Atlantic (Kunzlik 1988) and whilst this species is now strictly protected (Fowler 2005), estimates on population sizes and structure remain limited (Westgate *et al.* 2014; Gore *et al.* 2016). To that end, the analyses presented in this thesis demonstrate the complexities of tracking marine megavertebrates. Through this thesis I examine the movement ecology of basking sharks through the application of satellite telemetry, ecological modelling and remotely sensed data. Specifically, I describe the surface space-use in a summer foraging site in the Sea of the Hebrides (**Chapter 2**); further develop knowledge on long-term, wide-ranging over-wintering movements, uncovering individual plasticity (**Chapter 3**); quantify depth and temperature ranges throughout the annual cycle of basking sharks (**Chapter 4**); and employ Ensemble Ecological Niche Modelling (EENM) techniques using contemporaneous tag data and knowledge gathered from previous chapter analysis to predict areas of suitable habitat for basking sharks across the Atlantic Ocean (**Chapter 5**). This thesis forms the most detailed investigation of basking shark movement ecology in the north-east Atlantic, and for the species globally, over seasonal timescales informed by satellite tracking.

Basking shark movement ecology

Detailed knowledge of basking shark occurrence in the north-east Atlantic is largely derived from public sightings data (Southall *et al.* 2005; Witt *et al.* 2012) and boat-based, effort-corrected surveys (Southall *et al.* 2005; Speedie *et al.* 2009) when basking sharks are associated with surface waters within foraging grounds (Matthews & Parker 1950; Berrow & Heardman 1994; Sims *et al.* 2000). In **Chapter 2** I identify basking shark core activity occurs within boundaries of a proposed MPA, providing new information on fine-scale coastal movements. This chapter also reveals residency in this species to the area, and the first record of inter-annual site-fidelity. I show behavioural variation by individuals

within the tracked population, with individuals exhibiting one of three winter migration strategies occupying both coastal and oceanic habitats (**Chapter 3**). This work increases the knowledge base provided by previous tracking studies in the region, where campaigns were restricted by sample size and attachment durations (Sims *et al.* 2003, 2006; Shepard *et al.* 2006; Gore *et al.* 2008; Stéphan *et al.* 2011). Marine organisms function within three-dimensions and environmental conditions change with depth (Hussey *et al.* 2015). In the first long-term investigation of basking shark vertical space-use, I reveal seasonality in depth-use, with some individuals exhibiting extreme deep diving to greater than 1000 m during late winter/early spring (**Chapter 4**). I also show the first evidence for behavioural thermoregulation in basking sharks, a new insight into the ecology and behaviour of this species. The ability to apply predictive modelling techniques to basking sharks has been limited to the continental shelf waters (Siders *et al.* 2013; Paxton *et al.* 2014a; Lucifora *et al.* 2015), but has successfully been applied to other species (Zydelis *et al.* 2011; Scales *et al.* 2014; Sequeira *et al.* 2014; Pikesley *et al.* 2015). I employed an ensemble modelling approach (Araújo & New 2007) to predict suitable habitats for basking sharks (**Chapter 5**). I integrate multiple single-algorithm model predictions and evaluation metrics to reduce potential bias and increase confidence in predictions (Scales *et al.* 2015) using location data collected by satellite tags as the response variable in each ensemble model algorithm. This is the first time EENMs have been used to predict areas of suitable habitat for basking sharks over an oceanic scale and the first to apply three-dimensional oceanographic data based on vertical space-use behaviour to a large planktivorous fish species. I highlight potential areas of interest for future investigation and the potential for connectivity pathways at depth. These areas may represent critical habitats of this species of conservation concern, which is a major application of habitat suitability models for conservation purposes (Guisan *et al.* 2013).

Conservation

In order to employ appropriate protective measures for mobile species, key areas providing suitable conditions and where key life-history events occur need to be identified (Worm *et al.* 2003; Hooker & Gerber 2004). The Convention for Biological Diversity Aichi Targets strategic goals includes the conservation of at least 10% of coastal and marine ecosystems by 2020. The combination of analyses shown in this thesis; spatial movements in areas of key life-history events, broad-scale migrations highlighting most frequented migratory pathways, and a modelling approach to predict potential areas for future focus may provide a framework from which management strategies can be informed. Recently there has been a focus on designating remote Very Large Marine Protected Areas (VLMPAs; (Edgar *et al.* 2014; Singleton & Roberts 2014)), which can offer substantial levels of protection (White *et al.* 2017). However, in order to achieve the Aichi Targets through MPA designation, likely a combination of MPA types, including networks of smaller MPAs will be needed, especially in more intensely used areas (Jones & De Santo 2016). Threats still exist for basking sharks in the absence of directed fisheries, and as such, increased spatio-temporal understanding of their distribution and occurrence within particular habitats will likely help tailor MPA design and management strategies. This thesis is able to substantiate the importance of one such area for basking sharks and evaluate its use prior to designation, a process not usually afforded to most MPAs.

Limitations

Data transmitted via the ARGOS satellite system have inherent spatial accuracy errors associated with them (Witt *et al.* 2010), however, application of a filtering regime, including removal of error classes and restriction by speed of movement can create a representative reconstruction of animal movement (Witt *et al.* 2010).

Estimating locations derived from light-levels is based upon time of highest solar irradiance and length of day (time between sunrise and sunset or vice versa; Wilson *et al.* 1992), however, raw geolocations (i.e. unfiltered and uncorrected estimates), especially

for latitude, are often unreliable (Lam, Nielsen & Sibert 2008; Lisovski *et al.* 2012). Physical (e.g. days near the equinox, where day length is almost equal at all latitudes) and biological factors (e.g. vertical space-use) can reduce the reliability of the position estimation from light data even further (Hill & Braun 2001; Shepard *et al.* 2006; Lam *et al.* 2008). To account for these potential errors Hidden Markov Models (HMMs) were used as grid filters to estimate the daily probability density of the location of each tracked shark (Thygesen *et al.* 2009; Neilson *et al.* 2014). These models were further constrained by bathymetry, SST, and known deployment and pop-off locations to reduce location estimate error (Bias *et al.* 2017).

Spatio-temporal data may contain bias via spatial and temporal autocorrelation or pseudo-replication (Franklin 2010). Failure to account for these biases may increase the signal strength from some environmental variables causing an explanatory variable to be retained when it should not have been (Franklin 2010). To reduce the potential for spatial and temporal autocorrelation, all data used to construct habitat models were reduced to best daily locations. In order to obtain robust model predictions, spatial autocorrelation must be accounted for and if necessary reduced. Where EENMs were run, spatial autocorrelation within model residuals were investigated using Moran's I coefficients (Dormann *et al.* 2007). Using such methods, the ensemble model prediction surfaces produced within this thesis likely represent robust predictions of habitat suitability for basking sharks, based on key environmental variables most likely to be of importance.

Basking sharks approached for tag attachment were first assessed, where possible, for their sex, and estimates of body length. These are important physiological and morphometric data to be considered as many shark species show segregation by size and/or sex (Klimley 1987; Wearmouth & Sims 2008; Mucientes *et al.* 2009), and may impact movement patterns. However, due to fieldwork campaign limitations, the collection of these data was not always possible. This has therefore reduced the ability to observe any differences in space-use that could be influenced by sex, or body length, which may be a proxy for age. During the project there were no observations of juvenile

basking sharks and they therefore do not feature in the thesis. This size class likely have different requirements than mature individuals and may therefore exhibit differing movement behaviours (Knip *et al.* 2011; Ketchum, Galván-Magaña & Klimley 2013).

Individual variation in both horizontal and vertical movement behaviour has been described in this thesis, however the effect of which variables are driving movement patterns are largely unknown for basking sharks. In order to address this, more information on individuals tracked is required; accurate body size measurements (including body mass), sexing of all individuals, DNA samples (relatedness may drive movements in groups), and a combination of technologies providing real-time environmental conditions associated with location and programming of tags to reflect knowledge of species movements to gather more fine-scale data at a wider range of temperatures and depths occupied.

Notwithstanding these caveats, the analyses presented in this thesis emphasise the need for the development of multi-national marine conservation policies that will actively protect highly migratory species. These policies need to be coupled with effective enforcement and adaptability, to change as our knowledge of animal movement ecology increases allowing for more developed informing of distribution estimates.

Future research areas

The continued development of tag technology coupled with emphasis on reduction of impact of devices; in particular drag effects that may potential disrupt the mechanics of locomotion. Increasing battery life and minimising biofouling, will allow for longer attachment times, increasing the ability to observe movement patterns and the conditions under which they occur. This research can be coupled with other fast-developing techniques such as stable isotopes and genetic analysis to better estimate population sizes and relatedness to begin to understand foraging strategies. Animals equipped with telemetry devices encounter varying environmental conditions whilst carrying out core activities, and can therefore sample the water column they inhabit for many variables,

such as salinity, temperature, light levels, and oxygen concentration acting as “animal oceanographers” (Lydersen *et al.* 2002; Grist *et al.* 2011; Lowther *et al.* 2013; Roquet *et al.* 2013). These studies to date have been limited to mammalian species at high latitudes; however, the capacity for real-time data to be recorded is cause for the continued development and testing of these types of devices for non-mammalian pelagic species such as sharks.

Most satellite tracking studies for sharks have been limited to describing the “what” and “where” rather than the “why” aspects of shark behaviour and ecology (Hammerschlag *et al.* 2011). This is changing with the combination of sensors and transmitters being deployed to assess some of these questions, such as measuring tail-beat frequency and body orientation and dynamic movement using accelerometers (Gleiss, Norman & Wilson 2011), *in situ* observations of animals with automated underwater vehicles (Skomal *et al.* 2015), and combining techniques with animal-borne cameras to elucidate and ground-truth the data recorded on telemetry devices (Watanabe & Takahashi 2013). Further knowledge of threats to sharks, and basking sharks in particular needs to be gathered. Assessment of interactions with fisheries, marine civil engineering, eco-tourism, pollution, and climate change, together with quantification of probable impacts is required. There is a need for a robust study into population size, relatedness, connectivity of possible sub-populations, and sensitivity of species to identified threats to be carried out. This may aid updating population status and assess impacts of threats at local and global population levels. Fine scale environmental data of areas of high occupancy would further inform habitat suitability predictions. The Sea of the Hebrides is shown to be an area of high importance for basking sharks, with key life-history events taking place there. The ability to measure and monitor changes in conditions at a local scale where observations of high activity is occurring could provide better estimates of suitable habitat at larger scales if key drivers are identified. Other areas in the north-east Atlantic are highlighted as having large areas of suitable habitat, yet we have little to no evidence of basking sharks occupying these areas. This could be due overexploitation of fisheries leading to a loss of migratory behaviour to these areas as has been shown in other taxa (Caro & Sherman

2012). These other areas of suitable habitat could provide areas for basking sharks to expand into, potentially as the population recovers from exploitation or as climate change implications affect movement patterns.

Population recovery will need to be considered in any management strategy to ensure any MPA designated has potential to remain effective for an increasing protected population. However, in the absence of population estimates before high levels of exploitation, knowledge on basking shark population status is largely unknown. Life history traits of chondrichthyans, especially for large bodied, slow growing, late maturing, and coastal species with long gestation periods, such as the basking shark, the “rebound potential” for a population will take many decades (Smith, Au & Show 1998; Stevens 2000).

Concluding remarks

The focus of movement patterns of basking sharks in the north-east Atlantic has been largely at foraging grounds and in continental shelf waters, limiting our understanding of the range of this species and the behaviours occurring within an annual cycle. This study contributes to the growing knowledge of basking shark movements and behaviour, but provides the first in-depth account of movements throughout the winter. A large sample size of basking sharks tracked has facilitated investigation of individual level movements, which I have shown to differ. Combining detailed knowledge of space-use in all dimensions (latitude, longitude, depth, and time) for species of conservation concern will best inform on implementation of sustainable conservation and management strategies.

In order to develop governance frameworks for the marine realm, understanding the causes, changes, and ecological functions associated with species-environment interactions is crucial and can be obtained through data collected via telemetry devices (Hussey *et al.* 2015). This likely will close the gap between terrestrial and aquatic ecosystems (Beger *et al.* 2010). Throughout my PhD I have been constantly amazed by the rapid development of telemetry devices and analytical techniques. The ability to observe fine-scale data has revolutionised our understanding of how animals use the ocean. The

creation of sophisticated devices allows researchers to answer questions about marine species that may be considered “basic” in their terrestrial equivalents but have until recently eluded us. As we enter this “golden age” of satellite tracking, the insights into animal movement ecology in the ocean will dramatically increase providing exciting new discoveries into the ecology of marine species.

References

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, **31**, 140–160.
- Afonso, A.S. & Hazin, F.H.V. (2015) Vertical Movement Patterns and Ontogenetic Niche Expansion in the Tiger Shark, *Galeocerdo cuvier*. *Plos One*, **10**, e0116720.
- Allen, A.M. & Singh, N.J. (2016) Linking Movement Ecology with Wildlife Management and Conservation. *Frontiers in Ecology and Evolution*, **3**, 1–13.
- Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, **22**, 42–47.
- Ashe, E., Noren, D.P. & Williams, R. (2010) Animal behaviour and marine protected areas: Incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population. *Animal Conservation*, **13**, 196–203.
- Atwood, T.B., Connolly, R.M., Ritchie, E.G., Lovelock, C.E., Heithaus, M.R., Hays, G.C., Fourqurean, J.W. & Macreadie, P.I. (2015) Predators help protect carbon stocks in blue carbon ecosystems. *Nature Climate Change*, **5**, 1038–1045.
- Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3**, 327–338.
- Barnett, A., Abrantes, K.G., Stevens, J.D. & Semmens, J.M. (2011) Site fidelity and sex-specific migration in a mobile apex predator: implications for conservation and ecosystem dynamics. *Animal Behaviour*, **81**, 1039–1048.

- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-5. <http://CRAN.R-project.org/package=lme4>.
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003) Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, **299**, 389–392.
- Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A. & Edwards, M. (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694.
- Beger, M., Grantham, H.S., Pressey, R.L., Wilson, K.A., Peterson, E.L., Dorfman, D., Mumby, P.J., Lourival, R., Brumbaugh, D.R. & Possingham, H.P. (2010) Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biological Conservation*, **143**, 565–575.
- Berrow, S.D. (1994) Incidental capture of elasmobranchs in the bottom-set gill-net of the South Coast of Ireland. *Journal of the Marine Biological Association of the U.K.*, **74**, 837–847.
- Berrow, S.D. & Heardman, C. (1994) The Basking Shark *Cetorhinus maximus* (Gunnerus) in Irish Waters: Patterns of Distribution and Abundance. *Biology and Environment: Proceedings of the Royal Irish Academy*, **94**, 101–107.
- Berumen, M.L., Braun, C.D., Cochran, J.E.M., Skomal, G.B. & Thorrold, S.R. (2014) Movement Patterns of Juvenile Whale Sharks Tagged at an Aggregation Site in the Red Sea. *PLoS ONE*, **9**, e103536.
- Beyer, H.L. (2012) Geospatial Modelling Environment (version 0.7.2.1). <http://www.spataleecology.com/gme>.

- Bias, G., Coupeau, Y., Seret, B., Calmettes, B., Lopez, R., Hetherington, S. & Righton, D. (2017) Return migration patterns of porbeagle shark (*Lamna nasus*) in the Northeast Atlantic: implications for stock range and structure. *ICES Journal of Marine Science*, **doi:10.109**.
- Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A. & Fudge, D. (2001) Migratory movements, depth preferences, and thermal biology of Atlantic Bluefin Tuna. *Science*, **293**, 1310–1314.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W. & Costa, D.P. (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature*, **475**, 86–90.
- Bonfil, R., Meÿer, M., Scholl, M.C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D. & Paterson, M. (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science*, **310**, 100–103.
- Boustany, A.M., Davis, S.F., Pyle, P., Anderson, S.D., Le Boeuf, B.J. & Block, B.A. (2002) Expanded niche for white sharks. *Nature*, **415**, 36–37.
- Braun, C.D., Skomal, G.B., Thorrold, S.R. & Berumen, M.L. (2014) Diving Behavior of the Reef Manta Ray Links Coral Reefs with Adjacent Deep Pelagic Habitats. *PLoS ONE*, **9**, e88170.
- Bres, M. (1993) The behaviour of sharks. *Reviews in Fish Biology and Fisheries*, **3**, 133–159.
- Brunnschweiler, J.M., Baensch, H., Pierce, S.J. & Sims, D.W. (2009) Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. *Journal of fish biology*, **74**, 706–14.
- Calenge, C. (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

- Campana, S.E., Dorey, A., Fowler, M., Joyce, W., Wang, Z., Wright, D. & Yashayaev, I. (2011) Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic. *PLoS one*, **6**, e16854.
- Carey, F.G. & Scharold, J.V. (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, **106**, 329–342.
- Caro, T. & Sherman, P.W. (2012) Vanishing behaviors. *Conservation Letters*, **5**, 159–166.
- Cayula, J.-F. & Cornillon, P. (1992) Edge detection algorithm for SST images. *Journal of Atmospheric and Oceanic Technology*, **9**, 67–80.
- Chapman, D.D., Feldheim, K.A., Papastamatiou, Y.P. & Hueter, R.E. (2015) There and Back Again: A Review of Residency and Return Migrations in Sharks, with Implications for Population Structure and Management. *Annual Review of Marine Science*, **7**, 547–570.
- Chin, A., Heupel, M., Simpfendorfer, C. & Tobin, A. (2016) Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. *Marine Ecology Progress Series*, **544**, 197–211.
- Chin, A., Mourier, J. & Rummer, J.L. (2015) Blacktip reef sharks (*Carcharhinus melanopterus*) show high capacity for wound healing and recovery following injury. *Conservation Physiology*, **3**, 1–9.
- Clark, E. & Nelson, D.R. (1997) Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes*, **50**, 63–73.
- Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J.A., Goni, R., Borg, J.A., Forcada, A., De Lucia, G.A., Perez-Ruzafa, A., Afonso, P., Brito, A., Guala, I., Le Diréach, L., Sanchez-Jerez, P., Sommerfield, P.J. & Planes, S. (2009) Marine reserves : Fish life history and ecological traits matter. *Ecological Applications*, **20**, 830–839.

- Compagno, L.J.V. (1984) Sharks of the World. An annotated and illustrated catalogue of shark species to date. Part I (Hexanchiformes to Lamniformes). *FAO Fisheries Synopsis, FAO, Rome*.
- Compagno, L.J. V. (1990) Alternative life-history styles of cartilaginous fishes in time and space. *Environmental Biology of Fishes*, **28**, 33–75.
- Cooke, S.J. (2008) Biotelemetry and biologging in endangered species research and animal conservation: Relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research*, **4**, 165–185.
- Cortés, E. (2000) Life History Patterns and Correlations in Sharks. *Reviews in Fisheries Science*, **8**, 299–344.
- Cortés, E. (2002) Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. *Conservation Biology*, **16**, 1048–1062.
- Costa, D.P., Breed, G.A. & Robinson, P.W. (2012) New Insights into Pelagic Migrations: Implications for Ecology and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 73–96.
- Cotton, P. & Sims, D. (2005) The effects of climate variability on zooplankton and basking shark (*Cetorhinus maximus*) relative abundance off southwest Britain. *Fisheries Oceanography*, **14**, 151–155.
- Coyne, M.S. & Godley, B.J. (2005) Satellite Tracking and Analysis Tool (STAT): An integrated system for archiving, analyzing and mapping animal tracking data. *Marine Ecology Progress Series*, **301**, 1–7.
- Curtis, T., Zeeman, S., Summers, E., Cadrin, S. & Skomal, G. (2014) Eyes in the sky: linking satellite oceanography and biotelemetry to explore habitat selection by basking sharks. *Animal Biotelemetry*, **2**, 12.

- Dambach, J. & Rödder, D. (2011) Applications and future challenges in marine species distribution modeling. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **21**, 92–100.
- Dingle, H. (2014) *Migration: The Biology of Life on the Move. Second Edition*. Oxford University Press, Oxford.
- Doherty, P.D., Baxter, J.M., Gell, F.R., Godley, B.J., Graham, R.T., Hall, G., Hall, J., Hawkes, L.A., Henderson, S.M., Johnson, L., Speedie, C. & Witt, M.J. (2017a) Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic. *Scientific Reports*, **7**, doi:10.1038/srep42837.
- Doherty, P.D., Baxter, J.M., Godley, B.J., Graham, R.T., Hall, G., Hall, J., Hawkes, L.A., Henderson, S.M., Johnson, L., Speedie, C. & Witt, M.J. (2017b) Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed marine protected area. *Biological Conservation*, **209**, 68–75.
- Domeier, M. & Nasby-Lucas, N. (2008) Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Marine Ecology Progress Series*, **370**, 221–237.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, **30**, 609–628.
- Duffy, G. & Chown, S. (2017) Explicitly integrating a third dimension in marine species distribution modelling. *Marine Ecology Progress Series*, **564**, 1–8.

- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, M., Harrison, L.R., Carlson, J.K., Davidson, L.N.K., Fordham, S.V., Francis, M.P., Pollock, M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J.V., Ebert, D.A., Gibson, C., Heupel, M.R., S.R., L., Sanciangco, J.C., Stevens, J.D., Valenti, S. & Wjite, W.T. (2014) Extinction risk and conservation of the world 's sharks and rays. *eLife*, **3**, 1–35.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A. & Thomson, R.J. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature*, **506**, 216–220.
- Ellenberg, U., Mattern, T. & Seddon, P.J. (2013) Heart rate responses provide an objective evaluation of human disturbance stimuli in breeding birds. *Conservation Physiology*, **1**, 1–11.
- Engqvist, L. (2005) The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, **70**, 967–971.
- Escalle, L., Speed, C.W., Meekan, M.G., White, W.T., Babcock, R.C., Pillans, R.D. & Huvaneers, C. (2015) Restricted movements and mangrove dependency of the nervous shark *Carcharhinus cautus* in nearshore coastal waters. *Journal of Fish Biology*, **87**, 323–341.
- Farmer, N.A. & Ault, J.S. (2011) Grouper and snapper movements and habitat use in Dry Tortugas, Florida. *Marine Ecology Progress Series*, **433**, 169–184.
- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology letters*, **13**, 1055–71.

- Fossette, S., Witt, M.J., Miller, P., Nalovic, M.A., Albareda, D., Almeida, A.P., Broderick, A.C., Chacón-Chaverri, D., Coyne, M.S., Domingo, A., Eckert, S., Evans, D., Fallabrino, A., Ferraroli, S., Formia, A., Giffoni, B., Hays, G.C., Hughes, G., Kelle, L., Leslie, A., López-Mendilaharsu, M., Luschi, P., Prosdocimi, L., Rodriguez-Heredia, S., Turny, A., Verhage, S. & Godley, B.J. (2014) Pan-atlantic analysis of the overlap of a highly migratory species, the leatherback turtle, with pelagic longline fisheries. *Proceedings of the Royal Society B*, **281**, 20133065.
- Fossi, M.C., Coppola, D., Baini, M., Giannetti, M., Guerranti, C., Marsili, L., Panti, C., de Sabata, E. & Clò, S. (2014) Large filter feeding marine organisms as indicators of microplastic in the pelagic environment: The case studies of the Mediterranean basking shark (*Cetorhinus maximus*) and fin whale (*Balaenoptera physalus*). *Marine Environmental Research*, **100**, 17–24.
- Fowler, S.L. (2005) *Basking Shark (Cetorhinus Maximus)*. *The IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 17th September 2015.
- Francis, M.P. & Duffy, C. (2002) Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. *Marine Biology*, **140**, 831–842.
- Franklin, J. (2010) Mapping species distributions. Spatial inference and prediction. *Ecology, biodiversity and conservation*, **53**, 340.
- Gattuso, J.-P., Magnan, A., Bille, R., Cheung, W.W.L., Howes, E.L., Joos, F., Allemand, D., Bopp, L., Cooley, S.R., Eakin, C.M., Hoegh-Guldberg, O., Kelly, R.P., Portner, H.-O., Rogers, a. D., Baxter, J.M., Laffoley, D., Osborn, D., Rankovic, A., Rochette, J., Sumaila, U.R., Treyer, S. & Turley, C. (2015) Contrasting futures for ocean and society from different anthropogenic CO² emissions scenarios. *Science*, **349**, 45–55.
- Geelhoed, S.C.V., Janinhoff, N. & Verdaat, J.P. (2016) First visual record of a living basking shark *Cetorhinus maximus* in the Caribbean Sea. *Caribbean Journal of Science*, **49**, 76–78.

- Gerritsen, H.D. & Lordan, C. (2014) *Atlas of Commercial Fisheries Around Ireland*.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. (2007) LoCoH: Nonparameteric Kernel methods for constructing home ranges and utilization distributions. *PLoS ONE*, **2**, e207.
- Gitzen, R.A., Millspaugh, J.J. & Kernohan, B.J. (2006) Bandwidth Selection for Fixed-Kernel Analysis of Animal Utilization Distributions. *Journal of Wildlife Management*, **70**, 1334–1344.
- Gleiss, A.C., Norman, B. & Wilson, R.P. (2011) Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Functional Ecology*, **25**, 595–607.
- Goldbogen, J.A., Hazen, E.L., Friedlaender, A.S., Calambokidis, J., Deruiter, S.L., Stimpert, A.K. & Southall, B.L. (2015) Prey density and distribution drive the three-dimensional foraging strategies of the largest filter feeder. *Functional Ecology*, 1–11.
- Gonzalez-Carman, V., Mandiola, A., Alemany, D., Dassis, M., Pon, J.P.S., Prosdocimi, L., Ponce de Leon, A., Mianzan, H., Acha, E.M., Rodriguez, D., Favero, M. & Copello, S. (2016) Distribution of megafaunal species in the Southwestern Atlantic: key ecological areas and opportunities for marine conservation. *ICES Journal of Marine Science*, doi: 10.1093/icesjms/fsw019.
- Gore, M.A., Frey, P.H., Ormond, R.F., Allan, H. & Gilkes, G. (2016) Use of Photo-Identification and Mark-Recapture Methodology to Assess Basking Shark (*Cetorhinus maximus*) Populations. *Plos One*, **11**, e0150160.
- Gore, M.A., Rowat, D., Hall, J., Gell, F.R. & Ormond, R.F. (2008) Transatlantic migration and deep mid-ocean diving by basking shark. *Biology Letters*, **4**, 395–8.
- Graham, R.T., Roberts, C.M. & Smart, J.C.R. (2006) Diving behaviour of whale sharks in relation to a predictable food pulse. *Journal of the Royal Society, Interface*, **3**, 109–16.

- Graham, F., Rynne, P., Estevanez, M., Luo, J., Ault, J.S. & Hammerschlag, N. (2016) Use of marine protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean by large highly mobile sharks. *Diversity and Distributions*, **22**, 534–546.
- Grist, J.P., Josey, S.A., Boehme, L., Meredith, M.P., Davidson, F.J.M., Stenson, G.B. & Hammill, M.O. (2011) Temperature signature of high latitude Atlantic boundary currents revealed by marine mammal-borne sensor and Argo data. *Geophysical Research Letters*, **38**, 4–9.
- Grüss, A., Kaplan, D.M., Guénette, S., Roberts, C.M. & Botsford, L.W. (2011) Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation*, **144**, 692–702.
- Gschweng, M., Kalko, E.K. V., Berthold, P., Fiedler, W. & Fahr, J. (2012) Multi-temporal distribution modelling with satellite tracking data: predicting responses of a long-distance migrant to changing environmental conditions. *Journal of Applied Ecology*, **49**, 803–813.
- Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. & Perrins, C. (2011) A dispersive migration in the atlantic Puffin and its implications for migratory navigation. *PLoS ONE*, **6**, e21336.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., Mcdonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P. & Buckley, Y.M. (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, **16**, 1424–1435.

- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Guttridge, T.L., Gulak, S.J.B., Franks, B.R., Carlson, J.K., Gruber, S.H., Gledhill, K.S., Bond, M.E., Johnson, G. & Grubbs, R.D. (2015) Occurrence and habitat use of the critically endangered smalltooth sawfish *Pristis pectinata* in the Bahamas. *Journal of Fish Biology*, **87**, 1322–1341.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, K. V, Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.
- Halpern, B.S. & Warner, R.R. (2002) Marine reserves have rapid and lasting effects. *Ecology Letters*, **5**, 361–366.
- Hammerschlag, N., Gallagher, A.J. & Lazarre, D.M. (2011) A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology*, **398**, 1–8.
- Hart, K.M. & Hyrenbach, K.D. (2009) Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endangered Species Research*, **10**, 9–20.
- Hartigan, J.A. & Wong, M.A. (1979) Algorithm AS 136: A k-means clustering algorithm. *Applied Statistics*, **28**, 100–108.
- Harvey-Clark, C.J., Stobo, W.T., Helle, E. & Mattson, M. (1999) Putative Mating Behavior in Basking Sharks off the Nova Scotia Coast. *Copeia*, **3**, 780–782.

- Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H., Bailleul, F., Bowen, W.D., Caley, M.J., Costa, D.P., Eguíluz, V.M., Fossette, S., Friedlaender, A.S., Gales, N., Gleiss, A.C., Gunn, J., Harcourt, R., Hazen, E.L., Heithaus, M.R., Heupel, M., Holland, K., Horning, M., Jonsen, I., Kooyman, G.L., Lowe, C.G., Madsen, P.T., Marsh, H., Phillips, R.A., Righton, D., Ropert-Coudert, Y., Sato, K., Shaffer, S.A., Simpfendorfer, C.A., Sims, D.W., Skomal, G., Takahashi, A., Trathan, P.N., Wikelski, M., Womble, J.N. & Thums, M. (2016) Key Questions in Marine Megafauna Movement Ecology. *Trends in Ecology & Evolution*, **31**, 463–475.
- Hazen, E., Maxwell, S., Bailey, H., Bograd, S., Hamann, M., Gaspar, P., Godley, B. & Shillinger, G. (2012) Ontogeny in marine tagging and tracking science: technologies and data gaps. *Marine Ecology Progress Series*, **457**, 221–240.
- Hein, A.M., Hou, C. & Gillooly, J.F. (2012) Energetic and biomechanical constraints on animal migration distance. *Ecology Letters*, **15**, 104–110.
- Hetherington, S., Townhill, B., Borrow, K., Bendall, V. & Hunter, E. (2015) *Shark By-Watch UK 2. Research Priorities: Innovative Solutions for Reducing by-Catch & Dead Discards of Threatened Sharks, Skates & Rays*. Shark By-Watch UK.
- Heupel, M.R. & Simpfendorfer, C.A. (2005) Using acoustic monitoring to evaluate MPAs for shark nursery areas: The importance of long-term data. *Marine Technology Society Journal*, **39**, 10–18.
- Heupel, M.R., Simpfendorfer, C.A., Espinoza, M., Smoothey, A.F., Tobin, A. & Peddemors, V. (2015) Conservation challenges of sharks with continental scale migrations. *Frontiers in Marine Science*, **2:12**, doi: 10.3389/fmars.2015.00012.
- Hijmans, R.J. (2016) raster: Geographic Data Analysis and Modelling. R package version 2.5-8. <https://CRAN.R-project.org/package=raster>.

- Hill, R.D. & Braun, M.J. (2001) Geolocation by light level - the next step: latitude. *Electronic Tagging and Tracking in Marine Fisheries* (ed J.R. Sibert), pp. 315–330. Kluwer Academic Publishers.
- Hoelzel, A.R., Shivji, M.S., Magnussen, J. & Francis, M.P. (2006) Low worldwide genetic diversity in the basking shark (*Cetorhinus maximus*). *Biology letters*, **2**, 639–42.
- Hoffmann, M., Hilton-taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., Darwall, W.R.T., Dulvy, N.K., Harrison, L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F., Vié, J., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F., Andrew, P., Aquino Ortiz, A.L., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P., Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar-G, W., Burfield, I.J., Burton, J.A., Capper, D.R., Castro, F., Catullo, G., Cavanagh, R.D., Channing, A., Chao, N.L., Chenery, A.M., Chiozza, F., Clausnitzer, V., Collar, N.J., Collett, L.C., Collette, B.B., Cortez Fernandez, C.F., Craig, M.T., Crosby, M.J., Cumberlidge, N., Cuttelod, A., Derocher, A.E., Diesmos, A.C., Donaldson, J.S., Duckworth, J.W., Dutson, G., Dutta, S.K., Emslie, R.H., Farjon, A., Fowler, S., Freyhof, J.J., Garshelis, D.L., Gerlach, J., Gower, D.J., Grant, T.D., Hammerson, G.A., Harris, R.B., Heaney, L.R., Hedges, S.B., Hero, J.-M., Hughes, B., Hussain, S.A., Javier Icochea, M., Inger, R.F., Ishii, N., Iskandar, D.T., Jenkins, R.K.B., Kaneko, Y., Kottelat, M., Kovacs, K.M., Kuzmin, S.L., La Marca, E., Lamoreux, J.F., Lau, M.W.N., Lavilla, E.O., Leus, K., Lewison, R.L., Lichtenstein, G., Livingstone, S.R., Lukoschek, V., Mallon, D.P., McGowan, P.J.K., McIvor, A., Moehlman, P.D., Molur, S., Muñoz Alonso, A., Musick, J.A., Nowell, K., Nussbaum, R.A., Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro, B.A., Pourkazemi, M., Racey, P.A., Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin, A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., Sadovy de Mitcheson, Y., Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan, C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D.L., Smith, K.G., Smith, A.T., Snoeks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J., Timmins, R., Tobias, J.A., Tsytsulina, K.,

- Tweddle, D., Ubeda, C., Valenti, S. V., van Dijk, P.P., Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E.A., Xie, F., Young, B.E., Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., da Fonseca, G.A.B., Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S.A., McNeely, J.A., Mittermeier, R.A., Reid, G.M., Rodriguez, J.P., Rosenberg, A.A., Samways, M.J., Smart, J., Stein, B.A. & Stuart, S.N. (2010) The Impact of Conservation on the Status of the World 's Vertebrates. *Science*, **330**, 1503–1509.
- Holland, K.N., Brill, R.W., Randolph, K., Chang, R.K., Sibert, J.R. & Fournier, D.A. (1992) Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature*, **358**, 410–412.
- Hooker, S.K., Biuw, M., McConnell, B.J., Miller, P.J.O. & Sparling, C.E. (2007) Bio-logging science: Logging and relaying physical and biological data using animal-attached tags. *Deep-Sea Research Part II: Topical Studies in Oceanography*, **54**, 177–182.
- Hooker, S.K. & Gerber, L.R. (2004) Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna. *BioScience*, **54**, 27.
- Howe, J.A., Dove, D., Bradwell, T. & Gafeira, J. (2012) Submarine geomorphology and glacial history of the Sea of the Hebrides, UK. *Marine Geology*, **315–318**, 64–76.
- Howey-Jordan, L.A., Brooks, E.J., Abercrombie, D.L., Jordan, L.K.B., Brooks, A., Williams, S., Gospodarczyk, E. & Chapman, D.D. (2013) Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the western North Atlantic. *PloS one*, **8**, e56588.
- Humphries, N.E., Queiroz, N., Dyer, J.R.M., Pade, N.G., Musyl, M.K., Schaefer, K.M., Fuller, D.W., Brunnschweiler, J.M., Doyle, T.K., Houghton, J.D.R., Hays, G.C., Jones, C.S., Noble, L.R., Wearmouth, V.J., Southall, E.J. & Sims, D.W. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature*, **465**, 1066–9.

- Hussey, N.E., Kessel, S., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Mills Flemming, J.E. & Whoriskey, F.G. (2015) Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, **348**, 1221–1231.
- Hutchinson, G.E. (1959) Concluding remarks. *Cold Spring Harbor Symposium Quantitative Biology*, **22**, 415–427.
- Irvine, L.M., Mate, B.R., Winsor, M.H., Palacios, D.M., Bograd, S.J., Costa, D.P. & Bailey, H. (2014) Spatial and temporal occurrence of blue whales off the U.S. West Coast, with implications for management. *PLoS ONE*, **9**.
- Jackson, J.B.C. (2010) The future of the oceans past. *Philosophical transactions of the Royal Society of London B*, **365**, 3765–78.
- Jacoby, D.M.P., Siriwat, P., Freeman, R. & Carbone, C. (2015) Is the scaling of swim speed in sharks driven by metabolism? *Biology letters*, **11**, 20150781.
- Jeffers, V.F. & Godley, B.J. (2016) Satellite tracking in sea turtles: How do we find our way to the conservation dividends? *Biological Conservation*, **199**, 172–184.
- Jewell, O.J.D., Wcisel, M.A., Gennari, E., Towner, A. V., Bester, M.N., Johnson, R.L. & Singh, S. (2011) Effects of smart position only (SPOT) tag deployment on white sharks *Carcharodon carcharias* in South Africa. *PLoS ONE*, **6**, 4–7.
- Jones, T.T., Van Houtan, K.S., Bostrom, B.L., Ostafichuk, P., Mikkelsen, J., Tezcan, E., Carey, M., Imlach, B. & Seminoff, J.A. (2013) Calculating the ecological impacts of animal-borne instruments on aquatic organisms. *Methods in Ecology and Evolution*, **4**, 1178–1186.
- Jones, P.J.S. & De Santo, E.M. (2016) Viewpoint - Is the race for remote, very large marine protected areas (VLMPAs) taking us down the wrong track? *Marine Policy*, **73**, 231–234.

- Jorgensen, S.J., Klimley, P.A. & Muhlia-Melo, A.F. (2009) Scalloped hammerhead shark *Sphyrna lewini*, utilizes deep-water, hypoxic zone in the Gulf of California. *Journal of Fish Biology*, **74**, 1682–1687.
- Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S., Perle, C., Van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, P.A. & Block, B.A. (2010) Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society B*, **277**, 679–88.
- Kelly, C., Glegg, G.A. & Speedie, C.D. (2004) Management of marine wildlife disturbance. *Ocean and Coastal Management*, **47**, 1–19.
- Ketchum, J.T., Galván-Magaña, F. & Klimley, A.P. (2013) Segregation and foraging ecology of whale sharks, *Rhincodon typus*, in the southwestern Gulf of California. *Environmental Biology of Fishes*, **96**, 779–795.
- Klimley, P.A. (1987) The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes*, **18**, 27–40.
- Klimley, P.A., Beavers, S.C., Curtis, T.H. & Jorgensen, S.J. (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*, **63**, 117–135.
- Knip, D.M., Heupel, M.R. & Simpfendorfer, C.A. (2012a) To roam or to home: site fidelity in a tropical coastal shark. *Marine Biology*, **159**, 1647–1657.
- Knip, D.M., Heupel, M.R. & Simpfendorfer, C.A. (2012b) Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biological Conservation*, **148**, 200–209.
- Knip, D.M., Heupel, M.R., Simpfendorfer, C.A., Tobin, A.J. & Moloney, J. (2011) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. *Marine Ecology Progress Series*, **425**, 233–246.

- Kock, A., O’Riain, M.J., Mauff, K., Meÿer, M., Kotze, D. & Griffiths, C. (2013) Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PloS one*, **8**, e55048.
- Kokko, H. (2011) Directions in modelling partial migration: How adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos*, **120**, 1826–1837.
- Kokko, H. & Lopez-Sepulcre, A. (2006) From individual dispersal to species ranges: Perspectives for a changing world. *Science*, **313**, 789–791.
- Kunzlik, P.A. (1988) The Basking Shark. *Department of Agriculture and Fisheries for Scotland, Aberdeen, UK*, **14**, 1–21.
- Lam, C.H., Nielsen, A. & Sibert, J.R. (2008) Improving light and temperature based geolocation by unscented Kalman filtering. *Fisheries Research*, **91**, 15–25.
- Lauck, T., Clark, C.W., Mangel, M. & Munro, G.R. (1998) Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications*, **8**, 72–78.
- Lea, J.S.E., Wetherbee, B.M., Queiroz, N., Burnie, N., Aming, C., Sousa, L.L., Mucientes, G.R., Humphries, N.E., Harvey, G.M., Sims, D.W. & Shivji, M.S. (2015) Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Scientific Reports*, **5**, 11202.
- Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W. & Hahn, S. (2012) Geolocation by light: Accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, **3**, 603–612.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C. & Bay, M. (2006) Depletion, Degradation and Recovery Potential of Estuaries and Coastal Seas. *Science*, **312**, 1806–1809.

- Lowther, A.D., Harcourt, R.G., Page, B. & Goldsworthy, S.D. (2013) Steady as He Goes: At-Sea Movement of Adult Male Australian Sea Lions in a Dynamic Marine Environment. *PLoS ONE*, **8**.
- Lucifora, L.O., Barbini, S.A., Di Giacomo, E.E., Waessle, J.A. & Figueroa, D.E. (2015) Estimating the geographic range of a threatened shark in a data-poor region: *Cetorhinus maximus* in the South Atlantic Ocean. *Current Zoology*, **61**, 811–826.
- Lydersen, C., Nøst, O.A., Lovell, P., Mcconnell, B.J., Gammelsrød, T., Hunter, C., Fedak, M.A. & Kovacs, K.M. (2002) Salinity and temperature structure of a freezing Arctic fjord—monitored by white whales (*Delphinapterus leucas*). *Geophysical Research Letters*, **29**, 2119.
- Lyons, A.J., Turner, W.C. & Getz, W.M. (2013) Home Range Plus: A Space-Time Characterization of Movement Over Real Landscapes. *Movement Ecology*, **1–2**, 1–14.
- Macleod, C.D. (2014) *An Introduction to Using GIS in Marine Biology. Supplementary Workbook Four. Investigating Home Ranges of Individual Animals*. Pictish Beast Publications, Glasgow, UK.
- Matthews, L.H. (1962) The Shark That Hibernates. *New Scientist*, **280**, 756–759.
- Matthews, L.H. & Parker, H.W. (1950) Notes on the anatomy and biology of the Basking Shark (*Cetorhinus maximus* (Gunner)). *Proceedings of the Zoological Society of London*, **120**, 535–576.
- McNeill, S. (1994) The selection and design of marine protected areas : Australia as a case study. *Biodiversity and Conservation*, **3**, 586–605.
- Meyer, C.G., Holland, K.N. & Papastamatiou, Y.P. (2007) Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of Marine Protected Areas. *Marine Ecology Progress Series*, **333**, 13–25.

- Meyer, C.G., Papastamatiou, Y.P. & Holland, K.N. (2010) A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Marine Biology*, **157**, 1857–1868.
- Miller, P.I., Scales, K.L., Ingram, S.N., Southall, E.J. & Sims, D.W. (2015) Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic. *Functional Ecology*, **29**, 1099–1109.
- Milner-Gulland, E.J., Fryell, J.M. & Sinclair, A.R.E. (2011) *Animal Migration: A Synthesis*. Oxford University Press, New York.
- Mucientes, G.R., Queiroz, N., Sousa, L.L., Tarroso, P. & Sims, D.W. (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology letters*, **5**, 156–159.
- Myklevoll, S. (1946) Basking shark fishery. *Commercial Fisheries Review*, **30**, 59–63.
- Nakamura, I., Goto, Y. & Sato, K. (2015) Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. *Journal of Animal Ecology*, **84**, 590–603.
- Nakamura, I., Watanabe, Y.Y., Papastamatiou, Y.P., Sato, K. & Meyer, C.G. (2011) Yo-yo vertical movements suggest a foraging strategy for tiger sharks *Galeocerdo cuvier*. *Marine Ecology Progress Series*, **424**, 237–246.
- Nakaya, K., Matsumoto, R. & Suda, K. (2008) Feeding strategy of the megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae). *Journal of Fish Biology*, **73**, 17–34.
- Neilson, J.D., Loefer, J., Prince, E.D., Royer, F., Calmettes, B., Gaspar, P., Lopez, R. & Andrushchenko, I. (2014) Seasonal distributions and migrations of northwest atlantic Swordfish: Inferences from integration of Pop-Up satellite archival tagging studies. *PLoS ONE*, **9**, e112736.

- Nelms, S.E., Duncan, E.M., Broderick, A.C., Galloway, T.S., Godfrey, M.H., Hamann, M., Lindeque, P.K. & Godley, B.J. (2016) Plastic and marine turtles: a review and a call for research. *ICES Journal of Marine Science*, **73**, 165–181.
- Nelson, D.R., McKibben, J.N., Strong Jr, W.R., Lowe, C.G., Sisneros, J.A., Schroeder, D.M. & Lavenberg, R.J. (1997) An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes*, **49**, 389–399.
- New, L.F., Clark, J.S., Costa, D.P., Fleishman, E., Hindell, M.A., Klanjscek, T., Lusseau, D., Kraus, S., McMahon, C.R., Robinson, P.W., Schick, R.S., Schwarz, L.K., Simmons, S.E., Thomas, L., Tyack, P. & Harwood, J. (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Marine Ecology Progress Series*, **496**, 99–108.
- Noble, L.R., Jones, C.S., Sarginson, J., Metcalfe, J.D., Sims, D.W. & Pawson, M.G. (2006) *Conservation Genetics of Basking Sharks. Final Report for Defra Tender CR 0288*.
- O'Brien, K. & Whitehead, H. (2013) Population analysis of Endangered northern bottlenose whales on the Scotian Shelf seven years after the establishment of a Marine Protected Area. *Endangered Species Research*, **21**, 273–284.
- O'Connor, P.F. (1953) *Shark-O!* Secker & Warburg, London.
- Papastamatiou, Y.P., Meyer, C.G., Carvalho, F., Dale, J.J., Hutchinson, M.R. & Holland, K.N. (2013) Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology*, **94**, 2595–2606.
- Parker, H.W. & Boseman, M. (1954) The Basking Shark, *Cetorhinus maximus*, in winter. *Proceedings of the Zoological Society, London*, **124**, 185–194.
- Parker, H. & Stott, F. (1965) Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). *Zoologische mededelingen*, **40**, 305–320.

- Paxton, C.G.M., Scott-Hayward, L.A.S. & Rexstad, E. (2014a) Review of available statistical approaches to help identify Marine Protected Areas for cetaceans and basking shark. *Scottish Natural Heritage Commissioned Report No. 573*.
- Paxton, C.G.M., Scott-Hayward, L.A.S. & Rexstad, E. (2014b) SNH Commissioned Report 594: Statistical approaches to aid the identification of Marine Protected Areas for minke whale, Risso's dolphin, white-beaked dolphin and basking shark. , 1–133.
- Peterson, A.T. (2001) Predicting Species' Geographic Distributions Based on Ecological Niche Modeling. *The Condor*, **103**, 599–605.
- Pikesley, S.K., Broderick, A.C., Cejudo, D., Coyne, M.S., Godfrey, M.H., Godley, B.J., Lopez, P., López-Jurado, L.F., Elsy Merino, S., Varo-Cruz, N., Witt, M.J. & Hawkes, L.A. (2015) Modelling the niche for a marine vertebrate: A case study incorporating behavioural plasticity, proximate threats and climate change. *Ecography*, **38**, 803–812.
- Pratt, H.L. & Carrier, J.C. (2001) A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes*, **60**, 157–188.
- Provan, J., Beatty, G.E., Keating, S.L., Maggs, C.A. & Savidge, G. (2009) High dispersal potential has maintained long-term population stability in the North Atlantic copepod *Calanus finmarchicus*. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 301–307.
- R Core Team. (2014) R: A language and environment for statistical computing. (R Foundation for Statistical Computing.
- Del Raye, G., Jorgensen, S.J., Krumhansl, K., Ezcurra, J.M. & Block, B.A. (2013) Travelling light: white sharks (*Carcharodon carcharias*) rely on body lipid stores to power ocean-basin scale migration. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20130836.

- Righton, D.A., Andersen, K.H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., Michalsen, K., Hinrichsen, H.H., Bendall, V., Neuenfeldt, S., Wright, P., Jonsson, P., Huse, G., Van Der Kooij, J., Mosegaard, H., Hüsey, K. & Metcalfe, J. (2010) Thermal niche of Atlantic cod *Gadus morhua*: Limits, tolerance and optima. *Marine Ecology Progress Series*, **420**, 1–13.
- Roberts, C.M. (2000) Selecting Marine Reserve Locations: Optimally versus Opportunism. *Bulletin of Marine Science*, **66**, 581–592.
- Roberts, J.J., Best, B.D., Dunn, D.C., Treml, E.A. & Halpin, P.N. (2010) Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. *Environmental Modelling and Software*, **25**, 1197–1207.
- Robinson, R.A., Crick, H.Q.P., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F., Forchhammer, M.C., Francis, C.M., Gill, J.A., Godley, B.J., Harwood, J., Hays, G.C., Huntley, B., Hutson, A.M., Pierce, G.J., Rehfish, M.M., Sims, D.W., Begona Santos, M., Sparks, T.H., Stroud, D.A. & Visser, M.E. (2008) Travelling through a warming world: Climate change and migratory species. *Endangered Species Research*, **7**, 87–99.
- Roquet, F., Wunsch, C., Forget, G., Heimbach, P., Guinet, C., Reverdin, G., Charrassin, J.B., Bailleul, F., Costa, D.P., Huckstadt, L.A., Goetz, K.T., Kovacs, K.M., Lydersen, C., Biuw, M., Nøst, O.A., Bornemann, H., Ploetz, J., Bester, M.N., McIntyre, T., Muelbert, M.C., Hindell, M.A., McMahon, C.R., Williams, G., Harcourt, R., Field, I.C., Chafik, L., Nicholls, K.W., Boehme, L. & Fedak, M.A. (2013) Estimates of the Southern Ocean general circulation improved by animal-borne instruments. *Geophysical Research Letters*, **40**, 6176–6180.
- Rosenbaum, H.C., Maxwell, S.M., Kershaw, F. & Mate, B. (2014) Long-range movement of humpback whales and their overlap with anthropogenic activity in the South Atlantic Ocean. *Conservation Biology*, **28**, 604–615.

- Rowat, D., Meekan, M.G., Engelhardt, U., Pardigon, B. & Vely, M. (2006) Aggregations of juvenile whale sharks (*Rhincodon typus*) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes*, **80**, 465–472.
- Scales, K.L., Hazen, E.L., Jacox, M.G., Edwards, C.A., Boustany, A.M., Oliver, M.J. & Bograd, S.J. (2016) Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. *Ecography*, **40**, 210–220.
- Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. & Votier, S.C. (2014) On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, **51**, 1575–1583.
- Scales, K.L., Miller, P.I., Ingram, S.N., Hazen, E.L., Bograd, S.J. & Phillips, R.A. (2015) Identifying predictable foraging habitats for a wide-ranging marine predator using ensemble ecological niche models. *Diversity and Distributions*, **22**, 212–224.
- Schlaff, A.M., Heupel, M.R. & Simpfendorfer, C.A. (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. *Reviews in Fish Biology and Fisheries*, **24**, 1089–1103.
- Schorr, G.S., Falcone, E.A., Moretti, D.J. & Andrews, R.D. (2014) First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS ONE*, **9**.
- Scott, R., Hodgson, D.J., Witt, M.J., Coyne, M.S., Adnyana, W., Blumenthal, J.M., Broderick, A.C., Canbolat, A.F., Catry, P., Ciccione, S., Delcroix, E., Hitipeuw, C., Luschi, P., Pet-Soede, L., Pendoley, K., Richardson, P.B., Rees, A.F. & Godley, B.J. (2012) Global analysis of satellite tracking data shows that adult green turtles are significantly aggregated in Marine Protected Areas. *Global Ecology and Biogeography*, **21**, 1053–1061.

- Scottish Natural Heritage. (2014) *Further Advice to Scottish Government on the Selection of Nature Conservation Marine Protected Areas for the Development of the Scottish MPA Network. Commissioned Report No. 780.*
- Sepulveda, C.A., Kohin, S., Chan, C., Vetter, R. & Graham, J.B. (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Marine Biology*, **145**, 191–199.
- Sequeira, A.M.M., Mellin, C., Fordham, D.A., Meekan, M.G. & Bradshaw, C.J.A. (2014) Predicting current and future global distributions of whale sharks. *Global Change Biology*, **20**, 778–789.
- Sequeira, A., Mellin, C., Rowat, D., Meekan, M.G. & Bradshaw, C.J.A. (2012) Ocean-scale prediction of whale shark distribution. *Diversity and Distributions*, **18**, 504–518.
- Shaltout, M. & Omstedt, A. (2014) Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. *Oceanologia*, **56**, 411–443.
- Shepard, E.L.C., Ahmed, M.Z., Southall, E.J., Witt, M.J., Metcalfe, J.D. & Sims, D.W. (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology Progress Series*, **328**, 205–213.
- Shimada, T., Jones, R., Limpus, C. & Hamann, M. (2012) Improving data retention and home range estimates by data-driven screening. *Marine Ecology Progress Series*, **457**, 171–180.
- Siders, Z.A., Westgate, A.J., Johnston, D.W., Murison, L.D. & Koopman, H.N. (2013) Seasonal Variation in the Spatial Distribution of Basking Sharks (*Cetorhinus maximus*) in the Lower Bay of Fundy, Canada. *PLoS ONE*, **8**, e82074.
- Sims, D.W. (1999) Threshold foraging behaviour of basking sharks on zooplankton : life on an energetic knife-edge? *Proceedings of the Royal Society B*, **266**, 1437–1443.

- Sims, D.W. (2003) Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free ranging sharks. *Journal of fish biology*, **63**, 53–73.
- Sims, D.W. (2008) Sieving a living: a review of the biology, ecology and conservation status of the plankton-feeding basking shark *Cetorhinus maximus*. *Advances in marine biology*, **54**, 171–220.
- Sims, D.W., Fox, A.M. & Merrett, D.A. (1997) Basking shark occurrence off south-west England in relation to zooplankton abundance. *Journal of Fish Biology*, **51**, 436–440.
- Sims, D.W. & Merrett, D.A. (1997) Determination of zooplankton characteristics in the presence of surface feeding basking sharks *Cetorhinus maximus*. *Marine Ecology Progress Series*, **158**, 297–302.
- Sims, D.W. & Quayle, V.A. (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature*, **393**, 460–464.
- Sims, D.W. & Reid, P.C. (2002) Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark *Cetorhinus maximus* fishery catches off west Ireland. *Fisheries Oceanography*, **11**, 59–63.
- Sims, D.W., Southall, E.J., Quayle, V.A. & Fox, A.M. (2000) Annual social behaviour of basking sharks associated with coastal front areas. *Proceedings of the Royal Society B*, **267**, 1897–1904.
- Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C. & Metcalfe, J.D. (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series*, **248**, 187–196.
- Sims, D.W., Southall, E.J., Tarling, G.A. & Metcalfe, J.D. (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology*, **74**, 755–761.

- Sims, D.W., Witt, M.J., Richardson, A.J., Southall, E.J. & Metcalfe, J.D. (2006) Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society B*, **273**, 1195–201.
- Singleton, R.L. & Roberts, C.M. (2014) The contribution of very large marine protected areas to marine conservation: Giant leaps or smoke and mirrors? *Marine Pollution Bulletin*, **87**, 7–10.
- Skomal, G.B., Hoyos-Padilla, E.M., Kukulya, A. & Stokey, R. (2015) Subsurface observations of white shark *Carcharodon carcharias* predatory behaviour using an autonomous underwater vehicle. *Journal of Fish Biology*, **87**, 1293–1312.
- Skomal, G.B., Wood, G. & Caloyianis, N. (2004) Archival tagging of a basking shark, *Cetorhinus maximus*, in the western North Atlantic. *Journal of the Marine Biological Association of the UK*, **84**, 795–799.
- Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K.W. & Thorrold, S.R. (2009) Transequatorial migrations by basking sharks in the western Atlantic Ocean. *Current Biology*, **19**, 1019–1022.
- Smith, S.E., Au, D.W. & Show, C. (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*, **49**, 663.
- Southall, E.J., Sims, D.W., Metcalfe, J.D., Doyle, J.I., Fanshawe, S., Lacey, C., Shrimpton, J., Solandt, J.-L. & Speedie, C.D. (2005) Spatial distribution patterns of basking sharks on the European shelf: preliminary comparison of satellite-tag geolocation, survey and public sightings data. *Journal of the Marine Biological Association of the UK*, **85**, 1083–1088.
- Southall, E.J., Sims, D.W., Witt, M.J. & Metcalfe, J.D. (2006) Seasonal space-use estimates of basking sharks in relation to protection and political–economic zones in the North-east Atlantic. *Biological Conservation*, **132**, 33–39.

- Speed, C.W., Field, I.C., Meekan, M.G. & Bradshaw, C.J.A. (2010) Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series*, **408**, 275–293.
- Speed, C.W., Meekan, M.W., Field, I.C., McMahon, C.R. & Bradshaw, C.J.A. (2012) Heat-seeking sharks: support for behavioural thermoregulation in reef sharks. *Marine Ecology Progress Series*, **463**, 231–244.
- Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Stevens, J.D., McGregor, F., Huveneers, C., Berger, Y. & Bradshaw, C.J.A. (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Marine Ecology Progress Series*, **429**, 261–275.
- Speedie, C.D., Johnson, L.A. & Witt, M.J. (2009) Basking Shark Hotspots on the West Coast of Scotland : Key sites, threats and implications for conservation. *Scottish Natural Heritage Commissioned Report No.339*.
- Sprogis, K.R., Raudino, H.C., Rankin, R., Macleod, C.D. & Bejder, L. (2016) Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. *Marine Mammal Science*, **32**, 287–308.
- Stéphan, E., Gadenne, H. & Jung, A. (2011) Sur les traces du requin pèlerin Satellite tracking of basking sharks in the North-East Atlantic Ocean. *Association Pour l'Etude et la Conservation des Sélaciens*.
- Stevens, J. (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, **57**, 476–494.
- Stott, F.C. (1982) A note on catches of basking sharks, *Cetorhinus maximus* (Gunnerus), off Norway and their relation to possible migration paths. *Journal of Fish Biology*, **21**, 227–230.

- Sydeman, W.J., Poloczanska, E., Reed, T.E. & Thompson, S.A. (2015) Climate Change and Marine Vertebrates. *Science*, **350**, 171–193.
- Taylor, M.D. & Ko, A. (2011) Monitoring acoustically tagged king prawns (*Penaeus (Melicertus) plebejus*) in an estuarine lagoon. *Marine Biology*, **158**, 835–844.
- Thorrold, S.R., Afonso, P., Fontes, J., Braun, C.D., Santos, R.S., Skomal, G.B. & Berumen, M.L. (2014) Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nature Communications*, **5:4274**, doi: 10.1038/ncomms5274.
- Thuiller, W., Georges, D., Engler, R. & Breiner, F. (2016) biomod2: Ensemble Platform for Species Distribution Modelling.
- Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD - A platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.
- Thums, M., Meekan, M., Stevens, J., Wilson, S. & Polovina, J. (2013) Evidence for behavioural thermoregulation by the world's largest fish. *Journal of The Royal Society Interface*, **10**, 2–6.
- Thygesen, U.H., Pedersen, M.W. & Madsen, H. (2009) Geolocating fish using hidden Markov models and data storage tags. *Tagging and Tracking of Marine Animals with Electronic Devices. Methods and technologies in fish biology and fisheries Edited by J.L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage and J. Sibert*, **8**, 23–34.
- Tyminski, J.P., de la Parra-Venegas, R., González Cano, J. & Hueter, R.E. (2015) Vertical Movements and Patterns in Diving Behavior of Whale Sharks as Revealed by Pop-Up Satellite Tags in the Eastern Gulf of Mexico. *Plos One*, **10**, e0142156.
- Valeiras, J., Lopez, A. & Garcia, M. (2001) Geographical, seasonal occurrence and incidental fishing captures of basking shark *Cetorhinus maximus* (Chondrichthyes : Cetorhinidae). *Journal of the Marine Biological Association of the U.K.*, **81**, 183–184.

- Vaudo, J.J., Wetherbee, B.M., Harvey, G., Nemeth, R.S., Aming, C., Burnie, N., Howey-Jordan, L.A. & Shivji, M.S. (2014) Intraspecific variation in vertical habitat use by tiger sharks (*Galeocerdo cuvier*) in the western North Atlantic. *Ecology and Evolution*, **4**, 1768–1786.
- Vaudo, J., Wetherbee, B., Wood, A., Weng, K., Howey-Jordan, L., Harvey, G. & Shivji, M. (2016) Vertical movements of shortfin mako sharks *Isurus oxyrinchus* in the western North Atlantic Ocean are strongly influenced by temperature. *Marine Ecology Progress Series*, **547**, 163–175.
- Watanabe, Y.K. & Takahashi, A. (2013) Linking animal-borne video to accelerometers reveals prey capture variability. *Proceedings of the National Academy of Sciences*, **110**, 2199–2204.
- Watson, R. & Pauly, D. (2001) Systematic distortions in world fisheries catch trends. *Nature*, **414**, 534–536.
- Wearmouth, V.J. & Sims, D.W. (2008) Sexual segregation in marine fish, reptiles, birds and mammals behaviour patterns, mechanisms and conservation implications. *Advances in marine biology*, **54**, 107–70.
- Wegner, N.C. & Cartamil, D.P. (2012) Effects of prolonged entanglement in discarded fishing gear with substantive biofouling on the health and behavior of an adult shortfin mako shark, *Isurus oxyrinchus*. *Marine Pollution Bulletin*, **64**, 391–394.
- Weng, K.C. (2005) Satellite Tagging and Cardiac Physiology Reveal Niche Expansion in Salmon Sharks. *Science*, **310**, 104–106.
- Weng, K.C., Foley, D.G., Ganong, J.E., Perle, C., Shillinger, G.L. & Block, B.A. (2008) Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Marine Ecology Progress Series*, **372**, 253–264.

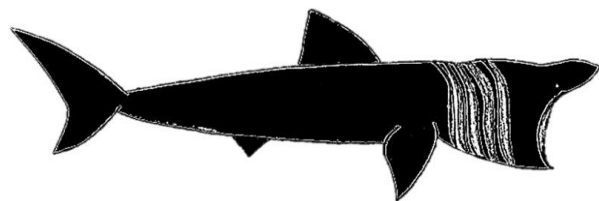
- Werry, J.M., Planes, S., Berumen, M.L., Lee, K.A., Braun, C.D. & Clua, E. (2014) Reef-Fidelity and Migration of Tiger Sharks, *Galeocerdo cuvier*, across the Coral Sea. *PLoS ONE*, **9**, e83249.
- Westgate, A.J., Koopman, H.N., Siders, Z.A., Wong, S.N.P. & Ronconi, R.A. (2014) Population density and abundance of basking sharks *Cetorhinus maximus* in the lower Bay of Fundy, Canada. *Endangered Species Research*, **23**, 177–185.
- White, T.D., Carlisle, A.B., Kroodsma, D.A., Block, B.A., Casagrandi, R., De Leo, G.A., Gatto, M., Micheli, F. & McCauley, D.J. (2017) Assessing the effectiveness of a large marine protected area for reef shark conservation. *Biological Conservation*, **207**, 64–71.
- Wilson, S.G. (2004) Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. *Fisheries Oceanography*, **13**, 283–286.
- Wilson, B. (2016) Might marine protected areas for mobile megafauna suit their proponents more than the animals? *Aquatic Conservation: Marine and Freshwater Ecosystems*, **26**, 3–8.
- Wilson, R.P., Ducamp, J.J., Rees, W.G., Culik, B.M. & Niekamp, K. (1992) Estimation of location: global coverage using light intensity. *Wildlife telemetry: remote monitoring and tracking of animals*, 131–134.
- Wilson, S.G., Polovina, J.J., Stewart, B.S. & Meekan, M.G. (2006) Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology*, **148**, 1157–1166.
- Witt, M.J., Åkesson, S., Broderick, A.C., Coyne, M.S., Ellick, J., Formia, A., Hays, G.C., Luschi, P., Stroud, S. & Godley, B.J. (2010) Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. *Animal Behaviour*, **80**, 571–581.

- Witt, M.J., Augowet Bonguno, E., Broderick, A.C., Coyne, M.S., Formia, A., Gibudi, A., Mounquengui Mounquengui, G.A., Moussounda, C., NSafou, M., Nougessono, S., Parnell, R.J., Sounguet, G.-P., Verhage, S. & Godley, B.J. (2011) Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic. *Proceedings of the Royal Society B*, **278**, 2338–2347.
- Witt, M.J., Broderick, A.C., Coyne, M.S., Formia, A., Nguouessono, S., Parnell, R.J., Sounguet, G.-P. & Godley, B.J. (2008) Satellite tracking highlights difficulties in the design of effective protected areas for Critically Endangered leatherback turtles *Dermochelys coriacea* during the inter-nesting period. *Oryx*, **42**, 296–300.
- Witt, M.J., Doherty, P.D., Godley, B.J., Graham, R.T., Hawkes, L.A. & Henderson, S.M. (2016) Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement, distribution and behaviour using satellite telemetry. Final Report. *Scottish Natural Heritage Commissioned Report No. 908*.
- Witt, M.J., Hardy, T., Johnson, L., McClellan, C.M., Pikesley, S.K., Ranger, S., Richardson, P.B., Solandt, J.-L., Speedie, C., Williams, R. & Godley, B.J. (2012) Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters. *Marine Ecology Progress Series*, **459**, 121–134.
- Womble, J.N., Blundell, G.M., Gende, S.M., Horning, M., Sigler, M.F. & Csepp, D.J. (2014) Linking marine predator diving behavior to local prey fields in contrasting habitats in a subarctic glacial fjord. *Marine Biology*, **161**, 1361–1374.
- Wood, L.J., Fish, L., Laughren, J. & Pauly, D. (2008) Assessing progress towards global marine protection targets: shortfalls in information and action. *Oryx*, **42**, 340–351.
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R. & Zeller, D. (2009) Rebuilding global fisheries. *Science*, **325**, 578–585.

- Worm, B., Lotze, H.K. & Myers, R.A. (2003) Predator diversity hotspots in the blue ocean. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 9884–9888.
- Zydelis, R., Lewison, R.L., Shaffer, S.A., Moore, J.E., Boustany, A.M., Roberts, J.J., Sims, M., Dunn, D.C., Best, B.D., Tremblay, Y., Kappes, M.A., Halpin, P.N., Costa, D.P. & Crowder, L.B. (2011) Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proceedings of the Royal Society B*, **278**, 3191–3200.

Appendices





Appendix A

Table A1. National and international regulations and protection measures for basking sharks.

Regulation	Year	Region
Wildlife & Countryside Act	1981	UK
Manx Wildlife Act	1990	Isle of Man
Biodiversity Action Plan (BAP) priority species	1997	UK
Countryside Rights of Way Act	2000	UK
CITES (Appendix II)	2003	Global
CMS (Appendix I & II)	2005	Global
European Common Fisheries Policy (EU CFP)	2007	Europe
OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic: OSPAR List of Threatened and/or Declining Species and Habitats	2008	Europe
Marine & Coastal Access Act	2009	UK
Marine (Scotland) Act	2010	Scotland
Marine Act (Northern Ireland)	2013	Northern Ireland

Table A2. Deployment information. Summary table of tags deployed between 2012 and 2014 transmitting near real-time locations (n = 36). In 2012 and 2013 tags transmitted Argos locations from basking shark tagged with SPOT and SPLASH-F tags. In 2014, SPALSH-F tags transmitted GPS locations. Ordered by deployment year, tag type and tag number. Max. displacement, Max. distance and Time spent in MPA refer to the 90-day post tag attachment (summertime) period.

	Model	Ptt	Deployment date	End	Sex	Body length (m)	Location	Summer duration (d)	Total duration (d)	Max. displacement (km)	Max. distance (km)	Time spent in MPA (%)	
2012	SPOT	119854	13/07/2012	31/05/2013	U	4 to 5	SW Tiree	52	322	32	376	100	
		119855	13/07/2012	02/08/2012	U	6 to 7	SW Tiree	20	20	26	168	100	
		119856	13/07/2012	16/10/2012	M	5 to 6	SW Tiree	47	96	105	495	31	
		120496	13/07/2012	22/10/2012	F	5 to 6	Gunna Sound	44	100	37	386	97	
		120497	14/07/2012	03/08/2012	F	4 to 5	Gunna Sound	20	20	36	171	100	
		120498	14/07/2012	26/11/2012	F	5 to 6	Gunna Sound	31	135	143	491	20	
		120499	14/07/2012	20/12/2012	M	7 to 8	Hyskeir	57	156	57	397	100	
		120500	17/07/2012	05/08/2012	M	6 to 7	Hyskeir	19	19	70	177	94	
		2013	SPLASH	129431	21/07/2013	17/09/2013	F	7 to 8	SW Tiree	30	57	57	335
129432	22/07/2013			05/09/2013	U	5 to 6	Skerryvore	35	45	64	552	94	
129433	28/07/2013			11/09/2013	M	7 to 8	SW Tiree	30	45	96	295	91	
129434	28/07/2013			11/09/2013	U	5 to 6	SW Tiree	45	45	86	447	100	
SPOT	129435			06/08/2013	18/09/2013	F	5 to 6	Gunna Sound	43	43	119	579	78
	129436			06/08/2013	09/12/2015	U	5 to 6	Gunna Sound	50	83	49	395	92
	129437			06/08/2013	16/08/2014	U	5 to 6	Gunna Sound	27	375	39	312	96
	129438			06/08/2013	30/09/2013	M	5 to 6	Gunna Sound	38	55	37	365	100
	129439			06/08/2013	17/08/2014	U	6 to 7	Gunna Sound	13	376	42	146	100
	129440		18/07/2013	05/09/2014	F	4 to 5	SW Tiree	59	414	53	712	91	
	129441		18/07/2013	30/03/2014	M	5 to 6	SW Tiree	63	254	127	1410	46	
	129443		21/07/2013	17/10/2013	F	6 to 7	Skerryvore	73	87	94	619	100	
	129444		21/07/2013	30/06/2014	U	7 to 8	SW Tiree	49	343	57	533	88	
129445	21/07/2013		10/05/2014	U	7 to 8	SW Tiree	21	292	23	138	100		
129446	29/07/2013		26/09/2013	U	5 to 6	SW Tiree	58	58	74	486	84		
129447	29/07/2013		08/09/2013	U	4 to 5	SW Tiree	41	41	30	202	95		
129448	29/07/2013		29/07/2014	U	5 to 6	SW Tiree	55	365	61	286	100		
129449	29/07/2013		31/07/2014	U	5 to 6	SW Tiree	43	367	126	533	95		
129450	29/07/2013	28/03/2014	F	5 to 6	SW Tiree	42	242	113	656	61			
2014	SPLASH	137645	24/07/2014	08/10/2014	U	7 to 8	Hawk's Bank	75	75	46	277	100	
		137646	24/07/2014	01/08/2014	M	6 to 7	Hawk's Bank	10	10	74	111	100	
		137648	25/07/2014	27/09/2014	F	6 to 7	West Coll	64	64	159	336	55	
		137649	28/07/2014	11/12/2014	U	6 to 7	Cairns of Coll	67	136	162	340	72	
		137650	28/07/2014	17/11/2014	F	7 to 8	Cairns of Coll	87	112	156	259	25	
		137651	28/07/2014	02/04/2015	F	5 to 6	Cairns of Coll	24	248	164	172	75	
		137652	29/07/2014	21/11/2014	U	6 to 7	East Coll	41	115	62	199	92	
		137653	29/07/2014	14/09/2014	M	7 to 8	East Coll	47	47	159	587	46	
		137654	29/07/2014	14/04/2015	U	7 to 8	East Coll	78	259	44	283	100	

Table A3. Summary table of sharks exhibiting inter-annual site fidelity.

Ptt	Max. displaced (km)	No. locations 2013	No. locations 2014	MCP area 2013 (km²)	MCP area 2014 (km²)	Distance between centroids (km)
129439	565	13	4	591.12	2536.93	28.56
129440	304	54	51	2870.95	10188.91	138.28
129449	1474	38	5	7147.66	217.29	23.99

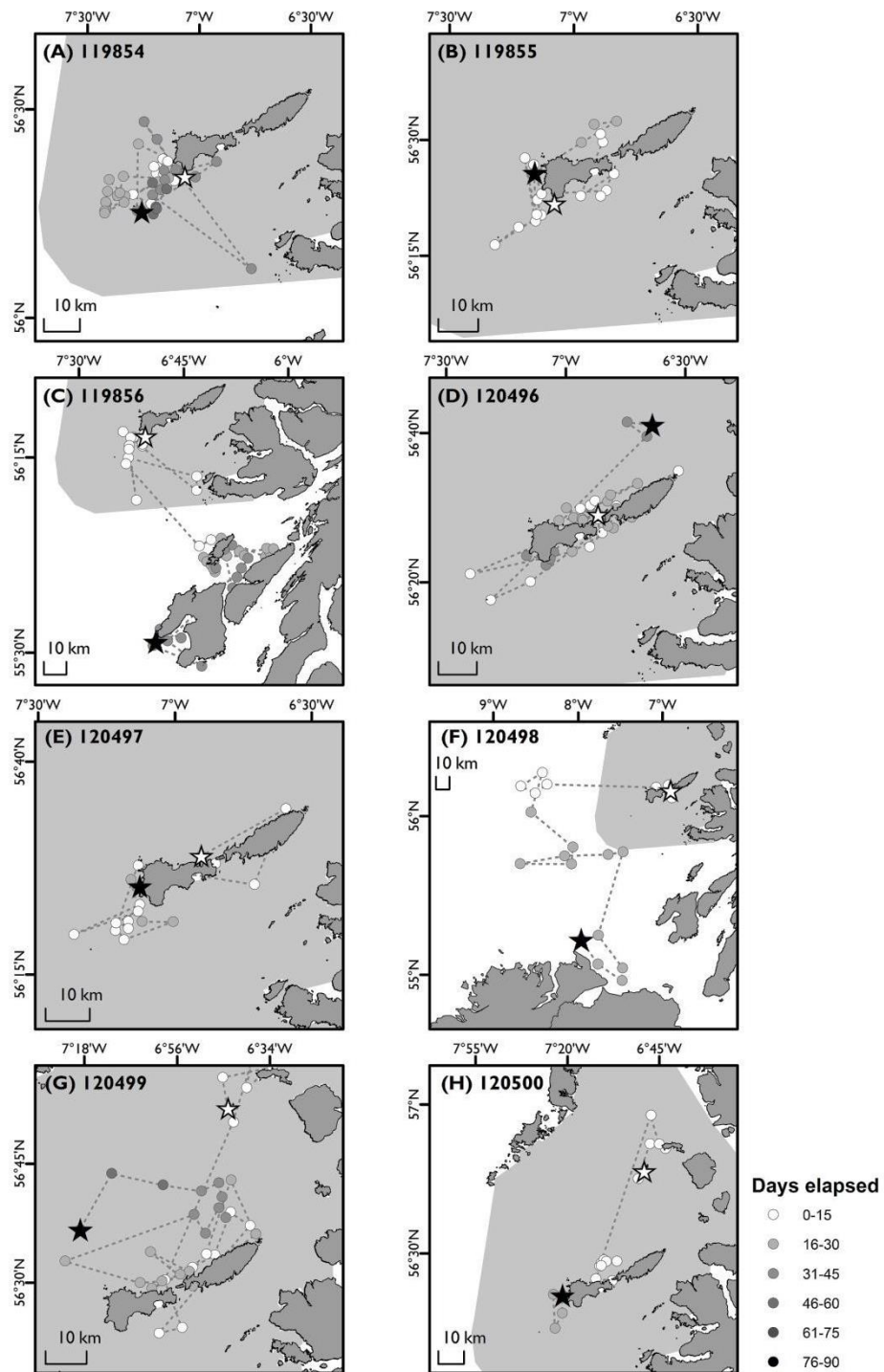


Figure A1. Individual movements of basking sharks exhibiting behaviour tagged in 2012. Satellite tracked data from basking sharks for summer months. Each circle represents best daily location, coloured by days elapsed. Dashed lines join consecutive locations but do not infer straight line movement. Shark tag ID. White stars denote tag deployment location, black stars denote track end point. Proposed MPA area (light grey polygon).

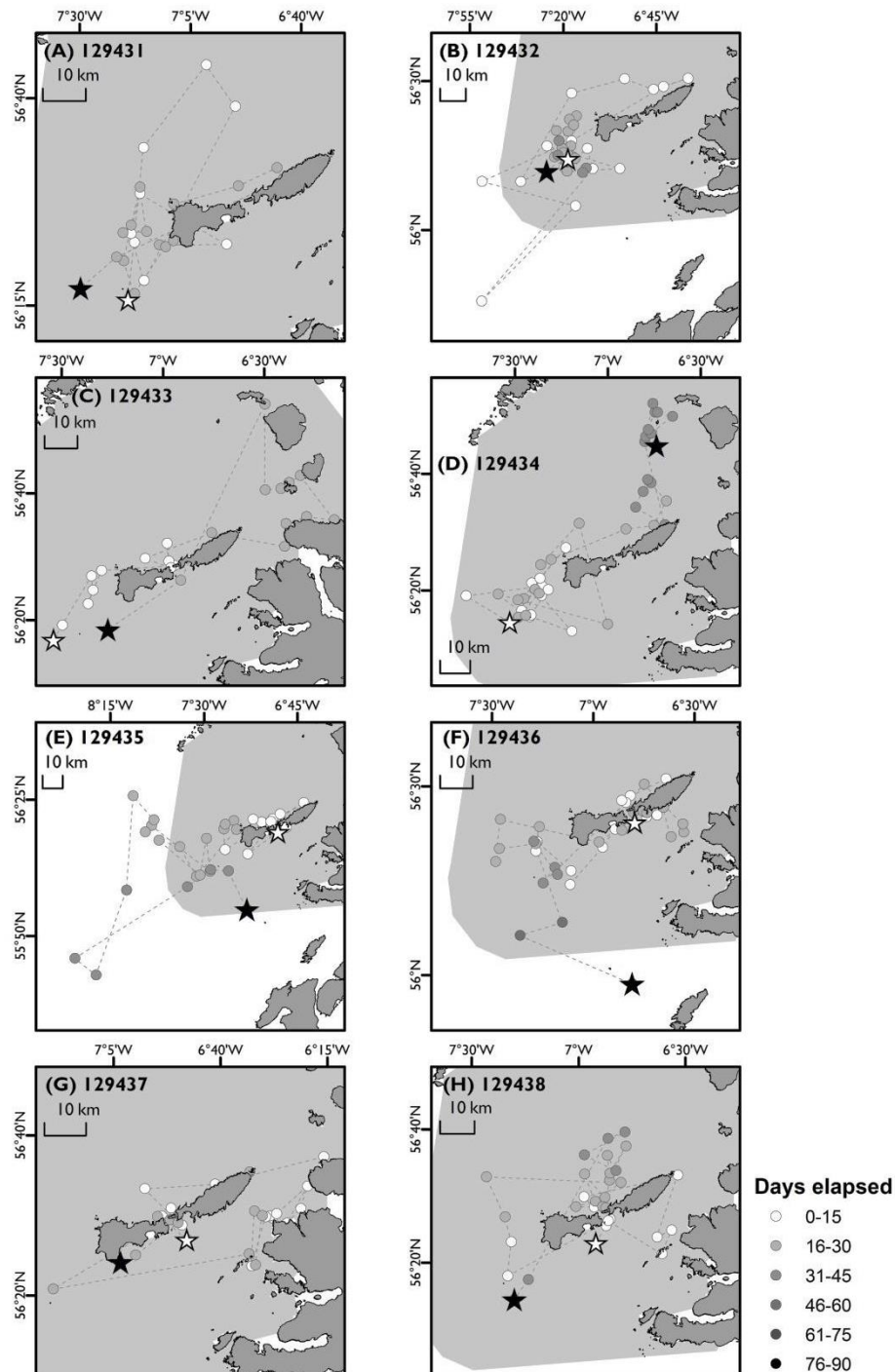


Figure A2. Individual movements of basking sharks exhibiting behaviour tagged in 2013.

Satellite tracked data from basking sharks for summer months. Each circle represents best daily location, coloured by days elapsed. Dashed lines join consecutive locations but do not infer straight line movement. Shark tag ID. White stars denote tag deployment location, black stars denote track end point. Proposed MPA area (light grey polygon).

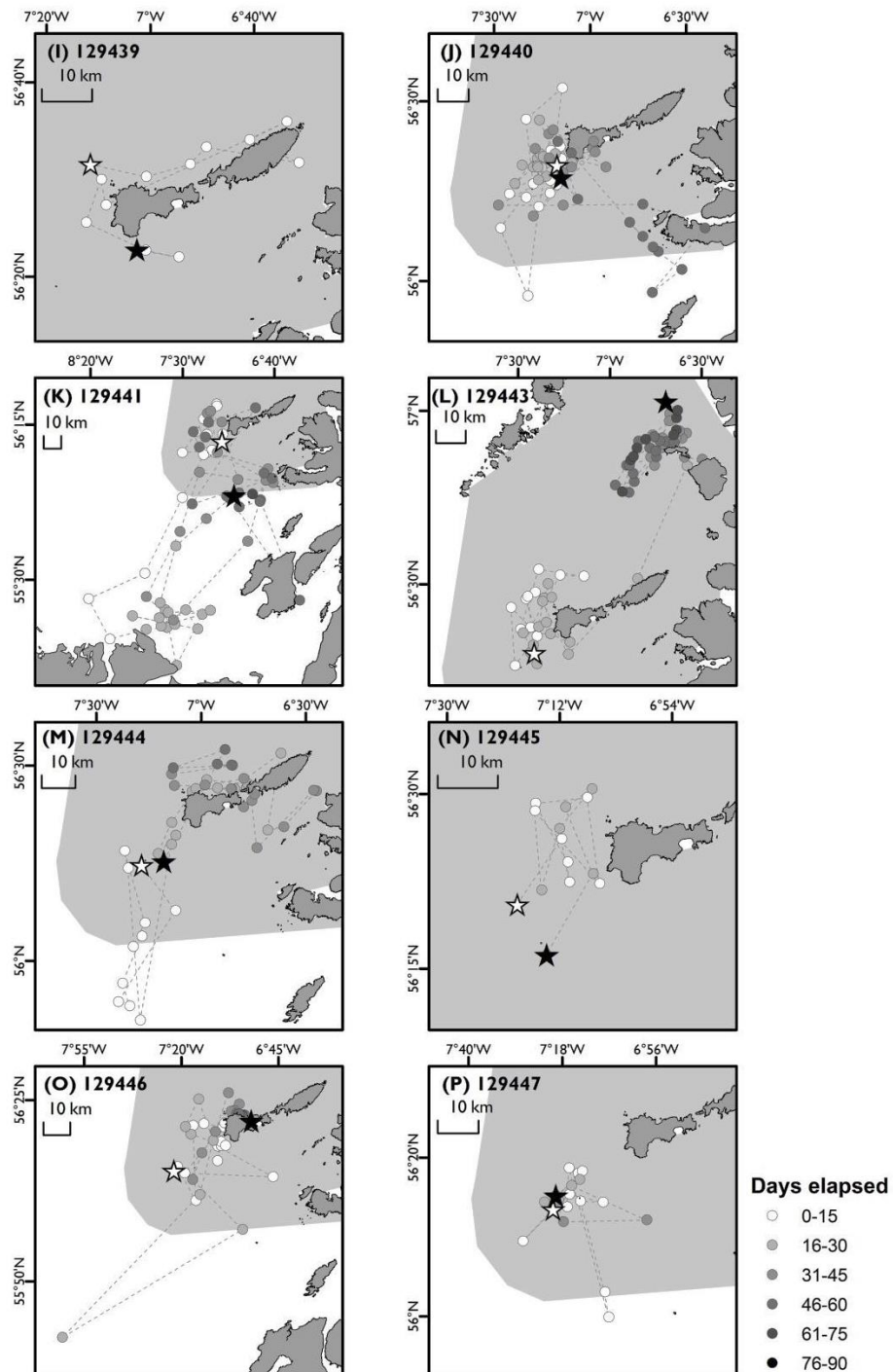


Figure A2. Individual movements of basking sharks exhibiting behaviour tagged in 2013
cont.

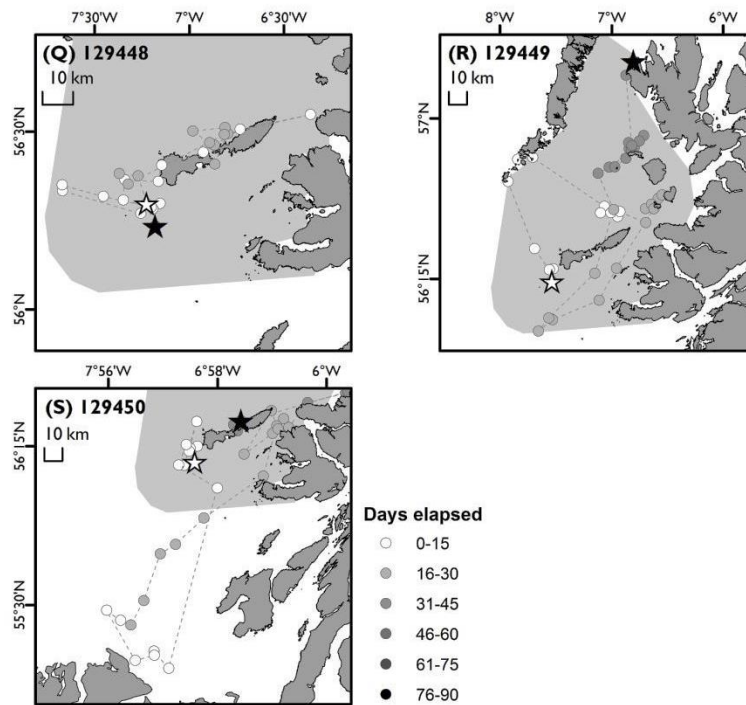


Figure A2. Individual movements of basking sharks exhibiting behaviour tagged in 2013 cont.

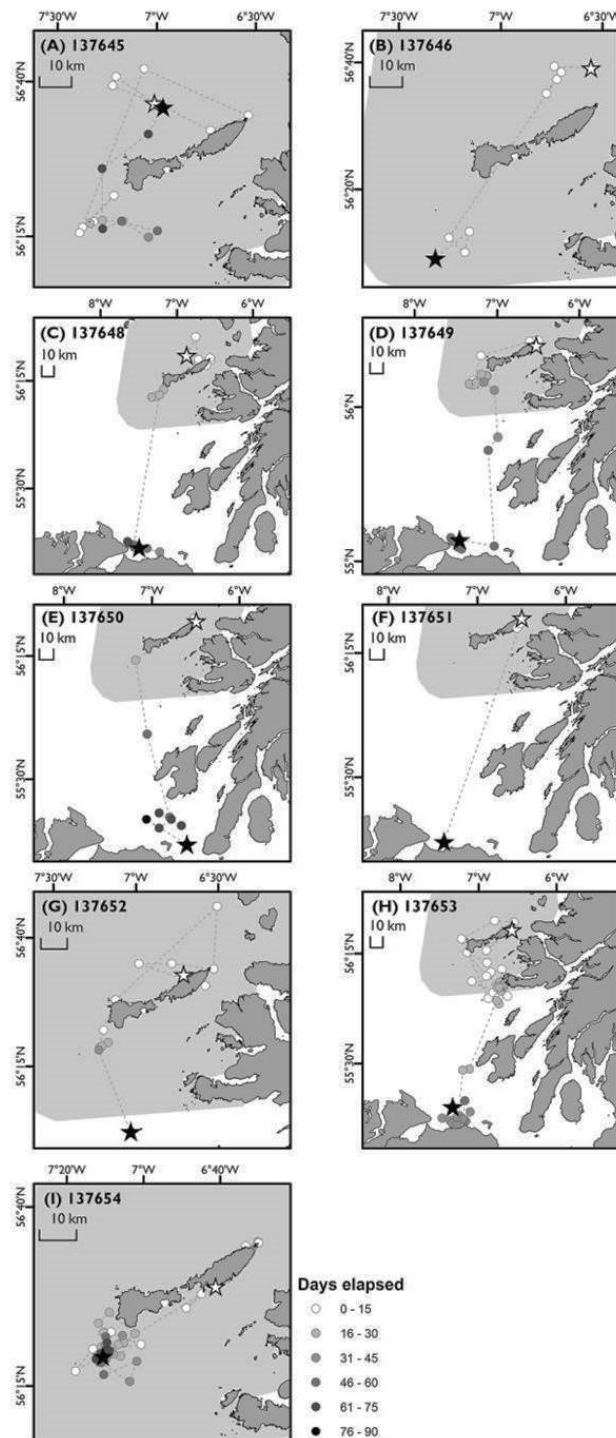


Figure A3. Individual movements of basking sharks exhibiting behaviour tagged in 2014.

Satellite tracked data from basking sharks for summer months. Each circle represents best daily location, coloured by days elapsed. Dashed lines join consecutive locations but do not infer straight line movement. Shark tag ID. White stars denote tag deployment location, black stars denote track end point. Proposed MPA area (light grey polygon).

Appendix B

Supplementary methods

The attachment of satellite transmitters in Scottish coastal waters protocol was approved by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (issuing Project Licence 30/2975). All work was carried out in accordance with the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971) and internally through the University of Exeter's animal welfare and ethics review board (AWERB). Licences to tag sharks in the Isle of Man were issued by the Department of Environment, Food and Agriculture (Isle of Man Government) under the Wildlife Act 1990. Sharks were approached with a boat from behind to avoid the shark's line of sight and to minimise disturbance. On approach to the sharks, the individuals were, where possible, sexed (female (n = 8), male (n = 8), and unknown (n = 12) using a pole mounted camera and total body length estimated (4-5 m (n = 6), 5-6 m (n = 12), 6-7 m (n = 5), 7-8 m (n = 4) and 8-9 m (n = 1) based on comparison to the length of the survey boat (10 m). Tags were deployed using a titanium M-style dart (Wildlife Computers) inserted into the sub-dermal layer at the base of the first dorsal fin with a modified pole spear and attached via a tether consisting of heat-shrink covered stainless steel flexible cable, a swivel and monofilament line attached to the satellite tag.

Four models of satellite tags were deployed; Smart Position or Temperature tags (SPOT; n = 32), transmitting location data when at the surface via the ARGOS satellite system. Pop-up Archival Transmitting with Fastloc™ GPS tags (PAT-F; n = 12), Mini Pop-up Archival Transmitting tags (MiniPAT; n = 12) and SPLASH-F archival tags (n = 14). All archival tags collected light, temperature and depth data at 10 second (PAT-F) or 15 second (MiniPAT & SPLASH-F) intervals. Throughout the project, satellite tags were attached to a total of 24 females, 19 males and 27 individuals of unknown sex, measuring 4-5m (n = 10), 5-6m (n = 30), 6-7m (n = 14), 7-8m (n = 13) and 8-9m (n = 3) estimated total length. Tags were programmed to record summarised percentage depth use across 12 depth ranges; 0-1m,

1-5m, 5-10m, 10-25m, 25-50m, 50-75m, 75-100m, 100-250m, 250-500m, 500-750m, 750-1000m and >1000m with this information created every four hours. Satellite transmitted archival maximum daily depths were used to estimate location within the water column during wide-ranging movements.

Location data from SPOT tags were subject to filtering, leaving only location classes 1 (accurate to 500-1500m), 2 (accurate to 250-500m), 3 (accurate to <250m), 'A' (three messages received but no accuracy estimation) and 'B' (one or two messages received but no accuracy estimation). A maximum plausible speed filter was applied removing locations if speed between two locations exceeded 10 km h^{-1} . These data were later reduced to a single, most accurate best daily location to minimise spatial and temporal autocorrelation.

Satellite tracking end points were determined by a pre-determined tag detachment date or earlier due to tag attachment failure or other unknown factors leading to detachment of tags. When an Argos Doppler derived location tag detaches from the study animal, it will float on the surface generating many high quality locations over several days. These data are unusual for tags attached to wild animals, as it does not reflect their natural behaviour, and as such provides a useful indicator that the tag has detached.

Table B1. Legislation. National and international regulations and protection measures for basking sharks.

Regulation	Year	Region
Wildlife & Countryside Act	1981	UK
Manx Wildlife Act	1990	Isle of Man
Biodiversity Action Plan (BAP) priority species	1997	UK
Countryside Rights of Way Act	2000	UK
CITES (Appendix II)	2003	Global
CMS (Appendix I & II)	2005	Global
European Common Fisheries Policy (EU CFP)	2007	Europe
OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic: OSPAR List of Threatened and/or Declining Species and Habitats	2008	Europe
Marine & Coastal Access Act	2009	UK
Marine (Scotland) Act	2010	Scotland
Marine Act (Northern Ireland)	2013	Northern Ireland

Table B2. Deployment information. Summary table of tags remaining attached for longer than 165 days, displaying ‘over-wintering’ behaviour used in this study (n = 28), plus one SPOT tracked sharks included for demonstration of behaviours at different time-scales. Ordered by deployment year and tag attachment duration.

Year	Ptt	Model	Deployment date	Sex	Body length (m)	Location	Duration (d)	Max. displacement (km)	Mean latitude error (km)	Light-curve locs (%)	Modelled locs (%)	Max. depth (m)	Prop. <200m
2012	¹ 120498	SPOT	14/07/2012	F	5 to 6	Gunna Sound	135	3088	-	-	-	-	-
	119846	PAT-F	30/07/2012	F	6 to 7	SW Tiree	170	455	95.46	33.33	66.67	248	1
	119845	PAT-F	20/07/2012	M	4 to 5	Hyskeir	204	854	59.94	61.46	38.54	1000	0.86
	119853	PAT-F	26/07/2012	M	6 to 7	SW Tiree	280	1211	58.83	35.82	64.18	1072	0.93
	119854	SPOT	13/07/2012	U	4 to 5	SW Tiree	322	2035	-	-	-	-	-
2013	129459	MiniPAT	31/07/2013	U	4 to 5	Skerryvore	165	823	107.67	12.88	87.12	375	0.81
	129457	MiniPAT	22/07/2013	U	7 to 8	Skerryvore	196	787	194.25	11.70	88.30	232	0.91
	129450	SPOT	29/07/2013	F	5 to 6	SW Tiree	242	571	-	-	-	-	-
	129441	SPOT	18/07/2013	M	5 to 6	SW Tiree	254	1127	-	-	-	-	-
	129454	MiniPAT	22/07/2013	F	5 to 6	Skerryvore	259	1244	77.7	32.76	67.24	1500	0.7
	129452	MiniPAT	31/07/2013	F	5 to 6	Skerryvore	280	1515	88.8	10.10	89.90	1192	0.8
	129455	MiniPAT	22/07/2013	F	5 to 6	Skerryvore	280	1161	79.92	18.32	81.68	1280	0.85
	129458	MiniPAT	31/07/2013	U	4 to 5	Skerryvore	280	2354	118.77	3.90	96.10	875	0.59
	129456	MiniPAT	22/07/2013	F	5 to 6	Skerryvore	281	1207	98.79	32.98	67.02	1500	0.84
	129442	MiniPAT	31/07/2013	U	4 to 5	Skerryvore	292	615	116.55	18.09	81.91	375	0.89
	129445	SPOT	21/07/2013	U	7 to 8	SW Tiree	292	988	-	-	-	-	-
	129182	SPOT	13/08/2013	M	6 to 7	Isle of Man	301	390	-	-	-	-	-
	129444	SPOT	21/07/2013	U	7 to 8	SW Tiree	343	1819	-	-	-	-	-
	129448	SPOT	29/07/2013	U	5 to 6	SW Tiree	365	1355	-	-	-	-	-
	129449	SPOT	29/07/2013	U	5 to 6	SW Tiree	367	1474	-	-	-	-	-
	129437	SPOT	06/08/2013	U	5 to 6	Gunna Sound	375	1210	-	-	-	-	-
	129439	SPOT	06/08/2013	U	6 to 7	Gunna Sound	376	565	-	-	-	-	-
	129183	SPOT	22/06/2013	M	5 to 6	Isle of Man	397	314	-	-	-	-	-
	129440	SPOT	18/07/2013	F	4 to 5	SW Tiree	414	304	-	-	-	-	-
	129185	SPOT	22/06/2013	M	6 to 7	Isle of Man	479	264	-	-	-	-	-
2014	137651	SPLASH	28/07/2014	F	5 to 6	Cairns of Coll	248	2711	-	-	-	-	-
	137654	SPLASH	29/07/2014	U	7 to 8	East Coll	259	533	76.59	55.38	44.62	1232	0.89
2015	138609	SPOT	07/08/2015	M	5 to 6	Isle of Man	241	327	-	-	-	-	-
	138610	SPOT	07/08/2015	M	8 to 9	Isle of Man	247	2385	-	-	-	-	-

*Does not meet tracking duration requirements for analysis, included for behaviour demonstrative purposes. Sex: M = male, F = female & U = unknown.

Table B3. Use of geo-political marine zones in the north-east Atlantic. Proportions of density values from daily distribution utilisation distributions within each sovereign state's marine boundaries. Table ordered by EEZ from most to least densely occupied zone.

EEZ	Prop	%
Ireland	0.51	50.65
UK	0.18	18.10
High seas	0.18	17.58
Spain	0.04	4.26
Portugal	0.04	3.57
France	0.03	3.41
Faeroe Islands	0.02	1.96
Morocco	<0.01	0.23
Iceland	<0.01	0.13
Madeira	<0.01	0.10

Table B4. K-means cluster analysis criteria.

Year	Ptt	Min. Latitude	Migration strategy
2012	119846	52.98	A
	119845	49.45	A
	119853	45.56	B
2013	129459	51.85	A
	129457	49.38	A
	129454	45.41	B
	129452	43.14	B
	129455	46.13	B
	129458	35.35	C
	129456	46.41	B
	129442	51.84	A
2014	137654	52.70	A

Table B5. Depth-use of satellite tracked basking sharks for post-summer (October onwards) movements. Proportions of locations received within specific depth classes. Separated by assigned migration strategy.

<i>(a) Celtic Seas</i>		
Depth class	No. Days	Prop.
0-25	34	0.04
26-50	57	0.07
51-100	293	0.34
101-200	411	0.47
201-500	58	0.07
501-750	5	0.01
751-1000	11	0.01
>1000	4	0
Total	873	
<i>(b) Bay of Biscay</i>		
Depth class	No. Days	Prop.
0-25	8	0.01
26-50	34	0.03
51-100	379	0.38
101-200	394	0.4
201-500	78	0.08
501-750	47	0.05
751-1000	36	0.04
>1000	12	0.01
Total	988	
<i>(c) Iberian Peninsula & North Africa</i>		
Depth class	No. Days	Prop.
0-25	4	0.06
26-50	5	0.07
51-100	6	0.08
101-200	27	0.38
201-500	20	0.28
501-750	7	0.10
751-1000	2	0.03
>1000	0	0.00
Total	71	

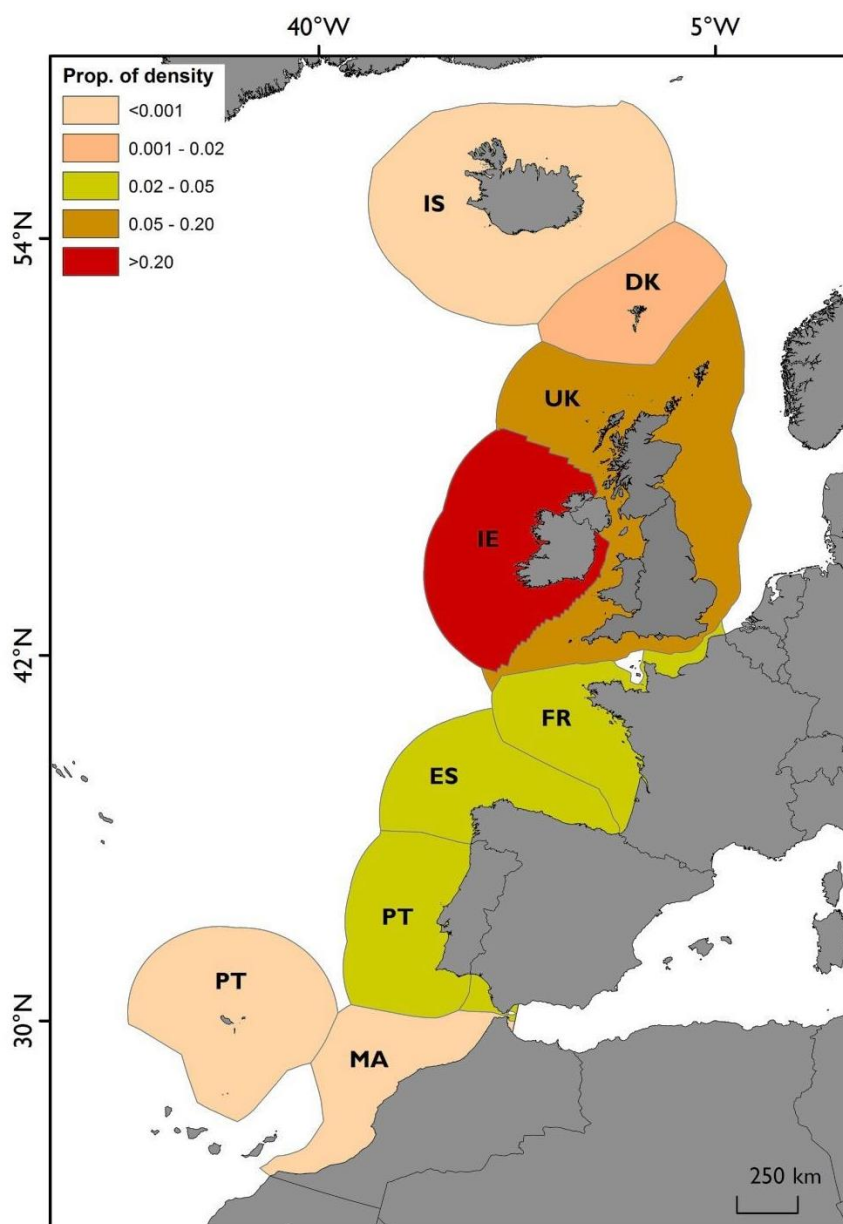


Figure B1. Geo-political zone use by tracked basking sharks. The north-east Atlantic split into Economic Exclusive Zones (EEZs) for each country in which tracking locations were received for satellite tracked basking sharks. Each EEZ coloured according to proportion of occupancy within its boundaries. EEZs labelled with international two letter initials for sovereign state of each region (IS=Iceland, DK=Denmark, UK=United Kingdom, IE=Ireland, FR=France, ES=Spain, PT=Portugal and MA=Morocco). Map created in ESRI ArcGIS version 10.1 ([Http://desktop.arcgis.com/en/arcmap](http://desktop.arcgis.com/en/arcmap)) using Esri land shapefiles and Flanders Marine Institute (VLIZ) Economic Exclusive Zone (EEZ) boundaries (<http://www.marineregions.org>).

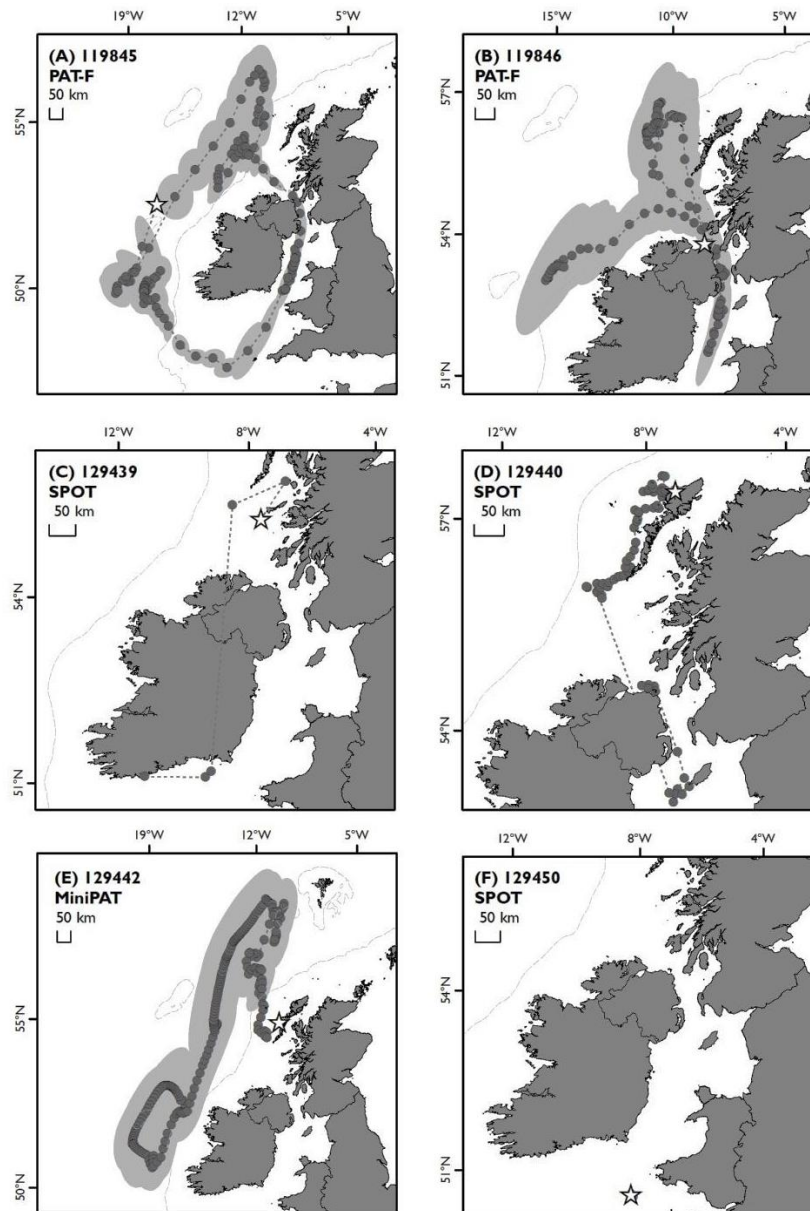


Figure B2. Individual movements of basking sharks exhibiting migration strategy A (*Celtic Seas*). Satellite tracked data from basking sharks for post-summer (October onwards) movements. Each circle represents best daily location, with associated error from light geolocation displayed as grey ellipses. Shark tag ID and tag model type displayed. Note figure parts are to differing scales. Broken grey line denotes 200 m bathymetric contour. White stars denote track end point for Argos Doppler-based geolocation tags or pop-off locations for light geolocation tags. Maps created in ESRI ArcGIS version 10.1 (<http://desktop.arcgis.com/en/arcmap>) using ESRI land shapefiles and GEBCO bathymetric contours (<http://www.gebco.net>).

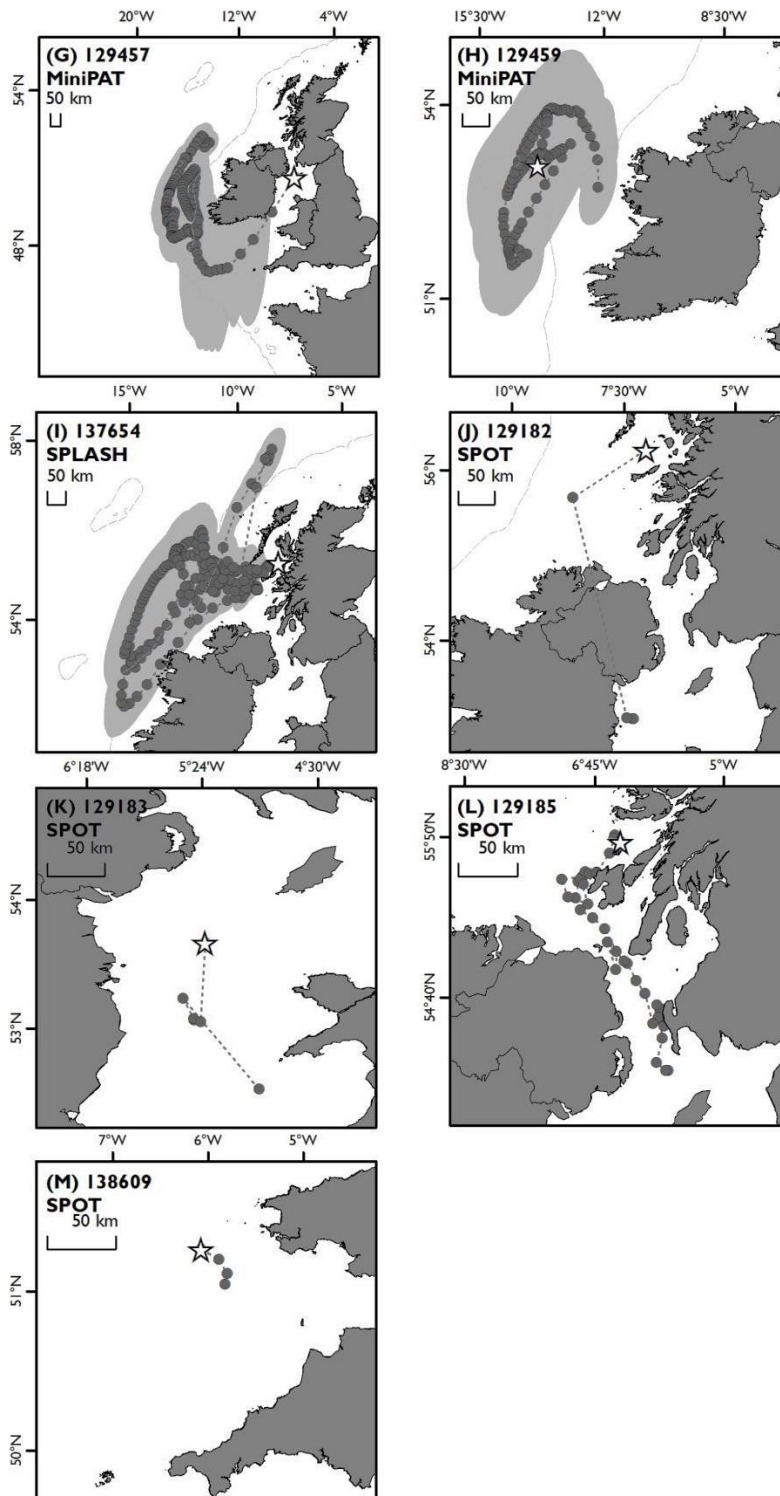


Figure B2. Individual movements of basking sharks exhibiting migration strategy A (Celtic Seas) cont.

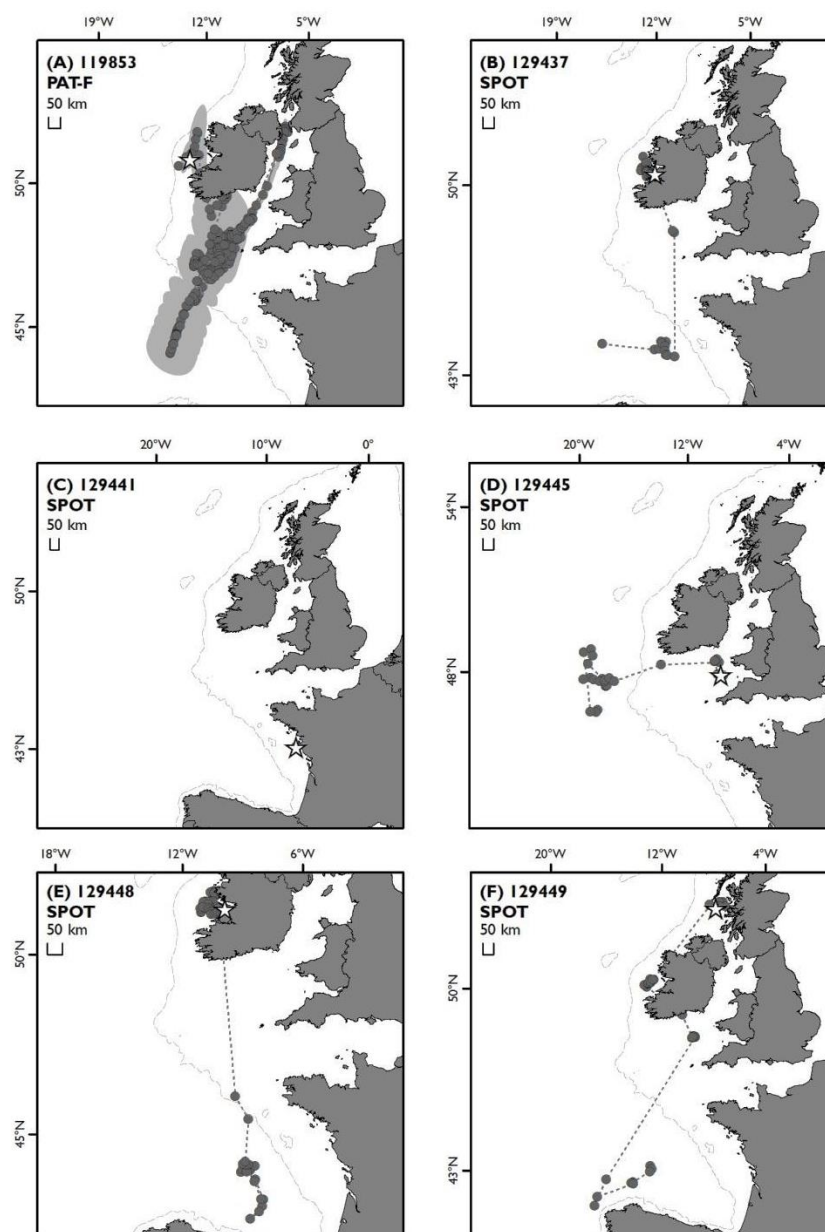


Figure B3. Individual movements of basking sharks exhibiting migration strategy B (*Bay of Biscay*). Satellite tracked data from basking sharks for post-summer (October onwards) movements. Each circle represents best daily location, with associated error from light geolocation displayed as grey ellipses. Shark tag ID and tag model type displayed. Note figure parts are to differing scales. Broken grey line denotes 200 m bathymetric contour. White stars denote track end point for Argos Doppler-based geolocation tags or pop-off locations for light geolocation tags. Maps created in ESRI ArcGIS version 10.1 (<http://desktop.arcgis.com/en/arcmap>) using ESRI land shapefiles and GEBCO bathymetric contours (<http://www.gebco.net>).

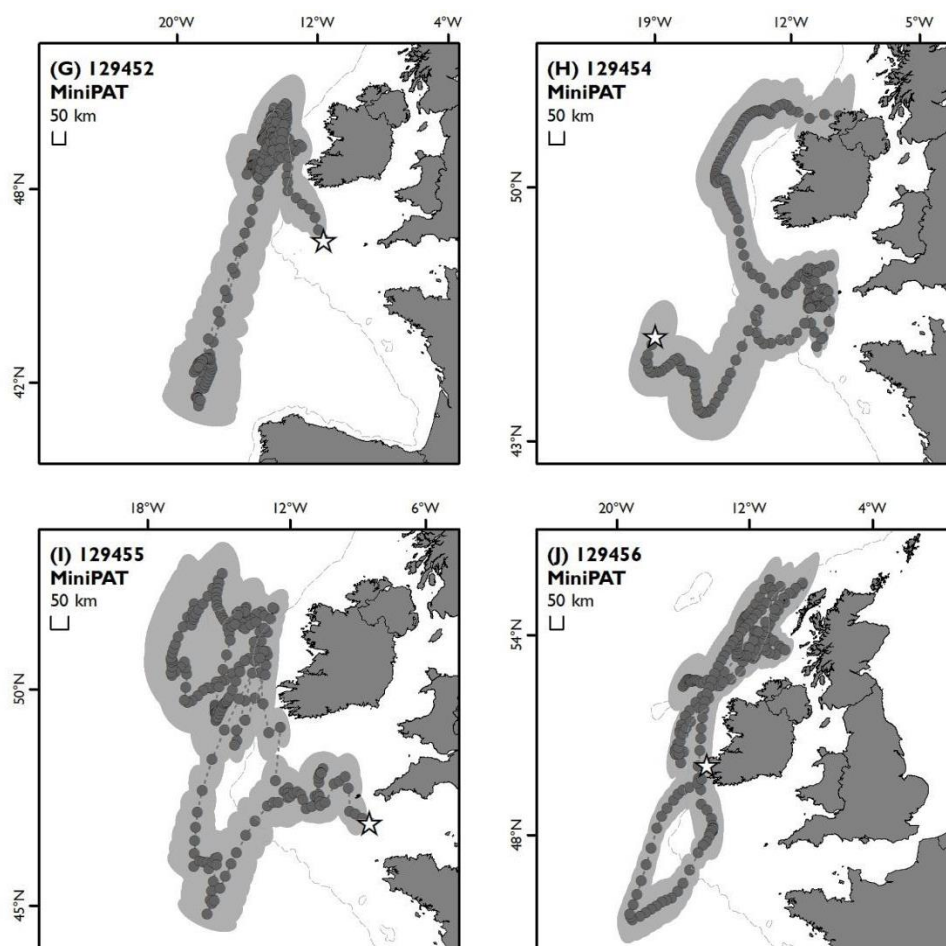


Figure B3. Individual movements of basking sharks exhibiting migration strategy B (Bay of Biscay) cont.

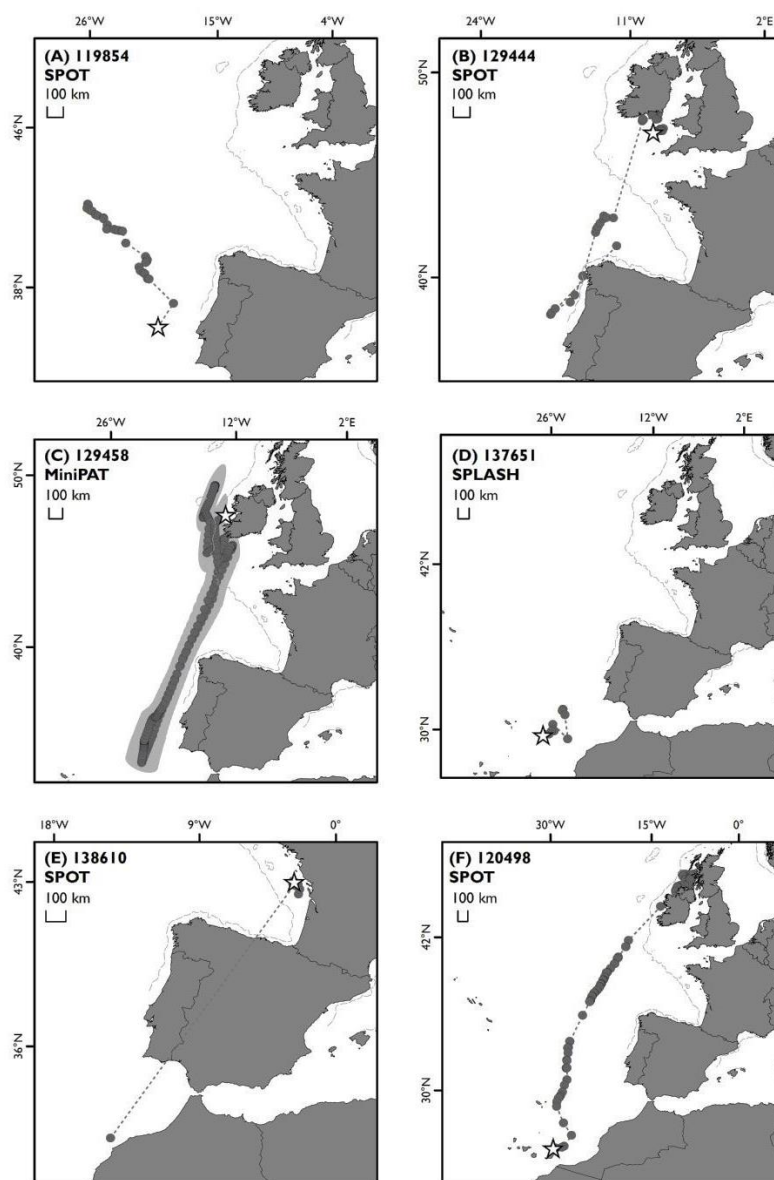


Figure B4. Individual movements of basking sharks exhibiting migration strategy C (Iberian Peninsula & North Africa). Satellite tracked data from basking sharks for post-summer (October onwards) movements, with additional shark tracked in 2012 exhibiting migration strategy C on a shorter time-scale (F). Each circle represents best daily location, with associated error from light geolocation displayed as grey ellipses. Shark tag ID and tag model type displayed. Note figure parts are to differing scales. Broken grey line denotes 200 m bathymetric contour. White stars denote track end point for Argos Doppler-based geolocation tags or pop-off locations for light geolocation tags. Maps created in ESRI ArcGIS version 10.1 (<http://desktop.arcgis.com/en/arcmap>) using ESRI ESRI land shapefiles and GEBCO bathymetric contours (<http://www.gebco.net>).

Appendix C

Table C1. Summary table of archival tags deployed between 2012 and 2014 contributing depth and temperature data (n = 32). Data type contribution from each tag shown (Histos = Summarised histograms at 4-hour intervals, Light geolocated = light geolocation methods applied to tags with long-term attachment (>165 days) providing daily minimum and maximum depths, and Time series = tags physically recovered for download providing depth and temperature data at 10 or 15 second intervals). Ordered by deployment year, tag type and tag number.

Year	PTT	Tag model	Sex	Body length (m)	Duration (days)	Max. Depth (m)	Histos	Light geolocated	Timeseries
2012	I19842	PAT-F280	Female	4 to 5	37	-	✓		
	I19843	PAT-F280	Male	7 to 8	140	-	✓		
	I19845	PAT-F280	Male	4 to 5	204	1000	✓	✓	✓
	I19846	PAT-F280	Female	6 to 7	170	248	✓	✓	
	I19848	PAT-F280	Unknown	5 to 6	20	-	✓		
	I19850	PAT-F280	Female	8 to 9	19	-	✓		
	I19851	PAT-F280	Unknown	5 to 6	45	227	✓		✓
	I19852	PAT-F280	Female	6 to 7	111	-	✓		
	I19853	PAT-F280	Male	6 to 7	280	1072	✓	✓	✓
	2013	I29431	SPLASH-F	Female	7 to 8	57	-	✓	
I29432		SPLASH-F	Unknown	5 to 6	34	-	✓		
I29433		SPLASH-F	Male	7 to 8	45	-	✓		
I29434		SPLASH-F	Unknown	5 to 6	45	178	✓		✓
I29442		MiniPAT-280	Unknown	4 to 5	292	375	✓	✓	
I29452		MiniPAT-280	Female	5 to 6	280	1192	✓	✓	
I29453		MiniPAT-365	Unknown	4 to 5	121	250	✓		✓
I29454		MiniPAT-280	Female	5 to 6	259	1500	✓	✓	✓
I29455		MiniPAT-280	Female	5 to 6	280	1280	✓	✓	
I29456		MiniPAT-280	Female	5 to 6	281	1500	✓	✓	✓
I29457		MiniPAT-365	Unknown	7 to 8	196	232	✓	✓	
I29458		MiniPAT-280	Unknown	4 to 5	280	875	✓	✓	
I29459		MiniPAT-280	Unknown	4 to 5	165	375	✓	✓	
I31890		MiniPAT-280	Unknown	5 to 6	64	259	✓		✓
2014	I37645	SPLASH-F	Unknown	7 to 8	75	-	✓		
	I37646	SPLASH-F	Male	6 to 7	10	82	✓		✓
	I37648	SPLASH-F	Female	6 to 7	64	-	✓		
	I37649	SPLASH-F	Unknown	6 to 7	136	165	✓		✓
	I37650	SPLASH-F	Female	7 to 8	112	-	✓		
	I37651	SPLASH-F	Female	5 to 6	248	-	✓		
	I37652	SPLASH-F	Unknown	6 to 7	115	-	✓		
	I37653	SPLASH-F	Male	7 to 8	47	208	✓		✓
	I37654	SPLASH-F	Unknown	7 to 8	259	1232	✓	✓	✓

Table C2. Summary table for General Linear Mixed Model (GLMM). Model contained random effects of shark identification number, tag model and month in which the dive event took place. Full model tested whether the log of minimum temperature experienced on a dive event (Min. temp) had an effect on the amount of time spent in shallow waters (<10 m) post-dive.

Fixed effect	β	SE	X^2	P
Intercept	3.40655	0.58180	-	-
Min. temp	-0.20883	0.04118	22.39	<0.001

Appendix D

Table D1. Deployment information. Summary table of tags used to provide locations to be used as presence data for model runs (n = 47). Ordered by deployment year and PTT number. Sex abbreviations; Male (M), Female (F), and Unknown (U).

Year	PTT	Tag type	Sex	Body length (m)	Duration (d)	Model	
2012	119845	PAT-F	M	4 to 5	204	Winter	
	119846	PAT-F	F	6 to 7	170	Winter	
	119853	PAT-F	M	6 to 7	280	Winter	
	119854	SPOT	U	4 to 5	322	Summer	
	119855	SPOT	U	6 to 7	20	Summer	
	119856	SPOT	M	5 to 6	96	Summer	
	120496	SPOT	F	5 to 6	100	Summer	
	120497	SPOT	F	4 to 5	20	Summer	
	120498	SPOT	F	5 to 6	135	Summer	
	120499	SPOT	M	7 to 8	156	Summer	
	120500	SPOT	M	6 to 7	19	Summer	
	2013	129431	SPLASH	F	7 to 8	57	Summer
		129432	SPLASH	U	5 to 6	45	Summer
129433		SPLASH	M	7 to 8	45	Summer	
129434		SPLASH	U	5 to 6	45	Summer	
129435		SPOT	F	5 to 6	43	Summer	
129436		SPOT	U	5 to 6	83	Summer	
129437		SPOT	U	5 to 6	375	Summer	
129438		SPOT	M	5 to 6	55	Summer	
129439		SPOT	U	6 to 7	376	Summer	
129440		SPOT	F	4 to 5	414	Summer	
129441		SPOT	M	5 to 6	254	Summer	
129442		MiniPAT	U	4 to 5	292	Winter	
129443		SPOT	F	6 to 7	87	Summer	
129444		SPOT	U	7 to 8	343	Summer	
129445		SPOT	U	7 to 8	292	Summer	
129446		SPOT	U	5 to 6	58	Summer	
129447		SPOT	U	4 to 5	41	Summer	
129448		SPOT	U	5 to 6	365	Summer	
129449		SPOT	U	5 to 6	367	Summer	
129450		SPOT	F	5 to 6	242	Summer	
129452		MiniPAT	F	5 to 6	280	Winter	
129454		MiniPAT	F	5 to 6	259	Winter	
129455		MiniPAT	F	5 to 6	280	Winter	
129456		MiniPAT	F	5 to 6	281	Winter	
129457		MiniPAT	U	7 to 8	196	Winter	
129458		MiniPAT	U	4 to 5	280	Winter	
129459	MiniPAT	U	4 to 5	165	Winter		
2014	137645	SPLASH	U	7 to 8	75	Summer	
	137646	SPLASH	M	6 to 7	10	Summer	
	137648	SPLASH	F	6 to 7	64	Summer	
	137649	SPLASH	U	6 to 7	136	Summer	
	137650	SPLASH	F	7 to 8	112	Summer	
	137651	SPLASH	F	5 to 6	248	Summer	
	137652	SPLASH	U	6 to 7	115	Summer	
	137653	SPLASH	M	7 to 8	47	Summer	
137654	SPLASH	U	7 to 8	259	Summer/Winter		

Table D2. Global Moran's I test for spatial autocorrelation. Summary table of Moran's Index test for spatial autocorrelation for input locations for each model.

Moran's Index	Expected Index	Variance	z-score	p-value	Model	n locations
0.0377	-0.0004	0.4735	0.0554	0.9558	Summer	1103
0.0808	-0.0005	0.0128	0.7173	0.4732	Winter: 0-10 m	959
0.0266	-0.0005	0.0307	0.1546	0.8771	Winter: 50-100 m	988
0.0476	-0.0006	0.0297	0.2971	0.7664	Winter: 150-250 m	569

Table D3. Average evaluation metrics of summer model runs. Summary table of Ensemble Ecological Model (EENM) evaluation metrics for 10-fold cross validation for summer (April-October). Model algorithm abbreviations; General Linear Model (GLM), Boosted Regression Tree (BRT), and General Additive Model (GAM). Evaluation metric abbreviations; Cohen's Kappa, Heidke skill score (KAPPA), True Skill Statistic (TSS), Area Under the Curve (AUC), Success Ratio (SR), and Fraction correct accuracy (ACCURACY).

Evaluation metric	Modelling algorithm		
	GAM	BRT	GLM
KAPPA	0.954	0.963	0.932
TSS	0.988	0.996	0.976
AUC	0.950	0.961	0.930
SR	0.983	0.993	0.976
ACCURACY	0.978	0.982	0.967
Mean	0.971	0.979	0.956
SD	0.016	0.015	0.021

Table D4. Average Relative Importance of the Contribution to the summer model Coefficients (RICC). Summary table of Ensemble Ecological Model (EENM) relative importance of each environmental variable averaged over 10-fold cross validation, and then averaged across model algorithms for summer (April-October). Model algorithm abbreviations; General Linear Model (GLM), Boosted Regression Tree (BRT), and General Additive Model (GAM). Environmental variable abbreviations; Sea Surface Temperature (SST; °C), Chlorophyll α concentration (Chl-a; mg/m^{-3}), persistent daily SST frontal activity (Fronts), bathymetric depth (Depth; m), and slope derived from bathymetric depth (Slope; °).

Modelling algorithm	Environmental variable			
	SST	Chla	Fronts	Depth
GAM	0.491	0.342	0.133	0.034
BRT	0.481	0.288	0.026	0.205
GLM	0.642	0.019	0.032	0.328
Mean	0.538	0.216	0.064	0.189
SD	0.073	0.141	0.049	0.121

Table D5. Average evaluation metrics of winter model runs. Summary table of Ensemble Ecological Model (EENM) evaluation metrics for 10-fold cross validation for winter (October-March). Model algorithm abbreviations; General Linear Model (GLM), Boosted Regression Tree (BRT), and General Additive Model (GAM). Evaluation metric abbreviations; Cohen’s Kappa, Heidke skill score (KAPPA), True Skill Statistic (TSS), Area Under the Curve (AUC), Success Ratio (SR), and Fraction correct accuracy (ACCURACY).

Evaluation metric	0-10 m			50-100 m			150-250 m		
	Modelling algorithm			Modelling algorithm			Modelling algorithm		
	GAM	BRT	GLM	GAM	BRT	GLM	GAM	BRT	GLM
KAPPA	0.926	0.948	0.907	0.974	0.979	0.977	0.960	0.963	0.961
TSS	0.914	0.946	0.908	0.974	0.979	0.977	0.962	0.965	0.962
AUC	0.983	0.990	0.979	0.992	0.994	0.994	0.992	0.995	0.992
SR	0.979	0.985	0.982	0.988	0.991	0.990	0.981	0.975	0.984
ACCURACY	0.962	0.973	0.953	0.987	0.989	0.989	0.982	0.983	0.982
Mean	0.953	0.968	0.946	0.983	0.986	0.985	0.975	0.976	0.976
SD	0.028	0.018	0.033	0.007	0.006	0.007	0.012	0.012	0.013

Table D6. Average Relative Importance of the Contribution to the winter model Coefficients (RICC). Summary table of Ensemble Ecological Model (EENM) relative importance of each environmental variable averaged over 10-fold cross validation, and then averaged across model algorithms for winter (October-March). Model algorithm abbreviations; General Linear Model (GLM), Boosted Regression Tree (BRT), and General Additive Model (GAM). Environmental variable abbreviations; Temperature-at-depth (Temp. at depth; HYCOM, °C), bathymetric depth (Depth; m), and slope derived from bathymetric depth (Slope; °).

Modelling algorithm	0-10 m			50-100 m			150-250 m		
	Environmental variables			Environmental variables			Environmental variables		
	Temp. at depth	Depth	Slope	Temp. at depth	Depth	Slope	Temp. at depth	Depth	Slope
GAM	0.904	0.085	0.011	0.684	0.310	0.006	0.618	0.307	0.075
BRT	0.715	0.283	0.003	0.633	0.364	0.003	0.584	0.411	0.005
GLM	0.945	0.055	0.000	0.656	0.343	0.001	0.656	0.309	0.035
Mean	0.855	0.141	0.004	0.658	0.339	0.003	0.619	0.342	0.038
SD	0.100	0.101	0.004	0.021	0.022	0.002	0.029	0.048	0.028

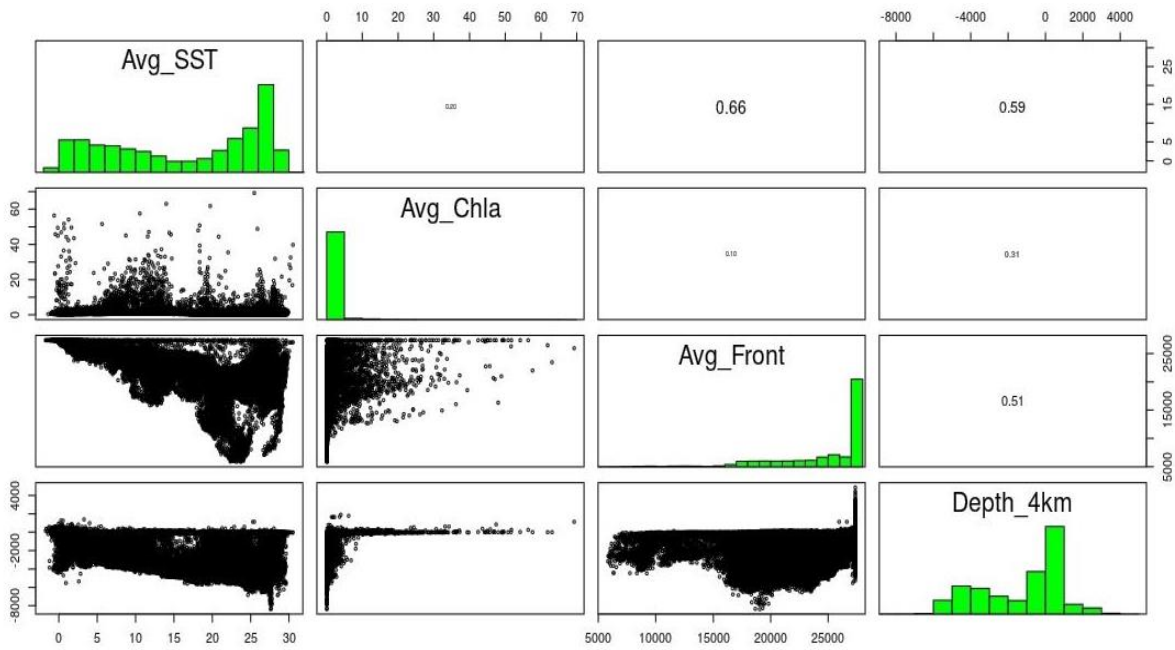


Figure D1. Co-variance plots for summer model environmental variables. Spearman's rank tests shown between all unique combinations of environmental data layers testing for correlation. Histograms represent the data contributed by each variable, scatterplots of each combination of variables, and Spearman's rank values, text sized by correlation. Environmental variable abbreviations; Mean Sea Surface Temperature (Avg_SST; °C), mean Chlorophyll α concentration (Avg_Chla; mg/m^3), mean persistent daily SST frontal activity (Avg_Front), and bathymetric depth (Depth_4km; m).

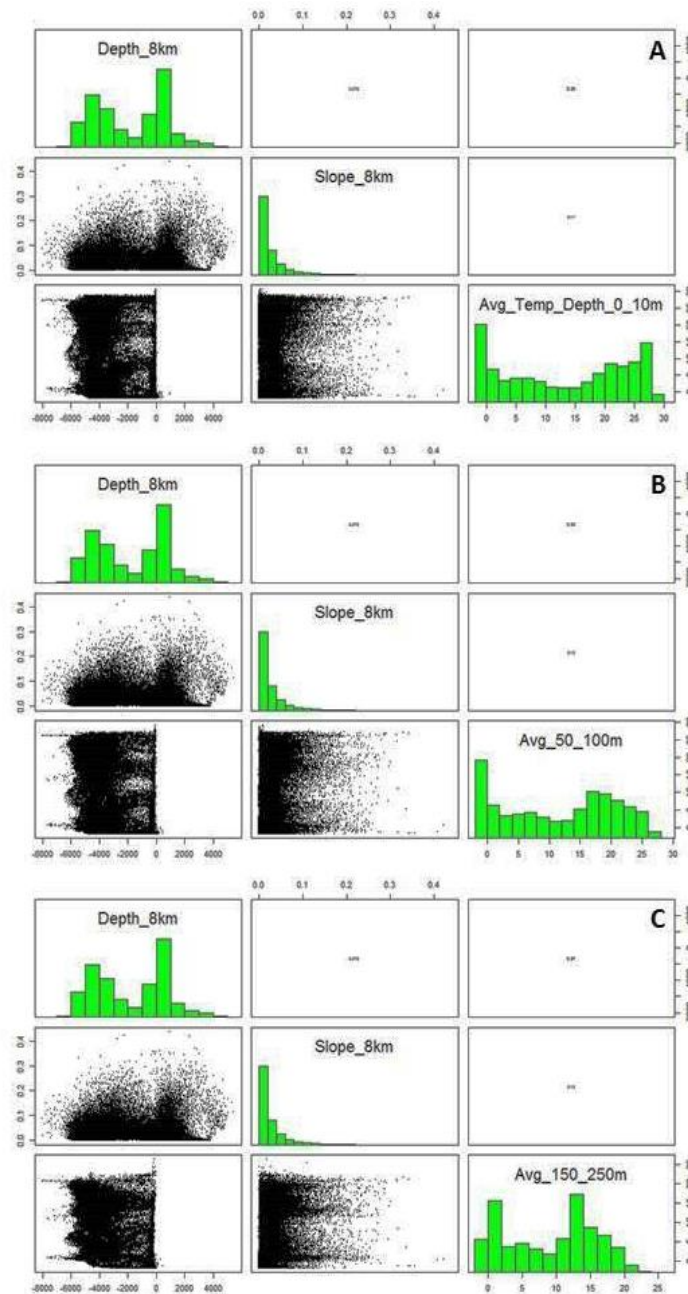


Figure D2. Co-variance plots for winter model environmental variables. Spearman's rank tests shown between all unique combinations of environmental data layers testing for correlation. Histograms represent range of data contributed by each variable, scatterplots of each combination of variables, and Spearman's rank values, text sized by correlation. Environmental variable abbreviations; (A) 0-10 m depth (Avg_Temp_Depth_0_10m, (B) 50-100 m depth (Avg_50_100m, and (C) 150-250 m depth (Avg_150_250m; HYCOM; °C). Each depth layer was modelled individually with bathymetric depth (Depth_8km; m), and slope derived from bathymetric depth (Slope_8km; °).

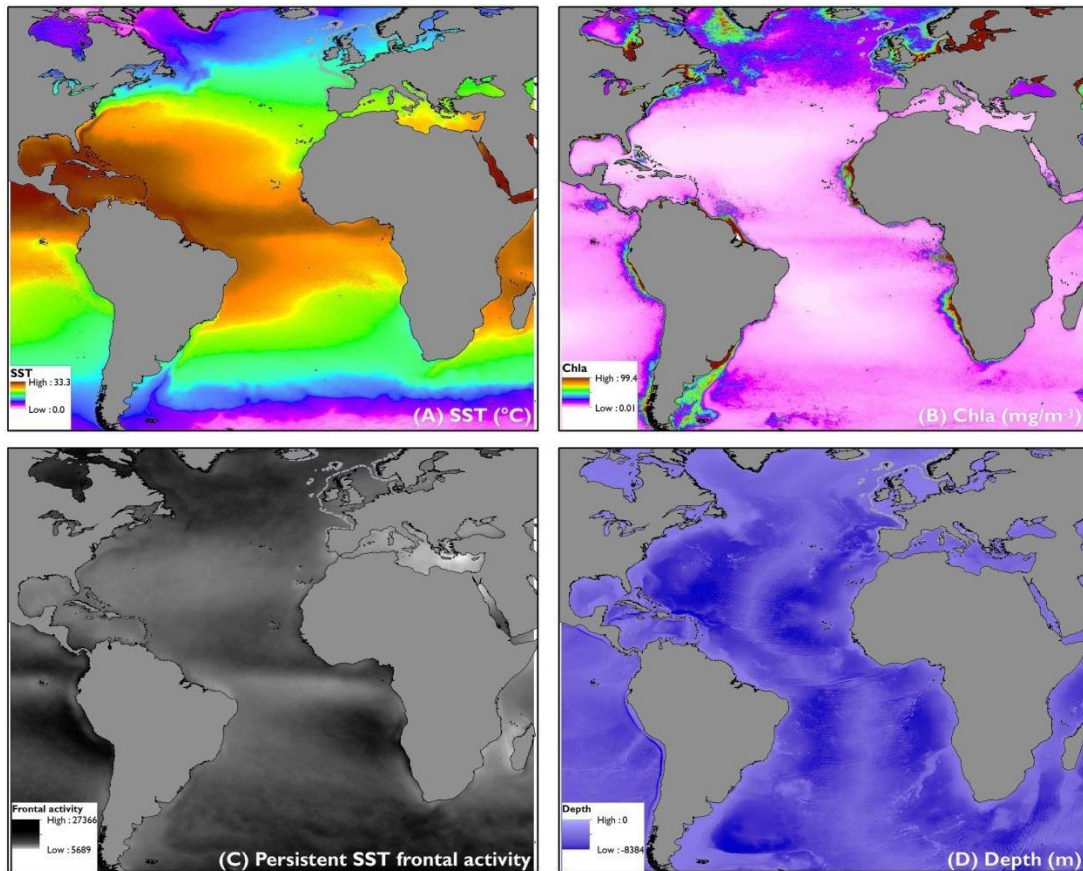


Figure D3. Summer Ensemble Ecological Niche Model (EENM) environmental variables. (A) Sea Surface Temperature (SST; °C), (B) Chlorophyll α concentration (Chla; mg/m⁻³), (C) persistent daily SST frontal activity, and (D) bathymetric depth (m). All data surfaces were sampled to 4 km x 4 km resolution using bilinear interpolation.

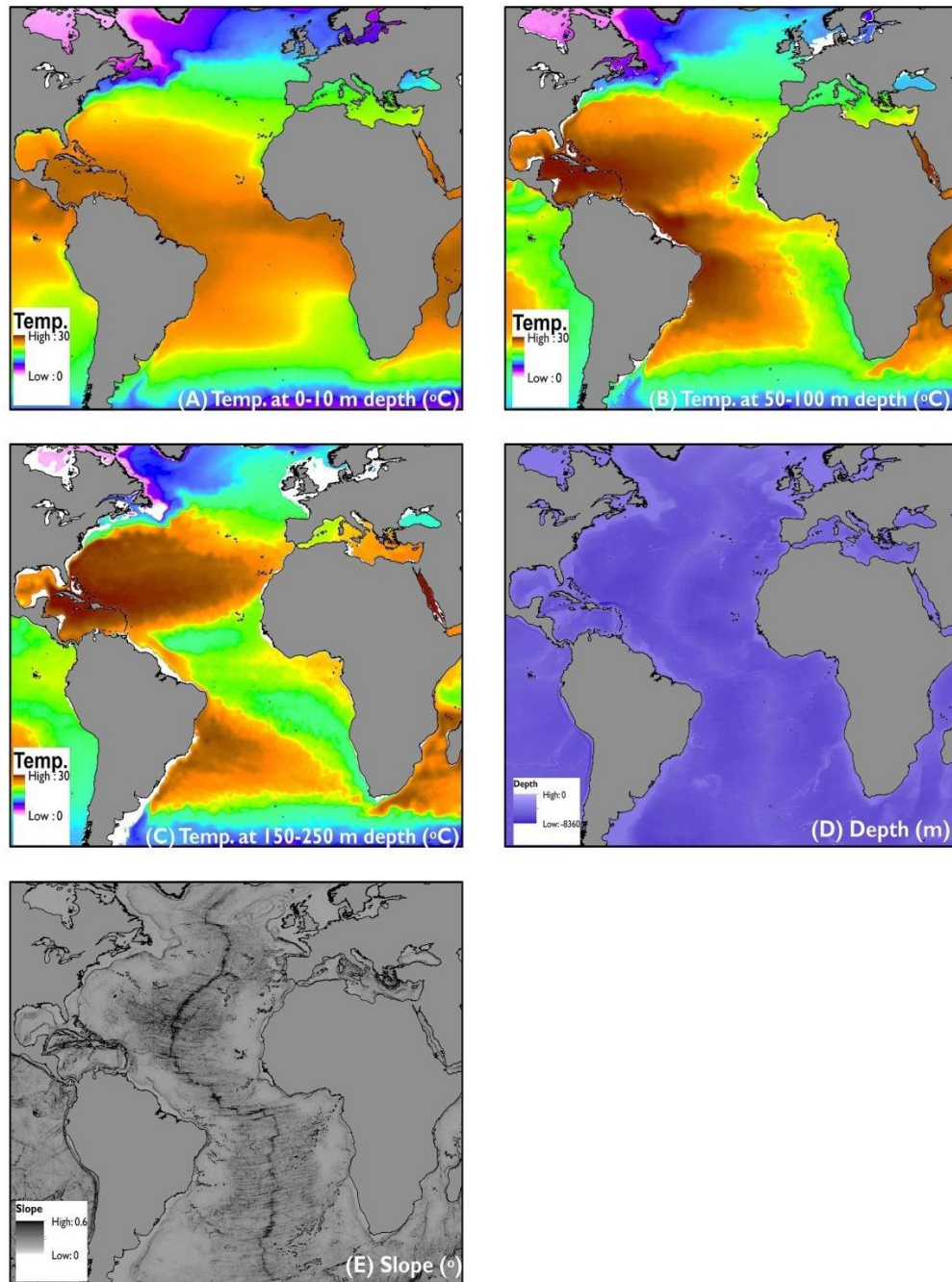
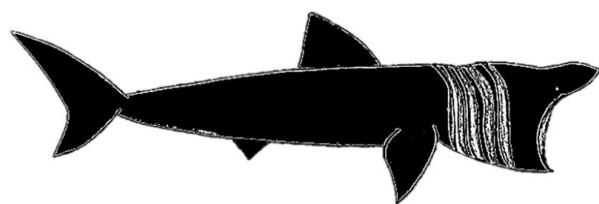


Figure D4. Winter Ensemble Ecological Niche Model (EENM) environmental variables. (A) 0-10 m depth, (B) 50-100 m depth, (C) 150-250 m depth (HYCOM; °C), (D) bathymetric depth (m), and (E) slope (°). All data surfaces were sampled to 8 km x 8 km resolution using bilinear interpolation.





Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed marine protected area

P.D. Doherty^{a,b}, J.M. Baxter^c, B.J. Godley^{a,b}, R.T. Graham^d, G. Hall^e, J. Hall^e, L.A. Hawkes^b, S.M. Henderson^f, L. Johnson^g, C. Speedie^g, M.J. Witt^{a,b,*}

^a Environment and Sustainability Institute, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK

^b Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK

^c Scottish Natural Heritage, Silvan House, 231 Corstorphine Road, Edinburgh EH12 7AT, UK

^d MarAlliance, PO Box 283, San Pedro, Ambergris Caye, Belize

^e Manx Basking Shark Watch, Glen Chass Farmhouse, Glen Chass, Port St Mary IM9 5PJ, Isle of Man

^f Scottish Natural Heritage, Great Glen House, Inverness, Scotland IV3 8NW, UK

^g Wave Action, 3 Beacon Cottages, Falmouth TR11 2LZ, UK

ARTICLE INFO

Article history:

Received 2 August 2016

Received in revised form 16 January 2017

Accepted 25 January 2017

Available online xxx

Keywords:

Animal movement
Cetorhinus maximus
Conservation
North-east Atlantic
Satellite tracking

ABSTRACT

There is a growing need to understand the inter-annual movements of mobile marine species of conservation concern to inform the design and placement of Marine Protected Areas (MPAs) to maximise their conservation potential. We use satellite telemetry data from 36 basking sharks (*Cetorhinus maximus*) tracked in 2012, 2013 and 2014 (cumulative total: 1598 days; median: 44 days; range: 10–87 days) to quantify movements in coastal waters off the west coast of Scotland within the Sea of the Hebrides proposed MPA. Sharks exhibited seasonal residency to the proposed MPA, with a mean of 84% of filtered best daily locations occurring within its boundaries (2012 = 80%, 2013 = 90% and 2014 = 74%). Three long-term tracked basking sharks demonstrated inter-annual site fidelity, returning to the same coastal waters in the year following tag deployment, with two returning to within the boundaries of the proposed MPA. These data likely suggest the area experiences favourable conditions and/or resources for basking sharks across years and, if designated, coupled with appropriate management, could afford protection during summer months.

© 2016 Published by Elsevier Ltd.

1. Introduction

With global declines in many marine fish populations and habitats (Watson and Pauly, 2001; Baum et al., 2003; Lotze et al., 2006) the use of Marine Protected Areas (MPAs) has become increasingly popular as a management tool to prevent further population decline, promote recovery and improve biodiversity conservation (Halpern and Warner, 2002; Wood et al., 2008). Studies have suggested that large, mobile species, with wide-ranging movements may benefit from MPAs, e.g. teleost fish (Farmer and Ault, 2011), turtles (Scott et al., 2012), whales (O'Brien and Whitehead, 2013), as well as sharks (Claudet et al., 2009; Barnett et al., 2011), depending on protective measures applied to these areas.

In particular, there is growing concern regarding the rate of decline of global shark populations due to overfishing (Dulvy et al., 2014). The proportion of time individuals spend within MPA boundaries will affect the degree to which these animals could be protected, should adequate management measures also be in place. This protection is likely to vary with species, life stage, sex, size, body condition and food availability (Speed et al., 2010; Escalle et al., 2015). De-

signing MPA boundaries and management measures to be effective for mobile species require detailed knowledge of the species' biology, movements and habitat use (Grüss et al., 2011; Chin et al., 2016). Establishing MPAs in areas that mobile species use consistently (e.g. areas of key life-history events) may offer some protection at a population level (Heupel and Simpfendorfer, 2005; Meyer et al., 2007), and protection will therefore depend on the degree of overlap between core activity areas and the area of protection (Knip et al., 2012).

Basking sharks were historically exploited in the north-east Atlantic for their meat, fins and large liver containing desired squalene oil; with directed fisheries from Norway, Scotland and Ireland. These fisheries landed 77,204 individuals between 1946 and 1986 (Kunzlik, 1988), leading to depletion in local stocks (Parker and Stott, 1965). Basking sharks are listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Appendices I and II in the Convention of Migratory Species (CMS; Table S1), and are listed as 'Vulnerable' globally by the International Union for Conservation of Nature (IUCN Red List), and 'Endangered' in the north-east Atlantic (Fowler, 2005). The Marine (Scotland) Act (2010) and the UK Marine and Coastal Access Act (2009) include powers for Scottish Ministers to designate MPAs in the seas around Scotland, one of which is the proposed 10,325 km² Sea of the Hebrides MPA, between the Isles of Skye, Mull and Outer

* Corresponding author at: Environment and Sustainability Institute, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK.
Email address: p.doherty@exeter.ac.uk (P.D. Doherty)

Hebrides (Scottish Natural Heritage, 2014). This area has been highlighted as a key area for surface sightings of basking sharks (Speedie et al., 2009; Witt et al., 2012) between July and August each year, and for minke whales (*Balaenoptera acutorostrata*) and was thus proposed for designation as a MPA (Scottish Natural Heritage, 2014).

In an attempt to increase protective measures for marine environments and to satisfy international conventions, many MPAs have been implemented opportunistically without prior knowledge of how they may contribute to biodiversity conservation (Roberts, 2000). Assessment of the efficacy of a MPA is important in order to maximise its conservation potential (McNeill, 1994), otherwise there is a possibility of tokenism if placed arbitrarily (Ashe et al., 2010). We used satellite tags in order to (1) describe the seasonal (summer months) space-use of coastal waters off the west coast of Scotland by basking sharks, (2) describe areas of inter- and intra-annual density and (3) evaluate the use of the Sea of the Hebrides proposed MPA and establish the amount of time sharks spent inside the proposed MPA thus quantify the potential importance of this area to basking sharks.

2. Materials & methods

2.1. Tag attachment and specification

Sixty-two satellite tags, communicating with the Argos System, were attached to basking sharks off the west coast of Scotland during July and August in 2012, 2013 and 2014. Basking sharks were approached by boat from behind to avoid the line of sight of the shark and to minimise disturbance. On approach to the shark, the individual was, where possible, sexed using a pole mounted camera and total body length was estimated based on comparison to the total length of the boat (10 m). Satellite tags were deployed using a titanium M-style dart (Wildlife Computers, Redmond, California, USA) inserted into the sub-dermal layer at the base of the first dorsal fin with a modified pole spear and attached via a tether consisting of heat-shrink covered stainless steel flexible cable, a swivel and monofilament line attached to the tag. Four models of satellite tags were deployed to gather a variety of information on the movements and distribution of tagged animals. Thirty-six satellite tags were used in this analysis; Smart Position or Temperature tags (SPOT; $n = 23$, Wildlife Computers, Redmond, California, USA) and SPLASH-F tags ($n = 13$, Wildlife Computers, Redmond, California, USA) and transmitted data in real-time while attached to study animals. Both tag models provided Argos Doppler-based estimates of location (termed Argos locations) during shark surfacing events. SPLASH-F tags also contained Fastloc™ GPS technology, providing GPS locations in addition to collecting light, temperature and depth data. Both, Argos and GPS locations were used for analysis of summer movement patterns and seasonal site fidelity. Remaining tags ($n = 24$) were Pop-up Archival tags fitted with Fastloc™ GPS technology (PAT-F; $n = 12$) and MiniPAT ($n = 12$; Wildlife Computers, Redmond, California, USA). These tags used to gather information on longer-range movements of basking sharks away from the west coast of Scotland using the principles of light geolocation (Doherty et al., 2017).

2.2. Location data processing

Analysis focused on coastal movement within the summer months; therefore, data were confined to 90 days (approx. mid July–mid October) following tag deployment and prior to the departure of sharks from the region. Data from satellite tags transmitting in the year following tag attachment were examined to ascertain inter-annual site fidelity. Argos location data from SPOT tags were subject

to filtering, retaining location classes 1 (accurate to 500–1500 m), 2 (accurate to 250–500 m), 3 (accurate to < 250 m), ‘A’ (three messages received but no accuracy estimation) and ‘B’ (one or two messages received but no accuracy estimation) (Witt et al., 2010). GPS location data from SPLASH-F tags deployed in 2014 were filtered to include only positions with a residual error value of < 30 and where five or more satellites were visible to estimate the location (Shimada et al., 2012). GPS locations from SPLASH-F tags in 2014 were favoured over Argos locations from the same tags as the number of GPS locations was more numerous (662 vs. 463 Argos locations; post-filtering) and GPS locations have a greater spatial accuracy (Table S2). A maximum plausible speed filter was applied to both datasets removing locations if speed between two locations exceeded 10 km h^{-1} . These data were later reduced to a single, most accurate best daily location (highest location class as described above for Argos locations and maximum number of visible satellites for GPS locations) to minimise spatial and temporal autocorrelation. All tag data were downloaded from CLS-Argos and archived using the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley, 2005).

2.3. Data analysis

We used four techniques to identify core activity areas of residency, these techniques were; Minimum Convex Polygons (MCPs), polygon sampling grid, Time Local Convex Hulls (T-LoCoh) and Kernel Density Estimation (KDE). MCPs create the smallest convex polygon that incorporates all filtered best daily locations. To determine areas of high relative importance, a polygon sampling grid (hexagonal cells; 2 km from each grid cell centroid to its perimeter; cell area 14 km^2) was spatially intersected with filtered best daily locations. The proportion of locations within each grid cell was calculated for each tracked shark; a mean proportion for each cell was then calculated. We used T-LoCoh to construct utilisation distributions by aggregating local MCPs around each point, which were then sorted and progressively merged to form isopleths. Local Convex Hull (LoCoH) methods have been shown to outperform traditional kernel-smoothing techniques in excluding areas known not to be used (Getz et al., 2007). These attributes make LoCoH methods applicable to analyse collective area use of multiple individuals. T-LoCoh offers an advantage over traditional approaches because it further improves the ability to partition area use and study patterns through time (Lyons et al., 2013). We applied the k-based method with no time-based weighting, constructing hulls for defined numbers of neighbouring points due to the absence of areas with high density of clustering as well as areas of sparsely distributed points (Lyons et al., 2013). We also applied KDE interpolation with barriers as described by Macleod (2014). KDE with barriers uses the shortest distance between points without intersecting a defined barrier, in this case land, allowing the contour of the kernel to change at the edge of the barrier (Sprogis et al., 2016). Output cell size was 250 m side length and the bandwidth (search radius) was 5000 m. The bandwidth is a smoothing value that determines the width of the kernel. Choice of bandwidth method may vary depending on the study goals, sample size and patterns of space use by the study species (Gitzen et al., 2006), therefore the bandwidth value was selected by iterative visual inspection of outputs and evaluating the results based on extant ecological knowledge of the species.

Individual trajectories of tracked basking sharks were separated into groups based on movements relative to the boundaries of the proposed MPA using k-means cluster analysis (Hartigan and Wong, 1979). Individual tracks were initially separated into *High-use* ($n = 29$) and *Low-use* ($n = 7$) groups based on time spent within the

boundaries of the proposed MPA. To ascertain the use of the proposed MPA movements of tracked basking sharks the *High-use* group was further split into *Near* ($n = 23$) and *Far* ($n = 6$) groups based on their maximum displacement distances from tagging location.

Data analysis was performed in R (R Core Team, 2014), with satellite tag location filtering applied using the *adehabitat* packages (Calenge, 2006) and T-LoCoH analysis using the *T-LoCoH* package (Lyons et al., 2013). All spatial analyses and maps were created using Geospatial Modelling Environment (GME v 0.7.2.1; Beyer, 2012) and ESRI ArcMap 10.1.

3. Results

The movements of 36 basking sharks were analysed comprising eight males, 11 females and 17 of unknown sex. Sharks ranged from four to eight metres in length (4–5 m, $n = 4$ sharks; 5–6 m, $n = 15$ sharks; 6–7 m, $n = 8$ sharks and 7–8 m, $n = 9$ sharks). Sharks were tracked for a cumulative summer duration of 1598 days (mid-July–mid-October; median: 44; range: 10–87 days), moved a median

minimum along-track straight-line distance of 353 km (Inter-Quartile Range (IQR): 260 km range: 111–1410 km; Table S2) and were displaced a median 63 km (IQR: 71 km; range: 23–167 km) during that time. Following summer movements, 20 of these sharks were tracked departing the region (Doherty et al., 2017).

Tracked basking sharks demonstrated three movement behaviours throughout the summer (Fig. 1; Figs S1–3), which was independent of tracking duration within the period (GLMM; $\chi^2_1 = 2.07$, $p = 0.15$); here, defined as (1) *High-use and near*, where sharks remain close to tagging location around the coastal waters of the Isles of Coll and Tiree within the boundaries of the proposed MPA ($n = 23$; Fig. 1B), (2) *High-use and far*, where sharks are mobile, using a high proportion of space within the proposed MPA, but away from tagging location, ($n = 6$; Fig. 1C) or (3) *Low-use*, where sharks leave the boundaries of the proposed MPA ($n = 7$) either permanently or re-entering at a later date within the same summer season (Fig. 1D).

Minimum Convex Polygons (MCPs) of tracked basking sharks across years reached from the tagging location and proposed MPA southwards to the coasts of Ireland and Northern Ireland, encompassing the waters off the Isles of Jura and Islay, west of the Outer He-

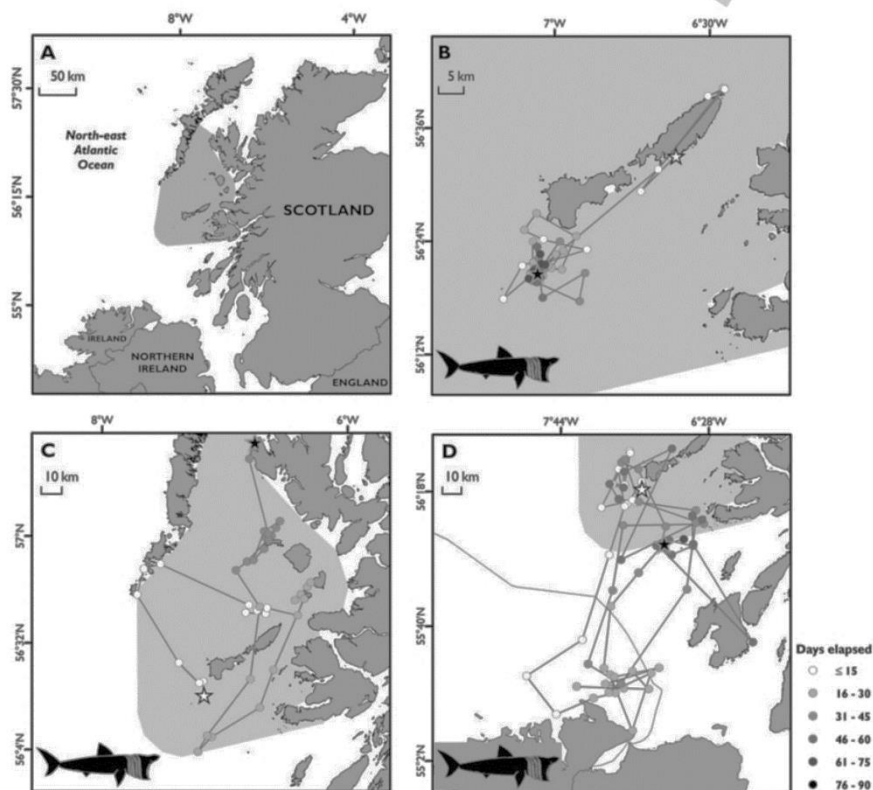


Fig. 1. Movement of tracked basking sharks in summer months (2012–2014; mid-July- to mid-October). (A) Study area; west coast of Scotland, showing proposed MPA (grey polygon). Examples of individual tracks that exemplify three modes of movements: (B) *High-use and near*, where sharks remain close to tagging location within the boundaries of the proposed MPA, PTT 137654 shown as example ($n = 23$); (C) *High-use and far*, where sharks are mobile, using a high proportion of space within the MPA away from tagging location, PTT 129449 shown as example ($n = 6$); (D) *Low-use*, where sharks leave the boundaries of the proposed MPA PTT 129441 shown as example ($n = 7$). White stars denote tag deployment, black stars denote track end point for the summer months. Solid line is representative of tracked movement. Economic Exclusive Zone (EEZ) between UK and Ireland (dashed grey line).

brides. The boundaries circumscribed areas of 21,182 km² in 2012, 24,532 km² in 2013, and 9403 km² in 2014. In 2014, Argos and GPS locations were available from SPLASH-F tags, the MCP from Argos locations was 8641 km² for Argos locations as compared to 9403 km² for GPS, we chose to use GPS locations in further analysis due to their greater volume, and hence likely improved chance to more accurately describe to occupied MCP in that season. The mean MCP areas of tracked sharks was 2605 km in 2012, 3154 km in 2013 and 3258 km in 2014 (applied to GPS locations compared to 1221 km² for Argos locations) (Table 1; Fig. 2A). The majority of filtered best daily locations (84%) occurred within the boundaries of the proposed MPA across all years (mean value, 2012 = 80%, 2013 = 90% and 2014 = 74%; Table 1, Figs 2A and S1–3). Grid density plots highlighted two common areas of high occupancy; to the south-west of the Isle of Coll and between the islands of Coll and Tiree, an area known as Gunna Sound (Fig. 2B). These areas were further identified using T-LoCoH and Kernel Density analysis, which show the extent of use of these hotspots. The approaches identified other areas to the north, in waters of the Isles of Hyskeir and Canna. Core activity areas were almost entirely encompassed within the proposed MPA boundaries (T-LoCoH 50% isopleth = 91%, KDE 50% contour = 97%).

Five basking sharks were tracked for longer than a year (> 365 days), and three of these sharks returned to the waters off the west coast of Scotland from over-wintering grounds the subsequent summer permitting insights into inter-annual site fidelity. The remaining two sharks were tracked in coastal waters off the west coast of Ireland the subsequent summer. The three returning sharks dispersed 565, 304 and 1474 km (minimum straight-line distance) from tag attachment location, these distances occurring in April, December and April respectively, and then returning to within 29, 138 and 24 km of the centroid of their core activity area from the first year of tracking respectively (Fig. 3). Two sharks returned to the waters of the proposed MPA in both years (Fig. 3A and C); the third shark was located outside the MPA boundary in the second year of tracking (Fig. 3B, Table S3).

4. Discussion

The need to identify key areas of activity of large marine vertebrates in coastal areas is essential in order to appropriately delineate areas, and their boundaries, where protection measures can be implemented.

Table 1

Space-use within proposed MPA boundaries. Shark locations within the proposed MPA boundaries per year, showing size and overlap of activity areas. MCP = Minimum Convex Polygon; MPA = Marine Protected Area; T-LoCoH = Time Local Convex Hull.

	2012	2013	2014
Geolocation method	Argos locations	Argos locations	GPS
Number of sharks	8	19	9
Number of best daily filtered locations	235	674	194
MCP area (km ²)	21,182	24,532	9402
Locations in MPA (median ± SD; range); %	80 ± 32 (20–100)	90 ± 14 (46–100)	74 ± 26 (25–100)
MCP area per shark (mean ± SD range); km ²	2605 ± 3610 (477–11,123)	3154 ± 2904 (250–10,470)	3258 ± 2344 (552–5984)
T-LoCoH isopleth area (50% hull (25–75%); km ²)	296 (88–1372)	591 (190–2282)	221 (52–1106)
T-LoCoH isopleth overlap with MPA (50% hull (25–75%); %)	93 (100–73)	90 (96–94)	91 (100–68)
Kernel area (50% contour (25–75%); km ²)	309 (97–728)	635 (181–1662)	211 (51–601)
Kernel overlap with MPA (50% contour (25–75%); %)	97 (100–87)	100 (100–100)	90 (100–72)

MPAs can benefit mobile marine species (Worm et al., 2003), including cetaceans, pinnipeds, sea otters, sea birds, sharks, cephalopods, and teleost fish (Hooker and Gerber, 2004). Our study showed that satellite tracked basking sharks in the north-east Atlantic exhibited seasonal residency and inter-annual site fidelity during summer months to a proposed MPA. The study area has been recognised as a basking shark aggregation site in the summer months from public sightings data (Southall et al., 2005; Witt et al., 2012) and boat-based, effort-corrected surveys (Southall et al., 2005; Speedie et al., 2009) where foraging behaviour can be observed (Matthews and Parker, 1950; Berrow and Heardman, 1994), but thus far high-resolution tracking data has been lacking.

4.1. Near real-time tracking – Argos locations & GPS

The ability to observe fine-scale movements of marine species of conservation concern provides novel insights into horizontal movements that cannot be gained from more traditional boat-based or aerial surveys (Westgate et al., 2014). Describing these movements has provided insight into home-ranges, core activity areas and seasonal use of distinct habitats, such as tiger sharks seasonally feeding on fledgling Albatross (*Phoebastria* spp.) at the French Frigate Shoals and subsequent migration once this resource is depleted (Meyer et al., 2010) and large-scale migrations of leatherback turtles (*Dermochelys coriacea*) from Central Africa (Witt et al., 2008). More recently, the development of Fastloc™ GPS technology in telemetry allows highly accurate locations to be acquired from very brief (millisecond) surfacing events. This has led to high-resolution coastal water use by reef manta rays (*Manta alfredi*; Braun et al., 2014) and whale sharks (*Rhincodon typus*; Berumen et al., 2014). Such high resolution data has also permitted the identification of habitat use of the Critically Endangered smalltooth sawfish (*Pristis pectinata*) (Guttridge et al., 2015). Here we have revealed diverse, fine-scale space-use by basking sharks, whereby collectively tracked sharks occupied the same area throughout the summer months, but movements within this area differed at an individual level, which is critical in understanding plasticity of space-use and habitat preference.

4.2. Residency and site fidelity

Residency, where an individual remains in a restricted geographic area for an extended period of time (Chapman et al., 2015), and site fidelity, the return of an individual to a location where it previously resided after having left for a sustained period of time (Speed et al., 2011; Chapman et al., 2015) are common in shark species, with most data for reef associated species (see Chapman et al., 2015 for review). There is, however, a paucity of information on intra- and inter-annual shared use of an area by multiple basking sharks. Tracked sharks exhibited seasonal summer residency to the coastal waters off the west coast of Scotland. The vast majority of tracked sharks (86%; $n = 31$) showed some degree of residency (> 50% locations) to the proposed MPA (Fig. 2). We reveal tracked sharks exhibiting inter-annual site fidelity returning to the coastal waters of West Scotland. Two individuals returned to waters encompassed by the proposed MPA in summer months in the year following tag attachment, returning to within 30 km of the centre of activity from the previous summer, with another shark returning to waters off the west coast of Scotland, 138 km from centre of activity from the previous summer in an area highlighted as having conditions suitable for basking sharks (Fig. 3; Paxton et al., 2014). Until the present study, attachment durations of tags to basking sharks have been insufficient to ascertain information on inter-seasonal migration routes; we present the first description of

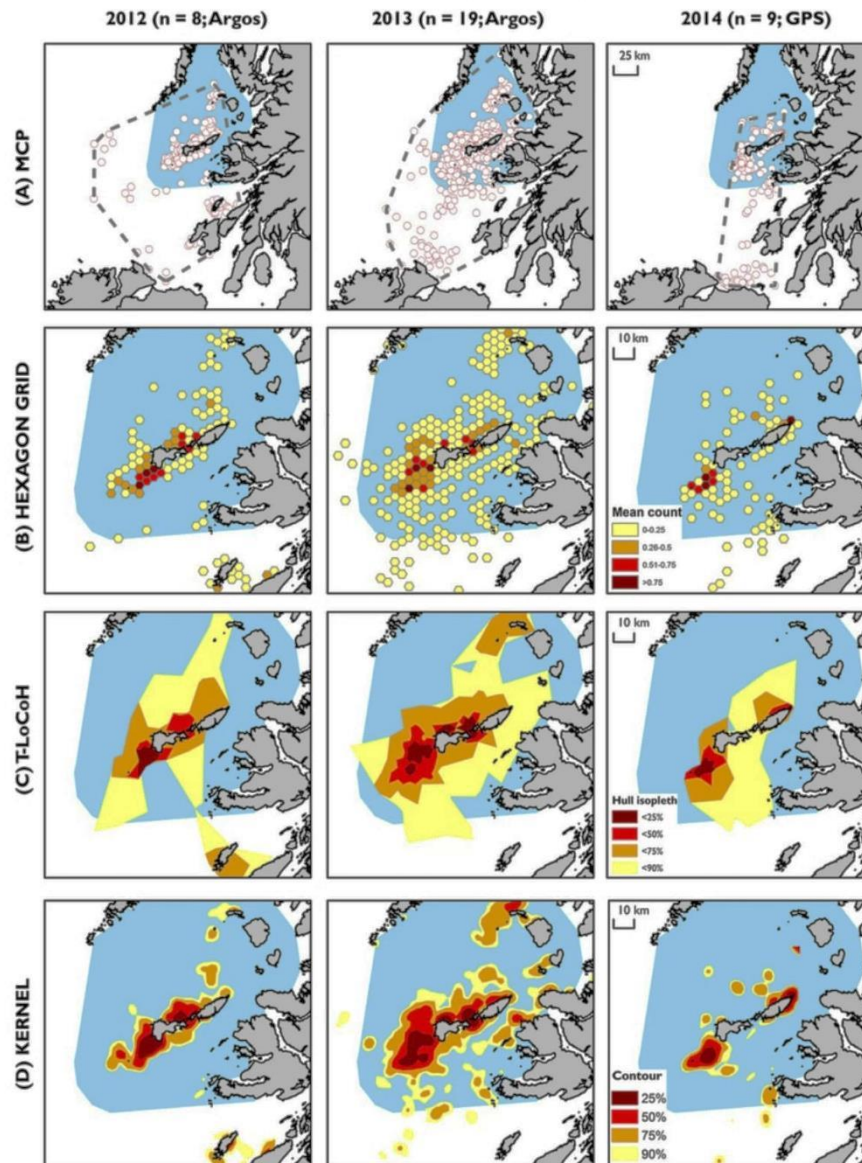
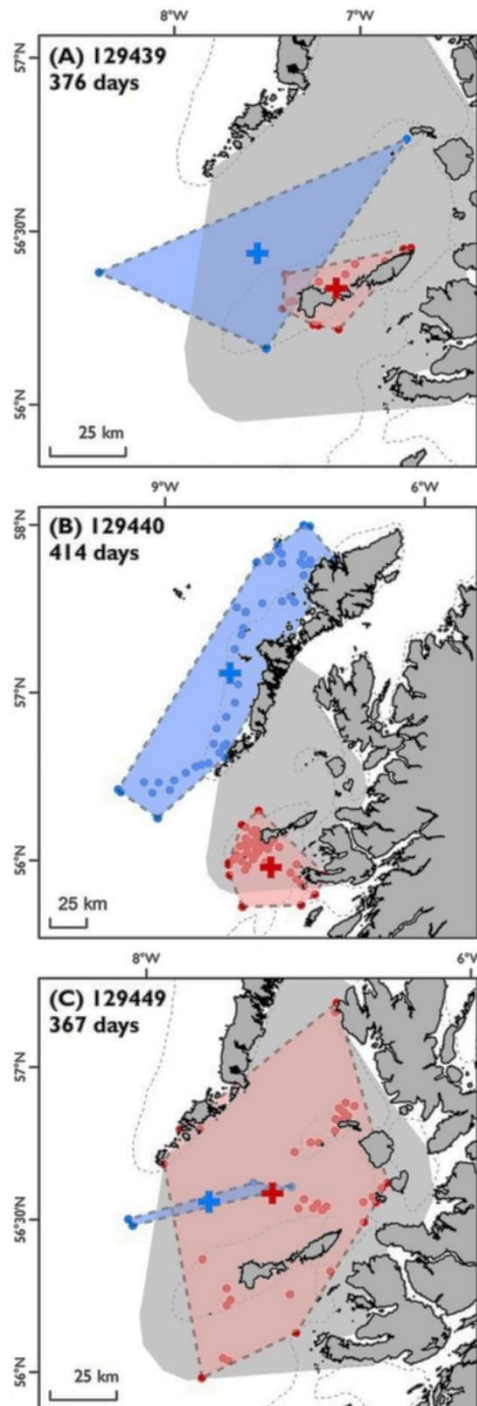


Fig. 2. Identifying areas of relative importance. Areas of relative importance for the summer months (2012 to 2014; July–October) estimated using (A) Minimum Convex Polygon (MCP), (B) Grid density estimation, (C) Time-Local Convex Hull analysis (T-LoCoH) and (D) Kernel density interpolation with barriers. In 2012 and 2013 locations (white circles) are daily highest quality Argos locations from basking shark tagged with SPOT and SPLASH-F tags. In 2014, locations (white circles) are daily highest quality GPS locations from SPLASH-F tags. Proposed MPA (blue polygon). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

multiple individuals exhibiting residency and site fidelity in this species.

Other tracking studies have indicated site fidelity and residency occurring in large, migratory sharks (e.g. white (*Carcharodon carcharias*), (Bonfil et al., 2005); whale, (Wilson et al., 2006); oceanic

whitetip (*Charcharhinus longimanus*), (Howey-Jordan et al., 2013)), highlighting specific areas of use by these animals that would be suitable for protection (Kock et al., 2013; Howey-Jordan et al., 2013; Graham et al., 2016). White sharks have been shown to exhibit a high degree of residency and site fidelity, returning to either the central



Californian coast (Jorgensen et al., 2010) or Guadalupe Island (Domeier and Nasby-Lucas, 2008) after migrating to a shared offshore foraging area in the Pacific Ocean. There is potential for a similar pattern of seasonal movement occurring in basking sharks in the north-east Atlantic, whereby the coastal waters off the west coast of Scotland serve as a shared, seasonal foraging site, with basking sharks moving away to separate over-wintering areas, as there is evidence for plasticity in dispersal behaviours during winter migrations (Doherty et al., 2017).

4.2.1. MPA use

Protection of highly migratory species throughout their range and life history is likely not feasible but MPAs can be used to protect areas of high relative importance or areas supporting key stages of life history ecology, such as breeding or foraging grounds (Lauck et al., 1998; Hooker and Gerber, 2004). Establishing management and protection measures for highly mobile species ranges will likely rely on the premise, that if protection of areas encompassing key life history events is achieved, populations may be better sustained (Speed et al., 2010). In a summary of evidence for the value of no-take zones for reef shark species, Escalle et al. (2015) found 65% of these studies deemed the protection area assessed to be beneficial to sharks, but 35% of studies suggested designated areas were too small based on residency, home-range and space-use; concluding that marine reserves have the potential to benefit sharks, but will be dependent on the amount of time individuals spend within reserve boundaries and the number of life-history stages catered for by the reserve.

Most protected areas are designated with their efficacy tested *post-hoc*, if at all, which may result in the assigned areas and boundaries being unsuitable. This can create a situation where adjustments in boundaries would be needed to provide protection of more appropriate areas, e.g. expansion of protective measures to include U.S. territorial waters would effectively protect 100% of core activity areas of highly mobile sharks in the north-west Atlantic (Graham et al., 2016), or a buffer zone of an MPA acting as a year round exclusion zone to industrial trawlers would greatly increase protection of turtles in central Africa (Witt et al., 2008). If MPAs are designed with prior knowledge of space-use by species of conservation concern, and designated based on those findings, then they will more likely serve their purpose. In the present study, we have been able to robustly test basking shark space-use of a proposed MPA, prior to designation, in order to evaluate its potential spatial efficacy. We determined a mean of 84% of locations occurred within the boundaries of this proposed MPA across three years of study (Table 1). Core activity areas were robustly tested across multiple analytical techniques, all of which resulted in overlap of these core areas (> 90%) with the proposed MPA (Fig. 2).

Basking sharks were observed foraging at the surface within the proposed MPA, however, there is potential for this area to provide suitable conditions for other life-history events. Nose-to-tail following and breaching behaviours were also observed in this area; behaviours that have previously been attributed to courtship (Harvey-Clark

Fig. 3. Inter-annual site fidelity. Best daily filtered locations (red and blue circles for 2013 and 2014 respectively) within summer months for three sharks demonstrating inter-annual site fidelity to coastal waters off the west coast of Scotland. Minimum Convex Polygons (red and blue polygons for 2013 and 2014 respectively), geographic mean centroid of Argos locations (red and blue crosses for 2013 and 2014 respectively). Shark ID and total tag attachment duration indicated for each figure part. Proposed MPA (grey polygon). 50 m bathymetry contour (grey broken line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 1999; Sims et al., 2000; Wilson, 2004), although mating has never been observed. Boat-based transects have also shown the area to have a high level of shark occurrence (mean 1.74 sharks hour⁻¹), where large groups (> 10 individuals) can be seen aggregating, with individuals within these large groups displaying courtship-like behaviour (Speedie et al., 2009), supporting the notion that this area is a *hotspot* for basking sharks.

4.3. Application and MPA management recommendations

MPAs can only be effective if appropriate management and enforcement are employed to reduce threats to species for which they are designated. We have observed basking shark behaviours, often at the surface, occurring within the waters off the west coast of Scotland. The threats to this species are therefore likely to primarily occur from boat strikes (leisure and tourist boats, commercial transportation and fishing vessels) or fisheries activity (entanglement or by-catch). It is often argued that MPAs are too small, often containing a small proportion of a population at any one time (Wilson, 2016). However, after testing the space-use of basking sharks in the region, we reveal that high levels of core activity occurred within the boundaries of the MPA. Nevertheless, there is evidence for complementary MPAs to encompass other areas of use observed in satellite tracked basking sharks. Most notably off the north-west coast of Ireland, the north coast of Northern Ireland and the waters to the west of the Outer Hebrides. We suggest that the areas of higher relative importance within the proposed MPA boundary should represent zones where vessel speeds are reduced, potentially seasonally between May and October (Speedie et al., 2009), fishing gear, in particular bottom set static gear (entanglement) or trawls (bycatch) are regulated and where leisure and tourist boats should adhere to the wildlife-watching best practise guidelines such as, Scottish Marine Wildlife Watching Code (SMWWC; www.marinecode.org) and the Wise Scheme (www.wisescheme.org) when sharing waters with marine wildlife.

5. Conclusion

Basking sharks are capable of extensive movement (Doherty et al., 2017; Gore et al., 2008; Skomal et al., 2009), and are an important species of conservation concern in UK coastal waters. Until now there has been a paucity of high-resolution, seasonal information on space-use in basking sharks. The present study provides near real-time tracking of multiple individuals at a shared foraging site in the coastal waters off the west coast of Scotland. We identify core activity areas occurring within the boundaries of the proposed MPA, providing an opportunity for specific management to be implemented within the area. Our work also highlights the repeated seasonal use and inter-annual site fidelity of this area, which may provide suitable conditions for other key life-history events as well as foraging. This study was able to substantiate the importance of the area and assess how basking sharks use the proposed MPA prior to designation, a process not usually afforded to most MPAs.

Acknowledgements

This project was funded by Scottish Natural Heritage and the University of Exeter. We extend our sincere thanks to the skippers and crew of the *Sula Crion* and *Bold Ranger* of Sealife Surveys, Tormory. The attachment of satellite transmitters was regulated by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and under the Wildlife & Countryside Act 1981 (as amended) (License(s): 13904,

13937 and 13971). PD was supported by a NERC PhD studentship NEL/L501669/1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.01.018>.

References

- Ashe, E., Noren, D.P., Williams, R., 2010. Animal behaviour and marine protected areas: incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population. *Anim. Conserv.* 13, 196–203.
- Barnett, A., Abrantes, K.G., Stevens, J.D., Semmens, J.M., 2011. Site fidelity and sex-specific migration in a mobile apex predator: implications for conservation and ecosystem dynamics. *Anim. Behav.* 81, 1039–1048.
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299, 389–392.
- Berrow, S.D., Heardman, C., 1994. The Basking Shark *Maximus Cetorhinus* (Gunnerus) in Irish waters: Patterns of Distribution and Abundance. 94B, 101–107.
- Berumen, M.L., Braun, C.D., Cochran, J.E.M., Skomal, G.B., Thorrold, S.R., 2014. Movement patterns of juvenile whale sharks tagged at an aggregation site in the Red Sea. *PLoS One* 9, e103536.
- Beyer, H.L., 2012. Geospatial Modelling Environment (version 0.7.2.1). (<http://www.spatialecology.com/gme>).
- Bonfil, R., MeYer, M., Scholl, M.C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D., Paterson, M., 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310, 100–103.
- Braun, C.D., Skomal, G.B., Thorrold, S.R., Berumen, M.L., 2014. Diving behavior of the reef manta ray links coral reefs with adjacent deep pelagic habitats. *PLoS One* 9, e88170.
- Calenge, C., 2006. The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519.
- Chapman, D.D., Feldheim, K.A., Papastamatiou, Y.P., Hueter, R.E., 2015. There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annu. Rev. Mar. Sci.* 7, 547–570.
- Chin, A., Heupel, M., Simpfendorfer, C., Tobin, A., 2016. Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. *Mar. Ecol. Prog. Ser.* 544, 197–211.
- Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J.A., Goni, R., Borg, J.A., Forcada, A., De Lucia, G.A., Perez-Ruzafa, A., Afonso, P., Brito, A., Guala, I., Le Diréach, L., Sanchez-Jerez, P., Sommerfield, P.J., Planes, S., 2009. Marine reserves: fish life history and ecological traits matter. *Ecol. Appl.* 20, 830–839.
- Coyne, M.S., Godley, B.J., 2005. Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Mar. Ecol. Prog. Ser.* 301, 1–7.
- Doherty, P.D., Baxter, J.M., Gell, F.R., Godley, B.J., Graham, R.T., Hall, G., Hall, J., Hawkes, L.A., Henderson, S.M., Johnson, L., Speedie, C., Witt, M.J., 2017. Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic.
- Domeier, M., Nasby-Lucas, N., 2008. Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Mar. Ecol. Prog. Ser.* 370, 221–237.
- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, M., Harrison, L.R., Carlson, J.K., Davidson, L.N.K., Sonja, V., 2014. Extinction risk and conservation of the world's sharks and rays. *eLife* 3, 1–35.
- Escale, L., Speed, C.W., Meekan, M.G., White, W.T., Babcock, R.C., Pillans, R.D., Huveneers, C., 2015. Restricted movements and mangrove dependency of the nervous shark *Carcharhinus caudatus* in nearshore coastal waters. *J. Fish Biol.* 87, 323–341.
- Farmer, N.A., Ault, J.S., 2011. Grouper and snapper movements and habitat use in Dry Tortugas, Florida. *Mar. Ecol. Prog. Ser.* 433, 169–184.
- Fowler, S.L., 2005. Basking Shark (*Cetorhinus Maximus*). The IUCN Red List of Threatened Species. (www.iucnredlist.org). Downloaded on 17th September 2015.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., Wilmsers, C.C., 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* 2, e207.
- Gitzen, R.A., Millsap, J.J., Kernohan, B.J., 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *J. Wildl. Manag.* 70, 1334–1344.
- Gore, M.A., Rowat, D., Hall, J., Gell, F.R., Ormond, R.F., 2008. Transatlantic migration and deep mid-ocean diving by basking shark. *Biol. Lett.* 4, 395–398.
- Graham, F., Rynne, P., Estevanez, M., Luo, J., Ault, J.S., Hammerslag, N., 2016. Use of marine protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean by large highly mobile sharks. *Divers. Distrib.* 22, 534–546.

- Grüss, A., Kaplan, D.M., Guénette, S., Roberts, C.M., Botsford, L.W., 2011. Consequences of adult and juvenile movement for marine protected areas. *Biol. Conserv.* 144, 692–702.
- Guttridge, T.L., Gulak, S.J.B., Franks, B.R., Carlson, J.K., Gruber, S.H., Gledhill, K.S., Bond, M.E., Johnson, G., Grubbs, R.D., 2015. Occurrence and habitat use of the critically endangered smalltooth sawfish *Pristis pectinata* in the Bahamas. *J. Fish Biol.* 87, 1322–1341.
- Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5, 361–366.
- Hartigan, J.A., Wong, M.A., 1979. Algorithm AS 136: a k-means clustering algorithm. *Appl. Stat.* 28, 100–108.
- Harvey-Clark, C.J., Stobo, W.T., Helle, E., Mattson, M., 1999. Putative mating behavior in basking sharks off the Nova Scotia coast putative mating behavior in basking sharks off the Nova Scotia coast. *Copeia* 3, 780–782.
- Heupel, M.R., Simpfendorfer, C.A., 2005. Using acoustic monitoring to evaluate MPAs for shark nursery areas: the importance of long-term data. *Mar. Technol. Soc. J.* 39, 10–18.
- Hooker, S.K., Gerber, L.R., 2004. Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. *Bioscience* 54, 27.
- Howey-Jordan, L.A., Brooks, E.J., Abercrombie, D.L., Jordan, L.K.B., Brooks, A., Williams, S., Gospodarczyk, E., Chapman, D.D., 2013. Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the western North Atlantic. *PLoS One* 8, e56588.
- Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S., Perle, C., Van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, A.P., Block, B.A., 2010. Philopatry and migration of Pacific white sharks. *Proc. R. Soc. B Biol. Sci.* 277, 679–688.
- Knip, D.M., Heupel, M.R., Simpfendorfer, C.A., 2012. To roam or to home: site fidelity in a tropical coastal shark. *Mar. Biol.* 159, 1647–1657.
- Kock, A., O'Riain, M.J., Maufl, K., Meyer, M., Kotze, D., Griffiths, C., 2013. Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS One* 8, e55048.
- Kunzlik, P.A., 1988. The Basking Shark. 14. Department of Agriculture and Fisheries for Scotland, Aberdeen, UK, 1–21.
- Lauck, T., Clark, C.W., Mangel, M., Munro, G.R., 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecol. Appl.* 8, 72–78.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., Bay, M., 2006. Depletion, degradation and recovery potential of estuaries and coastal seas. *Science* 312, 1806–1809.
- Lyons, A.J., Turner, W.C., Getz, W.M., 2013. Home range plus: a space-time characterization of movement over real landscapes. *Mov. Ecol.* 1–2, 1–14.
- Macleod, C.D., 2014. An Introduction to Using GIS in Marine Biology. Supplementary Workbook Four. Investigating Home Ranges of Individual Animals, Pictish Beast Publications, Glasgow, UK.
- Matthews, L.H., Parker, H.W., 1950. Notes on the anatomy and biology of the basking shark (*Cetorhinus maximus* (Gunner)). *Proc. Zool. Soc. London* 120, 535–576.
- McNeill, S., 1994. The selection and design of marine protected areas: australia as a case study. *Biodivers. Conserv.* 3, 586–605.
- Meyer, C.G., Holland, K.N., Papastamatiou, Y.P., 2007. Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine protected areas. *Mar. Ecol. Prog. Ser.* 333, 13–25.
- Meyer, C.G., Papastamatiou, Y.P., Holland, K.N., 2010. A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (Galeocerdo cuvier) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Mar. Biol.* 157, 1857–1868.
- O'Brien, K., Whitehead, H., 2013. Population analysis of endangered northern bottlenose whales on the Scotian shelf seven years after the establishment of a marine protected area. *Endanger. Species Res.* 21, 273–284.
- Parker, H., Stott, F., 1965. Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). *Zoologische mededelingen* 40, 305–320.
- Paxton, C.G.M., Scott-Hayward, L.A.S., Rexstad, E., 2014. Review of available statistical approaches to help identify Marine Protected Areas for cetaceans and basking shark. In: Scottish Natural Heritage Commissioned Report No. 573.
- R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
- Roberts, C.M., 2000. Selecting marine reserve locations: optimally versus opportunism. *Bull. Mar. Sci.* 66, 581–592.
- Scott, R., Hodgson, D.J., Witt, M.J., Coyne, M.S., Adnyana, W., Blumenthal, J.M., Broderick, A.C., Canbolat, A.F., Catry, P., Ciccione, S., Delcroix, E., Hitipeuw, C., Luschi, P., Pet-Soede, L., Pendoley, K., Richardson, P.B., Rees, A.F., Godley, B.J., 2012. Global analysis of satellite tracking data shows that adult green turtles are significantly aggregated in marine protected areas. *Glob. Ecol. Biogeogr.* 21, 1053–1061.
- Scottish Natural Heritage, 2014. Further Advice to Scottish Government on the Selection of Nature Conservation Marine Protected Areas for the Development of the Scottish MPA Network. (Commissioned Report No. 780).
- Shimada, T., Jones, R., Limpus, C., Hamann, M., 2012. Improving data retention and home range estimates by data-driven screening. *Mar. Ecol. Prog. Ser.* 457, 171–180.
- Sims, D.W., Southall, E.J., Quayle, V.A., Fox, A.M., 2000. Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B Biol. Sci.* 267, 1897–1904.
- Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K.W., Thorrold, S.R., 2009. Transoceanic migrations by basking sharks in the western Atlantic Ocean. *Curr. Biol.* 19, 1019–1022.
- Southall, E.J., Sims, D.W., Metcalfe, J.D., Doyle, J.I., Fanshawe, S., Lacey, C., Shrimpton, J., Solandt, J.-L., Speedie, C.D., 2005. Spatial distribution patterns of basking sharks on the European shelf: preliminary comparison of satellite-tag geolocation, survey and public sightings data. *J. Mar. Biol. Assoc. UK* 85, 1083.
- Speed, C.W., Field, I.C., Meekan, M.G., Bradshaw, C.J.A., 2010. Complexities of coastal shark movements and their implications for management. *Mar. Ecol. Prog. Ser.* 408, 275–293.
- Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Stevens, J.D., McGregor, F., Huveneers, C., Berger, Y., Bradshaw, C.J.A., 2011. Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Mar. Ecol. Prog. Ser.* 429, 261–275.
- Speedie, C.D., Johnson, L.A., Witt, M.J., 2009. Basking shark hotspots on the West Coast of Scotland: key sites, threats and implications for conservation. In: Scottish Natural Heritage Commissioned Report No.339.
- Sprogis, K.R., Raudino, H.C., Rankin, R., Macleod, C.D., Bejder, L., 2016. Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. *Mar. Mamm. Sci.* 32, 287–308.
- Watson, R., Pauly, D., 2001. Systematic distortions in world fisheries catch trends. *Nature* 414, 534–536.
- Westgate, A.J., Koopman, H.N., Siders, Z.A., Wong, S.N.P., Ronconi, R.A., 2014. Population density and abundance of basking sharks *Cetorhinus maximus* in the lower Bay of Fundy, Canada. *Endanger. Species Res.* 23, 177–185.
- Wilson, S.G., 2004. Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. *Fish. Oceanogr.* 13, 283–286.
- Wilson, B., 2016. Might marine protected areas for mobile megafauna suit their proponents more than the animals?. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 26, 3–8.
- Wilson, S.G., Polovina, J.J., Stewart, B.S., Meekan, M.G., 2006. Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Mar. Biol.* 148, 1157–1166.
- Witt, M.J., Broderick, A.C., Coyne, M.S., Formia, A., Nguouesso, S., Parnell, R.J., Sounguet, G.-P., Godley, B.J., 2008. Satellite tracking highlights difficulties in the design of effective protected areas for critically endangered leatherback turtles *Dermostochelys coriacea* during the inter-nesting period. *Oryx* 42, 296–300.
- Witt, M.J., Akesson, S., Broderick, A.C., Coyne, M.S., Ellick, J., Formia, A., Hays, G.C., Luschi, P., Stroud, S., Godley, B.J., 2010. Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. *Anim. Behav.* 80, 571–581.
- Witt, M.J., Hardy, T., Johnson, L., McClellan, C.M., Pikesley, S.K., Ranger, S., Richardson, P.B., Solandt, J.-L., Speedie, C., Williams, R., Godley, B.J., 2012. Basking sharks in the Northeast Atlantic: spatio-temporal trends from sightings in UK waters. *Mar. Ecol. Prog. Ser.* 459, 121–134.
- Wood, L.J., Fish, L., Laughren, J., Pauly, D., 2008. Assessing progress towards global marine protection targets: shortfalls in information and action. *Oryx* 42, 340–351.
- Worm, B., Lotze, H.K., Myers, R.A., 2003. Predator diversity hotspots in the blue ocean. *Proc. Natl. Acad. Sci. U. S. A.* 100, 9884–9888.

SCIENTIFIC REPORTS

OPEN

Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic

Received: 09 June 2016
Accepted: 16 January 2017
Published: xx xx xxx

P. D. Doherty^{1,2}, J. M. Baxter³, F. R. Gell⁴, B. J. Godley^{1,2}, R. T. Graham⁵, G. Hall⁶, J. Hall⁶, L. A. Hawkes², S. M. Henderson⁷, L. Johnson⁸, C. Speedie⁹ & M. J. Witt^{1,2}

Animal migration is ubiquitous in nature with individuals within a population often exhibiting varying movement strategies. The basking shark (*Cetorhinus maximus*) is the world's second largest fish species, however, a comprehensive understanding of their long-term wider-ranging movements in the north-east Atlantic is currently lacking. Seventy satellite tags were deployed on basking sharks over four years (2012–2015) off the west coast of Scotland and the Isle of Man. Data from 28 satellite tags with attachment durations of over 165 days⁵ reveal post-summer ranging behaviours. Tagged sharks moved a median minimum straight-line distance of 3,633 km; achieving median displacements of 1,057 km from tagging locations. Tagged individuals exhibited one of three migration behaviours: remaining in waters of UK, Ireland and the Faroe Islands; migrating south to the Bay of Biscay or moving further south to waters off the Iberian Peninsula, and North Africa. Sharks used both continental shelf areas and oceanic habitats, primarily in the upper 50–200 m of the water column, spanning nine geo-political zones and the High Seas, demonstrating the need for multi-national cooperation in the management of this species across its range.

Animal migration is based upon individuals or groups of individuals attempting to secure optimal environmental conditions and exploit habitats during seasonal changes, and is observed in a wide range of taxa¹. Some individuals within a population often adopt differing migration strategies, which may result from either inter- or intra-individual plasticity with regards to their fidelity to a particular site. The strength of such fidelity can be affected by food availability, reproductive status, competition, predation risk, or body condition². Describing seasonal and migratory movements in large marine vertebrates can be challenging, largely due to their wide ranging behaviour and the complexities of tracking individuals in water for durations sufficient to observe migratory behaviour³. However, advances in satellite tracking technologies and attachment techniques now allow for repeated observations of movements and insights into intra- and inter-individual variation over extended time-scales⁴, enhancing our ability to assess life history traits, distribution and extent of range, site fidelity, migratory movements^{4–6} and exposure to human threat.

Many sharks undertake migrations and utilise resources in different habitats with residency and fidelity varying at different spatial and temporal scales⁷, with further evidence of behavioural plasticity^{8–11}. The basking shark (*Cetorhinus maximus*) is the world's second largest fish species, historically overexploited for its large liver¹² resulting in large local population declines leading to recognition by the International Union for Conservation of Nature (IUCN) as Vulnerable globally, and Endangered in the north-east Atlantic¹³; with further designations on a range of conservation legislation in the UK and Europe and inclusion under several international conservation

¹Environment & Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK. ²Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK. ³Scottish Natural Heritage, Silvan House, 231 Corstorphine Road, Edinburgh, EH12 7AT, UK. ⁴Department of Environment, Food and Agriculture, Thie Sileau Whallian, Foxdale Road, St John's, Isle of Man, IM4 3AS. ⁵MarAlliance, PO Box 283, San Pedro, Ambergris Caye, Belize. ⁶Manx Basking Shark Watch, Glen Chass Farmhouse, Port St Mary, Isle of Man, IM9 5PJ. ⁷Scottish Natural Heritage, Great Glen House, Inverness, Scotland, IV3 8NW, UK. ⁸Wave Action, 3 Beacon Cottages, Falmouth, TR11 2LZ, UK. Correspondence and requests for materials should be addressed to M.J.W. (email: M.J.Witt@exeter.ac.uk)

treaties (Table S2). The species has a circumglobal distribution and can undertake extensive trans-oceanic basin migrations^{14,15}; although the relative frequency and function of these migrations is unknown. Aggregations of basking sharks occur seasonally in temperate continental shelf waters of the Atlantic, Pacific and Indian Oceans to feed, but potentially also for mating and parturition¹⁶. Population size and structure estimates for the basking shark in the north-east Atlantic are unknown¹⁷, although a sub-regional estimate has been conducted¹⁸. Tracking studies in the region have successfully tracked basking sharks for up to 245 days, showing movements into the open ocean, the waters of the Bay of Biscay^{19,20} and one trans-Atlantic crossing¹⁴. These studies however have been limited by sample size, with the majority of movements confined to the continental shelf of the north-east Atlantic ($n = 2^{14}$, $n = 7^{19,21,22}$, $n = 9^{20}$). With growing concern regarding the rate of decline of global shark populations²³, the importance of defining the extent and connectivity of mobile species populations has increased²⁴.

Basking sharks are considered to be vulnerable to interactions with commercial fishing; potentially becoming entangled in set nets, pot lines or caught incidentally in trawls and is considered as one of the more valued fins within the shark fin trade¹³.

Anthropogenic activity in the north-east Atlantic is increasing²⁵, therefore improved knowledge could be instrumental in supporting management decisions²⁶, including mitigation of putative threats such as fisheries bycatch²⁷. Area-based protection measures are often implemented based on the majority of individuals exhibiting repeated behaviours and movement patterns. Behavioural plasticity can result in a range of movement strategies, sometimes resulting in groups of individuals moving away from areas originally designated for their protection⁹. These groups may then remain at heightened risk of mortality. Consequently these behaviours may lead to specific groups (potentially based on sex, ages, reproductive status and condition) being at more risk²⁸. In this study, long-term movement data gathered from satellite tags attached to basking sharks at known summer 'hotspots' off the west coast of Scotland and the Isle of Man^{29,30}, were used to examine patterns of individual movement and subsequent post-summer migration strategies. Particular attention is given to over-wintering distributions as least is known of basking shark spatial ecology during this period, hence this represents one of the missing links to a more comprehensive understanding of their lifecycle.

Results

Satellite tracking. Basking sharks satellite tracked into the year following tag deployment ($n = 28$) using real-time tags (SPOT; Wildlife Computers) and light-geolocation archival tags (MiniPAT; Wildlife Computers) provided data for 281 days (IQR: 247–349; max. 479), moved a median minimum straight-line distance of 3,633 km (IQR 4,996–1,987, range: 469–8,081 km) and were displaced by a median of 1,057 km from their respective tagging locations (IQR: 1,384–557; range: 264–2,711 km). Sharks tracked using SPOTs collected data for a median 322 days (IQR: 252–375; max. 479), moved a median straight-line distance of 2,280 km (IQR: 3,375–1,456; range: 469–4,310 km) and were displaced by a median of 1,057 km from their respective tagging locations (IQR: 1,560–374; range: 264–2,711 km). Sharks tracked using MiniPATs collected data for a median 265 days (IQR: 280–199; max. 292), moved a median straight-line distance of 6,050 km (IQR: 7,029–4,044; range: 2,333–8,081 km) and were displaced by a median of 1,007 km from their respective tagging locations (IQR: 1,219–744; range: 455–2,354 km).

There was no significant interaction effect of sex and estimated body length on the maximum displacement or the minimum latitude recorded by these sharks (GLMM: $\chi^2 = 5.64$, $p = 0.06$ and $\chi^2 = 5.66$, $p = 0.06$ respectively). There were no significant effects of sex, body length or tag attachment duration on the maximum displacement or the minimum latitude recorded by these sharks (GLMM maximum displacement by sex: $n = 16$, $\chi^2 = 1.49$, $p = 0.47$; by body length: $n = 28$, $\chi^2 = 0.05$, $p = 0.83$ and by tag attachment duration: $\chi^2 = 0.42$, $p = 0.52$. GLMM minimum latitude by sex: $n = 16$, $\chi^2 = 0.74$, $p = 0.69$; by body length: $n = 28$, $\chi^2 = 0.16$, $p = 0.69$ and by tag attachment duration: $n = 28$, $\chi^2 = 0.21$, $p = 0.64$).

Migration strategies. Basking sharks exhibited wide-ranging post-summer movements, stretching from 33° to 61°N latitude (approx. 3,100 km) within a longitudinal range (2° to 20°W); along the eastern fringe of the North Atlantic Ocean (Fig. 1 and Figs S2–4). The general pattern of movement followed a transition to more southerly latitudes from October onwards in each year. These movements varied in distance and duration, with some individuals making short-range movements from the tagging areas and others undertaking longer-range movements (Fig. 2 and Figs S1 and S3–5). Three post-summer migration strategies were identified from archival tags ($n = 12$); (a) *Celtic Seas* - predominantly remaining in UK and Ireland, with some movement into waters of the Faroe Islands ($n = 6$; max. displacement range: 455–854 km; one female, one male, four unknown sex), (b) *Bay of Biscay* - movement south to the Bay of Biscay ($n = 5$; max. displacement range: 1,161–1,515 km; four females, one male), and (c) *Iberian Peninsula & North Africa* - movement further afield to waters off the west coast of Portugal and North Africa ($n = 1$; max. displacement: 2,354 km; one unknown sex; Fig. 2, Table S5). For Argos Doppler-based geolocation tags ($n = 16$; three females, six males, seven unknown sex), sharks were displaced by a range of 264–2,711 km.

The furthest movement observed was undertaken by a basking shark during a three-month tracking period using a SPOT tag. This individual departed the west of Scotland tagging area in the month following tag application (August 2012), transited to the west of Ireland and the European mainland and arrived in North African waters in November 2012, at which point the tag ceased transmission (Fig. S5F; minimum straight line along-track distance: 3,949 km, straight line displacement from tagging location: 3,088 km).

Return migrations. We observed varying degrees of return migration ($n = 15$ tags) in the years following tagging; which can be described as (i) departing the coastal regions of the UK, Isle of Man and Ireland (August to October), and return the following spring/summer (March to June) while remaining within the Exclusive

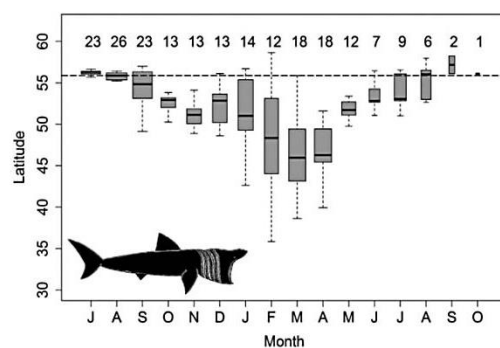


Figure 1. Minimum latitude observed for 28 satellite-tracked basking sharks. Box and whisker plots showing minimum latitudes per shark per month from tag deployment (July onwards). Boxes denote inter-quartile range; horizontal black bar indicates the median (whiskers extend to the 2.5th and 97.5th percentiles). Box width indicates relative data volume of (sample size) for each month; with number of individual sharks contributing to each box shown above corresponding box. Broken line indicates average latitude of tag deployments.

Economic Zone (EEZ) of the UK and Ireland throughout the winter (Fig. 4a and d, n = 6; tag numbers: 119846 (Fig. S2B), 129439 (Fig. S2C), 129440 (Fig. S2D), 129442 (Fig. S2E), 129457 (Fig. S2G) and 137654 (Fig. S2I)); (ii) movement outside the EEZ of the UK and Ireland during the winter, but return to the Celtic Seas (Fig. 4b and d, n = 3; tag numbers: 129452 (Fig. S3G), 129455 (Fig. S3I) and 129444 (Fig. S3B)); or West Ireland (n = 5; tag numbers: 119853 (Fig. S3A), 129437 (Fig. S3B), 129448 (Fig. S3E), 129456 (Fig. S3J), and 129458 (Fig. S4C)) in spring, having undertaken migration strategy b; *Bay of Biscay* (n = 6; tag numbers: 119853 (Fig. S3A), 129437 (Fig. S3B), 129448 (Fig. S3E), 129452 (Fig. S3G), 129455 (Fig. S3I), and 129456 (Fig. S3J)), or migration strategy c; *Iberian Peninsula & North Africa* (Fig. 4d, n = 2; PTT numbers: 129444 (Fig. S4B) and 129458 (Fig. S4C)); or (iii) full return migration, returning to the region of tag attachment (approx. 20 km) after over-wintering outside of UK and Irish waters (Fig. 4b, n = 1; PTT number 129449 (Fig. S3F)). This is the first observation of such return migration in this species.

Based on archival tag data, post-summer movements (October onwards) indicated basking sharks entered the EEZs of Iceland (<1% of all locations), Faroe Islands (2%), UK (18%), Ireland (51%), France (3%), Spain (4%), Portugal (4%), Madeira (<1%), Morocco (<1%), and the High Seas (18%; Fig. S1). Areas of relative high importance for the tracked sharks (Fig. 3) include the waters to the west coast of Scotland, the Celtic and Irish Seas and, in particular the areas west of Ireland along the continental shelf break. These areas experienced a relatively high degree of usage by tracked sharks, somewhat indicative of an overwintering ground that links foraging grounds in the waters off the west coast of the UK and Ireland to the destinations adopted by each of the three migration strategies observed (Fig. 3a).

Depth-use. For those basking sharks tracked with light-geolocation archival tags, data on depth-use were also available. These data highlighted sharks (n = 12) predominantly occupied the epipelagic zone (0–200 m depth; mean 84% of tracking time; Table S5) regardless of migration strategy ((a) *Celtic Seas*: 91%; (b) *Bay of Biscay*: 82%; (c) *Iberian Peninsula & North Africa*: 59%; Fig. 5; Table S5). Individuals exhibiting migration strategy a and b spent the majority of their time in waters 50–200 m deep (80.2% and 78.2% respectively); whereas, individuals exhibiting migration strategy c spent the majority of time in depths between 100 and 500 m (66.2%; Figs 4 and 5; Table S5).

Discussion

The ability to record intra- and inter-individual variation in the movement and distribution of large marine vertebrates is becoming increasingly possible and provides important information on species space-use^{3–5,31}, and has resulted in migration being observed in many taxa^{1,28}. Our study provides the most detailed investigation of basking shark ranging behaviours in the north-east Atlantic over seasonal timescales to be informed by satellite tracking³².

Little is known about basking shark habitat or site preference during the winter as their vertical distribution indicates they spend a large proportion of time away from the surface. Anatomical studies previously suggested that basking sharks hibernate in deep waters around the UK and Ireland during the winter^{33–35}. In recent years, however, theories around hibernation have become improbable due to increasing levels of information from electronic tags^{19,36,37}. Sims *et al.*¹⁹ showed that basking sharks do not lie dormant during the winter months, but show frequent vertical movements throughout the water column with close association to the continental shelf edge, providing evidence that these sharks likely do not hibernate. More recent studies have shown that this species makes oceanic scale movements post-summer, travelling towards Newfoundland from the Isle of Man¹⁴, although this has only been observed in a single individual. Extensive north-south autumn migrations have been observed from basking sharks tagged in coastal waters of north-east United States, with tracked individuals crossing the

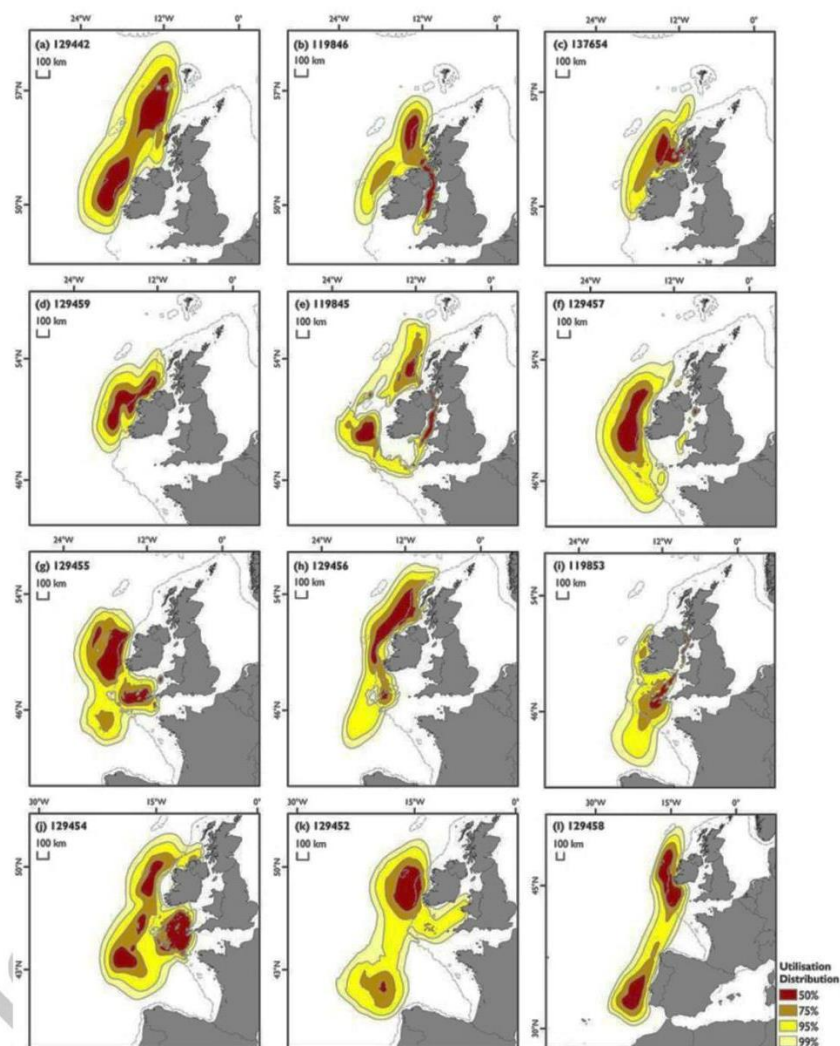
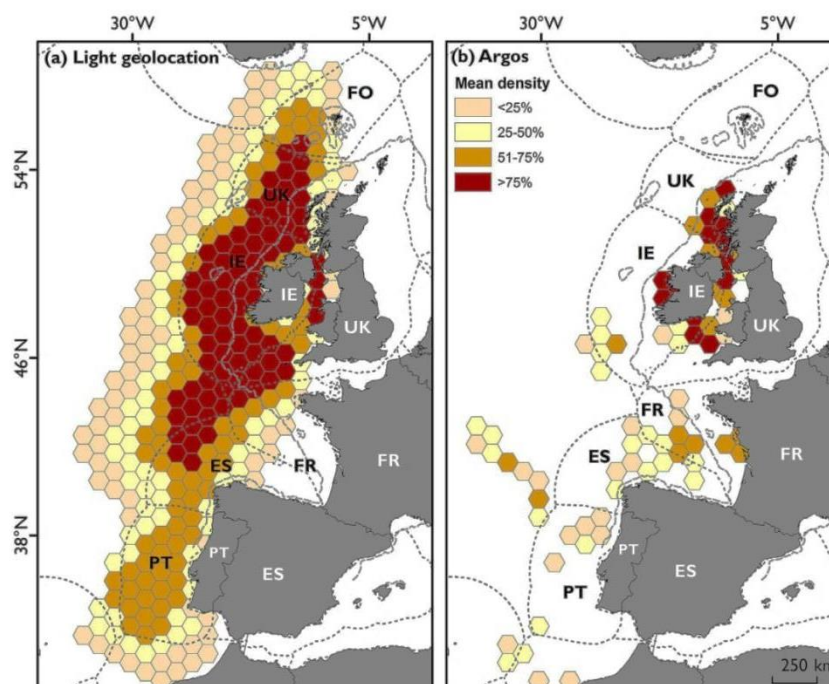


Figure 2. Overall post-summer (October onwards) distribution of individual tracked basking sharks from light-geolocation archival tags ($n = 12$). Normalised Utilisation Distributions (UDs); shaded according to probability of area of space-use. Panels ordered by migration range with tag number shown. Broken grey line indicates 200 m depth contour (source: <http://www.gebco.net>). Maps created in ESRI ArcGIS version 10.1 using ESRI land shapefiles.

equator into tropical waters off the coast of Brazil¹⁵. It seems increasingly improbable that this species exhibits a sedentary phase during winter months (based on an assessment of movement), and it remains unknown if basking sharks forage during this time, however, there is evidence for diel vertical migration (DVM) occurring away from the surface post-summer²², similar in form to DVM patterns seen in summer months attributed to associating with the diel vertically migrating *Calanus sp.* layer³⁸. There is the potential for basking sharks to subsist on fat reserves in the liver, which has been observed in white sharks (*Carcharodon carcharias*) where these sharks exhibited an increased vertical downward drift rate over the course of long migration movements (>4,000 km), which is indicative of decreased buoyancy caused by the depletion of liver lipid reserves³⁹. This depletion of lipid reserves has also been noted in historical testimonies from basking shark fishers claiming basking sharks caught earlier in the season had lighter livers⁴⁰.



Q2 **Figure 3.** Grid density enumeration identifying areas of relative importance for tracked basking sharks post-summer (October onwards; 2012–2016) for locations derived from light-geolocation archival tags (a; $n = 12$) and Argos real-time tracking tags (b; $n = 16$). Mean occurrences from individual basking sharks enumerated on a hexagonal grid (cell edge size: 50 km; cell area: 8,660 km²). Country Economic Exclusive Zones denoted by light-grey broken line with associated international two letter codes (white letters = land, black letters = EEZs; FO = Faroe Islands, UK = United Kingdom, IE = Ireland, FR = France, ES = Spain). Broken dark grey line denotes 200 m depth contour. Maps created in ESRI ArcGIS version 10.1 (<http://desktop.arcgis.com/en/arcmap>) using ESRI land shapefiles, GEBCO bathymetric contours (<http://www.gebco.net>) and Flanders Marine Institute (VLIZ) Economic Exclusive Zone (EEZ) boundaries (<http://www.marinerregions.org>).

Historically there have been contrasting opinions on this species' long-term movements and distribution, with suggestions of that basking sharks over-winter as a single population off the coast of North Africa returning North in the spring¹², however, there was a counter argument citing that there was no predictability in first appearance of basking sharks during the spring/summer season from Portugal/Spain northwards as the season progressed⁴¹. We show that it is unlikely that all basking sharks adopt a single migration strategy, but more likely plasticity occurs within the population, resulting in individuals performing varying movement strategies. It is not yet known whether adopted migration strategy by individuals is annually consistent or changes with body condition, reproductive status, resource availability or other factors.

The primary drivers behind basking shark migrations are still unclear, but may include; searching for foraging grounds, thermoregulation by moving to areas and/or depths of preferred temperature, movement towards mating grounds or natal homing. Skomal *et al.*¹⁵ hypothesised that within the north-east Atlantic, stable environmental conditions are mediated by the Gulf Stream, limiting the extent to which basking sharks need to move during winter months to find sufficient food. We find that at least some individuals do undertake large-scale latitudinal movements throughout the winter in the north-east Atlantic, somewhat similar to their results from the north-west Atlantic. We have observed the first evidence of round-trip migrations by individuals leaving UK and Irish waters, over-wintering elsewhere, returning to these coastal waters during the spring and summer. Some tracks ended off North Africa with no evidence of return movements, which may be an artefact of tag attachment duration, with premature tag detachment potentially occurring from biofouling of the tag, predation of the tag by other species or removal of the tag during incidental bycatch. There remains the possibility that sharks could move further south, as has been shown in the north-west Atlantic¹⁵. Shark movements were reconstructed for this study using Argos real-time Doppler geolocation and light-geolocation; these techniques differ in that Argos Doppler-based geolocation only provides estimates of locations when the tag is at the surface. During the winter, sharks spend proportionally less time at the surface, limiting opportunities to gather information on their location during this period. In contrast, light geolocation can be near-continuous, particularly when integrated with

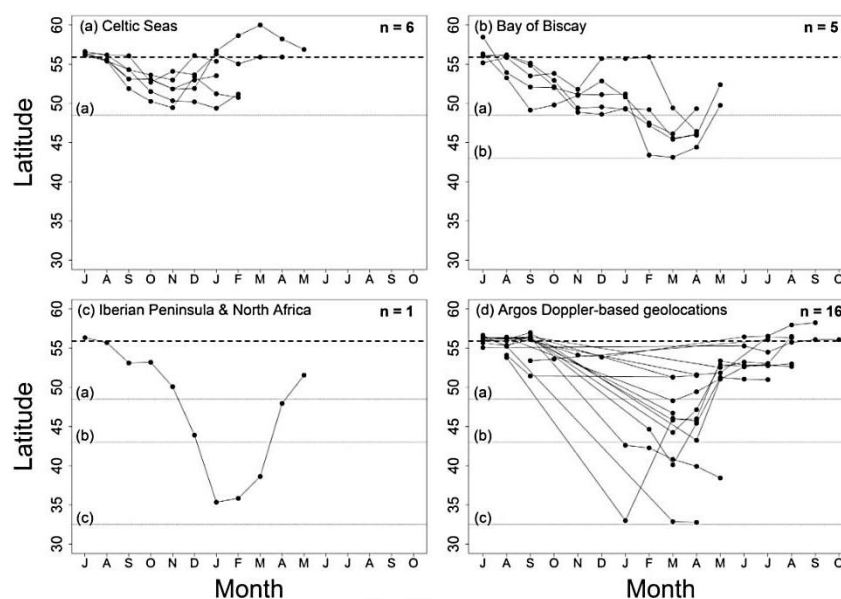


Figure 4. Plots showing minimum monthly latitudes occupied for each tracked shark from tag deployment (July onwards), derived from best daily location estimates from archival tags ($n = 12$) separated by migration strategy (a–c) and all Argos Doppler-based geolocation tracked sharks (d; $n = 16$). Maximum southerly latitude for migration strategies (narrow dashed horizontal and labelled lines). Tag deployment locations (thick dashed horizontal line).

predictive models of animal movement to provide estimates of location when light geolocation is unsuccessful. Our assignment of migration strategy likely underestimates the extent of potential movement for sharks tagged with SPOT tags. Nonetheless, all migration strategies (a to c) were observed independently in the light geolocation data; therefore, broad scale, geographic patterns of movement described here are likely not artefacts of the positioning technology used.

Continued development of tag technology and attachment techniques will allow for multi-year deployments, increasing the ability to quantify individual variability and highlight the likely potential for condition-dependent ranging. Further work is also required to quantify the frequency of newly observed ranging behaviours, whereby individuals adopt a differing behaviour to that of the modal strategy, as these individuals are likely important for maintaining genetic diversity (thought to be low⁴²) and ensure the species has the potential to exploit all areas of the realised or fundamental niche^{43,44}. Greater knowledge on behavioural plasticity may also help improve predictions on how this large planktivorous species might respond to environmental disturbance and climate change, where fidelity to areas may diminish or strengthen as locations that are regularly used by individuals become less suitable, either for foraging or breeding². This may be pertinent for basking sharks, as climate change has been suggested to influence the distribution of their preferred prey group (calanoid copepods^{45,46}), possibly making some areas less suitable for this species, offering one possible explanation for declines in basking shark sightings within areas of its historical range⁴⁷. Highlighting the full range of movements made by a species and partitioning of time within these areas is integral to implementing effective international conservation measures for highly mobile species^{7,48}.

In this study, satellite tracked basking sharks largely remained within the EEZs of the UK and Ireland; they also appeared to occupy waters of seven other geo-political zones and the High Seas. In a previous study⁴⁹ it was shown that basking sharks spent a higher proportion of their time in the UK EEZ (31%) to that of our study (18%), however, this study showed a much greater use of the France EEZ (22%) than our study (3%) and much less occupancy of the Ireland EEZ (15%) to that shown here (51%). No use of International waters away from the European continental shelf was shown, whereas we observed basking sharks showing appreciable levels of occupancy of the High Seas (18%). This may be due to shorter tag attachment durations of the previous study, resulting in more data from summer and autumn months. Our study therefore stresses the need for multi-national cooperation in developing a comprehensive conservation strategy for this species, which is still likely recovering from historical exploitation. This is especially apparent during winter months where plasticity in basking shark behaviour results in multiple geo-political zones being occupied by the population and often away from protective areas. Whilst there are no longer targeted fisheries for basking sharks, by-catch is an area of concern and research in UK waters⁵⁰ has identified incidental catches occurring in fisheries operating off south Ireland in surface and bottom set gill nets^{51,52}, north-west Iberian Peninsula in artisanal gill net fisheries⁵³ and in New Zealand, where

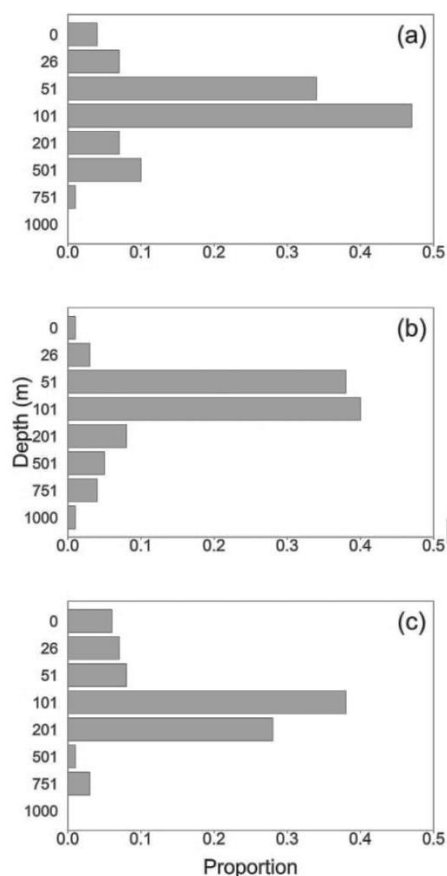


Figure 5. Proportion of daily maximum depths derived from archival tags within eight depth bins for associated migration strategy; (a) Celtic Seas, (b) Bay of Biscay and (c) Iberian Peninsula and North Africa.

basking sharks are a frequent bycatch of trawl and set net fisheries³⁶, all with uncertain levels of mortality. The waters to the west of Ireland and the Celtic and Irish Seas are likely important areas for basking sharks, acting as migratory pathways linking foraging areas in the waters off the west coast of Scotland to other areas of importance to basking shark life-history events, which may also include other seasonal foraging or breeding sites. Active fisheries operating within the Irish EEZ, include demersal otter trawling, (approx. 62% of total fishing hours between 2008 and 2012), longliners (15%), gill and trammel nets (7%) and pelagic trawlers (5%) the other most operated gear types⁵⁴. The majority of fishing activity within the Irish EEZ is by foreign vessels (Spanish = 30%, French = 20%, and the UK = 11%), with Irish vessels accounting for 36% of activity with combined landings of over 394,000 tonnes in 2012⁵⁴. The UK is a signatory to the Convention for Migratory Species with Ireland, France, Portugal, Spain and Morocco; all range states for basking sharks, mandating multi-national cooperation over management of shared activities within ranges of species of conservation concern. An onboard bycatch observer programme may provide a useful tool in which to assess the potential impact of bycatch on basking sharks³⁶. This would inform on the extent to which basking sharks are being incidentally caught, and provide baseline information on gear type, effort, and potentially mortality rates within these fisheries from which to form an evidence-based conservation programme.

Satellite tracking has greatly improved our understanding of animal movements. This study further contributes to the growing knowledge of basking shark movements and behaviour, especially for those aspects of movement that have remained elusive, such as during winter months in the north-east Atlantic. We show behavioural plasticity within the population, with individuals exhibiting one of three migration strategies and the capacity to move from coastal to oceanic habitats. Individuals can undertake movements at an oceanic scale, crossing multiple geo-political zones following periods of residency. Our work has highlighted a potentially important movement corridor along the continental shelf off western Ireland, which may leave a proportion of the population

vulnerable for extended periods to trawl and set–net fishery interactions. We did not detect segregation by sex or size in our study, behaviours that are often reported for sharks^{55,56}. We cannot fully ascertain whether this is not occurring in basking sharks, or whether sample size and access to a full range of size and sex in which to tag affected the results seen. The continued development of tag technology, in particular battery life and minimising biofouling, will allow for longer attachment times, which will increase our understanding of the drivers of movement in this species and intra- and inter-individual movement across multiple years, in order to identify key habitats and behaviours and overlap with potential threats. This research can be coupled with other fast-developing techniques such as stable isotopes and genetic analysis, to better estimate population sizes and relatedness and to begin to understand foraging strategies, especially during winter months.

Methods

Seventy satellite tags (Smart Position or Temperature tags; SPOT = 32; Pop-up Archival Transmitting with Fastloc™ GPS tags; PAT-F = 12; Mini Pop-up Archival Transmitting tag; Mini-PAT = 12; SPLASH-F = 14; Wildlife Computers, Washington, USA) were attached to basking sharks off the west coast of Scotland (n = 62) and Isle of Man (n = 8) during June, July and August in 2012 (n = 21), 2013 (n = 36), 2014 (n = 10) and 2015 (n = 3)³² (for tag programming and deployment see supplementary materials). The attachment of satellite transmitters in Scottish coastal waters protocol was approved by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (issuing Project Licence 30/2975). All work was carried out in accordance with the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971) and internally through the University of Exeter's animal welfare and ethics review board (AWERB). Licences to tag sharks in the Isle of Man were issued by the Department of Environment, Food and Agriculture (Isle of Man Government) under the Wildlife Act 1990. Data gathered from 29 sharks (SPOT = 16; PAT-F = 3; Mini-PAT = 8; SPLASH-F = 2) were selected for detailed analysis; these sharks were either tracked into at least the January following tag attachment (n = 28; >165 days of tracking; Table S2), or were tracked making long-range movements away from the north-east Atlantic over a shorter period of time (n = 1; Table S2). All tag data were downloaded from CLS-Argos and archived using the Satellite Tracking and Analysis Tool (STAT)⁵⁷. Basking sharks were geolocated during their tracking periods using either standard Argos Doppler-based geolocation when sharks were at the surface (n = 16; SPOT and SPLASH-F tags) or light-based geolocation throughout the tag attachment period (n = 12; PAT-F, Mini-PAT and SPLASH-F tags). These data were subsequently processed to single daily tracking locations for each individual. Argos Doppler-based geolocation filtering was achieved using the *adehabitat* package⁵⁸.

Light geolocation data were obtained from archival tags (n = 12, one SPLASH-F tag failed to transmit sufficient light level data for track reconstruction) and analysis of light level data was undertaken by *Collecte Localisation Satellites* (CLS-Argos) (www.argos-system.org). Obtaining daily estimates of location from gathered light data can be challenging for basking sharks as they often spend prolonged periods at depth or exhibit diel vertical migration (DVM), reducing reliability of some light data²². Therefore, to reconstruct the likely movement paths of basking sharks, we used Hidden Markov Models (HMM) implemented as grid filters⁵⁹ to estimate the daily probability density (or Utilisation Distribution; UD) of the location of tracked animals making use of validated light-based estimates of location to influence the resulting modelled trajectories⁶⁰. The HMM used a two-step process, whereby at each sampling time a position prediction step, solving the advection-diffusion equation for the two-dimensional probability of an animal's presence, was implemented⁶¹. An update step was then performed to combine the predicted probability density using information on latitude, longitude, SST (GHRSSST-OSTIA; <https://www.ghrsst.org/>) and depth (etopo2; <https://www.ngdc.noaa.gov/mgg/global/etopo2.html>) recorded onboard the tag to produce the posterior distribution of the individual⁶¹. Locations derived from light intensity (obtained using Wildlife Computers GPE2 software) were used as observations. These data were constrained by bathymetry⁶⁰, SST and known deployment and pop-off locations. The diffusion coefficient of the HMM model was set to 1,000 km²d⁻¹; the standard deviation of raw light based locations used in the update step was set to 1° longitude and 3.5° latitude and the standard deviation of the difference between recorded and satellite derived SST was set to 0.5 °C⁶¹. The best daily estimate of location for these tags was taken to be the geographic mean of the grid locations weighted by their probability. Once daily UDs were calculated for each tag for the duration of the tag attachment, these were normalised and summed to provide the probability of the animal's presence in the extent of the grid filter for its time at liberty. For each daily distribution probability raster, percentage volume contours (PVC) were calculated to produce density kernels exhibiting likelihood of presence (Fig. 2). UDs for each shark were created for entire time at liberty post-summer (October onwards). Data from PAT-F, MiniPAT and SPLASH-F tags recording depth (n = 12) were used to estimate time spent within pre-determined depth ranges.

To determine areas of high relative importance for tracked basking sharks polygon sampling grids bounded by the maximum limits of observed movement were spatially intersected with filtered tracking locations for Argos Doppler-based geolocation and raster values for light-based geolocation (hexagonal cells; 50 km from grid cell centroid to edge; cell area 8,660 km²). The size of the grid cells was based on the mean error across all light-based geolocation tags (97.68 km). The mean occurrence of daily locations within grid cells was calculated for each individual followed by a spatial mean calculated across all individuals. All spatial analyses and maps were created using Geospatial Modelling Environment (GME v 0.7.2.1)⁶² and ESRI ArcMap 10.1.

K-means cluster analysis was used to separate individual tracks into migration strategy groups⁶³ based on most southerly latitude observed using best daily locations, which was used as a proxy for putative migration strategy. This analysis was conducted using archival tags only (n = 12), as data provided information on the full extent of movement with robust evidence of most southerly latitude reached, followed by return movements North in the spring. All data analyses were performed in R⁶⁴.

To examine the effect of basking shark sex, body length and tag attachment duration on movement we used General Linear Mixed-effect Modelling (GLMMs; *lme4* package⁶⁵). For this analysis the maximal model was fitted with all biologically relevant interactions. The significance of fixed effects were assessed by comparing maximum likelihood ratios of the maximal model to the model without the fixed effect, with non-significant interactions removed to test the main effects⁶⁶.

References

- Dingle, H. *Migration: The Biology of Life on the Move*. Second Edition. (Oxford University Press, 2014).
- Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P. & Hueter, R. E. There and Back Again: A Review of Residency and Return Migrations in Sharks, with Implications for Population Structure and Management. *Ann. Rev. Mar. Sci.* **7**, 547–570 (2015).
- Hammerschlag, N., Gallagher, A. J. & Lazarre, D. M. A review of shark satellite tagging studies. *J. Exp. Mar. Biol. Ecol.* **398**, 1–8 (2011).
- Hussey, N. E. *et al.* Aquatic animal telemetry: A panoramic window into the underwater world. *Science* **348**, 1255642 (2015).
- Block, B. A. *et al.* Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90 (2011).
- Rosenbaum, H. C., Maxwell, S. M., Kershaw, F. & Mate, B. Long-range movement of humpback whales and their overlap with anthropogenic activity in the South Atlantic Ocean. *Conserv. Biol.* **28**, 604–615 (2014).
- Werry, J. M. *et al.* Reef-Fidelity and Migration of Tiger Sharks, *Galeocerdo cuvier*, across the Coral Sea. *PLoS One* **9**, e83249 (2014).
- Papastamatiou, Y. P. *et al.* Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology* **94**, 2595–2606 (2013).
- Lea, J. S. E. *et al.* Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Sci. Rep.* **5**, 11202 (2015).
- Weng, K. C. *et al.* Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Mar. Ecol. Prog. Ser.* **372**, 253–264 (2008).
- Boustany, A. M. *et al.* Expanded niche for white sharks. *Nature* **415**, 36–37 (2002).
- Kunzlik, P. A. The Basking Shark. *Dep. Agric. Fish. Scotland, Aberdeen, UK* **14**, 1–21 (1988).
- Fowler, S. L. Basking Shark (*Cetorhinus maximus*). The IUCN Red List of Threatened Species. www.iucnredlist. Downloaded on 17th September 2015. eT4292A107 (2005).
- Gore, M. A., Rowat, D., Hall, J., Gell, F. R. & Ormond, R. F. Transatlantic migration and deep mid-ocean diving by basking shark. *Biol. Lett.* **4**, 395–8 (2008).
- Skomal, G. B. *et al.* Transequatorial migrations by basking sharks in the western Atlantic Ocean. *Curr. Biol.* **19**, 1019–1022 (2009).
- Sims, D. W., Southall, E. J., Quayle, V. A. & Fox, A. M. Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B Biol. Sci.* **267**, 1897–1904 (2000).
- Sims, D. W. Sieving a living: a review of the biology, ecology and conservation status of the plankton-feeding basking shark *Cetorhinus maximus*. *Adv. Mar. Biol.* **54**, 171–220 (2008).
- Gore, M. A., Frey, P. H., Ormond, R. F., Allan, H. & Gilkes, G. Use of Photo-Identification and Mark-Recapture Methodology to Assess Basking Shark (*Cetorhinus maximus*) Populations. *PLoS One* **11**, e0150160 (2016).
- Sims, D., Southall, E., Richardson, A., Reid, P. & JD, M. Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Mar. Ecol. Prog. Ser.* **248**, 187–196 (2003).
- Stéphan, E., Gadenne, H. & Jung, A. Sur les traces du requin pélerin Satellite tracking of basking sharks in the North-East Atlantic Ocean. *Assoc. Pour l'Etude la Conserv. des Séliaciens* (2011).
- Sims, D. W., Witt, M. J., Richardson, A. J., Southall, E. J. & Metcalfe, J. D. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proc. Biol. Sci.* **273**, 1195–201 (2006).
- Shepard, E. *et al.* Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Mar. Ecol. Prog. Ser.* **328**, 205–213 (2006).
- Dulvy, N. K. *et al.* Extinction risk and conservation of the world's sharks and rays. *Elife* **3**, 1–35 (2014).
- Heupel, M. R. *et al.* Conservation challenges of sharks with continental scale migrations. *Front. Mar. Sci.* **2** (2015).
- Halpern, B. S. *et al.* A global map of human impact on marine ecosystems. *Science* (80–) **319**, 948–952 (2008).
- Allen, A. M. & Singh, N. J. Linking Movement Ecology with Wildlife Management and Conservation. *Front. Ecol. Evol.* **3**, 1–13 (2016).
- Witt, M. J. *et al.* Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic. *Proc. R. Soc. B Biol. Sci.* **278**, 2338–2347 (2011).
- Milner-Gulland, E. J., Fryell, J. M. & Sinclair, A. R. E. *Animal migration: A synthesis*. (Oxford University Press, 2011).
- Southall, E. J. *et al.* Spatial distribution patterns of basking sharks on the European shelf: preliminary comparison of satellite-tag geolocation, survey and public sightings data. *J. Mar. Biol. Assoc. UK* **85**, 1083 (2005).
- Witt, M. J. *et al.* Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters. *Mar. Ecol. Prog. Ser.* **459**, 121–134 (2012).
- Hart, K. M. & Hyrenbach, K. D. Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endanger. Species Res.* **10**, 9–20 (2009).
- Witt, M. J. *et al.* Basking shark satellite tagging project: insights into basking shark (*Cetorhinus maximus*) movement, distribution and behaviour using satellite telemetry. Final Report. *Scottish Nat. Herit. Comm. Rep. No. 908* (2016).
- Matthews, L. H. & Parker, H. W. Notes on the anatomy and biology of the Basking Shark (*Cetorhinus maximus* (Gunner)). *Proc. Zool. Soc. London* **120**, 535–576 (1950).
- Parker, H. W. & Boseman, M. The Basking Shark, *Cetorhinus maximus*, in winter. *Proc. Zool. Soc. London* **124**, 185–194 (1954).
- Matthews, L. H. The Shark That Hibernates. *New Sci.* **280**, 756–759 (1962).
- Francis, M. P. & Duffy, C. Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. *Mar. Biol.* **140**, 831–842 (2002).
- Skomal, G. B., Wood, G. & Caloyianis, N. Archival tagging of a basking shark, *Cetorhinus maximus*, in the western North Atlantic. *J. Mar. Biol. Assoc. UK* **84**, 795–799 (2004).
- Sims, D. W., Southall, E. J., Tarling, G. A. & Metcalfe, J. D. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J. Anim. Ecol.* **74**, 755–761 (2005).
- Del Raye, G., Jørgensen, S. J., Krumhansl, K., Ezcurra, J. M. & Block, B. A. Travelling light: white sharks (*Carcharodon carcharias*) rely on body lipid stores to power ocean-basin scale migration. *Proc. R. Soc. B Biol. Sci.* **280**, 20130836 (2013).
- O'Connor, P. F. *Shark-Of* (Secker & Warburg, 1953).
- Stott, F. C. A note on catches of basking sharks, *Cetorhinus maximus* (Gunnerus), off Norway and their relation to possible migration paths. *J. Fish Biol.* **21**, 227–230 (1982).
- Hoelzel, A. R., Shivji, M. S., Magnussen, J. & Francis, M. P. Low worldwide genetic diversity in the basking shark (*Cetorhinus maximus*). *Biol. Lett.* **2**, 639–42 (2006).
- Kokko, H. & Lopez-Sepulcre, A. From individual dispersal to species ranges: Perspectives for a changing world. *Science* (80–) **313**, 789–791 (2006).
- Kokko, H. Directions in modelling partial migration: How adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos* **120**, 1826–1837 (2011).

45. Sims, D. W., Fox, A. M. & Merrett, D. A. Basking shark occurrence off south-west England in relation to zooplankton abundance. *J. Fish Biol.* **51**, 436–440 (1997).
46. Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A. & Edwards, M. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* (**80-**) **296**, 1692–1694 (2002).
47. Sims, D. W. & Reid, P. C. Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark *Cetorhinus maximus* fishery catches off west Ireland, 1986–1990 (2002).
48. Knip, D. M., Heupel, M. R. & Simpfendorfer, C. A. Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biol. Conserv.* **148**, 200–209 (2012).
49. Southall, E. J., Sims, D. W., Witt, M. J. & Metcalfe, J. D. Seasonal space-use estimates of basking sharks in relation to protection and political-economic zones in the North-east Atlantic. *Biol. Conserv.* **132**, 33–39 (2006).
50. Hetherington, S., Townhill, B., Borrow, K., Bendall, V. & Hunter, E. Shark By-Watch UK 2. *Research priorities: Innovative solutions for reducing by-catch & dead discards of threatened sharks, skates & rays* (2015).
51. Berrow, S. D. Incidental capture of elasmobranchs in the bottom-set gill-net of the South Coast of Ireland. *J. Mar. Biol. Assoc. UK* **74**, 837–847 (1994).
52. Berrow, S. D. & Heardman, C. The Basking Shark *Cetorhinus maximus* (Gunnerus) in Irish Waters: Patterns of Distribution and Abundance. *Biol. Environ. Proc. R. Irish Acad.* **94**, 101–107 (1994).
53. Valeiras, J., Lopez, A. & Garcia, M. Geographical, seasonal occurrence and incidental fishing captures of basking shark *Cetorhinus maximus* (Chondrichthyes : Cetorhinidae). *J. Mar. Biol. Assoc. UK* **81**, 183–184 (2001).
54. Gerritsen, H. D. & Lordan, C. Atlas of Commercial Fisheries Around Ireland (2014).
55. Bres, M. The behaviour of sharks. *Rev. Fish Biol. Fish.* **3**, 133–159 (1993).
56. Wearmouth, V. J. & Sims, D. W. Sexual segregation in marine fish, reptiles, birds and mammals behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* **54**, 107–70 (2008).
57. Coyne, M. S. & Godley, B. J. Satellite Tracking and Analysis Tool (STAT): An integrated system for archiving, analyzing and mapping animal tracking data. *Mar. Ecol. Prog. Ser.* **301**, 1–7 (2005).
58. Calenge, C. The package 'adehabitat' for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**, 516–519 (2006).
59. Neilson, J. D. *et al.* Seasonal distributions and migrations of northwest atlantic Swordfish: Inferences from integration of Pop-Up satellite archival tagging studies. *PLoS One* **9** (2014).
60. Thygesen, U. H., Pedersen, M. W. & Madsen, H. In *Tagging and Tracking of Marine Animals with Electronic Devices. Methods and technologies in fish biology and fisheries* Edited by Nielsen, J. L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcuage, M. & Sibert, J. **8**, 23–34 (2009).
61. Bias, G. *et al.* Return migration patterns of porbeagle shark (*Lamna nasus*) in the Northeast Atlantic: implications for stock range and structure. *Rev.* (**2016**).
62. Beyer, H. L. Geospatial Modelling Environment (version 0.7.2.1). <http://www.spatial ecology.com/gme>, doi: <http://www.spatial ecology.com/gme> (2012).
63. Hartigan, J. A. & Wong, M. A. Algorithm AS 136: A k-means clustering algorithm. *Appl. Stat.* **28**, 100–108 (1979).
64. R Core Team. R: A language and environment for statistical computing. (R Foundation for Statistical Computing (2014).
65. Bates, D., Maechler, M., Bolker, B. & Walker, S. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-5. <http://CRAN.R-project.org/package=lme4> (2014).
66. Engqvist, L. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim. Behav.* **70**, 967–971 (2005).

Acknowledgements

Tagging in Scotland was funded by Scottish Natural Heritage and the University of Exeter. We extend our sincere thanks to the skippers and crew of the *Sula Crion* and *Bold Ranger* of Sealife Surveys, Tobermory. The attachment of satellite transmitters in Scottish coastal waters was regulated by the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence 30/2975) and under the Wildlife & Countryside Act 1981 (as amended) (Licence(s): 13904, 13937 and 13971). The Manx Basking Shark Watch gives sincere thanks for support from the Manx Wildlife Trust and for funding from The Manx Lottery Trust, The Department of Environment, Food and Agriculture (DEFA) and other local businesses. Licences to tag sharks in the Isle of Man were issued by DEFA under the Wildlife Act 1990. PD was supported by a NERC PhD studentship NEL/L501669/1.

Author Contributions

S.M.H., J.M.B. and M.J.W. conceived the study for Scotland and G.H. and J.H. for the Isle of Man. P.D.D., B.J.G., R.T.G., L.A.H., S.M.H., G.H. and J.H. and M.J.W. carried out fieldwork. P.D.D. performed the primary analysis. All authors were involved in developing the manuscript and P.D.D. took a lead role in writing.

Additional Information

Supplementary information accompanies this paper at <http://www.nature.com/srep>

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Doherty, P. D. *et al.* Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic. *Sci. Rep.* **7**, 42837; doi: 10.1038/srep42837 (2017).

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



This work is licensed under a Creative Commons Attribution 4.0 International License. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>

© The Author(s) 2017

