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The application of ocean front metrics for understanding habitat selection by marine predators

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The application of ocean front metrics for understanding habitat selection by marine predators

by

Kylie Lisa Scales

A thesis submitted to Plymouth University

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Science and Technology

Faculty of Marine Science and Engineering

In collaboration with

Plymouth Marine Laboratory

January 2015

"When we try to pick out anything by itself,
we find it hitched to everything else in the Universe."

- John Muir

The application of ocean front metrics for understanding habitat selection by marine predators

Kylie Lisa Scales

ABSTRACT

Marine predators such as seabirds, cetaceans, turtles, pinnipeds, sharks and large teleost fish are essential components of healthy, biologically diverse marine ecosystems. However, intense anthropogenic pressure on the global ocean is causing rapid and widespread change, and many predator populations are in decline. Conservation solutions are urgently required, yet only recently have we begun to comprehend how these animals interact with the vast and dynamic oceans that they inhabit. A better understanding of the mechanisms that underlie habitat selection at sea is critical to our knowledge of marine ecosystem functioning, and to ecologically-sensitive marine spatial planning.

The collection of studies presented in this thesis aims to elucidate the influence of biophysical coupling at oceanographic fronts – physical interfaces at the transitions between water masses – on habitat selection by marine predators. High-resolution composite front mapping via Earth Observation remote sensing is used to provide oceanographic context to several biologging datasets describing the movements and behaviours of animals at sea. A series of species-habitat models reveal the influence of mesoscale (10s to 100s of kilometres) thermal and chlorophyll-*a* fronts on habitat selection by taxonomically diverse species inhabiting contrasting ocean regions; northern gannets (*Morus bassanus*; Celtic Sea), basking sharks (*Cetorhinus maximus*; north-east Atlantic), loggerhead turtles (*Caretta caretta*; Canary Current), and grey-headed albatrosses (*Thalassarche chrysostoma*; Southern Ocean).

Original aspects of this work include an exploration of quantitative approaches to understanding habitat selection using remotely-sensed front metrics; and explicit investigation of how the biophysical properties of fronts and species-specific foraging ecology interact to influence associations. Main findings indicate that front metrics, particularly seasonal indices, are useful predictors of habitat preference across taxa. Moreover, frontal persistence and spatiotemporal predictability appear to mediate the use of front-associated foraging habitats, both in shelf seas and in the open oceans. These findings have implications for marine spatial planning and the design of protected area networks, and may prove useful in the development of tools supporting spatially dynamic ocean management.

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Acknowledgements

Creating this thesis has been a testing but deeply satisfying experience, at times frustrating and at others exciting and self-affirming. There are many people to whom I owe sincere thanks, both professionally and personally, for their part in this journey.

My foremost thanks go to my supervisors. I am profoundly grateful to Dr. Peter Miller for showing opportunity to my door; for his constant support and guidance, and patient responses to thousands of emails; for developing the remote sensing techniques that underlie the studies presented in this thesis; and for being a genuinely attentive and considerate supervisor. I am also extremely thankful for the supervision of Dr. Simon Ingram and Prof. David Sims, without whom the project would not have been possible and whose contributions have been indispensable.

The Natural Environment Research Council provided financial support through a studentship hosted at Plymouth Marine Laboratory, in collaboration with Plymouth University. I am grateful for this research funding, which has given me the means to attend several courses and conferences that have proven constructive in terms of professional development, and for the maintenance stipend that has allowed me to concentrate fully on my studies. I also extend thanks to the Plymouth Marine Science Education Foundation, PlyMSEF, for an additional travel grant to support the presentation of my work at the international Ocean Sciences conference in Hawaii in February 2014, an unforgettable experience.

I am forever indebted to several researchers that have acted as mentors and collaborators in research. I extend heartfelt gratitude to Prof. Brendan Godley, who changed my life with a phone call, and remains a major source of academic wisdom and honest, often hilarious, advice; to Dr. Stephen Votier – who has the impressive ability to stomach tinned sardines while surrounded by regurgitating gannets – for being a brilliant *de facto* supervisor, giving me the opportunity to spend some memorable and much appreciated time in the field, and patiently showing me how to become a better scientist; and to Dr. Richard Phillips, for being the ultimate master of all things grammatical and all things albatross, and an exceptionally kind and generous man. I would like to thank Dr. Lucy Hawkes, both for her collaborative role and, more generally, for setting the bar high and raising my aspirations. Dr. Clare Embling has also been a constant source of inspiration and encouragement, and a fantastic academic resource.

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Finally, heartfelt thanks are owed to my closest family and friends; to Pin and Pen, who have walked with me every step of the way, every day of my life, and who showed me how to live, love, learn, laugh and keep on trucking; to Clynton, for helping me with code; to Levi, for reminding me that stories are the most important things we have; and to both, for making me want to be better at things; to Tracy, for the pact we made in 2002; to Alistair and Brigi, for always being interested, supportive and extremely kind; to Bernie, for being the best pal ever; and, most importantly of all, to Simon – Scalsey number one, my J2 – thank you for your unfaltering support, tolerance and understanding, for listening to all of the details, for knowing how to make me laugh, and for always being positive and optimistic… I can't wait to begin our next adventure together.

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without the prior agreement of the Graduate Committee.

This study was financed with the aid of a studentship from the Natural Environment Research Council (NERC) and carried out in collaboration with Plymouth Marine Laboratory (PML). The work described in this thesis was conducted by the author, under the supervision of Dr. Peter Miller, Dr. Simon Ingram and Prof. David Sims. Dr. Stephen Votier, Dr. Richard Phillips, Prof. Brendan Godley and Dr. Lucy Hawkes provided data and guidance as collaborators in research presented in individual chapters.

Relevant scientific seminars and conferences were regularly attended, at which work was often presented. The author attended several specialist courses as part of research training. External institutions were visited for consultation purposes, and several papers were prepared for publication. Details of relevant publications are listed at the beginning of each chapter.

Presentations and Conferences Attended:

- Marine and Coastal Policy Forum, University of Plymouth, Plymouth, UK. Jun 2011
- International Seabird Group Conference, University of Plymouth, Plymouth, UK. Sept 2011
- Spatial Ecology and Conservation Conference, University of Birmingham, Birmingham, UK. Sept 2011
- Poster presentation to the Blue Horizons Conference, Plymouth Marine Laboratory, Plymouth, UK. Dec 2011. *"The Front Line: investigating the ecological significance of ocean fronts for marine megafauna"*
- Oral presentation to the South West Marine Ecosystems Conference, Marine Biological Association, Plymouth, UK. March 2012. *"Ocean front metrics for improving understanding of the dynamic distributions of marine top predators"*
- Poster presentation to the Oceans of Potential Conference, Plymouth Marine Laboratory, Plymouth, UK. Sept 2012. , *"The Front Line: investigating the influence of ocean fronts in marine top predator spatial ecology"*

- Oral presentation to the South West Marine Ecosystems Conference, Marine Biological Association, Plymouth, UK. March 2013. *"The influence of ocean fronts in marine apex predator spatial ecology".*
- Poster presentation to the 9th Ecology and Behaviour Meeting, CNRS, University of Strasbourg, France. April 2013. *"The Front Line: significance of ocean fronts to marine top predators".*

  Awarded Prize for Best Poster.
- Oral presentation to the Marine Biological Association Postgraduate Conference, University of Aberystwyth, Wales, UK. May 2013. *"Investigating the influence of ocean fronts in marine top predator spatial ecology".*

  Awarded Prize for Best Oral Presentation.
- Oral presentation to the Natural England Mini-Conference for South West Marine Team, Marine Biological Association, Plymouth, UK. May 2013. *"Ocean fronts as drivers of marine top predator spatial ecology"*. Invited presentation.
- Oral presentation to Seabird Tracking Group Meeting, Environment and Sustainability Institute, University of Exeter, Penryn, UK. Sept 2013. *"Do gannets forage at fronts?"*
- Oral presentation at Public Outreach event, "From Outer to Inner Space: Using Satellites to Monitor the Seas Around Us", Plymouth Marine Laboratory, Plymouth, UK. Oct 2013. *"Using satellites to understand the at-sea behaviours of marine megavertebrates"*.
- Oral presentation to the European Elasmobranch Association Conference, University of Plymouth, Plymouth, UK. Nov 2013. *"Basking sharks and oceanographic fronts: remotely-sensed front metrics for improving understanding of habitat use".*
- Poster presentation to the 'Advances in Approaches to Monitoring the Occurrence, Distribution and Behaviour of Top Predators' session at ASLO/AGU/TOS Ocean Sciences Meeting, Honolulu, Hawaii. Feb 2014. *"On the front line: ocean front metrics for understanding marine predator habitat use"*.
- Oral presentation to the International Seabird Group Meeting, Merton College, University of Oxford, Oxford, UK. March 2014. *"Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird"*.

  Awarded Prize for Best Oral Presentation.
- Oral presentation to South West Marine Ecosystems Conference, Plymouth Marine Laboratory, Plymouth, UK. April 2014. *"Marine predators and oceanographic fronts: are fronts used as foraging habitats?".*

- Poster presentation to the Remote Sensing for Biodiversity Conservation Symposium, Zoological Society of London, London, UK. May 2014. *"Composite front mapping for improving understanding of marine predator habitat use"*. Workshop invitation: Marine Remote Sensing and Conservation
- Poster presentation to 5th International Biologging Science Symposium, CNRS, University of Strasburg, France. Sept 2014. *"Composite front mapping for investigating oceanographic drivers of habitat use by marine predators"*.
- Oral presentation to the Challenger Society for Marine Science Conference, University of Plymouth, Plymouth, UK. Sept 2014. *"On the front line: composite front mapping for understanding marine predator habitat use"*.

External Training Courses Attended:

- Animal Movement Analysis Summer Course, University of Amsterdam, Netherlands. July 2012.
- Linear Effects Modelling and GLMM in R. Alain Zuur (Highland Statistics Ltd.) Lisbon, Portugal. Feb 2013.
- Introduction to Bayesian Analysis and MCMC. Prof. Alan Gelflund (Duke University), Dr. Sujit Sahu (University of Southampton), Southampton, UK. April 2013.
- MCMC, GLM and GAM in R. Alain Zuur, Highland Statistics Ltd., Scottish Association for Marine Science, Oban, Scotland, UK. June 2013.
- NERC 'ReBoot Camp' Statistics Course: dealing with non-independence. Dr. David Hodgson (Centre for Ecology and Conservation, University of Exeter). Cornwall, UK. Feb 2014.

Other Scientific Contributions:

- Interview for NERC Planet Earth podcast, *"Climate tipping points, basking sharks, primates"*

  http://planetearth.nerc.ac.uk/multimedia/story.aspx?id=1336&cookieConsent=A
- Blog post for Journal of Applied Ecology, *"Eyes in the sky see the secrets of the sea"*

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Introduction

Project Rationale

Understanding oceanographic influences on habitat selection by marine predators such as seabirds, turtles, cetaceans, pinnipeds, sharks and large teleost fish is a major challenge in marine ecology. A better comprehension of the ways in which these large vertebrate predators interact with their oceanic environment is fundamental both to our knowledge of marine ecosystem functioning (Pauly *et al.* 1998; Heithaus *et al.* 2008), and for designing appropriate management measures for populations of conservation concern (Game *et al.* 2009; Hooker *et al.* 2011; Maxwell *et al.* 2013). However, insights into habitat preferences can be difficult to obtain. Marine predators can range over vast distances, complicating monitoring of their movements and distributions. Moreover, pelagic environments are highly dynamic, and interactions between predators, prey and physical processes are complex, variable and problematic to observe.

Recent innovations in biologging, "the practice of logging and relaying physical and biological data using animal-attached tags" (see Hooker *et al.* 2007; Bograd *et al.* 2010; Shillinger *et al.* 2012), Earth Observation remote sensing (Palacios *et al.* 2006; Priede & Miller 2009; Grantham *et al.* 2011) and habitat modelling (Aarts *et al.* 2008; Wakefield, Phillips & Matthiopoulos 2009; Warton & Aarts 2013) can generate valuable insights into at-sea habitat use. Biologging facilitates remote observation of the movements and behaviours of known individuals moving freely through their natural environment. Remote sensing of environmental variables from satellite Earth Observation (EO) platforms provides data describing dynamic oceanographic processes over broad spatial scales, in near real-time. In conjunction with *in-situ* studies that elucidate fine-scale interactions between predators, prey and physical processes (e.g. Cox, Scott & Camphuysen 2013; Scott *et al.* 2013), these innovations provide powerful means for improving understanding of the mechanisms underlying habitat selection by marine predators.

A considerable body of evidence documents associations between marine predators and mesoscale (10s to 100s of kilometres) or sub-mesoscale (~1 kilometre) oceanographic features such as fronts (Bost *et al.* 2009; Scales *et al.* 2014b), eddies (Godø *et al.* 2012), regions of stratification (Scott *et al.* 2010) and tidal flow fields (Jones *et al.* 2014). The work presented in this thesis focuses on associations with ocean fronts – physical interfaces between water bodies of contrasting properties (i.e. temperature, salinity, density, turbidity, colour; Belkin, Cornillon & Sherman 2009). Biophysical coupling within these features can enhance prey accessibility for both planktivorous and piscivorous predators, leading to the propagation of pelagic foraging hotspots (Le Fevre 1986; Franks 1992b; Graham, Pages & Hamner 2001; Genin *et al.* 2005; Simpson & Sharples 2012).

Satellite remote sensing algorithms enable automatic and objective detection of the locations, properties and dynamics of fronts, improving methods for identification of biophysical hotspots. Fronts can be detected in remotely-sensed imagery as 'edges' that delineate boundaries between contrasting water masses, most usually through the use of the *gradient method* or *local-regional histogram analysis* (Cayula & Cornillon 1992). The *gradient method* derives a simple metric describing the 2-dimensional gradient in SST across image pixels, which can then be processed into composites that show only strong gradients (Belkin & Gordon 1996). The *Canny algorithm* (Canny 1986) identifies pixels in which temperature gradient is greater than a user-defined threshold (Castelao *et al.* 2006). However, these methods rely on significant smoothing of the SST field, and produce a continuous output variable rather than a precise front location. Moreover, smoother thermal transitions may not be detected (Cayula & Cornillon 1992).

Single-image edge detection (SIED; Cayula & Cornillon 1992) applies histogram analysis on a series of overlapping windows over a satellite image. Histograms of SST or other detected properties are bimodal when a front is present. The statistical relevance of each front determined from the relative shapes of these histograms, and the spatial cohesion of temperature fields is tested before pixels are flagged along the transition marking the front at the surface. SST gradient is then used to join isolated pixels into coherent frontal structures, using a contour-following regime (Cayula *et al.* 1991; Cayula & Cornillon 1992; Ullmann & Cornillon 2000). SIED is a robust and objective technique for characterising frontal structures, and its utility has been validated widely (see Kahru, Håkansson & Rud 1995; Ullmann & Cornillon 2000; Ullman, Cornillon & Shan 2007; Belkin, Cornillon & Sherman 2009).

Extensions of SIED enable visualisation of frontal dynamics over a sequence of images. Conventional compositing has relied on averaging of cloud-free values (e.g. Vasquez *et al.* 1994) or identification of clusters of fronts in an image sequence (e.g. Podestá, Browder & Hoey 1993), but this can mask spatiotemporal dynamics. Composite front mapping combines all cloud-free values of location, persistence and strength of all fronts detected over several days into a single synoptic chart (Miller 2009). A clustering algorithm simplifies multiple edges detected in image sequences into a single line for each frontal system. A set of quantitative front metrics (i.e. *fdens*, front density; *gdens,* frontal gradient density; *fdist,* distance to closest front; *fside*, warm or cold side; *ffreq,* front frequency) can be derived and time-matched with biologging datasets to inform habitat modelling, a major advantage of this technique over alternatives.

Composite front mapping techniques were adopted for this thesis, owing to these advantages and previous successful application for studying habitat selection by marine predators (e.g. Priede & Miller 2009). Rather than implementing and comparing the results of alternative front detection algorithms, this approach allowed for greater effort to be spent on applications of satellite front maps in modelling marine predator habitat selection. The studies presented in this thesis seek to integrate front detection and biologging techniques; to investigate the utility of remotely-sensed front metrics as environmental proxies in species-habitat modelling, and, more broadly, to generate further insight into the ecological significance of fronts for marine predators.

Aims

The major aims of this thesis are:

- to explore methods for the integrated use of animal tracking and remotely-sensed oceanographic data in quantitative investigations of habitat selection by marine predators.
- to elucidate associations between a range of marine predators and mesoscale fronts using remotely-sensed front metrics, and assess the utility of these metrics for this purpose.
- to consider implications for marine conservation planning and anthropogenic threat management.

Thesis Structure

This thesis is comprised of a series of chapters, each written as a stand-alone research paper. Each chapter can be considered in isolation, but the thesis is structured so as to present a coherent package of work focused on the ecological significance of ocean fronts across taxa. All appropriate copyright permissions regarding the inclusion of published works as chapters in this thesis have been obtained from respective publishers.

The literature review presented in chapter one provides as an introduction to the subject, synthesising current understanding of associations between marine predators and fronts from a global perspective. Taxon-specific investigations presented in chapters three to six have each been developed explicitly to advance understanding of the physical drivers of habitat selection by the focal species, based upon an assessment of the current literature in each taxon-specific sub-field.

Each of these taxon-specific chapters has been prepared in collaboration with data-providing partners at external research institutes, increasing the scope of this work through enabling the inclusion of a diverse set of model species tracked using different biologging technologies in contrasting ocean domains. Short summaries below highlight the main features and novel aspects of each chapter. Combined, these studies make a considerable original contribution to current understanding of oceanographic influences on habitat selection by marine predators, particularly with respect to the significance of mesoscale (10s to 100s of kilometres) frontal systems.

Chapter one presents a review of documented associations between marine predators and fronts, synthesising several decades of scientific literature to discuss the cross-taxa ecological importance of these oceanographic features. The first section highlights notable examples of associations documented in different oceanographic domains, ranging from ocean-basin scale to sub-mesoscale features, and from shelf seas to the open oceans. The influence of taxon-specific aspects of foraging ecology are discussed. The chapter then explores the key common biophysical characteristics of fronts that are known to attract foraging predators. Both of these themes are further explored in subsequent chapters.

The second part of this review discusses the potential role of frontal zones, here defined as *regions of frequent mesoscale frontal activity*, as priority at-sea conservation areas for marine predators. First, the role of frontal zones as regions of overlap between potentially critical habitats and spatially-explicit anthropogenic threat is considered. Second, recommendations are made regarding the role of EO remote sensing for identifying, monitoring and managing priority conservation areas, with specific reference to spatially dynamic ocean management.

This chapter was published as a review article in *Journal of Applied Ecology* in September 2014 as:

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. and 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**(6), 1575 – 1583. doi: 10.1111/1365-2664.12330

Chapter two presents the results of an investigation into the physical drivers of foraging habitat selection in a piscivorous marine predator, the northern gannet *Morus bassanus*. High-resolution GPS tracking was used to obtain detailed information on the movements of chick-rearing adults from a breeding colony in the Celtic Sea. Front metrics derived from composite front maps identified thermal and chlorophyll-*a* fronts occurring over two spatiotemporal scales, (i) mesoscale fronts contemporaneous to birds as they overflew the seascape and (ii) broad-scale regions of frequent front manifestation over the breeding season, termed *persistent frontal zones*. Main findings indicate that birds preferentially target foraging effort within these spatially predictable, persistent frontal zones – a novel result which suggests that learning and memory strongly influence foraging decisions in this species. This chapter is progressive in its methodological approach, and provides proof-of-concept that remotely-sensed front metrics are a useful tool for modelling habitat preference of piscivorous marine predators.

This chapter was published in *Journal of the Royal Society Interface* in August 2014 as:

Scales, K.L., Miller, P.I., Embling, C.B., Ingram, S.N., Pirotta, E. and Votier, S.C. (2014) Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of the Royal Society Interface* **11**, 20140679.
doi: 10.1098/rsif.2014.0679

Chapter three investigates associations between the planktivorous basking shark *Cetorhinus maximus* and thermal and chl-*a* fronts in the northeast Atlantic. Sharks were tracked over timescales of weeks to months during the regional surface sightings seasons (May – November) of 2001 and 2002, using fin-mounted Pop-up Satellite Archival Tags (PSATs).

Space use of tracked sharks (n=7) was compared to correlated random walk simulations (n=7000; 1000 per tracked individual), using Generalised Linear Mixed Modelling (GLMM) with iterative sub-sampling to account for serial autocorrelation. This analysis makes a substantial methodological contribution to the field – associations between basking sharks and tidal-mixing fronts had been previously observed in the region (Sims & Quayle 1998), but their significance never quantified. This work reveals associations between basking sharks and contemporaneous fronts, and also documents preferences for persistent frontal zones. Novel aspects of this chapter include explicit investigation of the influence of temporal persistence and cross-frontal gradient magnitude on associations between basking sharks and thermal fronts, confirming that sharks are more likely to be found in association with strong, persistent fronts than more ephemeral features.

This chapter was published in *Functional Ecology* in March 2015 as:
Scales, K.L*., Miller, P.I.*, Ingram, S.N., Southall, E.J., and Sims, D.W. (*Joint First Authors) Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic. *Functional Ecology*, In Press. doi: 10.1111/1365-2435.12423

<u>Chapter four</u> focuses on habitat preferences of loggerhead turtles *Caretta caretta* inhabiting the Canary Current Large Marine Ecosystem (LME), a major eastern boundary upwelling system off north-western Africa. Adult females (n=12) were tracked from a population nesting at Boa Vista, Cape Verde, using Argos-Platform Terminal Transmitter (PTT) technology, between 2004 and 2009. Previous work using this tracking dataset has discovered a foraging dichotomy within this population, challenging the accepted view that adult loggerheads forage exclusively in the neritic zone (<500m depth) and identifying a significant number of individuals that maintain an oceanic foraging strategy into adulthood (Hawkes *et al.* 2006). As epipelagic (near-surface) foragers, oceanic loggerheads represent an interesting model organism for investigation of the influence of surface fronts on foraging habitat selection in marine turtles. This chapter investigates the physical drivers of habitat

selection in a novel oceanographic context for this species, and explores methods for robust enumeration of environmental influences on animal movements observed using Argos-PTT technologies.

This chapter was published in *Marine Ecology Progress Series* in January 2015 as:

Scales, K.L., Miller, P.I., Varo-Cruz, N., Hodgson, D.J., Hawkes, L.A. and Godley, B.J. (2014) Oceanic loggerhead turtles associate with oceanographic fronts: evidence from the Canary Current Large Marine Ecosystem. *Marine Ecology Progress Series* **519**, 195-207.

doi: 10.3354/meps11075

Chapter five presents results of an ensemble ecological niche model (EENM) investigating foraging habitat selection by the grey-headed albatross *Thalassarche chrysostoma*. This approach combines outputs of multiple modelling algorithms into an EENM to identify suitable habitats based on combinations of environmental parameters. Adult birds (n=55) were tracked from the breeding colony at Bird Island, South Georgia during the brood-guard stage of the chick-rearing period, using a combination of GPS and geolocation-immersion loggers to record at-sea behaviours. High-resolution sea surface temperature (SST), chlorophyll-*a,* front frequency and depth data were used to identify oceanographic conditions characterising the locations of foraging events. These *presences* were statistically compared to sets of pseudo-absences sampled at random from within the region accessible to foraging birds. Model results were then projected to identify potentially suitable foraging conditions within this accessible range. This chapter explicitly investigates the importance of the Antarctic Polar Frontal Zone (APFZ) to this population, and explores key considerations for the use of EENM in characterising preferred foraging habitats of highly mobile species.

Chapter six is a general discussion of key themes running throughout this thesis. The first section synthesises findings of other chapters, summarising main conclusions and recommendations. The second section examines methodological approaches to linking animal movements with environmental conditions in dynamic marine systems. The final section of this chapter then discusses wider implications of research presented in this thesis, and how techniques might support the development of conservation and management strategies for marine predator populations.

Summary of collaborator contributions

Chapter I On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates

Kylie L. SCALES, Peter I. MILLER, Lucy A. HAWKES, Simon N. INGRAM,
David W. SIMS & Stephen C. VOTIER

This chapter presents a literature review, prepared independently but under the supervision of Dr. P.I. Miller (Plymouth Marine Laboratory), Dr. S.N. Ingram (University of Plymouth) and Prof. D.W. Sims (Marine Biological Association/University of Southampton). Each of these authors provided comments on manuscript drafts. Additional comments and suggestions were provided by Dr. S.C. Votier (University of Exeter) and Dr. L.A. Hawkes (University of Exeter). Dr. S.C. Votier made the most substantial input to the final draft (disucssions, plus several sets of comments), and so is listed as last author on the published paper. This chapter was published as a review article in the Journal of Applied Ecology in September 2014.

Chapter II Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird

Kylie L. SCALES, Peter I. MILLER, Clare B. EMBLING, Simon N. INGRAM, Enrico PIROTTA & Stephen C. VOTIER

Northern gannet tracking data used for this chapter were provided by Dr. S.C. Votier. Data processing and analysis were carried out independently but in consultation with Dr. P.I. Miller, Dr. S.C. Votier and Dr. S.N. Ingram. Technical aspects of modelling work were discussed further with Dr. C.B. Embling (University of Plymouth) and Dr. E. Pirotta (University of Aberdeen). All collaborators provided suggestions for edits to manuscript drafts. This chapter was published in the Journal of the Royal Society Interface in August 2014.

Chapter III Basking sharks and oceanographic fronts: quantifying associations in the northeast Atlantic

Kylie L. SCALES, Peter I. MILLER, Emily J. SOUTHALL & David W. SIMS

Basking shark tracking data used for this chapter were provided by Prof. D.W. Sims. Data processing and analysis were carried out independently, but in consultation with by Dr. P. I. Miller. Comments on manuscript drafts were provided by Prof. D.W. Sims and Dr. P.I. Miller. This chapter was published in Functional Ecology in March 2015.

Chapter IV Oceanic loggerhead turtles *Caretta caretta* associate with oceanographic fronts: evidence from the Canary Current Large Marine Ecosystem

Kylie L. SCALES, Peter I. MILLER, Nuria VARO-CRUZ, David J. HODGSON, Lucy A. HAWKES & Brendan J. GODLEY

Loggerhead turtle tracking data used for this chapter were provided by Prof. B.J. Godley and Dr. L.A. Hawkes (Centre for Ecology and Conservation, University of Exeter), and by Dr. N. Varo-Cruz (Universitad de Las Palmas de Gran Canaria). Data processing and analysis were carried out independently, but in consultation with Dr. P.I. Miller and Prof. B.J. Godley. Technical aspects of modelling work were further discussed with Dr. D.J. Hodgson (University of Exeter). All co-authors provided comments on manuscript drafts. This chapter was published in Marine Ecology Progress Series in January 2015.

Chapter V Ensemble ecological niche modelling identifies preferred foraging habitats of grey-headed albatrosses *Thalassarche chrysostoma*

Kylie L. SCALES, Peter I. MILLER, Simon N. INGRAM & Richard A. PHILLIPS

Grey-headed albatross tracking data used for this chapter were provided by Dr. R.A. Phillips (British Antarctic Survey). Data processing and analysis were carried out independently, in consulation with Dr. P.I. Miller and Dr. R.A. Phillips. Comments on manuscript drafts were provided by Dr. P.I. Miller and Dr. R.A. Phillips. This chapter is yet to be submitted for consideration for publication.

Chapter I

On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates

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ABSTRACT

Identifying priority areas for marine vertebrate conservation is complex because species of conservation concern are highly mobile, inhabit dynamic habitats and are difficult to monitor. Many marine vertebrates are known to associate with oceanographic fronts – physical interfaces at the transition between water masses – for foraging and migration, making them important candidate sites for conservation. Here, we review associations between marine vertebrates and fronts and how they vary with scale, regional oceanography, and foraging ecology. Accessibility, spatiotemporal predictability, and relative productivity of front-associated foraging habitats are key aspects of their ecological importance. Predictable meso-scale (10s–100s km) regions of persistent frontal activity (*frontal zones*) are particularly significant. Frontal zones are also hotspots of overlap between critical habitat and spatially explicit anthropogenic threats, such as the concentration of fisheries activity. As such, they represent tractable conservation units, in which to target measures for threat mitigation. Front mapping via Earth Observation (EO) remote sensing facilitates identification and monitoring of these hotspots of vulnerability. Seasonal or climatological products can locate biophysical hotspots, while near real-time front mapping augments the suite of tools supporting spatially dynamic ocean management. These insights are useful for marine spatial planning and marine biodiversity conservation, both within Exclusive Economic Zones and in the open oceans.

1.1 Introduction

Accommodating the conservation needs of large marine vertebrates such as seabirds, turtles, cetaceans, pinnipeds, sharks, and teleosts (e.g. tunas, billfish, sunfish) is a major challenge in marine management. These apex predators fulfil critical roles in ecosystem functioning (Heithaus *et al.* 2008), but are currently afforded only cursory or inadequate protection, particularly in the open oceans (Game *et al.* 2009). The combined effects of anthropogenic stressors (e.g. habitat degradation, overexploitation, fisheries bycatch and climate variability) are negatively impacting marine vertebrate populations (Halpern *et al.* 2008; Maxwell *et al.* 2013; Lewison *et al.* 2014), and in some cases resulting in dramatic declines (e.g. rockfishes, Ralston 2002; seabirds, Croxall *et al.* 2012). However, effective conservation is problematic. Large marine vertebrates are highly mobile, ranging great distances over the course of their lives. For example, many migrate across entire ocean basins (e.g. leatherback turtle, *Dermochelys coriacea*, Shillinger *et al.* 2008; Arctic tern, *Sterna paradisea*, Egevang *et al.* 2010; humpback whale, *Megaptera novaeangliae*, Robbins *et al.* 2011), epitomising the problems of conserving a moving target (Singh & Milner-Gulland 2011). Furthermore, the formation and propagation of pelagic foraging habitats is a function of complex oceanographic dynamics (see Hazen *et al.* 2013a), so *habitat* in the marine context does not always refer to fixed geographical space, but preferentially-used areas that may shift. Understanding how oceanographic processes influence marine vertebrate distributions is, therefore, crucial for effective conservation (Hooker *et al.* 2011).

Oceanographic conditions drive spatial structuring of predator abundance and diversity across the oceans. At a global scale, marine biodiversity is regulated by sea surface temperature, with diversity maxima occurring at mid-latitudes (Worm *et al.* 2005; Tittensor *et al.* 2010). At an ocean-basin scale, diversity is highest in productive zones associated with major water-mass transitions, currents, upwellings, and bathymetric features (Chavez & Messié 2009). Within these productive regions, meso- (10s – 100s km) and sub-mesoscale (~1km) oceanographic dynamics lead to the formation of ecologically significant features such as fronts and eddies (see Godø *et al.* 2012). Here, we focus on fronts - physical interfaces between water bodies that manifest as steep gradients in temperature, salinity, density, turbidity or colour (Belkin, Cornillon & Sherman 2009) – as important habitats for mobile marine vertebrates

Bio-physical coupling at fronts can lead to the formation of pelagic foraging hotspots. Mixing and nutrient retention enhance primary productivity (Traganza, Redalije & Garwood 1987; Franks 1992a) while plankton and small nekton may become entrained in convergent surface flow (Le Fevre 1986; Franks 1992b; Genin *et al.* 2005). Convergences aggregate zooplankton advected from surrounding water masses, driving bottom-up processes across multiple trophic levels up to apex predators (Graham, Pages & Hamner 2001; Bakun 2006). However, the productivity and degree of bio-aggregation along fronts varies according to physical characteristics such as spatiotemporal variability, gradient magnitude, type of front and properties of the surrounding water masses (Le Fevre 1986). Therefore a holistic understanding of how biophysical mechanisms interact to influence the degree of bio-aggregation at fronts, and their subsequent attractiveness to top predators, remains elusive.

A taxonomically diverse array of marine vertebrates have been shown to associate with fronts, and the scale, nature and significance of these associations to vary according to regional oceanography and taxon-specific life history characteristics. Ecologically significant features can range from ocean-basin scale, persistent frontal zones to fine-scale, ephemeral features in shelf seas (Le Fevre 1986; Belkin, Cornillon & Sherman 2009). Here, we review current understanding of associations between high trophic-level marine vertebrates and fronts, selecting key examples from contrasting oceanographic regions, and highlighting important biophysical characteristics of ecologically-significant frontal zones. We discuss implications for management and conservation, including overlap with anthropogenic threat, and highlight the potential role of front mapping via EO Remote Sensing to inform threat mitigation.

1.2 Ecological Importance of Frontal Zones

The mechanisms linking physical processes, prey dynamics and top predator foraging are complex and scale-dependent (Fauchald 2009). Understanding these mechanisms is crucial to understanding what makes front-associated foraging opportunities attractive to high trophic-level consumers. Use of frontal zones is mediated bottom-up by the spatial scale, persistence and biophysical properties of fronts, and top-down by aspects of foraging ecology, including life history mode (true pelagics vs. central-place foragers), physiological constraints (e.g. thermal range, diving capability), trophic level (planktivores vs piscivores), foraging guild (near-surface vs. sub-surface), foraging plasticity, ontogenetic stage, and whether foraging is opportunistic or mediated by learning and memory (Vilchis, Ballance & Fiedler 2006). Here, we review current literature documenting associations between marine vertebrates and fronts occurring over a range of scales, discussing key examples from contrasting oceanographic regions.

OCEAN-BASIN SCALE (1000s kms)

Ocean-basin scale regions of intense mesoscale dynamics, such as those associated with the major water mass transitions discussed below, are ecologically significant features in the largely oligotrophic open oceans (Belkin, Cornillon & Sherman 2009). These regions are important foraging and migration habitats for pelagic marine vertebrates (Tittensor *et al.* 2010).

North Pacific Transition Zone (NPTZ) This highly dynamic region delineates the boundary between warm, oligotrophic subtropical gyres and cold, productive subarctic gyres, and is a marine biodiversity hotspot of global significance (Sydeman *et al.* 2006). Numerous marine vertebrates with contrasting life histories preferentially use areas of the NPTZ, including elephant seals *Mirounga angustirostris*, salmon shark *Lamna ditropis* and blue shark *Prionace glauca*, bluefin *Thunnus thynnus* and albacore tunas *Thunnus alalunga*, Laysan *Phoebastria immutabilis* and black-footed albatrosses *P. nigripes*, and loggerhead *Caretta caretta* and olive ridley turtles *Lepidochelys olivacea* (Polovina *et al.* 2004; Kappes *et al.* 2010; Block *et al.* 2011; Robinson *et al.* 2012).

The NPTZ encompasses the Transition Zone Chlorophyll Front (TZCF), a surface convergence that extends over 8000km (Polovina *et al.* 2001). While the wider NPTZ is predictable at broad scales, the position of the TZCF is strongly influenced by climate (Kappes *et al.* 2010), leading to spatial variability in foraging associations. Some near-surface foragers, such as loggerhead turtles, can track the southward movement of the TZCF in winter (Howell *et al.* 2010). Other taxa constrained to a central place, such as albatrosses breeding on the Hawaiian Islands, have experienced reproductive failure as a result of spatial deviation (Kappes *et al.* 2010). In contrast, elephant seals, which forage along the sub-surface thermal boundary between gyres (Robinson *et al.* 2012), remain unaffected by the movement of surface features.

Equatorial Front (EF) Manifesting between the Equatorial upwelling to the South and warmer tropical waters to the North, the EF is a prominent feature of the tropical Eastern Pacific, characterised by steep gradients in temperature, salinity and nutrients (see Ballance, Pitman & Fiedler 2006). Planktivorous seabirds associate strongly with the semi-permanent EF, which entrains zooplankton in surface layers (Spear, Ballance & Ainley 2001). However, seabird densities observed were found to be closely coupled with climate-driven variability in frontal intensity, defined as the tightening of SST contours over a latitudinal section (*front width*; Spear, Balance & Ainley 2001). A significant interaction between season and phase of the El Niño Southern Oscillation (ENSO) was shown to influence planktivorous seabird densities, with greater numbers encountered during Autumn in the La Niña phase of ENSO.

Southern Ocean frontal zones The major frontal zones of the Southern Ocean determine the distributions of pelagic prey species in the region (Rodhouse & Boyle 2010). A range of marine predators utilise the southern boundary of the Antarctic Circumpolar Current (ACC), the subtropical front and the Subantarctic front (see Bost *et al.* 2009; Santora & Veit 2013). Penguins, albatrosses and seals travel from distant breeding colonies to forage along the subtropical and Polar fronts (Xavier *et al.* 2003; Bailleul *et al.* 2007; Scheffer, Bost & Trathan 2012). Although distant from land, Southern Ocean frontal zones provide suitable foraging conditions for both near-surface and deep-diving foragers, but are accessible only to those species with the capacity to navigate across oceanic seascapes.

MESOSCALE (10s – 100s kms) TO SUB-MESOSCALE (~1km)

Mesoscale and sub-mesoscale processes drive front formation within large-scale transition zones and in regions associated with currents, upwellings and bathymetric features, and appear to be of particular ecological importance. For example, hotspots of predatory fish diversity (tuna, billfish) are associated with mesoscale fronts within warm waters (~25°C) across all the major ocean basins (Worm *et al.* 2005).

Major currents Bio-aggregating thermal, colour and density fronts frequently form along the boundaries of major current systems (Fig. 1.1). Seabirds and neonate sea turtles associate strongly with fronts and eddies formed along the Gulf Stream (Haney 1986a; Witherington 2002; Thorne & Read 2013), and the Kuroshio current (Polovina *et al.* 2006). The peripheries of frontal eddies formed along these currents are also of ecological significance (Haney 1986b; Bailleul, Cotté & Guinet 2010; Godø *et al.* 2012).

Upwelling fronts Major Eastern boundary upwellings (e.g. Canary Current, Benguela Current, California Current, Humboldt Current) are hotspots of marine biodiversity (Chavez & Messié 2009) characterised by intense surface frontal activity. Mesoscale thermal and colour fronts mark the interface between cool, nutrient-rich upwelled water and warmer oligotrophic waters further offshore. Bio-aggregation in upwelling-driven frontal structures attracts foragers from diverse foraging guilds (see Nur *et al.* 2011; Sabarros *et al.* 2013). For example, strong associations have been documented between cetaceans (Tynan *et al.* 2005), seabirds

(Ainley *et al.* 2009) and upwelling fronts in the California Current. Similarly, coastal upwelling creates a persistent multiple trophic-level hotspot off Baja California, within which bio-aggregating thermal fronts are utilised by sub-surface predators such as blue whales *Balaenoptera musculus,* green *Chelonia mydas* and loggerhead turtles (Etnoyer *et al.* 2006; Wingfield *et al.* 2011).

Strong convergent fronts also manifest at the peripheries of upwelling shadows, where water upwelled offshore meets coastal water masses sheltered by coastline irregularities (Chavez & Messié 2009). Large upwelling shadows in the Southern California Bight (Fiedler & Bernard 1987; Hunt Jr & Schneider 1987) and off Southern Peru (Acha *et al.* 2004) are known hotspots. However, upwelling intensity is often seasonal, varying under climatic and oceanographic influence, affecting the predictability of foraging opportunities in these regions (Thompson *et al.* 2012).

Shelf edge frontal zones Shelf-edge systems - at the transitions between the abyssal oceans and shelf seas - are zones of intense mixing, resulting in the manifestation of strong thermohaline fronts. Nutrient enrichment in shelf-edge fronts enhances primary production, attracting grazers such as copepods, fish larvae and planktivorous fish, and their predators (Le Fevre 1986). For example, the Celtic Sea shelf-edge is an important over-wintering habitat for basking sharks *Cetorhinus maximus* (Sims *et al.* 2003). Both surface-feeding and diving seabirds aggregate along shelf-edge fronts (Skov & Durinck 1998). Downwelling shelf slopes, such as those found at the Mid Atlantic Bight (Ryan, Yoder & Cornillon 1999) and at the margins of the Bering Sea (Springer, McRoy & Flint 1996), are important seabird foraging areas. Shelf-edge fronts can also be significant habitat features for cetaceans, including deep-diving species that prey on squid and fish (Baumgartner 1997; Waring *et al.* 2001), rorquals (Azzellino *et al.* 2008) and some delphinids (Davis *et al.* 1998).

Mid-ocean bathymetrically-induced frontal zones Mid-ocean bathymetric features generate persistent fronts that can produce predictable foraging grounds. For example, the interaction of the North Atlantic Current with the Mid-Atlantic Ridge around the Charlie-Gibbs Fracture Zone (CGFZ) generates intense mesoscale frontal activity (Miller, Read & Dale 2013), attracting surface and near-surface foraging seabirds (Egevang *et al.* 2010; Frederiksen *et al.* 2012; Edwards *et al.* 2013). Piscivorous dolphins and whales also feed on mesopelagic fish and squid in this area (Doksæter *et al.* 2008; Skov *et al.* 2008).

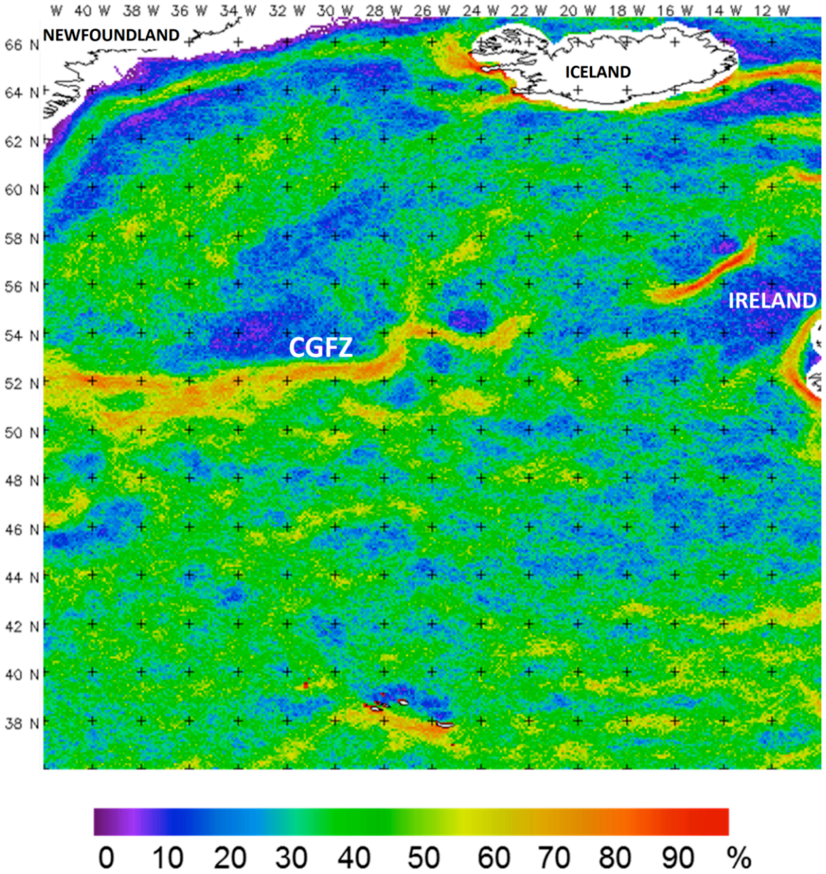

Figure 1.1 Front mapping via EO Remote Sensing. *Example imagery: seasonal front frequency map, N. Atlantic (percent time a front detected in each 1km pixel during spring, March-May). Regions of frequent mesoscale frontal activity along the North Atlantic Current are highlighted, including that associated with the Charlie Gibbs Fracture Zone. Useful as part of a suite of tools for locating priority conservation areas through identifying potential biophysical hotspots of significance to marine vertebrates, and their dynamics through time. Derived from merged microwave and infrared SST data, 2006-2011. Reproduced, with permission, from Miller et al. (2013).*

Shelf-sea tidal mixing fronts Tidal mixing fronts manifest in shelf seas between well-mixed and stratified waters (Pingree & Griffiths 1978). Nutrient retention and enhanced vertical mixing enhance seasonal phytoplankton production (Pingree 1975; Franks 1992a), attracting both pelagic and neritic foragers. For example, basking sharks forage for zooplankton at small-scale tidal fronts in UK waters (Sims & Quayle 1998), with sightings clustered around slicks indicative of convergent flow. Likewise, planktivorous ocean sunfish *Mola mola* are frequently encountered near fronts (Sims & Southall 2002). Similarly strong associations have been observed between rorquals and tidal fronts in the Gulf of St. Lawrence (Doniol-Valcroze *et al.* 2007). On the European Continental Shelf, piscivorous cetaceans use both seasonally persistent, mesoscale tidal mixing fronts (Goold 1998; Weir & O'Brien 2000) and finer-scale fronts that manifest in tidal inlets (Pirotta *et al.* 2013). In addition, numerous seabirds forage around mid-shelf fronts (Haney & McGillivary 1985; Hamer *et al.* 2009; Dean *et al.* 2013), sometimes in Multi-Species Foraging Associations (MSFAs; Camphuysen, Scott & Wanless 2006). Surface and near-surface foraging birds are frequently observed near convergent fronts (Durazo, Harrison & Hill 1998; Hunt Jr *et al.* 1999), whereas sub-surface foragers tend to associate with strong, vertically-structured fronts (Decker & Hunt Jr 1996; Begg & Reid 1997).

Tidal-topographic fronts In neritic waters, tidal-topographic interactions generate fine scale yet strongly bio-aggregating fronts (Le Fevre 1986). For example, 'island wake' effects lead to the development of surface convergences and eddies (Wolanski & Hamner 1988). Marine mammals (Johnston & Read 2007) and surface-foraging seabirds (Schneider 1990) associate with island wake fronts. Similarly, offshore banks can initiate front development, increasing prey accessibility in surface layers (Stevick *et al.* 2008). Tidal-topographic fronts over banks can cause the formation of sub-surface chlorophyll maxima (Franks 1992a), which are significant foraging areas for some diving predators (Scott *et al.* 2010). Tidal-topographic fronts are highly predictable, and may be especially important for central-place marine vertebrates. However, at very fine scales (<1km), other sub-surface physical processes may mediate predator foraging over bank systems (Scott *et al.* 2010; Cox, Scott & Camphuysen 2013).

Estuarine plume and tidal intrusion fronts Estuarine plume fronts are formed by interactions between tidal processes and river outflow. Entrainment of zooplankton (Govoni & Grimes 1992) attracts forage fish (Kaltenberg, Emmett & Benoit-Bird 2010), making plume fronts significant nearshore foraging features. Large aggregations of piscivorous seabirds have been documented around estuarine plume fronts (Skov & Prins 2001; Zamon, Phillips & Guy 2013).

KEY BIOPHYSICAL CHARACTERISTICS OF ECOLOGICALLY-SIGNIFICANT FRONTAL ZONES

Current understanding indicates that accessibility, spatio-temporal predictability and relative productivity are central to the ecological importance of frontal zones (Hunt Jr *et al.* 1999; Weimerskirch 2007). These insights are useful in predicting which taxa are likely to aggregate at frontal zones in different oceanographic regions, enhancing understanding of pelagic ecosystem function and identifying important at-sea habitats. For example, it is clear that large-scale frontal zones in the open oceans are often highly productive and persistent, and so predictable, yet only really accessible to oceanic species and far-ranging central-place foragers (Bost *et al.* 2009; Tittensor *et al.* 2010). Predictable, productive mesoscale frontal zones associated with bathymetric features, currents and major upwellings attract marine vertebrates from diverse foraging guilds in contrasting oceanographic regions (Chavez & Messié 2009; Block *et al.* 2011). Persistent shelf-sea tidal mixing and tidal-topographic fronts create predictable foraging opportunities, accessible to coastal species such as colonial seabirds and some cetaceans. Recent work in the Celtic Sea highlights temporal persistence as a key component of frontal zones used as foraging features for a piscivorous seabird (Scales *et al.* 2014a), presumably as persistence enhances both productivity and predictability.

The literature documenting associations between marine vertebrates and fronts has yielded valuable insights, yet many questions remain. For example, despite the implicit assumption that fronts generate suitable foraging conditions, the mechanisms linking physical processes and prey dynamics are not well understood (but see Cox, Scott & Camphuysen 2013). In many cases, it remains unclear how habitat utilisation changes through the annual cycle, through ontogenetic development and life cycle stages (i.e. breeding, migration; but see e.g. Votier *et al.* 2011). In addition, little is known about the ways in which many species perceive and respond to environmental cues (but see Nevitt & Bonadonna 2005; Tew Kai *et al.* 2009; Votier *et al.* 2013; Tremblay *et al.* 2014). Moreover, it is important to determine whether fronts are significant foraging features at the population level. This has not yet been achieved, to our knowledge, but is possible through estimation of the proportion of a population using a frontal zone, or the spatial range over which animals are attracted. Future work should address these questions, improving capacity to locate ecologically-significant features.

1.3 Frontal Zones as Priority Conservation Areas

HOTSPOTS OF ANTHROPOGENIC THREAT

Frontal zones appear to be hotspots of overlap between potentially critical at-sea habitats and spatially-explicit anthropogenic threat (e.g. fisheries), particularly in the coastal zone (Halpern *et al.* 2008). The major fisheries threats to marine vertebrates are bycatch (Gilman *et al.* 2008; Anderson *et al.* 2011; Žydelis, Small & French 2013; Lewison *et al.* 2014) and competition for resources (e.g. Bertrand *et al.* 2012). Comprehensive data are difficult to obtain, but industrialised fisheries, particularly pelagic long-lining fleets, target persistent frontal zones (Podestá, Browder & Hoey 1993; Hartog *et al.* 2011), generating significant risk of conflict with other apex consumers. Spatial overlap is particularly pronounced within the coastal zone, along shelf breaks and in upwelling regions (Halpern *et al.* 2008; Lewison *et al.* 2014), especially those around Africa and South America (Zeeberg, Corten & de Graaf 2006; Pichegru *et al.* 2009). Within these regions, frontal zones are logical areas in which to focus measures for mitigation of fisheries threat. In addition, convergent fronts can concentrate pollutants and floating debris such as oil and plastics, potentially increasing exposure of marine vertebrates aggregating to forage (Bourne & Clark 1984; González Carman *et al.* 2014).

On the continental shelf, the expansion of marine renewable energy installations (MREI) has the potential for direct and indirect effects on marine vertebrates (Inger *et al.* 2009; Grecian *et al.* 2010; Scott *et al.* 2014). MREIs that rely on tidal flow are likely to be concentrated in the vicinity of hydrographically-dynamic tidal mixing fronts (Miller & Christodoulou 2014), altering habitat dynamics and displacing foraging effort. These impacts may be particularly pronounced for coastal central-place foragers (Scott *et al.* 2014). While more research is needed to determine if MREIs have population-level effects, marine spatial planning can be improved by identification of vulnerability hotspots.

FRONT MAPPING TO IDENTIFY PRIORITY CONSERVATION AREAS

Technological innovations in remote sensing, biologging, autonomous marine vehicles and vessel monitoring hold promise for identification of priority conservation areas (Palacios *et al.* 2006; Grantham *et al.* 2011; Miller & Christodoulou 2014) and spatially dynamic, near real-time threat management (Hobday *et al.* 2014). Front mapping via EO Remote Sensing (Fig. 1.1; Miller 2009) enables high-resolution, automated detection of frontal zones anywhere in the global ocean. Seasonal/climatological products are potentially useful for marine spatial planning, identifying priority areas for threat mitigation both on-shelf (Miller & Christodoulou 2014) and in Areas Beyond National Jurisdiction (ABNJ; the 'high seas'). Moreover, near real-time front mapping augments the suite of tools with potential to inform spatially-dynamic ocean management (Hobday *et al.* 2014), enabling identification and monitoring of critical ephemeral habitats (Fig. 1.2).

Remotely-sensed oceanographic data have been used to inform spatially-dynamic fisheries management in several cases. For example, historical and near real-time SST imagery, coupled with satellite telemetry and spatially-explicit fisheries data, has been successfully used to reduce bycatch of loggerhead turtles along the TZCF north of Hawaii (Howell *et al.* 2008). The Australian fisheries authority has used a comparable approach using *in-situ* sensors to regulate exploitation of southern bluefin tuna (*Thunnus maccoyii*; Hobday & Hartmann 2006). Although there are few examples of such innovatively managed fisheries (Dunn, Boustany & Halpin 2011), similar methods are applicable to other species of conservation concern (Hobday & Hartmann 2006) and may be critical in mitigating future marine biodiversity loss.

Marine Protected Areas (MPAs) can regulate overlap between spatially-explicit threats and critical at-sea habitats. MPAs are most tractable on-shelf, within Exclusive Economic Zones (EEZ), where anthropogenic threats to marine vertebrate populations, such as fisheries pressure, MREI development, noise and habitat degradation, are also concentrated (Maxwell *et al.* 2013). Spatially predictable biophysical hotspots, such as those associated with persistent tidal mixing, tidal-topographic, and upwelling shadow fronts, are logical candidates for within-EEZ MPAs and easily identifiable. Indeed, hotspots associated with quasi-stationary frontal zones have been explicitly included in MPA design in the UK (Miller & Christodoulou 2014) and the Mediterranean (Panigada *et al.* 2008).

In the open oceans beyond EEZs, persistent frontal zones, such as that associated with the Charlie Gibbs Fracture Zone in the North Atlantic (Fig. 1.1), are also amenable to site-based management. However, effective conservation of pelagic biodiversity in ABNJ rests not only upon the identification of vulnerability hotspots, but also the capacity to track how these hotspots shift with changing oceanographic conditions (Hooker *et al.* 2011; Fig. 1.2; Lascelles *et al.* 2012). Spatially-dynamic ocean management (Hobday *et al.* 2014) may be more effective in managing threats to marine vertebrate populations in some highly dynamic regions, and for increasing adaptability as pelagic ecosystems undergo changes related to climate variability. High-resolution front frequency maps, both near real-time and seasonal/climatological (e.g. Fig. 1.1), coupled with real-time monitoring of anthropogenic activity and marine vertebrate habitat use (Fig. 1.2), present managers with data of value for more effective management of pelagic ecosystems.

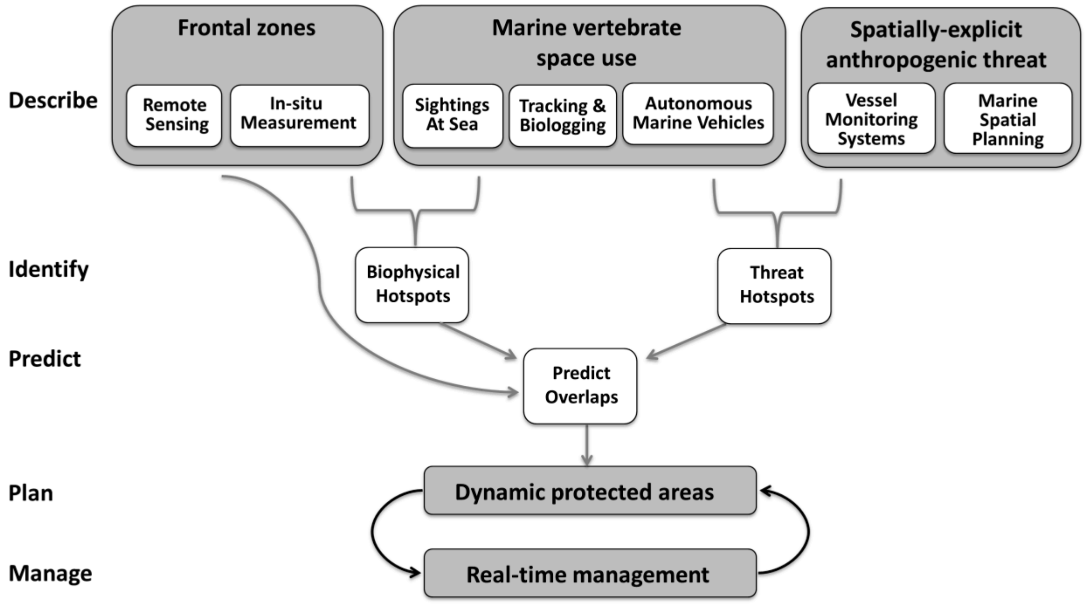

Figure 1.2 Frontal zones as priority conservation areas for marine vertebrates. *Understanding of associations between marine vertebrates and fronts can be enhanced using data describing i) the oceanographic environment, obtainable from remote sensing or in-situ measurement and ii) marine vertebrate space use, through at-sea sightings, tracking/biologging and autonomous marine vehicles. Insights can be fed forward into predictive habitat models, which can be used together with spatially-explicit information describing anthropogenic threat to predict and monitor regions of overlap.*

1.4 Conclusions

Associations between marine vertebrates and oceanographic fronts vary spatially, temporally and between taxa, influenced by both the biophysical properties of fronts and taxon-specific foraging ecology (Hunt Jr *et al.* 1999). Despite this variability, there now exists a considerable body of evidence indicating that persistent mesoscale frontal zones are ecologically significant across the oceans (e.g. Polovina *et al.* 2001; Bost *et al.* 2009). As areas of existing and potential overlap between critical habitats and anthropogenic threat, persistent frontal zones represent tractable conservation areas, in which to focus threat mitigation measures. Continued integration between remote sensing science, spatial ecology, oceanography and fisheries management has potential to improve marine biodiversity conservation by i) bridging the gaps in our understanding of the oceanographic drivers of marine vertebrate space use and ii) feeding into systematic conservation planning through mapping and real-time monitoring of threat hotspots (Grantham *et al.* 2011; Hobday *et al.* 2014). Such integration is vital if we are to balance the competing demands of anthropogenic activities and biodiversity conservation in the vast and dynamic oceans.

Chapter II

Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird

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ABSTRACT

The oceanographic drivers of marine vertebrate habitat use are poorly understood yet fundamental to our knowledge of marine ecosystem functioning. Here we use composite front mapping and high-resolution GPS tracking to determine the significance of mesoscale oceanographic fronts as physical drivers of foraging habitat selection in northern gannets *Morus bassanus*. We tracked 66 breeding gannets from a Celtic Sea colony over two years and used residence time (RT) to identify area-restricted search (ARS) behaviour. Composite front maps identified thermal and chlorophyll-a mesoscale fronts at two different temporal scales – (a) contemporaneous fronts and (b) seasonally persistent frontal zones. Using Generalised Additive Models (GAM), with Generalised Estimating Equations (GEE-GAM) to account for serial autocorrelation in tracking data, we found that gannets do not adjust their behaviour in response to contemporaneous fronts. However, ARS was more likely to occur within spatially predictable, seasonally persistent frontal zones (GAM). Our results provide proof-of-concept that composite front mapping is a useful tool for studying the influence of oceanographic features on animal movements. Moreover, we highlight that frontal persistence is a crucial element of the formation of pelagic foraging hotspots for mobile marine vertebrates.

2.1 Introduction

Marine predators, such as seabirds, cetaceans, pinnipeds, turtles and sharks, must locate sparsely-distributed prey in vast, heterogeneous and dynamic oceans. Although these diverse taxa differ greatly in foraging ecology, shared scale-dependent foraging strategies have evolved, presumably in response to the patchy, hierarchical distribution of pelagic prey (Weimerskirch, Gault & Cherel 2005; Sims *et al.* 2006; Fauchald 2009). These strategies enable predators to locate broad-scale foraging grounds and then adjust the scale of search effort to find prey aggregations nested within (Pinaud & Weimerskirch 2007; Fauchald 2009). Prey distributions are somewhat predictable at large- and meso-scales (10 s to 100s of kilometres; Weimerskirch 2007), but less so at sub-mesoscales (approx. 1 kilometre; Weimerskirch, Gault & Cherel 2005; Fauchald & Tveraa 2006), which may explain why foraging-site fidelity at broad and meso-scales is common among marine vertebrates (e.g. seabirds, turtles, seals; Bradshaw *et al.* 2004b; Hays *et al.* 2006; Broderick *et al.* 2007; Weimerskirch 2007; Patrick *et al.* 2014).

Oceanographic processes operating over a range of spatial and temporal scales regulate pelagic prey availability, and predictability, driving patterns of habitat utilisation for highly mobile marine predators. For instance, a taxonomically diverse range of marine vertebrates are known to associate with meso- (10s-100s kms) and sub-mesoscale (~1km) oceanographic features such as fronts and eddies (Polovina *et al.* 2001; Sims *et al.* 2003; Doniol-Valcroze *et al.* 2007; Weimerskirch 2007; Bost *et al.* 2009; Tew Kai *et al.* 2009; Godø *et al.* 2012; Sabarros *et al.* 2013). Fronts are transitions between water masses, which manifest at the surface as horizontal gradients in temperature, salinity, density, turbidity or colour (Le Fevre 1986; Belkin, Cornillon & Sherman 2009). Nutrient retention within fronts can significantly enhance primary production (Le Fevre 1986; Franks 1992a) and bio-physical coupling leads to aggregation and proliferation of zooplankton (Franks 1992b; Genin *et al.* 2005). These conditions are suitable for pelagic fish, which in turn are prey for higher predators, and hence, fronts may be foraging hotspots (Yoder *et al.* 1994; Genin *et al.* 2005). Despite the assumed significance of fronts as foraging locations, we still have a poor grasp of their ecological value for higher trophic level predators. Fronts occur throughout the oceans, yet differ considerably in strength, persistence, size and spatial variability (Belkin, Cornillon & Sherman 2009). This variability, as well as temporal and spatial lags in bio-aggregative effects (Owen 1981; Le Fevre 1986; Genin *et al.* 2005), influences the suitability of fronts for foraging, particularly for piscivores. Persistent fronts are assumed to present more predictable foraging opportunities than small-scale, ephemeral and/or superficial features (Sabatés & Masó 1990; Gregory Lough & Manning 2001), but direct tests of the significance of frontal predictability for predator foraging are lacking.

Recent methodological developments can address this discrepancy. Bio-logging technology and associated analytical techniques have enabled remote monitoring of individual animal distribution and behaviour, enriching our insight into habitat use by marine predators (Godley *et al.* 2008). However, a key constraint is the lack of data describing oceanographic processes and pelagic prey distributions at matching spatio-temporal scales. Although *in-situ* studies have yielded valuable insights into the fine-scale mechanisms underlying animal-oceanography interactions (e.g. Scott *et al.* 2010; Embling *et al.* 2012; Pirotta *et al.* 2013), this eulerian approach cannot provide information on behaviour throughout a foraging bout, limiting our understanding of broader-scale oceanographic influence. Remotely-sensed data can supplement bio-logging, identifying physical conditions that drive habitat selection in virtual real-time. Sea surface temperature (SST) and chlorophyll-a (chl-a) imagery are most widely used (Polovina *et al.* 2001; Block *et al.* 2011), but it is questionable whether these metrics are appropriate for defining foraging habitat, particularly for piscivores (Grémillet *et al.* 2008). Indeed, the use of chl-a imagery in shallow shelf seas could be misleading, as sub-surface chlorophyll maxima in stratified areas can present more attractive foraging opportunities than mixed waters with elevated surface chl-*a* (Scott *et al.* 2010). In contrast, sub-surface processes occurring along thermal fronts are known to increase prey accessibility for diving predators. Convergent flow fields and fine-scale downwelling aggregate plankton in the shallow thermocline (Franks 1992b; Genin *et al.* 2005), attracting higher trophic level consumers, including foraging seabirds (Durazo, Harrison & Hill 1998; Simpson & Sharples 2012). Front mapping is able to detect the surface profile of these important sub- and near-surface biophysical processes and is, therefore, a potentially powerful tool for identifying pelagic foraging hotspots.

Composite front mapping (Miller 2009) is a step forward in automated front detection via remote sensing, addressing the limitations of precursor methods. To date, the majority of studies including a measure of frontal activity have either identified fronts manually or used single-image edge detection (SIED; Cayula & Cornillon 1992) on single-day (e.g. Graham *et al.* 2012) or temporally averaged (e.g. Sabarros *et al.* 2013) images. However, limitations of these methods reduce their utility. For example, using single-day imagery can result in sacrifice of tracking data owing to cloud cover. Furthermore, temporally averaged imagery masks spatiotemporal dynamics of fronts, which can be highly variable in shelf seas, giving only an estimated average position of a wandering feature. Using SST/chl-a gradients it is not possible to recognise contiguous curvilinear frontal features and, when using temporally averaged images, can result in erroneous frontal locations. *Composite front mapping* addresses these limitations, enabling objective, automatic front detection over a sequence of images, removing cloud influence and allowing for the visualisation of frontal dynamics. In addition, high-resolution front metrics, such as the distance to the closest front or density of detected fronts, can be derived. These metrics facilitate objective quantification of the strength of predator-frontal associations and exploration of the effects of spatial scale, persistence, and magnitude of cross-frontal gradient, not always possible previously.

Here we use composite front mapping and high-resolution GPS tracking to investigate oceanographic drivers of habitat use in a piscivorous marine predator, the northern gannet *Morus bassanus* (hereafter, 'gannet'). Gannets are large, medium-ranging marine predators, which feed on a wide-variety of piscivorous prey (Martin 1989; Hamer *et al.* 2007; Votier *et al.*

2013; Patrick *et al.* 2014). Foraging plasticity in gannets has been linked to oceanographic variability over a range of scales (Garthe *et al.* 2007; Hamer *et al.* 2007; Hamer *et al.* 2009; Garthe, Montevecchi & Davoren 2011). We here assess the influence of mesoscale frontal activity on gannet foraging behaviour, and evaluate the utility of composite front mapping for elucidating oceanographic controls of habitat selection. Moreover, we explicitly assess the importance of frontal persistence by investigating gannets' behavioural responses to both contemporaneous and seasonally persistent thermal and chlorophyll fronts.

2.2 Methods

Device deployment

Chick-rearing gannets (n=66) were tracked from a large breeding colony (~40,000 breeding pairs) on Grassholm, Wales, UK (51° 43' N, 05° 28' W) over two breeding seasons (n=17, Jul 2010; n=49, Jun-Jul 2011; Fig. 2.1). All birds were equipped with 30g GPS loggers (i-gotU; MobileAction Technology; http://www.i-gotu.com), TESA-taped to feathers on the centre of the back. Previous studies indicate these devices have no deleterious effects on foraging gannets (Patrick *et al.* 2014). All birds were caught during changeover at the nest, to minimise time chicks spent alone and to ensure foraging trips began immediately following release. Handling time did not exceed 15 minutes. Devices were programmed to record location fixes at one- or two- minute intervals, and recovered after at least one complete foraging trip.

Behavioural classification

Area-Restricted Search (ARS) behaviour is characterised by low flight speed and frequent turning (Pinaud 2008) and can thus be distinguished from direct and fast transit to and from the colony. Previous work has revealed that ARS is triggered by the detection and pursuit of prey in gannets (Hamer *et al.* 2009). The pelagic prey field is patchy and hierarchically organised, with dense prey patches nested within broader-scale aggregation zones, and resultantly ARS is often observed at multiple nested scales (Fauchald, Erikstad & Skarsfjord 2000; Fauchald & Tveraa 2003; Fauchald & Tveraa 2006; Pinaud & Weimerskirch 2007).

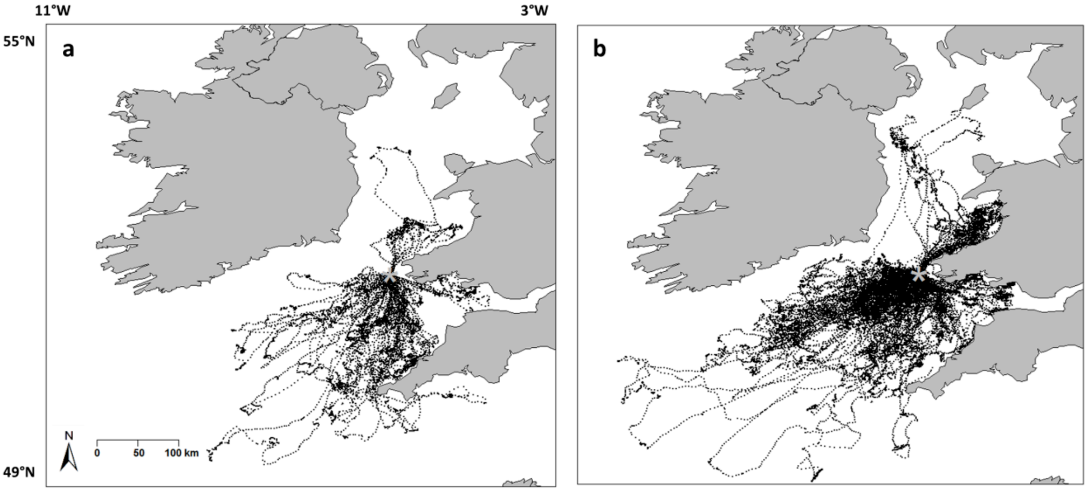


Figure 2.1 GPS tracking. *All foraging trips of birds GPS-tracked during 2010 (a, n=17) and 2011 breeding seasons (b, n=49). Grassholm colony shown as grey star.*

We used an approach based on residence time (RT; Barraquand & Benhamou 2008) to identify ARS bouts in all foraging tracks (adehabitatLT R package; Calenge 2006). To avoid artificial inflation of residence times, we excluded tracking locations recorded during hours of darkness and all locations within a radius of 1km of the colony (because gannets do not forage here but do frequently rest on the water). We then interpolated each daylight movement bout to 60 second intervals and calculated RT at each of these locations, using three radii (1km, 5km, 10km; 2 hours allowed outside circle before re-entering) to detect the scale at which birds performed ARS. These radii were chosen to cover the range of ARS observed previously in gannets (e.g. Hamer *et al.* 2009; average scale of search 9.1 ± 1.9km, with nested finer-scale search at 1.5 ± 0.8km). We used RT at each interpolated location to distinguish ARS from transit using an approach based on Lavielle segmentation (Barraquand & Benhamou 2008) , using both the mean and variance of each series with an 'Lmin' value of 3 (minimum number of observations in each segment) and a 'Kmax' value of 10 (maximum number of segments in movement burst; Supp. Fig. 2.1). We classified segments as periods of ARS or transit using a custom-written R function that identifies each segment as either above or below a threshold of residence time (seconds), with thresholds specified as mean values across all trips at each radius, resulting in a binary response variable (i.e. ARS or transit) for each radius (Supp. Fig.

2.2). We then used these multi-radii ARS classifications in subsequent analysis, investigating levels of scale-dependence in the influence of fronts on habitat selection at meso- (10s – 100s kms) and submeso- scales (~1km).

Composite front mapping

Thermal composite front maps were created for the area enclosing accessible habitat (see Wakefield *et al.* 2009 ; Fig. 2.2), using a radius of whole-dataset maximum displacement from colony (432km). Firstly, raw (level 0) Advanced Very High Resolution Radiometer (AVHRR) infrared data were converted to an index of Sea-Surface Temperature (SST; level 2). SST data were then mapped on to the United Kingdom Continental Shelf (UKCS) region in Mercator projection, with a spatial resolution of ~1.1km/pixel. Thermal fronts were detected in each scene using SIED. Thresholds used for SIED front definition are often selected arbitrarily, and yet are central to findings. We therefore actively varied the threshold for thermal front definition, enabling us to objectively assess the effects on model predictions. To investigate the influence of the magnitude of cross-frontal temperature gradient, we created separate thermal composite sets using 0.4°C and 1.0°C thresholds. All fronts detected over 7-day windows were included in composite front maps, rolling by one day and covering the entire tracking duration. We also produced composite chlorophyll-a (hereafter; chl-*a*) front maps from MODIS data using a similar protocol. However we only used a single front detection threshold for chl-*a* owing to the log-space scale of chl-*a* imagery (0.06 log mg chl-a m^{-3}). Resultant composite maps (Fig. 2.2) quantify frontal activity using arbitrary units (fcomp; Miller 2009), which are a combination of thermal gradient, persistence (ratio of front observations to cloud-free views) and proximity of neighbouring fronts.

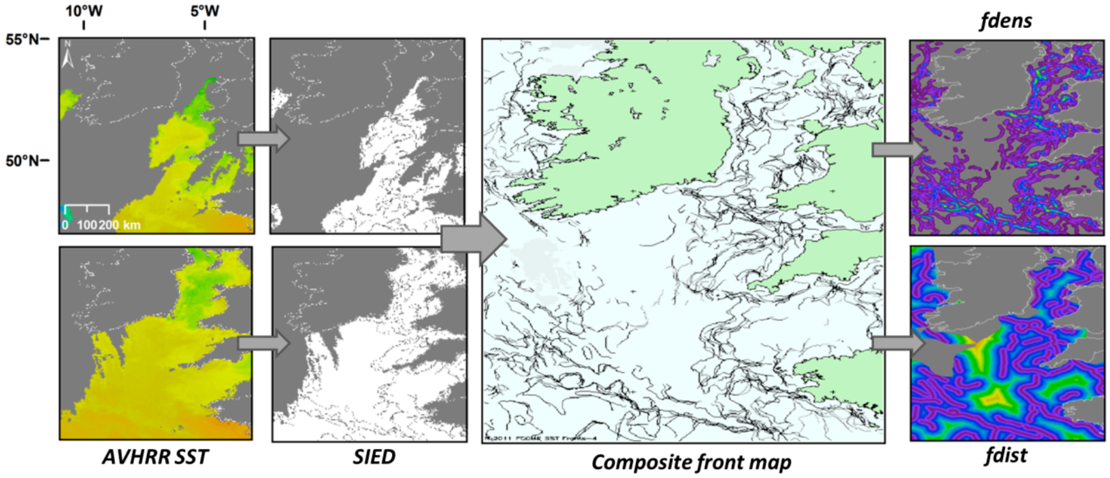


Figure 2.2 ***Composite front mapping.*** *Preparation of thermal composite front maps, and front metrics rasters, from Advanced Very High Resolution Radiometer (AVHRR) sea surface temperature (SST) images. Several satellite passes per day are mapped to the study area (e.g. a,b). Single-Image Edge Detection (SIED) detects fronts in each of these swaths, using a given threshold for front definition, here 0.4°C (c,d). Composite front maps are created from all fronts detected in imagery over a 7-day period (e; Miller, 2009), and spatially smoothed to generate a frontal density (fdens) metric (f) or simplified to generate a distance to closest front (fdist) metric (g).*

Composites were used to create a suite of metrics quantifying frontal activity designed for use with tracking data (Fig. 2.2). We simplified the composite maps to determine contiguous contours through the strongest front observations, using a novel clustering algorithm (Miller, *unpubl. data*) which first involves smoothing the front map with a Gaussian filter of five pixels width. From these we generated smoothed rasters describing distance to the closest front and frontal density, for use with tracking data. **Frontal distance (fdist)** describes distance from any point to the closest simplified front (Fig. 2.3). **Frontal density (fdens)** quantifies the relative strength of detected fronts, using fcomp units (gradient x persistence x proximity). This metric is derived using spatial smoothing of each composite front map to yield a continuous distribution of frontal activity (Fig. 2.3). We selected a smoothing parameter based on the level of detail in resultant products, choosing a value that did not oversmooth small-scale, ephemeral fronts. Thermal and chl-*a* front metrics were extracted for each location along each track using custom software. In addition, we extracted surface chl-*a* (mg m^{-3}; 7-day composite) for each location, as an indicator of levels of primary production in relation to frontal propagation.

Seasonal thermal front climatologies were also generated for each year (Jun-Aug; 2010-11), at 1.2km/pixel resolution. These **frequent front (ffreq)** maps (Fig. 2.4) identify seasonally persistent frontal zones by highlighting regions in which strong, persistent or frequently-occurring fronts manifest. We used a custom algorithm that estimates the percentage time in which a 'strong' front (here, $F_{comp} \geq 0.015$) is detected within each grid cell over a specified time period (Miller & Christodoulou 2014). This F_{comp} unit combines strength, persistence and proximity to other fronts (Miller 2009), and this threshold is used to exclude numerous weak and variable fronts that could confuse the seasonal frequency. Seasonal chl-*a* (median) composites were created at the same temporal and spatial resolution, to highlight areas of enhanced productivity in relation to persistent frontal zones.

Modelling responses to contemporaneous thermal and chlorophyll-a fronts

First, we tested the influence of contemporaneous thermal and chl-*a* fronts on the probability of observing ARS in gannets. Metrics describing frontal density (*fdens*), distance to closest simplified front (*fdist*), and chl-*a* concentration were extracted from rolling 7-day composites centred at the time of animal presence (Fig. 2.3). To account for the fact that gannet foraging range is influenced by intra-specific interactions and travelling costs (Wakefield *et al.* 2013), we also included distance to the colony of each GPS fix as a proportion of maximum displacement as a covariate in our models (Wakefield, Phillips & Matthiopoulos 2009). All explanatory covariates were standardised before inclusion by subtracting the mean and dividing by the standard deviation (Zuur 2012). We checked for multi-colinearity using Generalised Variance Inflation Factors (GVIF) and pairwise plots. Owing to observed colinearity, the *fdens* and *fdist* metrics were investigated using separate models for both thermal and chl-*a* fronts.

To account for strong intra-individual temporal autocorrelation, we used Generalised Estimating Equations (GEE; Liang & Zeger 1986), with each daylight movement bout as the blocking variable (see also Pirotta *et al.* 2011; Pirotta *et al.* 2013; Scott *et al.* 2013). We constructed GEE-GAMs with a binomial error structure and logistic ('logit') link function ('geepack' and 'splines' R packages; Højsgaard, Halekoh & Yan 2006). Quasi-likelihood under the model independence criterion (QIC; Pan 2004) was used to select between a working independence correlation structure and an autoregressive, AR1, correlation structure.

An approximated version of the QIC (QICu; Pan 2004) was used to select the most parsimonious set of explanatory variables from *a priori* candidate models. In order to ascertain the most appropriate form of each explanatory covariate, we compared the QICu of models with each term in its linear form, and as a B-spline with 4 degrees of freedom and a knot positioned at the mean. QICu can be over-conservative (Hardin & Hilbe 2003), so we used repeated Wald's tests to determine significance of retained explanatory covariates.

Goodness-of-fit of final models was evaluated using a confusion matrix comparing binary predictions to observed incidence of ARS in the original dataset. The probability cut-off above which a prediction was classified as an ARS point was selected using a Receiver Operating Characteristic (ROC) curve (Zweig & Campbell 1993). We computed the area under the ROC curve (AUC) as a further measure of model performance (closer to 1, better performance; Zweig & Campbell 1993). To obtain response curves, we predicted from the final model for each of the explanatory terms, holding all other terms constant. Terms retained by QICu model selection but found to be non-significant under more stringent Wald's tests were not removed from the model (Pirotta *et al.* 2011), and only significant relationships were plotted.

Modelling responses to seasonally persistent thermal and chlorophyll-a frontal zones

Second, we tested the influence of seasonally persistent thermal and chl-*a* frontal zones (Fig. 2.4) on gannet foraging habitat preference. As no intra-individual temporal autocorrelation existed in this time-aggregated dataset, we used a binomial Generalised Additive Model (GAM) with a logistic ('logit') link function to model presence/absence of ARS against front frequency for the 2011 breeding season ('mgcv' R package; Wood 2006). To achieve this, we created a grid at a matching spatial resolution to the seasonal frequent front maps (1.2km; 'raster' R package; Hijmans & van Etten 2012), and then determined presence/absence of ARS in each cell across all tracks. We were unable to do the same for 2010 because of low sample size. Environmental covariates were standardised before inclusion as explanatory terms, and multi-colinearity was checked using GVIF and pairwise plots. Co-linearity between the seasonal frequent front and chl-*a* metrics prevented simultaneous inclusion in the same model, so the terms were applied separately. An index of habitat accessibility, derived using the distance of each grid cell to the colony as a proportion of whole-dataset maximum displacement, was also included to control for greater accessibility of fronts close to the colony than in fringes of the foraging range (Wakefield, Phillips & Matthiopoulos 2009).

In order to ascertain the best form for each explanatory covariate, we fitted separate models with both linear and smoothed forms of each term, visualised the shape of smoothers and determined the effect of the inclusion of each form on Akaike Information Criteria (AIC). Smoothers were only included in final models where deemed biologically reasonable. For example, although the smoothed forms of the front frequency metrics (*mfreq*; *cfreq*) were associated with lower AIC, linear forms were preferred following visualisation of the smoother, as a conservative approach to prevent over-fitting. Forwards and backwards step-wise model selection using AIC identified the final model, which was then checked for overdispersion. Model residuals were checked for spatial autocorrelation (Zuur 2012).

2.3 Results

Gannet foraging trips

For the 66 birds tracked over the two breeding seasons, mean number of foraging trips was 3.8 ± 2.8 (range 1-12), with an average duration of 24.8 ± 22.7 hours (range 2 – 168 hours). The majority (76%) involved one or more nights spent away from the colony (mode 1; range 0-7). Maximum foraging range per trip ranged between 22.2 and 432.0 km from the colony, with an average of 178.3 ± 87.2 km. All foraging trips included at least one ARS zone.

Responses to contemporaneous thermal and chlorophyll-a fronts

We found no evidence that gannet ARS was associated with contemporaneous thermal or chlorophyll-*a* fronts, even when varying the threshold used for thermal front definition and the radius used to define ARS through the residence time analysis. Although QICu model selection retained contemporaneous front metrics in some model runs (Supp. Table 2.1), post-hoc repeated Wald's tests confirmed that only distance to colony explained a significant proportion of deviance in each of these model runs (Supp. Fig. 2.3).

Model validation confirmed goodness of fit of final models. True positive rates of model predictions, obtained from confusion matrices, are given in Supplementary Table 2.1. ROC curves confirmed models performed acceptably well. High levels of temporal autocorrelation (within-block correlation, e.g. thermal 0.4°C threshold, 5km RT radius *fdens* = 0.97 ± 0.04) justified the use of GEEs. QIC comparison confirmed an AR1 autoregressive correlation structure as best fit for the data for all models.

Use of seasonally persistent frontal zones

Seasonal thermal front frequency (mfreq; Fig. 2.4a) was retained by model selection (χ^2_1 = 322.5, p < 0.001; Fig. 2.4c; Table 2.2), with the probability of ARS twice as likely at high front frequency compared with low (Fig. 2.4c). A smoothed relationship with habitat accessibility was also retained (HabAccess, df = 8, p < 0.001; Supp. Fig. 2.4; Supp. Table 2.2). The model explained 33% of deviance and was not over-dispersed (dispersion statistic = 0.83). Colinearity between thermal front frequency (Fig. 2.4a) and seasonal average surface chl-*a* concentration also confirms that persistent frontal zones are areas of increased primary productivity.

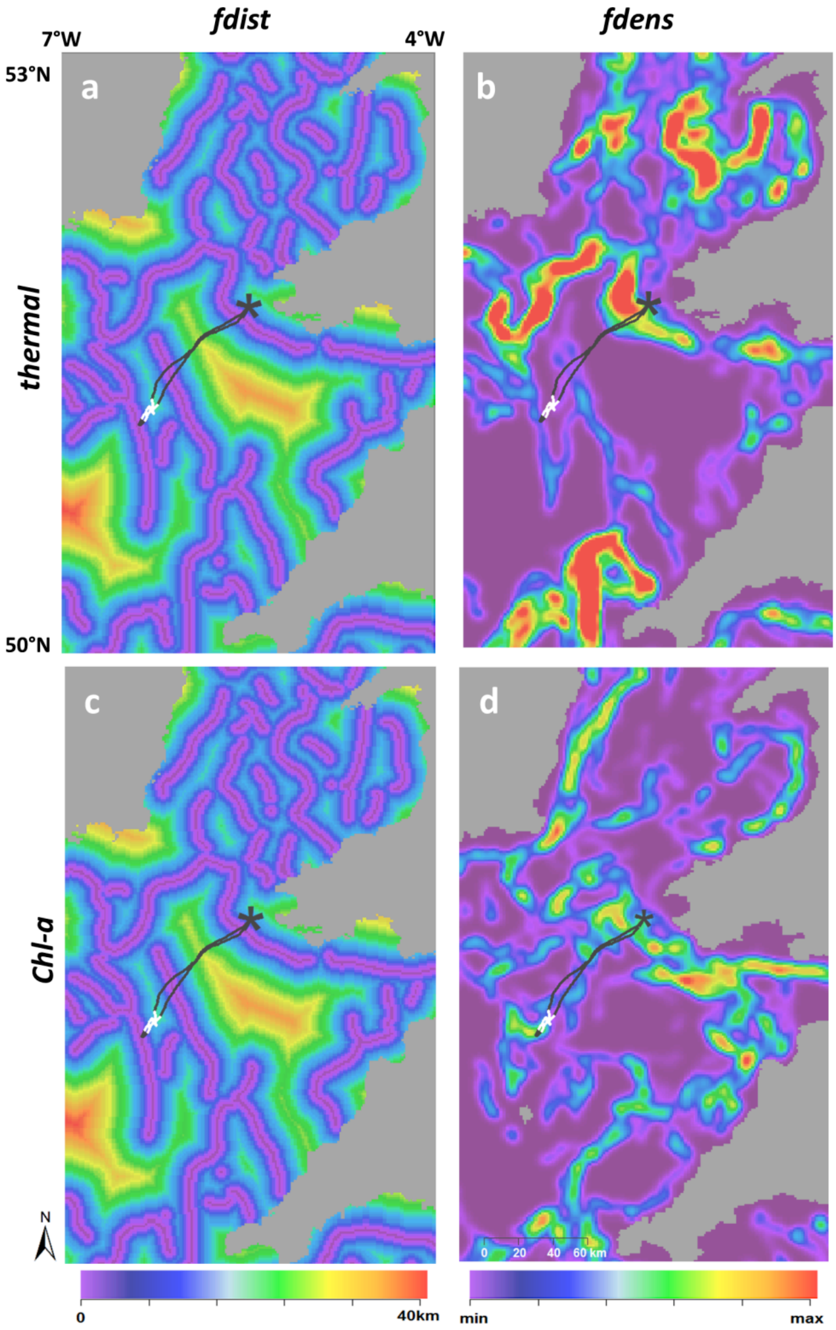


Figure 2.3 Contemporaneous front metrics time-matched to gannet foraging trip. *Distance to closest thermal front (fdist; 0.4°C threshold, a), thermal front density (fdens; 0.4°C threshold, b), distance to closest chl-a front (c) and chl-a front density (d) shown for one complete foraging trip (23 July 2011). Points designated as ARS by residence time analysis (5km radius) shown as white track sections, and commuting flight as black track sections. Colony location shown as black star.*

The seasonal front frequency index for chlorophyll-*a* fronts (cfreq; Fig. 2.4b) was also significant in explaining the spatial distribution of ARS over the breeding season ($\chi^2_1 = 3108$, $p < 0.001$; Fig. 2.4d; Supp. Table 2.2), alongside smoothed habitat accessibility ($p < 0.001$; Supp. Fig. 2.4; Supp. Table 2.2). The model explained 32% of deviance and was not over-dispersed (dispersion statistic = 0.88).

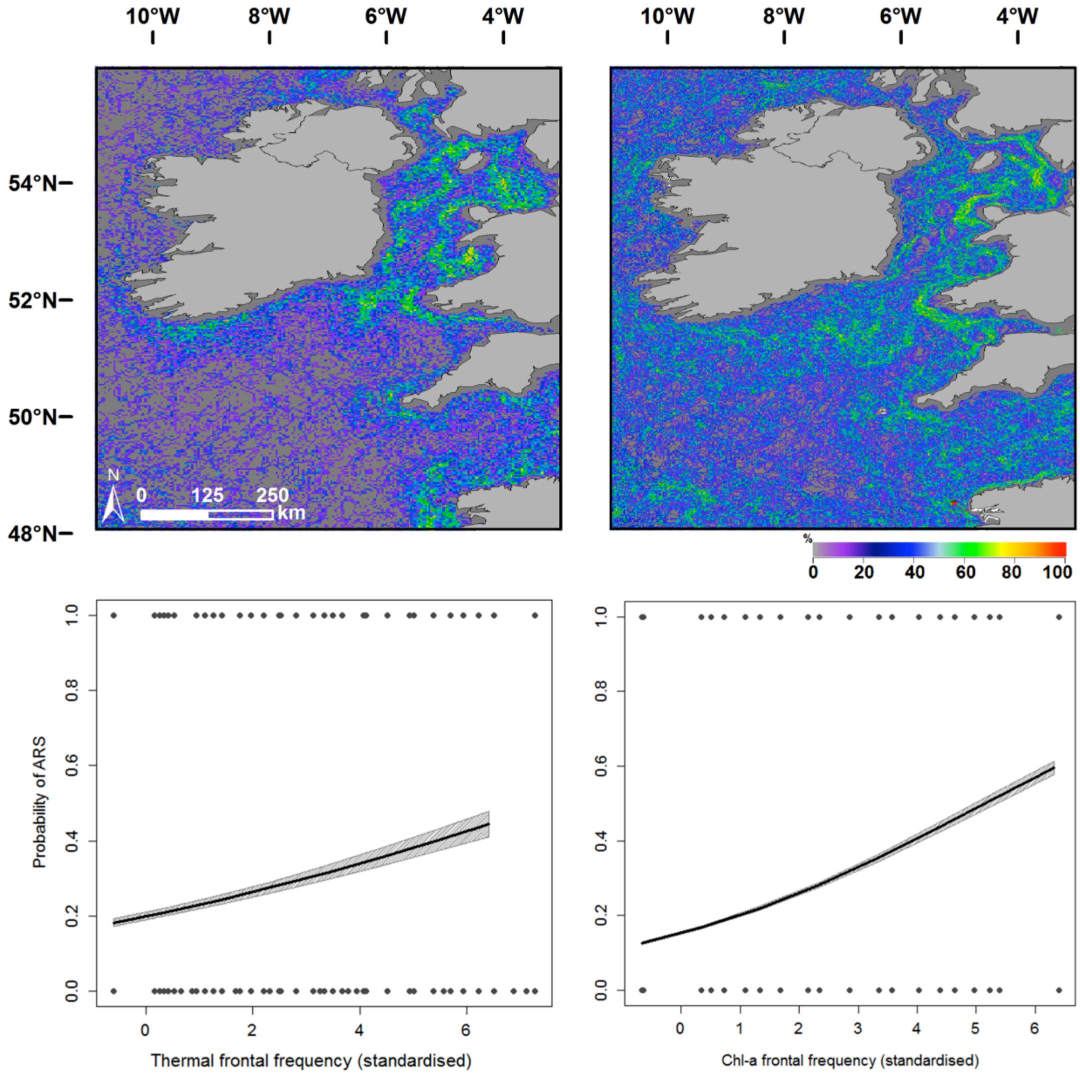


Figure 2.4 Modelling the effects of persistent frontal zones (thermal, chl-a) on the spatial distribution of gannet area-restricted search behaviour. *Seasonally persistent (Jun-Aug 2011) thermal frontal zones (a) and chl-a frontal zones (b), identified using frequent front (mfreq; cfreq) metrics. Model predictions for effects of seasonal thermal front frequency (c; model 4.1) and seasonal chl-a front frequency (d; model 4.2). Gannets are more likely to perform ARS behaviours within regions of frequent frontal activity.*

2.4 Discussion

Combining composite front mapping with high-resolution GPS tracking, this work has revealed that gannets are more likely to perform ARS within persistent mesoscale frontal zones than in other regions of accessible habitat. This is of particular significance since it not only shows that mesoscale fronts influence habitat selection, but also that remote sensing methods are able to identify features relevant to piscivorous marine vertebrates. Moreover, this work also illustrates that temporal scale is crucial - gannets do not tend to forage at ephemeral contemporaneous fronts, instead relying on spatially predictable, seasonally persistent zones of frequent frontal activity.

Mesoscale fronts and top predator foraging

Predictability of foraging grounds is known to strongly influence seabird habitat selection, and may partially explain our observed differences in front use (Weimerskirch 2007). Many marine predators, including seabirds, are known to repeatedly return to the same foraging areas (Hamer *et al.* 2007; Weimerskirch 2007; Pettex *et al.* 2010; Patrick *et al.* 2014), which is generally attributed to the presence of oceanographic features that are predictable in time and space. In the Celtic Sea, these predictable foraging areas are associated with persistent mesoscale thermal and chl-a frontal zones. The ultimate mechanisms by which these features are located are not known, although a combination of memory effects, local enhancement and colonies acting as information centres strongly influence observed foraging distributions in this species (Wakefield *et al.* 2013). Proximate environmental factors enabling front detection include visual cues associated with the accumulation of foam and detritus (Le Fevre 1986; Franks 1992b); flow patterns, including surface convergence (Franks 1992b) and cross-frontal jets (Simpson & Sharples 2012), or olfactory cues such as dimethyl sulphide (DMS; Nevitt & Bonadonna 2005). Persistent fronts probably produce a stronger surface signal than ephemeral features, increasing detectability.

Alongside greater spatial predictability and detectability, persistent mesoscale frontal zones also present more attractive foraging opportunities than ephemeral fronts. The bio-aggregative effects of fronts vary with temporal persistence, spatial scale, temperature gradient, strength of convergent flow and the properties of surrounding water masses, influencing their attractiveness as top predator foraging habitat. Ephemeral, weak or spatially-variable features may not propagate for sufficient time for biological enhancement to attract mid-trophic level consumers such as pelagic fish. In contrast, persistent frontal zones are associated with sustained primary productivity, and therefore more likely to attract the pelagic fish preyed upon by seabirds and other large marine vertebrates.

In contrast to our findings, the closely-related Cape gannet *Morus capensis* is known to initiate ARS-type behaviours at contemporaneous chl-*a* fronts in the Benguela (Sabarros *et al.* 2013). The reasons for these differences are not clear, but are likely to be related to differences in regional oceanography. Small-scale, superficial and ephemeral thermal fronts develop frequently in the Celtic Sea through tidal effects and cycles of stratification and mixing (Pirotta *et al.* 2013), but are not always associated with chl-*a* enrichment (Scott *et al.* 2010; Votier *et al.* 2010). In contrast, the Benguela is a major upwelling zone, in which upwelling filaments, eddies and strong vertically-structured fronts manifest. Although varying in seasonal intensity and position, upwelling fronts in the Benguela are less spatiotemporally variable than tidal fronts in the Celtic Sea over time scales of days to weeks, and so may be more predictable foraging habitats for seabirds using learning and memory effects to locate prey (Weimerskirch 2007). In addition, Cape gannets prey upon the mega-abundant sardines and anchovies in the Benguela (Sabarros *et al.* 2013). These fish are zooplanktivorous, and therefore more closely tied to oceanographic drivers, than the piscivorous fish (e.g. mackerel *Scomber scombrus*, garfish *Belone belone*) targeted by northern gannets in the Celtic Sea (Votier *et al.* 2013). Differences in the biophysical nature of fronts encountered by prospecting birds within these two contrasting oceanographic regions elicit different responses from these two closely-related species. These differences highlight the need for a comprehensive understanding of regional oceanography when investigating the drivers of habitat selection for mobile marine vertebrates.

Gannets in the Celtic Sea forage extensively at fishing vessels (Votier *et al.* 2010; Votier *et al.* 2013; Bodey *et al.* 2014), so fisheries activity could also influence the association between fronts and gannets reported here. Nevertheless, we believe that gannets are using persistent frontal zones as natural foraging sites for the following reasons. First, gannets switch between natural foraging and scavenging both within and among trips (Votier *et al.* 2013) and must therefore rely upon both natural foraging and scavenging. Second, analysis of a subset of ten gannets in 2011 equipped with bird-borne cameras enabled us to determine frontal activity in the presence and absence of fishing vessels. This revealed little difference between vessel-associated ARS instances, those associated with natural foraging and conditions experienced during transit (see Supp. Fig. 2.5). Third, the majority of trawlers that gannets follow in the Celtic Sea target demersal fish (Votier *et al.* 2013), and would presumably not benefit from fishing in frontal regions.

Composite front mapping for identifying marine predator foraging habitats

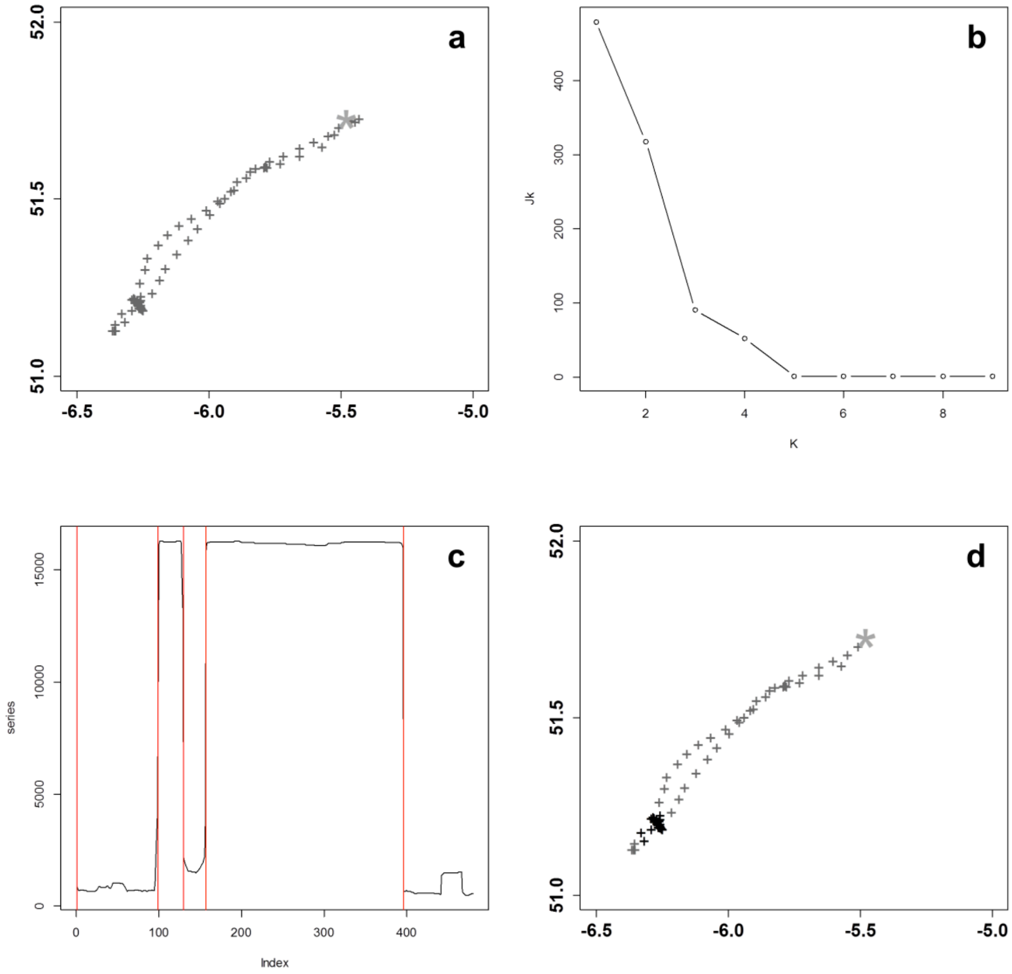
We have used multi-threshold objective front detection to produce composite thermal and chl-*a* front maps at 1km resolution, enabling us to quantify the influence of fronts on foraging habitat selection in gannets. Using this technique has negated sacrifice of tracking data as a result of cloud cover. Furthermore, using both temporally-matched 7-day front composites and seasonal front indices has revealed the importance of considering frontal persistence. However, composite front mapping does have limitations with implications for defining marine predator foraging habitats. In common with all remotely-sensed products, only the surface signature of complex three-dimensional oceanographic processes is visible. Resolution of imagery is also limited by sensor technology, restricting our ability to detect sub-mesoscale near-shore tidal fronts, potentially significant features in shallow shelf-seas (Mendes *et al.* 2002). Furthermore, using 7-day composites could mask real-time, fine-scale responses to environmental cues. Recent in-situ studies of fine-scale oceanographic influence on seabird foraging have identified tidal state, thermal stratification index, and sub-surface processes such as tidal shear at the thermocline, as significant influences on foraging decisions (Pirotta *et al.* 2011; Cox, Scott & Camphuysen 2013). These fine-scale processes cannot be detected using contemporary remote sensing techniques. However, remote sensing can provide oceanographic context for the movements of known individuals over broader spatial and temporal scales, generating insights of direct relevance to predictive habitat modelling (Oppel *et al.* 2012) and marine spatial planning (Miller & Christodoulou 2014).

2.5 Conclusions

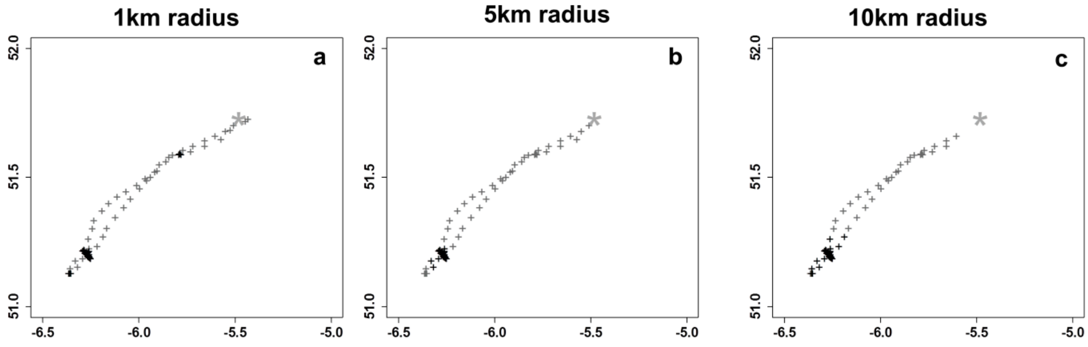
We here present proof of concept that objective front detection and composite front mapping (Miller 2009) can enhance the value of predator tracking data for habitat utilisation studies, and can improve understanding of mechanistic links between oceanographic processes and marine vertebrate foraging ecology. Novel front metrics used here provide capacity for quantification of the strength of predator-frontal relationships without neglecting the significance of frontal strength, persistence and scale. We have found that persistent frontal zones are preferred foraging habitats of a piscivorous top predator inhabiting a shallow shelf sea, but that responses to contemporaneous thermal and chl-*a* fronts vary. Persistent frontal zones are likely to represent predictably profitable foraging grounds for predators that use learning and memory effects to locate prey. In contrast, ephemeral, superficial fronts may not present attractive foraging opportunities owing to the spatial and temporal lags inherent in bio-aggregation. Furthermore, persistent fronts are more likely to generate environmental cues discernible to overflying gannets, and so more likely to become sites of local enhancement for these network foragers. These findings provide direct evidence that the temporal persistence of mesoscale fronts fundamentally regulates their value as foraging habitats for marine predators.

Although considerable advances have been made in our understanding of the oceanographic drivers of marine vertebrate habitat use in recent years, questions remain regarding the strength and nature of predator-frontal associations. Our methods have considerable scope for further application, providing opportunity for environmental contextualisation of habitat use, across foraging guild, trophic level and oceanographic region. Composite front mapping allows us to objectively detect thermal and chl-*a* fronts anywhere in the global ocean at high resolution, which could help in locating critical at-sea habitats for mobile marine vertebrates, many of which are of immediate conservation concern (Myers & Worm 2003; Croxall *et al.* 2012). Furthermore, continuous near-real time global satellite monitoring of environmental conditions, together with animal tracking and biologging, provides capacity for investigation of responses to global change.

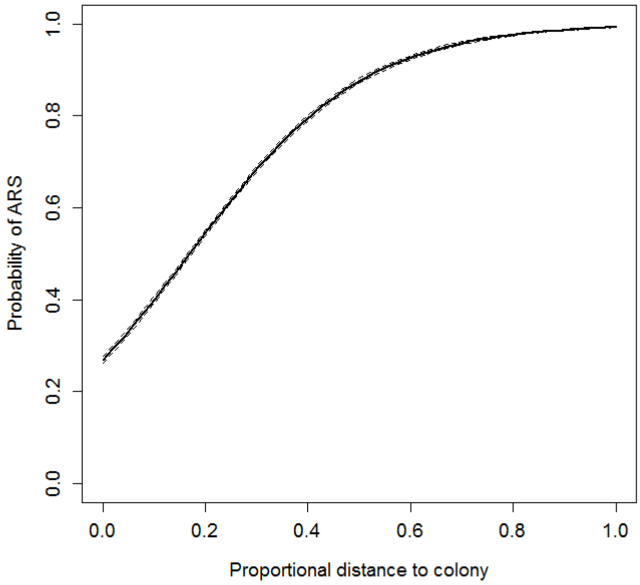
Supplementary Figures and Tables



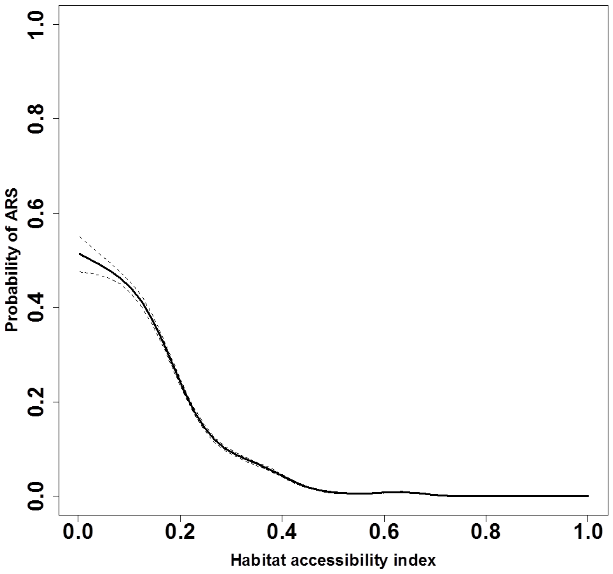
Supp. Figure 2.1 Behavioural classification: identifying ARS using residence time. *Example of ARS designation procedure using Lavielle segmentation. Each interpolated track section (a) underwent a two-stage Lavielle segmentation process, the first of which identifies the number of different segments in the series (b) and then relates these segments to locations (c,d). (d) Commuting flight shown in grey, ARS points (here, 5km RT radius) shown in black. Sub-sampled dataset (locations every 5 mins) plotted for clarity. Colony location as grey star.*



Supp. Figure 2.2 Behavioural classification: identifying ARS using residence time at radii of 1km, 5km and 10km. *Example of ARS designation using different radii for residence time analysis. Commuting flight shown in grey, ARS points identified at each radius shown in black. Sub-sampled dataset (locations every 5 mins) plotted for clarity. Colony location as grey star.*

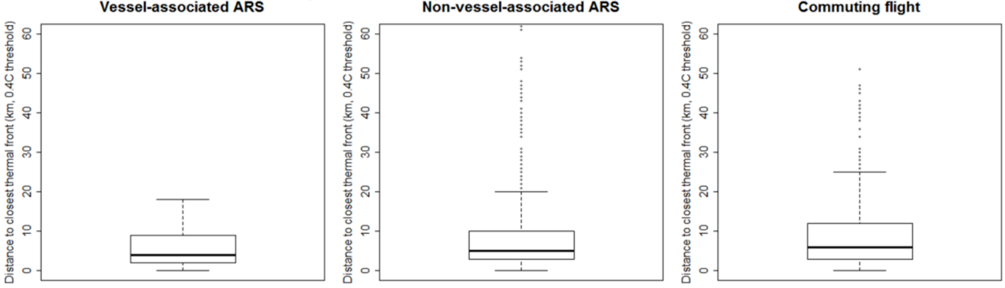


Supp. Figure 2.3 Modelling the effects of contemporaneous thermal fronts on gannet area-restricted search behaviour, using GEE-GAMs. *Contemporaneous front GEE-GAM results (model 1.1.2), showing predicted influence of proportional distance to colony. All other explanatory terms, including thermal and chlorophyll front metrics, were not statistically significant, so are not shown here. The higher probability of ARS further from the colony represents the tendency for ARS zones to take place at the distal point of foraging points. Confidence Intervals represented by dashed lines, here close to the main effect line, owing to small standard error on this coefficient estimate in model output.*

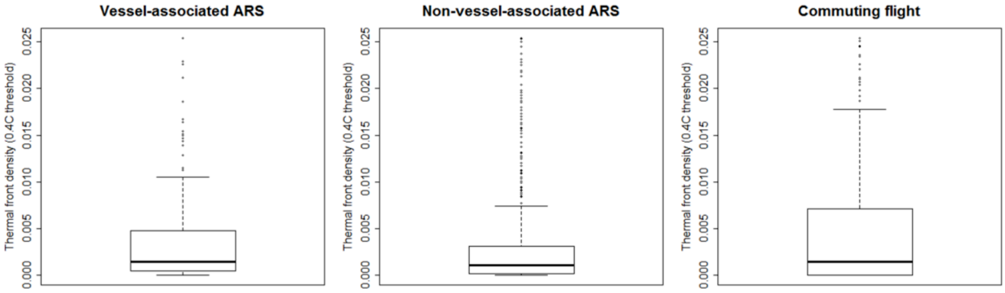


Supp. Figure 2.4 Modelling the effects of persistent frontal zones (thermal, chl-a) on the spatial distribution of gannet area-restricted search behaviour. *Habitat Accessibility index fitted to binomial GAM investigating the influence of persistent frontal zones on gannet ARS behaviour (models 4.1, 4.2) as a control for availability of fronts as a function of distance from colony.*

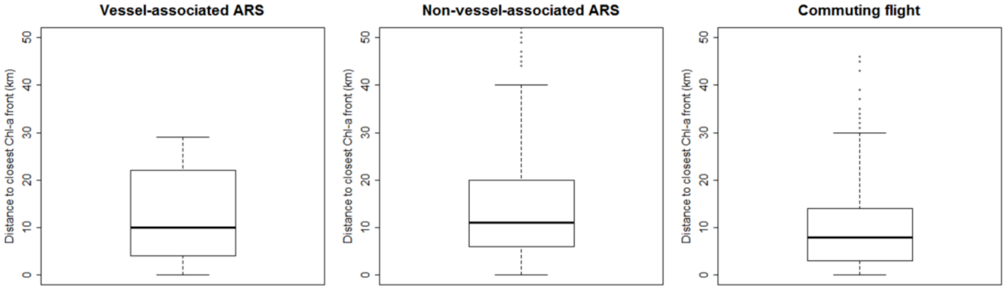
Distance to closest thermal front (0.4C threshold)



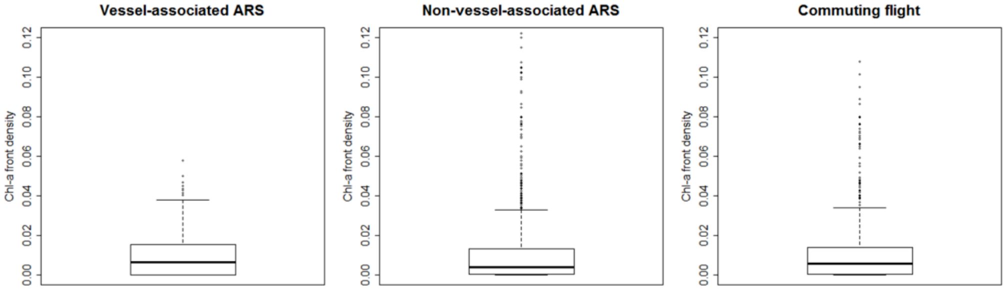
Thermal front density (0.4C threshold)



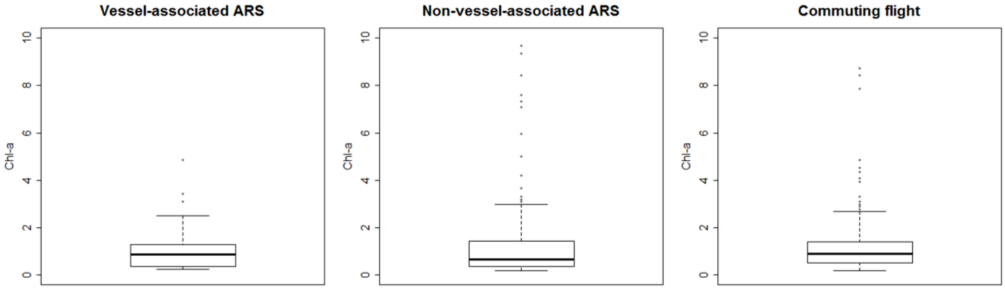
Distance to closest Chl-*a* front



Chl-*a* front density



Chl-*a* concentration (mg m^{-3})



Supp. Figure 2.5 Fisheries interactions. *Frontal activity, and Chl-a concentration, associated with ARS zones in the vicinity of fisheries vessels, with ARS zones classified as natural foraging and with commuting flight. No significant differences are evident for any of these metrics. From subset of GPS-tracked gannets also equipped with miniaturised cameras in 2011 (n=10).*

Supp. Table 2.1 *Modelling the effects of contemporaneous thermal fronts on gannet area-restricted search behaviour, using GEE-GAMs - parameter estimates, standard errors and Wald statistics for terms retained by QICu model selection for each model run, where pdistCol is proportional distance from colony, fdens is standardised frontal density, fdist is distance from the closest front, and chl-a is standardised surface chlorophyll concentration. f denotes the use of splines. fdens and fdist metrics applied in separate model runs, indicated by bold line, owing to colinearity between metrics.*

Parameter	co-efficient	std. error	Wald statistic	p-value
Thermal frontal density (fdens; 0.4°C threshold)				
Model 1.1.1: 1km RT radius			***QICu (ar1) = 30128***	
Intercept	-1.76	0.17		
pdistCol	5.64	0.80	49.3	<0.001
chl-a	-0.000006	0.009	0.0	1
Model 1.1.2: 5km RT radius			***QICu (ar1) = 29362***	
Intercept	-0.99	0.15		
pdistCol	5.89	0.84	48.9	<0.001
True positive prediction rate: 68%				
Model 1.1.3: 10km RT radius			***QICu (ar1) = 29055***	
Intercept	-0.99	0.15		
pdistCol	5.89	0.84	48.9	<0.001
Distance to closest thermal front (fdist; 0.4°C threshold)				
Model 1.2.1: 1km RT radius			***QICu (ar1) = 29887***	
Intercept	-1.78	0.18		
pdistCol	5.72	0.82	49.3	<0.001
fdist	-0.0121	0.036	0.1	0.74
chl-a	-0.00003	0.009	0.0	1
Model 1.2.2: 5km RT radius			***QICu (ar1) = 27893***	
Intercept	-1.50	0.18		
pdistCol	6.67	0.93	51.1	<0.001
True positive prediction rate: 68%				
Model 1.2.3: 10km RT radius			***QICu (ar1) = 28890***	
Intercept	-0.99	0.15		
pdistCol	5.89	0.84	48.9	<0.001
fdist	0.02	0.04	0.2	0.66
Thermal frontal density (fdens; 1.0°C threshold)				
Model 2.1.1: 1km RT radius			***QICu (ar1) = 29887***	
Intercept	-1.76	0.17		
pdistCol	5.64	0.8	49.3	<0.001
chl-a	-0.000006	0.008	0.0	1
Model 2.1.2: 5km RT radius			***QICu (ar1) = 27893***	
Intercept	-1.50	0.18		
pdistCol	6.67	0.93	51.1	<0.001
True positive prediction rate: 68%				
Model 2.1.3: 10km RT radius			***QICu (ar1) = 29055***	
Intercept	-0.99	0.15		
pdistCol	5.89	0.84	48.9	<0.001

Distance to closest thermal front (fdist; 1.0°C threshold)				
Model 2.2.1: 1km RT radius			***QICu (ar1) = 28963***	
Intercept	-1.89	0.19		
pdistCol	6.17	0.89	49.3	<0.001
fdist	-0.13	0.08	3.0	0.081
Model 2.2.2: 5km RT radius			***QICu (ar1) = 27643***	
Intercept	-1.53	0.19		
pdistCol	6.77	0.97	51.1	<0.001
fdist	-0.03	0.05	0.3	0.58
True positive prediction rate: 69%				
Model 2.2.3: 10km RT radius			***QICu (ar1) = 28764***	
Intercept	-1.02	0.16		
pdistCol	6.00	0.88	48.9	<0.001
fdist	-0.04	0.06	0.6	0.42
Chl-a frontal density (cdens; 0.06 log mg chl m^{-3} threshold)				
Model 3.1.1: 1km RT radius			***QICu (ar1) = 29437***	
Intercept	-1.82	0.18		
pdistCol	5.82	0.84	49.3	<0.001
Cdens	0.01	0.02	0.4	0.53
Model 3.1.2: 5km RT radius			***QICu (ar1) =30555***	
Intercept	-1.31	0.17		
pdistCol	6.03	0.87	51.1	<0.001
Cdens	-0.03	0.02	1.9	0.17
True positive prediction rate: 69%				
Model 3.1.3: 10km RT radius			***QICu (ar1) =29577***	
Intercept	-0.93	0.15		
pdistCol	5.71	0.83	48.9	<0.001
Cdens	-0.03	0.02	3.8	0.051
Distance to closest chl-a front (cdist; 0.06 log mg chl m^{-3} threshold)				
Model 3.2.1: 1km RT radius			***QICu (ar1) = 30004***	
Intercept	-1.77	0.17		
pdistCol	5.63	0.81	49.3	<0.001
Cdist	0.01	0.06	0.1	0.82
Model 3.2.2: 5km RT radius			***QICu (ar1) = 27422***	
Intercept	-1.47	0.18		
pdistCol	6.47	0.94	51.1	<0.001
Cdist	0.08	0.05	2.9	0.09
True positive prediction rate: 62%				
Model 3.2.3: 10km RT radius			***QICu (ar1) = 28279***	
Intercept	-0.99	0.15		
pdistCol	5.88	0.83	48.9	<0.001
Cdist	0.04	0.04	0.7	0.39

Supp. Table 2.2 Modelling the effects of persistent frontal zones (thermal, chl-a) on gannet area-restricted search behaviour. *Model selection for binomial GAM for presence/absence of ARS at whole dataset level (2011 breeding season) against seasonal environmental covariates. Akaike Information Criteria (AIC) and percentage of deviance explained for each term in both linear and smoothed forms, and effects of term additions, where: HabAccess is habitat accessibility index; mfreq is standardised seasonal thermal front frequency (0.4°C threshold; Jun-Aug 2011); chl-a is standardised seasonal average surface chl-a concentration, and cfreq is standardised seasonal chl-a front frequency. f() denotes the smoothed form of each variable. Separate model selection runs for thermal front frequency and chl-a front frequency separated by dotted line. Most parsimonious models, as identified by AIC, highlighted in bold.*

Explanatory term(s)	**AIC**	**deviance explained**	**linear coefficient**	**p-value**	**df of smooths**
Model 4.1; Thermal frontal zones					
Intercept only (null)	76103	0%	-	-	-
pdistCol	51910	32%	-10.20	<0.001	-
ƒ (pdistCol)	51602	32%	-	<0.001	7.957
mfreq	73448	4%	0.42	<0.001	-
ƒ (mfreq)	72256	5%	-	<0.001	7.786
chl-a	71273	6%	-3.53	<0.001	-
ƒ (chl-a)	67883	11%	-	<0.001	8.975
ƒ (pdistCol)			**-**	**<0.001**	**7.961**
+ mfreq	**51209**	**33%**	**0.19**	**<0.001**	**-**
Model 4.2; Chl-a frontal zones					
Intercept only (null)	202740	0%	-	-	-
pdistCol	141331	30%	-10.3359	<0.001	-
ƒ (pdistCol)	140627	31%	-	<0.001	8.39
cfreq	195489	4%	0.45367	<0.001	-
ƒ (cfreq)	190632	6%	-	<0.001	8.96
ƒ (pdistCol)			**-**	**<0.001**	**8.44**
+ cfreq	**137664**	**32%**	**0.33143**	**<0.001**	**-**

Chapter III

Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic

This chapter has been published as:

Scales, K.L*., Miller, P.I.*, Ingram, S.N., Southall, E.J., and Sims, D.W. (*Joint First Authors) Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic. *Functional Ecology*, In Press. doi: 10.1111/1365-2435.12423

ABSTRACT

Understanding the mechanisms linking oceanographic processes and marine vertebrate space use is critical to our knowledge of marine ecosystem functioning, and for effective management of populations of conservation concern. The basking shark *Cetorhinus maximus* has been observed in association with oceanographic fronts – physical interfaces at the transitions between water masses – exploiting foraging opportunities resulting from zooplankton aggregation. However, the scale, significance and variability of these associations have not previously been established. Here, we quantify the influence of thermal and chlorophyll-*a* fronts on basking shark habitat use in the northeast Atlantic. We use animal-mounted archival tracking with composite front mapping via Earth Observation (EO) remote sensing to provide an oceanographic context to individual shark movements. We investigate levels of association with fronts occurring over two spatio-temporal scales, (i) broad-scale, seasonally persistent frontal zones and (ii) contemporaneous thermal and chl-*a* fronts. Using random walk simulations and logistic regression within an iterative generalised linear mixed modelling (GLMM) framework, we find that seasonal front frequency is a significant predictor of shark presence. Oceanographic metrics time-matched to shark tracks indicate that sharks show a preference for productive regions, and associate with contemporaneous thermal and chl-*a* fronts more frequently than could be expected at random. Moreover, we highlight the importance of front persistence and cross-frontal temperature step, which appear to interact to affect the degree of prey aggregation along thermal fronts in this shelf-sea system. Our findings confirm that surface frontal activity is a predictor of basking shark presence in the northeast Atlantic, both over seasonal timescales and in near real-time. These insights have clear implications for understanding the preferred habitats of basking sharks in the context of anthropogenic threat management and marine spatial planning in the region.

3.1 Introduction

Understanding the ways in which large marine vertebrates optimise foraging efficiency in heterogeneous and dynamic pelagic environments has become a central issue in marine ecology. These animals are often highly mobile, moving over immense spatial scales in order to find suitable habitats in which to forage and reproduce. Moreover, zooplanktivorous megavertebrates such as the basking shark *Cetorhinus maximus*, whale shark *Rhincodon typus*, leatherback turtle *Dermochelys coriacea* and manta ray *Manta birostris* exist on an energetic 'knife-edge', and so must maximise prey encounter rates in patchy pelagic prey seascapes in order to survive (Sims 1999; Stevens 2007; Sims 2008; Fossette *et al.* 2010).

Underlying movement patterns that enhance foraging optimality, such as behaviours approximating theoretically optimal Lévy walks, have been identified in a variety of marine taxa (Visnawathan *et al.* 1996; Sims *et al.* 2008; Humphries *et al.* 2012) and linked to oceanographic context (Hays *et al.* 2006; Humphries *et al.* 2010) and prey fields (Sims *et al.* 2012). Biophysical habitat characteristics, including primary productivity and convergent front propagation, have been shown to influence behavioural switches between Lévy behaviour and Brownian movements in several species, including the basking shark (Humphries *et al.* 2010). Such behavioural switches indicate the concentration of area-restricted search (ARS), a proxy for foraging effort, in productive waters (Humphries *et al.* 2012). Broad-scale movements have also been linked to climatic influence over thermal resources, and finer-scale habitat use closely coupled with prey availability (Cotton *et al.* 2005; Siders *et al.* 2013; Curtis *et al.* 2014), indicating that bottom-up forcing and the propagation of oceanographic features that aggregate prey are likely to mediate foraging behaviour over a continuum of spatial scales.

A diverse range of large marine vertebrates have been shown to associate with mesoscale (10s – 100s km) and submesoscale (~ 1km) oceanographic features such as fronts, eddies and seamounts as foraging habitats, in contrasting ocean domains (Morato *et al.* 2010; Godø *et al.*

2012; Scales *et al.* 2014b). Here, we focus on mesoscale fronts – physical interfaces at the transitions between water masses that differ in temperature, salinity, density, turbidity or productivity (Belkin, Cornillon & Sherman 2009) – as features of potential significance to the basking shark in seasonally-stratified shelf seas in the northeast Atlantic.

Understanding the role of oceanographic processes as drivers of marine vertebrate habitat utilisation is fundamental to our knowledge of pelagic ecosystem functioning, and pivotal in identifying important habitats for species of conservation concern. Basking shark populations in the northeast Atlantic are still recovering from the effects of historical overexploitation (Southall *et al.* 2006), and the species is currently classified as *vulnerable* globally and *endangered* in the northeast Atlantic by the IUCN Red List of Threatened Species (Fowler 2005). A better understanding of the drivers of habitat utilisation is valuable for continued management of these enigmatic marine vertebrates, and indeed for marine vertebrates more generally. An ability to predict the locations of important habitats has relevance for the design of Marine Protected Area (MPA) networks and marine spatial planning (Miller & Christodoulou 2014; Paxton, Scott-Hayward & Rexstad 2014; Scales *et al.* 2014b), and could inform projections of habitat shifts occurring in the wake of future climate change.

Seasonal basking shark aggregations occur in coastal regions of Great Britain and Ireland from May – October each year, when they can be observed surface-feeding on dense zooplankton patches (Sims, Fox & Merrett 1997; Sims & Merrett 1997). Although sharks are generally present in shelf and shelf-edge waters year-round in this region (Sims *et al.* 2003), they also spend protracted periods in the open ocean and are rarely sighted at the surface at other times of year. Distinct seasonal sightings 'hotspots' are apparent off the southwest of England, the Isle of Man, western Scotland and in Irish waters (Berrow & Heardman 1994; Southall *et al.* 2005; Leeney *et al.* 2012; Witt *et al.* 2012). Associations between basking sharks and mesoscale thermal fronts have been observed repeatedly in the region, with sharks using front-associated habitat for both foraging (Sims & Quayle 1998; Priede & Miller 2009) and social interaction (Sims *et al.* 2000).

Bio-physical coupling along fronts is known to lead to the proliferation and aggregation of zooplankton (Le Fevre 1986; Franks 1992b; Genin *et al.* 2005), creating potentially profitable foraging opportunities for higher trophic level organisms (Belkin *et al.* 2014; Scales *et al.* 2014b). Tidally-mediated thermal fronts in seasonally-stratified shelf seas can be highly productive (Pingree 1975; Pingree & Griffiths 1978), and are known to be features around which the basking shark exploits foraging opportunities resulting from aggregation of its preferred *Calanus* prey (Sims, Fox & Merrett 1997; Sims & Merrett 1997; Sims & Quayle 1998).

Although broad-scale climatic drivers of basking shark abundance in the region (e.g. North Atlantic Oscillation, NAO; Cotton *et al.* 2005), and the finer-scale influence of prey dynamics on habitat selection (Continuous Plankton Recorder, CPR; Sims *et al.* 2006) have been investigated in some detail, associations between sharks and frontal activity have been described (Sims *et al.* 2003; Sims *et al.* 2006; Sims *et al.* 2008) but not yet adequately quantified. A recent study in the north-western Atlantic linked the movements of sharks tracked using biotelemetry over timescales of days to weeks with remotely-sensed oceanographic data, finding significant associations with sharp surface gradients in temperature and productivity in Cape Cod Bay during late summer (Curtis *et al.* 2014). These findings provided valuable insight into preferred oceanographic conditions, and the study represented a methodological forward step in quantitative investigation of habitat selection. However, the spatial resolution (0.05° pixel size) and temporal averaging (monthly composites) of remotely-sensed imagery, and the use of the gradient method to identify fronts, restricted the authors' ability to define mesoscale features accurately. Moreover, the latter study used non-parametric testing to compare oceanographic conditions encountered by tracked sharks to those encountered by 250 random walk simulations. This approach to investigating habitat preference is limited in its ability to quantify the influence of mesoscale oceanographic conditions.

Here, we use shark-attached satellite-linked archival tracking to investigate movements of individual sharks through their natural environment over timescales of weeks to months, alongside high-resolution composite front mapping (~1km pixel size; 7-day composites; Miller 2009) to characterise oceanographic conditions encountered. We test the hypothesis that surface frontal activity is a predictor of habitat preference for these planktivorous marine megavertebrates, and use a robust statistical modelling procedure to quantify associations occurring over two spatio-temporal scales: (i) seasonal associations with regions of frequent frontal activity, and (ii) near real-time associations with contemporaneous thermal and chlorophyll-*a* (chl-*a*) fronts. We aim to clarify factors affecting the degree of association between sharks and fronts through explicitly investigating the influence of cross-frontal temperature change and front persistence. In this way, we highlight the key biophysical characteristics of fronts that attract basking sharks, improving understanding of the foraging ecology of the species and building capacity for identification of potentially important habitats.

3.2 Materials And Methods

Satellite-linked archival tracking

Satellite-linked pop-up archival transmitting (PAT) tags (Wildlife Computers, Redmond, USA) were deployed on foraging sharks (n=21) off northwest Scotland and southwest England between May and August in 2001 and 2002. A detailed description of tag deployment and tracking data preparation protocols can be found in Sims *et al.* (2006). Briefly, PAT tags were attached to basking sharks by approaching them from behind in a small vessel and, using a modified speargun harpoon, tags were placed at the base of the first dorsal fin and held in position by a small stainless steel T-bar dart with a monofilament tether connected to the tag (Sims et al. 2003; 2006). Tagging was conducted under licences from the UK Home Office, English Nature and Scottish Natural Heritage. Shark locations during the period of tag attachment were derived using light-based geolocation (GLS), corrected for sea-surface temperature (SST), with a calculated error radius of 75.5 ± 54.5km (Sims et al. 2006). In order to account for this spatial uncertainty in further analyses, we resampled possible locations (n=10 per GLS-derived location) from within the mean radius of error (Fig. 3.1). Resampled possible 'presence' positions falling on land were discarded and replaced. We also resampled presence positions (n=10) in the initial (vessel dGPS, error radius <5m) and final (Argos pop-up location, error radius <1km) locations per track, for equal weighting of all presence positions. Locations derived from this combined dataset were treated as near-surface presence positions for statistical analysis.

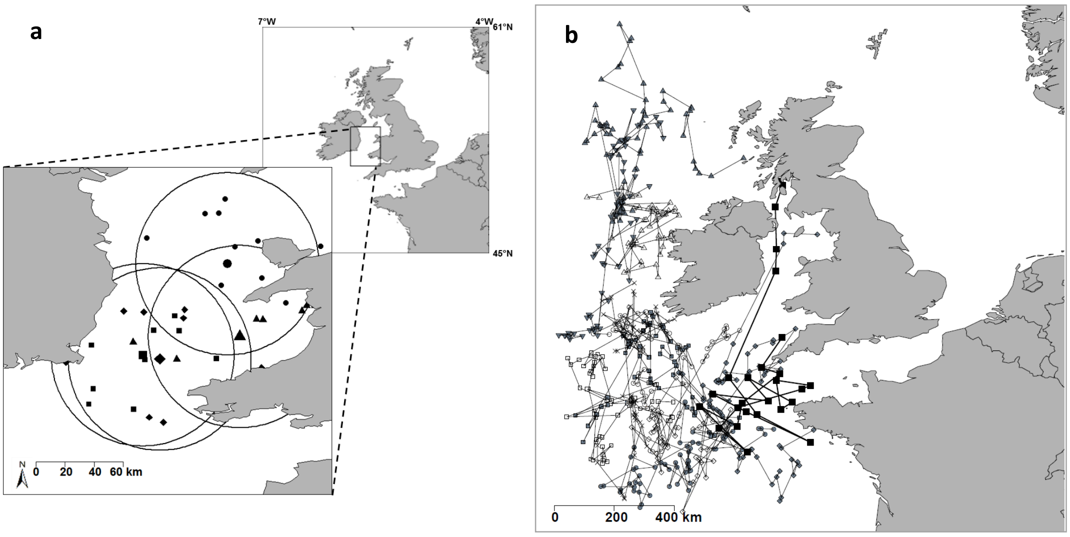


Figure 3.1 Derivation of presence/pseudo-absence dataset from tracking data. *(a) Example of resampling of possible presence locations from within calculated error radius of each geolocation-derived tracking location. (b) Example random walks (10 shown from n=1000), used to derive pseudo-absences for each shark. Geolocation-derived track as bold line.*

Random Walk Simulations

The use of presence-only, serially autocorrelated tracking data to infer habitat preference has inherent complications (Aarts *et al.* 2008; Warton & Aarts 2013). In order to account for regions of habitat accessible to, but not actively utilised by, tracked sharks, we used a randomisation procedure (cf. Heithaus *et al.* 2006; Sims *et al.* 2006) to generate correlated random walk simulations (n=1000 per shark, total=7000; adehabitatLT package for R; Calenge 2006). Simulated tracks were generated per shark such that total number of locations equalled the original track length, and step lengths and turning angles were derived from distributions in each original track. Simulations were permitted to approach, but not cross, land, were time-matched to original tracks, and were constrained within a region defined by the bounding box surrounding all locations obtained across all individuals (Fig. 3.1; 45° to 61° N, -15° to 6° W; hereafter 'study area'). This study area includes the UK and Irish continental shelf region, and the shelf break system (Fig. 3.2). Locations derived from this simulated dataset were treated as pseudo-absences for statistical analysis.

Environmental data

Composite front maps (7-day, rolling by 1 day; Miller 2009) were prepared for the study area using SST data obtained via the Advanced Very-High Resolution Radiometer (AVHRR) sensor and ocean colour data obtained via the Sea-Viewing Wide Field-of-View Sensor (SeaWIFS; Local Area Coverage, LAC), mapped to the study area at 1.1km resolution using a Mercator projection.

Seasonal front frequency maps quantifying the percentage time in which a front was detected in each pixel of the study area, as a ratio of positive detections to the number of cloud-free observations, were generated for each tracking year (Miller & Christodoulou 2014). As >95% of all tracking locations were obtained during the main UK basking shark sightings season (May – Oct), we used 7-day composite front maps from this period of each year (2001, 2002) to generate the front frequency datasets (thermal front detection threshold = 0.4°C; chl-*a* min. front detection threshold = 0.06 mg m^{-3}). We also generated seasonal front frequency maps for the preceding year, to assess the influence of the previous year's conditions on habitat selection (Fig. 3.2).

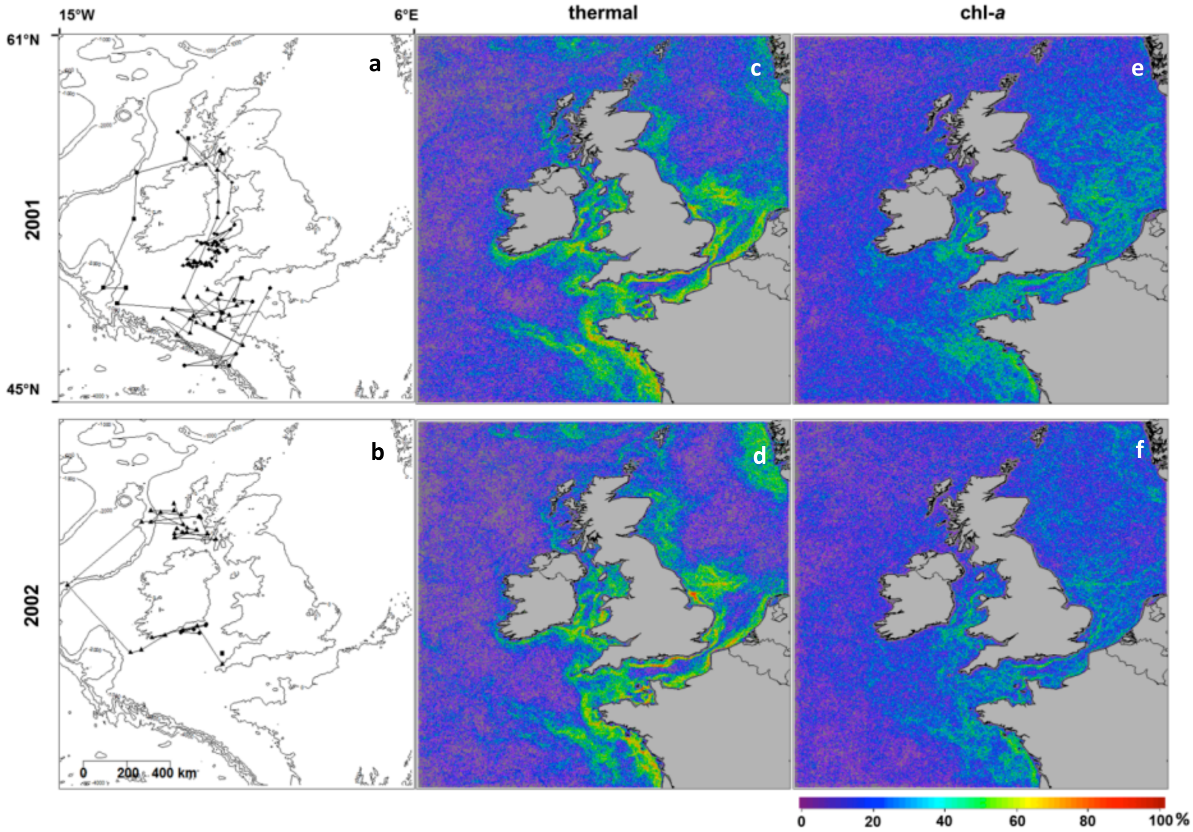


Figure 3.2 Associations with broad-scale, seasonally persistent frontal zones. *(a),(b) Shark tracking locations obtained from satellite-linked pop-up archival tags, with different icons identifying individual sharks overlaid over bathymetry contours of the study area, derived from the General Bathymetric Chart of the Oceans (GEBCO, 30 arc-second resolution). (c),(d) Seasonal thermal front frequency for the main UK basking shark sightings season (May – Oct) of each year at 1.1km resolution (0.4°C front detection threshold). (e),(f) Seasonal chlorophyll-a front frequency for the same period of each year (0.06 mg* m^{-3} *min. front detection threshold).*

Contemporaneous front metrics (front distance *fdist*, front gradient density *gdens*, front persistence *pfront*) were generated from composite front maps and time-matched to shark tracks (7-day, rolling by 1 day). Front distance (*fdist*) quantifies the distance from any location in the study area to the closest simplified front, using a custom simplification algorithm (Miller, P.I.; *unpubl. data*). Front gradient density (*gdens*) is the result of applying a Gaussian smoothing filter (sigma = 5 pixels) to a map of the mean gradient magnitude values. It is designed to provide a local neighbourhood average of frontal gradient, avoiding the discrete nature of individual detected front contours. Front persistence (*pfront*) is the fraction of cloud-free observations of a pixel for which a front is detected. Again, a Gaussian filter (sigma = 5 pixels) is applied, to provide a local neighbourhood average of frontal persistence.

Thresholds for front detection (Single-Image Edge Detection, SIED; Cayula & Cornillon 1992) are often chosen arbitrarily, yet the magnitude of cross-frontal temperature change is likely to influence associations between marine vertebrates and fronts (Etnoyer *et al.* 2006). We therefore systematically varied the SIED threshold used in preparation of thermal composite front maps, from 0.2°C (minimum detectable owing to SST scaling in original imagery) to 1.0°C, generating a set of time-matched front metrics at each threshold. Values were obtained for each of these metrics, plus SST and chl-*a* with no front detection, for each location of the full dataset (presence, resampled presence, pseudo-absence), and used as predictor variables in subsequent statistical modelling.

Statistical analysis

We carried out a use-availability analysis over two spatiotemporal scales: (i) seasonal associations with zones of frequent frontal activity, and (ii) near real-time associations with contemporaneous mesoscale thermal and chl-*a* fronts. We used logistic regression within a Generalised Linear Mixed Modelling framework (GLMM, lme4 package for R; Bates *et al.* 2014) to obtain estimates of the influence of each of the predictor variables on the probability of observing a presence (individual as random effect; binary presence/pseudo-absence response; binomial errors with logistic link function). Owing to serial autocorrelation in both tracking data and simulated tracks, which violates the assumption of independence essential to the use of GLMM, we used a non-parametric bootstrapping regime to iteratively resample both the presence and pseudo-absence datasets for each model fit. A total of 1000 presence and 1000 pseudo-absence locations, weighted as per the proportion of the complete tracking dataset contributed by each individual, were sub-sampled from each individual dataset for each iteration. Resultant presence/pseudo-absence datasets were then used to fit models over 1000 iterations.

We repeated this procedure using (i) seasonal front frequency metrics (thermal, chl-*a*) for both the season in which the sharks were tracked, and the preceding year, and (ii) 7-day contemporaneous front metrics (thermal, chl-*a*; distance to closest front *fdist*, frontal gradient density *gdens*, frontal persistence *pfront*), together with time-matched SST and chl-*a* values. All 7-day contemporaneous front metrics and SST were standardised across the entire presence/pseudo-absence dataset prior to the modelling procedure, by subtracting the mean and dividing by standard deviation (Zuur, Hilbe & Ieno 2013). This enables comparability of effect sizes between variables that are scaled differently in their original form. The distribution of chl-*a* was highly skewed, with a large predominance of small values. We therefore removed all spurious outlying values (>20 mg m^{-3}) and transformed the resulting dataset using a $\log_{10}$ transformation to generate an explanatory variable with a distribution approaching normal.

Owing to colinearity between predictor variables, which was detected using pairwise plots and Generalised Variance Inflation Factors (GVIF; Zuur, Hilbe & Ieno 2013), each variable was fitted via Maximum Likelihood estimation as a standalone explanatory term in separate model runs (1000 iterations per term). Parameter distributions generated by each set of model iterations were used to obtain the mean and standard deviation of model intercepts, regression coefficients and standard errors of fitted terms, deviance explained, and Chi-square statistic and p-value from a likelihood ratio test against a null model with no fixed effects (with Restricted Maximum Likelihood; Supp. Table 3.1). Confidence intervals (CIs; 95%) were also calculated for each of the parameter distributions. Mean values and CIs of regression coefficients were plotted and used to assess the influence of each term on the probability of shark presence (CIs overlapping zero indicates non-significant term). To assess the influence of thermal gradient magnitude on the strength of associations with fronts, we repeated this modelling procedure for each set of time-matched metrics derived using different front detection thresholds (0.2°C, 0.4°C, 0.6°C, 0.8°C, 1.0°C).

3.3 Results

Satellite-linked archival tracking

Of the 21 basking sharks tagged sufficient data to reconstruct tracks were received from 7 individuals (body length range 2.5 – 7.0m), which were tracked for a cumulative total of 964 days, ranging from 72 – 213 days per individual. A total of 186 light-level geolocations were obtained (0.2 ± 0.05 per day) during this period. Associated dive data indicated that all sharks spent a significant proportion of this time foraging at the sea surface (Sims *et al.* 2006).

Seasonal front frequency

Basking shark tracking locations were clustered within broad-scale regions of high seasonal front frequency, in both SST and chl-*a* fields (Fig. 3.2). Logistic regression reveals that the probability of shark presence was higher in regions of frequent or persistent frontal activity (*frontal zones*) during the basking shark surface sightings season (May – Oct) over two years (Fig. 3.3; Supp. Table 3.1). Thermal front frequency had a stronger influence over the probability of observing a presence than chl-*a* front frequency, although both contributed significant explanatory power to models (Fig. 3.3c; Supp. Table 3.1). The proportion of deviance explained was also found to be higher for thermal front frequency than for chl-*a* (thermal = 8.25 ± 2.32; chl-*a* = 1.65 ± 1.06).

Seasonal front frequency in the preceding year also had an influence on the probability of observing a presence (Fig. 3.3; Supp. Table 3.1). Model intercepts and regression coefficients were similar when modelling the influence of front frequency from the same year and from the preceding year on shark presence (Supp. Table 3.1). Inter-annual variability in front frequency was low in both thermal and chl-*a* fields between 2000 and 2002 (Fig. 3.2, Table 3.1). We also observed a high degree of spatial correlation between the thermal and chl-*a* seasonal front frequency metrics in each year (mean = 0.523 ± 0.04; 2000 = 0.476; 2001 = 0.561; 2002 = 0.533).

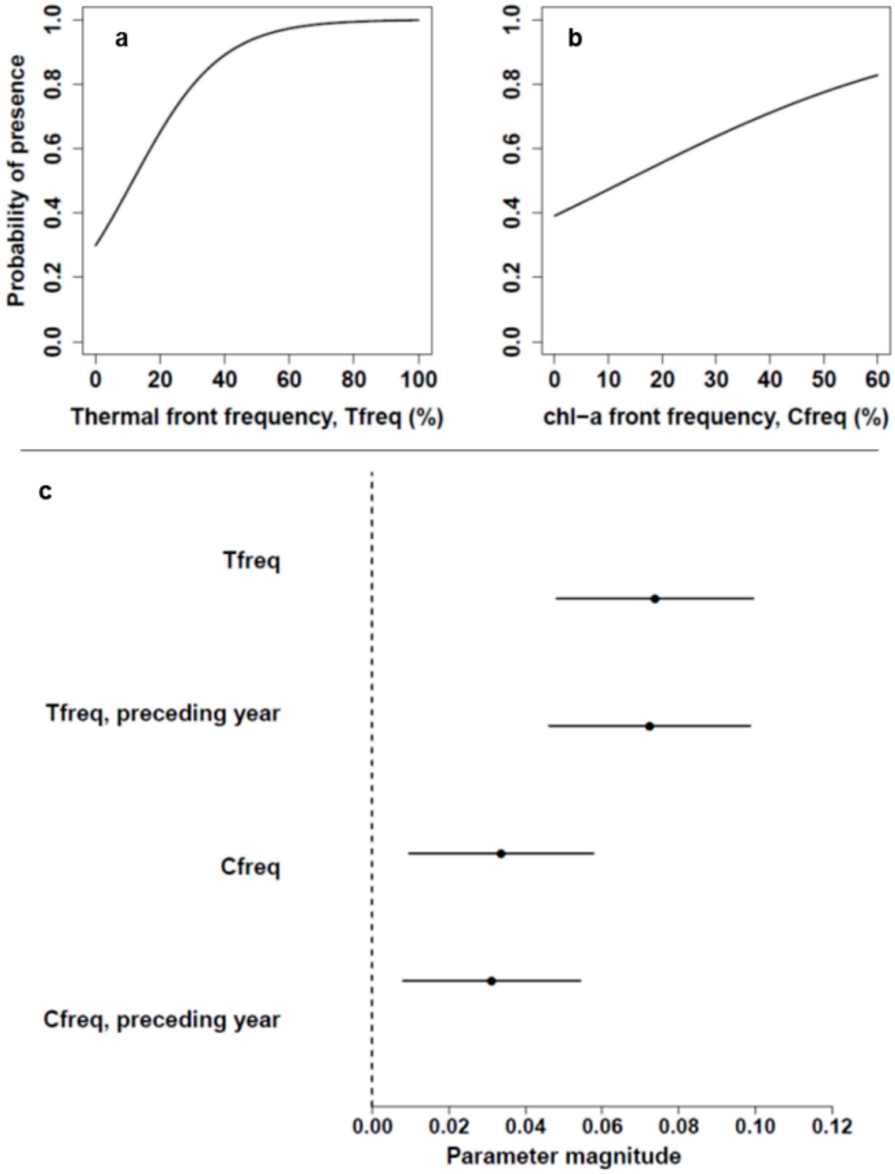


Figure 3.3 Modelling the influence of seasonal front frequency on probability of shark presence. *Mean regression coefficients for the influence of (a) thermal front frequency and (b) chl-a front frequency on probability of observing a shark presence vs. pseudo-absence derived from random walk simulations. (c) Distibution of each regression coefficient, obtained from 1000 model iterations, as mean with 95% CIs.*

Time-matched front metrics

Shark presence was significantly more likely to be associated with contemporaneous thermal and chl-*a* fronts than pseudo-absences derived from random walk simulations (Fig. 3.4; Supp. Tables 3.2 - 3.3). Distance to closest chl-a front (*fdist*) and all 7-day thermal front metrics (distance to closest simplified front, *fdist*; frontal gradient density, *gdens;* front persistence, *pfront*; 0.4°C front detection threshold) were significant predictors of shark presence. Shark presence was more likely to be observed in closer proximity to thermal and chl-*a* fronts, at higher thermal gradient densities and in association with persistent thermal fronts than pseudo-absences. Indeed, some individuals appeared to spend days to weeks tracking the surface profile of strong thermal fronts, presumably foraging on aggregated prey.

Overall, 7-day chl-*a* front metrics held less explanatory power than thermal metrics; while distance to closest simplified chl-*a* front *fdist* explained a significant proportion of deviance, *gdens* and *pfront* had a less pronounced effect on the probability of shark presence (Fig. 3.5; Supp. Table 3.3). In addition, confidence intervals of the distribution of regression coefficients from bootstrapping approached zero for chl-*a gdens* and overlapped zero for chl-*a pfront* (Fig. 3.5). We can surmise that shark presence positions are more likely to be observed in closer proximity to chl-*a* fronts than pseudo-absences, but that chl-*a gdens* and *pfront* metrics have a lesser influence on probability of shark presence, presumably as a result of the ephemeral nature of chl-*a* blooms at fronts, and the spatial smoothing involved in preparation of these metrics. These results indicate that time-matched thermal front metrics are more useful predictors of shark presence than comparable chl-*a* metrics in this case.

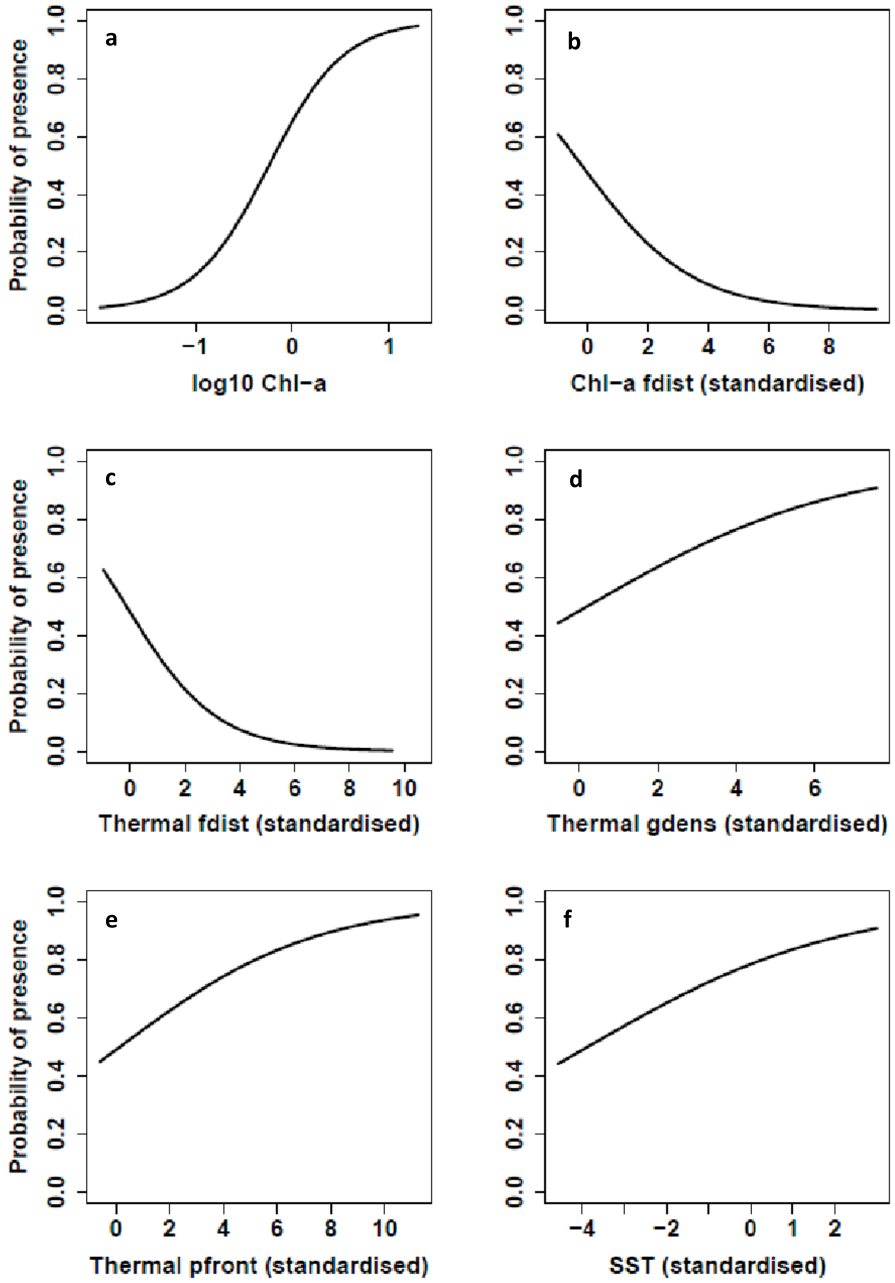


Figure 3.4 Modelling the influence of contemporaneous fronts on probability of shark presence. *(a – f) Mean effects of time-matched oceanographic metrics (**chl-a**, distance to closest simplified thermal or chl-a front **fdist**, frontal gradient density **gdens**, frontal persistence **pfront**, and sea surface temperature, **SST**) over 1000 model iterations.*

Varying the thermal front detection threshold had a considerable effect on the magnitude of the logistic regression coefficient for the thermal *fdist* metric (Fig. 3.6; Supp. Table 3.2). Effect size and proportion of deviance explained increased with a higher detection threshold. Shark presences were more likely to be associated with stronger thermal fronts (1.0°C cross-frontal temperature difference or “step”) than weaker features (0.2°C difference), although all detection thresholds resulted in significant predictors (Fig.3.6; Supp. Table 3.2). In contrast, altering the detection threshold had little influence over the effect sizes of the *gdens* and *pfront* metrics (Supp. Table 3.2), most likely as a result of the inclusion of the cross-frontal gradient in the *gdens* metric, and the tendency of fronts with a stronger cross-frontal gradient to persist through time (Bakun 2006).

Comparison with standard SST and chlorophyll-a fields

Chlorophyll-*a* concentration was found to have a significant effect on the probability of shark presence, with $\log_{10}$ transformed chl-*a* concentration explaining the highest proportion of deviance across model iterations (Fig. 3.5b; Supp. Table 3.3). Chl-*a* had a strongly positive effect as a predictor of shark presence, indicating that foraging habitat selection is tightly coupled with primary productivity. SST was also found to be a significant predictor, although this variable explained a considerably lower proportion of deviance than chl-*a* and time-matched front metrics, having a weak negative effect on the probability of shark presence (Fig. 3.5; Supp. Table 3.3).

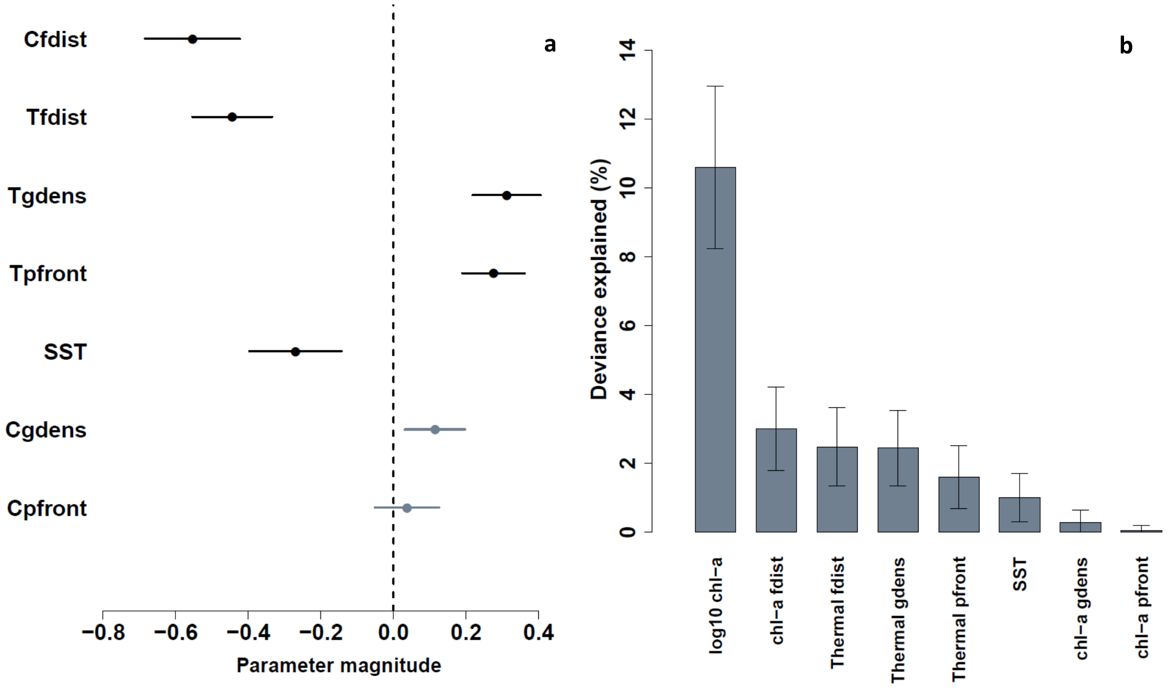


Figure 3.5 Modelling the influence of contemporaneous fronts on the probability of shark presence. *(a) Parameter distributions for regression coefficients, obtained from 1000 model iterations. Mean regression coefficient with 95% CIs. Significant terms in black, non-significant in grey. Coefficient for log*$_{10}$ *chl-a not shown owing to different scaling to standardised metrics. (b) Percentage of deviance explained by each of the time-matched oceanographic metrics. Mean value with 95% CIs, from 1000 model iterations.*

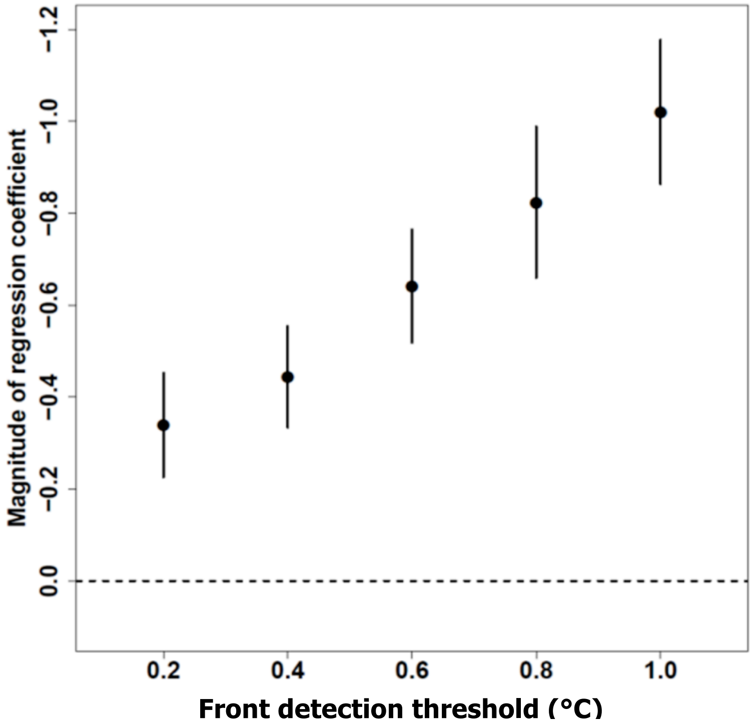


Figure 3.6 Effect of varying thermal front detection threshold on magnitude of effect size for distance to closest simplified thermal front (fdist). *Parameter distributions (mean + 95% CIs) for regression coefficient obtained from 1000 model iterations per threshold.*

3.4 Discussion

Our combined use of animal-attached satellite-linked archival tracking and composite front mapping (Miller 2009) provides novel insight into the influence of regional oceanography on habitat selection in this wide-ranging marine megavertebrate. This study builds upon prior observations of associations between the planktivorous basking shark and oceanographic fronts in coastal regions of the northeast Atlantic obtained from *in situ* work (Sims & Quayle 1998; Sims *et al.* 2000; Priede & Miller 2009), but is novel in that we provide a robust quantification of the influence of thermal and chl-*a* fronts on habitat selection for sharks tracked over timescales of weeks to months. Our analysis reveals associations between tracked sharks and seasonally persistent frontal zones, and a more proximate influence of contemporaneous mesoscale thermal and chl-*a* fronts on habitat selection.

Associations with seasonally persistent frontal zones

Seasonal front frequency, i.e. the number of times a front was detected in any one pixel (1.1km x 1.1km) of the study area over the main UK basking shark surface sightings season (May – Oct), was found to be a significant predictor of shark presence for both thermal and chl-*a* frontal activity. Presence locations of tracked sharks were more likely to be found in association with seasonally persistent frontal zones than in other regions of the study area, although thermal front frequency was found to have a stronger effect than chl-*a*, perhaps owing to the propensity of thermal fronts to manifest in similar locations more frequently than chl-*a* fronts over the season (cf. Kahru *et al.* 2012).

Furthermore, seasonal front frequency metrics from the preceding year were significant predictors of shark presence. Low inter-annual variability in the spatial extent of these persistent frontal zones over the study period (2000-2002) suggests that sharks may return to spatiotemporally predictable foraging grounds in which they have previously experienced profitable prey encounter rates. Although we only have tracking data from seven different individuals tagged over two successive years, and none spanning two years, and so cannot determine whether the same sharks could be returning to forage in previously profitable regions, we can surmise that predictability of foraging hotspots is likely to be high over seasonal timescales. Basking sharks, like many pelagic marine vertebrates, may optimise foraging efficiency through orientation to the same broad-scale regions to search for suitable foraging areas, then using random searches (Sims *et al.* 2008; Humphries *et al.* 2010) and more proximate clues to locate prey aggregations nested within (Cotton *et al.* 2005; Sims *et al.* 2006; Siders *et al.* 2013). Many marine vertebrates exhibit broad-scale foraging site fidelity over seasonal, annual or inter-annual timescales (e.g. seals, Bradshaw *et al.* 2004b; sharks, Pade *et al.* 2009; Queiroz *et al.* 2012; whales, Irvine *et al.* 2014; seabirds, Patrick *et al.* 2014), indicating that spatio-temporal predictability of prey encounter rates influences habitat selection across taxa (e.g. seabirds, marine mammals; Weimerskirch 2007; Bost *et al.* 2009).

Spatial correlation between the locations of thermal and chl-*a* frontal zones with which sharks associate was also found to be high within the study area, over the three years' of remotely-sensed data analysed for this study. The locations of thermal and chl-*a* fronts often coincide (Belkin, Cornillon & Sherman 2009), since chl-*a* fronts frequently manifest where convergent processes occurring around thermal discontinuities aggregate nutrients and plankton in productive regions with high background chl-*a* concentrations, such as at the peripheries of plankton blooms (Le Fevre 1986; Kahru *et al.* 2012). Although these mechanisms are not yet well understood, objective detection of regions of frequent frontal activity in both thermal and chl-*a* fields, such as that presented here, could aid in identification of biophysical hotspots. Persistent thermal and chl-*a* frontal zones in the Celtic Sea, identified using the same front frequency indices, have been found to be significant foraging features for breeding northern gannets *Morus bassanus* (hereafter, 'gannet'; Scales *et al.* 2014a). When considered together, these results suggest that persistent mesoscale frontal zones in UK shelf seas may have significant cross-taxa ecological importance, providing spatio-temporally predictable foraging opportunities for both planktivorous and piscivorous marine vertebrates.

Associations with contemporaneous thermal and chlorophyll-a fronts

Basking sharks were found to associate strongly with productive regions of the study area, indicating that the propagation of surface foraging opportunities is tightly coupled with bottom-up oceanographic forcing. Our analysis also reveals that over timescales of weeks to months, sharks associated with thermal and chl-*a* fronts within these productive areas. Time-matched front metrics were significant predictors of shark presence at the surface, with tracked shark locations more likely to be found in close proximity to thermal and chl-*a* fronts, at higher thermal gradient densities and in association with more persistent thermal fronts than pseudo-absences derived from random walk simulations. These findings are in concordance with those of another recent study conducted in the western North Atlantic (Curtis *et al.* 2014), and with our *a priori* assumption that foraging behaviour of these zooplanktivores is closely linked to low trophic-level enhancement. Comparable associations with thermal fronts in pelagic waters have been documented in other sharks and large teleosts, including the blue shark *Prionace glauca* (Queiroz *et al.* 2012), ocean sunfish *Mola mola* (Sims & Southall 2002), bluefin *Thunnus thynnus* (Schick, Goldstein & Lutcavage 2004), albacore *Thunnus alalunga* and skipjack *Katsuwonus pelamis* tunas (Fiedler & Bernard 1987) and swordfish *Xiphias gladius* (Podestá, Browder & Hoey 1993; Seki *et al.* 2002) in differing oceanographic regions, suggesting that thermal fronts could have multi-taxon ecological importance for pelagic predators.

Furthermore, shark presence was more likely to be associated with lower sea surface temperatures, indicating that fine-scale upwelling and vertical mixing, which transports nutrients to the surface and so enhances primary productivity, are likely to play a role in the propagation of profitable foraging opportunities. Upwelling fronts are sites of strong biophysical coupling, along which nutrient retention and vertical mixing increase primary productivity and attract grazers such as the calanoid prey of basking sharks (Smith *et al.* 1986; Franks 1992a; Sims & Quayle 1998; Shanks *et al.* 2000).

Through systematically varying the threshold used for detection of thermal fronts, our analysis has revealed that cross-frontal temperature difference is likely to be an important influence on foraging decisions. Regression coefficients and proportion of deviance explained across the model iterations per threshold indicate that stronger (1.0°C cross-frontal step) fronts have more influence over the probability of shark presence than thermal fronts with a weaker cross-frontal temperature step. The effect of the gradient density *gdens* metric also indicates that sharks are more likely to associate with stronger fronts. While part of this effect may be related to the spatial element of this study, in that stronger fronts are less numerous and so less likely to be encountered by random walk simulations, this nevertheless indicates that tracked sharks were found in closer proximity to these strong fronts than could be expected by chance. These findings highlight the importance of the choice of front detection threshold in studies investigating species-habitat relationships. The influence of relative sizes of fronts detected has not been explicitly considered here owing to methodological considerations, but may be an interesting subject for future research.

The magnitude of cross-frontal temperature difference is likely linked to persistence and the degree of bio-aggregation occurring at a front, owing to the spatial and temporal lags inherent in bio-physical coupling mechanisms (Le Fevre 1986). Stronger fronts are more likely to persist through time, and also potentially more likely to attract foraging sharks. The mechanisms through which basking sharks detect and respond to environmental clues associated with biophysical coupling at fronts are not yet well understood, but frontal propagation and frontogenesis are likely to induce the development of discernible environmental clues (e.g. surface and sub-surface flow patterns, tidal slicks and streams, accumulation of biota; Franks 1992b). These cues are likely to be more pronounced in the vicinity of stronger, more persistent fronts.

Modelling the influence of contemporaneous fronts on habitat selection has revealed that spatio-temporal persistence of thermal fronts may be an important aspect of their attractiveness as surface-foraging hotspots. Thermal fronts in shelf seas around Great Britain and Ireland form primarily as a result of interaction between tidal processes, seasonal stratification and bathymetric influence (Pingree & Griffiths 1978; Simpson & Sharples 2012). As a result, fronts range from ephemeral, only manifesting at certain stages of the tidal cycle, to quasi-stationary and seasonally persistent (Belkin, Cornillon & Sherman 2009; Simpson & Sharples 2012). Persistent fronts are more likely to be sites of bio-aggregation (Bakun 2006), and hence more likely to attract foraging marine vertebrates, than ephemeral features. Whilst gannets in the Celtic Sea appear to target foraging effort within seasonally persistent frontal zones, responses to contemporaneous fronts are highly variable (Scales *et al.* 2014a). We here provide evidence that basking sharks may associate with contemporaneous fronts more actively than these piscivorous birds, and while persistence evidently has an influence, sharks may also associate with more ephemeral features. We can surmise that aggregation of the sharks' preferred zooplankton prey does not involve the same spatial and temporal lags that would be required for bio-aggregation to propagate through the food chain from plankton to pelagic fish populations and, in turn, to their predators. This work highlights the importance of persistence, and spatio-temporal predictability, of fronts when considering their value as habitats for marine predators.

Technical Limitations

While this study enhances understanding of associations between basking sharks and fronts in the northeast Atlantic, it is not of course without limitations. Using archival tracking technologies based on light-level geolocation has intrinsic limitations, owing to the low level of spatial accuracy of location estimates. However, we have propagated this uncertainty through modelling by repeatedly resampling potential presence locations from within an experimentally-derived radius of error around each geolocation estimate, and randomly resampling from this presence dataset before fitting each model iteration. The future use of more accurate tracking technologies, such as fast-acquisition GPS systems (e.g. Fastloc™-GPS; Wildtrack Telemetry Systems Ltd., Leeds, UK) will enable finer-scale investigations into the drivers of habitat preference in this species and other pelagic marine vertebrates (e.g. Sims *et al.* 2009). The use of GPS-based tracking with composite front mapping or similar techniques would be a logical follow-up to the results presented here.

Moreover, our study has been restricted to analysis of movements of only a few individuals (n=7) over a few months within a year of their life cycle, so we are hesitant to extrapolate findings to the population level. Many aspects of the life cycle of the basking shark remain unknown, including the size of the population using shelf seas of the northeast Atlantic, and longer range migratory behaviour (Sims 2008). We cannot ascertain whether fronts are significant habitat features for basking sharks throughout the annual cycle or throughout their range. In the northwest Atlantic tracked basking sharks move from higher latitudes in summer to equatorial regions in winter (Skomal *et al.* 2009), but in the northeast Atlantic other tracking work has revealed that the shelf-break system, a region of frequent and intense surface frontal activity, may represent an important over-wintering habitat (Sims *et al.* 2003). Results presented here indicate that sharks also associate with thermal and chl-*a* fronts manifesting in coastal waters of the British Isles in summer, when sharks frequently feed at the surface and occasionally dive to the sea bottom (Sims *et al.* 2005), and so are at their most vulnerable to deleterious anthropogenic interactions (e.g. fisheries bycatch; development of Marine Renewable Energy Installations (MREI); impacts of maritime leisure). Composite front mapping is useful in identifying key habitats and potential regions of overlap with anthropogenic pressures within the Exclusive Economic Zones (EEZ) of stakeholder nations, and so could be of value in marine spatial planning and the formulation of management initiatives for species of conservation concern (Miller & Christodoulou 2014; Scales *et al.* 2014b).

Although oceanographic front metrics derived from composite front mapping have proven useful in this context, the technique has some constraints that must be taken into account. Along with all marine remote sensing applications, only the surface profile of complex three-dimensional oceanographic processes can be detected. However, surface frontal activity can be a useful indicator of sub-surface biophysical processes that influence prey availability (Le Fevre 1986; Genin *et al.* 2005). Moreover, this study focuses on basking sharks that spend long periods surface-feeding, which may be more closely associated with surface frontal activity than other deep-diving marine vertebrates (e.g. northern elephant seal Mirounga angustirostris; Robinson *et al.* 2012). In addition, the spatial resolution of SST and chl-*a* imagery used to derive the front indices is limited by the satellite-based sensors. Here, we use Local Area Coverage (LAC) to obtain 1.1km resolution products, but we cannot detect finer-scale oceanographic influence on shark movements. The issue of spatial resolution has an impact on the algorithm's ability to detect fine-scale tidal mixing fronts occurring near to the coastline, which have been identified as potentially significant features for marine vertebrates utilising the nearshore coastal zone (e.g. Jones *et al.* 2014). However, front metrics used here are appropriate for oceanographic contextualisation of animal movements occurring across pelagic seascapes over timescales of days-weeks-months, complementing the recent proliferation of data obtained through biologging.

3.5 Conclusions

In summary, we present evidence that basking sharks strongly associate with thermal and chl-*a* frontal activity in shelf seas of the northeast Atlantic. We provide a robust methodological approach to quantification of the influence of fronts on habitat selection by wide-ranging marine vertebrates. This analysis reveals that seasonal front frequency is a useful predictor of shark presence. Moreover, we highlight the tendency of sharks to associate with contemporaneous thermal and chl-*a* fronts, and the significant influence of cross-frontal temperature change and spatio-temporal persistence on the strength of associations. These findings have implications for management and conservation (Miller & Christodoulou 2014; Scales *et al.* 2014b), particularly in regard to the current marine spatial planning agenda in the northeast Atlantic.

Supplementary Figures and Tables

Supp. Table 3.1 Modelling the influence of seasonal front frequency *on the probability of observing shark presence vs. pseudo-absence derived from random walk simulations (n=1000 per shark). Parameter distributions obtained from 1000 model iterations, summarised as mean ± standard deviation, with range. The magnitude of regression coefficients here reflect the scaling of the predictor variable, which is presented as percentage time in which a front is detected in any pixel over the study area over the specified season of each tracking year (May – Oct, 2001-02).*

Predictor	**Intercept**	**Regression coefficient**	**Standard error**	**Deviance explained (%)**	**p-values < 0.05**
Thermal front frequency (Tfreq)	-0.85 ± 0.14 (-1.37 – -0.48)	0.07 ± 0.01 (0.04 – 0.12)	0.01 ± 0.00 (0.01 – 0.02)	8.25 ± 2.32 (2.83 – 16.22)	100%
Chl-*a* front frequency (Cfreq)	-0.44 ± 0.16 (-1.03 – -0.01)	0.03 ± 0.01 (0.00 – 0.08)	0.01 ± 0.00 (0.01 – 0.01)	1.65 ± 1.06 (0.00 – 6.58)	78%
Thermal front frequency (Tfreq), preceding year	-0.77 ± 0.14 (-1.28 – -0.34)	0.07 ± 0.01 (0.03 – 0.13)	0.01 ± 0.00 (0.01 – 0.02)	7.05 ± 2.11 (1.54 – 14.66)	100%
Chl-*a* front frequency (Cfreq), preceding year	-0.41 ± 0.15 (-0.90 – 0.09)	0.03 ± 0.01 (-0.01 – 0.07)	0.01 ± 0.00 (0.01 – 0.01)	1.48 ± 1.00 (0.01 – 6.09)	73%

Supp. Table 3.2 Modelling the influence of contemporaneous mesoscale thermal fronts on habitat selection. *Influence of time-matched metrics on the probability of observing shark presence vs. pseudo-absence derived from random walk simulations (n=1000 per shark) using different thermal front detection thresholds.*

Front detection threshold (°C)	Intercept	Regression coefficient	Standard error	Deviance explained (%)	p-values < 0.05
Thermal fdist					
0.2	0.03 ± 0.02 (-0.01 – 0.08)	-0.34 ± 0.06 (-0.52 – -0.11)	0.06 ± 0.00 (0.05 – 0.07)	1.47 ± 0.45 (0.17 – 2.93)	100%
0.4	-0.07 ± 0.02 (-0.12 – -0.01)	-0.44 ± 0.06 (-0.62 – -0.28)	0.06 ± 0.00 (0.05 – 0.06)	2.48 ± 0.58 (1.05 – 4.48)	100%
0.6	-0.07 ± 0.03 (-0.16 – 0.01)	-0.64 ± 0.06 (-0.82 – -0.45)	0.07 ± 0.00 (0.06 – 0.08)	4.21 ± 0.75 (2.02 – 6.68)	100%
0.8	-0.13 ± 0.04 (-0.26 – 0.00)	-0.82 ± 0.08 (-1.09 – -0.57)	0.08 ± 0.00 (0.07 – 0.09)	6.20 ± 1.01 (3.67 – 9.99)	100%
1.0	-0.29 ± 0.05 (-0.44 – -0.16)	-1.02 ± 0.08 (-1.28 – -0.78)	0.09 ± 0.00 (0.08 – 0.10)	8.53 ± 1.13 (5.25 ± 12.06)	100%
Thermal gdens					
0.2	-0.04 ± 0.02 (-0.10 – 0.00)	0.29 ± 0.05 (0.17 – 0.44)	0.04 ± 0.00 (0.04 – 0.05)	2.05 ± 0.50 (0.79 – 3.93)	100%
0.4	-0.07 ± 0.01 (-0.11 – -0.03)	0.31 ± 0.05 (0.17 – 0.48)	0.04 ± 0.00 (0.03 – 0.05)	2.44 ± 0.56 (0.83 – 4.50)	100%
0.6	-0.06 ± 0.01 (-0.11 – -0.02)	0.26 ± 0.04 (0.14 – 0.42)	0.04 ± 0.00 (0.03 – 0.05)	2.09 ± 0.51 (0.73 – 3.78)	100%
0.8	-0.05 ± 0.01 (-0.11 – -0.02)	0.24 ± 0.04 (0.13 – 0.46)	0.04 ± 0.00 (0.03 – 0.06)	1.91 ± 0.48 (0.60 – 4.13)	100%
1.0	-0.05 ± 0.01 (-0.10 – -0.01)	0.24 ± 0.05 (0.13 – 0.43)	0.04 ± 0.01 (0.03 – 0.07)	1.88 ± 0.47 (0.62 – 3.58)	100%
Thermal pfront					
0.2	0.01 ± 0.01 (-0.01 – 0.04)	0.10 ± 0.04 (-0.04 – 0.28)	0.04 ± 0.00 (0.04 – 0.05)	0.21 ± 0.17 (0.00 – 1.41)	57%
0.4	-0.04 ± 0.01 (-0.08 – -0.01)	0.28 ± 0.04 (0.15 – 0.44)	0.04 ± 0.00 (0.04 – 0.05)	1.61 ± 0.47 (0.48 – 3.55)	100%
0.6	-0.04 ± 0.01 (-0.07 – -0.01)	0.24 ± 0.04 (0.11 – 0.38)	0.04 ± 0.00 (0.04 – 0.05)	1.45 ± 0.44 (0.36 – 3.06)	100%
0.8	-0.05 ± 0.01 (-0.08 – -0.01)	0.24 ± 0.05 (0.12 – 0.42)	0.04 ± 0.00 (0.03 – 0.06)	1.60 ± 0.47 (0.42 – 3.45)	100%
1.0	-0.04 ± 0.01 (-0.08 – -0.01)	0.24 ± 0.05 (0.11 – 0.47)	0.04 ± 0.01 (0.03 – 0.07)	1.61 ± 0.47 (0.46 – 3.30)	100%

Supp. Table 3.3 Modelling the influence of contemporaneous mesoscale chlorophyll-a (chl-a) fronts, sea surface temperature (SST) and surface chl-a concentration on habitat selection. *Influence of time-matched metrics quantifying distance to closest simplified chl-a front fdist, chl-a gradient density gdens, temporal persistence of chl-a fronts pfront, SST and chl-a on the probability of observing shark presence vs. pseudo-absence derived from random walk simulations (n=1000 per shark). Significant relationships in black, non-significant in grey (Confidence Intervals of regression coefficients overlap zero, and low proportion of p-values below 0.05 threshold, low proportion of deviance explained).*

Predictor	Intercept	Regression coefficient	Standard error	Deviance explained (%)	p-values < 0.05
chl-a *fdist*	-0.10 ± 0.02 (-0.16 – -0.05)	-0.55 ± 0.07 (-0.76 – -0.38)	0.07 ± 0.00 (0.06 – 0.08)	3.01 ± 0.62 (1.48 – 5.06)	100%
chl-a *gdens*	0.00 ± 0.01 (-0.02 – 0.02)	0.11 ± 0.04 (-0.01 – 0.25)	0.04 ± 0.00 (0.04 – 0.05)	0.28 ± 0.18 (0.00 – 1.10)	75%
chl-a *pfront*	0.01 ± 0.01 (-0.01 – 0.02)	0.04 ± 0.05 (-0.09 – 0.20)	0.05 ± 0.00 (-0.09 – 0.20)	0.05 ± 0.00 (0.04 – 0.05)	10%
SST	-0.03 ± 0.01 (-0.07 – 0.01)	-0.27 ± 0.06 (-0.47 – -0.09)	0.05 ± 0.00 (0.05 – 0.06)	1.0 ± 0.36 (0.12 – 2.30)	100%
$\log_{10}$ chl-a	0.63 ± 0.05 (0.47 – 0.87)	2.6 ± 0.19 (2.00 – 3.42)	0.18 ± 0.01 (0.16 – 0.20)	10.6 ± 1.21 (6.99 – 15.19)	100%

Chapter IV

Oceanic loggerhead turtles *Caretta caretta* associate with oceanographic fronts: evidence from the Canary Current Large Marine Ecosystem

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ABSTRACT

Oceanographic fronts are physical interfaces between water masses that differ in properties such as temperature, salinity, turbidity and chlorophyll-*a* enrichment. Bio-physical coupling along fronts can lead to the development of pelagic biodiversity hotspots. A diverse range of marine vertebrates have been shown to associate with fronts, using them as foraging and migration habitats. Elucidation of the ecological significance of fronts generates a better understanding of marine ecosystem functioning, conferring opportunities to improve management of anthropogenic activities in the oceans. This study presents novel insight into the oceanographic drivers of habitat use in a population of marine turtles characterised by an oceanic-neritic foraging dichotomy. Using satellite tracking data from adult female loggerhead turtles nesting at Cape Verde (n=12), we test the hypothesis that oceanic-foraging loggerheads associate with mesocale (10s -100s km) thermal fronts. We use high-resolution (1km) composite front mapping to characterise frontal activity in the Canary Current Large Marine Ecosystem (LME) over two temporal scales – i) seasonal front frequency and ii) 7-day front metrics. Our use-availability analysis indicates that oceanic loggerheads show a preference for the highly productive upwelling region between Cape Verde and mainland Africa, an area of intense frontal activity. Within the upwelling region, turtles appear to forage epipelagically around mesoscale thermal fronts, exploiting profitable foraging opportunities resulting from physical aggregation of prey.

4.1 Introduction

Anthropogenic impacts on the marine environment are now evident in every major ocean basin and marine ecosystem type (Halpern *et al.* 2008). These impacts are consequent not only for continued use of marine ecosystem goods and services by humans, but also for management and conservation of marine biodiversity (Maxwell *et al.* 2013). Understanding the oceanographic drivers of marine vertebrate habitat use is essential to our knowledge of marine ecosystem functioning, and in locating critical habitats for species of conservation concern.

Oceanographic fronts are potentially significant habitat features, often associated with pelagic biodiversity hotspots (Le Fevre 1986; Belkin, Cornillon & Sherman 2009). Fronts are physical interfaces at the transitions between water masses, manifesting as surface features delineating abrupt changes in physical properties (i.e. temperature, salinity, colour). Fronts occur throughout the oceans, range from metres to thousands of kilometres in length and can be ephemeral or persistent (Belkin, Cornillon & Sherman 2009). Along some features, nutrient retention can enhance primary productivity (Traganza, Redalije & Garwood 1987; Franks 1992a). Zooplankton and small nekton may also become entrained and aggregated together by convergent flow fields (Franks 1992b; Graham, Pages & Hamner 2001; Genin *et al.* 2005). Together, this can provide rich foraging opportunities for higher marine vertebrates, from pelagic fish to apex predators.

Evidence suggests that a taxonomically diverse range of marine predators, including seabirds and pinnipeds, predatory fish, cetaceans, elasmobranchs and several species of sea turtle associate with fronts to some degree during their lifecycle (see Polovina *et al.* 2004; Mansfield & Putman 2013; Scales *et al.* 2014b & references therein). However, the nature, strength and variability of these associations remains unclear in many cases. Alongside taxon-specific aspects of foraging ecology, regional oceanographic character is likely to strongly influence the attractiveness of fronts as foraging features. Spatial scale, gradient magnitude and temporal persistence of fronts vary both within and between oceanographic regions, influencing the linkages between predators, prey, and physical processes. Foraging opportunities associated with bio-aggregation along fronts may be more profitable under certain oceanographic conditions, or exploitation of these opportunities may vary between populations or individuals (Scales *et al.* 2014b). More work is therefore needed to elucidate the influence of mesoscale oceanographic dynamics on habitat preference in different marine vertebrate populations.

Loggerhead turtles have been shown to migrate along the North Pacific Transition Zone (Polovina *et al.* 2000; Polovina *et al.* 2004; Kobayashi *et al.* 2008), forage around coastal upwelling fronts off Baja California (Etnoyer *et al.* 2006), and raft amongst floating *Sargassum* at fronts as neonates (Witherington 2002; Mansfield *et al.* 2014). However, loggerheads are circumglobally distributed, migratory predators that exhibit a high degree of foraging plasticity (Hatase *et al.* 2002; Hawkes *et al.* 2006; Frick *et al.* 2009; Hatase, Omuta & Tsukamoto 2013; Varo-Cruz *et al.* 2013), so questions remain regarding the generality of these findings across populations. Adult loggerheads in the classic life history model forage benthically in coastal waters of temperate and sub-tropical nations (Schroeder, Foley & Bagley 2003), yet oceanic foraging strategies have now been observed in populations in the Atlantic (Hawkes *et al.* 2006; Mansfield *et al.* 2009; Reich *et al.* 2010; Varo-Cruz *et al.* 2013), Pacific (Hatase *et al.* 2002), Indian ocean (Luschi *et al.* 2003), the Mediterranean (Casale *et al.* 2008) and Arabian seas (Rees *et al.* 2010). Oceanic loggerheads are thought to feed in the epipelagic zone (i.e. near the surface), preying opportunistically on planktonic and neustonic organisms, such as jellies, fish, crustaceans and their eggs and larvae (Frick *et al.* 2009; McClellan *et al.* 2010; Todd Jones & Seminoff 2013), organisms that are easily entrained along bio-aggregating fronts.

Here, we use high-resolution (1km) composite front mapping (Miller 2009) to provide a remotely-sensed oceanographic context to the movements of post-nesting female loggerheads tracked by satellite from Cape Verde, a population in which the oceanic foraging strategy seems to dominate (Hawkes *et al.* 2006; Eder *et al.* 2012; Varo-Cruz *et al.* 2013). Composite front mapping allows us to objectively locate thermal and chlorophyll-*a* fronts over ocean-basin scales, remove any obscuring influence of cloud and visualise spatiotemporal dynamics. High-level metrics describing frontal activity (distance to closest front, front density) can be time-matched to tracking data, and used as part of a suite of remotely-sensed products to contextualise animal movements. Using metrics describing oceanographic conditions over two temporal scales (seasonal, 7-day) in a multi-scale use-availability analytical framework, we aim to quantify associations between oceanic loggerheads and thermal fronts in a novel oceanographic region.

4.2 Materials And Methods

Tracking Data

A total of 24 adult females were equipped with Argos-PTT satellite tracking devices over three successive nesting seasons (n=10, 2004; n=3, 2005; n=11, 2006) at Boa Vista, Cape Verde (Lat. 16.1, Lon. -22.8; Hawkes *et al.* 2006 and L.A. Hawkes unpubl. data), using previously tested attachment methods (Godley *et al.* 2002). Transmitters used were Sirtrack Kiwisat model 101 (n=16), Telonics model ST-14 (n=2) and dive-recording Sea Mammal Research Unit (SMRU) 9000x Satellite Relay Data Loggers (SRDLs; n=6). As tags were attached to adult turtles only (Curved Carapace Length, CCL > 70cm), we assume that additional drag effects were minimal, following Todd Jones *et al.* (2013). Argos data were filtered to include only location classes (LC) A, B, 0, 1, 2 and 3, using the Satellite Tracking and Analysis Tool (Coyne & Godley 2005), excluding LC Z owing to low accuracy (Witt *et al.* 2010). All inter-nesting locations were removed. Unrealistic locations were also excluded (swimming speed > 5 km h^{-1}; positions on land). Only those turtles that exhibited an oceanic foraging strategy (n=12; Supp. Table 4.1; 98% locations >500m depth; Hawkes *et al.* 2006) were included in further analyses.

Track Interpolation using State-Space Modelling (SSM)

The majority (60%) of filtered Argos locations were of low accuracy (Location Classes A and B) and were irregular, with long data gaps (mean uplink frequency: one location per 11.2 hrs; Fig. 4.1). We thus excluded large gaps (>14 days), which reduced mean uplink frequency to one location per 8.1 hours, but variability remained high (range <1 to 332.5 hours between uplinks). Consequently, we interpolated between locations using a first differences correlated random walk SSM (DCRW; Jonsen, Flemming & Myers 2005) in R (R Core Development Team 2012) and Just Another Gibbs Sampler (JAGS) 3.2.0 (www.mcmc-jags.sourceforge.net). Model parameters were estimated for each track using two parallel Markov Chain Monte Carlo (MCMC) chains. We used 10,000 iterations after a burn-in phase of 30,000, and a thinning rate of every 10th sample. A time-step of 12 hours was used to generate two 'most likely' locations for each day of the tracking period from the posterior means of resultant distributions (Fig. 4.1).

BROAD-SCALE USE-AVAILABILITY ANALYSIS

High-use habitat over seasonal timescales was identified using kernel utilisation distributions (KUD) on interpolated tracks over a 1km resolution grid. Data were split into seasons (Winter: Dec – Feb; Spring: Mar – May; Summer: Jun – Aug; Autumn: Sep – Nov) across the entire tracking period and aggregated (adehabitatHR library for R; Calenge 2006). Low sample size prohibited further separation into seasons of each year. The KUD smoothing parameter was selected using the reference bandwidth (Kie 2013).

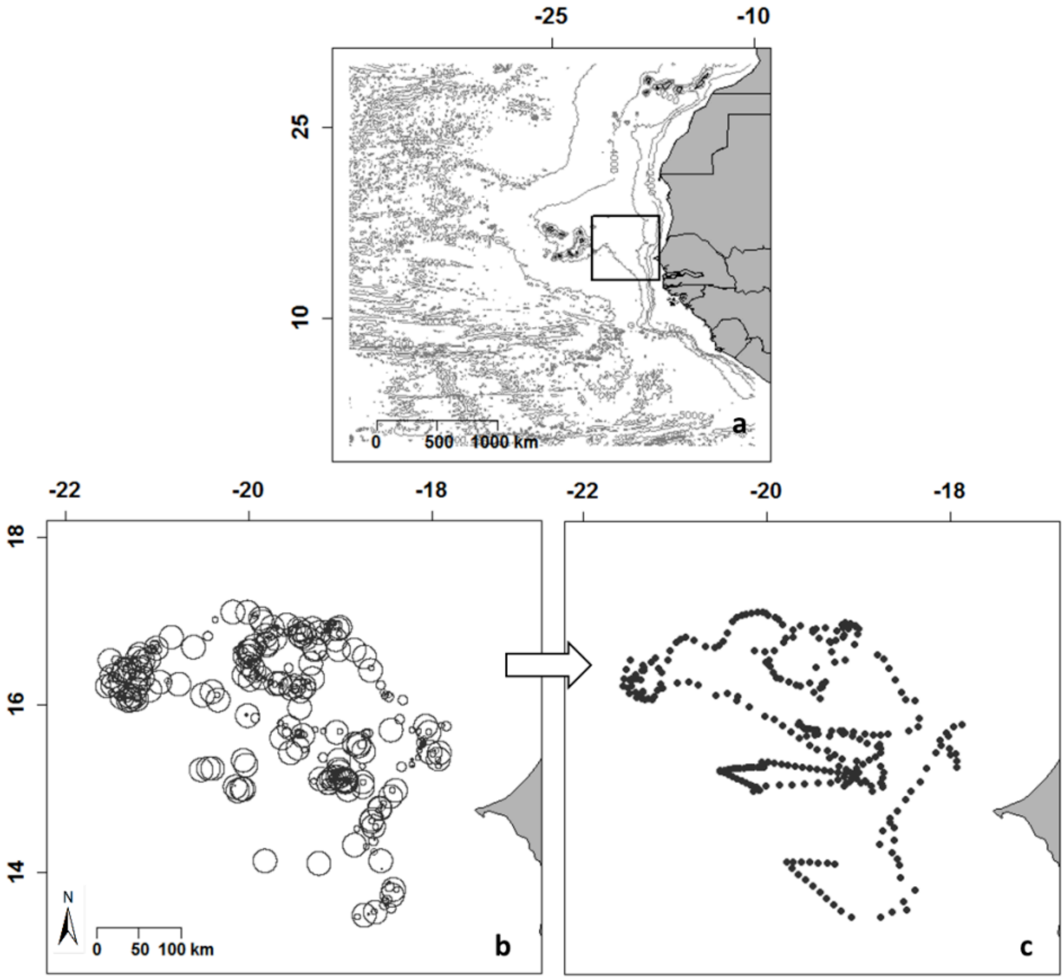

Figure 4.1 State-space modelling (SSM) for track interpolation. *Study area shown in (a), with bathymetric contours highlighted (GEBCO; 30 arc-second resolution) and smaller inset area encompassing individual track highlighted with bold black polygon (turtle 68558a). (b) Filtered Argos locations shown with error radius (from Witt et al., 2010) as open circles. (c) Interpolated, regularly-spaced locations generated by the SSM (2 locations day^{-1}).*

Seasonal Environmental Data

Thermal composite front maps were created at 1km resolution using NASA Multi-sensor Ultra-high Resolution Sea-Surface Temperature data (MUR SST). Daily SST imagery was mapped to the study area in geographic projection, and thermal fronts were detected in each scene using Single-Image Edge Detection (SIED; Cayula & Cornillon 1992; front detection threshold = 0.4°C). All fronts detected over 7-day windows were incorporated into composite front maps, rolling by one day and covering the entire tracking duration (July 2004 – Oct. 2009; Fig. 4.2). Using these 7-day composite front maps, seasonal thermal front climatologies were generated for the area enclosed by a radius described by the maximum displacement from origin (Lat: 0°N to 30°N; Long: 10°W to 40°W) for each season (Winter, Dec-Feb; Spring, Mar-May; Summer, Jun-Aug; Autumn, Sep-Nov; Fig. 4.3) over the entire tracking duration (2004-09). Resultant *frequent front* maps track each pixel through successive composites, quantifying the percentage time in which a front is detected and thereby highlighting regions in which fronts persist or manifest frequently (Miller & Christodoulou 2014). Sea Surface Temperature (SST; median) and chlorophyll-*a* (chl-*a*; median) imagery was processed from MODIS data at 4km resolution and mapped to the same region over matching seasonal timescales. General Bathymetric Chart of the Oceans (GEBCO_08 grid; http://www.gebco.net/) depth data were also obtained, at 30 arc-second resolution, and mapped to the study area ('raster' library for R; Hijmans & van Etten 2012).

MESOSCALE USE-AVAILABILITY ANALYSIS

Random Walk Simulations

Estimating habitat preference using presence-only, spatio-temporally autocorrelated telemetry data can be complex (Aarts *et al.* 2008). In order to generate a null model with which to test the habitat preference by loggerhead turtles, we used a randomisation procedure (cf. Heithaus *et al.* 2006) to generate pseudo-absence points for use within a regression-based statistical framework (Warton & Aarts 2013). One thousand correlated random walk (CRW) simulations were generated per individual and were time-matched to original tracks using step lengths, turning angles and total track length from each track (adehabitatLT library for R; Calenge 2006). To reflect spatial bias in presence data, random walk simulations had a fixed start at the nesting beach and were constrained within a habitat availability radius defined by the overall maximum displacement distance.

Temporally-matched Environmental Data

Thermal composite front maps (7-day, rolling by 1 day) were processed to generate a suite of time-matched rasters describing frontal activity (Fig. 4.2). Frontal density (*fdens*) quantifies the relative number and strength of all fronts detected over the study area, as a single metric that comprises both strength and persistence. *fdens* is prepared directly from *composite front* *maps* (Miller 2009), spatially smoothed to generate a continuous distribution quantifying relative frontal activity over the study area. The frontal distance (*fdist*) metric quantifies the distance from any location to the closest simplified front, using a custom simplification algorithm (Miller, P.I.; *unpubl. data*). Front metrics, SST and chl-*a* were extracted from temporally-matched rasters for each location along each track, both real and simulated.

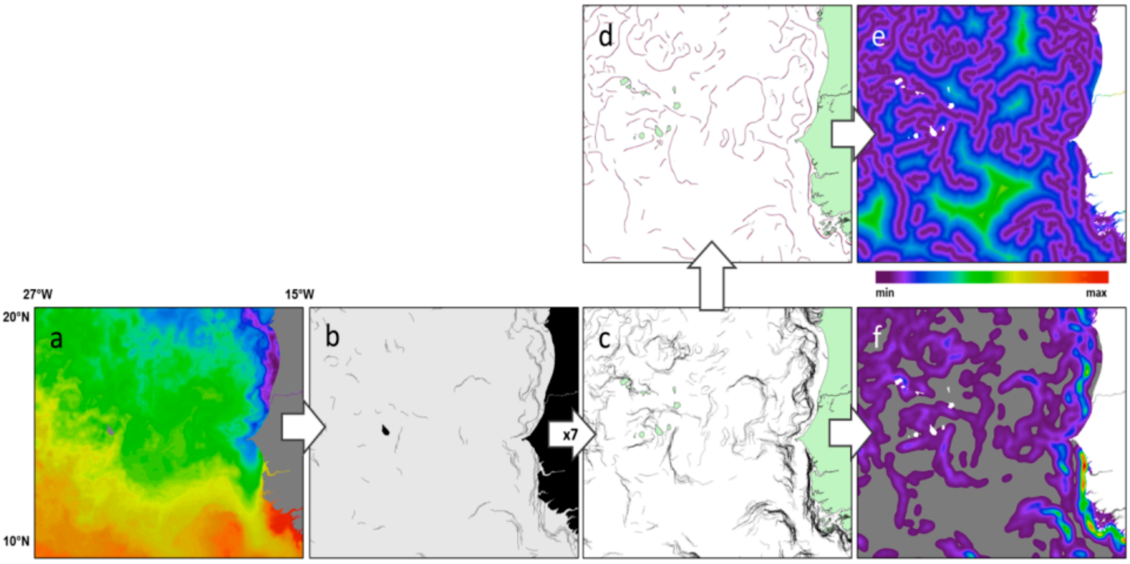

Figure 4.2 Composite front mapping protocol. *(a) Example daily NASA MUR SST product, (b) single-image edge detection, where edges are shown in grey (0.4°C threshold). (c) All fronts detected in 7 daily images combined to create 7-day composite front maps (Miller 2009), rolling by one day to cover entire tracking duration. (d) Composites simplified to a single line for each frontal feature (red = warm side, blue = cold side; width = relative strength), and (e) a continuous distance to closest front raster created from this simplified map (fdist). (f) Continuous frontal density (fdens) raster, created by spatial smoothing of the composite front map in (c).*

Statistical Analysis

First, we compared the proportion of time spent in proximity to mesoscale thermal fronts for real and simulated tracks (the null model). We derived the proportion of each track spent within four distance bins (2km, 5km, 7km, 10km) of the closest front, and compared the distributions. Distance bins were chosen to account for deviation between a front's surface manifestation and its sub-surface profile, advection of aggregated material, sub-mesoscale meanders undetectable at this spatial resolution, and potential measurement error.

A regression-based approach was then used to quantify the influence of oceanographic covariates on the probability of turtle presence. As tracking locations are serially autocorrelated, violating the assumption of independence held central to generalised linear modelling , we used a non-parametric bootstrap regression to repeatedly sub-sample the real (presence) and simulated (pseudo-absence) tracking datasets. Each sub-sampling iteration selected a total of 1000 presence and 1000 pseudo-absence points from the master dataset, weighted per the proportion of presences for each turtle. Presence/absence was then used as a binary response variable in binomial generalised linear mixed models (GLMM; lme4 package for R; Bates et al. 2014), with individual as a random effect, over 1000 bootstrap iterations. All environmental covariates were standardised before inclusion in models, by subtracting the mean and dividing by standard deviation (Zuur, Hilbe & Ieno 2013), enabling comparability of coefficient estimates.

Firstly, each environmental covariate was fitted as a standalone term in separate models, over 1000 iterations per term, to assess the effect of each on the probability of turtle presence. Parameter distributions drawn from model iterations were used to obtain mean values and standard deviations for model intercepts, regression coefficients and standard errors of fitted terms, percentage deviance explained, Chi-square statistic and p-value from a likelihood ratio test of each model iteration against a null model fitted with no fixed effects (Table 4.1). Next, multiple regression including all oceanographic covariates (*fdist*, *fdens*, chl-*a*, SST; all standardised) was used to determine relative contributions to the probability of turtle presence. Generalised Variance Inflation Factors (Zuur, Hilbe & Ieno 2013) confirmed that colinearity between oceanographic covariates was not prohibitively high for inclusion in the same model. We again used a non-parametric bootstrap, using a binomial GLMM with turtle ID as a random effect and removing each term from the maximal model in turn over 1000 iterations per term. We obtained estimates for regression coefficients, change in AIC and deviance explained on removal, and Chi-square statistic and p-value from a Chi-square test against the maximal model, to quantify the relative importance of each term to the model (Table 4.1).

Dive Behaviour

Two individuals were equipped with dive-logging devices, recording the location, depth and duration of dives (Supp. Table 4.1). We mapped dive locations, separated them into day/night using location-specific civil twilight times and then extracted temporally-matched environmental data ('maptools' library for R; Bivand & Lewin-Koh 2013). To test whether dive behaviour differed in association with mesoscale fronts, a negative binomial Generalised Additive Mixed Model (GAMM) was fitted, with maximum dive depth (m) as response and a smoother applied to the *fdist* (distance to closest front) metric, with individual as a random effect. The theta parameter was estimated by performance iteration, and scale parameter and model dispersion statistic were used for model validation (Zuur, Hilbe & Ieno 2013).

4.3 Results

Broad-scale, seasonal habitat associations

At broad scales, high-use habitat of oceanic loggerheads was strongly associated with the upwelling region off the coast of Northwest Africa, characterised by intense frontal activity and elevated chlorophyll-*a* concentrations (Fig. 4.3). Thermal front frequency was higher within regions of habitat used by tracked animals than the background level of frontal activity observed within the study area (Fig. 4.4).

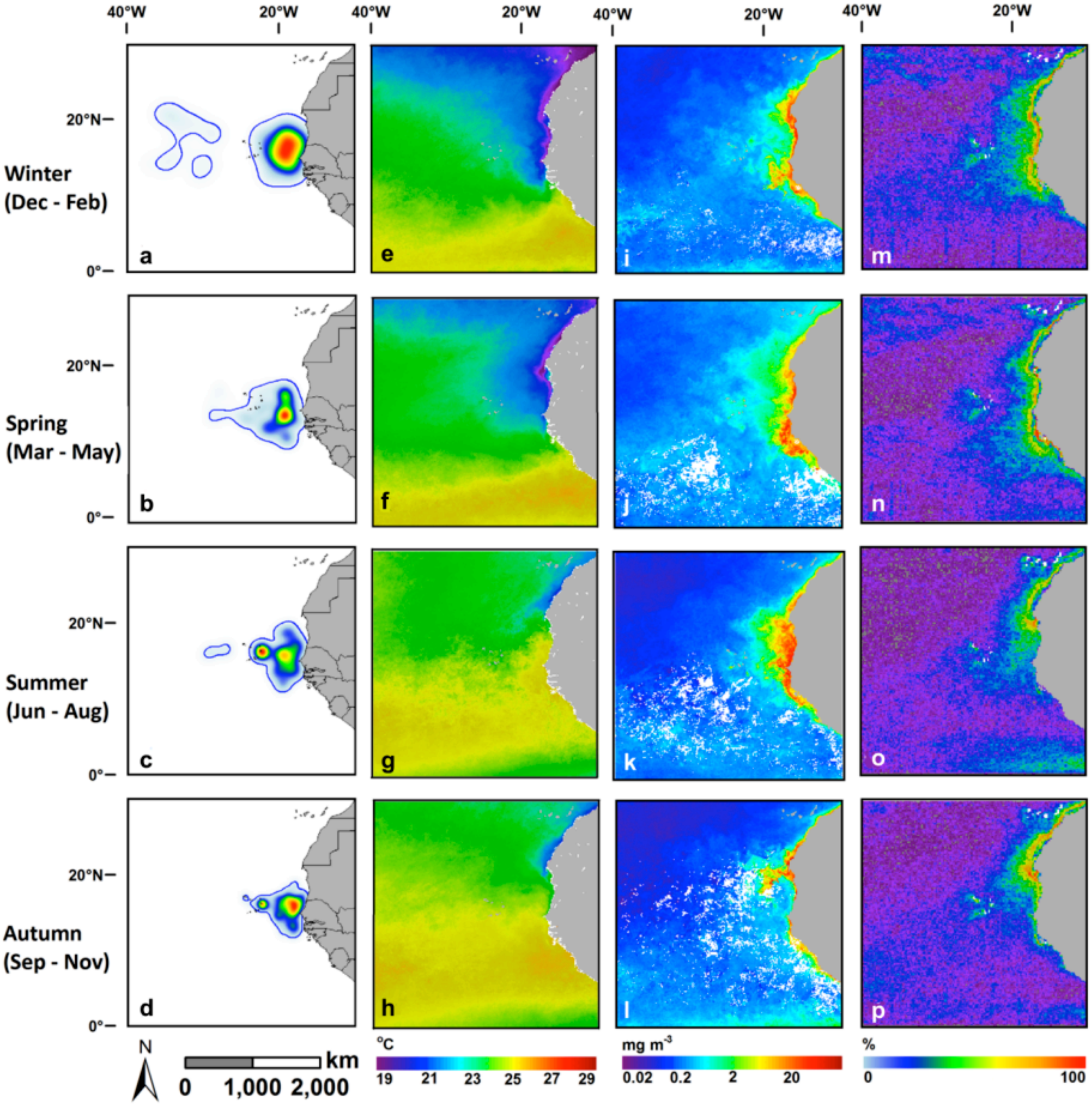

Figure 4.3 Broad-scale, seasonal habitat associations. *(a-d) Seasonal kernel utilisation distributions (KUD) for oceanic-foraging turtles only (n=12), identifying high-use habitat over the whole tracking duration, binned by season. KUD contours highlighted, with 95% contour as perimeter line. (e-h) Seasonally-averaged SST (2006 data) and (i-l) chlorophyll-a concentrations (2006 data). (m-p) Thermal front climatologies highlight areas of frequent, intense frontal activity over the tracking duration (2004-09).*

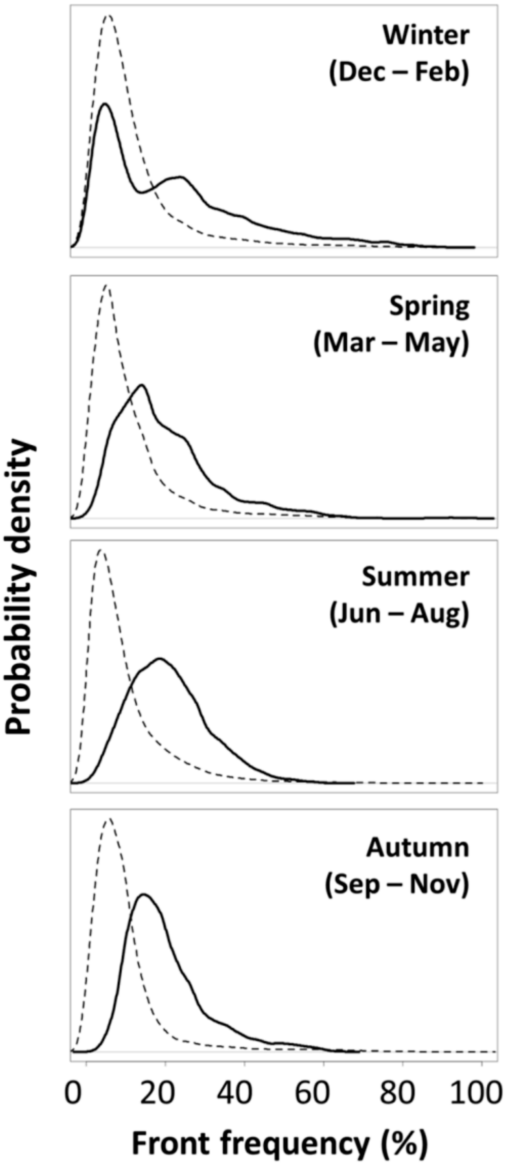

Figure 4.4 Broad-scale, seasonal habitat associations of oceanic-foraging loggerheads in Canary Current LME. *Distribution of front frequency (%) from habitat used, as defined by 95% KUD contours (solid line), against background level of front frequency (%) in all accessible habitat, as defined by radius of maximum displacement from nesting location (dashed line).*

Mesoscale habitat associations

Oceanic-foraging loggerhead turtles associated with mesoscale oceanographic fronts within the upwelling region significantly more than would be expected under a scenario of random habitat use.

The proportion of each track occurring within a spatial buffer (2km, 5km, 7km, 10km) of the closest detected front is, on average, higher for tracked turtles (2km, 0.10 ± 0.04; 5km, 0.25 ±

0.07; 7km, 0.33 ± 0.07; 10km, 0.47 ± 0.10) than for random walk simulations (2km, 0.07 ± 0.03; 5km, 0.19 ± 0.05; 7km, 0.26 ± 0.07; 10km, 0.39 ± 0.09), with four of twelve turtles associating with fronts significantly more frequently than random walks (Fig. 4.5; 5% significance level).

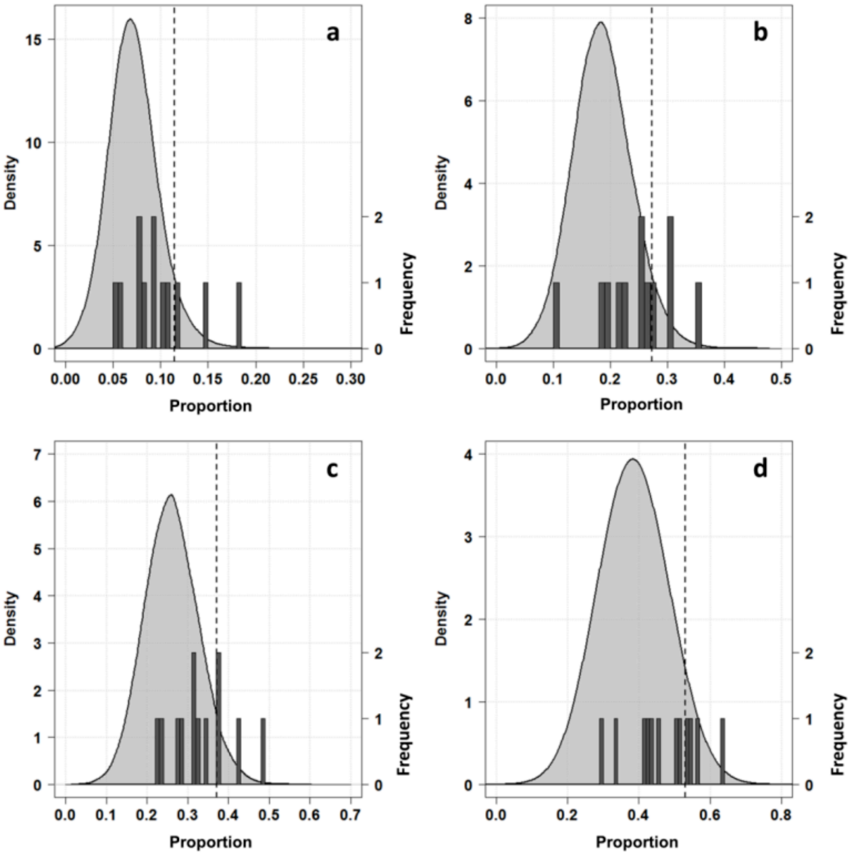

Figure 4.5 Use of mesoscale thermal fronts by oceanic-foraging loggerheads. *Proportion of each track (n=12) within 2km (a), 5km (b), 7km (c) and 10km (d) of closest front (grey bars). Proportion of simulated tracks (n=12000) within each distance threshold shown as grey curve. Upper 5% of distribution marked by dashed line.*

Presence/absence predictions from logistic regression suggests that front metrics (*fdens*, *fdist*) are significant predictors of turtle presence, both as standalone terms and in multiple regression. Presence points were more likely to occur closer to fronts and at higher frontal density than pseudo-absences derived from random walks (Fig. 4.6, Table 4.1). Confidence Intervals (CIs) of distributions of regression coefficient magnitude obtained from 1000 model iterations do not overlap zero for *fdens, fdist* or SST, indicating that these terms have significant explanatory power (Fig. 4.6e).

Further, *fdens* and *fdist* were found to be significant terms using likelihood ratio tests, with p-values indicating significance in all 1000 single-term model iterations. In contrast, SST and chl-*a* were weaker predictors of turtle presence. Confidence Intervals of regression coefficients for chl-*a* overlap zero, and a lower proportion of significant p-values were generated. In addition, *fdens*, *fdist* and SST made a more significant difference to the AIC of the multiple-regression model upon removal than chl-*a*. These results indicate that the 7-day front metrics *fdens* and *fdist* have better explanatory power in predicting turtle presence than the more-commonly used SST and chl-*a* metrics.

Dive data

The distribution of dive depth maxima clearly shows a predominance of shallow dives, with a median max. depth of 14.5m (Fig. 4.7a). Dives were marginally deeper during daylight than darkness hours (Fig. 4.7b). Moreover, dives during daylight hours tended to be shallower when closer to fronts (Fig. 4.7c).

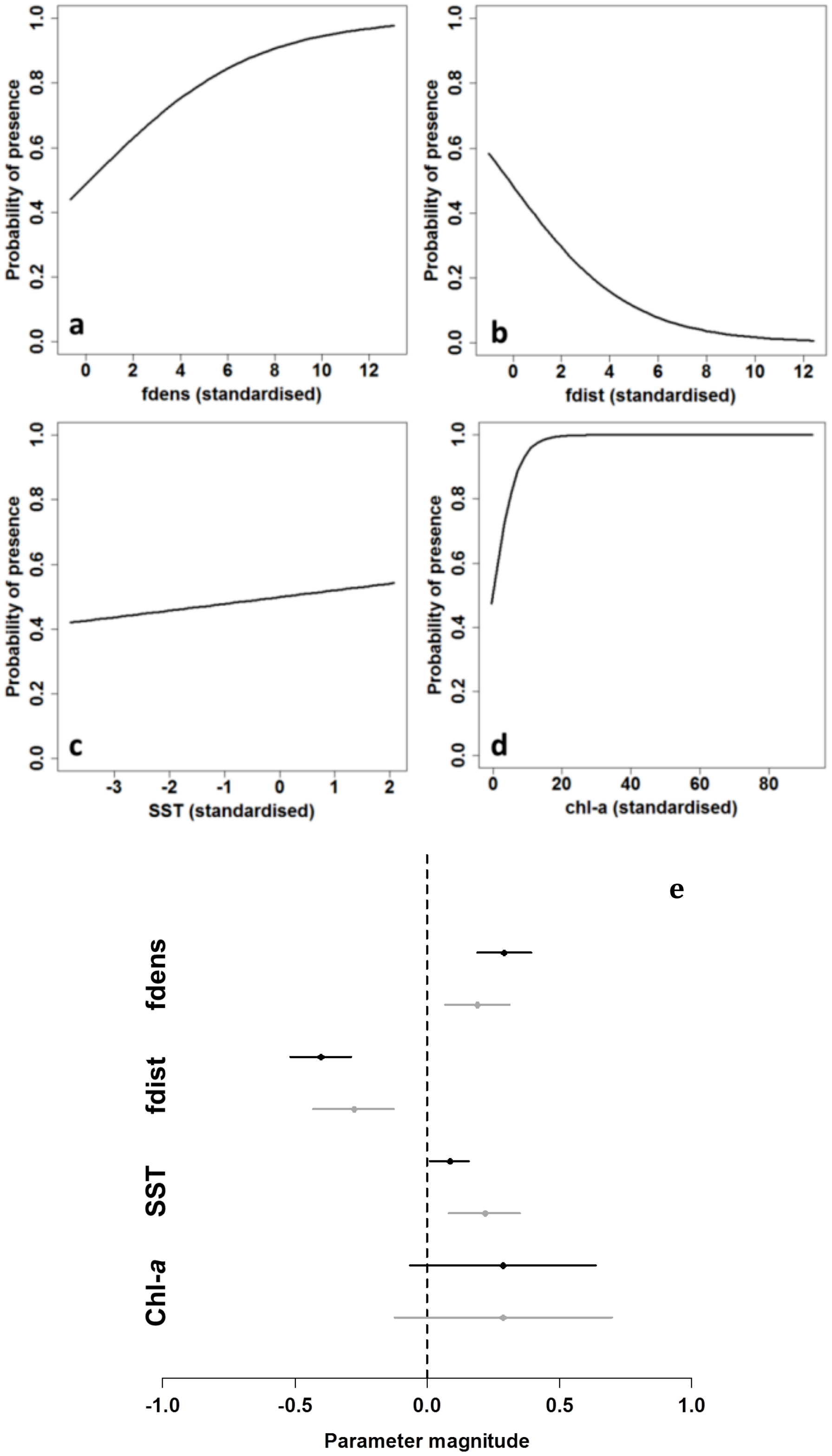

Figure 4.6 Modelling the influence of mesoscale fronts on habitat selection. *Effect of (a) frontal density, (b) distance to closest front, (c) SST and (d) surface chl-a concentration on probability of turtle presence (all covariates standardised). (e) Parameter distributions for regression coefficients from binomial GLMM (individual as random effect; 1000 iterations) shown for influence of frontal density (fdens), distance to closest front (fdist), SST and chl-a concentration. Mean value indicated by filled circle, 95% confidence intervals (CIs) shown as horizontal lines. Outputs from modelling of single terms in black, multiple regression in grey. Mean regression coefficients plotted on response scale (logistic link function; a-d). Confidence intervals for fdens, fdist and SST do not overlap zero, indicating significance explanatory power as predictors of turtle presence.*

Table 4.1 Modelling the influence of mesoscale fronts on habitat selection. *Model parameters (mean ± sd, range; binomial GLMM; 1000 iterations) for the influence of frontal density (fdens), distance to closest front (fdist), sea surface temperature (SST) and chl-a concentration (chl-a) on probability of observing a presence (locations sampled from filtered Argos dataset) or absence (pseudo-absences sampled from random walk locations). All environmental covariates standardised before inclusion, for comparability of coefficient sizes. Regression coefficients reported on untransformed scale.*

***a. Single terms*: presence (0/1) ~ metric + (1 | ID)**

Environmental covariate (standardised)	Intercept	Regression coefficient	Standard error	Deviance explained (%)	p-values < 0.05 (%)
fdens	-0.050 ± 0.01 (-0.08 – -0.03)	0.29 ± 0.05 (0.14 – 0.48)	0.04 ± 0.003 (0.034 – 0.054)	1.9 ± 0.53 (0.62 – 3.8)	100
fdist	-0.07 ± 0.01 (-0.12 – -0.03)	-0.40 ± 0.06 (-0.61 – -0.23)	0.6 ± 0.002 (0.05 – 0.07)	1.9 ± 0.51 (0.65 – 4.30)	100
SST	-0.005 ± 0.003 (-0.02 – 0.003)	0.08 ± 0.04 (-0.02 – 0.22)	0.04 ± 0.0004 (0.041 – 0.044)	0.16 ± 0.13 (0.00 – 0.92)	51
chl-a	0.02 ± 0.04 (-0.1 – 0.14)	0.29 ± 0.18 (-0.05 – 1.14)	0.1 ± 0.03 (0.02 – 0.18)	0.64 ± 0.53 (0.00 – 3.48)	75

***b. Multiple regression:* presence (0/1) ~ *fdens* + *fdist* + chl-*a* + SST + (1 | ID)**

Intercept = -0.05 ± 0.05 (-0.19 – 0.08)
AIC: 1531 ± 33.5 (1430 – 1645)
Total deviance explained (%) = 4.2 ± 1.0 (1.3 – 7.5)

Environmental covariate (standardised)	Regression coefficient	ΔAIC on removal	Δ deviance explained on removal (%)	Chi-sq statistic (df = 1)	p-values < 0.05 (%)
fdens	0.19 ± 0.06 (0.01 – 0.38)	+11.0 ± 7.1 (-1.9 – 36.6)	0.82 ± 0.45 (0.00 – 2.40)	13.0 ± 7.1 (0.07 – 38.6)	93
fdist	-0.28 ± 0.08 (-0.52 – 0.02)	+11.4 ± 6.8 (-1.9 – 40.3)	0.84 ± 0.43 (0.01 – 2.64)	13.4 ± 6.8 (0.09 – 42.3)	95
SST	0.22 ± 0.68 (-0.01 – 0.47)	+ 11.2 ± 7.6 (-1.9 – 51.4)	0.83 ± 0.51 (0.00 – 3.37)	13.2 ± 7.6 (0.05 – 53.4)	93
chl-a	0.29 ± 0.21 (-0.06 – 1.18)	+ 6.6 ± 8.1 (-2.0 – 52.5)	0.54 ± 0.51 (0.00 – 3.53)	8.6 ± 8.1 (0.0 – 54.5)	64

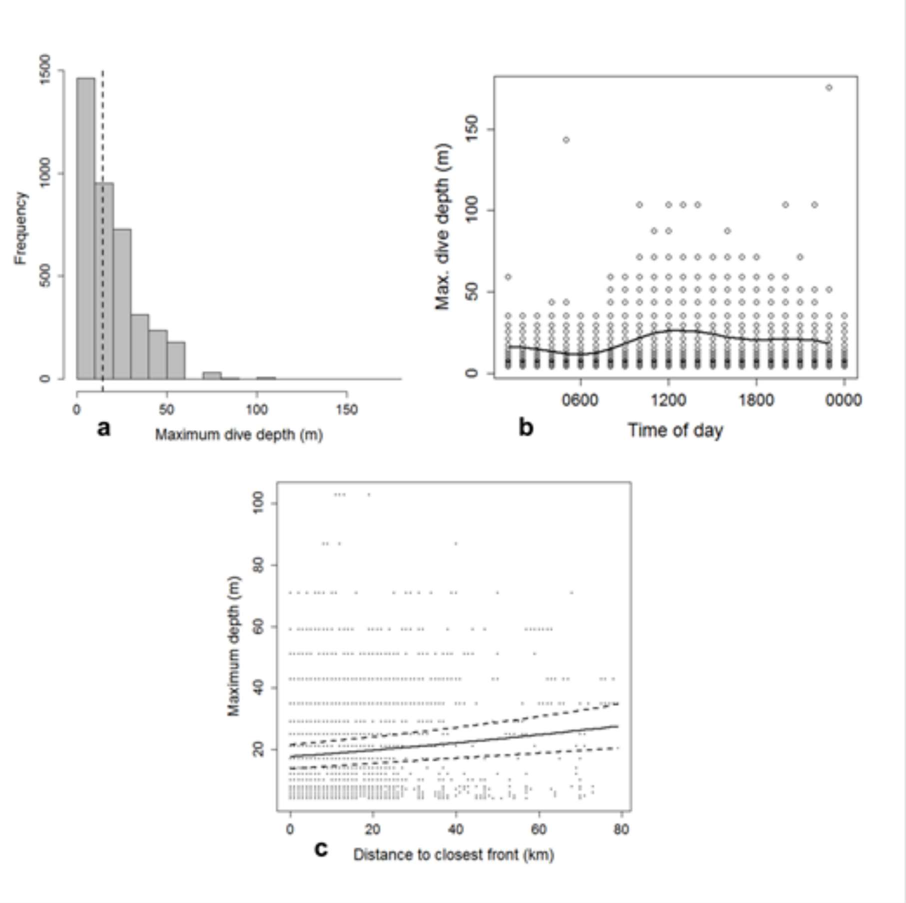

Figure 4.7 Dive behaviour of oceanic turtles. *(a) Distribution of maximum dive depths (metres), with median shown by dashed line, indicates epipelagic foraging. (b) Diel cycle of dive depths, with deeper dives during daylight hours. Points represent individual dives, aggregated by hour of day. Solid line shows predictions of generalised additive model of diel cycle in dive depths (c) Modelling the influence of mesoscale fronts on dive behaviour suggests that, during daylight hours, dives are shallower in proximity to fronts. Points represent individual dives. Solid line shows model predictions, with 95% confidence intervals as dashed lines.*

4.4 Discussion

Oceanic-foraging loggerheads inhabiting the Canary Current LME appear to associate strongly with the highly productive upwelling region off Northwest Africa between return migrations to nesting grounds at Cape Verde. At an ocean-basin scale and over seasonal timespans, high-use habitat overlaps with a region of intense frontal activity associated with this major Eastern boundary upwelling. Within the upwelling region, meso- and sub-mesoscale oceanographic dynamics influence prey availability. Oceanographic features, such as filaments, jets, eddies and internal waves, drive spatial structuring and front formation as cool, dense water is forced to the warmer surface (Chavez & Messié 2009). Filaments, tongueshaped extensions of coastally upwelled water, extend hundreds of kilometres offshore, transporting nutrients and entrained plankton to pelagic waters (Rodrıguez, Hernández-León & Barton 1999). Strong, persistent thermal fronts around filaments and eddies concentrate these nutrients and low trophic-level biota, increasing prey accessibility for higher-level consumers and their predators (Hernández-León *et al.* 2002).

Our use-availability analysis provides objective evidence that mesoscale oceanographic processes influence habitat selection by loggerhead turtles within this upwelling region. Tracked turtles spent more time in association with mesoscale thermal fronts than expected at random. Loggerheads are thought to be opportunistic foragers, feeding while travelling (Frick *et al.* 2009; Todd Jones & Seminoff 2013), so presumably use front-associated foraging opportunities as they encounter them.

While it is difficult to distinguish foraging dives from transit using dive depth alone, our dive data indicate some influence of front proximity on dive behaviour. Overall, dive data suggest that loggerheads forage epipelagically, and most particularly when associated with fronts (see also Polovina *et al.* 2000; Polovina *et al.* 2003; Mansfield & Putman 2013; Dalleau *et al.* 2014). As features in which the thermocline breaches the surface, fronts often act to increase prey accessibility in the surface ocean (Le Fevre 1986). We can therefore surmise that loggerheads likely dive epipelagically around thermal fronts to exploit profitable foraging opportunities resulting from physical aggregation of prey close to the surface.

As ectotherms, turtles must make energetic trade-offs between thermal constraints and availability of food resources when selecting pelagic habitats (Fossette *et al.* 2012). Habitats associated with the upwelling region favoured by this population are highly thermally dynamic, characterised by the intrusion of cool water into warmer tropical surface waters. As turtles do not invest in reproduction every year (mean interval 2.3 years, Marco *et al.* 2012), energetic trade-offs presumably enable the population to exploit profitable foraging opportunities associated with this upwelling in the intervening period. Seasonal patterns of space use show a range contraction through the year, coincident with variation in upwelling intensity. During the summer (Jun-Aug), when upwelling is at its most intense (Moyano *et al.* 2014), turtles remained within a core foraging area associated with the highly productive frontal zone.

While our analysis indicates that only four of twelve tracked turtles spent a significant proportion of time in the vicinity of strong fronts, use-availability regression models indicate that front metrics are significant predictors of turtle presence at the sampling level even when this inter-individual variability is explicitly accounted for. We postulate that this may be a function of limited sample size, or of individual behavioural differences during the tracking period – some turtles may move along fronts, presumably to exploit favourable conditions, while others may associate with front-associated habitat more opportunistically as they navigate the pelagic seascape. In addition, the degree of bio-aggregation at fronts, which varies according to the direction and strength of flow, temporal persistence and the properties of surrounding water masses (Bakun 1996), is likely to make some fronts more attractive than others - it has been shown that persistent fronts are more attractive to some high trophic-level organisms than ephemeral features (Scales *et al.* 2014a). Moreover, advection of prey items aggregated in convergent fronts could obscure the signal of frontal foraging. Importantly, front metrics (*fdens*, *fdist*) were found to be better predictors of turtle presence than SST or chl-*a*, parameters that are widely used to characterise habitat preference (e.g. Kobayashi *et al.* 2008; McCarthy *et al.* 2010). Thus, our approach offers advantages for future studies that wish to enumerate, robustly compare or predict the distribution of animals associating with oceanographic features.

Despite using the best available data and a progressive methodological approach, technical limitations meant that we were unable to investigate these mesoscale associations in further detail. We have used, for the first time to our knowledge, high-resolution (MUR SST; 1km) composite front mapping, which addresses many of the caveats of precursor front detection methods, alongside MODIS chl-*a* (4km), to provide novel context for the movements of tracked animals. Our use-availability analysis considers multiple nested spatial and temporal scales, defined by the oceanographic processes that underlie foraging habitat use and preference. We have used a regression-based technique that explicitly accounts for non-independence in tracking data to quantify, rather than just describe, associations with fronts.

However, limitations of data frequency and accuracy have precluded further investigation into the role of ocean currents in this system. Consideration of current flow is an important aspect in analysis of marine vertebrate space use (Luschi, Hays & Papi 2003; Gaspar *et al.* 2006). Broad-scale current flows experienced as hatchlings are known to influence foraging site selection in adult turtles (Scott, Marsh & Hays 2014). The influence of currents on the movements and behaviour of adult hard-shelled turtles, which have sufficient motility to actively swim against or across current fields, are less clear – and under debate (see Hays *et al.* 2014; Kobayashi *et al.* 2014). Advances in biologging technologies, including the advent of fast-acquisition GPS-based tags, (e.g. Fastloc™-GPS; Wildtrack Telemetry Systems Ltd., Leeds, UK) enable high resolution investigation of space use (Shillinger *et al.* 2012). Using directly measured, modelled or remotely sensed oceanographic data (c.f. McCarthy *et al.* 2010) alongside GPS-tracking technologies to investigate interactions between frontogenesis, mesoscale current fields and turtle habitat selection would be a logical follow-up to this study.

In a wider context, insights into the oceanographic drivers of marine vertebrate habitat use contribute to our understanding of pelagic ecosystem functioning, and thereby confer opportunities to improve biodiversity conservation as anthropogenic impacts on the global ocean intensify (Halpern *et al.* 2008). Such insights are useful in identifying ecologically significant marine areas, and assessing the extent of overlap between critical habitats and anthropogenic threat (McCarthy *et al.* 2010; Pikesley *et al.* 2013; Pikesley *et al.* 2014). At a regional level, intense fisheries pressure leads to high rates of incidental capture, 'bycatch'

(Zeeberg, Corten & de Graaf 2006), threatening this globally significant loggerhead population which also experiences direct take on the nesting grounds (Marco *et al.* 2012). Bycatch remains a major threat to many marine vertebrate populations of conservation concern (Lewison *et al.* 2014). As fisheries also target productive fronts, these threats are likely to be concentrated in ecologically-significant frontal zones (see Seki *et al.* 2002; Alemany, Acha & Iribarne 2014; Scales *et al.* 2014b). As a tool for identification of vulnerability hotspots, front mapping could inform a more spatially dynamic management paradigm (cf. Howell *et al.* 2008), designed to incorporate the conservation needs of highly mobile marine vertebrates.

Supplementary Figures and Tables

Supp. Table 4.1 *Summary of filtered Argos-PTT tracking dataset for oceanic-foraging turtles tracked from Boa Vista, Cape Verde 2004-06 (n=12; Hawkes et al. 2006). Individuals equipped with dive-loggers (n=2) highlighted (*).*

ID	CCL (cm)	Deployment date	Tracking duration (days)	Total number of location fixes	Max. displacement (km)
4413a	-	18-Aug-2004	24	89	555
4416a	78.50	04-Oct-2004	132	195	663
49819a	71.50	08-Aug-2004	596	1708	746
49827a	74.00	28-Jul-2004	345	1440	683
49829a	76.00	30-Jul-2004	221	747	640
52200a*	84.00	14-Aug-2004	83	158	652
57393a	86.00	07-Jul-2005	144	218	604
34208a*	86.00	19-Aug-2006	250	353	605
64702a	89.00	25-Aug-2006	714	484	635
68125a	-	03-Sep-2006	565	1654	666
68554a	76.00	18-Aug-2006	118	95	1292
68558a	90.00	30-Aug-2006	149	337	540

Chapter V

Ensemble ecological niche modelling identifies preferred foraging habitats of grey-headed albatrosses *Thalassarche chrysostoma*

ABSTRACT

Ecological niche modelling can provide insight into species' environmental preferences, enabling prediction of key habitats for populations of conservation concern. Here, we integrate biologging, Earth Observation remote sensing and ensemble ecological niche modeling (EENM) with two key aims: i) to identify the conditions that characterise foraging habitat for a globally significant seabird population; and ii) to explore the utility of EENM for predicting the locations of suitable habitats. GPS and geolocation-immersion loggers were used to track the at-sea activities of grey-headed albatrosses (*Thalassarche chrysostoma*; GHA) over the brood-guard phase of two breeding seasons (n=55). An EENM combines predictions of multiple algorithms (Generalised Additive Models, GAM; Maximum Entropy Modelling, MaxEnt; Random Forest, RF; Boosted Regression Trees, BRT) to identify conditions characterising foraging locations, using a suite of oceanographic predictors (Sea Surface Temperature, SST; Chlorophyll-*a*, chl-*a*, Thermal front frequency, *Ffreq*, Water depth). Model performance was assessed through iterative cross-validation. Although evaluation metrics indicated that algorithms performed comparably well (AUC GAM=0.9349, MaxEnt=0.9381, RF=0.9477, BRT=0.9390; TSS GAM=0.7960, MaxEnt=0.7743, RF=0.8036, BRT=0.7834), spatial predictions of habitat suitability varied markedly between model projections. EENM predictions identified suitable foraging conditions in neritic (<500m depth), shelf-break and oceanic waters, reflecting the variety of foraging locations targeted by GHA. Sea surface temperature and chl-*a* concentration were identified as important oceanographic predictors. Suitable foraging habitats (Habitat Suitability Index, HSI > 0.25) were associated with particular SST ranges (3-8°C, 12-13°C) and productive regions (chl-*a* >0.5mg m^{-3}). Water depth and the frequency of mesoscale thermal front manifestation (*Ffreq*) were also contributory variables, although less important owing to individual-level variability in foraging site selection. Moreover, EENM performed well in predicting the locations of suitable foraging habitats in the contemporaneous season, but forward projection indicates lack of transferability among years. Lack of transferability has important implications for the use of EENM in informing conservation and management.

5.1 Introduction

The energetic demands of reproduction strongly influence the spatial ecology of wide-ranging pelagic seabirds. During the breeding season, the constraints of incubation and chick-provisioning impose a central-place foraging mode, as trips are restricted to waters within an accessible range of the colony (Weimerskirch *et al.* 1993). Individuals face trade-offs between the costs of flight and the necessity for reliable acquisition of prey of sufficient quality to meet the demands of chick provisioning in addition to their own energetic requirements, including for self-maintenance (Weimerskirch, Mougey & Hindermeyer 1997). These constraints are particularly pronounced during the brood-guard period of chick-rearing, when chicks require continual attendance by a parent to avoid chilling, are at their most vulnerable to predation, and have a small stomach volume so require frequent small meals (Weimerskirch *et al.* 1988; Xavier *et al.* 2003; Wakefield *et al.* 2011).

Breeding success is therefore conditional upon the abilities of each bird to find suitable foraging habitats within a commutable distance of the colony. The seascape over which oceanic seabirds search for food is characterised by extreme heterogeneity, with prey distributed within a *nested patch hierarchy* (Fauchald, Erikstad & Skarsfjord 2000; Pinaud & Weimerskirch 2007). Suitable foraging habitats, within which prey of sufficient number and quality are accessible within the diving capabilities of the species, are formed by complex and stochastic biophysical processes; hence, exploitable prey aggregations are unpredictable in location as a result of oceanographic dynamics. Mechanisms for optimisation of foraging success have therefore evolved in response to the spatially heterogeneous and temporally dynamic nature of the oceanic environment.

Optimal search patterns (e.g. Lévy walks) have been observed in several marine vertebrate taxa, including albatrosses (Humphries *et al.* 2012, but see Edwards et al. 2007), although these scale-invariant mechanisms are likely to be prevalent where animals have little knowledge of resource distributions (Regular, Hedd & Montevecchi 2013). In seabirds, cognitive processes such as learning and memory appear to mediate navigation to broad-scale foraging grounds, which are often associated with persistent oceanographic conditions and so can be spatially predictable (Piatt *et al.* 2006; Weimerskirch 2007; Scales *et al.* 2014a). The prey-finding abilities of seabirds are enhanced by the capacity to detect and respond to real-time environmental cues, such as olfactory and visual stimuli that signal the presence of prey aggregations (Nevitt & Bonadonna 2005; Rodhouse & Boyle 2010). As Procellariiformes ('tube-noses'), albatrosses are known to use atmospheric gradients of dimethyl sulphide (DMS) as long-distance foraging cues; (Nevitt, Losekoot & Weimerskirch 2008). Social information transfer and flock facilitation, both between con-specifics and hetero-specifics, is also known to be an important influence on seabird foraging behaviour over more proximate scales (Silverman, Veit & Nevitt 2004; Thiebault *et al.* 2014; Tremblay *et al.* 2014). Foraging behaviour is therefore likely to be mediated by both intrinsic and extrinsic influences that operate over a range of spatial and temporal scales, and to incorporate both prior knowledge and real-time information.

Grey-headed albatrosses (GHA) *Thalassarche chrysostoma*, in common with many Southern Ocean predators , are known to exploit profitable foraging opportunities generated through bio-physical coupling along ocean fronts – physical interfaces between contrasting water bodies (Belkin, Cornillon & Sherman 2009; Bost *et al.* 2009). The Antarctic Polar Frontal Zone (APFZ), an extensive, dynamic region that marks the northern boundary of the Antarctic Circumpolar Current (ACC), is known to be an important feature for seabirds and marine mammals in this sector of the Southern Ocean (Catry *et al.* 2004; Bost *et al.* 2009; Wakefield *et al.* 2011; Scales *et al.* 2014b). Within the broad-scale APFZ, intense oceanographic dynamics lead to the generation of chaotic eddies and the manifestation of mesoscale (10s -100s of kilometres) or sub-mesoscale (~1 kilometre) thermohaline fronts. Aggregations of preferred prey of Southern Ocean predators, such as the mesopelagic fish and cephalopods often targeted by the grey-headed albatross (Rodhouse & White 1995; Reid, Croxall & Prince 1996;

Catry *et al.* 2004; Rodhouse & Boyle 2010), can be concentrated within this zone, both through processes of mechanical entrainment and bottom-up forcing.

However, habitat preference of Southern Ocean seabirds varies among species (Commins, Ansorge & Ryan 2014), populations (Nel *et al.* 2001; Louzao *et al.* 2011; Joiris & Dochy 2013), and individuals (Phillips *et al.* 2006; Patrick & Weimerskirch 2014); between sexes (Phillips *et al.* 2004b); with life history stage (Phillips *et al.* 2005); through the annual cycle (Phillips *et al.* 2006; Wakefield *et al.* 2011); and in response to changes in prevailing oceanographic conditions (Xavier *et al.* 2013). While previous work has identified the APFZ as a key habitat feature for grey-headed albatrosses from South Georgia, its importance as a regional foraging hotspot depends on a combination of all these factors. Further investigation of the drivers of habitat preference is therefore essential to our understanding of how these seabirds interact with their environment, and can advance our knowledge of pelagic ecosystem functioning in the Southern Ocean. Ecological niche modelling (also known as species-habitat, predictive habitat or species distribution modelling) provides a valuable framework for understanding habitat preferences of wide-ranging marine vertebrates, and has shown widespread application, particularly since the recent proliferation of studies using biologging technologies to track animal movement in unprecedented detail (Elith *et al.* 2011; Merow, Smith & Silander 2013).

Here, an ensemble ecological niche modelling approach (EENM; Araújo & New 2007; Oppel *et al.* 2012) is applied to high resolution GPS tracking and remotely-sensed environmental data to investigate habitat preference of GHA breeding at Bird Island, South Georgia, with three key aims; i) to identify preferred foraging conditions; ii) to investigate the contribution of mesoscale frontal activity as a determinant of habitat preference; and iii) to develop model predictions identifying suitable foraging habitats for the population as a whole, based on the preferences of tracked birds.

5.2 Methods

Tracking device deployment

Adult birds were tracked from Colony B at Bird Island, South Georgia (54°00'S 38°03'W) in December-January in two austral breeding seasons (total n=55 birds; n=25 in 2009/10; n=30 in 2011/12), during the brood-guard stage of chick-rearing. GPS loggers were i-gotU (MobileAction Technology; http://www.i-gotu.com; 30g mass), earth & Ocean Technology (e&O-Tec) MiniGPSlog (29g) or e&O-Tec MicroGPSlog (10g) and were attached using Tesa marine cloth tape to mantle feathers. Devices were programmed to record fixes at 10 or 15 minute intervals and were recovered after one complete foraging trip, when the instrumented bird returned to the nest. Birds were also equipped with geolocation-immersion loggers (British Antarctic Survey; Mk 13; ~2g mass), attached to a standard British Trust for Ornithology metal ring or plastic ring using a cable tie. These loggers test for saltwater immersion every 3 seconds, indicating time periods when the leg is submerged. Birds were restrained on the nest only during device deployment, and handling time during deployment and retrieval was minimised (5-10 mins).

Behavioural classification

Landing rate (number of landings per hour) was used to identify foraging bouts (Dias *et al.* 2010). Take-off from the water surface is energetically costly for albatrosses, so we assume that immersion events indicate prey capture attempts (Wakefield *et al.* 2011). Estimated locations of immersions were derived through linear interpolation of GPS tracks to 3-second intervals, using custom code written in R. All original GPS locations were also classified as 'wet' or 'dry' by matching the timing with the immersion data. As birds frequently rest on the surface of the water overnight (Catry *et al.* 2004), and night-time foraging cannot be differentiated reliably from resting using immersion data, only those locations recorded in daylight hours were used in further analysis. The times of civil twilight (solar zenith angle of -6°) were used to distinguish periods of daylight, twilight and darkness. All locations within a 50km radius of the colony were excluded from analysis, as birds frequently alight on the surface to preen soon after leaving the nest. Landing rate was derived using a sliding window summing the number of immersion events in the 30 minutes preceding, and 30 minutes following, each location. GPS locations along each track were then classified as either 'foraging' – associated with at least one immersion event within that hour – or 'transit' – not associated with an immersion (Fig. 5.1a). Foraging events more than 60 minutes apart were classed as distinct bouts.

To validate this approach, the resultant behavioural classifications were compared with those derived from a residence-time analysis (Barraquand & Benhamou 2008) using an equal area projection, a radius around each location of 10km and maximum time outside that radius of four hours (adehabitatLT library for R, Calenge 2006; Fig. 5.1). The threshold for determination of high residence time was based on the 75% quartile of the whole tracking dataset (5,385 seconds).

The study area was defined as the area enclosed by a radius corresponding to the absolute maximum displacement from the colony by any tracked bird (1185km). To obtain an indication of the spatial distribution of foraging events over the whole tracking period, a 2-dimensional regular grid of the study area (Lat: 71°S to 32°S; Lon: 55°W to 21°W) was created at 0.5° resolution (Kaschner *et al.* 2006). A binary classification index of grid cell usage was used to identify foraging regions - any grid cell in which foraging behaviour was recorded over the course of the tracking period was designated as '1', and grid cells that only contained transit locations, or no bird presence, were designated as '0' (Fig. 5.2)

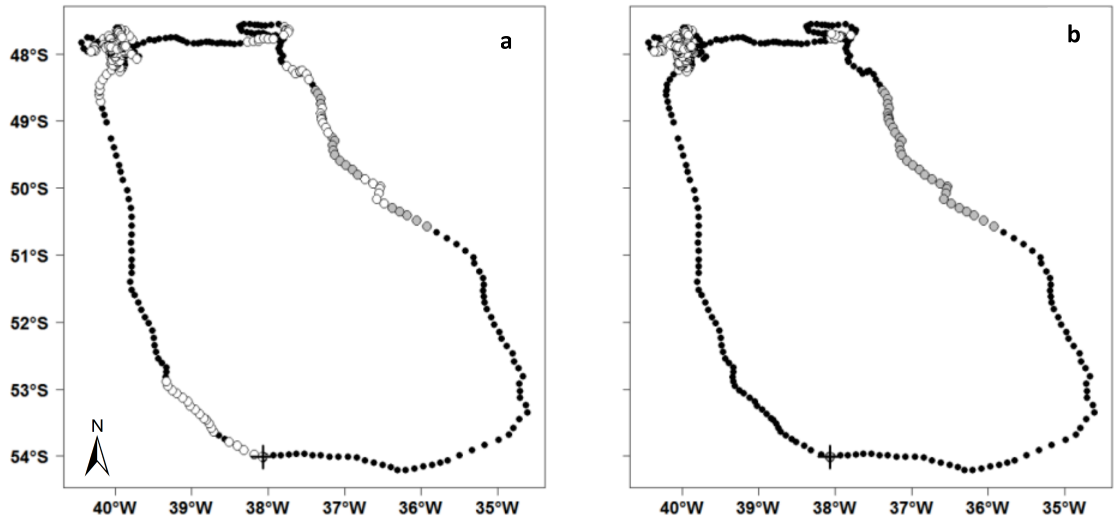

***Figure 5.1 Behavioural classification within foraging trips**. (a) Identification of foraging and transit behaviours using landing rate. Filled black circles are transit locations; white circles are foraging locations during daylight, defined by at least one immersion event within the hour; grey circles are GPS locations during darkness, which were removed from analysis. (b) Identification of foraging and transit behaviours using residence time within a 10km radius. Black circles denote transit, white filled circles are foraging locations during daylight with a residence time greater than the 75% quartile for the complete dataset (5,385 sec). Exclusion radius around colony (black cross) not shown.*

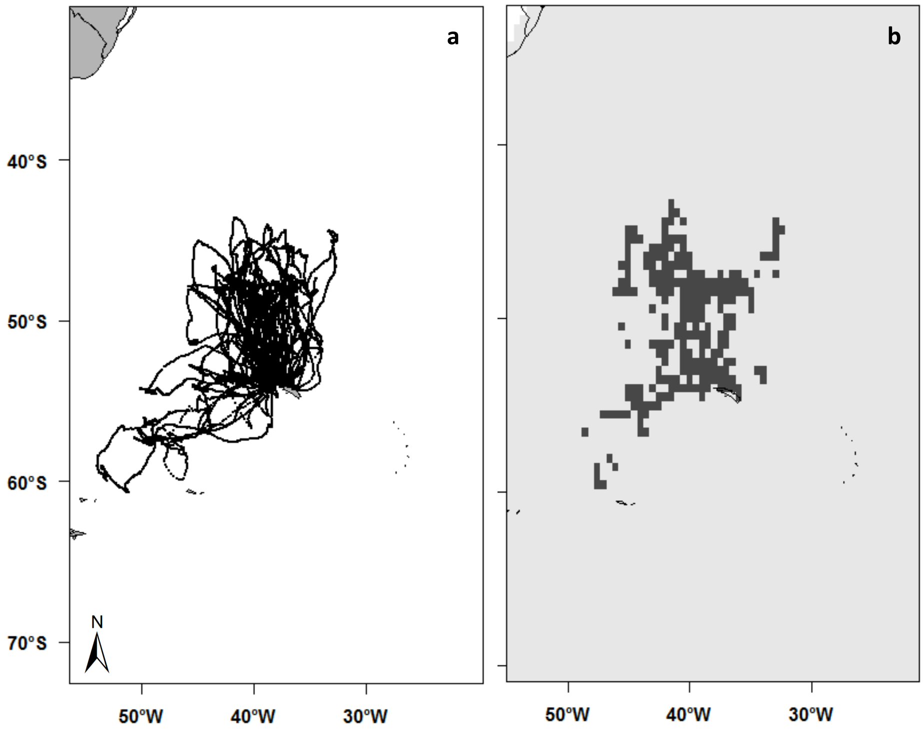

***Figure 5.2 Spatial distribution of foraging events** of birds tracked during the brood-guard period in 2009/10 (n=25). (a) GPS locations of all recorded foraging trips from Bird Island. Map shows South Georgia (54°00'S 38°03'W) and part of the South American coastline. (b) Regular grid (0.5 degree resolution) of foraging events over the tracking period, derived using landing rate to identify foraging behaviour in individual tracks. Dark grey grid cells identified as locations in which foraging events were observed.*

Environmental data

Environmental data describing oceanographic conditions during the brood-guard period (late December – end January) of each tracking season (2009/10; 2011/12) were obtained via Earth Observation Remote Sensing (Fig. 5.3). Daily NASA Multi-Sensor Merged Ultra-High Resolution (MUR) Sea Surface Temperature (SST) imagery was downloaded via OpenDAP, and daily chlorophyll-*a* (chl-*a*) imagery was processed from MODIS-Aqua data; both were mapped to the study area in geographic projection at 1.2km resolution. Daily images were then used to generate monthly median SST and chl-*a* (log-scaling) composites. Bathymetric data were obtained for a matching spatial extent via the General Bathymetric Chart of the Oceans (GEBCO_08 grid; http://www/gebco.net; Fig. 5.3d), and used to derive depth at 30 arc-second resolution.

Thermal composite front maps (Miller 2009) were generated from MUR SST data, covering rolling 7-day time windows throughout the tracking period. Thermal fronts were detected in each MUR SST scene using Single-Image Edge Detection (SIED; Cayula & Cornillon 1992; front detection threshold = 0.4°C). Successive 7-day composites were then used to prepare monthly *front frequency* (*ffreq*) rasters, which quantify how frequently a front is detected in each pixel (~1.2km pixel size) over the time period of interest (here, late December – early January; 2009/10, 2011/12; Fig. 5.3c) as a ratio of the number of positive front detections to the number of cloud-free observations. A threshold of four detections in each pixel was used to exclude those pixels where fronts were rare during the study period. All environmental data layers were standardised at 0.5 degree resolution, to match that of the usage grid, through bilinear interpolation ('raster' package for R; Hijmans & van Etten 2012; Fig. 5.4).

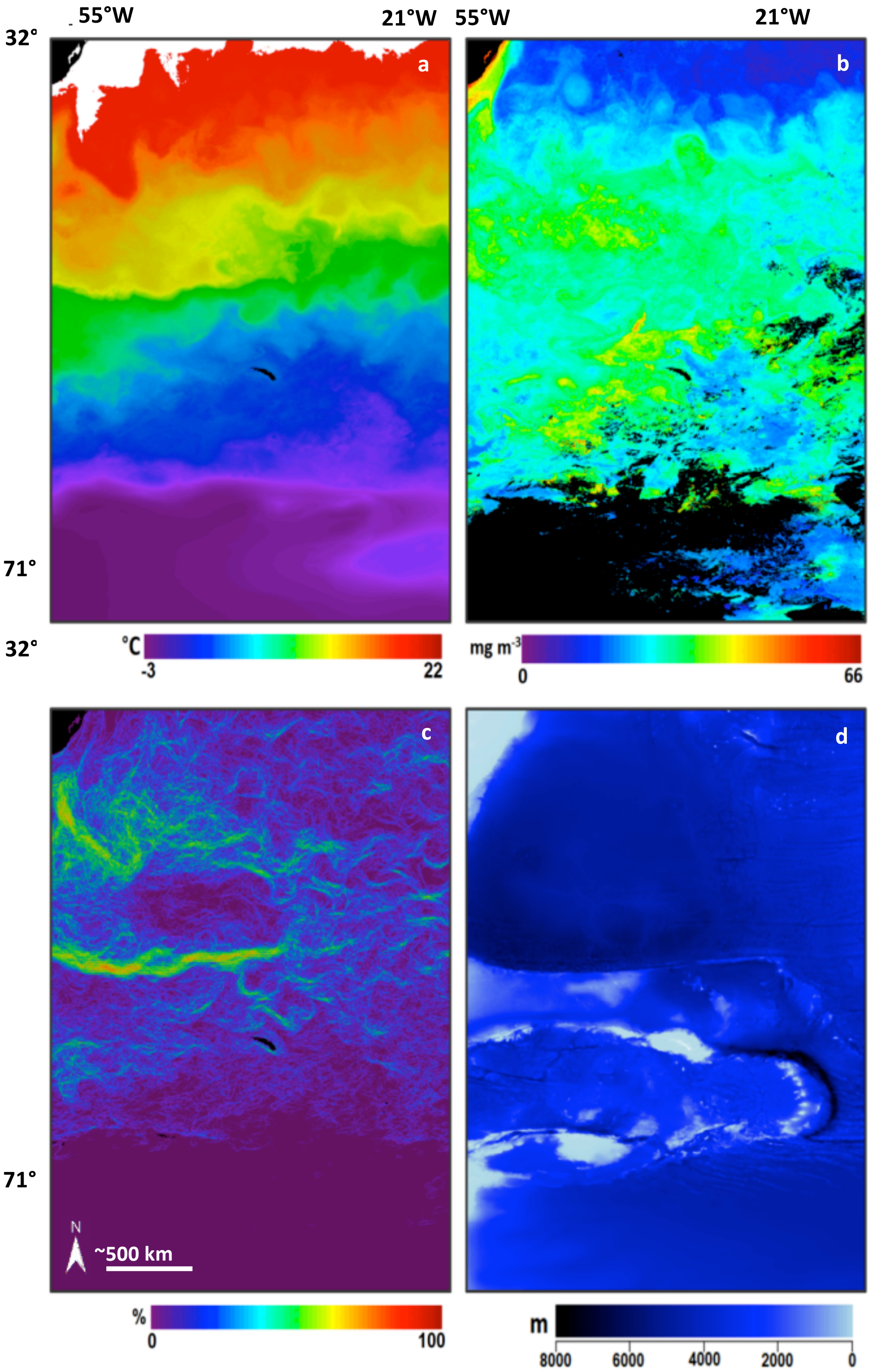

Figure 5.3 Environmental data layers for the study region, January 2010.*(a) Sea Surface Temperature (SST, °C; 1km resolution; monthly median composite), (b) Chlorophyll-a (chl-a, mg m*$^{-3}$*; 1km resolution; monthly median composite), (c) Front frequency (Ffreq, % time; 1km resolution; 0.4°C front detection threshold; monthly synoptic composite) (d) GEBCO Depth (30 arc-second resolution). SST scaling ranges from -3 to 22°C. Regions of higher SST (here, white) outside foraging range of birds, and removed from models.*

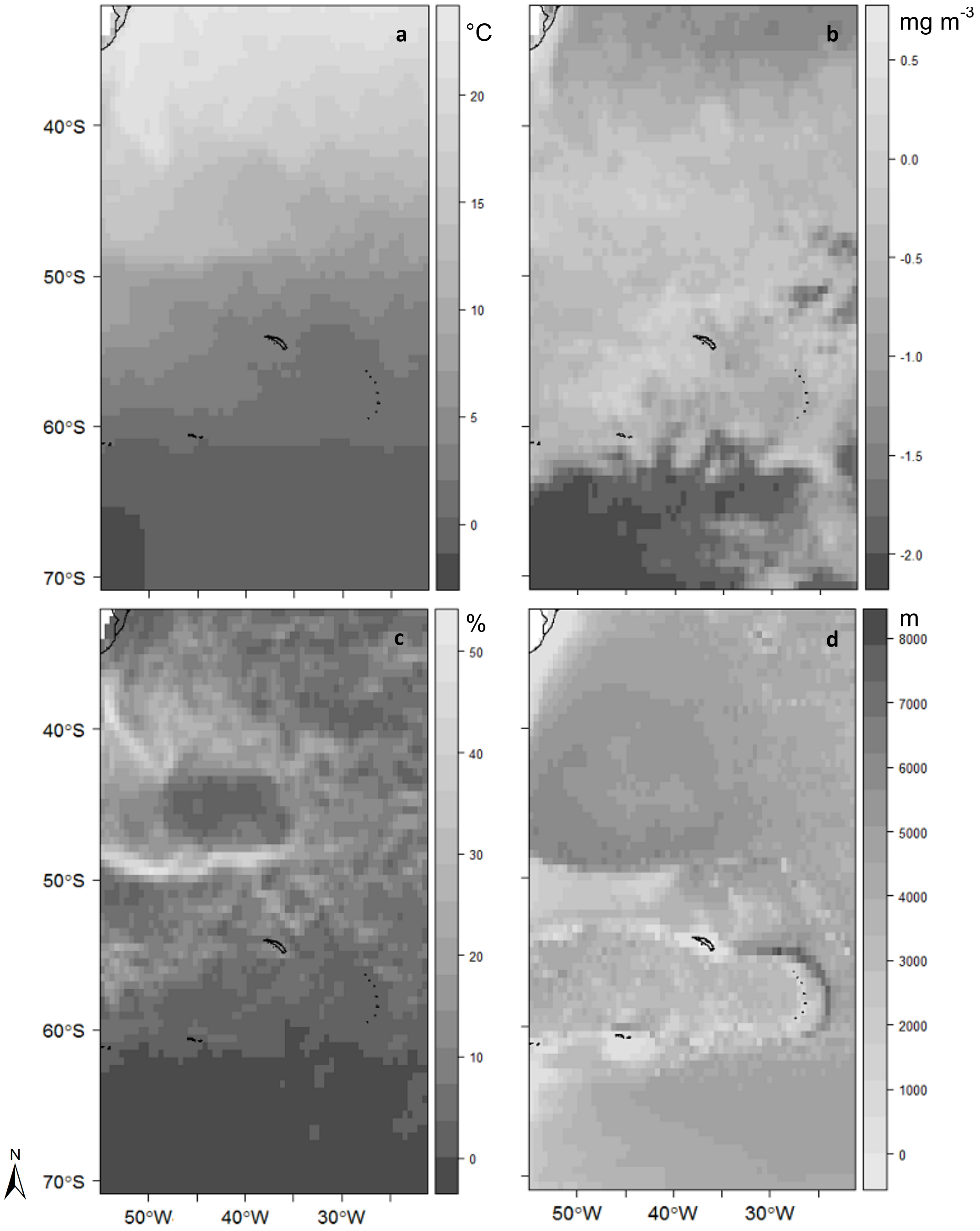

Figure 5.4 Environmental data layers used in ecological niche modelling, January 2010. *(a) Sea Surface Temperature (SST, °C; monthly median composite), (b) Chlorophyll-a (chl-a, mg m*$^{-3}$*; monthly median composite; log-transformed), (c) Front frequency (ffreq, % time; 0.4°C front detection threshold; monthly synoptic composite). (d) GEBCO Depth (30 arc-second resolution). All layers standardised at 0.5 degree spatial grid resolution through bilinear interpolation.*

Ensemble ecological niche modelling (EENM)

Previous work comparing the efficacy of different modelling algorithms for identifying and predicting habitat preferences in seabirds concluded that an ensemble modelling approach was preferable to the use of a single algorithm (Oppel *et al.* 2012). Ensemble ecological niche modelling was therefore used to determine the habitat preferences of grey-headed albatrosses by identifying the oceanographic conditions under which foraging behaviour was observed. Ecological niche models (ENMs) were fitted to the GHA tracking data from 2009/10 using the Generalised Additive Modelling (GAM), Maximum Entropy (MaxEnt), Random Forest (RF) and Boosted Regression Tree (BRT) algorithms within the biomod2 package for R (Thuiller, Georges & Engler 2014), and the efficacy tested using data from the 2011/12 season (see below).

The biomod2 modelling platform applies a use-availability framework to identify preferred environmental conditions. 'Presences' were defined as grid cells in which foraging behaviour was observed (usage= '1'). As grid cells in which no foraging events were observed cannot be accurately classified as true absences in this instance, pseudo-absences were iteratively resampled from within a radius of the colony that represents accessible habitat (1185km; see above). Five iterations of 1000 randomly-selected pseudo-absences were used over successive model runs, to avoid the introduction of spatial bias. Each model run used 10-fold cross-validation, with data randomly apportioned to a 75% / 25% split for model calibration and testing phases.

Parameterisations for model algorithms run within biomod2 were as follows:

- GAM: package = 'mgcv', family = 'binomial' (link = 'logit'),
  type = 's' (spline-based smooth);
- MaxEnt ,: maximum training iterations = 200,
  linear/quadratic/product/threshold/hinge features enabled,
  default prevalence = 0.5;

- Random Forest: number of trees = 500, node size = 5;
- Boosted Regression Trees: distribution = 'bernoulli', number of trees = 2500, shrinkage = 0.001, bag fraction = 0.5, train fraction = 1, cross-validation folds = 3.

Metrics used for model evaluation and comparison were the area under the Receiver Operating Characteristic (ROC) curve (AUC; Jiménez-Valverde 2012) and the True Skill Statistic (TSS; Allouche, Tsoar & Kadmon 2006). The mean of each of these metrics was derived over each model run per iteration of pseudo-absences, and then the mean-of-means was used to rank model performance (Table 5.1).

Relative importance of each environmental variable was determined using the built-in method in biomod2, which overcomes difficulties associated with comparing different model-specific outcomes through the use of a randomisation procedure (Thuiller *et al.* 2009). This procedure fits a Pearson correlation between the fitted values and predictions, where each variable has been randomly permutated. If the two predictions are similar, i.e., the correlation is high, the variable is considered of little importance to the model. This procedure was repeated 10 times for each variable within each individual model run. The overall relative importance of each environmental variable (Relative Importance of the Contribution to the model Coefficients, RICC) is then scaled by subtracting the resultant mean correlation coefficient from 1. The overall explanatory power of the environmental variables within different modelling frameworks was derived using the mean-of-means of standardised variable importance over all model iterations per algorithm (Table 5.2).

An ensemble model was then generated, combining predictions from the individual GAM, MaxEnt, RF and BRT model runs. Only those models with a True Skill Statistic equal to or greater than 0.7 were included, to avoid the inclusion of poorly-performing models. The ensemble projection was created using a weighted average across all models, accounting for differences in algorithm performance. Ensemble model projections were based on a habitat suitability index (HSI), scaled between 0 and 1, where 1 represents greatest suitability.

The resultant ensemble ecological niche model underwent a three-fold evaluation process, using the TSS and AUC metrics to rank performance. First, the evaluation metrics were obtained for the model fitted to the training data set. Secondly, ensemble model predictions were compared to observed habitat use over the full dataset from the 2009/10 breeding season. Thirdly, ensemble model projections for 2011/12 were quantitatively compared to the observed distribution of foraging events. Model predictions were also projected onto the 2011/12 combined environmental data surface for visual comparison with observed habitat use.

5.3 Results

Foraging trip metrics

GPS data from the 55 birds tracked showed that maximum displacement of each bird from the colony ranged between 153km and 1185km, with a mean ± SD of 744 ± 249km. Foraging trip duration ranged between 0.6 and 6.1 days, with a mean of 2.9 ± 1.3 days. Some birds exhibited extensive looping movements, characterised by multiple immersion events within both linear and tortuous track sections (Fig. 5.5a). Others exhibited more directed commuting movements, with immersion events clustered within tortuous track sections, usually at the distal point (Fig. 5.5b). Foraging trips were not classified into these modes, but visual inspection of plotted tracks revealed a range of looping and commuting types of behaviour.

Behavioural classification

All trips involved at least one foraging event (based on landing rate), with a mean of 6.1 ± 3.7 foraging events per trip (range 2 – 17). Foraging events were observed both in areas of high track tortuosity, and within linear track sections. Results of behavioural classification using landing rate, and that using residence time, were comparable. Clear instances of area restricted search (ARS) behaviour were highlighted using both methods. However, visual inspection of plotted tracks indicates that landing rate identified a greater proportion of linear track sections in which a prey capture attempt was likely to have taken place, which were not apparent using residence time (Fig. 5.1). Empirical evidence from previous work on this population very clearly shows that birds catch prey in very rapid directed flight, with no sign of ARS behaviour (Catry *et al.* 2004).

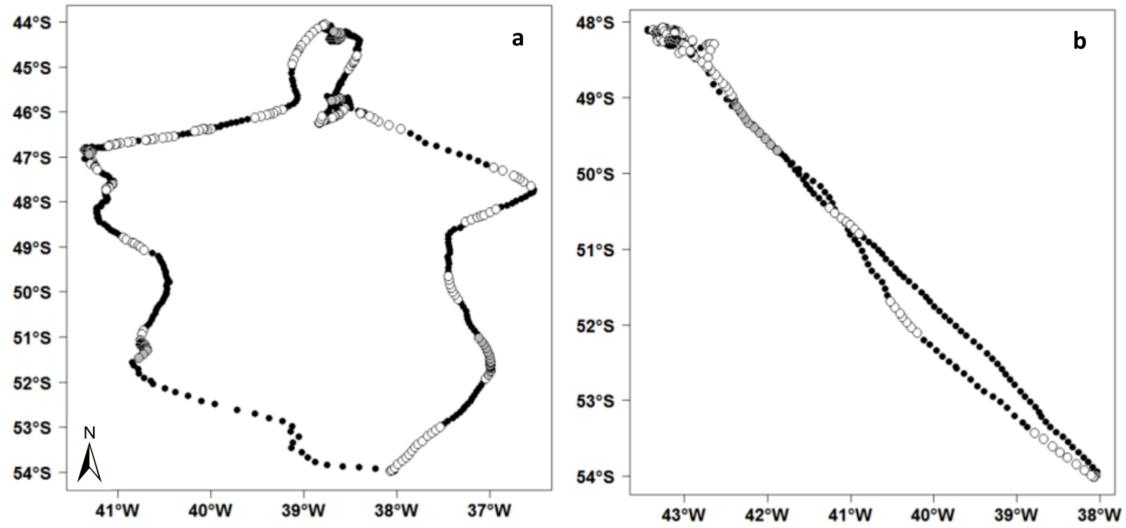

Figure 5.5 Foraging trip characteristics. *(a) Example of an extensive, looping trajectory. (b) Example of a directed commuting trajectory. Black circles denote transit locations; white circles denote foraging events (based on landing rate); grey circles are locations during darkness.*

Habitat modelling

Evaluation metrics indicated that all model algorithms performed well (Table 5.1). Differences in mean AUC and TSS metrics over all model runs per algorithm were small. However, habitat suitability predictions varied markedly in terms of spatial extent (Fig. 5.6). The Random Forest algorithm was identified as the best performing model by both evaluation metrics (mean of means AUC 0.948, TSS 0.804), and resulted in the most spatially conservative habitat suitability predictions (Fig. 5.6). Aside from the identification of RF as the best performing model by both metrics, ranking of model performance by AUC and TSS differed for other algorithms (AUC ranking: RF, BRT, MaxEnt, GAM; TSS ranking: RF, GAM, BRT, MaxEnt; Table 5.1).

Sea surface temperature and chl-*a* concentration were identified as the most important contributory environmental variables by all of the modelling algorithms (Table 5.2). Concordance in variable importance between modelling algorithms was high, with RF, BRT and GAM models ranking environmental variables in the same order (SST, chl-*a*, depth, *ffreq*; Table 5.2). MaxEnt differed in that *ffreq* had a higher mean RICC score (0.107) than depth (0.042).

Ensemble ecological niche model

Combining all models for each algorithm into an EENM identified suitable foraging conditions (i.e. those in which foraging events were recorded) in neritic (<500m depth), shelf-break and oceanic regions (Fig. 5.7), reflecting observed habitat use from the GHA tracks recorded in both the 2009/10 (Fig. 5.2) and 2011/12 (Fig. 5.8a) breeding seasons. The EENM identified SST and chl-*a* as the most important environmental covariates governing the locations of foraging events (Table 5.2). Suitable foraging habitats (HSI > 0.25) were associated with particular SST ranges (3-8°C, 12-13°C) and more productive regions (chl-*a* >0.5 mg m^{-3}) of the area accessible to foraging birds. Although *Ffreq* values over the study area were generally low (Fig. 5.3c), regions in which fronts manifested frequently over the study period, such as the APFZ, were consistently identifed as suitable foraging habitats (Fig. 5.6, Fig. 5.7). All grid cells in which *Ffreq* values were greater than 5% were identified as suitable for foraging (HSI > 0.25).

Based on the whole-dataset maximum displacement from the colony, the total area of accessible habitat during the brood-guard period was 4,411,503km^2. By comparison, the total area of suitable foraging habitat predicted by the EENM (HSI > 0.5) was c. 1,055,820km^2 (24% of the accessible area). Based on a more conservative threshold (HSI > 0.75), there was c. 335,323km^2 of suitable foraging habitat (8% of total accessible area). The projections of the EENM onto environmental conditions in the 2011/12 brood-guard period indicated comparable levels of suitable habitat within the total accessible area (HSI > 0.5, approx. 933,837km^2, 21% total accessible area; HSI > 0.75, approx. 412,054km^2, 9% total accessible area), although the spatial extent of these suitable foraging areas differed considerably between years (Figs. 5.7, 5.8b) as a result of annual variability in oceanographic conditions.

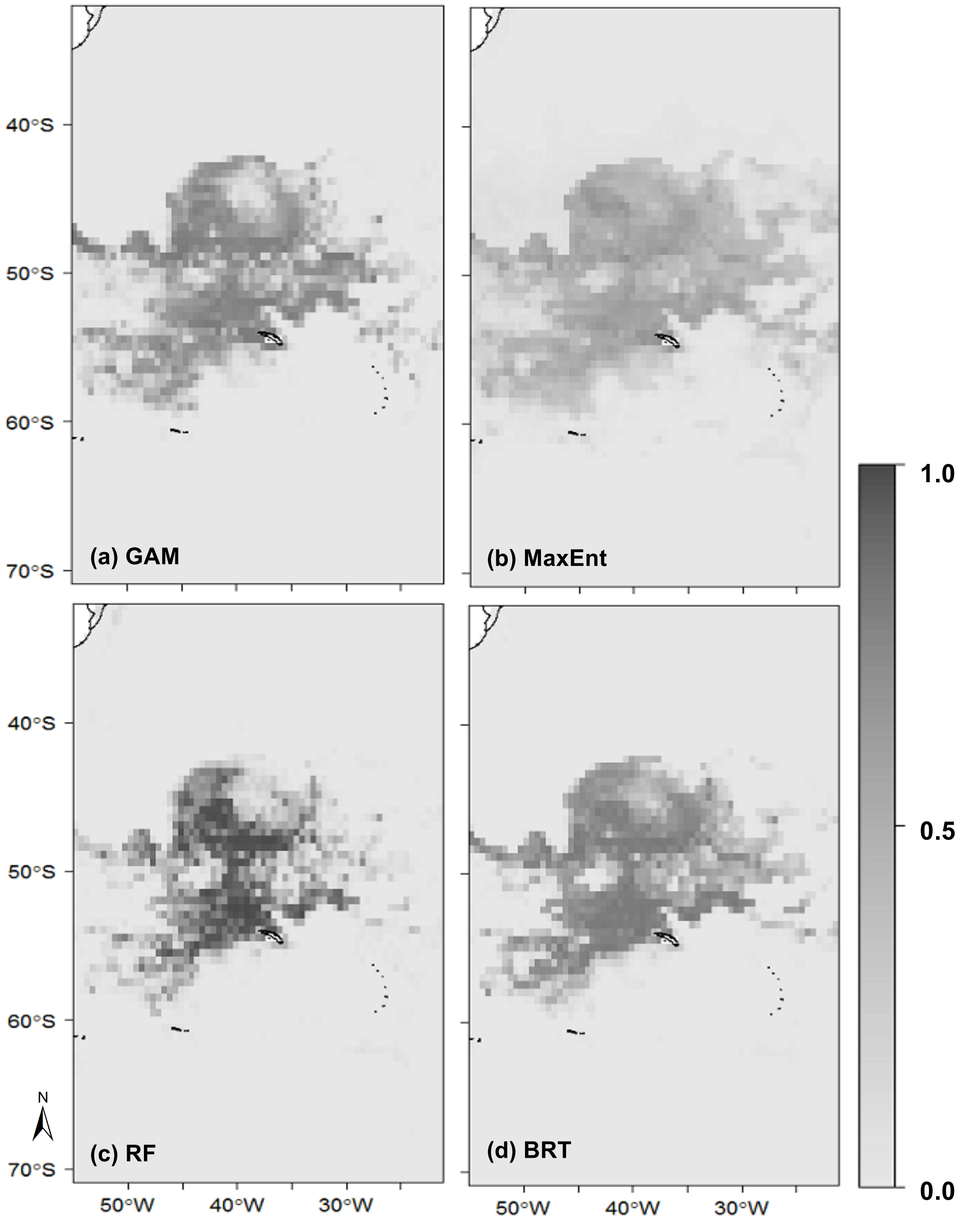

Figure 5.6 Ecological niche models (a, Generalised Additive Model, GAM; b, Maximum Entropy, MaxEnt; c, Random Forest, RF; d, Boosted Regression Trees, BRT). *Mean habitat suitability predictions for each modelling algorithm. Habitat Suitability Index (HSI) of each 0.5 degree grid cell of the study area, derived through projection of the overall model using each algorithm on the combined environmental data surface for the 2009/10 brood-guard period.*

Table 5.1 Ecological niche modelling. *Evaluation metrics (Area Under Receiver Operating Curve, AUC; True Skill Statistic, TSS). Mean over model runs (10-fold cross-validation) per pseudo-absence iteration, for each model algorithm (Generalised Additive Models, GAM; Maximum Entropy modelling, MaxEnt; Random Forest, RF; Boosted Regression Trees, BRT).*

Pseudo-Absence Iteration	**Evaluation Metric**	**Model Algorithm** (mean over 10 runs per Pseudo-Absence iteration)			
		GAM	**MaxEnt**	**RF**	**BRT**
1	**AUC**	0.9347	0.9338	0.9487	0.9359
	TSS	0.7761	0.7519	0.7898	0.7718
2	**AUC**	0.9438	0.9438	0.9491	0.9428
	TSS	0.8065	0.7759	0.8029	0.7828
3	**AUC**	0.9278	0.9327	0.9447	0.9376
	TSS	0.7871	0.7834	0.8119	0.7869
4	**AUC**	0.9413	0.9420	0.9541	0.9440
	TSS	0.8183	0.7855	0.8131	0.7978
5	**AUC**	0.9268	0.9380	0.9417	0.9344
	TSS	0.7922	0.7746	0.8005	0.7779
mean of means	**AUC**	0.9349	0.9381	0.9477	0.9390
	TSS	0.7960	0.7743	0.8036	0.7834

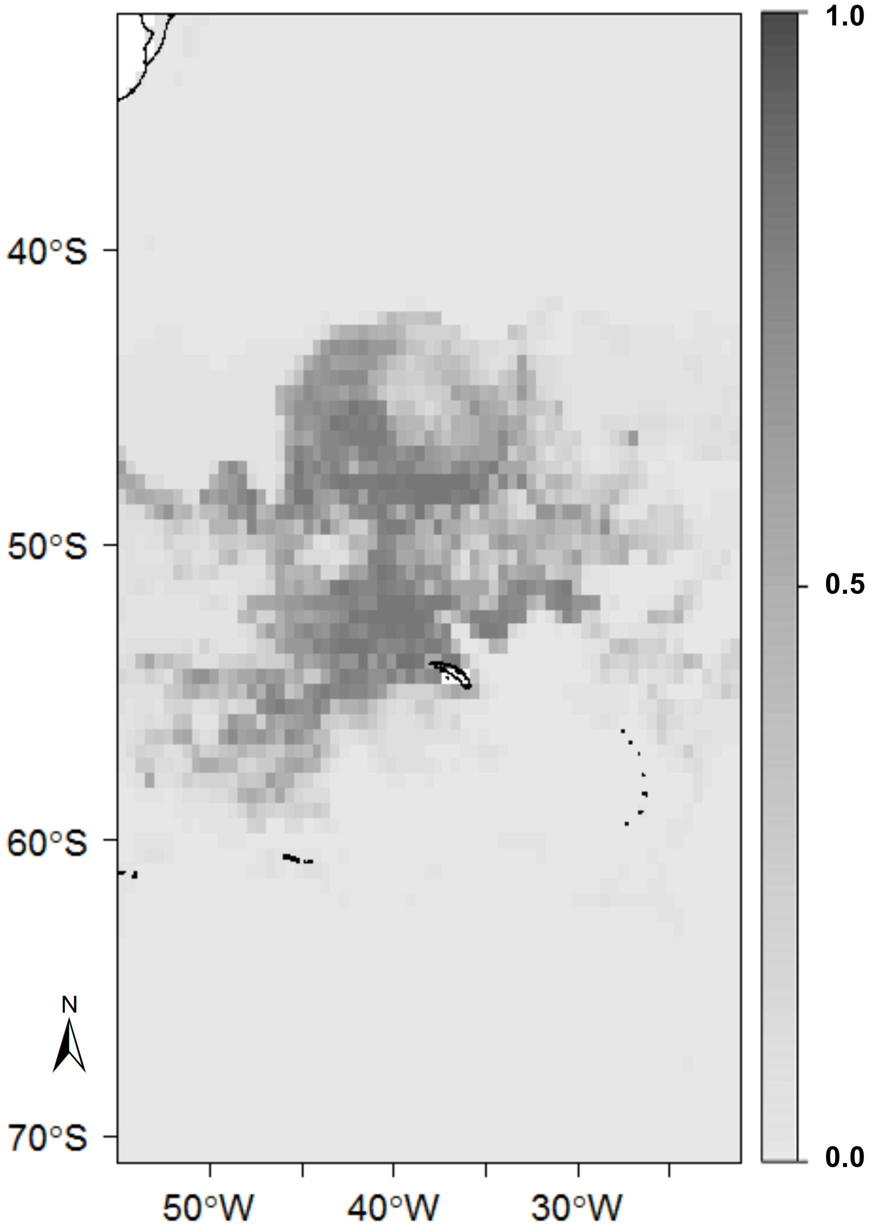

***Figure 5.7 Ensemble ecological niche model predictions** (weighted mean), highlighting suitable foraging habitat in the 2009/10 brood-guard period. Habitat Suitability Index (HSI) of each 0.5 degree grid cell of the study area surrounding South Georgia, as identified by the projection of the ensemble model on to the combined environmental data surface for January 2010.*

Table 5.2 Ecological niche modelling. Variable Importance (standardised according to the Relative Importance of the Contribution to the Model Coefficients, RICC). *Mean importance of each environmental variable (Sea Surface Temperature, SST; Chlorophyll-a, chl-a; thermal front frequency, Tfreq; depth) over model runs (10-fold cross-validation) per pseudo-absence iteration, for each model algorithm (Generalised Additive Models, GAM; Maximum Entropy modelling, MaxEnt; Random Forest, RF; Boosted Regression Trees, BRT).*

Pseudo-Absence Iteration	**Model Algorithm**	**Variable Importance** (mean over 10 runs per pseudo-absence iteration)			
		SST	**Chl-*a***	**TFreq**	**Depth**
1	**GAM**	0.5818	0.4241	0.1167	0.2587
	MaxEnt	0.4416	0.3993	0.1201	0.0435
	RF	0.5495	0.4779	0.1268	0.2901
	BRT	0.5939	0.5097	0.0365	0.1320
2	**GAM**	0.6248	0.4361	0.1116	0.2190
	MaxEnt	0.4932	0.4001	0.0927	0.0448
	RF	0.4893	0.4886	0.1398	0.2607
	BRT	0.6036	0.5075	0.0509	0.0902
3	**GAM**	0.6258	0.3981	0.0820	0.1929
	MaxEnt	0.5109	0.3412	0.1217	0.0371
	RF	0.5225	0.4689	0.1493	0.2563
	BRT	0.6189	0.4933	0.0582	0.0857
4	**GAM**	0.6422	0.4240	0.0245	0.2960
	MaxEnt	0.4984	0.3624	0.1202	0.0408
	RF	0.4850	0.4964	0.1067	0.3113
	BRT	0.6093	0.5052	0.0171	0.1079
5	**GAM**	0.5905	0.4315	0.0741	0.2213
	MaxEnt	0.4791	0.3972	0.0800	0.0439
	RF	0.4866	0.4833	0.1102	0.3040
	BRT	0.5776	0.5029	0.0435	0.1200
mean of means	**GAM**	0.6130	0.4228	0.0818	0.2376
	MaxEnt	0.4846	0.3800	0.1070	0.0420
	RF	0.5066	0.4830	0.1266	0.2845
	BRT	0.6007	0.5037	0.0412	0.1072

Given the differences in performance of the modelling algorithms, the weighted mean EENM (wEENM) was preferred, although little difference in evaluation metrics was observed between the wEENM and the regular mean EENM (Table 5.3). Evaluation of wEENM performance showed good predictive capability for both the test and full datasets for the 2009/10 brood-guard period (Table 5.3). The wEENM, fitted using 2009/10 data exclusively, did not perform as well when evaluated against observed habitat use in the 2011/12 breeding season (AUC = 0.884, TSS = 0.578), although some spatial concordance was identifiable between model projections for January 2012 and observed space use during the same time period (Fig. 5.8).

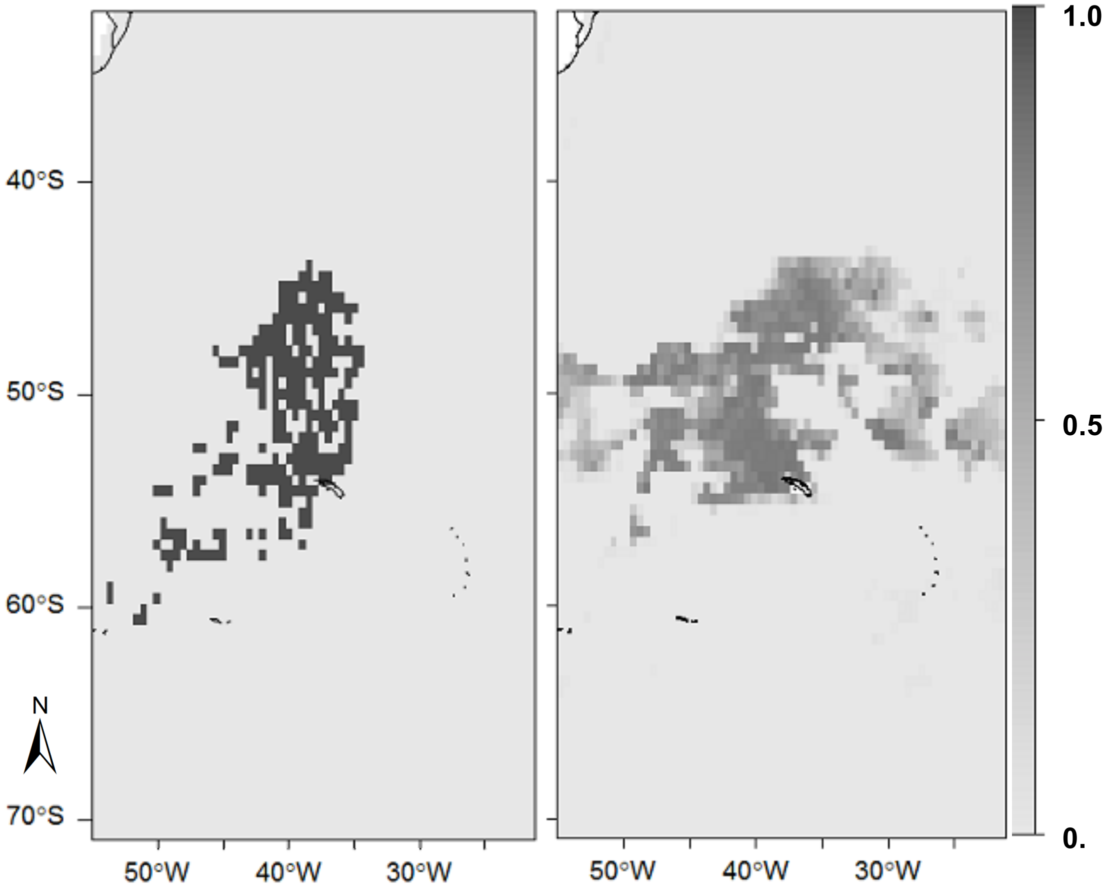

Figure 5.8 Comparing foraging habitat preference in 2011/12 brood-guard period to that predicted by ensemble ecological niche modelling. *(a) Regular grid (0.5 degree resolution) showing spatial distribution of foraging events in the 2011/12 brood-guard period, derived using landing rate to identify individual foraging events. Dark grey grid cells identified as locations in which foraging events were observed. (b) Ensemble ecological niche model predictions (weighted mean), highlighting suitable foraging habitat in the 2011/12 brood-guard period. Habitat Suitability Index (HSI) of each 0.5 degree grid cell of the study area, as identified by the projection of the ensemble model on to the combined environmental data surface for January 2012.*

Table 5.3 Ensemble Ecological Niche Models. *Evaluation metrics (Area Under Receiver Operating Curve, AUC; True Skill Statistic, TSS). Mean over model runs (10-fold cross-validation) per pseudo-absence iteration, for each model algorithm (Generalised Additive Models, GAM; Maximum Entropy modelling, MaxEnt; Random Forest, RF; Boosted Regression Trees, BRT).*

Evaluation dataset	**Ensemble model**	**Evaluation Metric**	
		TSS	**ROC**
Testing data	Weighted Mean	0.849	0.974
Testing data	Mean	0.849	0.974
Full 2010	Weighted Mean	0.748	0.920
Full 2010	Mean	0.748	0.920
Full 2012	Weighted Mean	0.578	0.884
Full 2012	Mean	0.578	0.884

5.4 Discussion

Habitat Selection

Ensemble ecological niche modelling highlighted sea surface temperature (SST) and chl-*a* concentration as determinants of foraging habitat suitability for grey-headed albatrosses (GHA) from South Georgia. Habitat selection was also related to water depth and the frequency of mesoscale thermal front manifestation (*ffreq*), although the relative contributions of these environmental parameters were smaller. Model predictions identified neritic (<500m), shelf-edge and oceanic waters to the north and west of South Georgia, including the Antarctic Polar Frontal Zone (APFZ), as suitable foraging habitats.

GHA are known to feed predominantly on ommastrephid squid (e.g. *Martialia hyadesi*), crustaceans (e.g. Antarctic krill *Euphasia superba*) and, less commonly, lamprey *Geotria australis*, mesopelagic fish and gelatinous zooplankton (Rodhouse *et al.* 1990; Reid, Croxall & Prince 1996; Xavier *et al.* 2003; Catry *et al.* 2004). Although the diet of tracked birds was not determined, their distribution was broadly comparable with previous years when all these types of prey were recorded (Xavier *et al.* 2003; Catry *et al.* 2004). This indicates that the environmental conditions identified through this modelling procedure reflect the key habitats and main prey that are targeted by this population of GHA, which represent c. 50% of the global breeding population (ACAP 2009).

SST is a proxy for the spatial structuring of the Southern Ocean, as distinct classes of predator exploit prey types that associate with particular temperature ranges (Commins, Ansorge & Ryan 2014). Indeed, major fronts in the region act as biogeographical boundaries, and can mechanically entrain and aggregate prey items (Graham, Pages & Hamner 2001; Genin *et al.* 2005; Rodhouse & Boyle 2010). The contribution of SST to the EENM indicates that birds may have targeted prey species that associate with particular water masses. Narrow SST contours and high *ffreq* values highlight the APFZ, which was identified by the EENM as a region of above-average habitat suitability. Plunge-diving grey-headed albatrosses have been observed in association with large aggregations of *M. hyadesi* at the surface within the APFZ (Rodhouse & Boyle 2010). It is therefore likely that tracked birds foraging at the APFZ were targeting ommastrephid squid. The APFZ lies near the northernmost extreme of the observed foraging range during brood-guard for this population, which might suggest that reproductive constraints influenced the strength of the association with this feature. Further investigation of the use of the APFZ, and of the suite of environmental conditions targeted by foraging birds during other breeding stages (incubation and chick-rearing), and in the non-breeding period, is necessary to assess the full significance of this feature for this population.

Chlorophyll-*a* concentration was also identified as a predictor of the spatial distribution of foraging events. Overall, foraging activity was more likely in productive regions within the accessible area. Surface chl-*a* concentrations were found to be highest on-shelf, with peak values recorded to the south-west of the study colony. The APFZ was not characterised by elevated productivity over the period investigated in this model. Birds foraging in more productive shelf waters around South Georgia are more likely to be targeting Antarctic krill and icefish *Champsocephalus gunnari*, which are more closely tied to bottom-up forcing mechanisms than the squid and mesopelagic fish found in the APFZ (Wakefield, Phillips & Belchier 2012).

The identification of both neritic and oceanic regions as suitable habitats could be explained by specialisation in foraging strategies at the individual level. Although there has been no direct test of individual specialisation in grey-headed albatrosses, non-breeding adults tend to use the same regions in consecutive years, indicating some consistency in habitat preferences (Croxall *et al.* 2005), and there is increasing evidence for individual foraging specialisation in other species of albatross (Ceia *et al.* 2012; Granadeiro, Brickle & Catry 2014; Patrick *et al.* 2014). In addition, there is some evidence from previous tracking and stable isotope studies that female GHA tend to feed further north than males at certain times of year (Phillips *et al.* 2004b; Phillips *et al.* 2011). Foraging at the APFZ seemed to be associated most frequently with trips that involved direct commuting movements to and from the colony. Foraging events identified during looping movements may be indicative of an opportunistic foraging strategy, with birds targeting prey items such as krill that are patchily distributed in waters close to the colony. Foraging in nearby neritic habitats could therefore be a less risky strategy for birds that are constrained to return to a small chick. The influence of individual specialisation, and indeed of sexual segregation, on habitat preferences of grey-headed albatrosses, and interactions between these intrinsic drivers and environmental determinants of foraging ecology, warrant further investigation.

The spatial distribution of foraging events, and the resulting influence on diet and intake rates, have been linked in a number of species with variation in breeding success between years of contrasting oceanographic conditions (Peck *et al.* 2004; Pinaud, Cherel & Weimerskirch 2005; Scott *et al.* 2006; Garthe, Montevecchi & Davoren 2011). Years in which grey-headed albatrosses at South Georgia have experienced poor breeding success (e.g. 1999-2000, only ~17% chicks fledged) have been linked to abnormally warm SST in the adjacent shelf. The resultant lack of food was evident from a mid-season switch from a diet dominated by cephalopods, to one of Antarctic krill (Xavier *et al.* 2013), indicating foraging plasticity. Differences in the spatial distribution of foraging effort have also been observed between years of good and poor conditions, with low availability of cephalopods at the APFZ forcing more birds to target krill aggregations around the South Shetland Islands and Antarctic Peninsula (Xavier *et al.* 2003). Although oceanographic conditions varied between the two breeding seasons in our study, we can assume that in neither case were these conditions strikingly different from the average, given the overall distribution broadly mirrored that for the same breeding stage in previous years (Phillips *et al.* 2004b). For this reason, it is likely that the same broad-scale habitat preferences identified in our models reflect the key oceanographic drivers of prey availability in other years, and are fundamental for successful breeding in this population.

Behavioural classification

The combined use of GPS and immersion loggers has here enabled behavioural classification of movements into *foraging* and *transit* modes, using landing rate. While there is good empirical support for the use of immersion events to define at-sea behaviours of albatrosses, for which take-off is energetically expensive (Weimerskirch *et al.* 2000), and evidence that immersions during daylight are associated with prey capture events (Catry *et al.* 2004), the choice of method for behavioural classification is an important consideration (Wakefield, Phillips & Matthiopoulos 2009; Louzao *et al.* 2011). Behavioural classifications using landing rate were comparable with those based on residence time, although landing rate provided a much better means of identifying foraging events in linear track sections. Concurrent use of stomach temperature loggers (Catry *et al.* 2004; Louzao *et al.* 2011) could have refined behavioural classifications, but this technique is more invasive than external tag attachment, limiting sample size. Stomach temperature loggers would also facilitate an investigation of whether sit-and-wait foraging during darkness (Catry *et al.* 2004) is associated with fronts, which would be an interesting question for future work.

Ensemble Ecological Niche Modelling

EENMs can incorporate differing predictions from models fitted using alternative algorithms. By better incorporating uncertainty, EENMs therefore provide a more robust basis for recommendations relating to the conservation and management of mobile species (Marmion *et al.* 2009; Oppel *et al.* 2012). However, there are several pertinent considerations inherent in creating an EENM. The choice of environmental data layers, selection and parameterisation of modelling algorithms, and approach to model validation and evaluation can have a marked effect on predictive capacity, and so should be considered explicitly during model creation.

Choice of environmental data layers

The selection of environmental data for model training and evaluation is critical to the performance of habitat models (Guisan & Zimmerman 2000; Hirzel *et al.* 2006), including those resulting from an ensemble approach. Given the vast at-sea ranges of albatrosses, Earth Observation Remote Sensing (RS) is presently the only technique available for obtaining environmental data that can be matched spatially and temporally to the movements of known individuals. The remotely-sensed environmental data layers used here were selected on the basis of availability, spatial coverage and previously demonstrated influence on habitat selection by GHA and other species in the region (Xavier *et al.* 2003; Phillips *et al.* 2006; Wakefield *et al.* 2011; Ballard *et al.* 2012; Scheffer, Bost & Trathan 2012).

EENMs for wide-ranging marine vertebrates can only be accurate where they incorporate the dynamic nature of pelagic environments, and so can be optimised by including both static and dynamic habitat variables (e.g. Louzao *et al.* 2011; Bombosch *et al.* 2014). Both static (i.e. bathymetry) and dynamic variables (i.e. SST, chl-*a*, *Tfreq*) were significant predictors of GHA foraging events. In previous studies in the region, the spatial extent of the APFZ has been estimated using historical or averaged data, which did not match the temporal resolution of animal tracking data. For example, Xavier *et al.* (2003) used the position of the Polar Front

(PF) derived from survey data in 1997 to investigate habitat preference of birds tracked in 2000. However, the APFZ is a highly dynamic feature, characterised by intense mesoscale variability, and the PF can vary in position by as much as 100km in 10 days (Trathan, Brandon & Murphy 1997). The path of a front in a temporally-averaged SST composite belies the dynamic nature of these features. The front frequency index *ffreq*, used here for the first time in the Southern Ocean, is an objective, synoptic product that can account for this mesoscale variability. It can be matched temporally and spatially to the movements of tracked individuals, providing valuable information on processes that influence prey abundance or accessibility, and therefore has potential for wide application to other species.

Spatial resolution and temporal coverage of environmental data layers used are pivotal considerations. Matching the spatial resolution of RS data with the scales over which animals search for prey remains a major challenge in habitat modelling (Storch 2002; Luoto, Virkkala & Heikkinen 2007), particularly in the marine realm (Araújo & Guisan 2006; Hirzel *et al.* 2006). In our study, environmental data layers were interpolated to a standard 0.5 degree grid resolution, which was appropriate given the extent of the area used by the tracked birds. Too fine a resolution can underestimate the influence of ambient conditions on behaviour by assigning a single pixel value to tracking locations, and too coarse a resolution can mask mesoscale dynamics. In addition, temporal averaging can obscure responses to contemporaneous environmental conditions, yet it is also necessary to avoid too fine a timescale, as prey aggregations develop over periods of days to weeks. Here, we have restricted temporal averaging to one month, which matches the duration of the brood-guard period at this location.

Further limitations of RS data might also have influenced model predictions. First, cloud cover can be extensive over the Southern Ocean, limiting satellite coverage. Here, we use a merged infra-red and microwave SST product– where cloud prevents infra-red detection, microwave data are interpolated to cover the missing area. Although this can lead to some differences in detail between regions, it prevents complete data loss. Second, RS data detect surface parameters only, providing little information on processes occurring at depth. This can be problematic if RS data are used to investigate habitat preference of diving predators (Bradshaw *et al.* 2004a). However, water column processes often manifest as surface variability, particularly in the formation and propagation of fronts and eddies (Owen 1981). Moreover, GHA are known to capture prey predominantly by surface-seizing, seldom diving deeper than 2-3 m (Huin & Prince 1997). Prey aggregation near the surface is likely to be driven by mechanical processes occurring around fronts (Graham, Pages & Hamner 2001; Genin *et al.* 2005; Rodhouse & Boyle 2010). The use of RS imagery is therefore deemed appropriate for this application.

Choice of modelling algorithms

Both the performance and predictions of ENMs depend on the algorithm used, and different methods can generate contrasting results (Guisan & Zimmerman 2000; Thibaud *et al.* 2014). Choosing a set of algorithms to fit an EENM is, therefore, central to its predictive capability. Here, several widely used algorithms were combined to produce a single ensemble model. GAM, a regression-based technique, is often used to fit nonlinear responses to environmental conditions (Wakefield, Phillips & Matthiopoulos 2009). Of the three machine learning techniques used here, MaxEnt has proven the most popular to date (Merow, Smith & Silander 2013), undergoing widespread use for marine vertebrate habitat modelling (Friedlaender *et al.* 2006; Arcos *et al.* 2012; Ballard *et al.* 2012; McKinney *et al.* 2012; Bombosch *et al.* 2014). A major advantage of MaxEnt is that it can fit complex models using presence-only data (Elith *et al.* 2011). RF and BRT, both machine learning techniques based on classification trees, can fit complex models using large datasets and often result in more conservative predictions than MaxEnt; these are used increasingly for modelling complex species-environment relationships (Olden, Lawler & Poff 2008). Although all four algorithms performed well in our study, evaluation metrics indicated that the models fitted using machine learning, particularly RF, were the most effective. Finally, the choice of method for building a consensus among models fitted using different algorithms for an EENM is important (Marmion *et al.* 2009).

Approach to model validation and evaluation

Differences in rankings of algorithm performance, and of the importance of each variable suggest that the approach to model evaluation is also central to ensuring accuracy. Previous work suggests that the AUC statistic can be misleading with binary presence-absence input data (Lobo, Jiménez-Valverde & Real 2008). TSS is robust and independent of sample size, unlike the commonly used *kappa* statistic (Allouche, Tsoar & Kadmon 2006), so may be preferable in this context. The use of multiple metrics is clearly preferable to any single metric, allowing for an overall judgement regardless of discrepancies between measures (Allouche, Tsoar & Kadmon 2006; Jiménez-Valverde 2012; Thibaud *et al.* 2014).

Here, iterative 10-fold cross-validation with a 75%/25% data split was used for model validation, training models on a randomly apportioned subset of data and validating outputs against the remainder. While this is effective at validating each model run over the same time period and spatial extent over which the training model was fitted, ENMs can have limited transferability across space and time (Randin *et al.* 2006; Torres *et al. In Press*). Here, projections of the model developed from data collected in 2009/10 onto conditions in 2011/12 highlighted some suitable habitat in similar regions to those used by foraging GHA tracked in the latter period, but also identified areas that were not utilised. TSS and AUC scores indicate relatively poor transferability between these years of contrasting conditions. Slight differences in the importance assigned to particular environmental variables can have notable effects on model predictions, which has considerable implications for forecasting. Future work should investigate the degree of annual variability in preferred foraging regions and relate these differences to prevailing oceanographic conditions before any firm conclusions can be made regarding population-level habitat preference.

Implications for management and conservation

The GHA population at South Georgia, which is the largest worldwide, has undergone substantial decline in recent decades, the reasons for which are uncertain (Poncet *et al.* 2006). GHA are extremely long-lived, defer first breeding for many years after fledging, and have low fecundity, such that most individuals breed biennially at best (Ryan *et al.* 2007). These aspects of life history make the species especially vulnerable to fisheries mortality. In addition, there is evidence that sympatric species that are also dependent on Antarctic krill have been impacted by the effects of climatic change in the region (Reid & Croxall 2001). An improved understanding of the interactions between oceanographic conditions, habitat preference and spatially-explicit anthropogenic threat is an important goal for future work, and an essential step in designing ecosystem-level management strategies for GHA and other species in the region.

5.5 Conclusions

Ensemble ecological niche modelling identified preferred foraging conditions for adult grey-headed albatrosses. Foraging effort over the brood-guard period extended over neritic, shelf-break and oceanic waters. Foraging habitat preference appeared to be most closely associated with particular SST and chl-*a* regimes. Tracked birds displayed both directed, commuting movements from the colony at Bird Island, South Georgia to the Antarctic Polar Frontal Zone (APFZ), and more opportunistic, looping movements, which may reflect variability in individual foraging strategies. The APFZ was an important feature for this population during brood-guard, and is likely to be even more significant during other breeding stages, when birds are less constrained.

Using an ensemble technique incorporates uncertainties resulting from differences in model algorithms, and therefore has broad utility in modelling complex interactions between wide-ranging marine vertebrates and pelagic environments (Oppel *et al.* 2012; Pikesley *et al.* 2013). However, the technique requires care, as building an appropriate model depends on the choice of environmental data, modelling algorithms, and the approach to model validation and evaluation. Moreover, models may have limited transferability across space and time (Randin *et al.* 2006; Torres *et al. In Press*).

In combination with oceanographic modelling, techniques presented here have scope for forecasting the locations of suitable at-sea habitats as the oceans change. However, further investigation of ontogenetic changes in habitat preference, at other stages in the breeding cycle, under contrasting oceanographic conditions, and between individuals and populations is necessary before accurate species-level predictions are possible. Nonetheless, ecological niche modelling provides insights of value, both for understanding the spatial ecology of these wide-ranging marine vertebrates, and in informing threat mitigation for species of conservation concern.

Chapter VI

General Discussion

Understanding habitat selection by marine predators requires datasets describing the distributions, movements and behaviours of animals, oceanographic data describing the dynamic physical environments that they inhabit, and analytical solutions that can link these data. Previous chapters have demonstrated several progressive methods for linking animal movements to environmental conditions in dynamic systems, providing original reference material for others seeking to enumerate the influence of the physical environment on habitat selection.

This chapter examines how the studies presented in this thesis extend current understanding, drawing the findings of previous chapters together into a critique of methodological and analytical approaches. The following sections revisit the aims of this thesis; discuss key considerations and limitations of techniques used; consider questions raised, data gaps and areas for further research; and summarise the main contributions of this thesis to current understanding of oceanographic influences on habitat selection by marine predators. The final section discusses wider implications of this research and makes recommendations pertinent to the conservation of predator populations and the management of anthropogenic activities in the oceans.

Main findings: oceanographic fronts and marine predator habitat selection

The main findings of studies presented in this thesis make an original contribution to current understanding of biophysical interactions between top predators and mesoscale oceanography in pelagic systems. The frequency of thermal front manifestation (*ffreq*) over monthly or seasonal timescales was found to be a significant predictor of broad-scale habitat preference in all four species-specific investigations. Many marine predators are known to exhibit strong foraging site fidelity, including sharks (Jorgensen *et al.* 2010; Barnett *et al.* 2011), pinnipeds (Bradshaw *et al.* 2004b; Call *et al.* 2008; Chilvers 2008), cetaceans (Baird *et al.* 2008; Foote *et al.* 2010), turtles (Broderick *et al.* 2007; Schofield *et al.* 2010) and seabirds (Weimerskirch 2007; Navarro & González-Solís 2009; Patrick *et al.* 2014). This may be related to cognitive processes such as learning and memory in some taxa, for example long-lived seabirds, in that spatiotemporal predictability of foraging opportunities is linked to prevailing oceanographic conditions and the persistence of environmental gradients (Piatt *et al.* 2006; Weimerskirch 2007; Regular, Hedd & Montevecchi 2013). Studies presented in this thesis indicate that persistent or frequent frontal activity over seasonal timescales is a contributing factor to the preferential selection of regions of accessible habitat for a range of species, in particular those that forage in epipelagic waters.

Responses to contemporaneous thermal and chl-*a* fronts appear to be more variable, differing according to both the biophysical properties of fronts and species-specific aspects of foraging ecology. Associations with contemporaneous mesoscale thermal fronts were found to be more significant for those species that feed at intermediate trophic levels, the basking shark and loggerhead turtle, than for higher trophic-level seabirds. Furthermore, the strength and persistence of contemporaneous fronts influenced observed associations. For example, basking sharks in seasonally-stratified shelf seas around the UK were more likely to be associated with persistent fronts with a stronger cross-frontal temperature step than more ephemeral features. We postulate that there may be considerable variability in marine predator responses to fronts at species, population, and individual levels, which warrants further investigation.

Major findings of studies presented in this thesis indicate that the temporal lags inherent in nutrient enrichment, enhancement of primary productivity and mechanical aggregation of zooplankton along fronts influence the attractiveness of these features for foraging predators. Planktivorous predators are more closely tied to the bottom-up mechanisms forcing the development of pelagic foraging hotspots at fronts, so can find foraging opportunities associated with both persistent and more ephemeral fronts. Sufficient time is required for low trophic-level enhancement to propagate through to attract pelagic fish (Le Fevre 1986; Franks 1992a; Genin *et al.* 2005), so piscivorous predators may be less likely to associate with ephemeral features. We therefore recommend that explicit consideration of spatial scale, front strength and persistence is incorporated in future habitat modelling studies incorporating measures of frontal activity. Consideration of the biophysical characteristics of fronts accessible to predator populations is essential to understanding the mechanistic links between animal movements and environmental conditions in dynamic marine systems.

Linking animal movements to environmental conditions in dynamic marine systems

The foraging behaviours of marine predators are governed by complex, variable and scale-dependent interactions between predators, prey and biophysical processes (Fauchald, Erikstad & Skarsfjord 2000). This section examines approaches to understanding the mechanisms that underlie habitat selection. First, current data gaps and the limitations of using remotely-sensed surface variables to define three-dimensional pelagic habitats are discussed. Main insights generated by studies presented in this thesis regarding the utility of remotely-sensed front metrics are then considered. Finally, the complications inherent in habitat modelling using biologging and remotely-sensed oceanographic data are examined, and recommendations are made for maximising the value of these datasets in understanding habitat selection.

The 'trophic gap'

The dynamic distributions of pelagic fish are influenced by stochastic processes (Van der Kooij, Scott & Mackinson 2008; Embling *et al.* 2012), leading to high levels of heterogeneity in prey availability over three dimensions (Weimerskirch, Gault & Cherel 2005). In addition, data describing pelagic prey distributions are logistically difficult to obtain, particularly in spatial and temporal congruence with biologging data (McIntyre *et al.* 2012). Understanding the mechanisms linking physical processes, prey distributions and predator behaviour is currently constrained by this *trophic gap*, particularly for piscivorous species.

A range of approaches have been used to bridge the trophic gap and characterise prey fields for biologging datasets. Zooplankton abundance, derived from Continuous Plankton Recorder (CPR) records or inferred from acoustic backscatter, have been used as measures of prey availability (Witt *et al.* 2007; Fossette *et al.* 2010; Patrick *et al.* 2014). However, there is unlikely to be direct correlation between high zooplankton densities and pelagic fish aggregations, restricting the utility of these methods for piscivores. In addition, the low spatial resolution of CPR datasets can restrict their utility (Patrick *et al.* 2014). Mapping hotspots of fisheries effort highlights more predictable forage fish aggregations over broad scales (Witt & Godley 2007), but access to vessel monitoring systems (VMS) is restricted by the fishing industry, so these data are rarely available to ecologists.

Alternatively, dietary analysis or stable isotope analysis of body tissues of instrumented animals can provide valuable evidence of prey types targeted, and relate this information to movement patterns (Catry *et al.* 2004), but the spatial resolution of insights generated is coarse and can not always be linked to mesoscale oceanographic conditions (Jaeger *et al.* 2013; Patrick *et al.* 2014). Consequently, the majority of studies seeking to define foraging habitat preferences of marine predators from tracking data use EO remote sensing to contextualise observed movements. However, this begs the question of whether remotely-sensed surface variables are good proxies for prey availability.

Are remotely-sensed variables good proxies for prey availability?

The use of sea-surface temperature (SST) and chlorophyll-*a* (chl-*a*) imagery has been prevalent to date in studies of habitat preference (e.g. Polovina *et al.* 2001; Sims *et al.* 2009; Block *et al.* 2011). Satellite altimetry is also used, both in isolation (Nel *et al.* 2001) and alongside other covariates (Zainuddin, Saitoh & Saitoh 2008; Sims *et al.* 2009; Teo & Block 2010). Suites of remotely-sensed environmental variables have been used in synchrony to characterise biological *hotspots* (Palacios *et al.* 2006; Grantham *et al.* 2011; Wingfield *et al.* 2011).

Remotely-sensed variables were found to be useful predictors of the locations of preferred habitats in the studies presented in this thesis. In addition to front metrics, chl-*a* was found to be a significant predictor of habitat preference in loggerhead turtles, basking sharks and grey-headed albatrosses in studies presented here. Two-dimensional spatial correlation observed between seasonal or monthly front frequency and chl-*a* concentration in several cases indicates a correlation between persistent frontal activity and primary productivity, particularly in stratified shelf seas. In contrast, SST held less explanatory value as a predictor of habitat preference over these spatiotemporal scales, but is known to strongly regulate marine biodiversity over ocean basin scales (Tittensor *et al.* 2010), and is a useful indicator of important sub-surface processes such as cold-water upwelling (Croll *et al.* 2005; Chavez & Messié 2009; Wingfield *et al.* 2011).

However, the use of remotely-sensed parameters in characterising foraging habitats assumes that variables detected are proxies for prey availability, which often lacks coherent supporting evidence (Ballance, Pitman & Fiedler 2006). For example, Grémillet *et al.* (2008) found a strong association between seabirds and primary productivity in the Benguela upwelling, but a spatial mismatch between primary productivity and pelagic fish distributions. A mismatch between primary productivity and zooplankton distributions has also been observed at the Celtic Boundary Front (Mcginty, Johnson & Power 2014).

In addition, while there is evidence that biophysical coupling along fronts can lead to low trophic-level enhancement (Franks 1992b; Genin *et al.* 2005), there is a paucity of data showing a similar effect for larger nekton. Frontal associations have been demonstrated for planktivorous fish species (e.g. Maravelias 1997; Marchand, Simard & Gratton 1999), particularly for larval stages (e.g. Munk 2002), but only in fine-scale tidally-driven fronts. Mechanical aggregation of zooplankton in convergent fronts presumably enhances food availability for mid-level consumers, but there are currently few accounts of bait fish aggregation at fronts (but see Belkin *et al.* 2014). While we can assume that fronts visible at the surface have a sub-surface profile in which biophysical coupling is likely to enhance prey accessibility for both planktivorous and piscivorous predators (see Chapter I, and references therein), questions remain regarding the efficacy of surface parameters for identifying preferred habitats that are formed by sub-surface processes.

Surface parameters; sub-surface processes

Remotely-sensed variables can detect two-dimensional surface parameters only, while the foraging decisions made by marine predators are governed by three-dimensional processes. *In-situ* surveys that incorporate oceanographic sampling, predator observation and hydroacoustic sampling have proven critical in revealing sub-surface mechanisms, including the influence of regions of stratification (Scott *et al.* 2010; Cox, Scott & Camphuysen 2013); tidal shear (Scott *et al.* 2013); interactions between sub-surface current flows and bathymetry (Jones *et al.* 2014); internal waves (Scott *et al.* 2013); and mesopelagic boundary layers (Benoit-Bird & Au 2003) on vertical distributions of prey species in the water column, and corresponding predator foraging decisions. Sub-surface or deep chlorophyll-*a* maxima (DCM) resulting from biophysical coupling in hydrodynamic features of the water column appear to be particularly significant (Baker, Polovina & Howell 2007; Scott *et al.* 2010; Williams *et al.* 2011).

While remote sensing can not resolve the influence of these sub-surface processes on habitat selection, it enables derivation of useful indices describing broad- to meso-scale oceanographic dynamics. Indeed, surface variables often reflect sub-surface variability. For example, DCM can manifest in association with frontal dynamics visible at the surface

(Fasham *et al.* 1985). However, bridging the *trophic gap* between predators and processes over the range of spatial and temporal scales relevant to their foraging ecology requires both top-down, broad-scale and bottom-up, fine-scale approaches. Remotely-sensed data are most useful for studies investigating the influence of broad- to meso-scale oceanography on habitat selection decisions, while in situ work is critical for understanding mechanisms occurring at the sub-mesoscale. For example, the use of vessel- or seabed- mounted technologies that can record both physical oceanographic data and indices of pelagic fish abundance alongside predator abundance and behaviour (Begg & Reid 1997; Doksæter *et al.* 2009; Cox, Scott & Camphuysen 2013; Jones *et al.* 2014; Williamson *et al.* 2014), Autonomous Underwater Vehicles (Gillespie *et al.* 2014; Suberg *et al.* 2014) and multi-parameter ocean observatories (Manderson *et al.* 2011) are now providing invaluable insight into biophysical mechanisms regulating habitat selection.

Studies presented in this thesis focus on surface or near-surface foragers, rather than deep-diving species. Although surface frontal activity appears to be a good indicator of the locations of sub-surface processes that can increase prey accessibility in these case studies, habitat preferences of deep-diving foragers may be better investigated using techniques described above, or animal-attached tags that can directly sense oceanographic parameters (e.g. Charrassin *et al.* 2008). Concurrent use of these tags with remotely-sensed metrics could be an interesting method of ground-truthing, and for investigating relationships between surface variables, sub-surface processes and predator habitat use in future studies. Despite shortcomings of remote sensing for habitat characterisation, many studies have documented clear associations between marine predators and surface features, including frontal systems, using remotely-sensed data (see preceding chapters, and references therein). Environmental conditions appear to strongly influence foraging habitat selection over broad to meso-scales.

Predators respond to environmental conditions

Although the ways in which marine predators sense and respond to environmental gradients are not yet well-understood, there is compelling evidence that environmental conditions influence spatial and foraging ecology across taxa (e.g. Block *et al.* 2011; Louzao *et al.* 2011; Commins, Ansorge & Ryan 2014). Indeed, some species seem to respond to environmental gradients in preference to real-time prey distributions (Benoit-Bird & Au 2003; Torres, Read & Halpin 2008). Using remotely sensed variables to characterise physical properties of preferred habitats can, therefore, circumvent the need for prey distribution data. In addition, remotely-sensed data can yield valuable information about the physical characteristics of areas available to, but not used by, focal species. However, issues associated with spatial scale and oceanographic dynamics are essential to consider. Moreover, it is critical that variables used are meaningful in terms of the ecology of focal species, and not just those that are most convenient for us to measure.

Utility of remotely-sensed front metrics

A major advantage of composite front mapping over alternative techniques is the capacity for generating metrics that are useful for objectively identifying frontal systems, and visualising their dynamics through time. This provides capacity for robust quantification of the influence of fronts in habitat models. Front metrics quantifying both contemporaneous and longer-term frontal activity have proven useful in modelling habitat preferences of marine predators, in the studies presented in this thesis and in other recent investigations (e.g. Oppel *et al.* 2012; Chivers *et al.* 2013; Edwards *et al.* 2013; Pirotta *et al.* 2013).

While none of the oceanographic predictors included in models presented in preceding chapters explained a high proportion of deviance, it is well established that the foraging decisions of marine predators are governed by multiple complex and interacting factors, both extrinsic and intrinsic to each individual. It would be unreasonable, therefore, to expect a single environmental variable to predict foraging habitat preference in highly dynamic pelagic systems. The proportions of deviance explained by front metrics significant to models presented here are in accordance with those documented by other habitat modelling studies (e.g. Embling *et al.* 2010; Wakefield *et al.* 2011; Oppel *et al.* 2012; Chivers *et al.* 2013).

Contemporaneous (7-day) front metrics provide capacity for high-resolution investigation of behavioural responses to environmental stimuli when coupled with GPS tagging, as demonstrated in chapter two. Use with other tag types (GLS, Argos-PTT) can elucidate levels of association with mesoscale thermal and chl-*a* fronts, as shown in chapters three and four. *fdist* showed the greatest utility for investigating responses to contemporaneous fronts in virtual real-time, and was the most convenient for interpretation of results. *gdens* was found to be preferable to *fdens*, owing to the relative ease of interpretation of model outcomes. The preparation of *fdens* involves data processing steps (multiplication of *gdens* with *pfront* and proximity to other features, and an uneven representation of front-positive pixels where satellite passes vary in number) that can confound interpretation. Exploratory data analysis showed little influence of the *fside* metric in any of the studies presented here, so it was not included as a predictor in models. In summary, *ffreq*, *fdist* and *gdens* metrics proved to be most informative, and have wide scope for further application in habitat modelling studies.

However, remotely-sensed front metrics have limitations that must be considered. In common with all remote sensing applications, detection of properties is limited to the uppermost surface layers of the ocean, and areas of imagery can be obscured by persistent cloud cover. The spatial resolution of imagery is a function of sensor sensitivity, and satellite coverage is variable across the globe. Other limitations are specific to these metrics. Although multi-day compositing circumvents problems associated with cloud cover, resultant composites can not strictly be regarded as representations of conditions experienced by animals in real-time. Preparation of composite front maps, and thus of the *fdens* metric, can be affected by the frequency of satellite passes, detracting from comparability of metrics between different regions and time periods.

In addition, several parameters for metric preparation, for example the temperature gradient threshold for front detection, degree of spatial smoothing in *fdens/gdens* and *hysteresis* settings for the algorithm, have to be set by the user. While this allows for greater flexibility in application, it can introduce subjectivity into analyses. Studies presented in this thesis identify optimum values, and it is recommended that parameter selection is matched with the spatial and temporal scales defining the research question. For example, maximum spatial detail is useful for investigating near real-time responses to contemporaneous conditions, whereas seasonal front frequency maps require less detail so as to minimise noise. Overall, the studies presented in previous chapters indicate that front metrics are useful oceanographic variables for investigating predator habitat preference, providing they are used with an awareness of the complications inherent in habitat modelling.

Habitat modelling – complications and solutions

Concurrent use of biologging and remote sensing leads to the generation of large, complex datasets. Sophisticated analytical methodologies are necessary to maximise the value of these data in quantifying the influence of environmental variables on habitat selection. Techniques used to achieve this aim are known by a range of terms including *habitat models, species-habitat models, species distribution models, predictive habitat models* and *ecological niche models*. Many of these techniques are based around Resource Selection Functions (RSFs), which quantify habitat use through statistical comparison of areas used to those available to an individual or population (Boyce *et al.* 2002; Aarts *et al.* 2013).

Regression-based techniques (i.e. Generalised Linear Models, GLM; Generalised Linear Mixed Models, GLMM; Generalised Additive Models, GAM; Generalised Additive Mixed Models, GAMM; (Bolker *et al.* 2009; Zuur, Hilbe & Ieno 2013) are widely used (Becker *et al.* 2012; Bailey, Hammond & Thompson 2014; Sequeira *et al.* 2014). Habitat modelling techniques are comprehensively reviewed in Aarts *et al.* (2008); Wakefield, Phillips and Matthiopoulos

(2009); and Warton and Aarts (2013). Analyses presented in chapters two to four demonstrate the use of GAM and GLMM. Machine learning techniques such as MaxEnt and boosted regression trees are also of utility, particularly for predictive modelling, as demonstrated in chapter five (see also Afán *et al.* 2014; Bombosch *et al.* 2014; Torres *et al. In Press*).

The nature of biologging datasets complicates habitat modelling in several respects, most notably spatial accuracy and temporal frequency of location fixes, statistical non-independence of successive locations, and the sampling of areas available to, but not used by, tracked animals (Aarts *et al.* 2008; Schick *et al.* 2008; Warton & Aarts 2013). The degree of spatial accuracy and the frequency of location fixes are both functions of tag types used. For example, geolocation (GLS) and Argos-PTT datasets are far less accurate, and more sparse, than most GPS datasets (Phillips *et al.* 2004a; Costa *et al.* 2010; Witt *et al.* 2010). However, the choice of tags used for a particular application is subject to multiple considerations, including financial cost, battery life, instrument burden, and requirements for surfacing or recapture (Bograd *et al.* 2010). Hence, analytical solutions have emerged that can minimise the effects of accuracy and regularity limitations of GLS and Argos-PTT, for example State-Space or Hidden Markov Modelling (Patterson *et al.* 2008; Bailey *et al.* 2009; Patterson *et al.* 2009), as demonstrated in chapter three.

In terms of statistical non-independence, both repeated measures from the same individual and serial autocorrelation in tracking data violate the assumption of independence central to the use of many modelling frameworks (Aarts *et al.* 2008). Mixed models explicitly account for non-independence resulting from repeated measures (Bolker *et al.* 2009), and were used in chapters three and four for this purpose. The analysis of gannet responses to contemporaneous fronts presented in chapter two uses Generalised Estimating Equations (Hardin & Hilbe 2003) to partition the dataset at the individual movement burst level. Ecological niche modelling presented in chapter five collapses the individual-level information in the dataset, examining the spatial distribution of foraging events over the whole tracking period, and so repeated measures are not a confounding influence in this analysis.

Serial autocorrelation can also lead to the artificial inflation of parameter significance if not accounted for (Fieberg *et al.* 2010). The degree of serial autocorrelation in a dataset is dependent on tag type and sampling frequency, and so is more pronounced in GPS tracking datasets than GLS or Argos-PTT. Studies presented in this thesis use several strategies to account for serial autocorrelation. Chapter two fits an autoregressive correlation structure at the individual movement burst level using GEE. Interestingly, explanatory terms found to be non-significant using GEEs were attributed false significance when fitted in a GAM with no autocorrelation term. The second analysis in chapter two, which investigated habitat selection in gannets over seasonal time scales, collapsed the time element of tracks and investigated the spatial distribution of foraging effort over the entire breeding season, removing serial autocorrelation. This approach was also used in chapter five. Finally, analyses described in chapters three and four used iterative resampling of both presence and pseudo-absence datasets to remove serial autocorrelation and prevent zero-inflation of the response variable in model runs.

Spatial autocorrelation in environmental data is a further complication (Dormann *et al.* 2007), although its effects on predictive accuracy have been shown to be less pronounced (Thibaud *et al.* 2014). Models presented in this thesis were checked for spatial autocorrelation by plotting model residuals in space, where model frameworks allowed. No substantial effects were detected. Model frameworks used here preclude the inclusion of multiple correlation structures, so serial autocorrelation was accounted for in preference. However, further exploration of the possible effects of spatial autocorrelation, and interaction with the spatial resolution of remotely-sensed data, could have enhanced investigations presented here.

Multi-colinearity between explanatory variables can confound habitat modelling. The complex interrelationships between physical and biological parameters in the marine environment can frequently lead to colinearity between commonly-used measures, for example, sea surface temperature and depth. Analyses presented in this thesis checked for colinearity between predictor variables using Generalised Variance Inflation Factors (GVIFs; Zuur, Ieno & Elphick 2010), a threshold-based pre-selection method that has been proven effective (Dormann *et al.* 2013). Where colinearity was detected, separate models were used to compare the significance of predictor variables.

In addition, tracking data are presence only, and so useful for identifying high-use areas (Tancell *et al.* 2013), yet an understanding of habitat preference requires comparison of conditions characterising high-use areas to those in other accessible regions. The generation of pseudo-absence locations is one strategy for representing accessible habitat, but the way in which pseudo-absences are generated can have a considerable impact on model outputs (Phillips *et al.* 2009). Simulations such as correlated random walks (CRWs; Heithaus *et al.* 2006) can be useful, as demonstrated in chapters three and four. The selection of parameters describing movement, the number of simulations and the spatial extent over which CRWs are permitted to roam are important considerations. In addition, CRWs are less applicable to central-place foragers that are constrained to periodically return to a particular location. Alternatively, pseudo-absences can be selected at random from a predefined study area. For chapter five, which focuses on a central-place forager, sets of pseudo-absences were selected at random from within the accessible range of the colony repeatedly over several iterations.

However, these presence-absence approaches cannot incorporate information on relative usage of different areas. Large, multi-individual biologging datasets can allow for calculation of relative density surfaces, which are more informative than simple presence-absence (e.g. Hazen *et al.* 2013b). Lack of spatial and temporal overlap between datasets used for this thesis precluded such an approach, but measures of relative importance are likely to become more commonly used as biologging datasets increase in number and detail.

Solutions to many of these complications are being made more accessible to ecologists as statistical methodologies improve. For example, Bayesian approaches such as Markov Chain Monte Carlo simulations (MCMC; Wade 2000; Ellison 2004; Zuur, Hilbe & Ieno 2013) and the Integrated Nested Laplace Approximation (INLA; Illian, Sørbye & Rue 2012) are becoming more commonly used (Lecomte *et al.* 2013; Pennino *et al.* 2013). Integration into packages for the R software platform (e.g. R-INLA, Rue, Martino & Chopin 2009; MCMCglmm, Hadfield 2010) is facilitating further uptake. These techniques enable the incorporation of random effects, multiple correlation structures and multivariate responses in models, so can circumvent complications listed above and incorporate several species' responses in one model, where datasets allow. Use of Bayesian approaches to build more sophisticated models would be a logical follow-up to the work presented in this thesis. Models presented in this thesis are progressive in terms of quantifying habitat preference using frequentist methods, and have generated insights that make an original contribution to current understanding of biophysical interactions in pelagic systems. These insights have implications for the conservation of marine biodiversity, and potential real-world application for improving marine management.

Implications for conservation and management

UK context

The waters surrounding the United Kingdom are among the busiest anywhere in the global ocean. Marine predator populations in the region are under intense anthropogenic pressure (Leeney *et al.* 2012; Votier *et al.* 2013). Marine policy and regulation in the UK is set by the governmental Department for the Environment, Food and Rural Affairs (Defra), which has the responsibility for including global and European legislation in management frameworks. The European Union (EU) Marine Strategy Framework Directive (MSFD; 2008/56/EC) includes requirements for member states to meet 11 descriptors of Good Environmental Status (GES) by 2020, including a requirement (D1) that "biological diversity is maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions". This legislation bridges requirements specified in the EU Birds (2009/147/EC) and Habitats (92/43/EEC) Directives for maintenance of *favourable conservation status* of marine vertebrate populations.

Defra's *Biodiversity 2020* strategy, an update to the *Biodiversity Action Plan*, sets out to foster "a more integrated large-scale approach to conservation […] at sea" (DEFRA 2011). This strategy seeks to meet global targets agreed under the UN Convention on Biological Diversity (CBD), one of which is to protect 10% of coastal and marine areas, "especially areas of particular importance for biodiversity and ecosystem services" ('Aichi' Target 11, Strategic Goal C; http://www.cbd.int/sp). In addition, the UK Marine and Coastal Access Act 2009 and Marine Policy Statement 2011 set commitments for the creation of an *ecologically coherent* network of Marine Conservation Zones (MCZs) as the primary strategy for achieving Good Environmental Status.

Composite front mapping, specifically the *frequent front* metric, was used in the Defra consultation for the identification of candidate sites for these MCZs (Miller & Christodoulou 2014). The metric contributed to the identification of 11 sites of importance for pelagic biodiversity. However, political inertia has prevented the designation of these sites as real protected areas. Only 27 of the originally proposed 127 sites are to be designated under current plans, and mobile species are not included. Moreover, *Biodiversity 2020* includes only two indicators of marine ecosystem health, the abundance of breeding seabirds around the coasts of England and the size structure of commercially exploited fish populations in the north-western North Sea. While there is an intention to widen the taxonomic scope of the first, current measures are not sufficient to protect marine predator populations in UK seas.

The marine spatial planning (MSP) agenda in the UK further complicates marine conservation strategy, often conflicting with MFSD implementation (Brennan *et al.* 2014). The expansion of the marine renewable energy industry has implications pertinent to the management of marine predator populations, particularly in Scotland where the sector is rapidly developing (Bailey, Brookes & Thompson 2014; Davies, Watret & Gubbins 2014). Marine Renewable Energy Installations (MREI) such as offshore wind farms, tidal turbines and wave-powered devices have several potential impacts on marine biodiversity, including the risk of increased mortality through direct collision (Grecian *et al.* 2010; Furness, Wade & Masden 2013; Waggitt & Scott 2014).

Moreover, MREIs are likely to be sited in hydrographically dynamic areas. This could lead to the displacement of marine predators from key foraging habitats, or displacement of the habitats themselves (Langton, Davies & Scott 2011; Scott *et al.* 2014) - but see Russell *et al.* (2014). Modelling habitat selection in marine predators, using techniques such as those presented in this thesis, could inform MSP through identification of these key habitats and investigation of how these habitats change or shift following MREI installation.

Global context

Marine Protected Areas (MPAs) currently cover less than 0.1% of the pelagic realm (Game *et al.* 2009). Although several large marine areas have been designated as protected sites in recent years (e.g. Chagos Archipelago, Indian Ocean; Sheppard *et al.* 2012), biodiversity conservation in Areas Beyond National Jurisdiction (ABNJ, the 'high seas') is currently inadequate (Sumaila *et al.* 2007; Ban *et al.* 2014). Under the CBD targets, the international community is required to identify *Ecologically or Biologically Significant Areas* (EBSAs) in the oceans that are in need of protection (Dunn *et al.* 2014). The *frequent front* metric has been used as part of a broad suite of measures to identify EBSAs in the Pacific (http://www.cbd.int/ebsa/). .

Identification of biophysical hotspots in this way can contribute to ecosystem-level management (Hyrenbach, Forney & Dayton 2000; Crowder & Norse 2008) and systematic conservation planning in the oceans (Ban *et al.* 2014). Species Distribution Modelling (SDM) incorporating both biotic and abiotic descriptors of pelagic environments is likely to become an important tool in marine conservation planning (Robinson *et al.* 2011; Marshall, Glegg & Howell 2014). As described in chapter one, tools such as those presented in this thesis could contribute to the identification of areas of overlap between critical habitats and anthropogenic threat, for example fisheries activity (e.g. Petersen *et al.* 2008; Fossette *et al.* 2014). SDM coupled with modelling of future climate scenarios could be used to forecast changes in the distributions of marine predator populations and key habitats as the oceans undergo climate-driven change (Hazen *et al.* 2013b; Marshall, Glegg & Howell 2014).

However, identification and protection of hotspots in this way may not be sufficient to protect marine predator populations. A recent meta-analysis suggests that a main reason that MPAs fail to conserve marine biodiversity is movement of animals outside boundaries (Edgar *et al.* 2014). For highly mobile species, connectivity between key habitats is especially important (Runge *et al.* 2014). While there are calls for 'Big Ocean' sites – very large-scale MPAs – to halt the loss of marine biodiversity (Toonen *et al.* 2013), it is difficult to see how these could be tractable and enforceable. Marine conservation planning should reflect the spatiotemporal dynamism inherent in marine predator space use if it is to prevent further decline of mobile populations of conservation concern (Hooker *et al.* 2011; Runge *et al.* 2014). Moving from static protected areas towards a more adaptive, spatially dynamic ocean management paradigm is necessary to achieve this aim.

Dynamic Ocean Management – the future of marine conservation?

Dynamic ocean management (DOM) is an emerging approach to management of marine resources that explicitly accounts for the dynamic movements of the ocean, marine animals, and human users (Hobday *et al.* 2014). DOM can regulate overlap between high-use areas for marine predators and anthropogenic threat through the establishment of protected areas that function in near real-time and can move, like the species they aim to protect.

Chapter one describes situations in which DOM has worked, to regulate tuna fisheries in South Australia and to reduce fisheries bycatch of loggerhead turtles in the North Pacific Transition Zone. A DOM approach is to be trialled further in the United States in upcoming years, including a novel approach to mitigating impacts of ship strike on the blue whale *Balaenoptera musculus* population along the Pacific coast (Irvine *et al.* 2014). DOM could facilitate better balance between anthropogenic interests and biodiversity conservation in the oceans, particularly in the coastal zone in which anthropogenic threat is largely concentrated (Maxwell *et al.* 2013). Moreover, a spatially dynamic approach to marine conservation could provide opportunity for adaptation of conservation strategies in the wake of future climatic change (Hazen *et al.* 2013b).

Satellite remote sensing of real-time oceanography is an essential component of current plans for establishment of DOM (Hazen *et al.* 2013b; Muller-Karger *et al.* 2013; Hobday *et al.* 2014). Given the ecological importance of persistent frontal zones, both near real-time and seasonal or climatological front mapping could be extremely useful as part of the suite of tools supporting DOM, provided that data are made freely and easily available to management bodies (Hobday *et al.* 2014). In synergy with vessel-based technologies, large biologging datasets and high-resolution habitat modelling, front mapping could prove a useful component of the suite of technological solutions to managing the marine biodiversity crisis.

References

Aarts, G., Fieberg, J., Brasseur, S. & Matthiopoulos, J. (2013) Quantifying the effect of habitat availability on species distributions. *Journal of Animal Ecology,* **82,** 1135-1145.

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.

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M. & Bava, J. (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *Journal of Marine systems,* **44,** 83-105.

Afán, I., Navarro, J., Cardador, L., Ramírez, F., Kato, A., Rodríguez, B., Ropert-Coudert, Y. & Forero, M.G. (2014) Foraging movements and habitat niche of two closely related seabirds breeding in sympatry. *Marine Biology,* **161,** 657-668.

Agreement on the Conservation of Albatrosses and Petrels, ACAP (2009) ACAP Species assessment: Grey-headed Albatross Thalassarche chrysostoma. Downloaded from http://www.acap.aq on 24 September 2014.

Ainley, D.G., Dugger, K.D., Ford, R.G., Pierce, S.D., Reese, D.C., Brodeur, R.D., Tynan, C.T. & Barth, J.A. (2009) Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. *Marine Ecology Progress Series,* **389,** 271-294.

Alemany, D., Acha, E.M. & Iribarne, O.O. (2014) Marine fronts are important fishing areas for demersal species at the Argentine Sea (Southwest Atlantic Ocean). *Journal of Sea Research,* **87,** 56-67.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology,* **43,** 1223-1232.

Anderson, O.R., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.J., Yates, O. & Black, A. (2011) Global seabird bycatch in longline fisheries. *Endangered Species Research,* **14,** 91-106.

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography,* **33,** 1677-1688.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution,* **22,** 42-47.

Arcos, J.M., Bécares, J., Villero, D., Brotons, L., Rodríguez, B. & Ruiz, A. (2012) Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain. *Biological Conservation,* **156,** 30-42.

Azzellino, A., Gaspari, S., Airoldi, S. & Nani, B. (2008) Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. *Deep Sea Research Part I: Oceanographic Research Papers,* **55,** 296-323.

Bailey, H., Brookes, K.L. & Thompson, P.M. (2014) Assessing environmental impacts of offshore wind farms: lessons learned and recommendations for the future. *Aquatic biosystems,* **10,** 8.

Bailey, H., Hammond, P.S. & Thompson, P.M. (2014) Modelling harbour seal habitat by combining data from multiple tracking systems. *Journal of Experimental Marine Biology and Ecology,* **450,** 30-39.

Bailey, H., Mate, B.R., Palacios, D.M., Irvine, L., Bograd, S.J. & Costa, D.P. (2009) Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research,* **10,** 93-106.

Bailleul, F., Charrassin, J.B., Monestiez, P., Roquet, F., Biuw, M. & Guinet, C. (2007) Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical Transactions of the Royal Society of London B Biological Sciences,* **362,** 2169-2181.

Bailleul, F., Cotté, C. & Guinet, C. (2010) Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Marine Ecology Progress Series,* **408,** 251-264.

Baird, R.W., Gorgone, A.M., McSweeney, D.J., Webster, D.L., Salden, D.R., Deakos, M.H., Ligon, A.D., Schorr, G.S., Barlow, J. & Mahaffy, S.D. (2008) False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: Long-term site fidelity, inter-island movements, and association patterns. *Marine Mammal Science,* **24,** 591-612.

Baker, J.D., Polovina, J.J. & Howell, E.A. (2007) Effect of variable oceanic productivity on the survival of an upper trophic predator, the Hawaiian monk seal *Monachus schauinslandi*. *Marine Ecology Progress Series,* **346,** 277-283.

Bakun, A. (1996) *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. California Sea Grant College System, NOAA, California.

Bakun, A. (2006) Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina,* **70,** 105-122.

Ballance, L.T., Pitman, R.L. & Fiedler, P.C. (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in Oceanography,* **69,** 360-390.

Ballard, G., Jongsomjit, D., Veloz, S.D. & Ainley, D.G. (2012) Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. *Biological Conservation,* **156,** 72-82.

Ban, N.C., Bax, N.J., Gjerde, K.M., Devillers, R., Dunn, D.C., Dunstan, P.K., Hobday, A.J., Maxwell, S.M., Kaplan, D.M. & Pressey, R.L. (2014) Systematic conservation planning: a better recipe for managing the high seas for biodiversity conservation and sustainable use. *Conservation Letters,* **7,** 41-54.

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.

Barraquand, F. & Benhamou, S. (2008) Animal movements in heterogenous landscapes: identifying profitable places and homogenous movement bouts. *Ecology,* **89,** 3336-3348.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. *http://CRAN.R-project.org/package=lme4*.

Baumgartner, M.F. (1997) The distribution of Risso's dolphin (Grampus griseus) with respect to the physiography of the northern Gulf of Mexico. *Marine Mammal Science,* **13,** 614-638.

Becker, E., Foley, D., Forney, K., Barlow, J., Redfern, J. & Gentemann, C. (2012) Forecasting cetacean abundance patterns to enhance management decisions. *Endangered Species Research,* **16,** 97-112.

Begg, G.S. & Reid, J.B. (1997) Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. *ICES Journal of Marine Science: Journal du Conseil,* **54,** 552-565.

Belkin, I.M., Cornillon, P.C. & Sherman, K. (2009) Fronts in large marine ecosystems. *Progress in Oceanography,* **81,** 223-236.

Belkin, I.M. & Gordon, A.L. (1996) Southern Ocean fronts from the Greenwich meridian to Tasmania. *Journal of Geophysical Research,* **101,** 3675-3696.

Belkin, I.M., Hunt Jr, G.L., Hazen, E.L., Zamon, J.E., Schick, R.S., Prieto, R., Brodziak, J., Teo, S.L.H., Thorne, L., Bailey, H., Itoh, S., Munk, P., Musyl, M.K., Willis, J.K. & Zhang, W. (2014) Special Issue: Fronts, fish, and predators. *Deep Sea Research Part II: Topical Studies in Oceanography,* **107**.

Benoit-Bird, K.J. & Au, W.W. (2003) Prey dynamics affect foraging by a pelagic predator (Stenella longirostris) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology,* **53,** 364-373.

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,* **94B,** 101-107.

Bertrand, S., Joo, R., Arbulu Smet, C., Tremblay, Y., Barbraud, C. & Weimerskirch, H. (2012) Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology,* **49,** 1168-1177.

Bivand, R. & Lewin-Koh, N. (2013) Maptools: Tools for reading and handling spatial objects. R package version 0.8-27.

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.

Bodey, T.W., Jessopp, M.J., Votier, S.C., Gerritsen, H.D., Cleasby, I.R., Hamer, K.C., Patrick, S.C., Wakefield, E.D. & Bearhop, S. (2014) Seabird movement reveals the ecological footprint of fishing vessels. *Current Biology,* **24,** R514-R515.

Bograd, S.J., Block, B.A., Costa, D.P. & Godley, B.J. (2010) Biologging technologies: new tools for conservation. *Endangered Species Research,* **10,** 1-7.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution,* **24,** 127-135.

Bombosch, A., Zitterbart, D.P., Van Opzeeland, I., Frickenhaus, S., Burkhardt, E., Wisz, M.S. & Boebel, O. (2014) Predictive habitat modelling of humpback (*Megaptera novaeangliae*) and Antarctic minke (*Balaenoptera bonaerensis*) whales in the Southern

Ocean as a planning tool for seismic surveys. *Deep Sea Research Part I: Oceanographic Research Papers,* **91,** 101-114.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G. & Weimerskirch, H. (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine systems,* **78,** 363-376.

Bourne, W. & Clark, G. (1984) The occurrence of birds and garbage at the Humboldt Front off Valparaiso, Chile. *Marine Pollution Bulletin,* **15,** 343-344.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling,* **157,** 281-300.

Bradshaw, C., Higgins, J., Michael, K., Wotherspoon, S. & Hindell, M. (2004a) At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. *ICES Journal of Marine Science,* **61,** 1014-1027.

Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D. & Michael, K.J. (2004b) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour,* **68,** 1349-1360.

Brennan, J., Fitzsimmons, C., Gray, T. & Raggatt, L. (2014) EU marine strategy framework directive (MSFD) and marine spatial planning (MSP): Which is the more dominant and practicable contributor to maritime policy in the UK? *Marine Policy,* **43,** 359-366.

Broderick, A.C., Coyne, M.S., Fuller, W.J., Glen, F. & Godley, B.J. (2007) Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society B: Biological Sciences,* **274,** 1533.

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.

Call, K.A., Ream, R.R., Johnson, D., Sterling, J.T. & Towell, R.G. (2008) Foraging route tactics and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the Pribilof Islands. *Deep Sea Research Part II: Topical Studies in Oceanography,* **55,** 1883-1896.

Camphuysen, C.J., Scott, B.E. & Wanless, S. (2006) Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multispecies foraging assemblages and habitat-specific feeding strategies. *Top Predators in Marine Ecosystems: Their Role in Monitoring and Management* (eds I.L. Boyd, S. Wanless & C.J. Camphuysen), pp. 82-97. Cambridge University Press, Cambridge.

Canny, J. (1986) A computational approach to edge detection. *Pattern Analysis and Machine Intelligence, IEEE Transactions on***,** 679-698.

Casale, P., Abbate, G., Freggi, D., Conte, N., Oliverio, M. & Argano, R. (2008) Foraging ecology of loggerhead sea turtles Caretta caretta in the central Mediterranean Sea: evidence for a relaxed life history model. *Marine Ecology Progress Series,* **372,** 265-276.

Castelao, R.M., Mavor, T.P., Barth, J.A. & Breaker, L.C. (2006) Sea surface temperature fronts in the California Current System from geostationary satellite observations. *Journal of Geophysical Research: Oceans (1978–2012),* **111,** C09026.

Catry, P., Phillips, R.A., Phalan, B., Silk, J.R.D. & Croxall, J.P. (2004) Foraging strategies of grey-headed albatrosses Thalassarche chrysostoma: integration of movements, activity and feeding events. *Marine Ecology Progress Series,* **280,** 261-273.

Cayula, J.-F. & Cornillon, P.C. (1992) Edge detection algorithm for SST images. *Journal of Atmospheric and Oceanic Technology,* **9,** 67-80.

Cayula, J.F., Cornillon, P., Holyer, R. & Peckinpaugh, S. (1991) Comparative study of two recent edge-detection algorithms designed to process sea-surface temperature fields. *Geoscience and Remote Sensing, IEEE Transactions on,* **29,** 175-177.

Ceia, F.R., Phillips, R.A., Ramos, J.A., Cherel, Y., Vieira, R.P., Richard, P. & Xavier, J.C. (2012) Short-and long-term consistency in the foraging niche of wandering albatrosses. *Marine Biology,* **159,** 1581-1591.

Charrassin, J.B., Hindell, M., Rintoul, S.R., Roquet, F., Sokolov, S., Biuw, M., Costa, D., Boehme, L., Lovell, P., Coleman, R., Timmermann, R., Meijers, A., Meredith, M., Park, Y.H., Bailleul, F., Goebel, M., Tremblay, Y., Bost, C.A., McMahon, C.R., Field, I.C., Fedak, M.A. & Guinet, C. (2008) Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. *Proceedings of the National Academy of Sciences,* **105,** 11634-11639.

Chavez, F.P. & Messié, M. (2009) A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography,* **83,** 80-96.

Chilvers, B. (2008) Foraging site fidelity of lactating New Zealand sea lions. *Journal of Zoology,* **276,** 28-36.

Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D.R. & Reid, N. (2013) Identifying optimal feeding habitat and proposed Marine Protected Areas (pMPAs) for the black-legged kittiwake (*Rissa tridactyla*) suggests a need for complementary management approaches. *Biological Conservation,* **164,** 73-81.

Commins, M.L., Ansorge, I. & Ryan, P.G. (2014) Multi-scale factors influencing seabird assemblages in the African sector of the Southern Ocean. *Antarctic Science,* **26,** 38-48.

Costa, D.P., Robinson, P.W., Arnould, J.P.Y., Harrison, A.L., Simmons, S.E., Hassrick, J.L., Hoskins, A.J., Kirkman, S.P., Oosthuizen, H. & Villegas-Amtmann, S. (2010) Accuracy of ARGOS locations of pinnipeds at-sea estimated using fastloc GPS. *PLoS ONE,* **5,** e8677.

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

Cox, S., Scott, B. & Camphuysen, C. (2013) Combined spatial and tidal processes identify links between pelagic prey species and seabirds. *Marine Ecology Progress Series,* **479,** 203-221.

Coyne, M. & 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.

Croll, D.A., Marinovic, B., Benson, S., Chavez, F.P., Black, N., Ternullo, R. & Tershy, B.R. (2005) From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series,* **289,** 117-130.

Crowder, L. & Norse, E. (2008) Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Marine Policy,* **32,** 772-778.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International,* **22,** 1-34.

Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. (2005) Global Circumnavigations: Tracking Year-Round Ranges of Nonbreeding Albatrosses. *Science,* **307,** 249-250.

Curtis, T.H., Zeeman, S.I., Summers, E.L., Cadrin, S.X. & Skomal, G.B. (2014) Eyes in the sky: linking satellite oceanography and biotelemetry to explore habitat selection by basking sharks. *Animal Biotelemetry,* **2,** 1-15.

Dalleau, M., Benhamou, S., Sudre, J., Ciccione, S. & Bourjea, J. (2014) The spatial ecology of juvenile loggerhead turtles (*Caretta caretta*) in the Indian Ocean sheds light on the "lost years" mystery. *Marine Biology,* **161,** 1835-1849.

Davies, I.M., Watret, R. & Gubbins, M. (2014) Spatial planning for sustainable marine renewable energy developments in Scotland. *Ocean & Coastal Management,* **99,** 72-81.

Davis, R., Fargion, G., May, N., Leming, T., Baumgartner, M., Evans, W., Hansen, L. & Mullin, K. (1998) Physical habitat of cetaceans along the continental slope in the northcentral and western Gulf of Mexico. *Marine Mammal Science,* **14,** 490-507.

Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R.A., Perrins, C.M. & Guilford, T. (2013) Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of The Royal Society Interface,* **10,** 20120570.

Decker, M.B. & Hunt Jr, G.L. (1996) Foraging by murres (Uria spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Marine Ecology Progress Series,* **139,** 1-10.

Dias, M.P., Granadeiro, J.P., Phillips, R.A., Alonso, H. & Catry, P. (2010) Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings of the Royal Society B: Biological Sciences*, rspb20102114.

Doksæter, L., Godø, O.R., Olsen, E., Nøttestad, L. & Patel, R. (2009) Ecological studies of marine mammals using a seabed-mounted echosounder. *ICES Journal of Marine Science: Journal du Conseil,* **66,** 1029-1036.

Doksæter, L., Olsen, E., Nøttestad, L. & Fernö, A. (2008) Distribution and feeding ecology of dolphins along the Mid-Atlantic Ridge between Iceland and the Azores. *Deep Sea Research Part II: Topical Studies in Oceanography,* **55,** 243-253.

Doniol-Valcroze, T., Berteaux, D., Larouche, P. & Sears, R. (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Series,* **335,** 207-216.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B. & Leitão, P.J. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography,* **36,** 027-046.

Dormann, F.C., McPherson, M.J., Araújo, B.M., Bivand, R., Bolliger, J., Carl, G., G Davies, R., Hirzel, A., Jetz, W. & Daniel Kissling, W. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography,* **30,** 609-628.

Dunn, D.C., Ardron, J., Bax, N., Bernal, P., Cleary, J., Cresswell, I., Donnelly, B., Dunstan, P., Gjerde, K. & Johnson, D. (2014) The Convention on Biological Diversity's Ecologically or Biologically Significant Areas: Origins, development, and current status. *Marine Policy,* **49,** 137-145.

Dunn, D.C., Boustany, A.M. & Halpin, P.N. (2011) Spatio-temporal management of fisheries to reduce by-catch and increase fishing selectivity. *Fish and Fisheries,* **12,** 110-119.

Durazo, R., Harrison, N. & Hill, A. (1998) Seabird observations at a tidal mixing front in the Irish Sea. *Estuarine, Coastal and Shelf Science,* **47,** 153-164.

Eder, E., De León, A., Martins, S., Pérez-García, H., Marín, I., Marco, A. & Cardona, L. (2012) Foraging dichotomy in loggerhead sea turtles Caretta caretta off northwestern Africa. *Marine Ecology Progress Series,* **47,** 113-122.

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. & Berkhout, J. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature*.

Edwards, A.M., Phillips, R.A., Watkins, N.W., Freeman, M.P., Murphy, E.J., Afanasyev, V., Buldyrev, S.V., da Luz, M.G.E., Raposo, E.P., Stanley, H.E. & Viswanathan, G.M. (2007) Revisiting Levy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature,* **449,** 1044-1048.

Edwards, E.W., Quinn, L.R., Wakefield, E.D., Miller, P.I. & Thompson, P.M. (2013) Tracking a northern fulmar from a Scottish nesting site to the Charlie-Gibbs Fracture Zone: Evidence of linkage between coastal breeding seabirds and Mid-Atlantic Ridge feeding sites. *Deep Sea Research Part II: Topical Studies in Oceanography,* **98,** 438-444.

Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. (2010) Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. *Proceedings of the National Academy of Sciences,* **107,** 2078-2081.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions,* **17,** 43-57.

Ellison, A.M. (2004) Bayesian inference in ecology. *Ecology Letters,* **7,** 509-520.

Embling, C.B., Gillibrand, P.A., Gordon, J., Shrimpton, J., Stevick, P.T. & Hammond, P.S. (2010) Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). *Biological Conservation,* **143,** 267-279.

Embling, C.B., Illian, J., Armstrong, E., van der Kooij, J., Sharples, J., Camphuysen, K.C.J. & Scott, B.E. (2012) Investigating fine-scale spatio-temporal predator–prey patterns in dynamic marine ecosystems: a functional data analysis approach. *Journal of Applied Ecology,* **49,** 481-492.

Etnoyer, P., Canny, D., Mate, B., Morgan, L., Ortegaortiz, J. & Nichols, W. (2006) Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography,* **53,** 340-358.

Fasham, M., Platt, T., Irwin, B. & Jones, K. (1985) Factors affecting the spatial pattern of the deep chlorophyll maximum in the region of the Azores front. *Progress in Oceanography,* **14,** 129-165.

Fauchald, P. (2009) Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series,* **391,** 139-151.

Fauchald, P., Erikstad, K.E. & Skarsfjord, H. (2000) Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology,* **81,** 773-783.

Fauchald, P. & Tveraa, T. (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology,* **84,** 282-288.

Fauchald, P. & Tveraa, T. (2006) Hierarchical patch dynamics and animal movement pattern. *Oecologia,* **149,** 383-395.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S. & Frair, J.L. (2010) Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 2233-2244.

Fiedler, P.C. & Bernard, H.J. (1987) Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental shelf research,* **7,** 871-881.

Foote, A.D., Similä, T., Víkingsson, G.A. & Stevick, P.T. (2010) Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolutionary Ecology,* **24,** 803-814.

Fossette, S., Hobson, V.J., Girard, C., Calmettes, B., Gaspar, P., Georges, J.-Y. & Hays, G.C. (2010) Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *Journal of Marine systems,* **81,** 225-234.

Fossette, S., Schofield, G., Lilley, M.K.S., Gleiss, A.C. & Hays, G.C. (2012) Acceleration data reveal the energy management strategy of a marine ectotherm during reproduction. *Functional Ecology,* **26,** 324-333.

Fossette, S., Witt, M., Miller, P., Nalovic, M., Albareda, D., Almeida, A., Broderick, A., Chacón-Chaverri, D., Coyne, M. & Domingo, A. (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: Biological Sciences,* **281,** 20133065.

Fowler, S.L. (2005) *Cetorhinus maximus*. The IUCN Red List of Threatened Species. Version 2014.3.

Franks, P.J.S. (1992a) Phytoplankton blooms at fronts: patterns, scales, and physical forcing mechanisms. *Reviews in Aquatic Sciences,* **6,** 121-137.

Franks, P.J.S. (1992b) Sink or swim: accumulation of biomass at fronts. *Marine Ecology Progress Series,* **82,** 1-12.

Frederiksen, M., Moe, B., Daunt, F., Phillips, R.A., Barrett, R.T., Bogdanova, M.I., Boulinier, T., Chardine, J.W., Chastel, O. & Chivers, L.S. (2012) Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions,* **18,** 530-542.

Frick, M.G., Williams, K.L., Bolten, A.B., Bjorndal, K.A. & Martins, H.R. (2009) Foraging ecology of oceanic-stage loggerhead turtles Caretta caretta. *Endangered Species Research,* **9,** 91-97.

Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D. & Read, A.J. (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series,* **317,** 297-310.

Furness, R.W., Wade, H.M. & Masden, E.A. (2013) Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of environmental management,* **119,** 56-66.

Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P. & Richardson, A.J. (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution,* **24,** 360-369.

Garthe, S., Montevecchi, W.A., Chapdelaine, G., Rail, J.F. & Hedd, A. (2007) Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Marine Biology,* **151,** 687-694.

Garthe, S., Montevecchi, W.A. & Davoren, G.K. (2011) Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnology and Oceanography,* **56,** 802-812.

Gaspar, P., Georges, J.-Y., Fossette, S., Lenoble, A., Ferraroli, S. & Le Maho, Y. (2006) Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proceedings of the Royal Society B: Biological Sciences,* **273,** 2697-2702.

Genin, A., Jaffe, J.S., Reef, R., Richter, C. & Franks, P.J.S. (2005) Swimming against the flow: a mechanism of zooplankton aggregation. *Science,* **308,** 860-862.

Gillespie, D.M., Johnson, M., Harris, D. & Gkikopoulou, K. (2014) Small cetacean monitoring from surface and underwater autonomous vehicles. *The Journal of the Acoustical Society of America,* **136,** 2117-2117.

Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J., Mangel, J., Petersen, S., Piovano, S., Thomson, N. & Dalzell, P. (2008) Shark interactions in pelagic longline fisheries. *Marine Policy,* **32,** 1-18.

Godley, B., Bearhop, S., Cooke, S., Dixson, A., Hodgson, D., Marsh, H., Matthiopoulos, J., Wilson, R. & (Eds.) (2008) Tracking vertebrates for conservation. *Endangered Species Research [Special Issue],* **4**.

Godley, B.J., Richardson, S., Broderick, A.C., Coyne, M.S., Glen, F. & Hays, G.C. (2002) Long term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography,* **25,** 352-362.

Godø, O.R., Samuelsen, A., Macaulay, G.J., Patel, R., Hjøllo, S.S., Horne, J., Kaartvedt, S. & Johannessen, J.A. (2012) Mesoscale eddies are oases for higher trophic marine life. *PLoS ONE,* **7,** e30161.

González Carman, V., Acha, E.M., Maxwell, S.M., Albareda, D., Campagna, C. & Mianzan, H. (2014) Young green turtles, Chelonia mydas, exposed to plastic in a frontal area of the SW Atlantic. *Marine Pollution Bulletin,* **78,** 56-62.

Goold, J.C. (1998) Acoustic assessment of populations of common dolphin off the west Wales coast, with perspectives from satellite infrared imagery. *Journal of the Marine Biological Association of the United Kingdom,* **78,** 1353-1364.

Govoni, J.J. & Grimes, C.B. (1992) The surface accumulation of larval fishes by hydrodynamic convergence within the Mississippi River plume front. *Continental shelf research,* **12,** 1265-1276.

Graham, R.T., Witt, M.J., Castellanos, D.W., Remolina, F., Maxwell, S., Godley, B.J. & Hawkes, L.A. (2012) Satellite tracking of manta rays highlights challenges to their conservation. *PLoS ONE,* **7,** e36834.

Graham, W.M., Pages, F. & Hamner, W.M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia,* **451,** 199-212.

Granadeiro, J.P., Brickle, P. & Catry, P. (2014) Do individual seabirds specialize in fisheries' waste? The case of black-browed albatrosses foraging over the Patagonian Shelf. *Animal Conservation,* **17,** 19-26.

Grantham, H.S., Game, E.T., Lombard, A.T., Hobday, A.J., Richardson, A.J., Beckley, L.E., Pressey, R.L., Huggett, J.A., Coetzee, J.C., van der Lingen, C.D., Petersen, S.L., Merkle, D. & Possingham, H.P. (2011) Accommodating dynamic oceanographic processes and pelagic biodiversity in marine conservation planning. *PLoS ONE,* **6,** e16552.

Grecian, W.J., Inger, R., Attrill, M.J., Bearhop, S., Godley, B.J., Witt, M.J. & Votier, S.C. (2010) Potential impacts of wave-powered marine renewable energy installations on marine birds. *Ibis,* **152,** 683-697.

Gregory Lough, R. & Manning, J.P. (2001) Tidal-front entrainment and retention of fish larvae on the southern flank of Georges Bank. *Deep Sea Research Part II: Topical Studies in Oceanography,* **48,** 631-644.

Grémillet, D., Lewis, S., Drapeau, L., van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S. & Ryan, P.G. (2008) Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology,* **45,** 610-621.

Guisan, A. & Zimmerman, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling,* **135,** 147-186.

Hadfield, J.D. (2010) MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. *Journal of Statistical Software,* **33,** 1-22.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C. & Fox, H.E. (2008) A global map of human impact on marine ecosystems. *Science,* **319,** 948-952.

Hamer, K., Humphreys, E., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Phillips, R., Harris, M. & Wanless, S. (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series,* **338,** 5-305.

Hamer, K., Humphreys, E., Magalhaes, M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Skov, H. & Wanless, S. (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *Journal of Animal Ecology,* **78,** 880-889.

Haney, J.C. (1986a) Seabird affinities for Gulf Stream frontal eddies: responses of mobile marine consumers to episodic upwelling. *Journal of Marine Research,* **44,** 361-384.

Haney, J.C. (1986b) Seabird segregation at Gulf Stream frontal eddies. *Marine Ecology Progress Series,* **28,** 279-285.

Haney, J.C. & McGillivary, P.A. (1985) Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance. *Biological oceanography,* **3,** 401-430.

Hardin, J.W. & Hilbe, J.M. (2003) *Generalized Estimating Equations (GEE).* Chapman & Hall/CRC, Boca Raton, Florida.

Hartog, J.R., Hobday, A.J., Matear, R. & Feng, M. (2011) Habitat overlap between southern bluefin tuna and yellowfin tuna in the east coast longline fishery–implications for present and future spatial management. *Deep Sea Research Part II: Topical Studies in Oceanography,* **58,** 746-752.

Hatase, H., Omuta, K. & Tsukamoto, K. (2013) A mechanism that maintains alternative life histories in a loggerhead sea turtle population. *Ecology,* **94,** 2583-2594.

Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N. & Fujiwara, T. (2002) Size-related differences in feeding habitat use of adult female loggerhead turtles Caretta caretta around Japan determined by stable isotope analyses and satellite telemetry. *Marine Ecology Progress Series,* **233,** 273-281.

Hawkes, L.A., Broderick, A.C., Coyne, M.S., Godfrey, M.H., Lopez-Jurado, L.-F., Lopez-Suarez, P., Merino, S.E., Varo-Cruz, N. & Godley, B.J. (2006) Phenotypically Linked Dichotomy in Sea Turtle Foraging Requires Multiple Conservation Approaches. *Current Biology,* **16,** 990-995.

Hays, G.C., Christensen, A., Fossette, S., Schofield, G., Talbot, J. & Mariani, P. (2014) Route optimisation and solving Zermelo's navigation problem during long distance migration in cross flows. *Ecology Letters,* **17,** 137-143.

Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D. & Sims, D. (2006) Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology,* **87,** 2647-2656.

Hazen, E.L., Bograd, S., Suryan, R.M., Watanuki, Y. & Wilson, R. (2013a) Biophysical coupling of marine hotspots. *Marine Ecology Progress Series,* **487,** 176-304.

Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer, S.A., Dunne, J.P., Costa, D.P. & Crowder, L.B. (2013b) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change,* **3,** 234-238.

Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution,* **23,** 202-210.

Heithaus, M.R., Hamilton, I.M., Wirsing, A.J. & Dill, L.M. (2006) Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. *Journal of Animal Ecology,* **75,** 666-676.

Hernández-León, S., Almeida, C., Portillo-Hahnefeld, A., Gómez, M., Rodriguez, J. & Arístegui, J. (2002) Zooplankton biomass and indices of feeding and metabolism in relation to an upwelling filament off northwest Africa. *Journal of Marine Research,* **60,** 327-346.

Hijmans, R.J. & van Etten, J. (2012) raster: Geographic analysis and modelling with raster data. *R package version 2.0-08 http://CRAN.R-project.org/package=raster*.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling,* **199,** 142-152.

Hobday, A., Maxwell, S., Forgie, J., McDonald, J., Darby, M., Seto, K., Bailey, H., Bograd, S., Briscoe, D. & Costa, D. (2014) Dynamic ocean management: Integrating scientific and technological capacity with law, policy and management. *Stanford Environmental Law Journal,* **33,** 125-168.

Hobday, A.J. & Hartmann, K. (2006) Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fisheries Management and Ecology,* **13,** 365-380.

Højsgaard, S., Halekoh, U. & Yan, J. (2006) The R package geepack for Generalized Estimating Equations. *Journal of Statistical Software,* **15,** 1-11.

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., Cañadas, A., Hyrenbach, K.D., Corrigan, C., Polovina, J.J. & Reeves, R.R. (2011) Making protected area networks effective for marine top predators. *Endangered Species Research,* **13,** 203-218.

Howell, E.A., Dutton, P.H., Polovina, J.J., Bailey, H., Parker, D.M. & Balazs, G.H. (2010) Oceanographic influences on the dive behavior of juvenile loggerhead turtles (Caretta caretta) in the North Pacific Ocean. *Marine Biology,* **157,** 1011-1026.

Howell, E.A., Kobayashi, D.R., Parker, D.M., Balazs, G.H. & Polovina, J.J. (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles Caretta caretta in the Hawaii-based pelagic longline fishery. *Endangered Species Research,* **5,** 267-278.

Huin, N. & Prince, P. (1997) Diving behaviour of the grey-headed albatross. *Antarctic Science,* **9,** 243-249.

Humphries, N.E., Queiroz, N., Dyer, J.R., Pade, N.G., Musyl, M.K., Schaefer, K.M., Fuller, D.W., Brunnschweiler, J.M., Doyle, T.K. & Houghton, J.D. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature,* **465,** 1066-1069.

Humphries, N.E., Weimerskirch, H., Queiroz, N., Southall, E.J. & Sims, D.W. (2012) Foraging success of biological Lévy flights recorded in situ. *Proceedings of the National Academy of Sciences,* **109,** 7169-7174.

Hunt Jr, G., Mehlum, F., Russell, R., Irons, D., Decker, M. & Becker, P. (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. *Proc. 22nd Int. Ornithol. Congr.* (eds A. N.J. & R. Slotow), pp. 2040-2056. BirdLife South Africa, Durban.

Hunt Jr, G. & Schneider, D. (1987) Scale-dependent processes in the physical and biological environment of marine birds. *Seabirds: feeding ecology and role in marine ecosystems*, 7-41.

Hyrenbach, K.D., Forney, K.A. & Dayton, P.K. (2000) Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **10,** 437-458.

Illian, J.B., Sørbye, S.H. & Rue, H. (2012) A toolbox for fitting complex spatial point process models using integrated nested Laplace approximation (INLA). *The Annals of Applied Statistics,* **6,** 1499-1530.

Inger, R., Attrill, M.J., Bearhop, S., Broderick, A.C., James Grecian, W., Hodgson, D.J., Mills, C., Sheehan, E., Votier, S.C., Witt, M.J. & Godley, B.J. (2009) Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology*.

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 US west coast, with implications for management. *PLoS ONE,* **9,** e102959.

Jaeger, A., Jaquemet, S., Phillips, R.A., Wanless, R.M., Richard, P. & Cherel, Y. (2013) Stable isotopes document inter-and intra-specific variation in feeding ecology of nine large southern Procellariiformes. *Marine Ecology Progress Series,* **490,** 255-266.

Jiménez-Valverde, A. (2012) Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography,* **21,** 498-507.

Johnston, D. & Read, A. (2007) Flow-field observations of a tidally driven island wake used by marine mammals in the Bay of Fundy, Canada. *Fisheries Oceanography,* **16,** 422-435.

Joiris, C.R. & Dochy, O. (2013) A major autumn feeding ground for fin whales, southern fulmars and grey-headed albatrosses around the South Shetland Islands, Antarctica. *Polar Biology,* **36,** 1649-1658.

Jones, A., Hosegood, P., Wynn, R., De Boer, M., Butler-Cowdry, S. & Embling, C. (2014) Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. *Progress in Oceanography,* **128,** 30-48.

Jonsen, I.D., Flemming, J.M. & Myers, R.A. (2005) Robust state-space modeling of animal movement data. *Ecology,* **86,** 2874-2880.

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. *Proceedings of the Royal Society B: Biological Sciences,* **277,** 679-688.

Kahru, M., Di Lorenzo, E., Manzano-Sarabia, M. & Mitchell, B.G. (2012) Spatial and temporal statistics of sea surface temperature and chlorophyll fronts in the California Current. *Journal of Plankton Research,* **34,** 749-760.

Kahru, M., Håkansson, B. & Rud, O. (1995) Distributions of the sea-surface temperature fronts in the Baltic Sea as derived from satellite imagery. *Continental shelf research,* **15,** 663-679.

Kaltenberg, A.M., Emmett, R.L. & Benoit-Bird, K.J. (2010) Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. *Marine Ecology Progress Series,* **419,** 171-184.

Kappes, M.A., Shaffer, S.A., Tremblay, Y., Foley, D.G., Palacios, D.M., Robinson, P.W., Bograd, S.J. & Costa, D.P. (2010) Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress in Oceanography,* **86,** 246-260.

Kaschner, K., Watson, R., Trites, A. & Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series,* **316,** 285-310.

Kie, J.G. (2013) A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry,* **1,** 1-12.

Kobayashi, D., Polovina, J., Parker, D., Kamezaki, N., Cheng, I., Uchida, I., Dutton, P. & Balazs, G. (2008) Pelagic habitat characterization of loggerhead sea turtles, Caretta caretta, in the North Pacific Ocean (1997–2006): Insights from satellite tag tracking and remotely sensed data. *Journal of Experimental Marine Biology and Ecology,* **356,** 96-114.

Kobayashi, D.R., Farman, R., Polovina, J.J., Parker, D.M., Rice, M. & Balazs, G.H. (2014) "Going with the Flow" or Not: Evidence of Positive Rheotaxis in Oceanic Juvenile Loggerhead Turtles (Caretta caretta) in the South Pacific Ocean Using Satellite Tags and Ocean Circulation Data. *PLoS ONE,* **9,** e103701.

Langton, R., Davies, I. & Scott, B. (2011) Seabird conservation and tidal stream and wave power generation: Information needs for predicting and managing potential impacts. *Marine Policy,* **35,** 623-630.

Lascelles, B.G., Langham, G.M., Ronconi, R.A. & Reid, J.B. (2012) From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe. *Biological Conservation,* **156,** 5-14.

Le Fevre, J. (1986) Aspects of the biology of frontal systems. *Advances in Marine Biology,* **23,** 164-299.

Lecomte, J., Benoît, H., Etienne, M., Bel, L. & Parent, E. (2013) Modeling the habitat associations and spatial distribution of benthic macroinvertebrates: A hierarchical Bayesian model for zero-inflated biomass data. *Ecological Modelling,* **265,** 74-84.

Leeney, R.H., Witt, M.J., Broderick, A.C., Buchanan, J., Jarvis, D.S., Richardson, P.B. & Godley, B.J. (2012) Marine megavertebrates of Cornwall and the Isles of Scilly: relative abundance and distribution. *Journal of the Marine Biological Association of the United Kingdom,* **92,** 1823-1833.

Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydelis, R., McDonald, S., DiMatteo, A., Dunn, D.C. & Kot, C.Y. (2014) Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences,* **111,** 5271-5276.

Liang, K.-Y. & Zeger, S.L. (1986) Longitudinal data analysis using generalized linear models. *Biometrika,* **73,** 13-22.

Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography,* **17,** 145-151.

Louzao, M., Pinaud, D., Peron, C., Delord, K., Wiegand, T. & Weimerskirch, H. (2011) Conserving pelagic habitats: seascape modelling of an oceanic top predator. *Journal of Applied Ecology,* **48,** 121-132.

Luoto, M., Virkkala, R. & Heikkinen, R.K. (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecology and Biogeography,* **16,** 34-42.

Luschi, P., Hays, G.C. & Papi, F. (2003) A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos,* **103,** 293-302.

Luschi, P., Hughes, G.R., Mencacci, R., Bernardi, E., Sale, A., Broker, R., Bouwer, M. & Papi, F. (2003) Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open sea. *Marine Biology,* **143,** 793-801.

Manderson, J., Palamara, L., Kohut, J. & Oliver, M.J. (2011) Ocean observatory data are useful for regional-habitat modeling of species with different vertical habitat preferences. *Marine Ecology Progress Series,* **438,** 1-17.

Mansfield, K.L. & Putman, N.F. (2013) Oceanic Habits and Habitats: Caretta caretta. *The Biology of Sea Turtles* (eds J. Wyneken, K.J. Lohmann & J.A. Musick), pp. 189 - 210. CRC Press, Boca Raton, Florida, USA.

Mansfield, K.L., Saba, V.S., Keinath, J.A. & Musick, J.A. (2009) Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. *Marine Biology,* **156,** 2555-2570.

Mansfield, K.L., Wyneken, J., Porter, W.P. & Luo, J. (2014) First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. *Proceedings of the Royal Society B: Biological Sciences,* **281,** 20133039.

Maravelias, C.D. (1997) Trends in abundance and geographic distribution of North Sea herring in relation to environmental factors. *Marine Ecology Progress Series,* **159,** 151-164.

Marchand, C., Simard, Y. & Gratton, Y. (1999) Concentration of capelin (Mallotus villosus) in tidal upwelling fronts at the head of the Laurentian Channel in the St. Lawrence estuary. *Canadian Journal of Fisheries and Aquatic Sciences,* **56,** 1832-1848.

Marco, A., Abella, E., Liria-Loza, A., Martins, S., López, O., Jiménez-Bordón, S., Medina, M., Oujo, C., Gaona, P. & Godley, B. (2012) Abundance and exploitation of loggerhead turtles nesting in Boa Vista island, Cape Verde: the only substantial rookery in the eastern Atlantic. *Animal Conservation,* **15,** 351-360.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions,* **15,** 59-69.

Marshall, C.E., Glegg, G.A. & Howell, K.L. (2014) Species distribution modelling to support marine conservation planning: The next steps. *Marine Policy,* **45,** 330-332.

Martin, A. (1989) The diet of Atlantic Puffin Fratercula arctica and Northern Gannet Sula bassana chicks at a Shetland colony during a period of changing prey availability. *Bird Study,* **36,** 170-180.

Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern, B.S., Breed, G.A., Nickel, B., Teutschel, N.M., Crowder, L.B., Benson, S., Dutton, P.H., Bailey, H., Kappes, M.A., Kuhn, C.E., Weise, M.J., Mate, B., Shaffer, S.A., Hassrick, J.L., Henry, R.W., Irvine, L.M., McDonald, B.I., Robinson, P.W., Block, B.A. & Costa, D.P. (2013) Cumulative human impacts on marine predators. *Nature Communications,* **4,** 2688.

McCarthy, A.L., Heppell, S., Royer, F., Freitas, C. & Dellinger, T. (2010) Identification of likely foraging habitat of pelagic loggerhead sea turtles (*Caretta caretta*) in the North Atlantic through analysis of telemetry track sinuosity. *Progress in Oceanography,* **86,** 224-231.

McClellan, C.M., Braun-McNeill, J., Avens, L., Wallace, B.P. & Read, A.J. (2010) Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. *Journal of Experimental Marine Biology and Ecology,* **387,** 44-51.

Mcginty, N., Johnson, M.P. & Power, A.M. (2014) Spatial mismatch between phytoplankton and zooplankton biomass at the Celtic Boundary Front. *Journal of Plankton Research,* **36,** 1446-1460.

McIntyre, T., Ansorge, I., Bornemann, H., Plötz, J., Tosh, C. & Bester, M. (2012) Elephant seal foraging dives do indeed track prey distribution, but temperature influences the distribution of prey: Reply to Boersch-Supan et al. (2012). *Marine Ecology Progress Series,* **461,** 299-303.

McKinney, J.A., Hoffmayer, E.R., Wu, W., Fulford, R. & Hendon, J. (2012) Feeding habitat of the whale shark Rhincodon typus in the northern Gulf of Mexico determined using species distribution modelling. *Marine Ecology Progress Series,* **458,** 199-211.

Mendes, S., Turrell, W., Lütkebohle, T. & Thompson, P.M. (2002) Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. *Marine Ecology Progress Series,* **239,** 221-229.

Merow, C., Smith, M.J. & Silander, J.A. (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography,* **36,** 1058-1069.

Miller, P. (2009) Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. *Journal of Marine systems,* **78,** 327-336.

Miller, P.I. & Christodoulou, S. (2014) Frequent locations of ocean fronts as an indicator of pelagic diversity: application to marine protected areas and renewables. *Marine Policy,* **45,** 318-329.

Miller, P.I., Read, J.F. & Dale, A.C. (2013) Thermal front variability along the North Atlantic Current observed using microwave and infrared satellite data. *Deep Sea Research Part II: Topical Studies in Oceanography,* **98,** 244-256.

Morato, T., Hoyle, S.D., Allain, V. & Nicol, S.J. (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences,* **107,** 9707-9711.

Moyano, M., Rodríguez, J.M., Benítez-Barrios, V.M. & Hernández-León, S. (2014) Larval fish distribution and retention in the Canary Current system during the weak upwelling season. *Fisheries Oceanography,* **23,** 191-209.

Muller-Karger, F., Roffer, M., Walker, N., Oliver, M., Schofield, O., Abbott, M., Graber, H., Leben, R. & Goni, G. (2013) Satellite Remote Sensing in Support of an Integrated Ocean Observing System. *Geoscience and Remote Sensing Magazine, IEEE,* **1,** 8-18.

Munk, P. (2002) Distribution of the Early Larval Stages of Cod, Plaice and Lesser Sandeel across Haline Fronts in the North Sea. *Estuarine, Coastal and Shelf Science,* **55,** 139-149.

Myers, R.A. & Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature,* **423,** 280-283.

Navarro, J. & González-Solís, J. (2009) Environmental determinants of foraging strategies in Cory's shearwaters Calonectris diomedea. *Marine Ecology Progress Series,* **378,** 259-267.

Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G. & Klages, N.T.W. (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Marine Ecology Progress Series,* **217,** 15-26.

Nevitt, G.A. & Bonadonna, F. (2005) Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biology letters,* **1,** 303-305.

Nevitt, G.A., Losekoot, M. & Weimerskirch, H. (2008) Evidence for olfactory search in wandering albatross, Diomedea exulans. *Proceedings of the National Academy of Sciences,* **105,** 4576-4581.

Nur, N., Jahncke, J., Herzog, M.P., Howar, J., Hyrenbach, K.D., Zamon, J.E., Ainley, D.G., Wiens, J.A., Morgan, K. & Ballance, L.T. (2011) Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. *Ecological Applications,* **21,** 2241-2257.

Olden, J.D., Lawler, J.J. & Poff, N.L. (2008) Machine learning methods without tears: a primer for ecologists. *The Quarterly review of biology,* **83,** 171-193.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I. & Louzao, M. (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation,* **156,** 94-104.

Owen, R.W. (1981) Fronts and Eddies in the Sea: Mechanisms, Interactions and Biological Effects. *Analysis of marine ecosystems* (ed. A.R. Longhurst), pp. 197-233. Academic Press, New York.

Pade, N.G., Queiroz, N., Humphries, N.E., Witt, M.J., Jones, C.S., Noble, L.R. & Sims, D.W. (2009) First results from satellite-linked archival tagging of porbeagle shark, Lamna nasus: area fidelity, wider-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology,* **370,** 64-74.

Palacios, D., Bograd, S., Foley, D. & Schwing, F. (2006) Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. *Deep Sea Research Part II: Topical Studies in Oceanography,* **53,** 250-269.

Pan, W. (2004) Akaike's information criterion in generalized estimating equations. *Biometrics,* **57,** 120-125.

Panigada, S., Zanardelli, M., MacKenzie, M., Donovan, C., Mélin, F. & Hammond, P.S. (2008) Modelling habitat preferences for fin whales and striped dolphins in the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. *Remote Sensing of Environment,* **112,** 3400-3412.

Patrick, S., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W.J., Bodey, T.W., Hamer, K.C., Wakefield, E., Le Nuz, M. & Votier, S.C. (2014) Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos,* **123,** 33-40.

Patrick, S.C. & Weimerskirch, H. (2014) Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. *Biology letters,* **10,** 20140630.

Patterson, T., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008) State–space models of individual animal movement. *Trends in Ecology & Evolution,* **23,** 87-94.

Patterson, T.A., Basson, M., Bravington, M.V. & Gunn, J.S. (2009) Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology,* **78,** 1113-1123.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres Jr, F. (1998) Fishing down marine food webs. *Science,* **279,** 860-863.

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. *Scottish Natural Heritage Commissioned Report No. 573*.

Peck, D.R., Smithers, B.V., Krockenberger, A.K. & Congdon, B.C. (2004) Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. *Marine Ecology Progress Series,* **281,** 259-266.

Pennino, M.G., Muñoz, F., Conesa, D., López-Quílez, A. & Bellido, J.M. (2013) Modeling sensitive elasmobranch habitats. *Journal of Sea Research,* **83,** 209-218.

Petersen, S.L., Phillips, R.A., Ryan, P.G. & Underhill, L.G. (2008) Albatross overlap with fisheries in the Benguela Upwelling System: implications for conservation and management. *Endangered Species Research,* **5,** 117-127.

Pettex, E., Bonadonna, F., Enstipp, M., Siorat, F. & Grémillet, D. (2010) Northern gannets anticipate the spatio–temporal occurrence of their prey. *Journal of Experimental Biology,* **213,** 2365-2371.

Phillips, R., Silk, J., Croxall, J., Afanasyev, V. & Briggs, D. (2004a) Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series,* **266,** 265-272.

Phillips, R.A., McGill, R.A., Dawson, D.A. & Bearhop, S. (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Marine Biology,* **158,** 2199-2208.

Phillips, R.A., Silk, J.R., Croxall, J.P. & Afanasyev, V. (2006) Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biological Conservation,* **129,** 336-347.

Phillips, R.A., Silk, J.R., Croxall, J.P., Afanasyev, V. & Bennett, V.J. (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology,* **86,** 2386-2396.

Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P. & Croxall, J.P. (2004b) Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **271,** 1283-1291.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications,* **19,** 181-197.

Piatt, J.F., Wetzel, J., Bell, K., DeGange, A.R., Balogh, G.R., Drew, G.S., Geernaert, T., Ladd, C. & Byrd, G.V. (2006) Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. *Deep Sea Research Part II: Topical Studies in Oceanography,* **53,** 387-398.

Pichegru, L., Ryan, P., Le Bohec, C., van der Lingen, C., Navarro, R., Petersen, S., Lewis, S., van der Westhuizen, J. & Grémillet, D. (2009) Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine Ecology Progress Series,* **391,** 199-208.

Pikesley, S.K., Broderick, A.C., Cejudo, D., Coyne, M.S., Godfrey, M.H., Godley, B.J., Lopez, P., López-Jurado, L.F., Merino, S.E., Varo-Cruz, N., Witt, M.J. & Hawkes, L.A. (2014) Modelling the niche for a marine vertebrate: a case study incorporating behavioural plasticity, proximate threats and climate change. *Ecography***,** In Press.

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

Pinaud, D. (2008) Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems. *Journal of Applied Ecology,* **45,** 91-99.

Pinaud, D., Cherel, Y. & Weimerskirch, H. (2005) Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Marine Ecology Progress Series,* **298,** 295-304.

Pinaud, D. & Weimerskirch, H. (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *Journal of Animal Ecology,* **76,** 9-19.

Pingree, R. (1975) The advance and retreat of the thermocline on the continental shelf. *Journal of the Marine Biological Association of the United Kingdom,* **55,** 965-974.

Pingree, R. & Griffiths, D. (1978) Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical Research,* **83,** 4615-4622.

Pirotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L. & Rendell, L. (2011) Modelling sperm whale habitat preference: a novel approach combining transect and follow data. *Marine Ecology Progress Series,* **436,** 257-272.

Pirotta, E., Thompson, P.M., Miller, P.I., Brookes, K.L., Cheney, B., Barton, T.R., Graham, I.M. & Lusseau, D. (2013) Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. *Functional Ecology,* **28,** 206-217.

Podestá, G.P., Browder, J.A. & Hoey, J.J. (1993) Exploring the association between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. *Continental shelf research,* **13,** 253-277.

Polovina, J., Uchida, I., Balazs, G., Howell, E.A., Parker, D. & Dutton, P. (2006) The Kuroshio Extension Bifurcation Region: A pelagic hotspot for juvenile loggerhead sea turtles. *Deep Sea Research Part II: Topical Studies in Oceanography,* **53,** 326-339.

Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P. & Dutton, P.H. (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography,* **13,** 36-51.

Polovina, J.J., Howell, E., Kobayashi, D. & Seki, M.P. (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography,* **49,** 469-483.

Polovina, J.J., Howell, E., Parker, D.M. & Balazs, G.H. (2003) Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: Might deep longline sets catch fewer turtles? *Fisheries Bulletin,* **101,** 189-193.

Polovina, J.J., Kobayashi, D.B., Parker, D.M., Seki, M.P. & Balazs, G. (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997-1998. *Fisheries Oceanography,* **9,** 71-82.

Poncet, S., Robertson, G., Phillips, R.A., Lawton, K., Phalan, B., Trathan, P.N. & Croxall, J.P. (2006) Status and distribution of wandering, black-browed and grey-headed albatrosses breeding at South Georgia. *Polar Biology,* **29,** 772-781.

Priede, I. & Miller, P. (2009) A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing II: New analysis reveals orientation to a thermal front. *Fisheries Research,* **95,** 370-372.

Queiroz, N., Humphries, N.E., Noble, L.R., Santos, A.M. & Sims, D.W. (2012) Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLoS ONE,* **7,** e32374.

Ralston, S. (2002) West coast groundfish harvest policy. *North American Journal of Fisheries Management,* **22,** 249-250.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography,* **33,** 1689-1703.

Rees, A.L.F., Saady, S.A., Broderick, A.C., Coyne, M.S., Papathanasopoulou, N. & Godley, B.J. (2010) Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles Caretta caretta. *Marine Ecology Progress Series,* **418,** 201-212.

Regular, P.M., Hedd, A. & Montevecchi, W.A. (2013) Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Animal Behaviour,* **86,** 545-552.

Reich, K., Bjorndal, K., Frick, M., Witherington, B., Johnson, C. & Bolten, A. (2010) Polymodal foraging in adult female loggerheads (*Caretta caretta*). *Marine Biology,* **157,** 113-121.

Reid, K., Croxall, J. & Prince, P. (1996) The fish diet of black-browed albatrossDiomedea melanophris and grey-headed albatrossD. Chrysostoma at South Georgia. *Polar Biology,* **16,** 469-477.

Reid, K. & Croxall, J.P. (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **268,** 377-384.

Robbins, J., Rosa, L.D., Allen, J.M., Mattila, D.K., Secchi, E.R., Friedlaender, A.S., Stevick, P.T., Nowacek, D.P. & Steel, D. (2011) Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: a seasonal migration record. *Endangered Species Research,* **13,** 117-121.

Robinson, L., Elith, J., Hobday, A., Pearson, R., Kendall, B., Possingham, H. & Richardson, A. (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography,* **20,** 789-802.

Robinson, P.W., Costa, D.P., Crocker, D.E., Gallo-Reynoso, J.P., Champagne, C.D., Fowler, M.A., Goetsch, C., Goetz, K.T., Hassrick, J.L. & Hückstädt, L.A. (2012) Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PLoS ONE,* **7,** e36728.

Rodhouse, P., Prince, P., Clarke, M. & Murray, A. (1990) Cephalopod prey of the grey-headed albatrossDiomedea chrysostoma. *Marine Biology,* **104,** 353-362.

Rodhouse, P.G. & Boyle, P.R. (2010) Large aggregations of pelagic squid near the ocean surface at the Antarctic Polar Front, and their capture by grey-headed albatrosses. *ICES Journal of Marine Science,* **67,** 1432-1435.

Rodhouse, P.G. & White, M.G. (1995) Cephalopods Occupy the Ecological Niche of Epipelagic Fish in the Antarctic Polar Frontal Zone. *The Biological Bulletin,* **189,** 77-80.

Rodrıguez, J., Hernández-León, S. & Barton, E. (1999) Mesoscale distribution of fish larvae in relation to an upwelling filament off Northwest Africa. *Deep Sea Research Part I: Oceanographic Research Papers,* **46,** 1969-1984.

Rue, H., Martino, S. & Chopin, N. (2009) Approximate Bayesian inference for latent Gaussian models using integrated nested Laplace approximations. *Journal of the Royal Statistical Society, Series B,* **71,** 319-392.

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G. & Fuller, R.A. (2014) Conserving mobile species. *Frontiers in Ecology and the Environment,* **12,** 395-402.

Russell, D.J., Brasseur, S.M., Thompson, D., Hastie, G.D., Janik, V.M., Aarts, G., McClintock, B.T., Matthiopoulos, J., Moss, S.E. & McConnell, B. (2014) Marine mammals trace anthropogenic structures at sea. *Current Biology,* **24,** R638-R639.

Ryan, J.P., Yoder, J.A. & Cornillon, P.C. (1999) Enhanced chlorophyll at the shelfbreak of the Mid-Atlantic Bight and Georges Bank during the spring transition. *Limnology and Oceanography,* **44,** 1-11.

Ryan, P.G., Phillips, R.A., Nel, D.C. & Wood, A.G. (2007) Breeding frequency in Grey-headed Albatrosses *Thalassarche chrysostoma*. *Ibis,* **149,** 45-52.

Sabarros, P.S., Grémillet, D., Demarcq, H., Moseley, C., Pichegru, L., Mullers, R.H., Stenseth, N.C. & Machu, E. (2013) Fine-scale recognition and use of mesoscale fronts by foraging Cape gannets in the Benguela upwelling region. *Deep Sea Research Part II: Topical Studies in Oceanography,* **107,** 77-84.

Sabatés, A. & Masó, M. (1990) Effect of a shelf-slope front on the spatial distribution of mesopelagic fish larvae in the western Mediterranean. *Deep Sea Research Part A. Oceanographic Research Papers,* **37,** 1085-1098.

Santora, J.A. & Veit, R.R. (2013) Spatio-temporal persistence of top predator hotspots near the Antarctic Peninsula. *Mar Ecol Prog Ser,* **487,** 287-304.

Scales, K.L., Miller, P.I., Embling, C.B., Ingram, S.N., Pirotta, E. & Votier, S.C. (2014a) Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of The Royal Society Interface,* **11,** 20140679.

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. & Votier, S.C. (2014b) On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology,* **51,** 1575 - 1583.

Scheffer, A., Bost, C. & Trathan, P. (2012) Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. *Marine Ecology Progress Series,* **465,** 281-297.

Schick, R., Goldstein, J. & Lutcavage, M. (2004) Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). *Fisheries Oceanography,* **13,** 225-238.

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M. & Clark, J.S. (2008) Understanding movement data and movement processes: current and emerging directions. *Ecology Letters,* **11,** 1338-1350.

Schneider, D.C. (1990) Seabirds and fronts: a brief overview. *Polar Research,* **8,** 17-21.

Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K., Katselidis, K.A. & Hays, G.C. (2010) Biodiversity Research: fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Diversity and Distributions,* **16,** 840-853.

Schroeder, B.A., Foley, A.M. & Bagley, D.A. (2003) Nesting patterns, reproductive migrations, and adult foraging areas of loggerhead turtles. *Loggerhead Sea Turtles* (eds A.B. Bolten & B.E. Witherington), pp. 114-124. Smithsonian Institution Press, Washington DC.

Scott, B., Sharples, J., Wanless, S., Ross, O.N., Frederiksen, M. & Daunt, F. (2006) The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. *Top Predators in Marine Ecosystems: their Role in Monitoring and Management* (eds I.L. Boyd, S. Wanless & C.J. Camphuysen), pp. 46-62. Cambridge University Press, Cambridge, UK.

Scott, B., Webb, A., Palmer, M., Embling, C. & Sharples, J. (2013) Fine scale bio-physical oceanographic characteristics predict the foraging occurrence of contrasting seabird species; Gannet (*Morus bassanus*) & Storm Petrel (*Hydrobates pelagicus*). *Progress in Oceanography,* **117,** 118-129.

Scott, B.E., Langton, R., Philpott, E. & Waggitt, J.J. (2014) Seabirds and marine renewables: Are we asking the right questions? *Marine Renewable Energy Technology and Environmental Interactions*, pp. 81-92. Springer.

Scott, B.E., Sharples, J., Ross, O.N., Wang, J., Pierce, G.J. & Camphuysen, C.J. (2010) Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Marine Ecology Progress Series,* **408,** 207-226.

Scott, R., Marsh, R. & Hays, G. (2014) Ontogeny of long distance migration. *Ecology,* **95,** 2840-2850.

Seki, M.P., Polovina, J.J., Kobayashi, D.R., Bidigare, R.R. & Mitchum, G.T. (2002) An oceanographic characterization of swordfish (*Xiphias gladius*) longline fishing grounds in the springtime subtropical North Pacific. *Fisheries Oceanography,* **11,** 251-266.

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.

Shanks, A.L., Largier, J., Brink, L., Brubaker, J. & Hooff, R. (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnology and Oceanography,* **45,** 230-236.

Sheppard, C., Ateweberhan, M., Bowen, B., Carr, P., Chen, C., Clubbe, C., Craig, M., Ebinghaus, R., Eble, J. & Fitzsimmons, N. (2012) Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **22,** 232-261.

Shillinger, G.L., Hazen, E.L., Bailey, H., Bograd, S.J., Godley, B.J., Wilson, R.P., Gaspar, P., Hamann, M., Spotila, J.R. & (Eds.) (2012) Tagging through the stages: ontogeny in biologging. *Marine Ecology Progress Series [Special Issue],* **457,** 163-301.

Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., Eckert, S.A. & Block, B.A. (2008) Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biology,* **6,** e171.

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.

Silverman, E.D., Veit, R.R. & Nevitt, G.A. (2004) Nearest neighbors as foraging cues: information transfer in a patchy environment. *Marine Ecology Progress Series,* **277,** 25-36.

Simpson, J.H. & Sharples, J. (2012) *Introduction to the physical and biological oceanography of shelf seas*. Cambridge University Press, Cambridge.

Sims, D. (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., 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. & Merrett, D.A. (1997) Determination of zooplankton charactersitics in the presence of surface feeding basking sharks *Cetorhinus maximus*. *Marine Ecology Progress Series,* **158,** 297-302.

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

Sims, D., 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. (1999) Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **266,** 1437-1443.

Sims, D.W., Humphries, N.E., Bradford, R.W. & Bruce, B.D. (2012) Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of Animal Ecology,* **81,** 432-442.

Sims, D.W., Queiroz, N., Humphries, N.E., Lima, F.P. & Hays, G.C. (2009) Long-term GPS tracking of ocean sunfish *Mola mola* offers a new direction in fish monitoring. *PLoS ONE,* **4,** e7351.

Sims, D.W. & Southall, E.J. (2002) Occurrence of ocean sunfish, *Mola mola* near fronts in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom,* **82,** 927-928.

Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J. & Metcalfe, J.D. (2008) Scaling laws of marine predator search behaviour. *Nature,* **451,** 1098-1102.

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: Biological Sciences,* **267,** 1897-1904.

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: Biological Sciences,* **273,** 1195-1201.

Singh, N.J. & Milner-Gulland, E.J. (2011) Conserving a moving target: planning protection for a migratory species as its distribution changes. *Journal of Applied Ecology,* **48,** 35-46.

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.

Skov, H. & Durinck, J. (1998) Constancy of frontal aggregations of seabirds at the shelf break in the Skagerrak. *Journal of Sea Research,* **39,** 305-311.

Skov, H., Gunnlaugsson, T., Budgell, W., Horne, J., Nøttestad, L., Olsen, E., Søiland, H., Víkingsson, G. & Waring, G. (2008) Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. *Deep Sea Research Part II: Topical Studies in Oceanography,* **55,** 254-268.

Skov, H. & Prins, E. (2001) Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. *Marine Ecology Progress Series,* **214,** 279-287.

Smith, S., Jones, B., Atkinson, L. & Brink, K. (1986) Zooplankton in the upwelling fronts off Pt. Conception, California. *Elsevier Oceanography Series,* **42,** 195-213.

Southall, E.J., Sims, D., Metcalfe, J.D., Doyle, J.I., Fanshaw, 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 United Kingdom,* **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.

Spear, L.B., Ballance, L.T. & Ainley, D.G. (2001) Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Marine Ecology Progress Series,* **219,** 275-289.

Springer, A.M., McRoy, C.P. & Flint, M.V. (1996) The Bering Sea Green Belt: shelf-edge processes and ecosystem production. *Fisheries Oceanography,* **5,** 205-223.

Stevens, J.D. (2007) Whale shark (Rhincodon typus) biology and ecology: A review of the primary literature. *Fisheries Research,* **84,** 4-9.

Stevick, P.T., Incze, L.S., Kraus, S.D., Rosen, S., Wolff, N. & Baukus, A. (2008) Trophic relationships and oceanography on and around a small offshore bank. *Marine Ecology Progress Series,* **363,** 15-28.

Storch, I. (2002) On spatial resolution in habitat models: can small-scale forest structure explain capercaillie numbers? *Conservation Ecology,* **6,** 6.

Suberg, L., Wynn, R.B., van der Kooij, J., Fernand, L., Fielding, S., Guihen, D., Gillespie, D., Johnson, M., Gkikopoulou, K.C. & Allan, I.J. (2014) Assessing the potential of autonomous submarine gliders for ecosystem monitoring across multiple trophic levels (plankton to cetaceans) and pollutants in shallow shelf seas. *Methods in Oceanography,* **10,** 70-89.

Sumaila, U.R., Zeller, D., Watson, R., Alder, J. & Pauly, D. (2007) Potential costs and benefits of marine reserves in the high seas. *Marine Ecology Progress Series,* **345,** 305-310.

Sydeman, W., Brodeur, R., Grimes, C., Bychkov, A. & McKinnell, S. (2006) Marine habitat "hotspots" and their use by migratory species and top predators in the North Pacific Ocean: Introduction. *Deep Sea Research Part II: Topical Studies in Oceanography,* **53,** 247-249.

Tancell, C., Phillips, R.A., Xavier, J.C., Tarling, G.A. & Sutherland, W.J. (2013) Comparison of methods for determining key marine areas from tracking data. *Marine Biology,* **160,** 15-26.

Teo, S.L.H. & Block, B.A. (2010) Comparative Influence of Ocean Conditions on Yellowfin and Atlantic Bluefin Tuna Catch from Longlines in the Gulf of Mexico. *PLoS ONE,* **5,** e10756.

Tew Kai, E., Rossi, V., Sudre, J., Weimerskirch, H., Lopez, C., Hernandez-Garcia, E., Marsac, F. & Garçon, V. (2009) Top marine predators track Lagrangian coherent structures. *Proceedings of the National Academy of Sciences,* **106,** 8245.

Thibaud, E., Petitpierre, B., Broennimann, O., Davison, A.C. & Guisan, A. (2014) Measuring the relative effect of factors affecting species distribution model predictions. *Methods in Ecology and Evolution,* **5,** 947-955.

Thiebault, A., Mullers, R.H., Pistorius, P.A. & Tremblay, Y. (2014) Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology,* **25,** 1302-1310.

Thompson, S.A., Sydeman, W.J., Santora, J.A., Black, B.A., Suryan, R.M., Calambokidis, J., Peterson, W.T. & Bograd, S.J. (2012) Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. *Progress in Oceanography,* **101,** 106-120.

Thorne, L. & Read, A. (2013) Fine-scale biophysical interactions drive prey availability at a migratory stopover site for Phalaropus spp. in the Bay of Fundy, Canada. *Marine Ecology Progress Series,* **487,** 261-273.

Thuiller, W., Georges, D. & Engler, R. (2014) biomod2: Ensemble platform for species distribution modeling.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography,* **32,** 369-373.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature,* **466,** 1098-1101.

Todd Jones, T. & Seminoff, J.A. (2013) Feeding Biology: Advances from Field-Based Observations, Physiological Studies, and Molecular Techniques. *The Biology of Sea Turtles* (eds J. Wyneken, K.J. Lohmann & J.A. Musick), pp. 211 - 247. CRC Press, Boca Raton, Florida, USA.

Todd Jones, 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.

Toonen, R.J., Wilhelm, T.A., Maxwell, S.M., Wagner, D., Bowen, B.W., Sheppard, C.R.C., Taei, S.M., Teroroko, T., Moffitt, R., Gaymer, C.F., Morgan, L., Lewis, N.a., Sheppard, A.L.S., Parks, J. & Friedlander, A.M. (2013) One size does not fit all: The emerging frontier in large-scale marine conservation. *Marine Pollution Bulletin,* **77,** 7-10.

Torres, L.G., Read, A.J. & Halpin, P. (2008) Fine-scale habitat modelling of a top marine predator: Do prey data improve predictive capacity? *Ecological Applications,* **18,** 1702-1717.

Torres, L.G., Sutton, P., Thompson, D.R., Delord, K., Weimerskirch, H., Sagar, P.M., Sommer, E., Dilley, B.J., Ryan, P.G. & Phillips, R.A. (*In Press*) Poor transferability of species distribution models for a pelagic predator, the grey petrel, indicates contrasting habitat preferences across ocean basins. *PLoS ONE*.

Traganza, E.D., Redalije, D.G. & Garwood, R.W. (1987) Chemical flux, mixed layer entrainment and phytoplankton blooms at upwelling fronts in the California coastal zone. *Continental shelf research,* **7,** 89-105.

Trathan, P., Brandon, M. & Murphy, E. (1997) Characterization of the Antarctic Polar Frontal Zone to the north of South Georgia in summer 1994. *Journal of Geophysical Research: Oceans (1978–2012),* **102,** 10483-10497.

Tremblay, Y., Thiebault, A., Mullers, R. & Pistorius, P. (2014) Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS ONE,* **9,** e88424.

Tynan, C.T., Ainley, D.G., Barth, J.A., Cowles, T.J., Pierce, S.D. & Spear, L.B. (2005) Cetacean distributions relative to ocean processes in the northern California Current System. *Deep Sea Research Part II: Topical Studies in Oceanography,* **52,** 145-167.

Ullman, D.S., Cornillon, P.C. & Shan, Z. (2007) On the characteristics of subtropical fronts in the North Atlantic. *J. Geophys. Res.,* **112,** C01010.

Ullmann, D.S. & Cornillon, P.C. (2000) Evaluation of front detection methods for satellite-derived SST data using in situ observations. *Journal of Atmospheric and Oceanic Technology,* **17,** 1667-1675.

Van der Kooij, J., Scott, B. & Mackinson, S. (2008) The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. *Journal of Sea Research,* **60,** 201-209.

Varo-Cruz, N., Hawkes, L.A., Cejudo, D., López, P., Coyne, M.S., Godley, B.J. & López-Jurado, L.F. (2013) Satellite tracking derived insights into migration and foraging strategies of male loggerhead turtles in the eastern Atlantic. *Journal of Experimental Marine Biology and Ecology,* **443,** 134-140.

Vasquez, J., Hamilton, M., Van Tran, A. & Sumagausay, R. (1994) JPL physical oceanography DAAC reprocesses 10 years of sea-surface temperature measurements from NOAA AVHRR. *The Earth Observer,* **ESA 6,** 16-17.

Vilchis, L.I., Ballance, L.T. & Fiedler, P.C. (2006) Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. *Marine Ecology Progress Series,* **315,** 279-292.

Visnawathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Prince, P.A. & Stanley, H.E. (1996) Levy flight search patterns of wandering albatrosses. *Nature,* **381,** 413-415.

Votier, S., Grecian, W., Patrick, S. & Newton, J. (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology,* **158,** 355-362.

Votier, S.C., Bearhop, S., Witt, M.J., Inger, R., Thompson, D. & Newton, J. (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology,* **47,** 487-497.

Votier, S.C., Bicknell, A., Cox, S.L., Scales, K.L. & Patrick, S.C. (2013) A bird's eye view of discard reforms: bird-borne cameras reveal seabird/fishery interactions. *PLoS ONE,* **8,** e57376.

Wade, P.R. (2000) Bayesian methods in conservation biology. *Conservation Biology,* **14,** 1308-1316.

Waggitt, J. & Scott, B. (2014) Using a spatial overlap approach to estimate the risk of collisions between deep diving seabirds and tidal stream turbines: A review of potential methods and approaches. *Marine Policy,* **44,** 90-97.

Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J., Grémillet, D. & Jackson, A.L. (2013) Space partitioning without territoriality in gannets. *Science,* **341,** 68-70.

Wakefield, E.D., Phillips, R.A. & Belchier, M. (2012) Foraging black-browed albatrosses target waters overlaying moraine banks-a consequence of upward benthic-pelagic coupling? *Antarctic Science,* **24,** 269-280.

Wakefield, E.D., Phillips, R.A. & Matthiopoulos, J. (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series,* **391,** 165-182.

Wakefield, E.D., Phillips, R.A., Trathan, P.N., Arata, J., Gales, R., Huin, N., Robertson, G., Waugh, S.M., Weimerskirch, H. & Matthiopoulos, J. (2011) Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs,* **81,** 141-167.

Waring, G., Hamazaki, T., Sheehan, D., Wood, G. & Baker, S. (2001) Characterization of beaked whale (*Ziphiidae*) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast US. *Marine Mammal Science,* **17,** 703-717.

Warton, D. & Aarts, G. (2013) Advancing our thinking in presence-only and used-available analysis. *Journal of Animal Ecology,* **82,** 1125-1134.

Weimerskirch, H. (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography,* **54,** 211-223.

Weimerskirch, H., Bartle, J.A., Jouventin, P. & Stahl, J.C. (1988) Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor,* **90,** 214-219.

Weimerskirch, H., Gault, A. & Cherel, Y. (2005) Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology,* **86,** 2611-2622.

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. & Costa, D. (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **267,** 1869-1874.

Weimerskirch, H., Mougey, T. & Hindermeyer, X. (1997) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology,* **8,** 635.

Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *The Auk,* **110,** 325-342.

Weir, C.R. & O'Brien, S.H. (2000) Association of the harbour porpoise (*Phocoena phocoena*) with the western Irish sea front in: PGH Evans, R. Pitt-Aiken & E. Rogan. *European Research on Cetaceans,* **14,** 61-65.

Williams, G., Hindell, M., Houssais, M.-N., Tamura, T. & Field, I. (2011) Upper ocean stratification and sea ice growth rates during the summer-fall transition, as revealed by Elephant seal foraging in the Adélie Depression, East Antarctica. *Ocean Science,* **7,** 185-202.

Williamson, B., Scott, B., Waggitt, J., Blondel, P., Armstrong, E., Hall, C. & Bell, P. (2014) Using the FLOWBEC seabed frame to understand underwater interactions between diving seabirds, prey, hydrodynamics and tidal and wave energy structures. *Proceedings of the 2nd EIMR conference, 28 April–02 May 2014, Stornoway, Isle of Lewis, Outer Hebrides, Scotland*.

Wingfield, D.K., Peckham, S.H., Foley, D.G., Palacios, D.M., Lavaniegos, B.E., Durazo, R., Nichols, W.J., Croll, D.A. & Bograd, S.J. (2011) The making of a productivity hotspot in the coastal ocean. *PLoS ONE,* **6,** e27874.

Witherington, B. (2002) Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. *Marine Biology,* **140,** 843-853.

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., Broderick, A.C., Johns, D.J., Martin, C., Penrose, R., Hoogmoed, M.A. & Godley, B.J. (2007) Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Marine Ecology Progress Series,* **337,** 231-244.

Witt, M.J. & Godley, B.J. (2007) A step towards seascape scale conservation: Using Vessel Monitoring Systems (VMS) to map fishing activity. *PLoS ONE,* **2,** e1111.

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. (2012) Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters. *Marine Ecology Progress Series,* **459,** 121-134.

Wolanski, E. & Hamner, W.M. (1988) Topographically controlled fronts in the ocean and their biological significance. *Science,* **241,** 177-181.

Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R.* Chapman and Hall/CRC.

Worm, B., Sandow, M., Oschlies, A., Lotze, H.K. & Myers, R.A. (2005) Global patterns of predator diversity in the open oceans. *Science,* **309,** 1365-1369.

Xavier, J., Croxall, J., Trathan, P. & Wood, A. (2003) Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Marine Biology,* **143,** 221-232.

Xavier, J., Louzao, M., Thorpe, S., Ward, P., Hill, C., Roberts, D., Croxall, J.P. & Phillips, R.A. (2013) Seasonal changes in the diet and feeding behaviour of a top predator indicate a flexible response to deteriorating oceanographic conditions. *Marine Biology,* **160,** 1597-1606.

Yoder, J.A., Ackleson, S.G., Barber, R.T., Flament, P. & Balch, W.M. (1994) A line in the sea. *Nature,* **371,** 689-692.

Zainuddin, M., Saitoh, K. & Saitoh, S.-I. (2008) Albacore (*Thunnus alalunga*) fishing ground in relation to oceanographic conditions in the western North Pacific Ocean using remotely sensed satellite data. *Fisheries Oceanography,* **17,** 61-73.

Zamon, J.E., Phillips, E.M. & Guy, T.J. (2013) Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. *Deep Sea Research Part II: Topical Studies in Oceanography,* **107,** 85-95.

Zeeberg, J., Corten, A. & de Graaf, E. (2006) Bycatch and release of pelagic megafauna in industrial trawler fisheries off Northwest Africa. *Fisheries Research,* **78,** 186-195.

Zuur, A. (2012) *A Beginner's Guide to Generalized Additive Models with R*. Highland Statistics Ltd., Newburgh.

Zuur, A., Hilbe, J.M. & Ieno, E.N. (2013) *A Beginner's Guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists*. Highland Statistics Ltd., Newburgh, UK.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* **1,** 3-14.

Zweig, M.H. & Campbell, G. (1993) Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical chemistry,* **39,** 561-577.

Žydelis, R., Small, C. & French, G. (2013) The incidental catch of seabirds in gillnet fisheries: A global review. *Biological Conservation,* **162,** 76-88.

Appendix I

Peer-Reviewed Publications

50 YEARS WITH IMPACT Journal of Applied Ecology 1913 2013 British Ecological Society CELEBRATING 100 YEARS

Journal of Applied Ecology 2014 doi: 10.1111/1365-2664.12330

REVIEW

On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates

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Summary

1. Identifying priority areas for marine vertebrate conservation is complex because species of conservation concern are highly mobile, inhabit dynamic habitats and are difficult to monitor.
2. Many marine vertebrates are known to associate with oceanographic fronts – physical interfaces at the transition between water masses – for foraging and migration, making them important candidate sites for conservation. Here, we review associations between marine vertebrates and fronts and how they vary with scale, regional oceanography and foraging ecology.
3. Accessibility, spatiotemporal predictability and relative productivity of front-associated foraging habitats are key aspects of their ecological importance. Predictable mesoscale (10s–100s km) regions of persistent frontal activity ('frontal zones') are particularly significant.
4. Frontal zones are hotspots of overlap between critical habitat and spatially explicit anthropogenic threats, such as the concentration of fisheries activity. As such, they represent tractable conservation units, in which to target measures for threat mitigation.
5. Front mapping via Earth observation (EO) remote sensing facilitates identification and monitoring of these hotspots of vulnerability. Seasonal or climatological products can locate biophysical hotspots, while near-real-time front mapping augments the suite of tools supporting spatially dynamic ocean management.
6. *Synthesis and applications*. Frontal zones are ecologically important for mobile marine vertebrates. We surmise that relative accessibility, predictability and productivity are key biophysical characteristics of ecologically significant frontal zones in contrasting oceanographic regions. Persistent frontal zones are potential priority conservation areas for multiple marine vertebrate taxa and are easily identifiable through front mapping via EO remote sensing. These insights are useful for marine spatial planning and marine biodiversity conservation, both within Exclusive Economic Zones and in the open oceans.

Key-words: composite front mapping, foraging, habitat, marine protected areas, marine top predator, marine vertebrate, ocean front, oceanographic front, pelagic predator, remote sensing

Introduction

Accommodating the conservation needs of large marine vertebrates such as seabirds, turtles, cetaceans, pinnipeds and sharks is a major challenge in marine management. These apex predators fulfil critical roles in ecosystem functioning (Heithaus *et al.* 2008), but are currently afforded only cursory or inadequate protection, particularly in the open oceans (Game *et al.* 2009). The combined effects of anthropogenic stressors (e.g. habitat degradation, overexploitation, fisheries bycatch and climate variability) are

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negatively impacting marine vertebrate populations (Halpern *et al.* 2008; Maxwell *et al.* 2013; Lewison *et al.* 2014), and in some cases resulting in dramatic declines (e.g. rockfishes, Ralston 2002; seabirds, Croxall *et al.* 2012). However, effective conservation is problematic. Large marine vertebrates are highly mobile, ranging great distances over the course of their lives. For example, many migrate across entire ocean basins (e.g. leatherback turtle *Dermochelys coriacea*, Shillinger *et al.* 2008; Arctic tern *Sterna paradisaea*, Egevang *et al.* 2010; humpback whale *Megaptera novaeangliae*, Robbins *et al.* 2011), epitomizing the problems of conserving a moving target (Singh & Milner-Gulland 2011). Furthermore, the formation and propagation of pelagic foraging habitats is a function of complex oceanographic dynamics (see Hazen *et al.* 2013), so habitat in the marine context does not always refer to fixed geographical space, but preferentially used areas that may shift. Understanding how oceanographic processes influence marine vertebrate distributions is, therefore, crucial for effective conservation (Hooker *et al.* 2011).

Oceanographic conditions drive spatial structuring of predator abundance and diversity across the oceans. At a global scale, marine biodiversity is regulated by sea surface temperature, with diversity maxima occurring at mid-latitudes (Worm *et al.* 2005; Tittensor *et al.* 2010). At an ocean-basin scale, diversity is highest in productive zones associated with major water mass transitions, currents, upwellings and bathymetric features (Chavez & Messié 2009). Within these productive regions, meso- (10s - 100s km) and sub-mesoscale (*c.* 1 km) oceanographic dynamics lead to the formation of ecologically significant features such as fronts and eddies (see Godø *et al.* 2012). Here, we focus on fronts – physical interfaces between water bodies that manifest as steep gradients in temperature, salinity, density, turbidity or colour (Belkin, Cornillon & Sherman 2009) – as important habitats for mobile marine vertebrates.

Biophysical coupling at fronts can lead to the formation of pelagic foraging hotspots. Mixing and nutrient retention enhance primary productivity (Traganza, Redalije & Garwood 1987; Franks 1992a), while plankton and small nekton may become entrained in convergent surface flow (Le Fevre 1986; Franks 1992b; Genin *et al.* 2005). Convergences aggregate zooplankton advected from surrounding water masses, driving bottom-up processes across multiple trophic levels up to apex predators (Graham, Pages & Hamner 2001; Bakun 2006). However, the productivity and degree of bioaggregation along fronts varies according to physical characteristics such as spatiotemporal variability, gradient magnitude, type of front and properties of the surrounding water masses (Le Fevre 1986). Therefore, a holistic understanding of how biophysical mechanisms interact to influence the degree of bioaggregation at fronts, and their subsequent attractiveness to top predators, remains elusive.

A taxonomically diverse array of marine vertebrates have been shown to associate with fronts, and the scale, nature and significance of these associations to vary according to regional oceanography and taxon-specific life-history characteristics. Ecologically significant features can range from ocean-basin scale, persistent frontal zones in the open oceans to fine-scale, ephemeral features in shelf seas (Le Fevre 1986; Belkin, Cornillon & Sherman 2009). Here, we review current understanding of associations between high trophic-level marine vertebrates and fronts, selecting key examples from contrasting oceanographic regions and highlighting important biophysical characteristics of ecologically significant frontal zones. We discuss implications for management and conservation, including overlap with anthropogenic threats, and highlight the potential role of front mapping via Earth observation (EO) remote sensing to inform threat mitigation.

Ecological importance of frontal zones

The mechanisms linking physical processes, prey dynamics and top predator foraging are complex and scale dependent (Fauchald 2009). Understanding these mechanisms is crucial to understanding what makes front-associated foraging opportunities attractive to high trophic-level consumers. Use of frontal zones is mediated bottom-up by the spatial scale, persistence and biophysical properties of fronts, and top-down by aspects of foraging ecology, including life-history mode (true pelagics vs. central-place foragers), physiological constraints (e.g. thermal range, diving capability), trophic level (planktivores vs piscivores), foraging guild (near-surface vs. subsurface), foraging plasticity, ontogenetic stage and whether foraging is opportunistic or mediated by learning and memory (Vilchis, Ballance & Fiedler 2006).

OCEAN-BASIN SCALE (1000s KM)

Ocean-basin scale regions of intense mesoscale dynamics, such as those associated with the major water mass transitions discussed below, are ecologically significant features in the largely oligotrophic open oceans (Belkin, Cornillon & Sherman 2009). These regions are important foraging and migration habitats for pelagic marine vertebrates (Tittensor *et al.* 2010).

North Pacific Transition Zone (NPTZ)

This highly dynamic region delineates the boundary between warm, oligotrophic subtropical gyres and cold, productive subarctic gyres and is a marine biodiversity hotspot of global significance (Sydeman *et al.* 2006). Numerous marine vertebrates with contrasting life histories preferentially use areas of the NPTZ, including northern elephant seals *Mirounga angustirostris*, salmon shark *Lamna ditropis* and blue shark *Prionace glauca*, bluefin *Thunnus thynnus* and albacore tunas *Thunnus alalunga*, Laysan *Phoebastria immutabilis* and black-footed albatrosses *Phoebastria nigripes*, and loggerhead *Caretta*

caretta and olive ridley turtles *Lepidochelys olivacea* (Polovina *et al.* 2004; Kappes *et al.* 2010; Block *et al.* 2011; Robinson *et al.* 2012).

The NPTZ encompasses the transition zone chlorophyll front (TZCF), a surface convergence that extends over 8000 km (Polovina *et al.* 2001). While the wider NPTZ is predictable at broad scales, the position of the TZCF is strongly influenced by climate (Kappes *et al.* 2010), leading to spatial variability in foraging associations. Some near-surface foragers, such as loggerhead turtles, can track the southward movement of the TZCF in winter (Howell *et al.* 2010). Other taxa constrained to a central place, such as albatrosses breeding on the Hawaiian Islands, have experienced reproductive failure as a result of spatial deviation (Kappes *et al.* 2010). In contrast, elephant seals, which forage along the subsurface thermal boundary between gyres (Robinson *et al.* 2012), remain unaffected by the movement of surface features.

Equatorial Front (EF)

Manifesting between the equatorial upwelling to the South and warmer tropical waters to the North, the EF is a prominent feature of the tropical eastern Pacific, characterized by steep gradients in temperature, salinity and nutrients (Ballance, Pitman & Fiedler 2006). Planktivorous seabirds strongly associate with the EF, which entrains zooplankton in surface layers (Spear, Ballance & Ainley 2001). However, seabird densities are also closely coupled with climate-driven variability in frontal intensity.

Southern Ocean frontal zones

The major frontal zones of the Southern Ocean determine the distributions of pelagic prey species in the region (Rodhouse & Boyle 2010). A range of marine predators utilize the southern boundary of the Antarctic Circumpolar Current, the subtropical front and the Subantarctic Front (see Bost *et al.* 2009; Santora & Veit 2013). Penguins, albatrosses and seals travel from distant breeding colonies to forage along the subtropical and Polar Fronts (Xavier *et al.* 2003; Bailleul *et al.* 2007; Scheffer, Bost & Trathan 2012). Although distant from land, Southern Ocean frontal zones provide suitable foraging conditions for both near-surface and deep-diving foragers, but are accessible only to those species with the capacity to navigate across oceanic seascapes.

MESOSCALE (10s–100s KM) TO SUB-MESOSCALE (*C.* 1 KM)

Mesoscale and sub-mesoscale oceanographic processes drive front formation within large-scale transition zones and in regions associated with currents, upwellings and bathymetric features and appear to be of particular ecological importance. For example, hotspots of predatory fish diversity (tuna, billfish) are associated with mesoscale fronts within warm waters (*c.* 25 °C) across all the major ocean basins (Worm *et al.* 2005).

Major currents

Bioaggregating thermal, colour and density fronts frequently form along the boundaries of major current systems (Fig. 1). Seabirds and neonate sea turtles associate strongly with fronts and eddies formed along the Gulf Stream (Haney 1986; Witherington 2002; Thorne & Read 2013) and the Kuroshio Current (Polovina *et al.* 2006). The peripheries of frontal eddies formed along these currents are also of ecological significance (Haney 1986; Bailleul, Cotté & Guinet 2010; Godø *et al.* 2012).

Upwelling fronts

Major Eastern boundary upwellings (e.g. Canary Current, Benguela Current, California Current, Humboldt Current) are hotspots of marine biodiversity (Chavez & Messié 2009) characterized by intense surface frontal activity. Mesoscale thermal and colour fronts mark the interface between cool, nutrient-rich upwelled water and warmer oligotrophic waters further offshore. Bioaggregation in upwelling-driven frontal structures attracts foragers from diverse foraging guilds (Nur *et al.* 2011;

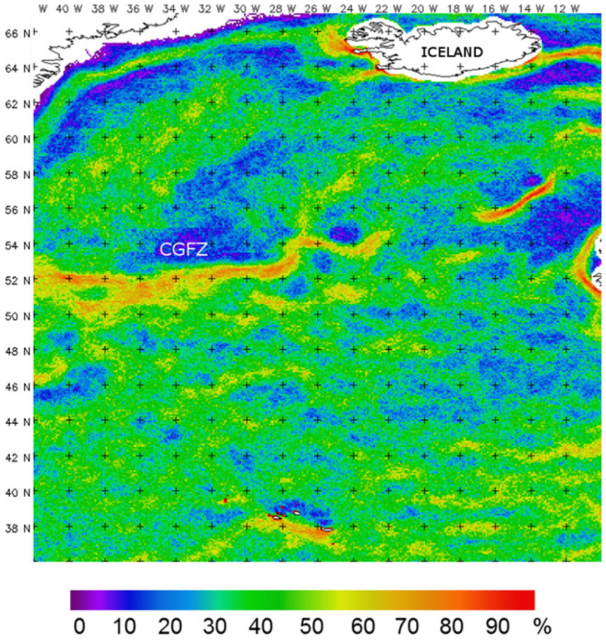

Fig. 1. Front mapping via Earth observation (EO) remote sensing. Example imagery: seasonal front frequency map, N. Atlantic (percentage time front detected in each 1 km pixel, March–May). Regions of intense mesoscale activity along the North Atlantic Current are highlighted, including that associated with the Charlie Gibbs Fracture Zone (CGFZ). Useful as part of a suite of tools for locating biophysical hot spots and their dynamics through time. Derived from merged microwave and infrared SST data, 2006–2011. Reproduced, with permission, from Miller, Read & Dale (2013).

Sabarros *et al.* 2013). For example, strong associations have been documented between cetaceans (Tynan *et al.* 2005), seabirds (Ainley *et al.* 2009) and upwelling fronts in the California Current. Similarly, coastal upwelling creates a persistent multiple trophic-level hotspot off Baja California, within which bioaggregating thermal fronts are utilized by subsurface predators, such as blue whales *Balaenoptera musculus*, green *Chelonia mydas* and loggerhead turtles (Etnoyer *et al.* 2006; Wingfield *et al.* 2011).

Strong convergent fronts also manifest at the peripheries of upwelling shadows, where water upwelled offshore meets coastal water masses sheltered by coastline irregularities (Chavez & Messié 2009). Large upwelling shadows in the Southern California Bight (Fiedler & Bernard 1987; Hunt & Schneider 1987) and off southern Peru (Acha *et al.* 2004) are known hotspots. However, upwelling intensity is often seasonal, varying under climatic and oceanographic influence, affecting the predictability of foraging opportunities in these regions (Thompson *et al.* 2012).

Shelf-edge frontal zones

Shelf-edge systems - at the transitions between the abyssal oceans and shelf seas - are zones of intense mixing, resulting in the manifestation of strong thermohaline fronts. Nutrient enrichment in shelf-edge fronts enhances primary production, attracting grazers such as copepods, fish larvae and planktivorous fish, and their predators (Le Fevre 1986). For example, the Celtic Sea shelf edge is an important overwintering habitat for basking sharks *Cetorhinus maximus* (Sims *et al.* 2003). Both surface-feeding and diving seabirds aggregate along shelf-edge fronts (Skov & Durinck 1998). Downwelling shelf slopes, such as those found at the Mid-Atlantic Bight (Ryan, Yoder & Cornillon 1999) and at the margins of the Bering Sea (Springer, McRoy & Flint 1996), are important seabird foraging areas. Shelf-edge fronts can also be significant habitat features for cetaceans, including deep-diving species that prey on squid and fish (Baumgartner 1997; Waring *et al.* 2001), rorquals (Azzellino *et al.* 2008) and some delphinids (Davis *et al.* 1998).

Mid-ocean bathymetrically-induced frontal zones

Mid-ocean bathymetric features generate persistent fronts that can produce predictable foraging grounds. For example, the interaction of the North Atlantic Current with the Mid-Atlantic Ridge around the Charlie-Gibbs Fracture Zone generates intense mesoscale frontal activity (Fig. 1; Miller, Read & Dale 2013), attracting surface and near-surface-foraging seabirds (Egevang *et al.* 2010; Frederiksen *et al.* 2012; Edwards *et al.* 2013). Piscivorous dolphins and whales also feed on mesopelagic fish and squid in this area (Doksæter *et al.* 2008; Skov *et al.* 2008).

Shelf-sea tidal mixing fronts

Tidal mixing fronts manifest in shelf seas between well-mixed and stratified waters (Pingree & Griffiths 1978). Nutrient retention and enhanced vertical mixing increase seasonal phytoplankton production (Pingree *et al.* 1975; Franks 1992a), attracting both pelagic and neritic foragers. For example, basking sharks forage for zooplankton at small-scale tidal fronts in UK waters (Sims & Quayle 1998), with sightings clustered around slicks indicative of convergent flow. Likewise, planktivorous ocean sunfish *Mola mola* are frequently encountered near fronts (Sims & Southall 2002). Similarly, strong associations have been observed between rorquals and tidal fronts in the Gulf of St. Lawrence (Doniol-Valcroze *et al.* 2007). On the European Continental Shelf, piscivorous cetaceans use both seasonally persistent tidal mixing fronts (Goold 1998; Weir & O'Brien 2000) and finer-scale fronts that manifest in tidal inlets (Pirotta *et al.* 2013). In addition, numerous seabirds forage around mid-shelf fronts (Haney & McGillivary 1985; Hamer *et al.* 2009; Dean *et al.* 2012), sometimes in Multi-Species Foraging Associations (MSFAs; Camphuysen, Scott & Wanless 2006). Surface and near-surface-foraging birds are frequently observed near convergent fronts (Durazo, Harrison & Hill 1998; Hunt *et al.* 1999), whereas subsurface foragers tend to associate with strong, vertically structured fronts (Decker & Hunt 1996; Begg & Reid 1997).

Tidal topographic fronts

In neritic waters, tidal topographic interactions generate fine-scale, yet strongly bioaggregating fronts (Le Fevre 1986). For example, 'island wake' effects lead to the development of surface convergences and eddies (Wolanski & Hamner 1988). Marine mammals (Johnston & Read 2007) and surface-foraging seabirds (Schneider 1990) associate with island wake fronts. Similarly, offshore banks can initiate front development, increasing prey accessibility in surface layers (Stevick *et al.* 2008). Tidal-topographic fronts over banks can cause the formation of subsurface chlorophyll maxima (Franks 1992a), which are significant foraging areas for some diving predators (Scott *et al.* 2010). Tidal-topographic fronts are highly predictable and may be especially important for central-place marine vertebrates. However, at very fine scales (<1 km), other subsurface physical processes may mediate predator foraging over bank systems (Scott *et al.* 2010; Cox, Scott & Camphuysen 2013).

Estuarine plume and tidal intrusion fronts

Estuarine plume fronts are formed by interactions between tidal processes and river outflow. Entrainment of zooplankton (Govoni & Grimes 1992) attracts forage fish

(Kaltenberg, Emmett & Benoit-Bird 2010), making plume fronts significant nearshore foraging features. Large aggregations of piscivorous seabirds have been documented around some estuarine plume fronts (Skov & Prins 2001; Zamon, Phillips & Guy 2013).

KEY BIOPHYSICAL CHARACTERISTICS OF ECOLOGICALLY SIGNIFICANT FRONTAL ZONES

Current understanding indicates that accessibility, spatiotemporal predictability and relative productivity are central to the ecological importance of frontal zones (Hunt *et al.* 1999; Weimerskirch 2007). These insights are useful in predicting which taxa are likely to aggregate at frontal zones in different oceanographic regions, enhancing understanding of pelagic ecosystem function and identifying important at-sea habitats. For example, it is clear that large-scale frontal zones in the open oceans are often highly productive and persistent, and so predictable, yet are only really accessible to oceanic species and far-ranging central-place foragers (Bost *et al.* 2009; Tittensor *et al.* 2010). Predictable, productive mesoscale frontal zones associated with bathymetric features, currents and major upwellings attract marine vertebrates from diverse foraging guilds in contrasting oceanographic regions (Chavez & Messié 2009; Block *et al.* 2011). Persistent shelf-sea tidal mixing and tidal-topographic fronts create predictable foraging opportunities, accessible to coastal species such as colonial seabirds and some cetaceans. Recent work in the Celtic Sea highlights temporal persistence as a key component of frontal zones used as foraging features for a piscivorous seabird (Scales *et al.* 2014), presumably as persistence enhances both productivity and predictability.

The literature documenting associations between marine vertebrates and fronts has yielded valuable insights, yet many questions remain. For example, despite the implicit assumption that fronts generate suitable foraging conditions, the mechanisms linking physical processes and prey dynamics are not well understood (but see Cox, Scott & Camphuysen 2013). In many cases, it remains unclear how habitat utilization changes through the annual cycle, through ontogenetic development and through life cycle stages (i.e. breeding, migration; but see e.g. Votier *et al.* 2011). In addition, little is known about the ways in which many species perceive and respond to environmental cues (but see Nevitt & Bonadonna 2005; Tew Kai *et al.* 2009; Votier *et al.* 2013; Tremblay *et al.* 2014). Moreover, it is important to determine whether fronts are significant foraging features at the population level. This has not yet been achieved, to our knowledge, but is possible through estimation of the proportion of a population using a frontal zone, or the spatial range over which animals are attracted. Future work should address these questions, improving capacity to locate ecologically significant features.

Frontal zones as priority conservation areas

HOTSPOTS OF ANTHROPOGENIC THREAT

Frontal zones appear to be hot spots of overlap between potentially critical at-sea habitats and spatially explicit anthropogenic threats (e.g. fisheries), particularly in the coastal zone (Halpern *et al.* 2008). The major fisheries threats to marine vertebrates are bycatch (Gilman *et al.* 2008; Anderson *et al.* 2011; Žydelis, Small & French 2013; Lewison *et al.* 2014) and competition for resources (e.g. Bertrand *et al.* 2012). Comprehensive data are difficult to obtain, but industrialized fisheries, particularly pelagic long-lining fleets, target persistent frontal zones (Podestá, Browder & Hoey 1993; Hartog *et al.* 2011), generating significant risk of conflict with other apex consumers. Spatial overlap is particularly pronounced within the coastal zone, along shelf breaks and in upwelling regions (Halpern *et al.* 2008; Lewison *et al.* 2014), especially those around Africa and South America (Zeeberg, Corten & de Graaf 2006; Pichegru *et al.* 2009). Within these regions, frontal zones are logical areas in which to target measures for mitigation of fisheries threats. In addition, convergent fronts can concentrate pollutants and floating debris such as oil and plastics, potentially increasing exposure of marine vertebrates aggregating to forage (Bourne & Clark 1984; González Carman *et al.* 2014).

On the continental shelf, the expansion of marine renewable energy installations (MREIs) has the potential for direct and indirect effects on marine vertebrates (Inger *et al.* 2009; Grecian *et al.* 2010; Scott *et al.* 2014). MREIs that rely on tidal flow are likely to be concentrated in the vicinity of hydrographically dynamic tidal mixing fronts (Miller & Christodoulou 2014), altering habitat dynamics and displacing foraging effort. These impacts may be particularly pronounced for coastal central-place foragers (Scott *et al.* 2014). While more research is needed to determine whether MREIs have population-level effects, marine spatial planning can be improved by identification of vulnerability hotspots.

FRONT MAPPING TO IDENTIFY PRIORITY CONSERVATION AREAS

Technological innovations in remote sensing, biologging, autonomous marine vehicles and vessel monitoring hold promise for identification of priority conservation areas (Palacios *et al.* 2006; Grantham *et al.* 2011; Miller & Christodoulou 2014) and spatially dynamic, near-real-time threat management (Hobday *et al.* 2014). Front mapping via EO remote sensing (Fig. 1; Miller 2009) enables high-resolution, automated detection of frontal zones anywhere in the global ocean. Seasonal or climatological products are potentially useful for marine spatial planning, identifying priority areas for threat mitigation both on-shelf (Miller & Christodoulou 2014) and in areas beyond national jurisdiction (ABNJ; the 'high seas'). Moreover, near-real-time front mapping augments the suite of tools with potential to inform spatially dynamic ocean management (Hobday *et al.* 2014), enabling identification and monitoring of critical ephemeral habitats (Fig. 2).

Remotely sensed oceanographic data have been used to inform spatially dynamic fisheries management in several cases. For example, historical and near-real-time SST imagery, coupled with satellite telemetry and spatially explicit fisheries data, has been successfully used to reduce bycatch of loggerhead turtles along the TZCF north of Hawaii (Howell *et al.* 2008). The Australian Fisheries Management Authority has used a comparable approach using *in situ* sensors to regulate exploitation of southern bluefin tuna *Thunnus maccoyii* (Hobday & Hartmann 2006). Although there are few examples of such innovatively managed fisheries (Dunn, Boustany & Halpin 2011), similar methods are applicable to other species of conservation concern (Hobday & Hartmann 2006) and may be critical in mitigating future marine biodiversity loss.

Marine protected areas (MPAs) can regulate overlap between spatially explicit threats and critical at-sea habitats. MPAs are most tractable on-shelf, within Exclusive Economic Zones (EEZs), where anthropogenic threats to marine vertebrate populations, such as fisheries pressure, MREI development, noise and habitat degradation, are also concentrated (Maxwell *et al.* 2013). Spatially predictable biophysical hotspots, such as those associated with persistent tidal mixing, tidal-topographic and upwelling shadow fronts, are logical candidates for within-EEZ MPAs and easily identifiable. Indeed, hot spots associated with quasi-stationary frontal zones have been explicitly included in MPA design in the UK (Miller & Christodoulou 2014) and the Mediterranean (Panigada *et al.* 2008).

In the open oceans beyond EEZs, persistent frontal zones, such as that associated with the Charlie Gibbs Fracture Zone in the North Atlantic (Fig. 1), are also amenable to site-based management. However, effective conservation of pelagic biodiversity in ABNJ rests not only upon the identification of vulnerability hotspots but also upon the capacity to track how these hotspots shift with changing oceanographic conditions (Hooker *et al.* 2011; Lascelles *et al.* 2012; Fig. 2). Spatially dynamic ocean management (Hobday *et al.* 2014) may be more effective in managing threats to marine vertebrate populations in some highly dynamic regions, and for increasing adaptability as pelagic ecosystems undergo changes related to climate variability. High-resolution front frequency maps, both near-real-time and seasonal/climatological (e.g. Fig. 1), coupled with real-time monitoring of anthropogenic activity and marine vertebrate habitat use (Fig. 2), present managers with data of value for more effective management of pelagic ecosystems.

CONCLUSIONS

Associations between marine vertebrates and oceanographic fronts vary spatially, temporally and between taxa, influenced by both the biophysical properties of fronts and taxon-specific foraging ecology (Hunt *et al.* 1999). Despite this variability, there now exists a considerable body of evidence indicating that persistent mesoscale frontal zones are ecologically significant across the oceans (e.g. Polovina *et al.* 2001; Bost *et al.* 2009). As areas of existing and potential overlap between critical habitats and anthropogenic threat, persistent frontal zones represent tractable conservation areas, in which to target threat mitigation measures. Continued integration between remote sensing science, spatial ecology, oceanography and fisheries management has potential to improve marine biodiversity conservation by (i) bridging the gaps in our understanding of the oceanographic drivers of marine vertebrate space use and (ii) feeding into systematic conservation planning through mapping and real-time monitoring of threat hot spots (Grantham *et al.* 2011; Hobday *et al.* 2014). Such integration is vital if we are to balance the competing demands of anthropogenic activities and biodiversity conservation in the vast and dynamic oceans.

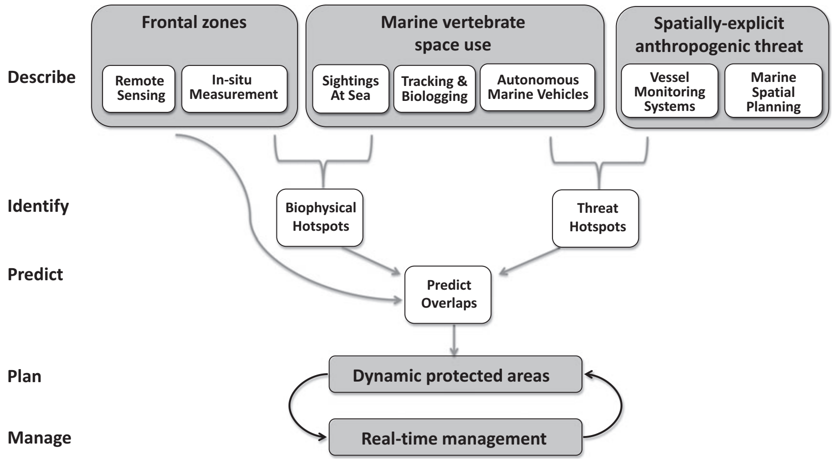

Fig. 2. Frontal zones as priority conservation areas for marine vertebrates. Understanding of associations between marine vertebrates and fronts can be enhanced using data describing (i) the oceanographic environment, obtainable from remote sensing or *in situ* measurement, and (ii) marine vertebrate space use, through at-sea sightings, tracking/biologging and autonomous marine vehicles. Insights can be fed forward into predictive habitat models, which can be used together with spatially explicit information describing anthropogenic threat to predict and monitor regions of overlap.

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References

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M. & Bava, J. (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *Journal of Marine Systems*, **44**, 83–105.

Ainley, D.G., Dugger, K.D., Ford, R.G., Pierce, S.D., Reese, D.C., Brodeur, R.D., Tynan, C.T. & Barth, J.A. (2009) Association of predators and prey at frontal features in the California current: competition, facilitation, and co-occurrence. *Marine Ecology Progress Series*, **389**, 271–294.

Anderson, O.R., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.J., Yates, O. & Black, A. (2011) Global seabird bycatch in longline fisheries. *Endangered Species Research*, **14**, 91–106.

Azzellino, A., Gaspari, S., Airoldi, S. & Nani, B. (2008) Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, **55**, 296–323.

Bailleul, F., Cotté, C. & Guinet, C. (2010) Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Marine Ecology Progress Series*, **408**, 251–264.

Bailleul, F., Charrassin, J.B., Monestiez, P., Roquet, F., Biuw, M. & Guinet, C. (2007) Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, **362**, 2169–2181.

Bakun, A. (2006) Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina*, **70**, 105–122.

Ballance, L.T., Pitman, R.L. & Fiedler, P.C. (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Progress in Oceanography*, **69**, 360–390.

Baumgartner, M.F. (1997) The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Marine Mammal Science*, **13**, 614–638.

Begg, G.S. & Reid, J.B. (1997) Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. *ICES Journal of Marine Science: Journal du Conseil*, **54**, 552–565.

Belkin, I.M., Cornillon, P.C. & Sherman, K. (2009) Fronts in large marine ecosystems. *Progress in Oceanography*, **81**, 223–236.

Bertrand, S., Joo, R., Smet, C.A., Tremblay, Y., Barbraud, C. & Weimerskirch, H. (2012) Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology*, **49**, 1168–1177.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J. *et al.* (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature*, **475**, 86–90.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G. & Weimerskirch, H. (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, **78**, 363–376.

Bourne, W. & Clark, G. (1984) The occurrence of birds and garbage at the Humboldt Front off Valparaiso, Chile. *Marine Pollution Bulletin*, **15**, 343–344.

Camphuysen, C.J., Scott, B.E. & Wanless, S. (2006) Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multispecies foraging assemblages and habitat-specific feeding strategies. *Top Predators in Marine Ecosystems: Their Role in Monitoring and Management* (eds I.L. Boyd, S. Wanless & C.J. Camphuysen), pp. 82–97. Cambridge University Press, Cambridge.

Chavez, F.P. & Messié, M. (2009) A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography*, **83**, 80–96.

Cox, S., Scott, B. & Camphuysen, C. (2013) Combined spatial and tidal processes identify links between pelagic prey species and seabirds. *Marine Ecology Progress Series*, **479**, 203–221.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, **22**, 1–34.

Davis, R., Fargion, G., May, N., Leming, T., Baumgartner, M., Evans, W., Hansen, L. & Mullin, K. (1998) Physical habitat of cetaceans along the continental slope in the northcentral and western Gulf of Mexico. *Marine Mammal Science*, **14**, 490–507.

Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R.A., Perrins, C.M. & Guilford, T. (2012) Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of The Royal Society Interface*, **10**, rsif20120570.

Decker, M.B. & Hunt, G.L. Jr (1996) Foraging by murres (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Marine Ecology Progress Series*, **139**, 1–10.

Doksæter, L., Olsen, E., Nøttestad, L. & Fernö, A. (2008) Distribution and feeding ecology of dolphins along the Mid-Atlantic Ridge between Iceland and the Azores. *Deep Sea Research Part II: Topical Studies in Oceanography*, **55**, 243–253.

Doniol-Valcroze, T., Berteaux, D., Larouche, P. & Sears, R. (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Series*, **335**, 207–216.

Dunn, D.C., Boustany, A.M. & Halpin, P.N. (2011) Spatio-temporal management of fisheries to reduce by-catch and increase fishing selectivity. *Fish and Fisheries*, **12**, 110–119.

Durazo, R., Harrison, N. & Hill, A. (1998) Seabird observations at a tidal mixing front in the Irish Sea. *Estuarine, Coastal and Shelf Science*, **47**, 153–164.

Edwards, E.W., Quinn, L.R., Wakefield, E.D., Miller, P.I. & Thompson, P.M. (2013) Tracking a northern fulmar from a Scottish nesting site to the Charlie-Gibbs Fracture Zone: evidence of linkage between coastal breeding seabirds and Mid-Atlantic Ridge feeding sites. *Deep Sea Research Part II: Topical Studies in Oceanography*, **98**, 438–444.

Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences*, **107**, 2078–2081.

Etnoyer, P., Canny, D., Mate, B., Morgan, L., Ortegaortiz, J. & Nichols, W. (2006) Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 340–358.

Fauchald, P. (2009) Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series*, **391**, 139–151.

Fiedler, P.C. & Bernard, H.J. (1987) Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental Shelf Research*, **7**, 871–881.

Franks, P.J.S. (1992a) Phytoplankton blooms at fronts: patterns, scales, and physical forcing mechanisms. *Reviews in Aquatic Sciences*, **6**, 121–137.

Franks, P.J.S. (1992b) Sink or swim: accumulation of biomass at fronts. *Marine Ecology Progress Series*, **82**, 1–12.

Frederiksen, M., Moe, B., Daunt, F., Phillips, R.A., Barrett, R.T., Bogdanova, M.I. *et al.* (2012) Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions*, **18**, 530–542.

Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E. *et al.* (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution*, **24**, 360–369.

Genin, A., Jaffe, J.S., Reef, R., Richter, C. & Franks, P.J.S. (2005) Swimming against the flow: a mechanism of zooplankton aggregation. *Science*, **308**, 860–862.

Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J., Mangel, J. *et al.* (2008) Shark interactions in pelagic longline fisheries. *Marine Policy*, **32**, 1–18.

Godø, O.R., Samuelsen, A., Macaulay, G.J., Patel, R., Hjøllo, S.S., Horne, J., Kaartvedt, S. & Johannessen, J.A. (2012) Mesoscale eddies are oases for higher trophic marine life. *PLoS ONE*, **7**, e30161.

González Carman, V., Acha, E.M., Maxwell, S.M., Albareda, D., Campagna, C. & Mianzan, H. (2014) Young green turtles, *Chelonia mydas*, exposed to plastic in a frontal area of the SW Atlantic. *Marine Pollution Bulletin*, **78**, 56–62.

Goold, J.C. (1998) Acoustic assessment of populations of common dolphin off the west Wales coast, with perspectives from satellite infrared imagery. *Journal of the Marine Biological Association of the United Kingdom*, **78**, 1353–1364.

Govoni, J.J. & Grimes, C.B. (1992) The surface accumulation of larval fishes by hydrodynamic convergence within the Mississippi River plume front. *Continental Shelf Research*, **12**, 1265–1276.

Graham, W.M., Pages, F. & Hamner, W.M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, **451**, 199–212.

Grantham, H.S., Game, E.T., Lombard, A.T., Hobday, A.J., Richardson, A.J., Beckley, L.E. *et al.* (2011) Accommodating dynamic oceanographic processes and pelagic biodiversity in marine conservation planning. *PLoS ONE*, **6**, e16552.

Grecian, W.J., Inger, R., Attrill, M.J., Bearhop, S., Godley, B.J., Witt, M.J. & Votier, S.C. (2010) Potential impacts of wave-powered marine renewable energy installations on marine birds. *Ibis*, **152**, 683–697.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C. *et al.* (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.

Hamer, K., Humphreys, E., Magalhaes, M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Skov, H. & Wanless, S. (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *Journal of Animal Ecology*, **78**, 880–889.

Haney, J.C. (1986) Seabird segregation at Gulf Stream frontal eddies. *Marine Ecology Progress Series*, **28**, 279–285.

Haney, J.C. & McGillivary, P.A. (1985) Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance. *Biological Oceanography*, **3**, 401–430.

Hartog, J.R., Hobday, A.J., Matear, R. & Feng, M. (2011) Habitat overlap between southern bluefin tuna and yellowfin tuna in the east coast longline fishery–implications for present and future spatial management. *Deep Sea Research Part II: Topical Studies in Oceanography*, **58**, 746–752.

Hazen, E.L., Bograd, S., Suryan, R.M., Watanuki, Y. & Wilson, R. (2013) Biophysical coupling of marine hotspots. *Marine Ecology Progress Series*, **487**, 176–304.

Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, **23**, 202–210.

Hobday, A.J. & Hartmann, K. (2006) Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fisheries Management and Ecology*, **13**, 365–380.

Hobday, A., Maxwell, S., Forgie, J., McDonald, J., Darby, M., Seto, K. *et al.* (2014) Dynamic ocean management: integrating scientific and technological capacity with law, policy and management. *Stanford Environmental Law Journal*, **33**, 125–168.

Hooker, S.K., Cañadas, A., Hyrenbach, K.D., Corrigan, C., Polovina, J.J. & Reeves, R.R. (2011) Making protected area networks effective for marine top predators. *Endangered Species Research*, **13**, 203–218.

Howell, E.A., Kobayashi, D.R., Parker, D.M., Balazs, G.H. & Polovina, J.J. (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endangered Species Research*, **5**, 267–278.

Howell, E.A., Dutton, P.H., Polovina, J.J., Bailey, H., Parker, D.M. & Balazs, G.H. (2010) Oceanographic influences on the dive behavior of juvenile loggerhead turtles (*Caretta caretta*) in the North Pacific Ocean. *Marine Biology*, **157**, 1011–1026.

Hunt, G. Jr & Schneider, D. (1987) Scale-dependent processes in the physical and biological environment of marine birds. *Seabirds: Feeding Ecology and Role in Marine Ecosystems* (ed. J.P. Croxall), pp. 7–41. Cambridge University Press, Cambridge.

Hunt, G. Jr, Mehlum, F., Russell, R., Irons, D., Decker, M. & Becker, P. (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. *Proc. 22nd Int. Ornithol. Congr.* (eds N.J. Adams & R. Slotow), pp. 2040–2056. BirdLife South Africa, Durban, Johannesburg.

Inger, R., Attrill, M.J., Bearhop, S., Broderick, A.C., James Grecian, W., Hodgson, D.J. *et al.* (2009) Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology*, **46**, 1145–1153.

Johnston, D. & Read, A. (2007) Flow-field observations of a tidally driven island wake used by marine mammals in the Bay of Fundy, Canada. *Fisheries Oceanography*, **16**, 422–435.

Kaltenberg, A.M., Emmett, R.L. & Benoit-Bird, K.J. (2010) Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. *Marine Ecology Progress Series*, **419**, 171–184.

Kappes, M.A., Shaffer, S.A., Tremblay, Y., Foley, D.G., Palacios, D.M., Robinson, P.W., Bograd, S.J. & Costa, D.P. (2010) Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress in Oceanography*, **86**, 246–260.

Lascelles, B.G., Langham, G.M., Ronconi, R.A. & Reid, J.B. (2012) From hotspots to site protection: identifying marine protected areas for seabirds around the globe. *Biological Conservation*, **156**, 5–14.

Le Fevre, J. (1986) Aspects of the biology of frontal systems. *Advances in Marine Biology*, **23**, 164–299.

Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydelis, R. *et al.* (2014) Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences*, **111**, 5271–5276.

Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern, B.S., Breed, G.A., Nickel, B. *et al.* (2013) Cumulative human impacts on marine predators. *Nature Communications*, **4**, 2688.

Miller, P. (2009) Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. *Journal of Marine systems*, **78**, 327–336.

Miller, P.I. & Christodoulou, S. (2014) Frequent locations of ocean fronts as an indicator of pelagic diversity: application to marine protected areas and renewables. *Marine Policy*, **45**, 318–329.

Miller, P.I., Read, J.F. & Dale, A.C. (2013) Thermal front variability along the North Atlantic Current observed using microwave and infrared satellite data. *Deep Sea Research Part II: Topical Studies in Oceanography*, **98**, 244–256.

Nevitt, G.A. & Bonadonna, F. (2005) Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biology Letters*, **1**, 303–305.

Nur, N., Jahncke, J., Herzog, M.P., Howar, J., Hyrenbach, K.D., Zamon, J.E. *et al.* (2011) Where the wild things are: predicting hotspots of seabird aggregations in the California current system. *Ecological Applications*, **21**, 2241–2257.

Palacios, D., Bograd, S., Foley, D. & Schwing, F. (2006) Oceanographic characteristics of biological hot spots in the North Pacific: a remote sensing perspective. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 250–269.

Panigada, S., Zanardelli, M., MacKenzie, M., Donovan, C., Mélin, F. & Hammond, P.S. (2008) Modelling habitat preferences for fin whales and striped dolphins in the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. *Remote Sensing of Environment*, **112**, 3400–3412.

Pichegru, L., Ryan, P., Le Bohec, C., van der Lingen, C., Navarro, R., Petersen, S., Lewis, S., van der Westhuizen, J. & Grémillet, D. (2009) Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine Ecology Progress Series*, **391**, 199–208.

Pingree, R. & Griffiths, D. (1978) Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical Research*, **83**, 4615–4622.

Pingree, R.D., Pugh, P.R., Holligan, P.M. & Forster, G.R. (1975) Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English channel. *Nature*, **258**, 672–677.

Pirotta, E., Thompson, P.M., Miller, P.I., Brookes, K.L., Cheney, B., Barton, T.R., Graham, I.M. & Lusseau, D. (2013) Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. *Functional Ecology*, **28**, 206–217.

Podestá, G.P., Browder, J.A. & Hoey, J.J. (1993) Exploring the association between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. *Continental Shelf Research*, **13**, 253–277.

Polovina, J.J., Howell, E., Kobayashi, D. & Seki, M.P. (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography*, **49**, 469–483.

Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P. & Dutton, P.H. (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography*, **13**, 36–51.

Polovina, J., Uchida, I., Balazs, G., Howell, E.A., Parker, D. & Dutton, P. (2006) The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 326–339.

Ralston, S. (2002) West coast groundfish harvest policy. *North American Journal of Fisheries Management*, **22**, 249–250.

Robbins, J., Rosa, L.D., Allen, J.M., Mattila, D.K., Secchi, E.R., Friedlaender, A.S., Stevick, P.T., Nowacek, D.P. & Steel, D. (2011) Return movement of a humpback whale between the Antarctic Peninsula and

American Samoa: a seasonal migration record. *Endangered Species Research*, **13**, 117–121.

Robinson, P.W., Costa, D.P., Crocker, D.E., Gallo-Reynoso, J.P., Champagne, C.D., Fowler, M.A. *et al.* (2012) Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PLoS ONE*, **7**, e36728.

Rodhouse, P.G. & Boyle, P.R. (2010) Large aggregations of pelagic squid near the ocean surface at the Antarctic Polar Front, and their capture by grey-headed albatrosses. *ICES Journal of Marine Science*, **67**, 1432–1435.

Ryan, J.P., Yoder, J.A. & Cornillon, P.C. (1999) Enhanced chlorophyll at the shelfbreak of the Mid-Atlantic Bight and Georges Bank during the spring transition. *Limnology and Oceanography*, **44**, 1–11.

Sabarros, P.S., Grémillet, D., Demarcq, H., Moseley, C., Pichegru, L., Mullers, R.H., Stenseth, N.C. & Machu, E. (2013) Fine-scale recognition and use of mesoscale fronts by foraging Cape gannets in the Benguela upwelling region. *Deep Sea Research Part II: Topical Studies in Oceanography*, doi: 10.1016/j.dsr2.2013.06.023. (in press).

Santora, J.A. & Veit, R.R. (2013) Spatio-temporal persistence of top predator hotspots near the Antarctic Peninsula. *Marine Ecology Progress Series*, **487**, 287–304.

Scales, K.L., Miller, P.I., Embling, C.B., Ingram, S.N., Pirotta, E. & Votier, S.C. (2014) Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of the Royal Society Interface*, **11**, 20140679.

Scheffer, A., Bost, C. & Trathan, P. (2012) Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. *Marine Ecology Progress Series*, **465**, 281–297.

Schneider, D.C. (1990) Seabirds and fronts: a brief overview. *Polar Research*, **8**, 17–21.

Scott, B.E., Sharples, J., Ross, O.N., Wang, J., Pierce, G.J. & Camphuysen, C.J. (2010) Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Marine Ecology Progress Series*, **408**, 207–226.

Scott, B.E., Langton, R., Philpott, E. & Waggitt, J.J. (2014) Seabirds and marine renewables: are we asking the right questions? *Marine Renewable Energy Technology and Environmental Interactions* (eds. M.A. Shields & A.I.L. Payne), pp. 81–92. Springer, Netherlands

Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P. *et al.* (2008) Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biology*, **6**, e171.

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

Sims, D.W. & Southall, E.J. (2002) Occurrence of ocean sunfish, *Mola mola* near fronts in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **82**, 927–928.

Sims, D., 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.

Singh, N.J. & Milner-Gulland, E.J. (2011) Conserving a moving target: planning protection for a migratory species as its distribution changes. *Journal of Applied Ecology*, **48**, 35–46.

Skov, H. & Durinck, J. (1998) Constancy of frontal aggregations of seabirds at the shelf break in the Skagerrak. *Journal of Sea Research*, **39**, 305–311.

Skov, H. & Prins, E. (2001) Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. *Marine Ecology Progress Series*, **214**, 279–287.

Skov, H., Gunnlaugsson, T., Budgell, W., Horne, J., Nøttestad, L., Olsen, E., Søiland, H., Víkingsson, G. & Waring, G. (2008) Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. *Deep Sea Research Part II: Topical Studies in Oceanography*, **55**, 254–268.

Spear, L.B., Ballance, L.T. & Ainley, D.G. (2001) Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Marine Ecology Progress Series*, **219**, 275–289.

Springer, A.M., McRoy, C.P. & Flint, M.V. (1996) The Bering Sea Green Belt: shelf-edge processes and ecosystem production. *Fisheries Oceanography*, **5**, 205–223.

Stevick, P.T., Incze, L.S., Kraus, S.D., Rosen, S., Wolff, N. & Baukus, A. (2008) Trophic relationships and oceanography on and around a small offshore bank. *Marine Ecology Progress Series*, **363**, 15–28.

Sydeman, W.J., Brodeur, R.D., Bychkov, A.S., Grimes, C.B. & McKinnell, S.M. (2006) Top predator "hotspots" in the North Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 247–450.

Tew Kai, E., Rossi, V., Sudre, J., Weimerskirch, H., Lopez, C., Hernandez-Garcia, E., Marsac, F. & Garçon, V. (2009) Top marine predators track Lagrangian coherent structures. *Proceedings of the National Academy of Sciences*, **106**, 8245.

Thompson, S.A., Sydeman, W.J., Santora, J.A., Black, B.A., Suryan, R.M., Calambokidis, J., Peterson, W.T. & Bograd, S.J. (2012) Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. *Progress in Oceanography*, **101**, 106–120.

Thorne, L. & Read, A. (2013) Fine-scale biophysical interactions drive prey availability at a migratory stopover site for *Phalaropus* spp. in the Bay of Fundy, Canada. *Marine Ecology Progress Series*, **487**, 261–273.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature*, **466**, 1098–1101.

Traganza, E.D., Redalije, D.G. & Garwood, R.W. (1987) Chemical flux, mixed layer entrainment and phytoplankton blooms at upwelling fronts in the California coastal zone. *Continental Shelf Research*, **7**, 89–105.

Tremblay, Y., Thiebault, A., Mullers, R. & Pistorius, P. (2014) Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS ONE*, **9**, e88424.

Tynan, C.T., Ainley, D.G., Barth, J.A., Cowles, T.J., Pierce, S.D. & Spear, L.B. (2005) Cetacean distributions relative to ocean processes in the northern California Current System. *Deep Sea Research Part II: Topical Studies in Oceanography*, **52**, 145–167.

Vilchis, L.I., Ballance, L.T. & Fiedler, P.C. (2006) Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. *Marine Ecology Progress Series*, **315**, 279–292.

Votier, S., Grecian, W., Patrick, S. & Newton, J. (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology*, **158**, 355–362.

Votier, S.C., Bicknell, A., Cox, S.L., Scales, K.L. & Patrick, S.C. (2013) A bird's eye view of discard reforms: bird-borne cameras reveal seabird/fishery interactions. *PLoS ONE*, **8**, e57376.

Waring, G., Hamazaki, T., Sheehan, D., Wood, G. & Baker, S. (2001) Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast US. *Marine Mammal Science*, **17**, 703–717.

Weimerskirch, H. (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, **54**, 211–223.

Weir, C.R. & O'Brien, S.H. (2000) Association of the harbour porpoise (*Phocoena phocoena*) with the western Irish sea front. *European Research on Cetaceans*, **14**, 61–65.

Wingfield, D.K., Peckham, S.H., Foley, D.G., Palacios, D.M., Lavaniegos, B.E., Durazo, R., Nichols, W.J., Croll, D.A. & Bograd, S.J. (2011) The making of a productivity hotspot in the coastal ocean. *PLoS ONE*, **6**, e27874.

Witherington, B. (2002) Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. *Marine Biology*, **140**, 843–853.

Wolanski, E. & Hamner, W.M. (1988) Topographically controlled fronts in the ocean and their biological significance. *Science*, **241**, 177–181.

Worm, B., Sandow, M., Oschlies, A., Lotze, H.K. & Myers, R.A. (2005) Global patterns of predator diversity in the open oceans. *Science*, **309**, 1365–1369.

Xavier, J., Croxall, J., Trathan, P. & Wood, A. (2003) Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Marine Biology*, **143**, 221–232.

Zamon, J.E., Phillips, E.M. & Guy, T.J. (2013) Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. *Deep Sea Research Part II: Topical Studies in Oceanography*, doi: 10.1016/j.dsr2.2013.03.031. in press.

Zeeberg, J., Corten, A. & de Graaf, E. (2006) Bycatch and release of pelagic megafauna in industrial trawler fisheries off Northwest Africa. *Fisheries Research*, **78**, 186–195.

Žydelis, R., Small, C. & French, G. (2013) The incidental catch of seabirds in gillnet fisheries: a global review. *Biological Conservation*, **162**, 76–88.

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Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic

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Summary

1. Understanding the mechanisms that link oceanographic processes and marine vertebrate space use is critical to our knowledge of marine ecosystem functioning, and for effective management of populations of conservation concern.

2. The basking shark *Cetorhinus maximus* has been observed in association with oceanographic fronts – physical interfaces at the transitions between water masses – exploiting foraging opportunities resulting from zooplankton aggregation. However, the scale, significance and variability of these associations have not previously been established.

3. Here, we quantify the influence of thermal and chlorophyll-*a* fronts on basking shark habitat use in the north-east Atlantic. We use animal-mounted archival tracking together with composite front mapping via Earth Observation (EO) remote sensing to provide an oceanographic context to shark movements.

4. We investigate levels of association with fronts occurring over two spatio-temporal scales, (i) broad-scale, seasonally persistent frontal zones and (ii) contemporaneous thermal and chl-*a* fronts. Using random walk simulations and logistic regression within an iterative generalized linear mixed modelling (GLMM) framework, we find that seasonal front frequency is a significant predictor of shark presence.

5. Oceanographic metrics time-matched to shark tracks indicate that sharks show a preference for productive regions and associate with contemporaneous thermal and chl-*a* fronts more frequently than could be expected at random. Moreover, we highlight the importance of front persistence and cross-frontal temperature step, which appear to interact to affect the degree of prey aggregation along thermal fronts in this shelf-sea system.

6. Our findings confirm that surface frontal activity is a predictor of basking shark presence in the north-east Atlantic, both over seasonal timescales and in near real-time. These insights have clear implications for understanding the preferred habitats of basking sharks in the context of anthropogenic threat management and marine spatial planning in the region.

Key-words: animal tracking, biologging, front mapping, habitat preference, habitat use, marine megavertebrate, marine vertebrate, remote sensing

Introduction

Understanding the ways in which large marine vertebrates optimize foraging efficiency in heterogeneous and dynamic pelagic environments has become a central issue in marine ecology. These animals are often highly mobile, moving over immense spatial scales in order to find suitable

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habitats in which to forage and reproduce. Moreover, zooplanktivorous megavertebrates such as the basking shark, *Cetorhinus maximus*; whale shark, *Rhincodon typus*; leatherback turtle, *Dermochelys coriacea;* and manta ray, *Manta birostris* exist on an energetic 'knife-edge', and so must maximize prey encounter rates in patchy pelagic prey seascapes in order to survive (Sims 1999, 2008; Hays *et al.* 2006; Stevens 2007; Fossette *et al.* 2010).

Underlying movement patterns that enhance foraging optimality, such as behaviours approximating theoretically optimal Lévy walks, have been identified in a variety of marine taxa (Viswanathan *et al.* 1999; Sims *et al.* 2008; Humphries *et al.* 2012) and linked to oceanographic context (Hays *et al.* 2006; Humphries *et al.* 2010) and prey fields (Sims *et al.* 2012). Biophysical habitat characteristics, including primary productivity and convergent front propagation, have been shown to influence behavioural switches between Lévy behaviour and Brownian movements in several species, including the basking shark (Humphries *et al.* 2010). Such behavioural switches indicate the concentration of area-restricted search (ARS), a proxy for foraging effort, in productive waters (Humphries *et al.* 2012). Broad-scale movements have also been linked to climatic influence over thermal resources, and finer-scale habitat use closely coupled with prey availability (Cotton *et al.* 2005; Siders *et al.* 2013; Curtis *et al.* 2014), indicating that bottom-up forcing and the propagation of oceanographic features that aggregate prey are likely to mediate foraging behaviour over a continuum of spatial scales.

A diverse range of large marine vertebrates have been shown to associate with mesoscale (10 s–100 s km) and submesoscale (*c.* 1 km) oceanographic features such as fronts, eddies and seamounts as foraging habitats, in contrasting ocean domains (Morato *et al.* 2010; Godø *et al.* 2012; Scales *et al.* 2014b). Here, we focus on mesoscale fronts – physical interfaces at the transitions between water masses that differ in temperature, salinity, density, turbidity or productivity (Belkin, Cornillon & Sherman 2009) – as features of potential significance to the basking shark in seasonally stratified shelf seas in the north-east Atlantic.

Understanding the role of oceanographic processes as drivers of marine vertebrate habitat utilization is fundamental to our knowledge of pelagic ecosystem functioning and pivotal in identifying important habitats for species of conservation concern. Basking shark populations in the north-east Atlantic are still recovering from the effects of historical overexploitation (Southall *et al.* 2006), and the species is currently classified as *vulnerable* globally and *endangered* in the north-east Atlantic by the IUCN Red List of Threatened Species (Fowler 2005). A better understanding of the drivers of habitat utilization is valuable for the management of populations of these enigmatic marine vertebrates, and indeed for marine vertebrates more generally. An ability to predict the locations of important habitats has relevance for the design of marine protected area (MPA) networks and marine spatial planning (Miller & Christodoulou 2014; Paxton, Scott-Hayward & Rexstad 2014; Scales *et al.* 2014b) and could inform projections of habitat shifts occurring in the wake of future climate change.

Seasonal basking shark aggregations occur in coastal regions of Great Britain and Ireland from May to October each year, when they can be observed surface-feeding on dense zooplankton patches (Sims, Fox & Merrett 1997; Sims & Merrett 1997). Although sharks are generally present in shelf and shelf-edge waters year-round in this region (Sims *et al.* 2003), they also spend protracted periods in the open ocean and are rarely sighted at the surface at other times of year. Distinct seasonal sightings 'hotspots' are apparent off the south-west of England, the Isle of Man, western Scotland and in Irish waters (Berrow & Heardman 1994; Southall *et al.* 2005; Leeney *et al.* 2012; Witt *et al.* 2012).

Associations between basking sharks and mesoscale thermal fronts have been observed repeatedly in the region, with sharks using front-associated habitat for both foraging (Sims & Quayle 1998; Priede & Miller 2009) and social interaction (Sims *et al.* 2000). Biophysical coupling along fronts is known to lead to the proliferation and aggregation of zooplankton (Le Fevre 1986; Franks 1992b; Genin *et al.* 2005), creating potentially profitable foraging opportunities for higher trophic-level organisms (Belkin *et al.* 2014; Scales *et al.* 2014b). Tidally mediated thermal fronts in seasonally stratified shelf seas can be highly productive (Pingree *et al.* 1975; Pingree & Griffiths 1978) and are known to be features around which the basking shark exploits foraging opportunities resulting from aggregation of its preferred *Calanus* prey (Sims, Fox & Merrett 1997; Sims & Merrett 1997; Sims & Quayle 1998).

Although broad-scale climatic drivers of basking shark abundance (e.g. North Atlantic Oscillation, NAO; Cotton *et al.* 2005) and the finer-scale influence of prey dynamics on habitat selection (Continuous Plankton Recorder, CPR; Sims *et al.* 2006) have been investigated in some detail, associations between sharks and frontal activity in the region have been described (e.g. Sims *et al.* 2003, 2006; Sims 2008) but not yet adequately quantified. A recent study in the north-western Atlantic linked the movements of sharks tracked using biotelemetry over timescales of days to weeks with remotely sensed oceanographic data, finding significant associations with sharp surface gradients in temperature and productivity in Cape Cod Bay during late summer (Curtis *et al.* 2014). These findings provided valuable insight into preferred oceanographic conditions, and the study represented a methodological forward step in quantitative investigation of habitat selection. However, the spatial resolution (0·05° pixel size) and temporal averaging (monthly composites) of remotely sensed imagery and the use of the gradient method to identify fronts restricted the authors' ability to define mesoscale features accurately. Moreover, the latter study used nonparametric testing to compare oceanographic conditions encountered by tracked sharks to those encountered by 250 random walk simulations. This approach to investigating habitat preference is limited in its ability to quantify the influence of mesoscale oceanographic conditions.

Here, we use satellite-linked archival tracking to investigate movements of individual sharks through their natural environment over timescales of weeks to months, alongside high-resolution composite front mapping (*c.* 1 km pixel size; 7-day composites; Miller 2009) to characterize oceanographic conditions encountered. We test the hypothesis that surface frontal activity is a predictor of habitat preference for these planktivorous megavertebrates, and use a robust mixed modelling procedure to quantify associations occurring over two spatio-temporal scales: (i) seasonal associations with regions of frequent frontal activity, and (ii) near real-time associations with contemporaneous thermal and chlorophyll-*a* (chl-*a*) fronts. We aim to clarify factors affecting the degree of association between sharks and fronts through explicitly investigating the influence of cross-frontal temperature change and front persistence. In this way, we highlight the key biophysical characteristics of fronts that attract basking sharks, improving understanding of the foraging ecology of the species and building capacity for identification of potentially important habitats.

Materials and methods

SATELLITE-LINKED ARCHIVAL TRACKING

Satellite-linked pop-up archival transmitting (PAT) tags (Wildlife Computers, Redmond, WA, USA) were deployed on foraging sharks ($n = 21$) off north-west Scotland and south-west England between May and August in 2001 and 2002. A detailed description of tag deployment and tracking data preparation protocols can be found in Sims *et al.* (2006). Briefly, PAT tags were attached to basking sharks by first approaching them from behind in a small vessel. Using a modified speargun harpoon, tags were placed at the base of the first dorsal fin and held in position by a small stainless steel T-bar dart with a monofilament tether connected to the tag (Sims *et al.* 2003, 2006). Tagging was conducted under licences from the UK Home Office, English Nature and Scottish Natural Heritage. Shark locations during the period of tag attachment were derived using light-based geolocation (GLS), corrected for sea-surface temperature (SST), with a calculated error radius of 75·5 ± 54·5 km (Sims *et al.* 2006). In order to account for this spatial uncertainty, we resampled possible locations ($n = 10$ per GLS-derived location) from within the mean radius of error (Fig. 1). Resampled presence positions falling on land were discarded and replaced. We also resampled presence positions ($n = 10$) in the initial (vessel dGPS, error radius <5 m) and final (Argos pop-up location, error radius <1 km) locations per track, for equal weighting of all presence positions. All locations derived from this combined data set were treated as near-surface presence positions in further analyses.

RANDOM WALK SIMULATIONS

The use of presence-only, serially autocorrelated tracking data to infer habitat preference has inherent complications (Aarts *et al.* 2008; Warton & Aarts 2013). In order to account for regions of habitat accessible to, but not actively utilized by, tracked sharks, we used a randomization procedure (cf. Heithaus *et al.* 2006; Sims *et al.* 2006) to generate correlated random walk simulations ($n = 1000$ per shark, total = 7000; ADEHABITATLT package for R; Calenge 2006). Simulated tracks were generated per shark such that the total number of locations equalled the original track length, and step lengths and turning angles were derived from distributions in each original track. Simulations were permitted to approach, but not cross, land, were time-matched to original tracks and were constrained within a region defined by the bounding box surrounding all locations obtained across all individuals (Fig. 1; 45° to 61° N, −15° to 6° W; hereafter 'study area'). This study area includes the UK and Irish continental shelf region, and the shelf-break system (Fig. 2). Locations derived from this simulated data set were treated as pseudo-absences for statistical analysis.

ENVIRONMENTAL DATA

Composite front maps (7-day, rolling by 1 day; Miller 2009) were prepared for the study area using SST data obtained via the Advanced Very-High Resolution Radiometer (AVHRR) sensor and ocean colour data obtained via the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS; Local Area Coverage, LAC), mapped to the study area at 1·1 km resolution using Mercator projection.

Seasonal front frequency maps quantifying the percentage time in which a front was detected in each pixel of the study area, as a ratio of positive detections to the number of cloud-free observations, were generated for each tracking year (Miller & Christodoulou 2014). As >95% of all tracking locations were obtained during the main UK basking shark sightings season (May–October), we used 7-day composite front maps from this period of each year (2001, 2002) to generate the front frequency data sets (thermal front detection threshold = 0·4 °C; chl-*a* min. front detection threshold = 0·06 mg m^{-3}). We also generated seasonal front frequency maps for the preceding year, to assess the influence of the previous year's conditions on habitat selection (Fig. 2).

Contemporaneous front metrics (front distance *fdist*, front gradient density *gdens*, front persistence *pfront*) were generated from

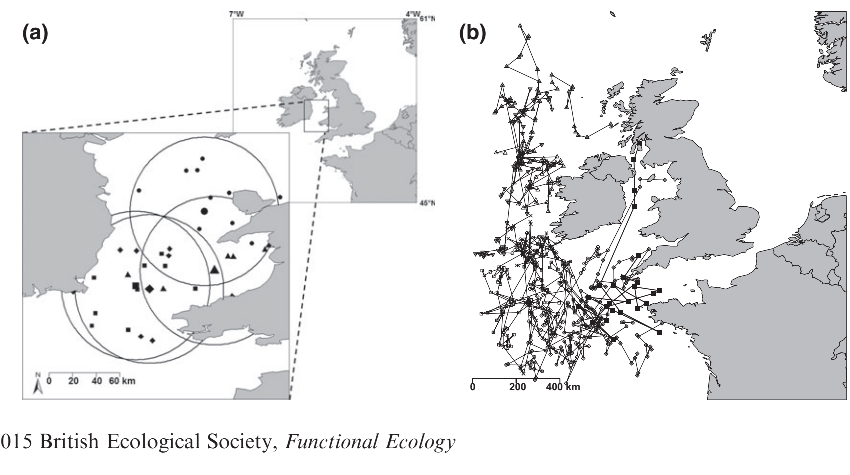

Fig. 1. Derivation of presence/pseudo-absence data set from tracking data. (a) Example of resampling of possible presence locations from within calculated error radius of each geolocation-derived tracking location. (b) Example random walks (10 shown from $n = 1000$), used to derive pseudo-absences for each shark. Geolocation-derived track as bold line.

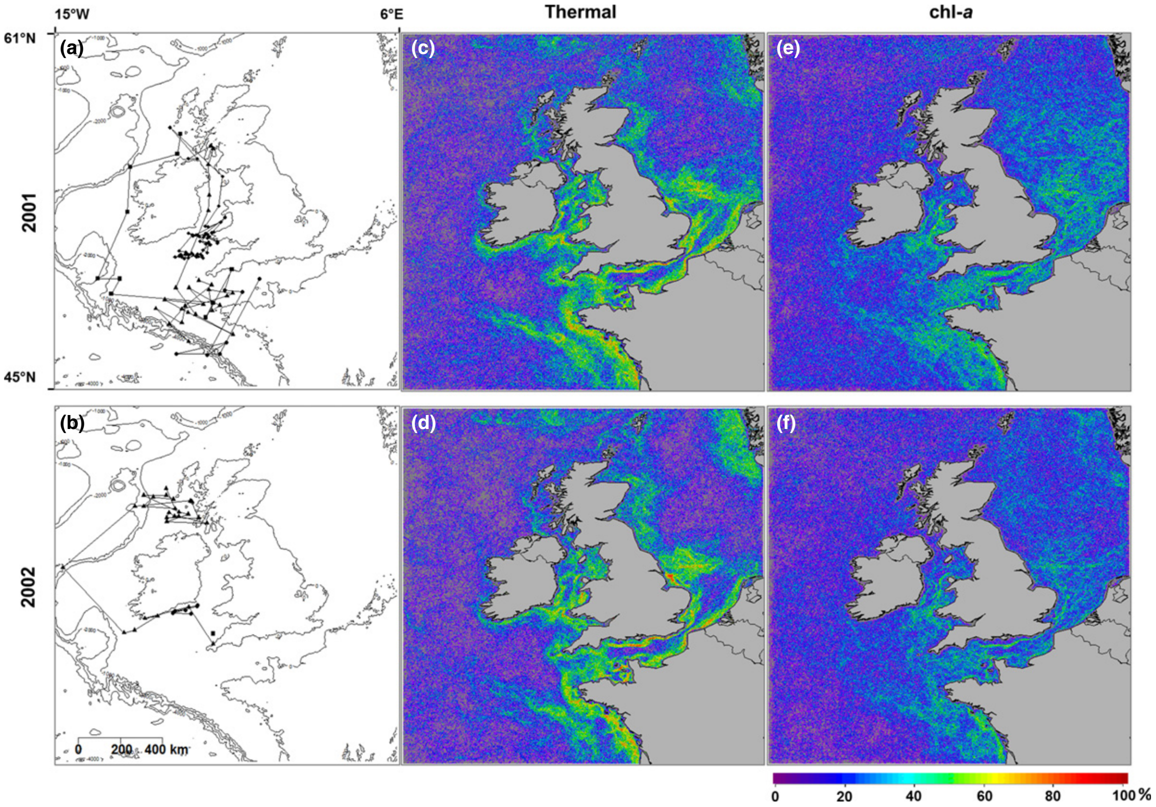

Fig. 2. Associations with broad-scale, seasonally persistent frontal zones. (a), (b) Shark tracking locations obtained from satellite-linked pop-up archival tags, with different icons identifying individual sharks overlaid over bathymetry contours of the study area, derived from the General Bathymetric Chart of the Oceans (GEBCO, 30 arc-second resolution). (c), (d) Seasonal thermal front frequency for the main UK basking shark sightings season (May–October) of each year at 1·1 km resolution (0·4 °C front detection threshold). (e), (f) Seasonal chlorophyll-*a* front frequency for the same period of each year (0·06 mg m^{-3} min. front detection threshold).

composite front maps and time-matched to shark tracks (7-day, rolling by 1 day). Front distance (*fdist*) quantifies the distance from any location in the study area to the closest simplified front, using a custom simplification algorithm (P. I. Miller, unpubl. data). Front gradient density (*gdens*) is the result of applying a Gaussian smoothing filter ($\sigma = 5$ pixels) to a map of the mean gradient magnitude values. It is designed to provide a local neighbourhood average of frontal gradient, avoiding the discrete nature of individual detected front contours. Front persistence (*pfront*) is the fraction of cloud-free observations of a pixel for which a front is detected. Again, a Gaussian filter ($\sigma = 5$ pixels) was applied, to provide a local neighbourhood average of frontal persistence.

Thresholds for front detection (Single-Image Edge Detection, SIED; Cayula & Cornillon 1992) are often chosen arbitrarily, yet the magnitude of cross-frontal temperature change is likely to influence associations between marine vertebrates and fronts (Etnoyer *et al*. 2006). We therefore systematically varied the SIED threshold used in the preparation of thermal composite front maps, from 0·2 °C (minimum detectable owing to SST scaling in original imagery) to 1·0 °C, generating a set of time-matched front metrics at each threshold. Values were obtained for each of these metrics, plus SST and chl-*a* with no front detection, for each location of the full data set (presence, resampled presence, pseudo-absence), and used as predictor variables in subsequent statistical modelling.

STATISTICAL ANALYSIS

We carried out a use–availability analysis over two spatiotemporal scales: (i) seasonal associations with zones of frequent frontal activity and (ii) near real-time associations with contemporaneous mesoscale thermal and chl-*a* fronts. We used logistic regression within a generalized linear mixed modelling framework (GLMM, LME4 package for R; Bates *et al.* 2014) to obtain estimates of the influence of each of the predictor variables on the probability of observing a presence (individual as random effect; binary presence/pseudo-absence response; binomial errors with logistic link function). Owing to serial autocorrelation in both tracking data and simulated tracks, which violates the assumption of independence essential to the use of GLMM, we used a nonparametric bootstrapping regime to iteratively resample both the presence and the pseudo-absence data sets for each model fit (Scales *et al.* 2015). A total of 1000 presence and 1000 pseudo-absence locations, weighted as per the proportion of the complete tracking data set contributed by each individual, were subsampled from each individual data set for each iteration. Resultant presence/pseudo-absence data sets were then used to fit models over 1000 iterations.

We repeated this procedure using (i) seasonal front frequency metrics (thermal, chl-*a*) for both the season in which the sharks were tracked, and the preceding year, and (ii) 7-day contemporaneous front metrics (thermal, chl-*a*; distance to closest front *fdist*, frontal gradient density *gdens*, frontal persistence *pfront*), together with time-matched SST and chl-*a* values. All 7-day contemporaneous front metrics and SST were standardized across the entire presence/pseudo-absence data set prior to the modelling procedure, by subtracting the mean and dividing by standard deviation (Zuur, Hilbe & Ieno 2013). This enables comparability of effect sizes between variables that are scaled differently in their original form. The distribution of chl-*a* was highly skewed, with a large predominance of small values. We therefore removed all spurious outlying values (>20 mg m^{-3}) and transformed the resulting data set using a $\log_{10}$ transformation to generate an explanatory variable with a distribution approaching normal.

Owing to colinearity between predictor variables, which was detected using pairwise plots and generalized variance inflation factors (GVIF; Zuur, Hilbe & Ieno 2013), each variable was fitted via maximum likelihood estimation as a standalone explanatory term in separate model runs (1000 iterations per term). Parameter distributions generated by each set of model iterations were used to obtain the mean and standard deviation of model intercepts, regression coefficients and standard errors of fitted terms, deviance explained and chi-square statistic and *P*-value from a likelihood ratio test against a null model with no fixed effects (with Restricted Maximum Likelihood; Table S1, Supporting information). Confidence intervals (CIs; 95%) were also calculated for each of the parameter distributions. Mean values and CIs of regression coefficients were plotted and used to assess the influence of each term on the probability of shark presence (CIs overlapping zero indicates non-significant term). To assess the influence of thermal gradient magnitude on the strength of associations with fronts, we repeated this modelling procedure for each set of time-matched metrics derived using different front detection thresholds (0·2, 0·4, 0·6, 0·8, 1·0 °C).

Results

SATELLITE-LINKED ARCHIVAL TRACKING

Of the 21 basking sharks tagged, sufficient data to reconstruct tracks were received from seven individuals (body length range 2·5–7·0 m), which were tracked for a cumulative total of 964 days, ranging from 72 to 213 days per individual. A total of 186 light-level geolocations were obtained (0·2 ± 0·05 per day) during this period. Associated dive data indicated that all sharks spent a significant proportion of this time foraging at the sea surface (Sims *et al.* 2006).

SEASONAL FRONT FREQUENCY

Basking shark tracking locations were clustered within broad-scale regions of high seasonal front frequency, in both SST and chl-*a* fields (Fig. 2). Logistic regression revealed that the probability of shark presence was higher in regions of frequent or persistent frontal activity ('frontal zones') during the basking shark surface sightings season (May–October) over 2 years (Fig. 3; Table S1). Thermal front frequency had a stronger influence over the probability of observing a presence than chl-*a* front frequency, although both contributed significant explanatory power to models (Fig. 3c; Table S1). The proportion of deviance explained was also found to be higher for thermal front frequency than for chl-*a* (thermal = 8·25 ± 2·32; chl-*a* = 1·65 ± 1·06).

Seasonal front frequency in the preceding year also had an influence on the probability of observing a presence (Fig. 3; Table S1). Model intercepts and regression coefficients were similar when modelling the influence of front frequency from the contemporaneous year and from the preceding year on shark presence (Table S1). Interannual variability in front frequency was low in both thermal and chl-*a* fields between 2000 and 2002 (Fig. 2, Table 1). We also observed a high degree of spatial correlation between the thermal and the chl-*a* seasonal front frequency metrics in each year (mean = 0·523 ± 0·04; 2000 = 0·476; 2001 = 0·561; 2002 = 0·533).

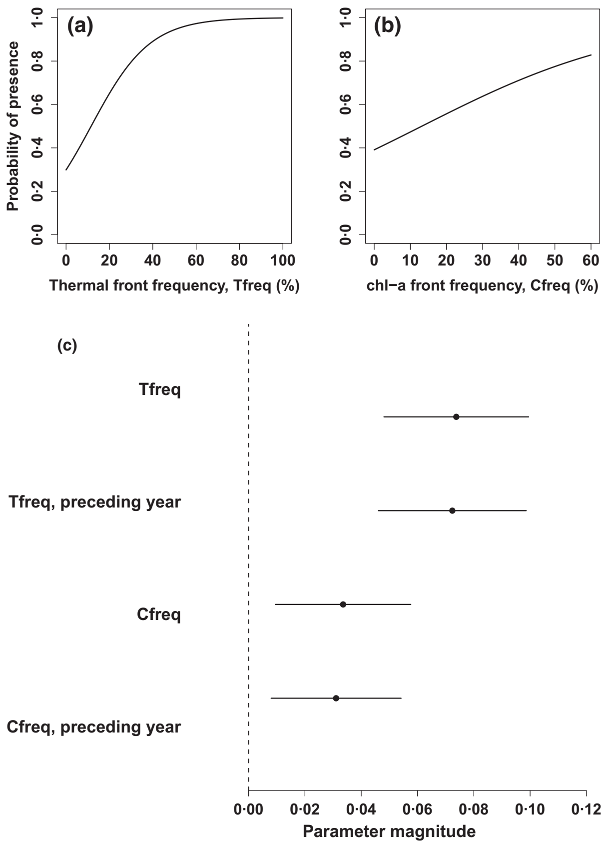

Fig. 3. Modelling the influence of seasonal front frequency on probability of shark presence. Mean regression coefficients for the influence of (a) thermal front frequency and (b) chl-*a* front frequency on probability of observing a shark presence vs. pseudo-absence derived from random walk simulations. (c) Distribution of each regression coefficient, obtained from 1000 model iterations, as mean with 95% CIs.

Table 1. Interannual variability in seasonal front frequency (May –October, 2000–2002). Pearson product-moment correlation coefficient for spatial correlation between years

	2000	2001	2002
Thermal front frequency			
Mean = 0·635 ± 0·03			
2000	1·0	0·619	0·617
2001	0·619	1·0	0·670
2002	0·617	0·670	1·0
Chl-*a* front frequency			
Mean = 0·581 ± 0·02			
2000	1·0	0·577	0·566
2001	0·577	1·0	0·599
2002	0·566	0·599	1·0

TIME-MATCHED FRONT METRICS

Shark presence locations were significantly more likely to be associated with contemporaneous thermal and chl-*a* fronts than pseudo-absences derived from random walk simulations (Fig. 4; Tables S2 and S3, Supporting information). Distance to closest chl-*a* front (*fdist*) and all 7-day thermal front metrics (distance to closest simplified front, *fdist*; frontal gradient density, *gdens;* front persistence, *pfront*; 0·4 °C front detection threshold) were significant predictors of shark presence. Shark presence was more likely to be observed in closer proximity to thermal and chl-*a* fronts, at higher thermal gradient densities and in association with persistent thermal fronts than pseudo-absences. Indeed, some individuals appeared to spend days to weeks tracking the surface profile of strong thermal fronts, presumably foraging on aggregated prey (see Video S1, Supporting information).

Overall, 7-day chl-*a* front metrics held less explanatory power than thermal metrics, while distance to closest simplified chl-*a* front *fdist* explained a significant proportion of deviance, *gdens* and *pfront* had a less pronounced effect on the probability of shark presence (Fig. 5; Table S3). In addition, confidence intervals of the distribution of regression coefficients from bootstrapping approached zero for chl-*a gdens* and overlapped zero for chl-*a pfront* (Fig. 5). We can surmise that shark presence positions are more likely to be observed in closer proximity to chl-*a* fronts than pseudo-absences, but that chl-*a gdens* and *pfront* metrics have a lesser influence on probability of shark presence, presumably as a result of the ephemeral nature of chl-*a* blooms at fronts, and the spatial smoothing involved in preparation of these metrics. These results indicate that time-matched thermal front metrics are more useful predictors of shark presence than comparable chl-*a* metrics in this case.

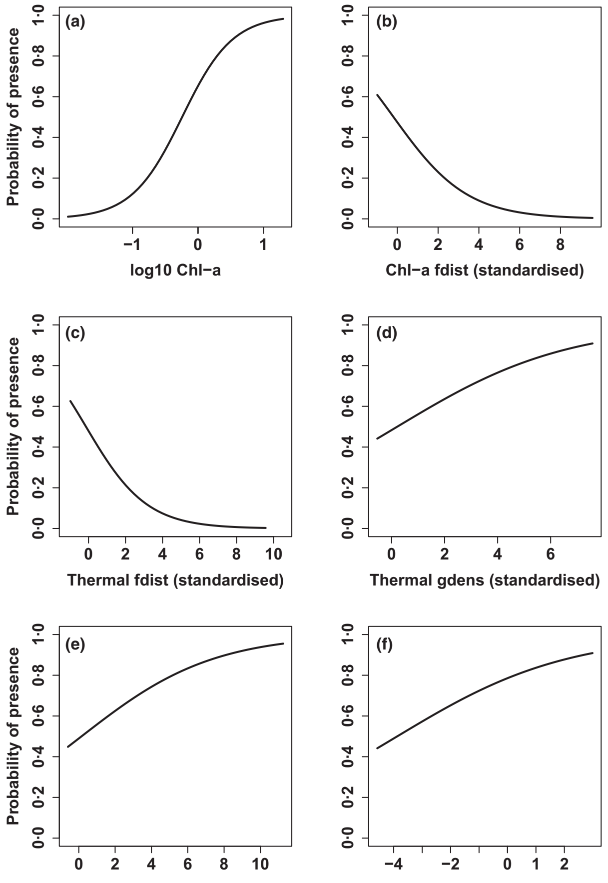

Fig. 4. Modelling the influence of contemporaneous fronts on probability of shark presence. (a–f) Mean effects of time-matched oceanographic metrics (chl-*a*, distance to closest simplified thermal or chl-*a* front *fdist*, frontal gradient density *gdens*, frontal persistence *pfront*, and sea-surface temperature, SST) over 1000 model iterations.

Varying the thermal front detection threshold had a considerable effect on the magnitude of the logistic regression coefficient for the thermal *fdist* metric (Fig. 6; Table S2). Effect size and proportion of deviance explained increased with a higher detection threshold. Shark presences were more likely to be associated with stronger thermal fronts (1·0 °C cross-frontal temperature difference or 'step') than weaker features (0·2 °C difference), although all detection thresholds resulted in significant predictors (Fig. 6; Table S2). In contrast, altering the detection threshold had little influence over the effect sizes of the *gdens* and *pfront* metrics (Table S2), most likely as a result of the inclusion of the cross-frontal gradient in the *gdens* metric, and the tendency of fronts with a stronger cross-frontal gradient to persist through time (Bakun 2006).

COMPARISON WITH STANDARD SST AND CHL-*A* FIELDS

Chlorophyll-*a* concentration was found to have a significant effect on the probability of shark presence, with $\log_{10}$-transformed chl-*a* concentration explaining the highest proportion of deviance across model iterations (Fig. 5b; Table S3). Chl-*a* had a strongly positive effect as a predictor of shark presence, indicating that foraging habitat selection is tightly coupled with primary productivity. SST was also found to be a significant predictor, although this variable explained a considerably lower proportion of deviance than chl-*a* and time-matched front metrics, having a weak negative effect on the probability of shark presence (Fig. 5; Table S3).

Discussion

Our combined use of animal-attached, satellite-linked archival tracking and composite front mapping (Miller 2009) provides novel insight into the influence of regional oceanography on habitat selection in this wide-ranging marine megavertebrate. This study builds upon prior observations of associations between the planktivorous basking shark and oceanographic fronts in coastal regions of the north-east Atlantic obtained from *in situ* work (Sims & Quayle 1998; Sims *et al.* 2000; Priede & Miller 2009), but is novel in that we provide a robust quantification of the influence of thermal and chl-*a* fronts on habitat selection for sharks tracked over timescales of weeks to months. Our analysis reveals associations between tracked sharks and seasonally persistent frontal zones, and a more proximate influence of contemporaneous mesoscale thermal and chl-*a* fronts on habitat selection.

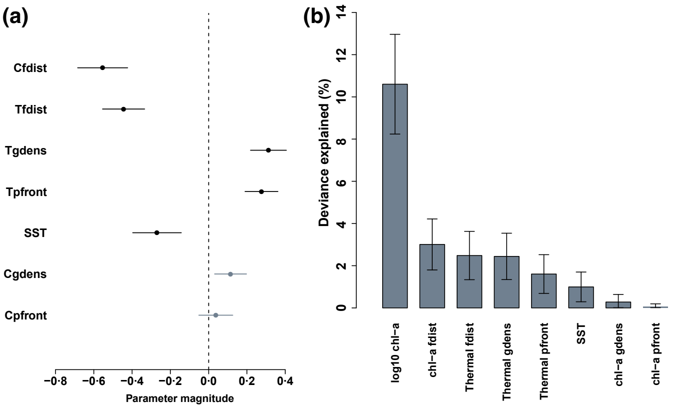

Fig. 5. Modelling the influence of contemporaneous fronts on the probability of shark presence. (a) Parameter distributions for regression coefficients, obtained from 1000 model iterations. Mean regression coefficient with 95% CIs. Significant terms in black, non-significant in grey. Coefficient for $\log_{10}$ chl-*a* not shown owing to different scaling to standardized metrics. (b) Percentage of deviance explained by each of the time-matched oceanographic metrics. Mean value with 95% CIs, from 1000 model iterations.

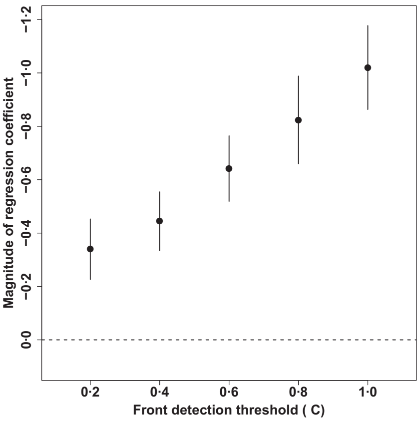

Fig. 6. Effect of varying thermal front detection threshold on magnitude of effect size for distance to closest simplified thermal front (*fdist*). Parameter distributions (mean + 95% CIs) for regression coefficient obtained from 1000 model iterations per threshold.

ASSOCIATIONS WITH SEASONALLY PERSISTENT FRONTAL ZONES

Seasonal front frequency, that is the number of times a front was detected in any one pixel (1·1 × 1·1 km) of the study area over the main UK basking shark surface sightings season (May–October), was found to be a significant predictor of shark presence for both thermal and chl-*a* frontal activity. Presence locations of tracked sharks were more likely to be found in association with seasonally persistent frontal zones than in other regions of the study area, although thermal front frequency was found to have a stronger effect than chl-*a*, perhaps owing to the propensity of thermal fronts to manifest in similar locations more frequently than chl-*a* fronts over the season (Kahru *et al.* 2012).

Furthermore, seasonal front frequency metrics from the preceding year were significant predictors of shark presence. Low interannual variability in the spatial extent of these persistent frontal zones over the study period (2000–2002) indicates that sharks may return to spatiotemporally predictable foraging grounds, in which they have previously experienced profitable prey encounter rates. Although we only have tracking data from seven different individuals tagged over two successive years, and none spanning 2 years, and so cannot determine whether the same sharks could be returning to forage in previously profitable regions, we can surmise that predictability of foraging hotspots is likely to be high over seasonal timescales. Basking sharks, like many pelagic marine vertebrates, may optimize foraging efficiency through orientation to the same broad-scale regions to search for suitable foraging areas, then using search patterns consistent with optimal random searches (Sims *et al.* 2008; Humphries *et al.* 2010) and more proximate clues to locate prey aggregations nested within (Cotton *et al.* 2005; Sims *et al.* 2006; Siders *et al.* 2013). Many marine vertebrates exhibit broad-scale foraging site fidelity over seasonal, annual or interannual timescales (e.g. seals, Bradshaw *et al.* 2004; sharks, Pade *et al.* 2009; Queiroz *et al.* 2012; whales, Irvine *et al.* 2014; seabirds, Patrick *et al.* 2014), indicating that spatio-temporal predictability of prey encounter rates influences habitat selection across taxa (e.g. seabirds, marine mammals; Weimerskirch 2007; Bost *et al.* 2009).

Spatial correlation between the locations of thermal and chl-*a* frontal zones with which sharks associate was also found to be high within the study area, over the 3 years' of remotely sensed data analysed for this study. The locations of thermal and chl-*a* fronts often coincide (Le Fevre 1986; Belkin, Cornillon & Sherman 2009), since chl-*a* fronts frequently manifest where convergent processes occurring around thermal discontinuities aggregate nutrients and plankton in productive regions with high-background chl-*a* concentrations, such as at the peripheries of plankton blooms (Le Fevre 1986; Kahru *et al.* 2012). Although these mechanisms are not yet well understood, objective detection of regions of frequent frontal activity in both thermal and chl-*a* fields, such as that presented here, could aid in the identification of biophysical hotspots. Persistent thermal and chl-*a* frontal zones in the Celtic Sea, identified using the same front frequency indices, have been found to be significant foraging features for breeding northern gannets *Morus bassanus* (Scales *et al.* 2014a). When considered together, these results suggest that persistent mesoscale frontal zones in UK shelf seas may have significant cross-taxa ecological importance, providing spatio-temporally predictable foraging opportunities for both planktivorous and piscivorous marine vertebrates.

ASSOCIATIONS WITH CONTEMPORANEOUS THERMAL AND CHL-*A* FRONTS

Basking sharks were found to associate strongly with productive regions of the study area, indicating that the propagation of surface-foraging opportunities is tightly coupled with bottom-up oceanographic forcing. Our analysis also reveals that over timescales of weeks to months, sharks associated with thermal and chl-*a* fronts within these productive areas. Time-matched front metrics were significant predictors of shark presence at the surface. Tracking locations were more likely to be found in close proximity to thermal and chl-*a* fronts, at higher thermal gradient densities and in association with more persistent thermal fronts than pseudo-absences derived from random walk simulations. These findings are in concordance with those of Curtis *et al.* (2014), and with our *a priori* assumption that foraging behaviour of these planktivores is closely tied to low trophic-level enhancement. Comparable associations with thermal fronts in pelagic waters have been documented in other sharks and large teleosts, including the blue shark *Prionace glauca* (Queiroz *et al.* 2012), ocean sunfish *Mola mola* (Sims & Southall 2002), bluefin *Thunnus thynnus* (Schick, Goldstein & Lutcavage 2004), albacore *Thunnus alalunga* and skipjack *Katsuwonus pelamis* tunas (Fiedler & Bernard 1987) and swordfish *Xiphias gladius* (Podestá, Browder & Hoey 1993; Seki *et al.* 2002) in differing oceanographic regions, suggesting that thermal fronts could have multitaxon ecological importance for pelagic predators.

Furthermore, basking shark presence was more likely to be associated with lower SSTs, indicating that fine-scale upwelling and vertical mixing are likely to influence the propagation of profitable foraging opportunities. Upwelling fronts are sites of strong biophysical coupling, along which nutrient retention and vertical mixing increase primary productivity and attract grazers such as the calanoid prey of basking sharks (Smith *et al.* 1986; Franks 1992a; Sims & Quayle 1998; Shanks *et al.* 2000).

Through systematically varying the threshold used for the detection of thermal fronts, our analysis has revealed that cross-frontal temperature difference is likely to be an important influence on foraging decisions. Regression coefficients and proportion of deviance explained across the model iterations per threshold indicate that stronger (1·0 °C cross-frontal step) fronts have more influence over the probability of shark presence than thermal fronts with a weaker cross-frontal temperature step. In addition, the effect of the gradient density *gdens* metric indicates that sharks are more likely to associate with stronger fronts. While part of this effect may be related to the spatial element of this study, in that stronger fronts are less numerous and so less likely to be encountered by random walk simulations, this nevertheless indicates that tracked sharks were found in closer proximity to these strong fronts than could be expected by chance. These findings highlight the importance of the choice of front detection threshold in studies investigating species–habitat relationships. The influence of relative sizes of fronts detected has not been explicitly considered here owing to methodological considerations, but may be an interesting subject for future research.

The magnitude of cross-frontal temperature difference is likely linked to persistence and the degree of bioaggregation occurring at a front, owing to the spatial and temporal lags inherent in biophysical coupling mechanisms (Le Fevre 1986). Stronger fronts are more likely to persist through time and also potentially more likely to attract foraging sharks. The mechanisms through which basking sharks detect and respond to environmental clues associated with biophysical coupling at fronts are not yet well understood, but frontogenesis and front propagation are likely to induce the development of discernible environmental clues (e.g. surface and subsurface flow patterns, tidal slicks and streams, accumulation of biota; Franks 1992b). These cues are likely to be more pronounced in the vicinity of stronger, more persistent fronts.

Modelling the influence of contemporaneous fronts on habitat selection has revealed that spatio-temporal persistence of thermal fronts is an important aspect of their attractiveness as surface-foraging hotspots. Thermal fronts in shelf seas around Great Britain and Ireland form primarily as a result of interaction between tidal processes, seasonal stratification and bathymetric influence (Pingree & Griffiths 1978; Simpson & Sharples 2012). As a result, fronts range from ephemeral, only manifesting at certain stages of the tidal cycle, to quasi-stationary and seasonally persistent (Belkin, Cornillon & Sherman 2009; Simpson & Sharples 2012).

Persistent fronts are more likely to be sites of bioaggregation (Bakun 2006), and hence more likely to attract foraging marine vertebrates, than ephemeral features. While gannets in the Celtic Sea appear to target foraging effort within seasonally persistent frontal zones, responses to contemporaneous fronts are highly variable (Scales *et al.* 2014a). We here provide evidence that basking sharks may associate with contemporaneous fronts more actively than these piscivorous birds, and while persistence evidently has an influence, sharks may also associate with more ephemeral features. We can surmise that aggregation of the sharks' preferred zooplankton prey does not involve the same spatial and temporal lags that would be required for bioaggregation to propagate through the food chain from plankton to pelagic fish populations and, in turn, to their predators. This work highlights the importance of persistence, and spatio-temporal predictability, of fronts when considering their value as habitats for marine predators.

TECHNICAL LIMITATIONS

While this study enhances understanding of associations between basking sharks and fronts in the north-east Atlantic, it is not of course without limitations. Using archival tracking technologies based on light-level geolocation has intrinsic limitations, owing to the low level of spatial accuracy of location estimates. However, we have propagated this uncertainty through modelling by repeatedly resampling potential presence locations from within an experimentally-derived radius of error around each geolocation estimate, and randomly resampling from this presence data set before fitting each model iteration. The future use of more accurate tracking technologies, such as fast-acquisition GPS systems (e.g. Fastloc™-GPS; Wildtrack Telemetry Systems Ltd., Leeds, UK), will enable finer-scale investigations into the drivers of habitat preference in this species and other pelagic marine vertebrates (e.g. Sims *et al.* 2009). The use of GPS-based tracking with composite front mapping or similar techniques would be a logical follow-up to the results presented here.

Moreover, our study has been restricted to the analysis of movements of only a few individuals ($n = 7$) over part of one year of their life cycle, so we are hesitant to extrapolate findings to the population level. Many aspects of the life cycle of the basking shark remain unknown, including the size of the population using shelf seas of the north-east Atlantic, and longer range migratory behaviour (Sims 2008). We cannot ascertain whether fronts are significant habitat features for basking sharks throughout the annual cycle or throughout their range. In the north-west Atlantic, tracked basking sharks move from higher latitudes in summer to equatorial regions in winter (Skomal *et al.* 2009), but in the north-east Atlantic other tracking work has revealed that the shelf-break system, a region of frequent and intense surface frontal activity, may represent an important over-wintering habitat (Sims *et al.* 2003).

Results presented here indicate that sharks also associate with thermal and chl-*a* fronts manifesting in coastal waters of the region in summer, when sharks frequently feed at the surface and occasionally dive to the sea bottom (Sims *et al.* 2005), and so are at their most vulnerable to deleterious anthropogenic interactions [e.g. fisheries bycatch; development of Marine Renewable Energy Installations (MREI); impacts of maritime leisure]. Composite front mapping is useful in identifying key habitats and potential regions of overlap with anthropogenic pressures within the Exclusive Economic Zones (EEZ) of nations, and so could be of value in marine spatial planning and the formulation of management initiatives for species of conservation concern (Miller & Christodoulou 2014; Scales *et al.* 2014b).

Although oceanographic front metrics derived from composite front mapping have proven useful in this context, the technique has some constraints that must be taken into account. Along with all marine remote sensing applications, only the surface profile of complex three-dimensional oceanographic processes can be detected. However, surface frontal activity can be a useful indicator of subsurface biophysical processes that influence prey availability (Le Fevre 1986; Genin *et al.* 2005). Moreover, this study focuses on basking sharks that spend long periods surface-feeding, which may be more closely associated with surface frontal activity than other deep-diving marine vertebrates (e.g. northern elephant seal *Mirounga angustirostris*; Robinson *et al.* 2012). In addition, the spatial resolution of SST and chl-*a* imagery used to derive the front indices is limited by the satellite-based sensors. Here, we use LAC to obtain 1·1 km resolution products, but we cannot detect finer-scale oceanographic influence on shark movements. The issue of spatial resolution has an impact on the algorithm's ability to detect fine-scale tidal mixing fronts occurring near to the coastline, which have been identified as potentially significant features for marine vertebrates utilizing the nearshore coastal zone (e.g. Jones *et al.* 2014). However, front metrics used here are appropriate for oceanographic contextualization of animal movements occurring across pelagic seascapes over timescales of days–weeks–months, complementing the recent proliferation of data obtained through biologging.

Conclusions

In summary, we present evidence that basking sharks associate strongly with thermal and chl-*a* frontal activity in shelf seas of the north-east Atlantic. We provide a robust methodological approach to quantification of the influence of fronts on habitat selection by wide-ranging marine vertebrates. This analysis reveals that seasonal front frequency is a useful predictor of shark presence. Moreover, we highlight the tendency of sharks to associate with contemporaneous thermal and chl-*a* fronts, and the significant influence of cross-frontal temperature change and spatio-temporal persistence on the strength of associations. These findings have implications for management and conservation (Miller & Christodoulou 2014; Scales *et al.* 2014b), particularly in regard to the current marine spatial planning agenda in the north-east Atlantic.

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Data accessibility

GLS tracking data and associated time-matched front metrics are deposited in the Dryad Digital Repository (doi: 10.5061/dryad.d0h7s) (Miller *et al.* 2015).

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.

Bakun, A. (2006) Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina*, **70**, 105–122.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. http://CRAN.R-project.org/package = lme4.

Belkin, I.M., Cornillon, P.C. & Sherman, K. (2009) Fronts in large marine ecosystems. *Progress in Oceanography*, **81**, 223–236.

Belkin, I.M., Hunt Jr, G.L., Hazen, E.L., Zamon, J.E., Schick, R.S., Prieto, R. *et al.* (2014) Special issue: fronts, fish, and predators. *Deep Sea Research Part II: Topical Studies in Oceanography*, **107**, 1–2.

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*, **94B**, 101–107.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C. *et al.* (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, **78**, 363–376.

Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D. & Michael, K.J. (2004) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour*, **68**, 1349–1360.

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.

Cayula, J.-F. & Cornillon, P.C. (1992) Edge detection algorithm for SST images. *Journal of Atmospheric and Oceanic Technology*, **9**, 67–80.

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

Curtis, T.H., Zeeman, S.I., Summers, E.L., Cadrin, S.X. & Skomal, G.B. (2014) Eyes in the sky: linking satellite oceanography and biotelemetry to explore habitat selection by basking sharks. *Animal Biotelemetry*, **2**, 1–15.

Etnoyer, P., Canny, D., Mate, B., Morgan, L., Ortegaortiz, J. & Nichols, W. (2006) Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 340–358.

Fiedler, P.C. & Bernard, H.J. (1987) Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental Shelf Research*, **7**, 871–881.

Fossette, S., Hobson, V.J., Girard, C., Calmettes, B., Gaspar, P., Georges, J.-Y. *et al.* (2010) Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *Journal of Marine systems*, **81**, 225–234.

Fowler, S.L. (2005) *Cetorhinus maximus*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 September 2014.

Franks, P.J.S. (1992a) Phytoplankton blooms at fronts: patterns, scales, and physical forcing mechanisms. *Reviews in Aquatic Sciences*, **6**, 121–137.

Franks, P.J.S. (1992b) Sink or swim: accumulation of biomass at fronts. *Marine Ecology Progress Series*, **82**, 1–12.

Genin, A., Jaffe, J.S., Reef, R., Richter, C. & Franks, P.J.S. (2005) Swimming against the flow: a mechanism of zooplankton aggregation. *Science*, **308**, 860–862.

Godø, O.R., Samuelsen, A., Macaulay, G.J., Patel, R., Hjøllo, S.S., Horne, J. *et al.* (2012) Mesoscale eddies are oases for higher trophic marine life. *PLoS ONE*, **7**, e30161.

Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D. & Sims, D.W. (2006) Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology*, **87**, 2647–2656.

Heithaus, M.R., Hamilton, I.M., Wirsing, A.J. & Dill, L.M. (2006) Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. *Journal of Animal Ecology*, **75**, 666–676.

Humphries, N.E., Queiroz, N., Dyer, J.R., Pade, N.G., Musyl, M.K., Schaefer, K.M. *et al.* (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature*, **465**, 1066–1069.

Humphries, N.E., Weimerskirch, H., Queiroz, N., Southall, E.J. & Sims, D.W. (2012) Foraging success of biological Lévy flights recorded in situ. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 7169–7174.

Irvine, L.M., Mate, B.R., Winsor, M.H., Palacios, D.M., Bograd, S.J., Costa, D.P. *et al.* (2014) Spatial and temporal occurrence of blue whales off the U.S. West Coast, with implications for management. *PLoS ONE*, **9**, e102959.

Jones, A.R., Hosegood, P., Wynn, R.B., De Boer, M.N., Butler-Cowdry, S. & Embling, C.B. (2014) Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. *Progress in Oceanography*, **128**, 30–48.

Kahru, M., Di Lorenzo, E., Manzano-Sarabia, M. & Mitchell, B.G. (2012) Spatial and temporal statistics of sea surface temperature and chlorophyll fronts in the California Current. *Journal of Plankton Research*, **34**, 749–760.

Le Fevre, J. (1986) Aspects of the biology of frontal systems. *Advances in Marine Biology*, **23**, 164–299.

Leeney, R.H., Witt, M.J., Broderick, A.C., Buchanan, J., Jarvis, D.S., Richardson, P.B. *et al.* (2012) Marine megavertebrates of Cornwall and the Isles of Scilly: relative abundance and distribution. *Journal of the Marine Biological Association of the United Kingdom*, **92**, 1823–1833.

Miller, P. (2009) Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. *Journal of Marine systems*, **78**, 327–336.

Miller, P.I. & Christodoulou, S. (2014) Frequent locations of ocean fronts as an indicator of pelagic diversity: application to marine protected areas and renewables. *Marine Policy*, **45**, 318–329.

Miller, P.I., Scales, K.L., Ingram, S.N., Southall, E. & Sims, D.W. (2015) Data from: Basking sharks *Cetorhinus maximus* and oceanographic fronts: quantifying associations in the north-east Atlantic. *Dryad Digital Repository*, doi:10.5061/dryad.d0h7s.

Morato, T., Hoyle, S.D., Allain, V. & Nicol, S.J. (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 9707–9711.

Pade, N.G., Queiroz, N., Humphries, N.E., Witt, M.J., Jones, C.S., Noble, L.R. *et al.* (2009) First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: area fidelity, wider-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology*, **370**, 64–74.

Patrick, S., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W.J., Bodey, T.W. *et al.* (2014) Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos*, **123**, 33–40.

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. *Scottish Natural Heritage Commissioned Report No. 573*.

Pingree, R. & Griffiths, D. (1978) Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical Research*, **83**, 4615–4622.

Pingree, R.D., Pugh, P.R., Holligan, P.M. & Forster, G.R. (1975) Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English channel. *Nature*, **258**, 672–677.

Podestá, G.P., Browder, J.A. & Hoey, J.J. (1993) Exploring the association between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. *Continental Shelf Research*, **13**, 253–277.

Priede, I. & Miller, P. (2009) A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing II: new analysis reveals orientation to a thermal front. *Fisheries Research*, **95**, 370–372.

Queiroz, N., Humphries, N.E., Noble, L.R., Santos, A.M. & Sims, D.W. (2012) Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLoS ONE*, **7**, e32374.

Robinson, P.W., Costa, D.P., Crocker, D.E., Gallo-Reynoso, J.P., Champagne, C.D., Fowler, M.A. *et al.* (2012) Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PLoS ONE*, **7**, e36728.

Scales, K.L., Miller, P.I., Embling, C.B., Ingram, S.N., Pirotta, E. & Votier, S.C. (2014a) Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of the Royal Society Interface*, **11**, 20140679.

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. & Votier, S.C. (2014b) 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., Varo-Cruz, N., Hodgson, D.J., Hawkes, L.A. & Godley, B.J. (2015) Do oceanic loggerhead turtles *Caretta caretta* associate with oceanographic fronts? Evidence from the Canary Current Large Marine Ecosystem. *Marine Ecology Progress Series*, **519**, 195–207.

Schick, R., Goldstein, J. & Lutcavage, M. (2004) Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). *Fisheries Oceanography*, **13**, 225–238.

Seki, M.P., Polovina, J.J., Kobayashi, D.R., Bidigare, R.R. & Mitchum, G.T. (2002) An oceanographic characterization of swordfish (*Xiphias gladius*) longline fishing grounds in the springtime subtropical north Pacific. *Fisheries Oceanography*, **11**, 251–266.

Shanks, A.L., Largier, J., Brink, L., Brubaker, J. & Hooff, R. (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnology and Oceanography*, **45**, 230–236.

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.

Simpson, J.H. & Sharples, J. (2012) *Introduction to the Physical and Biological Oceanography of Shelf Seas*. Cambridge University Press, Cambridge.

Sims, D.W. (1999) Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266**, 1437–1443.

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. & Southall, E.J. (2002) Occurrence of ocean sunfish, *Mola mola* near fronts in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **82**, 927–928.

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 of London. Series B: Biological Sciences*, **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 of London. Series B: Biological Sciences*, **273**, 1195–1201.

Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W. *et al.* (2008) Scaling laws of marine predator search behaviour. *Nature*, **451**, 1098–1102.

Sims, D.W., Queiroz, N., Humphries, N.E., Lima, F.P. & Hays, G.C. (2009) Long-term GPS tracking of ocean sunfish *Mola mola* offers a new direction in fish monitoring. *PLoS ONE*, **4**, e7351.

Sims, D.W., Humphries, N.E., Bradford, R.W. & Bruce, B.D. (2012) Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of Animal Ecology*, **81**, 432–442.

Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K.W. *et al.* (2009) Transequatorial migrations by basking sharks in the Western Atlantic Ocean. *Current Biology*, **19**, 1019–1022.

Smith, S., Jones, B., Atkinson, L. & Brink, K. (1986) Zooplankton in the upwelling fronts off Pt. Conception, California. *Elsevier Oceanography Series*, **42**, 195–213.

Southall, E.J., Sims, D., Metcalfe, J.D., Doyle, J.I., Fanshaw, S., Lacey, C. *et al.* (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 United Kingdom*, **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.

Stevens, J.D. (2007) Whale shark (*Rhincodon typus*) biology and ecology: a review of the primary literature. *Fisheries Research*, **84**, 4–9.

Viswanathan, G., Buldyrev, S.V., Havlin, S., Da Luz, M., Raposo, E. & Stanley, H.E. (1999) Optimizing the success of random searches. *Nature*, **401**, 911–914.

Warton, D. & Aarts, G. (2013) Advancing our thinking in presence-only and used-available analysis. *Journal of Animal Ecology*, **82**, 1125–1134.

Weimerskirch, H. (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, **54**, 211–223.

Witt, M.J., Hardy, T., Johnson, L., McClellan, C.M., Pikesley, S.K., Ranger, S. *et al.* (2012) Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters. *Marine Ecology Progress Series*, **459**, 121–134.

Zuur, A., Hilbe, J.M. & Ieno, E.N. (2013) *A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists*. Highland Statistics Ltd., Newburgh, UK.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Modelling the influence of seasonal front frequency on the probability of observing shark presence vs. pseudo-absence derived from random walk simulations (n = 1000 per shark).

Table S2. Modelling the influence of contemporaneous mesoscale thermal fronts on habitat selection.

Table S3. Modelling the influence of contemporaneous mesoscale chlorophyll-*a* (chl-*a*) fronts, sea surface temperature (SST) and surface chl-*a* concentration on habitat selection.

Video S1. Visualising associations between basking sharks and oceanographic fronts in the north-east Atlantic, using a Google-Earth approach to data visualisation for animal tracking data and composite front mapping.