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Cox, Samantha Lucy

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The Role of Physical Oceanography on the Distributions and Foraging Behaviours of Marine Mammals and Seabirds in Shelf-Seas

by

Samantha Lucy Cox

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THE ROLE OF PHYSICAL OCEANOGRAHY ON THE DISTRIBUTIONS AND FORAGING BEHAVIOURS OF MARINE MAMMALS AND SEABIRDS IN SHELF-SEAS

Samantha Lucy Cox

ABSTRACT

Mid-latitude shelf-seas are highly productive regions that host a rich diversity of animals including large numbers of marine mammals and seabirds. These large vertebrate predators play a crucial role in the functioning of shelf-sea ecosystems. However, the combined effects of multiple anthropogenic stressors are driving unprecedented declines in many of their populations. Mitigating this depends upon effective conservation and integrated ecosystem based approaches to management, which require a comprehensive understanding of the habitat needs of marine predators.

The foraging efficiencies of marine predators are closely tied to the availability of a number of oceanographic features. As such, these physical habitats represent critical locations within a species' range whose preservation and protection should be of high priority. The collection of studies presented in this thesis aims to improve our understanding of the physical oceanographic processes that underlie the at-sea behaviours and distributions of marine mammals and seabirds in coastal and shelf-sea environments. A combination of at-sea boat surveying, animal-borne biologging, satellite remote-sensing, passive acoustics and numerical modelling was used to collect information on the distributions and foraging behaviours of a range of marine predators alongside the bio-physical characteristics of the oceanographic habitats they occupied. These data were then used to (1) examine the use of oceanographic habitats generated around tidal-mixing fronts and coastal topographic structures by a range of piscivorous species including bottlenose dolphins *Tursiops truncatus*, common dolphins *Delphinus delphis*, harbour porpoises *Phocoena phocoena* and northern gannets *Morus bassanus*, and (2) identify the physical processes underlying their creation.

Original aspects of this work include the examination of the fine-scale bio-physical mechanisms that link marine predators to tidal-mixing fronts and coastal tidal-topographic structures. Main findings indicate that offshore habitats around tidal-mixing fronts are used by both common dolphins and northern gannets for foraging. Individuals associated with patches of increased sub-surface primary productivity, which were generated via a bi-weekly cycle of episodic turbulent mixing and stratification following an adjustment in the spatial position of a front with the spring-neap cycle. Moreover, around fronts, the dives of gannets were likely to be short and of a V-shaped strategy (with little active swim phase), which likely reflects an increase in the accessibility and catchability of their prey. In a coastal estuarine system, bottlenose dolphins were shown to associate with predictable downwelling features generated during flood tidal flows that were thought to act as a foraging aid. Together, these findings highlight the fundamental role physical oceanographic processes play in the structuring of marine ecosystems by providing vulnerable marine predators with prosperous and reliable foraging resources that they can exploit. This work has implications for both future studies of marine predator foraging ecology and the management of anthropogenic activities in coastal and shelf-seas.

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 prior agreement of the graduate committee. Work submitted for this research degree at Plymouth University has not formed part of any other degree either at Plymouth University of at another establishment.

This study was financed with the aid of a studentship from the Natural Environment Research Council (NERC) and carried out in collaboration with Exeter University. Additional funding for fieldworks in Chapter's III, V and VI was provided by NERC (grant reference NE/I001832/1), Plymouth Marine Institute, Exeter University, Natural Resources Wales (NRW) and the Royal Society for the Protection of Birds (RSPB).

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Relevant scientific seminars and conferences were regularly attended at which work from this project was often presented. The author attended specialist courses as part of research training. Work from the project and collaborations established during this project lead to a number of manuscripts that will be or have been submitted for peer review publication.

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SCIENTIFIC COMMUNICATIONS AND TRAINING COURSES ATTENDED DURING THE PHD

Scientific publications

Carter MID; **Cox SL**; Scales KL; Bicknell A; Bearhop S; Nicholson M; Atkins K; Morgan G; Morgan L; Grecian J; Patrick S; Votier SC. (*accepted*) GPS tracking reveals rafting behaviour of Northern Gannets (*Morus bassanus*): Implications for foraging ecology and conservation

Cox SL; Scott BE; Camphuysen CJ (2013) Combined spatial and tidal processes identify links between pelagic prey species and seabirds. Mar Ecol Prog Ser 479: 203-221

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Conference presentations

Cox SL; Hosegood PJ; Embling CB; Votier SC; Ingram SN. Shelf-sea fronts: Localised oceanographic features with important ecological roles. 5 minute oral presentation at ICCB-ECCB: 27th International Congress for Conservation Biology, 4th European Congress for Conservation Biology. August 2015. Montpellier, France.

Cox, SL; Hosegood PJ; Embling CB; Englund AM; Votier SC; Rogan E; Ingram SN. The use of tidally driven hydrodynamic features by a coastal top predator. Poster presentation at ICCB-ECCB: 27th International Congress for Conservation Biology, 4th European Congress for Conservation Biology. August 2015. Montpellier, France.

Cox SL; Miller PM; Embling CB; Scales KL; Hosegood PJ; Ingram SN; Votier SC. 3D movements of gannets alter in areas of frequent frontal activity. Poster presentation at Plymouth marine science and education foundation annual student conference. February 2015. Plymouth, UK

Cox SL; Miller PM; Embling CB; Scales KL; Hosegood PJ; Ingram SN; Votier SC. 3D movements of gannets alter in areas of frequent frontal activity. Poster presentation at the 5th international bio-logging science symposium (BLS5). September 2014. Strasbourg, France

Hosegood PJ; **Cox SL**; Schwarz J; Zanacchi M; Torres R. Does the extraction of energy from the sea surface really impact on regional physical and biological processes? Poster presentation at the 1st annual conference of the partnership in research in marine renewable energy (PRIMARE). June 2014, Plymouth, UK

Cox SL; Hosegood PJ; Embling CB; Votier SC; Ingram SN. Interactions between oceanography and marine top predators at a frontal system off the North Cornwall coast. 5 minute oral presentation at southwest marine ecosystems conference (SWME). April 2014. Plymouth, UK

Cox, SL; Hosegood PJ; Embling CB; Votier SC; Ingram SN. Interactions between oceanography and seabirds at a frontal system off the North Cornwall coast. 15 minute oral presentation at the 12th international seabird group conference. March 2014. Oxford, UK

Cox SL; Hosegood PJ; Embling CB; Votier SC; Ingram SN. Defining the foraging habitats of marine top predators. 15 minute oral presentation at Plymouth marine science and education foundation annual student conference. November 2013. Plymouth, UK

Cox SL; Hosegood PJ; Embling CB; Votier SC; Ingram SN. Physical drivers of predator foraging in the marine environment. 15 minute oral presentation at the United Kingdom and Ireland regional student chapter of the society for marine mammology annual conference. January 2012. St Andrews, UK

Specialist training courses attended

Zero-inflated models and generalized linear mixed models with R. Dr Alain Zuur and Dr Elena Ieno (Highland Statistics Ltd). Elche, Spain, May 2013.

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LIST OF ABBREVIATIONS

ACF	Auto-correlation function plot
ADCP	Acoustic Doppler current profiler
AIC	Akaike's information criterion
AUC	Area under the receiver operating characteristic curve
AVHRR	Advanced very high resolution radiometer
BirdID	Bird ID
BODC	British oceanography data centre
CI	Confidence intervals (95% limits)
CorStructSp	Spatial correlation structure
CorStructTp	Temporal correlation structure
CReSS	Complex region spatial smoother
CTD	Conductivity-temperature-depth
CurrentSpeed	Current speed
DecTime	Decimal time of day
DepthChange	Depth change
DPH	Detection positive hours per day
DOM	Dynamic ocean management
EEZ	Exclusive economic zone
Fdist	Distance to closest front
Ffreq	Front frequency
FrontIndex	Front index
GAMM	Generalised additive mixed effects model
Gdens	Front gradient intensity
GEE-GAM	Generalised additive estimating equations
GLM	Generalised linear model
GLMM	Generalised linear mixed effects model
INFOMAR	Integrated mapping for the sustainable development of Ireland's marine resource program
KCV	K-folds cross validation
LogMaxShear	Logged maximum shear
LMM	Linear mixed effects model

MaxFluorescence	Maximum relative fluorescence
ML	Maximum likelihood
MPA	Marine protected area
MREI	Marine renewable energy installation
MSS	Microstructure profiler
NEODAAS	Natural environment research centre Earth observation data acquisition and analysis service
NERC	Natural environment research centre
QIC$_{u}$	Quasi-likelihood criterion
REML	Restricted maximum likelihood
RIB	Rigid inflatable boat
ROC	Receiver operating characteristic curve
ROFI	Region of freshwater influence
SAC	Special area of conservation
SALSA	Spatially adaptive local smoothing algorithm
SeaState	Sea state corresponding to the Beaufort scale
SpringNeapCycle	Relative position in the spring-neap cycle
SST	Sea surface temperature
ThermStrat	Thermal stratification
TideDir	Direction of tidal flow
TDR	Time-depth recorder
UKHO	United Kingdom hydrographic office
UTM	Universal transverse Mercator

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CHAPTER I

General introduction and overview

1.1 Context and project rationale

Large marine vertebrate predators, such as marine mammals and seabirds, occupy critical roles in the functioning of marine ecosystems (Heithaus et al. 2008). However the combined and cumulative effects of multiple anthropogenic stressors, including fisheries by-catch, habitat degradation, resource competition and climatic variability, are negatively impacting their populations (Halpern et al. 2008, Estes et al. 2009, Cury et al. 2011, Lewison et al. 2014, McCauley et al. 2015). Mitigating this depends upon the effective conservation of marine ecosystems (Taylor et al. 2005), which requires an in-depth understanding of how marine predators interact with their environment (Hooker & Gerber 2004, Hooker et al. 2011).

Mid-latitude shelf-seas are highly productive regions that host a rich diversity of marine predators including large numbers of marine mammals and seabirds (Stone et al. 1995, Reid et al. 2003, Simpson & Sharples 2012). These environments are inherently dynamic in their oceanography owing to the combined effects of seasonal variation in solar irradiation, strong tidal currents and complex shallow (typically less than 200m) topography, which ultimately drive the accumulation and distribution of primary productivity and small nekton. As such, heterogeneity in resources is a key feature of mid-latitude shelf-seas (Franks 1992b, Genin et al. 2005) with concomitant consequences for higher trophic level consumers. Whilst many large marine vertebrate predators display complex and highly mobile behaviours (Block et al. 2011), they typically concentrate at discrete foraging ‘hotspot’ locations (Sydeman et al. 2006, Weimerskirch 2007) which, following optimal foraging theory (Stephens & Krebs 1986), should reflect the patchily distributed availability of their prey.

The dynamic nature of shelf-seas means marine predators face substantial challenges when locating and capturing their prey, which are sparsely distributed across these vast environments (Fauchald 2009). A number of oceanographic features, such as fronts (Scales et al. 2014b), stratified regions with a defined thermocline (Scott et al. 2010, Pelletier et al. 2012), offshore banks where internal waves propagate (Stevick et al. 2008) and tidally active topographic structures around the coast (Benjamins et al. 2015), are known to regulate the accessibility and availability of prey (Vlietstra et al. 2005, Bertrand et al. 2008, Stevick et al. 2008, Hazen et al. 2011, Embling et al. 2012, Embling et al. 2013) in a persistent and/or predictable manner, providing a resource that marine predators can repetitively exploit (Irons 1998, Bailey & Thompson 2010, Scales et al. 2014a). As such, foraging habitat can be thought of as a point or region in environment space and time, the location of which is determined by a specific set of bio-physical oceanographic covariates (Aarts et al. 2008).

The foraging efficiencies of marine predators are closely tied to the availability of oceanographic habitats, suggesting these features represent critical locations within a species’ range (Ropert-Coudert et al. 2009b, Borstad et al. 2011, Pelletier et al. 2012). Effective conservation of marine predator populations and the ecosystems they occupy therefore requires that these critical habitats are preserved and protected (Taylor et al. 2005). Achieving this requires both the identification of important oceanographic features and the physical processes that drive their creation, alongside a good understanding of the functional mechanisms that link them to marine predators. However, the variable nature of the numerous habitats available to marine predators across shelf-seas means that in many cases this remains elusive.

The relative accessibility of shelf-sea environments makes them particularly well suited for investigating interactions between marine predators and oceanography through the use of a number of methodological approaches. Traditionally, at-sea, vessel based surveying has been used to directly observe the behaviours of predators within their natural environment (Ainley et al. 2012). Whilst limited in their spatio-temporal coverage, the possibility to integrate a suite of instruments capable of obtaining *in-situ* oceanographic measurements, often of the entire water column, makes this method still highly relevant for examining the bio-physical characteristics of marine predator foraging habitats. More recently, innovations in biologging technologies mean unprecedented levels of information on the movements of an individual can be obtained across its complete range (Costa et al. 2010, Block et al. 2011). In some instances, sensors may also be capable of making *in-situ* measurements of bio-physical oceanographic conditions (Charrassin et al. 2008). These data can be integrated with remotely-sensed environmental information from satellite earth observation platforms that can provide valuable information on the characteristics and occurrences of oceanographic habitats that present with a distinct surface signature (e.g. fronts; Miller 2009). Finally, point locations around the coast can be monitored from land-based observation sites or, for echolocating cetaceans, using passive acoustics which may also be deployed further offshore over extended periods of time.

1.2 Aims, objectives and structure of the thesis

This thesis investigates interactions between marine predators, namely seabirds and marine mammals, and physical oceanography in shelf-seas. The overarching aim of the thesis is to provide a better understanding of the physical oceanographic processes that underlie the at-sea behaviours and distributions of large marine vertebrate predators in coastal and shelf-sea environments. Specifically the objectives are to:

1. Review and synthesise associations between large marine predators (seabirds and marine mammals) and physical oceanographic processes in mid-latitude shelf-sea environments from the current literature.
2. Investigate fine-scale links between marine predators (seabirds and marine mammals) and physical oceanography around a tidal-mixing front in the southern Celtic Sea.
3. Explore the temporal use of a seasonally forming tidal-mixing front in the southern Celtic Sea by small cetaceans.
4. Examine the fine-scale diving behaviours of northern gannets *Morus bassanus* in relation to shelf-sea fronts across their entire range in the Celtic Sea.
5. Investigate links between bottlenose dolphins *Tursiops truncatus* and tide in a topographically complex estuarine system on the west coast of Ireland.

The thesis is comprised of a series of chapters, each written as a stand-alone piece of research that addresses one of the objectives outlined above and can be read in isolation without the need for cross-reference. The work presented in each chapter results from separate studies that each use a contrasting set of methods and together seek to provide a unique insight of the physical oceanographic processes associated with habitat use by marine predators. Below, a brief outline of the aims, approaches, main findings and novel contribution of each of the chapters is provided.

Chapter II provides an introduction to the subject and synthesises current understanding of interactions between large marine vertebrate predators (marine mammals and seabirds) and shelf-sea oceanography. Key oceanographic features across the continental shelf are identified and described. Documented associations with marine predators, encompassing several decades of scientific literature, are then reviewed and the factors that drive their ecological significance discussed.

Chapter III aims to (1) characterise the fine-scale oceanographic dynamics of a seasonally forming tidal-mixing front in the southern Celtic Sea and (2) establish how two large marine vertebrate predators, the northern gannet and the common dolphin *Delphinus delphis*, respond to oceanographic conditions at and surrounding the front. Data were collected during stationary and transect surveys across and around a pre-selected tidal-mixing front in the southern Celtic Sea in August of two years, 2012 and 2013. Fine-scale *in-situ* measurements of oceanography spanning the entire water column were used to characterise the dynamics of the front. Simultaneously recorded distributions of northern gannets and common dolphins from transect surveys were then compared to these *in-situ* oceanographic measurements using zero-inflated hurdle models and generalised linear models (GLM). Main findings indicate that the occurrence of both species around the front is concentrated in localised regions of increased sub-surface fluorescence, indicative of chlorophyll production, which form as a result of episodic water mixing with the spring-neap adjustment of the tidal-mixing front. Novel aspects of this chapter include (1) the use of simultaneously collected fine-scale data on animal behaviours and *in-situ* oceanography around a tidal-mixing front, (2) the use of full water column micro-structure profiling to characterise the dynamic nature of the front across both spring and neap conditions, and (3) the exploration of links between sub-surface primary production and large marine vertebrate predators foraging at a front.

Chapter IV aims to investigate temporal variability in the use of a shelf-sea tidal-mixing front in the southern Celtic Sea by small cetaceans and establish if the detection frequencies of harbour porpoises *Phocoena phocoena* and dolphins (unspecified

Delphinids) are tied to the seasonal manifestation of the tidal-mixing front and fine-scale adjustments in its position across the summer. Five years of passive acoustic monitoring data (CPODs) were sourced through collaboration with Prof Brendan Godley and Dr Matthew Witt of Exeter University. This was then coupled to (1) remotely-sensed front data obtained through collaboration with Dr Peter Miller of Plymouth Marine Laboratory, (2) remotely-sensed sea surface temperature (SST) and chlorophyll data provided by NEODAAS (Plymouth Marine Laboratory) and (3) tidal height predictions obtained from Polpred tidal prediction model (via Dr Matthew Witt). Generalised additive mixed effects models (GAMM) were used both to allow for non-linearity in relationships between the occurrence of cetaceans and oceanographic measurements and to account for differences in the detection capabilities of acoustic devices. The main findings of this chapter indicate that harbour porpoises and dolphins show contrasting patterns in the temporal usage of the site with peaks in harbour porpoises occurring in the spring (January to March) and dolphins in the summer (July to September). For dolphins, this coincided with increased frontal activity and SST. Novel aspects of this work are the use of long term passive acoustics to examine the temporal usage of a site characterised by the seasonal formation of a dynamic tidal-mixing front.

Chapter V aims to examine the fine-scale diving behaviours of northern gannets in relation to remotely-sensed shelf-sea fronts across the Celtic Sea. High resolution GPS and time-depth recorder (TDR) data were collected from 53 birds tracked over one to seven day deployments across the summer breeding seasons of two years, 2012 and 2013, at Grassholm Island (Wales). Remotely-sensed front metrics were provided by Dr Peter Miller and Dr Kylie Scales of Plymouth Marine Laboratory. A habitat-use availability analysis was performed to establish if gannets preferentially dived around fronts. Following this, the characteristics of dives were then compared at and away from fronts to determine whether gannets switched foraging strategy in response to the presence of these features. In all analyses, a mixed modelling framework was used (generalised linear and linear mixed effects models; GLMM and LMM). Main findings indicate that gannets preferentially dive at and around shelf-sea fronts and that dives performed within these regions were likely to be short and shallow in their characteristics. Novel aspects of this chapter are the explicit investigation of fine-scale seabird diving behaviours in relation to shelf-sea fronts that are discretely defined via earth observation composite front mapping.

Chapter VI aims to explore relationships between bottlenose dolphins and tide across an estuarine system on the west coast of Ireland. Data from standardised animal surveys encompassing the time period of 1997-2007 were analysed together with current velocity data collected during repeat mini-circuit oceanographic surveys. Tidal predictions from 1997 to 2007 were obtained via the United Kingdom hydrographic office. Patterns in dolphin presence were examined against a number of tidal measurements using generalised additive estimating equations (GEE-GAM). Main findings indicate that the use of discrete areas across the estuary by dolphins is tidally dependent, particularly in a narrow scoured channel of the central estuary where concentrated activity occurs almost exclusively on the flood tide. Within this region strong downwelling features were identified that were most prominent during the flood tide at the times associated with increased dolphin activity. Novel aspects of this work include the use of repeat standardised surveys across an estuarine environment to identify fine-scale links between small cetaceans and tide, and the unique insight provided by the *in-situ* oceanographic data.

Chapter VII examines the main findings from the thesis in combination and discusses their ecological significance and application to marine conservation and management. Insight obtained from the use of multiple methodological approaches is summarised and opportunities for future research identified.

CHAPTER II

Physical oceanography and habitat use by large marine vertebrate predators in shelf-seas: a review

ABSTRACT

Large marine vertebrate predators, such as marine mammals and seabirds, occupy a vital role in ecosystem functioning yet the combined effects of multiple anthropogenic stressors are negatively impacting their populations, particularly in shelf-sea environments. Typically, these predators concentrate at discrete foraging locations which can be thought of as critical in occurrence. Evidence suggests these habitats form primarily as a result of bottom-up complex oceanographic dynamics. However, in many cases the involved functional mechanisms remain elusive. Here I (1) review associations between large marine vertebrate predators and physical oceanographic processes in mid-latitude shelf-sea environments, (2) highlight the characteristics of key features that make them attractive as foraging habitats and (3) discuss how these insights are useful for effectively conserving and managing marine environments. Across the literature associations between marine predators and physical features were numerous, varied over a number of spatio-temporal scales, and were subject to both species specificity and regionality. Preferentially targeted physical features included shelf-edge, upwelling and tidal-mixing fronts, offshore banks and internal waves, regions of stratification and topographically complex coastal areas subject to strong tidal flow. Current understanding suggests that the ecological significance of these features stems from their capacity to alter the densities, distributions (both horizontally and vertically) and behaviours of prey resources in a persistent and/or predictable manner that increases accessibility for large marine vertebrate predators. Future work should aim to further our current understanding of the functional mechanisms linking physical oceanography, prey and predators. Identifying the physical oceanographic habitats used by marine predators and understanding the functional mechanisms that

link the two can contribute towards both our comprehension of how the marine environment operates and achieving the objectives of ecosystem based management and marine conservation.

2.1 Introduction

Large marine vertebrate predators, such as marine mammals and seabirds, occupy a vital role in the structure, functionality and resilience of marine ecosystems, yet are highly sensitive to disturbance (Furness & Tasker 2000, Heithaus et al. 2008). The combined and cumulative effects of anthropogenic stressors such as climate change (Gremillet & Boulinier 2009), habitat alteration (Furness et al. 2013), fisheries by-catch (Lewison et al. 2004) and resource competition (Pichegru et al. 2009, Bertrand et al. 2012) have negatively impacted both their distributions and abundances (Bertrand et al. 2012, McCauley et al. 2015, Paleczny et al. 2015). Mitigating this depends upon the effective conservation and integrated management of marine ecosystems (Hooker & Gerber 2004), which requires a comprehensive understanding of marine predator ecology (Hooker et al. 2011, Waggitt & Scott 2014).

Large marine vertebrate predators are highly mobile yet, whilst capable of using vast areas of the ocean (Block et al. 2011), typically concentrate in discrete and localised 'hotspot' regions to forage (Hastie et al. 2004, Sydeman et al. 2006, Weimerskirch 2007). Distributional patterns are therefore expected to match those of their prey but demonstrating this has proved challenging (Logerwell et al. 1998, Fauchald & Erikstad 2002, Gremillet et al. 2008, Torres et al. 2008). Increasing evidence indicates that bottom-up complex oceanographic dynamics, that vary in space and time, are important, and that bio-physical coupling at these sites propagates multiple trophic levels (Bakun 2006, Alemany et al. 2014) to create a prosperous prey resource that a number of marine predators have been shown to regularly target (Hunt et al. 1999, Bost et al. 2009, Wakefield et al. 2009, Scales et al. 2014b). As such, a more mechanistic approach is required to better understand the distributional patterns of large marine vertebrate predators, and a crucial first step is to identify and characterise the oceanographic habitats that marine predators are known to favour.

Mid-latitude shelf-seas are highly productive regions and, despite covering less than 10% of the oceans total area, account for over 15% of global primary productivity (Simpson

& Sharples 2012). Subsequently, high levels of biodiversity are commonly observed, and these regions host a varied array of marine predators including a number of marine mammal and seabird species (Stone et al. 1995, Reid et al. 2003). Anthropogenic activities and their impacts are particularly concentrated within shelf-sea environments (Pauly et al. 2002, Halpern et al. 2008, Lewison et al. 2014, McClellan et al. 2014) and so there is a pressing need for information on how these regions function, especially given current calls for the implementation of integrative ecosystem based approaches to management (Hyrenbach 2000, Pikitch et al. 2004, Crowder & Norse 2008). Compared to deep-sea open ocean environments, the relatively shallow depths of continental shelf-seas mean that, in addition to seasonal fluctuations in heat flux, both topography and tidal currents play a dominant role in the structuring of these regions (Hunt et al. 1999, Simpson & Sharples 2012) and so a number of dynamic features are available for marine predators to forage at (Figure 2.1). However, associations are diverse and often mediated through species specific aspects of foraging ecology (Vilchis et al. 2006, Drew et al. 2013) such as life history mode (central placed foragers versus free ranging), prey type (planktivorous or piscivorous) and physiological constraint (diving capabilities and energetic requirements). Subsequently, there are a number of functional mechanisms that could link these features to large marine vertebrate predators which, as yet, have not been comprehensively reviewed.

Within this study I aim to provide an extensive overview of the literature documenting associations between large marine vertebrate predators (marine mammals and seabirds) and ecologically significant physical oceanographic processes in mid-latitude shelf-sea environments. I first identify and describe key physical features present across the continental shelf, working systematically from the shelf-edge to the shore line (Figure 2.1), and discuss links to marine predators. I then highlight the characteristics of these features that, as current understanding indicates, make them attractive as foraging habitats and as such ecologically significant. Finally, I briefly discuss the implications of these insights for the effective conservation and management of marine environments.

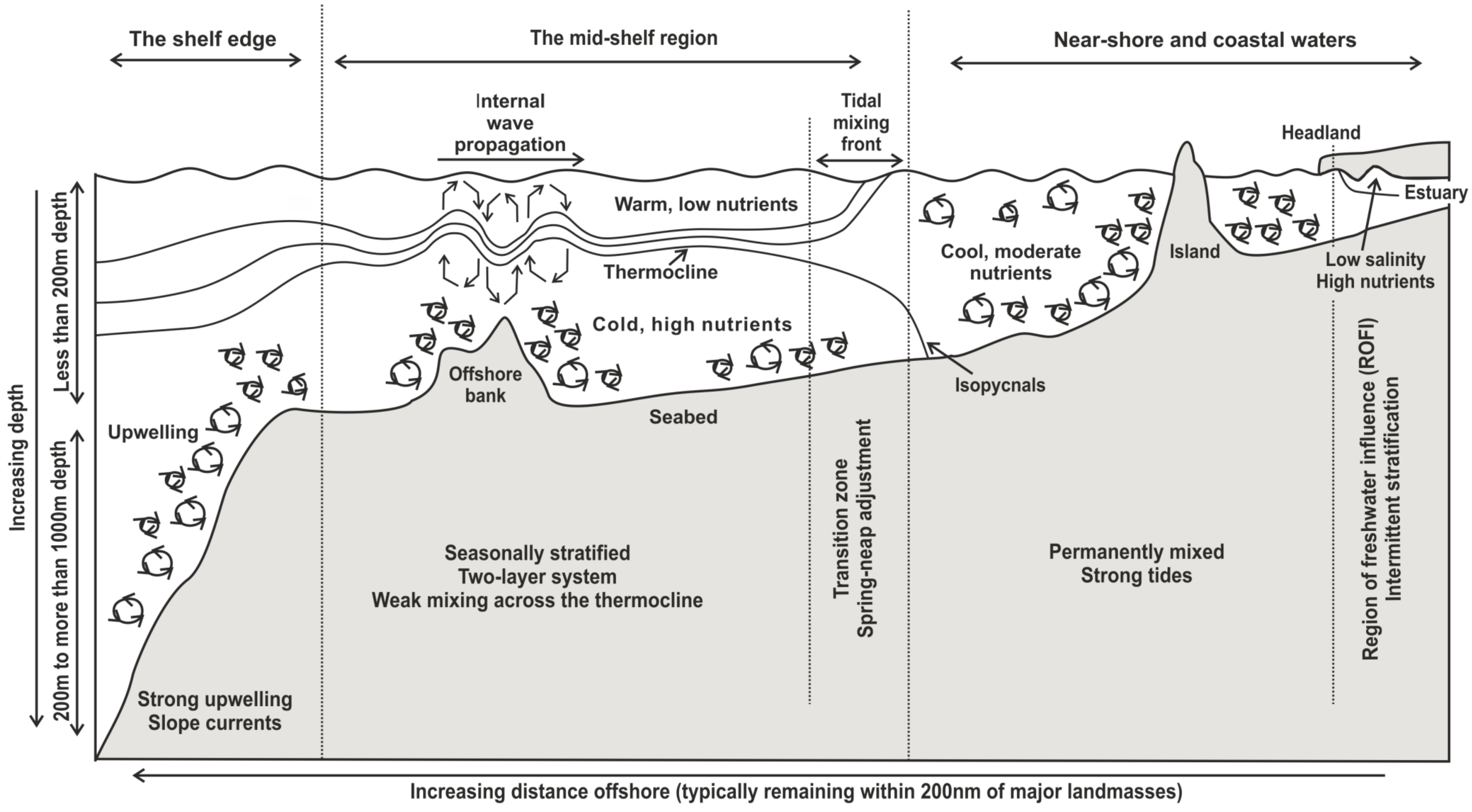

Figure 2.1 Cross shelf schematic giving an overview of the typical oceanography of shelf-sea environments at mid-latitudes during the summer months. Adapted from Simpson & Sharples (2012). Black directional arrows show (1) turbulent mixing around the seabed, offshore banks and islands (circular arrows), and (2) convergent and divergent upwelling and downwelling currents associated with the passage of internal waves (angled arrows).

2.2 The shelf-edge

The shelf-edge marks the transition zone from the comparatively shallow (usually less than 200m) waters of the continental shelf to the deep (generally exceeding 2000m) abyssal plains of the open ocean (Simpson & Sharples 2012). This region is relatively narrow, with a typical lateral distance of around 50km, and so generally characterised by a steep sloping profile (e.g. the European continental shelf-edge). Strong gradients in salinity, and sometimes temperature, mark the positions of shelf-edge fronts where exchange with the open ocean facilitates nutrient enrichment and primary production (Springer et al. 1996, Ryan et al. 1999). This productivity attracts planktivorous grazers and their predators, that may become further concentrated by convergent current flows that are often associated with shelf-edge fronts (Sabatés & Olivar 1996, Greer et al. 2015). High numbers of marine predators, particularly those capable of performing far-ranging foraging trips (e.g. black petrel *Procellaria parkinsoni*, northern fulmar *Fulmarus glasialis,* short-tailed albatross *Phoebastria albatrus* and short-tailed shearwater *Puffinus tenuirostris*; Ladd et al. 2005, Piatt et al. 2006, Freeman et al. 2010) or that are not restricted to a central location for breeding (e.g. Curvier's beaked whale *Ziphius cavirostris*, Risso's dolphin *Grampus griseus*, sperm whale *Physeter microcephalus* and spotted dolphin *Stenella attenuata*; Baumgartner 1997, Azzellino et al. 2008, Scott & Chivers 2009), are regularly observed foraging at these features.

In shelf-edge regions where seasonally persistent cross-shore winds are experienced, primary productivity levels, driven by the upwelling of deep ocean nutrient rich water (Franks 1992a, Kampf et al. 2004), are among the highest observed globally (Longhurst et al. 1995) and draw in dense concentrations of phytoplankton grazers (Bjorkstedt et al. 2002, Genin 2004), which in turn attract large numbers of forage fish (Ayon et al. 2008) and large marine vertebrate predators (Forney & Barlow 1998, Croll et al. 2005, Tynan et al. 2005, Thompson et al. 2012). Upwelling features are particularly pronounced along the eastern margins of subtropical ocean gyres in regions where the full extent of the continental shelf narrow, such as western North America (the California current upwelling system; Ainley et al. 2005, Croll et al. 2005), Peru (the Humboldt current system; Weichler et al. 2004), and western Africa (the Benguela upwelling system and the Canary current; Camphuysen & van der Meer 2005, Sabarros et al. 2013). Within these systems a number of marine predators are known to forage around frontal convergent zones (e.g. Cape gannet *Morus capensis* and rhinoceros auklet *Cerorhinca monocerata*; Ainley et al. 2005, Sabarros et al. 2014), likely because prey further aggregate here (Reese et al. 2011) which can create localised foraging opportunities, sometimes near the surface (Weichler et al. 2004). The transport of deep ocean, nutrient rich water onshore means variability in the intensity of upwelling features can have substantial effects across associated on-shelf ecosystems, with concomitant effects on large marine vertebrate predators (Becker & Beissinger 2003, Black et al. 2011, Reese et al. 2011).

2.3 The mid-shelf region: from the shelf-edge to near-shore coastal waters

The mid-shelf region extends from the shelf-edge to near-shore coastal waters (Figure 2.1) with topographic depths typically ranging from around 40m to 200m. The region seasonally stratifies between late spring and autumn, when increased solar irradiation heats surface waters sufficiently so as to increase buoyancy levels and overcome tidal and wind driven mixing (Pingree 1975, Pingree et al. 1976, Simpson & Sharples 2012). A two-layer system is formed, characterised by a top layer of warm nutrient deficient water and a bottom boundary layer of dense and cold nutrient rich water (Figure 2.1). Peaks in the occurrence of many of the marine mammal and seabird species present in these regions coincide with this stratification of the water column (Stone et al. 1995) which underlies a number of oceanographic processes that appear important to marine predators, particularly in areas where the spatial extent of the continental on-shelf region is large and tidal ranges considerable (e.g. the Canadian, European and northeast USA continental shelves).

2.3.1 The annual spring bloom

The onset of stratification in the early to late spring drives a significant annual peak in phytoplankton production known as the spring bloom (Pingree et al. 1976, Sharples et al. 2006). The timing of this bloom varies inter-annually as a result of fluctuations in spring air temperature and wind stress (Sharples et al. 2006), which can lead to a temporal mismatch between fish spawning and peak plankton production (match-mismatch hypothesis; Cushing 1975) with concomitant consequences for fish recruitment in the following months (Beaugrand & Kirby 2010). This can have bottom-up impacts at higher trophic levels, influencing the availability of food during the early life stages of marine predators (Durant et al. 2007), which has been shown to effect the breeding successes of a number of seabirds including; Atlantic puffin *Fratercula arctica*, black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge* and rhinoceros auklet (Durant et al. 2006, Scott et al. 2006, Borstad et al. 2011).

2.3.2 The thermocline and sub-surface productivity

Following the spring bloom, productivity within the mid-shelf region redistributes and is maintained by a number of oceanographic processes. An important feature is the vertical interface between low nutrient warm surface waters and cold dense high nutrient bottom waters where steep vertical gradients in temperature, density and/or salinity are observed (Figure 2.1). This is referred to as the thermocline, pycnocline and/or the halocline respectively and acts as a barrier between surface and bottom boundary waters, inhibiting the vertical exchange of nutrients and plankton (Stepputtis et al. 2011).

High levels of sub-surface primary productivity are often concentrated around the thermocline and can account for over 50% of water column productivity (Richardson et al. 2000, Weston et al. 2005). This is maintained through the summer months by episodic short-term mixing events attributable to interactions between topography and spring tidal currents (Sharples et al. 2001, Sharples 2008). The additional presence of shear boundaries (strong vertical gradients in horizontal currents) around the thermocline traps small organisms such as phytoplankton to further enhance productivity levels (Franks 1995, Durham et al. 2009, Cheriton et al. 2010), whilst a synchronous accumulation of zooplankton (McManus et al. 2005) can result in an upward propagation of food supply across multiple trophic levels.

Sub-surface productivity at the thermocline has been linked to a number of marine predators, such as northern fulmar, northern gannet *Morus bassanus* and grey seal *Halichoerus grypus*, that preferentially forage in stratified waters (Skov & Durinck 2000, Scott et al. 2010). In diving species, individuals have been shown to repetitively descend to the thermocline (e.g. northern fur seal *Callorhinus ursinus*, rhinoceros auklet and thick-billed murre *Uria lomvia*; Matsumoto et al. 2008, Takahashi et al. 2008, Kuhn 2011), where peaks in prey presence (Hansen et al. 2001, Baumgartner et al. 2003) have been shown to increase foraging efficiency (Pelletier et al. 2012). In years when the thermocline is absent or highly dispersed, corresponding reductions in foraging efficiencies have negatively impacted measures of fitness such as breeding success of, for example, the little penguin *Eudyptula minor* of the Bass Strait ecosystem in southern Australia (Ropert-Coudert et al. 2009b). Alternatively, thick-billed murre in the southeastern Bering Sea have been shown to shift to forage in other, possibly less desirable, habitats in years when the thermocline of preferred stratified waters was not well defined (Kokubun et al. 2010).

The depth of the thermocline is also thought to be an important determinant of its suitability as marine predator foraging habitat (Hunt et al. 1993, Skov & Durinck 2000, Nordstrom et al. 2013). Increased light attenuation with depth means productivity around shallower thermoclines is likely enhanced compared with deeper thermoclines (Skov & Durinck 2000). Moreover, for surface feeders a shallower thermocline may aid in prey accessibility (Haney 1991, Skov & Durinck 2000), and for those that dive from the surface, reduce foraging energetic costs (Langton et al. 2011).

2.3.3 Offshore banks and internal waves

Offshore banks and areas of complex topography within stratified regions can interrupt a stabilised water column through localised mixing events (Moum & Nash 2000, Mann & Lazier 2006). The raised and uneven topography of a bank acts as a barrier against which tidal currents are forced upwards toward the surface. This can trigger the formation of internal waves that can alter the depth of the thermocline by upwards of 30m (Witman et al. 1993). The simultaneous creation of a number of convergent (aggregating) and divergent (dispersing) zones (Figure 2.1) may act to alter the vertical distributions of plankton and small nekton (Lennert-Cody & Franks 1999, McManus et al. 2005, Bertrand et al. 2008). A number of marine predators are known to forage at these features (Moore & Lien 2007, Stevick et al. 2008, Scott et al. 2013).

These features appear to be especially important to those species that specialise in near-surface feeding on plankton and/or forage fish such as black-legged kittiwake, humpback whale *Megaptera novaeangliae* and several species of petrel and shearwater (Haney 1987, Stevick et al. 2008, Hazen et al. 2009, Embling et al. 2012). Observations indicate that internal waves are capable of forcing large aggregations of prey items to the surface (Embling et al. 2013). The occurrence of internal waves is often tidally mediated (Pineda et al. 2015), and surface prey aggregations and corresponding patterns of predator foraging activity regularly reflect this (Hazen et al. 2009, Embling et al. 2012). In some cases, further complexities in the topography of an offshore bank (e.g. steep sided crests and mounts) are thought to enhance the density of surface aggregations by moderating the passage of internal waves (Stevick et al. 2008).

2.3.4 Tidal-mixing fronts

Tidal-mixing fronts mark the transition zone between the stratified waters of the mid-shelf region and the well mixed waters of coastal regions (Figure 2.1; Simpson & Hunter 1974, Pingree & Griffiths 1978), where the thermocline of the stratified mid-shelf region meets the surface and there are strong horizontal gradients in sea surface temperatures (SST; Miller 2009). Their positions are dependent upon the ability of tidal currents to overcome the buoyant effects of surface heat fluxes and mix the entire water column (Franks 1992a). This is a function of the total depth of the water column, and so the position of a tidal-mixing front can be predicted from the ratio between the total water depth (h) and tidal velocity (u) as h/u^3 (known as the Simpson-Hunter parameter; Simpson & Hunter 1974, Simpson & Sharples 2012). Once established, localised variation in the position of a tidal-mixing front occurs predominantly in response to changes in the strength of tidal currents with the spring-neap cycle (Simpson & Sharples 2012), although further alteration to their positions can result from variation in heat flux and wind-driven mixing with prevailing weather conditions (Nahas et al. 2005, Pisoni et al. 2015).

Tidal-mixing fronts are often associated with elevated and persistent productivity levels that have the potential to propagate across multiple trophic levels (Munk et al. 1995, Gregory Lough & Manning 2001). Where the thermocline of stratified offshore waters shallows to meet inshore mixing waters, increased light exposure supplemented with nutrients from mixing coastal waters often results in productivity levels several orders of magnitude higher than those observed in surrounding waters (Simpson et al. 1979, Franks 1992a). Additional convergent flows redistribute the horizontal and vertical distributions of weak or passively swimming organisms (e.g. plankton grazers attracted to the high productivity levels of the front) to create a number of retention and accumulation zones that often occur near the surface (Franks 1992b, Epstein & Beardsley 2001).

A diverse range of marine predators have been shown to preferentially forage around tidal-mixing fronts (Begg & Reid 1997, Goold 1998, Hunt et al. 1999, Weir & O'Brien 2000). Such associations are particularly prominent in colonial seabird species, possibly due to the often proximate locations of these features to land-based breeding sites (Hunt 1997). Large numbers of near-surface feeding planktivorous species, such as least auklet *Aethia pusilla* and short-tailed shearwater, have been observed foraging at and around tidal-mixing fronts in concordance with patches of increased zooplankton abundance (Jahncke et al. 2005) that were often found to be concentrated near the sea surface (Russell et al. 1999). These features have also been shown to attract large cetacean species including a number of rorqual whales that practice surface lunge feeding (e.g. blue whale *Balaenoptera musculus*, fin whale *Balaenoptera physalus* and humpback whale; Doniol-Valcroze et al. 2007, Dalla Rosa et al. 2012). Piscivorous species, such as black-legged kittiwake, common guillemot, Magellanic penguin *Spheniscus magellanicus* and northern gannet, are frequently observed foraging at tidal-mixing fronts (Durazo et al. 1998, Boersma et al. 2009, Scales et al. 2014a) likely because the aggregating effects of these features on plankton predictably attract high densities of forage fish (Hansen et al. 2001). Indeed, in a number of cases across the southeastern Bering Sea, individuals present at these features have been observed feeding on high density patches of acoustically determined fish biomass (Decker & Hunt 1996, Kokubun et al. 2008) where capture rates were increased (Vlietstra et al. 2005).

2.4 Near-shore coastal waters and estuaries

On the shoreward side of the tidal-mixing front, shallow depths allow turbulence generated through friction between tidal currents and the seabed to extend the entire water column and prevent stratification (Simpson & Sharples 2012). As such, these regions remain permanently mixed throughout the year. Concentrated patches of productivity are generally limited to regions of fresh water influence (ROFIs) around estuarine systems. Other notable areas of interest to marine predators, such as tidally active topographic structures, likely function by temporarily mechanically altering the behaviours and distributions of zooplankton and fish prey as indicated by periodicity in their use (Zamon 2002, Zamon 2003). Unlike the mid-shelf region, where the seasonal development of thermal stratification plays a dominant role in the formation of foraging habitat, features occurring in near-shore coastal waters may persist throughout the year and, in some cases, are targeted perennially by marine predators (Skov & Prins 2001).

2.4.1 Channels, headland and island wakes, nearshore reefs and bays

In near-shore coastal regions, predators frequently target areas that are tidally active (Nol & Gaskin 1987, Marubini et al. 2009, Anderwald et al. 2012, Benjamins et al. 2015) and subsequently, there are often distinct regularities in their foraging behaviours that coincide with particular tidal phases (Irons 1998, Isojunno et al. 2012, De Boer et al. 2014). Specifically, areas such as narrow channels, headlands, islands, reefs and bays often function as periodic foraging hotspots, where interactions between strong tidal currents (often exceeding 1.5ms^{-1}) and complex topography provide prosperous foraging opportunities and attract high numbers of individuals from multiple trophic levels (Zamon 2003, Benjamins et al. 2015).

2.4.1.1 Channels

Narrow channels or passes are typical features found around estuaries, fjords and groups of islands. During strong tidal flows, these features are thought to act as bottlenecks (Zamon 2001, Pierpoint 2008, Bailey & Thompson 2010) creating predictable and exploitable concentrations of zooplankton and fish prey, whilst their steep sides provide a barrier against which the latter of these may be herded during capture events (Heimlich-Boran 1988). These features appear to be particularly important foraging habitats for a number of piscivorous small cetaceans and pinnipeds, such as bottlenose dolphin *Tursiops truncatus*, harbour porpoise *Phocoena phocoena*, harbour seal *Phoca vitulina* and killer whale *Orcinus orca*, which employ complex foraging strategies (Simila & Ugarte 1993, Fertl & Wilson 1997, Duffy-Echevarria et al. 2008). Where the profile of a channel or narrow pass causes its steep sides to act as a barrier to tidal currents (e.g. in the presence of shallow banks or sharp meanders), resultant upwelling can force advected zooplankton, and sometimes small nekton (e.g. forage fish) into dense aggregations (Lavoie et al. 2000, Davies et al. 2013) that are often driven towards the surface (Simard et al. 2002), making these features attractive to both bulk-feeding baleen whales (Cotté & Simard 2005) and surface feeding birds (e.g. a number of auklet species and Bonaparte's *Larus Philadelphia* and Mew *Larus canus* gulls; Vermeer et al. 1987, Hunt et al. 1998).

2.4.1.2 Headland and island wakes

When headland and island features interrupt the passage of strong tidal current flows, a leeward wake (or eddy) may form, within which calm waters provide fish refuge from strong tidal currents (Liao 2007). At the interface with non-wake waters, shear induced hydrographic fronts may occur (Johnston & Read 2007) that can trap zooplankton and/or disorientate fish prey (Tarrade et al. 2008), creating a predictable foraging resource for a number of predator species. For example, in the Bay of Fundy, harbour porpoise and fin and minke *Balaenoptera acutorostrata* whales have regularly been observed exploiting dense patches of euphasiid *Meganyctiphanes norvegica* and herring *Clupea harengus* along the edge of an island wake during flood tides (Johnston et al. 2005a, Johnston et al. 2005b). In some instances, fish have been shown to avoid turbulent flows, such as those associated with hydrographic fronts, that can be disorientating (Nichol & Somerton 2002). As such, some predators (e.g. bottlenose dolphin and killer whale) may additionally use these features as a foraging aid, against which to herd and trap prey (Heimlich-Boran 1988, Benjamins et al. 2015).

2.4.1.3 Nearshore reefs and banks

Where current flows run adjacent to the coast, under specific tidal conditions friction with topographically complex structures, such as nearshore reefs and banks, can generate shear instabilities and turbulence (Jones et al. 2014). Peaks in the occurrence of harbour porpoise corresponding to the times at which these hydrographic features occur suggest they alter prey distributions and/or aid in prey capture (Skov & Thomsen 2008, Jones et al. 2014).

2.4.1.4 Bays

In some instances, the curvature of a headland or a series of small islands can result in the formation of a bay. Tidal circulation patterns enforced by the curved profile of the bay accumulate plankton and small nekton through advection and retention (Gomez-Gutierrez & Robinson 2006, Rogachev et al. 2008). In bays characterised by the presence of steep topographic barriers and ledges, interactions with these circulation patterns can generate localised upwellings. This can force accumulated biomass into dense surface aggregations, and appears to provide an important foraging resource to a number of planktivorous species that either surface feed (e.g. black-legged kittiwake and red-necked phalarope *Phalaropus lobatus*; Drew et al. 2013, Thorne & Read 2013) and/or bulk feed (e.g. bowhead whale *Balaena mysticetus* and north Atlantic right whale *Eubalaena glacialis*; Jiang et al. 2007, Rogachev et al. 2008).

2.4.2 Regions of freshwater influence (ROFIs): estuarine plume and tidal intrusion fronts

Within estuarine systems, typical circulation patterns, forcing dense water below less dense water, promote the two-layer stratification of outflowing nutrient rich freshwater and intruding saline waters (Simpson & Sharples 2012). Where this stratification meets coastal mixing waters, high horizontal gradients in salinity and density mark the position of either a tidal intrusion front (dense saline coastal water intruding into the estuary) or a plume front (brackish water discharging out of the estuary; Simpson & Nunes 1981, Lewis 1984). Stratification increases stability in the water column, and allows plankton to redistribute and settle at, or above, the halocline/pycnocline where waters are nutrient rich and light exposure is increased. Subsequent high levels of productivity (Cloern 1991) may attract large numbers of zooplankton and forage fish (Govoni et al. 1989, Kaltenberg et al. 2010), which may be concentrated at the surface signature of the front as a result of additional convergent flows (Govoni et al. 1989). A number of piscivorous species, such as black and red throated diver *Gavia stellata/arctica*, bottlenose dolphin, common guillemot, little penguin and sooty shearwater *Puffinus griseus*, have been shown to regularly feed at estuarine plume and tidal intrusion fronts (Skov & Prins 2001, Mendes et al. 2002, Zamon et al. 2014, Kowalczyk et al. 2015). In some instances, the occurrence of these features may be tidally mediated (Mendes et al. 2002).

2.5 Key characteristics of ecologically significant physical habitats

Current understanding suggests a number of oceanographic features in shelf-sea environments are capable of generating high quality habitats that are preferentially targeted by a range of large marine vertebrate predators. These ecologically significant features appear to be characterised by the capacity to increase prey accessibility in a persistent and/or predictable manner that allows for the use of efficient and effective behaviours by a number of predator species (Pelletier et al. 2012). As such, the habitats created by physical oceanographic processes can be thought of as critical in occurrence and vital to ecosystem functioning (Hennicke & Culik 2005, Boersma & Rebstock 2009).

At a number of oceanographic habitats, changes in important aspects of prey accessibility, such as depth distribution (Friedlaender et al. 2006, Benoit-Bird et al. 2011, Boyd et al. 2015), density (Enstipp et al. 2007, Benoit-Bird et al. 2013, Goldbogen et al. 2015) and behaviour (Crook & Davoren 2014), have been either directly observed or implied by the behaviours of associated predators (e.g. Russell et al. 1999, Vlietstra et al. 2005, Stevick et al. 2008, Takahashi et al. 2008, Kuhn 2011, Embling et al. 2012, Embling et al. 2013). Surface convergent zones at shelf-edge, upwelling and tidal-mixing fronts appeared particularly important to surface foragers as did localised interactions between topography and tidal currents at offshore banks and around coasts. In a number of cases, individuals foraging at these features were directly linked to shallow aggregations of prey (Russell et al. 1999, Stevick et al. 2008, Embling et al. 2012). Diving predators were also shown to forage at these features, possibly because associated changes in the depth distributions of their prey reduced the energetic cost of prey capture (Ropert-Coudert et al. 2009a, Goldbogen et al. 2015). At other sub-surface features (e.g. the thermocline) this was also found to be an important component of habitat attractiveness. Prey were measured in dense concentrations at a number of physical features (e.g. Decker & Hunt 1996, Vlietstra et al. 2005, Stevick et al. 2008), which was thought to occur as a result of either elevated levels of associated primary productivity that propagated multiple trophic levels (e.g. shelf-edge, upwelling and tidal-mixing fronts) or specific flow characteristics (e.g. convergent zones or where interactions between tides and topography occurred). In some cases these habitats were linked to increases in prey capture rates and/or yields (Vlietstra et al. 2005, Rogachev et al. 2008), and so may be particularly important for species with especially high energetic needs and/or whose foraging strategies are particularly costly (Green et al. 2009, Goldbogen et al. 2011). Evidence of changes in prey behaviours were limited but thought to occur in a manner that likely further increased their vulnerability to predation (e.g. avoidance of turbulent flows; Benjamins et al. 2015).

The exploitation of a prey resource is dependent upon the ability of a predator to locate it, and so its spatio-temporal persistence and/or predictability is also fundamental to its accessibility and ecological significance (Gende & Sigler 2006, Davoren 2013). In particular, predictability was a common characteristic across the majority of physical features used by foraging predators. If predators can learn and remember the locations at which encountering prey is more probable (Regular et al. 2013), behaviours can be adjusted accordingly (possibly through the use of additional environmental cues) to maximise search effort within these areas (Hamer et al. 2009, Pettex et al. 2010, Dragon et al. 2012, Patrick et al. 2014) and increase foraging efficiency (Stephens & Krebs 1986). Targeted search patterns have indeed been shown to coincide with the occurrence of a number of oceanographic features that are repetitively visited (Bailey & Thompson 2010, Sabarros et al. 2014, Scales et al. 2014a).

The literature describing interactions between large marine vertebrate predators and physical oceanography in shelf-seas has yielded valuable insights. However, there are still many unanswered questions. Most prominently, direct evidence of the functional mechanisms that increase prey accessibility at oceanographic habitats, namely depth distribution, density, behavioural changes and predictability, is sparse and *in-situ* measurements of oceanography, encompassing the entire water column, would aid in this as would addressing a distinct lack of fine-scale information on prey densities, distributions and behaviours, particularly at mid-trophic levels (but see Embling et al. 2012 and Embling et al. 2013). Furthermore, while it may be presumed that foraging efficiency is maximised by targeting these features, few studies have explicitly tested this hypothesis. Fine-scale, three-dimensional measurements of predator behaviours alongside estimates of prey capture rates and energetic expenditure would aid in this (Viviant et al. 2010, Watanabe & Takahashi 2013), as would comparative measures of fitness between years of contrasting oceanographic activity (e.g. reproductive output; Borstad et al. 2011). Finally, it is unclear how animals perceive their environment and a greater understanding of the relative roles of knowledge transfer (Machovsky-Capuska et al. 2014), memory (Regular et al. 2013), sight (Bodey et al. 2014, Tremblay et al. 2014, Bairos-Novak et al. 2015) and smell (Savoca & Nevitt 2014) would be beneficial.

Future work should aim to address these questions if we are to improve our understanding of the key components that characterise high quality foraging habitats and how these relate to physical oceanographic processes.

2.6 Implications for conservation and management

Ecologically significant oceanographic features in shelf-seas represent critical habitat locations for a number of large marine vertebrate predators, particularly during the summer months. These features are often relied upon during crucial life cycle stages such as breeding (Hunt 1997) and migration (McKnight et al. 2013), and so disturbance at their locations can have severe consequences for involved populations (e.g. declines in the reproductive output of colonial seabirds during the breeding season; Hennicke & Culik 2005, Boersma & Rebstock 2009). This may arise as a result of a number of spatially explicit anthropogenic activities including, but not limited to, aquaculture, artisanal and commercial fishing, coastal development, marine renewable energy installations (MREIs), mineral resource extraction (i.e. gas and oil) and recreational and industrial shipping, alongside the environmental effects of climate change.

There has been a recent shift in marine management practices away from traditional single species methods to more inclusive integrative approaches that aim to incorporate the ecosystem as a whole (Pikitch et al. 2004, Arkema et al. 2006), and ensuring the critical foraging habitats of large marine vertebrate predators are protected is vital for this to prove effective (Taylor et al. 2005, Heithaus et al. 2008). Many of these features fall within exclusive economic zones (EEZs) and so their incorporation into conservation and management is tractable. Where they are predictable on localised spatio-temporal scales (e.g. tidally mediated topographic structures), marine protected areas (MPAs; Hyrenbach 2000, Gormley et al. 2012) can often regulate overlap with a number of the above-mentioned anthropogenic activities whilst adaptive approaches such as dynamic ocean management (DOM; Lewison et al. 2015, Maxwell et al. 2015) can be used to incorporate those features that are more progressive in their occurrence and so unsuited to static methods (e.g. shelf-edge, upwelling and tidal-mixing fronts whose geographical positions may alter in response to environmental variability). This may aid in minimising a number of pressures, such as fisheries by-catch and collision mortality with MREIs and commercial shipping, which result from direct interaction with marine predators. For those stressors that may alter the structuring of important oceanographic habitat features and lead to habitat loss (e.g. climate change, coastal development, oil and gas extraction and MREIs; Shields et al. 2011), a good understanding of the physical processes associated with their creation is essential to be able to adequately quantify this a priori and mitigate against it (Waggitt & Scott 2014).

2.7 Conclusions

Interactions between marine predators and physical oceanographic processes in shelf-sea environments are diverse and complex in their nature. Associations vary over a number of spatio-temporal scales, are species specific and subject to both regionality and seasonality. Despite this variability, there is now a considerable body of evidence indicating that physical oceanography plays an important role in the creation of foraging habitat for a number of large marine vertebrate predators. Current understanding suggests that the ecological significance of important physical features stems from their capacity to alter the densities, distributions (both horizontally and vertically) and behaviours of prey resources in a persistent and/or predictable manner that increases accessibility for a number of marine predators. In the majority of cases, intricate interactions between tidal currents and topography alongside the seasonal stratification of offshore waters appear key to this. Future work should aim to further our current understanding of the functional mechanisms linking physical oceanography, prey and predators and would greatly benefit from the additional incorporation of detailed three-dimensional measurements of prey behaviours, densities and distributions. The availability of high quality foraging habitats to marine predators is critical to ecosystem functioning. As such, identifying the physical processes that underlie their creation and understanding the functional mechanisms that link them to marine predators is fundamental to increasing our knowledge of how the marine environment operates and achieving the objectives of ecosystem based management and marine conservation.

CHAPTER III

Fine-scale dynamics of primary productivity around a tidal-mixing front and links to large marine vertebrate predators

ABSTRACT

The at-sea distributions and behaviours of large marine vertebrate predators, such as marine mammals and seabirds, are heterogeneous and often concentrated in discrete and localised foraging regions. These ‘hotspot’ locations are thought to form as a result of physical oceanographic processes that provide an accessible and often predictable prey resource and as such, play an important role in the structuring of marine ecosystems. Here I aim to (1) characterise the fine-scale oceanographic dynamics of a seasonally forming tidal-mixing front in the southern Celtic Sea, and (2) establish how two marine predators, the northern gannet *Morus bassanus* and the common dolphin *Delphinus delphis* respond to fine-scale oceanographic conditions at and around the front. First, I provide a comprehensive overview of the front using detailed *in-situ* oceanographic profiling of the entire water column taken across complete semi-diurnal tidal cycles during spring and neap conditions. Second, I couple continuous *in-situ* measurements of oceanography, taken during transect surveys across the front, to simultaneously collected observations of animal behaviours in order to establish how marine predators respond to the dynamic nature of this system. I show that around the front, the occurrence of both gannets and common dolphins is limited and correlated with regions of increased sub-surface fluorescence (indicative of increased primary productivity), which occurs on its stratified side in thin layers at and around the thermocline. I show that the production of this fluorescence is variable and mediated by a bi-weekly tidally induced cycle of thermal stratification and episodic water mixing that follows an offshore-inshore adjustment in the position of the front with the spring-neap cycle. Subsequently, these habitats may not be predictable over localised spatio-temporal scales and evolved hierarchical search strategies likely reflect this. My findings suggest

that fronts and the waters immediately surrounding them are locations within which localised ephemeral and transient foraging opportunities are reliably found. As such, these physical features likely represent an important habitat resource to a range of large marine vertebrate predators.

3.1 Introduction

Heterogeneity is a key feature of the marine environment (Worm et al. 2005, Weimerskirch 2007). As such, the locations where prey are available to large marine vertebrate predators, such as marine mammals and seabirds, are spatio-temporally limited and therefore likely critical in occurrence (Taylor et al. 2005, Fauchald 2009, Embling et al. 2012, Boyd et al. 2015). Increasing evidence suggests a number of dynamic oceanographic features, that occur as a result of bottom-up, complex, physical processes, play a fundamental role in the structuring of marine ecosystems and so likely constitute important foraging locations for a number of marine predators (Ballance et al. 2006, Bost et al. 2009, Scales et al. 2014b). A detailed understanding of these oceanographic habitats and their use by large marine vertebrate predators can provide valuable insight toward the mechanisms that both drive the at-sea behaviours and distributions of these animals, and sustain ecosystem functioning.

Shelf-sea environments are highly dynamic, and as such, there are a number of oceanographic habitats available for marine predators to forage at (Wolanski & Hamner 1988, Hunt et al. 1999, Stevick et al. 2008, Benjamins et al. 2015). Tidal-mixing fronts occur in the summer and mark the transitional zones between inshore coastal mixing and offshore seasonally stratifying waters (Simpson & Hunter 1974, Pingree 1975, Pingree & Griffiths 1978). These features both sustain high levels of primary productivity (Franks 1992a, Yoder et al. 1994) and mechanically accumulate plankton and small nekton (Franks 1992b, Genin et al. 2005, Bakun 2006). The combined effects of this propagate across multiple trophic levels resulting in the predictable formation of dense near-surface aggregations of forage and pelagic fish (Decker & Hunt 1996, Hansen et al. 2001), that provide large marine vertebrate predators with a highly accessible and exploitable prey resource (Russell et al. 1999, Vlietstra et al. 2005). As such, a number of species are known to regularly forage around these features (Jahncke et al. 2005, Kokubun et al. 2008, Scales et al. 2014b).

Tidal-mixing fronts and the oceanographic conditions of the waters immediately surrounding them vary over localised spatio-temporal scales in response to fluctuations in a number of dynamic physical processes including heat-flux, wind stress and tidal currents (Nahas et al. 2005, Pisoni et al. 2015). Away from fronts, these processes are known to drive the occurrence of a number of habitat features that marine predators forage at, such as localised increases in sub-surface chlorophyll production (Scott et al. 2010, Embling et al. 2012) and shear (vertical gradients in horizontal currents) capable of generating turbulent mixing (Scott et al. 2013). Whilst the fine-scale distributions of marine predators foraging at and around fronts are also known to respond to similarly characterised changes in localised surface and sub-surface oceanographic conditions, evidence is limited to only a handful of studies (Durazo et al. 1998). Physical and biological investigations are rarely conducted simultaneously over the spatio-temporal scales required to observe and resolve the fine-scale dynamics of tidal-mixing fronts and how predators respond to them (e.g. Begg & Reid 1997, Doniol-Valcroze et al. 2007, Scales et al. 2014a).

Within this study I aim to (1) characterise the fine-scale oceanographic dynamics of a seasonally forming tidal-mixing front in the southern Celtic Sea (Figure 3.1), and (2) establish how large marine vertebrate predators respond to oceanographic conditions at and surrounding the front. I first provide a comprehensive overview of the front using detailed *in-situ* oceanographic profiling of the entire water column across complete semi-diurnal tidal cycles during spring and neap conditions at two stations (Figure 3.1). Second, I couple continuous *in-situ* measurements of oceanography, taken during transect surveys across the latitudinal axis of the front (Figure 3.1), to simultaneously collected observations of animal behaviours to establish how marine predators respond to the dynamic nature of this system.

Corresponding analyses concentrated on two of the most abundant species in this oceanographically complex region; the northern gannet *Morus bassanus* and the common dolphin *Delphinus delphis* (Leeney et al. 2008, Votier et al. 2011, Votier et al. 2013). These species feed on the pelagic shoaling fish expected around fronts (Hansen et al. 2001, Hamer et al. 2007, Brophy et al. 2009). Moreover, gannets have previously been shown to forage in areas where fronts frequently manifest across a season (Scales et al. 2014a), suggesting this species preferentially targets the oceanographic habitats generated at and around fronts. I focus specifically on understanding how predators relate to patches of sub-surface primary productivity on the stratified side of the front (Franks 1992a, Scott et al. 2010), shear capable of generating turbulent mixing and altering the distributions of plankton and small nekton (Scott et al. 2013), and possible convergent zones present at the fronts interface between mixing and stratified waters (Franks 1992b).

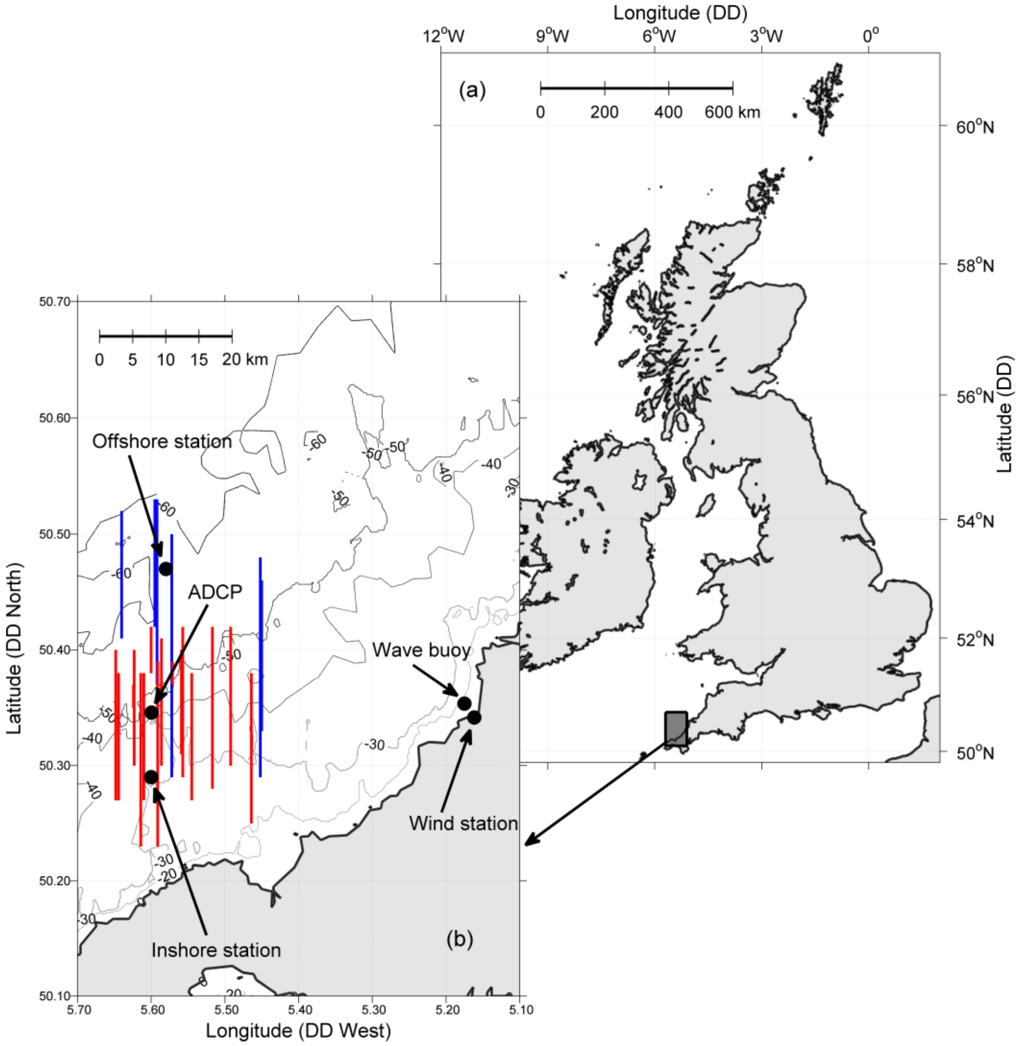

Figure 3.1 Top right (a) shows the location of the study site off the north Cornwall coast within the context of the entire UK. Bottom left (b) shows the distribution of survey effort within the study site. Front transect survey routes are shown in blue (2012) and red (2013). The locations of the two (inshore/offshore) oceanographic tidal stations, ADCP (acoustic Doppler current profiler) mooring, Perranporth wave buoy and Perranporth wind station are also indicated. Bathymetric contours of the region are marked in grey.

3.2 Methods

This study was conducted in the shelf-sea waters of the southern Celtic Sea, UK during the months of August 2012 and 2013 (Figures 3.1 and 3.2).

3.2.1 Contextualising meteorological and oceanographic conditions during survey periods

An upwards facing 614kHz ADCP (acoustic Doppler current profiler), that was configured to measure current speeds and directions over a vertical bin size of 1m with a ping frequency of 2 seconds, was deployed on the seabed between the 11th August and 2nd November 2012. Wave height and wind speed were taken from the Perranporth wave buoy and meteorological station (Figure 3.1) respectively (channel coastal observatory; www.channelcoast.org) for the time period running the 2nd to 23rd August 2012 and the 4th to 16th August 2013. Tidal height and current speeds were taken between the 11th and 21st August 2012 from the OTIS tidal prediction model (volkov.oce.orst.edu/tides/), run for the location of the moored ADCP (Figure 3.1). To be able to determine the relative importance of wind and tidal driven forcing on measured current speeds, residual current speeds (Figure 3.2) were calculated by subtracting predicted tidal current speeds (obtained via the OTIS tidal prediction model) from those measured by the moored ADCP.

3.2.2 Characterising the fine-scale oceanographic dynamics of the front

3.2.2.1 Data acquisition: sea surface temperature (SST) maps

Sea surface temperature (SST) maps (Figure 3.3) were based on advanced very high resolution radiometer (AVHRR) level 3 data taken over weekly composites for August 2012, as provided by the NERC Earth Observation Acquisition and Analysis Service (NEODAAS, Plymouth, UK).

3.2.2.2 Data collection: oceanographic tidal stations

Oceanographic tidal stations were conducted at two locations (Figure 3.1) on the 12th and 13th (neap tides), and the 19th and 21st (spring tides), of August 2012 (Figure 3.2). These were positioned roughly inshore (12th and 19th August) and offshore (13th and 21st August) of the anticipated position of the front as predetermined from remotely-sensed SST maps (Figure 3.3). Oceanographic measurements were collected throughout entire tidal cycles, and acquired from within 5m of the sea surface to the seabed via a free fall microstructure profiler (MSS; the ISW Wassermesstechnik MSS-90) equipped with microscale shear, temperature, conductivity, pressure and chlorophyll fluorescence sensors operating at 1024Hz. Profiles took around two minutes to complete at a fall speed of approximately 0.5ms^{-1} whilst the vessel drifted. Data were collected in groups of seven profiles, at the end of which the vessel was repositioned back to its starting location (Figure 3.1). Drift speeds were such that the vessel remained within 1km of this start position throughout each group. Current speeds and directions were measured via a hull mounted downwards facing 300kHz ADCP operating over a vertical bin size of 2m with a ping frequency of 1.5 seconds.

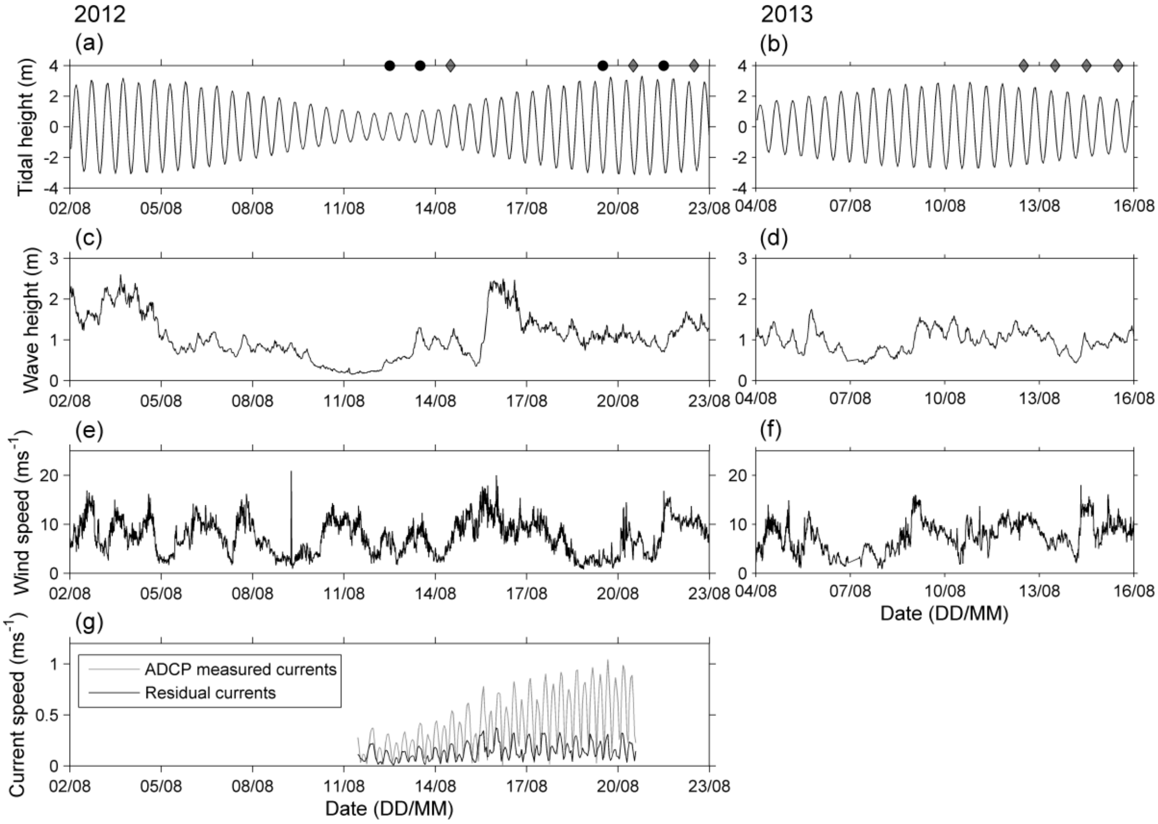

Figure 3.2 Prevailing tidal height, wave height, wind speed and water currents during survey periods in 2012 (the first column; a, c, e & g) and 2013 (the second column; b, d & f). Black circles represent the dates on which oceanographic tidal stations were conducted whilst grey diamonds mark dates on which cross-front transects were run. The top row (a & b) shows the position in the spring-neap cycle of surveys as indicated by tidal heights taken from the OTIS tidal prediction model. The second row (c & d) shows wave height as measured by the Perranporth wave buoy. The third row shows wind speed as measured at Perranporth meteorological weather station. The fourth row (g) shows in grey the depth averaged speeds of water currents measured by the moored ADCP and in black the speeds of residual currents calculated by subtracting tidal current speed predictions (obtained from the OTIS tidal prediction model) from those measured by the moored ADCP. Note there is still a tidal signal in the residual current suggesting the tidal component has not been completely removed.

3.2.2.3 Data presentation and processing

Temperature, conductivity and fluorescence measurements from each MSS profile were averaged into 1m vertical depth bins. Outputs from the fluorometer were normalised by dividing each value by the maximum measurement observed across all profiles, to give relative fluorescence. Turbulent kinetic energy was estimated as described by Osborn (1980) from the microscale shear measurements as $\varepsilon = 7.5\nu \,\langle(\partial u/\partial z)^2\rangle$, where ν is the kinematic viscosity (which in seawater is approximately 10^{-6}m^{2}s^{-1}) and $\partial u/\partial z$ represents the vertical gradient (z) of the turbulent horizontal current component (u). The angled brackets denote a suitable time average, which here is 2 seconds (the time taken to pass through a metre of the vertical water column with an approximate free fall speed of 0.5ms^{-1}) and the units are W kg^{-1}. Brunt-Väisälä (buoyancy) frequencies N^2 were calculated as $N^2 = (-\,g/\rho_0)\,(\partial\rho/\partial p)$, where g is the acceleration due to gravity, ρ_0 is a reference density, $\partial\rho$ is the change in density (ρ) and ∂p is the change in pressure (p) in dbars.

The northern and eastern velocity components measured by the ADCP were cleaned to reduce noise using: (1) a median filter of two standard deviations across two minutes of measurements horizontally and five bins vertically, and (2) a running average across one minute of measurements horizontally and three bins vertically. Current speeds and directions were then calculated over one minute block averages at depth intervals of 2m (one bin vertically). The two bins closest to the surface and seabed were excluded to remove inflated values associated with acoustical interference. Vertical shear in the horizontal currents S^2 was then calculated, using block averages of one minute horizontally and two bins vertically (to reduce noise in estimates) as $S^2 = (\partial u/\partial z)^2 + (\partial v/\partial z)^2$, where $\partial u/\partial z$ and $\partial v/\partial z$ represent the vertical gradients (z) of the northern (u) and eastern (v) horizontal velocity components over an interval of 4m respectively. To indicate the potential of this shear to overcome the stabilising influence of stratification, Richardson numbers Ri were computed as $Ri = N^2/S^2$. Values of less than 0.25 are indicative of conditions where shear can disrupt the tendency of a water column to remain stratified. Due to differences between the temporal resolutions of the MSS profiles and ADCP measurements, for this calculation N^2 values from the MSS data (generated as outlined above) were interpolated to the resolution of the S^2estimates.

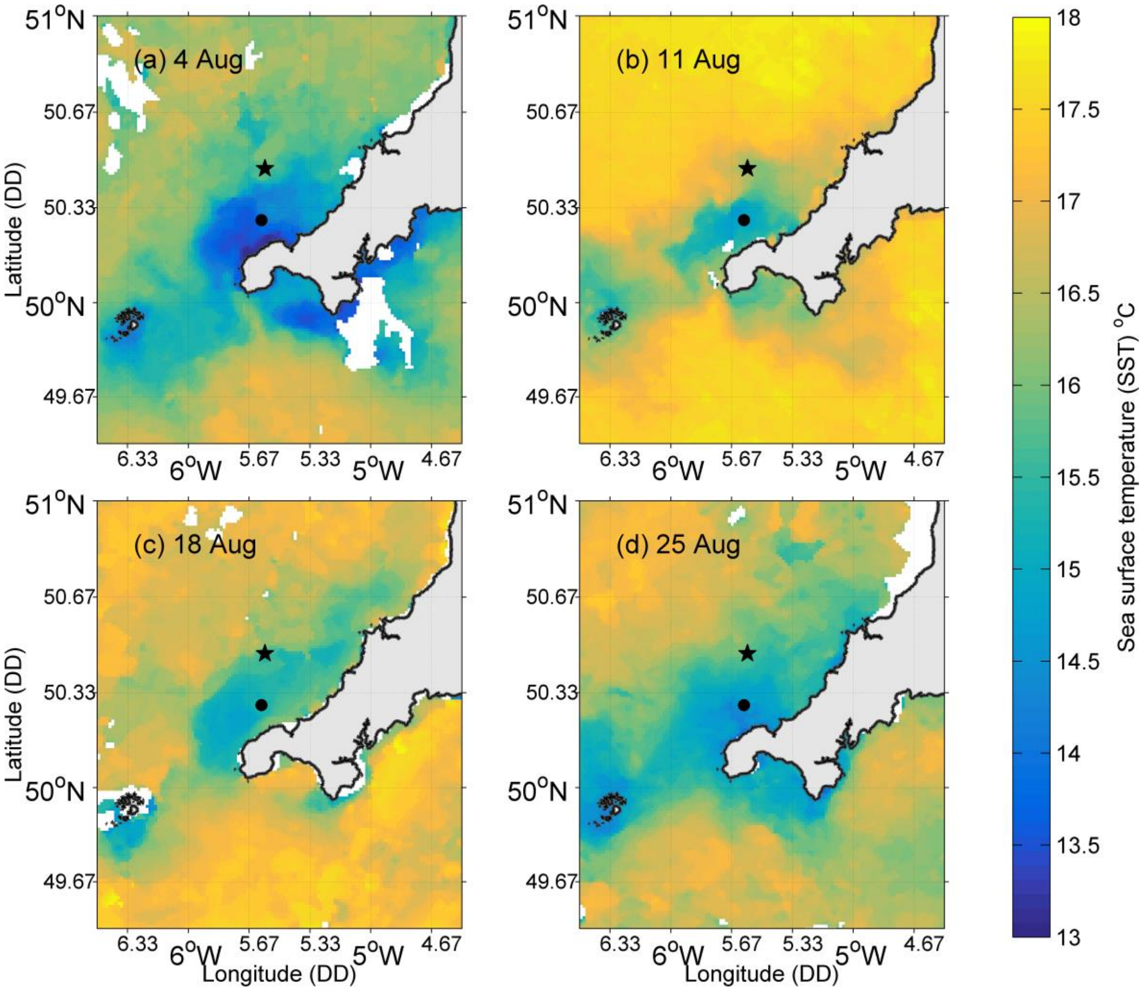

Figure 3.3 Seven day composite sea surface temperature (SST) maps for the southeast Celtic Sea at weekly intervals through August (2012). Dates indicated are centred to the middle of the composite seven day time period. From top left: (a) 04th August, (b) 11th August, (c) 18th August and (d) 25th August. The 4th August occurs within a day of peak spring tides. Offshore surface temperatures are around 16°C. Inshore waters are characterised by a pronounced pool of cool waters with temperatures of around 13°C. The 11th August occurs within a day of peak neap tides when offshore water temperatures have increased to around 18°C and extended inshore. The cool pool of water has retracted and temperatures have increased to around 15°C. The 18th of August occurs around a day before peak spring tides and sees a decrease in offshore water temperatures of around 1°C. The 25th of August occurs a day before peak neap tides and conditions are reflective of those a week previously. The locations of the inshore and offshore tidal stations are indicated by the black filled circle and star respectively. SST maps for 2013 are available in Appendix A1.1.

3.2.3 Investigating links with marine predators

3.2.3.1 Data collection: cross-front transects

At-sea transect surveys were conducted on the 14th, 20th and 22nd of August in 2012, and between the 12th and 15th of August inclusive in 2013 (Figure 3.1 and 3.2). Reciprocal north-south transects of 5 to 30km were run to traverse the anticipated location of the front based on recent SST maps (Figure 3.3). Real time observations of temperature from an undulating CTD (Conductivity-Temperature-Depth) allowed the length of transects to be altered to sample both the mixing and stratified sides of the constantly evolving front (Figure 3.3).

Pressure, temperature, conductivity and chlorophyll fluorescence were measured at a rate of 24Hz with an AML Micro CTD sensor and external Turner Cyclops fluorometer, which were mounted on an OSIL MiniBAT FC60 that undulated between depths of 3m and 20m (the maximum depth range attainable with the instrumentation) whilst being towed at a speed of four knots. Each undulation took between 1.5 and 2.5 minutes to complete resulting in a horizontal spatial resolution of around 150m. Current speeds and directions were measured continuously via a hull mounted 300kHz ADCP operating over a vertical bin size of 2m with a ping frequency of 1.5 seconds.

Table 3.1 Behaviour criteria for foraging and searching gannets *Morus bassanus*. Adapted from Camphuysen & Garthe (2004).

Behaviour	Description
Foraging naturally	Scooping prey from surface, deep plunging, shallow plunging, pursuit dives.
Active searching	Bird is flying with head down and circling. Sometimes dipping in the air.

Simultaneous to oceanographic sampling, animal observations were made based on strip transect techniques standardised for ship-based surveys (Tasker et al. 1984, Camphuysen et al. 2004). Two observers kept continuous watch and recorded the abundance and behaviour of gannets and common dolphins within 300m to the side of the boat with the least glare. Counts were made in five minute segments from a platform 2.3m and 4.9m above sea level in 2012 and 2013 respectively. The boat speed was maintained at 4 knots, and so an average distance of 650m was covered over each segment. Gannets actively searching or foraging for prey were distinguished from non-foraging/searching birds including those associated with or attracted by the research vessel or sitting on the water, which were not included in final analyses (behaviour criteria shown in Table 3.1; Camphuysen & Garthe 2004). All common dolphin sightings were included in analyses due to a lack of definitive foraging cues. Sea state, corresponding to the Beaufort scale, was recorded at 15 minute intervals, or when conditions changed.

Table 3.2. Methods for summarising high resolution oceanographic measurements from the CTD (conductivity-temperature-depth) and ADCP (acoustic Doppler current profiler).

Environmental variable	Description
ThermStrat	Thermal stratification. Difference between the mean temperature at 3m and 20m. Measurements taken from the undulating CTD.
FrontIndex	Front index. The difference between the minimum and maximum 3-20m temperature difference divided by the total distance travelled in each segment to give a standardised average change in thermal stratification. Top (3m) to mid-bottom (20m) temperature differences were calculated from a linear interpolation at one minute intervals, which was based on measurements at corresponding depths from the undulating CTD.
MaxFluorescence	Maximum relative fluorescence. Relative voltage from the fluorometer on the undulating CTD. This is used as a proxy for chlorophyll biomass (Lorenzen 1966). Maximum values within each five minute segment taken, regardless of position in the water column (between 3-20m).
DepthChange	Depth change used as a proxy for slope. Average difference in maximum and minimum depth over 100m within each five minute segment. Measurements taken from the ADCP.
Depth	Depth. Average depth for each five minute segment. Measurements taken from the ADCP.
CurrentSpeed	Current speed. Average speed through the entire water column for each five minute segment using the northern and eastern velocity components measured by the hull mounted ADCP.
TideDir	Direction of tidal flow. The average direction through the entire water column for each five minute segment was calculated from the northern and eastern velocity components measured by the ADCP and used to create a two stage flood-ebb factor variable. Flood directions were classified as those occurring between 340° and 160°, whilst ebb directions occurred between 160° and 340°. These criteria were determined via visual inspection of a tidal ellipse plot (Figure 3.4) generated from an ADCP mooring deployed between August and November 2012 in region (as shown in Figure 3.1.b).
LogMaxShear	Maximum shear. The maximum vertical gradient in horizontal velocity taken as $S^2 = (\partial u/\partial z)^2 + (\partial v/\partial z)^2$ where $\partial u/\partial z$ and $\partial v/\partial z$ represent the vertical (z) gradient of the northern (u) and eastern (v) horizontal current components respectively. Shear was computed over a one minute time average at 4m vertical intervals. The bottom and top bins were cut to exclude artificially inflated values associated with acoustical interference at the surface and seabed. Estimates are presented on a logarithmic scale.
DecTime	Time of day converted from 00:00 to 24:00 to a decimal between 0 and 1 (e.g. 0.5 is equivalent to mid-day).
SeaState	Sea state corresponding to the Beaufort scale. Average taken for each five minute segment.

3.2.3.2 Data preparation and processing

Outputs from the fluorometer were again normalised by dividing each measurement by the maximum value recorded across all transect surveys. For plotting purposes, raw CTD measurements were interpolated to a one second interval corresponding to the resolution of the GPS data to fill in gaps between undulations.

For comparison to the concurrent animal observations, undulations of raw CTD measurements were split into profiles, defined as a set of continuous measurements spanning the upper and lower depths reached by the CTD. These were then averaged over 1m depth intervals. Velocity measurements from the ADCP were cleaned and used to calculate current speeds and directions and S^2 (shear) as previously outlined. To be able to incorporate oceanographic measurements into statistical models of the animal observations, summaries were made to represent bio-physical conditions within each five minute observational segment that may be important to foraging predators. In addition to descriptions below, a reference overview is provided in Table 3.2.

3.2.3.2.1 Fronts and stratification

Two descriptors of thermal conditions were created; *ThermStrat* and *FrontIndex*. *ThermStrat* was used to identify regions where the water column was fully mixing or thermally stratified, and was taken as the difference between the mean temperature at 3m and 20m, as measured by the undulating CTD within each five minute segment. Although measurements of temperature were restricted to the top 20m of the water column, the typically shallow depth of the thermocline (around 10-15m) means this range should be sufficient to distinguish between waters of varying thermal stratification. *FrontIndex* was used as an indication of the strength of potential frontal convergent zones occurring between areas of disparate stratification. Top (3m) to mid-bottom (20m) temperature differences were calculated from a linear interpolation at one minute intervals, which was based on measurements at corresponding depths from the undulating CTD. The difference between the minimum and maximum 3-20m temperature difference within each five minute segment was then taken and divided by the total distance travelled during the segment to give a standardised average change in thermal stratification.

3.2.3.2.2 Sub-surface primary productivity

Relative fluorescence was used as a proxy for chlorophyll production (Lorenzen 1966). As patches of elevated primary productivity may not always occur at the surface (Weston et al. 2005, Sharples et al. 2007), the maximum value within each five minute segment was taken from measurements spanning the entire water column sampled (3-20m) to give *MaxFluorescence*.

3.2.3.2.3 Shear

The maximum S^2 value was taken for each five minute segment and presented on a logarithmic scale to give $LogMaxShear$.

3.2.3.2.4 Topography and water currents

The frontal system selected for this study is located in near-shore shelf waters with depths of between 30m and 60m. Due to this specificity, additional factors to temperature, primary productivity and shear may influence how prey are distributed. To ensure these were not missed, four further habitat descriptors were tested in analyses.

Depth (depth), was taken as the average depth, as measured by the ADCP, for each five minute segment, and was included to determine potential preferences for shallow versus deep waters (Marubini et al. 2009). *DepthChange* (change in depth), was taken as the difference between the maximum and minimum depths observed within each five minute segment, and was included as a proxy for slope and the presence of small topographic structures, both of which may potentially influence water mixing and prey distributions via the generation of localised upwelling (Nimmo Smith et al. 1999) and/or internal waves (Moum & Nash 2000).

Tidal current flows in and out of the region were associated with the transport of waters of differing oceanographic properties reflective of the variable conditions experienced around the Cornish coast. To determine the potential for this to influence prey and hence predators distributions, descriptors of tidal currents were also included in analyses. The average current speed was calculated for each five minute segment using velocity measurements from the ADCP spanning the entire water column to give *CurrentSpeed* (current speed). The corresponding average current direction was used to create a two stage flood-ebb factor variable, *TideDir*. Flood directions were classified as those occurring between 340° and 160°, whilst ebb directions occurred between 160° and 340° (Figure 3.4). These criteria were determined via visual inspection of a tidal ellipse generated using current measurements from the ADCP mooring (deployment period 22nd August to 2nd November 2012; Figure 3.4.a). It should be noted that due to daily access constraints at the harbour, sampling occurred predominantly during ebb tides (Figure 3.4.b).

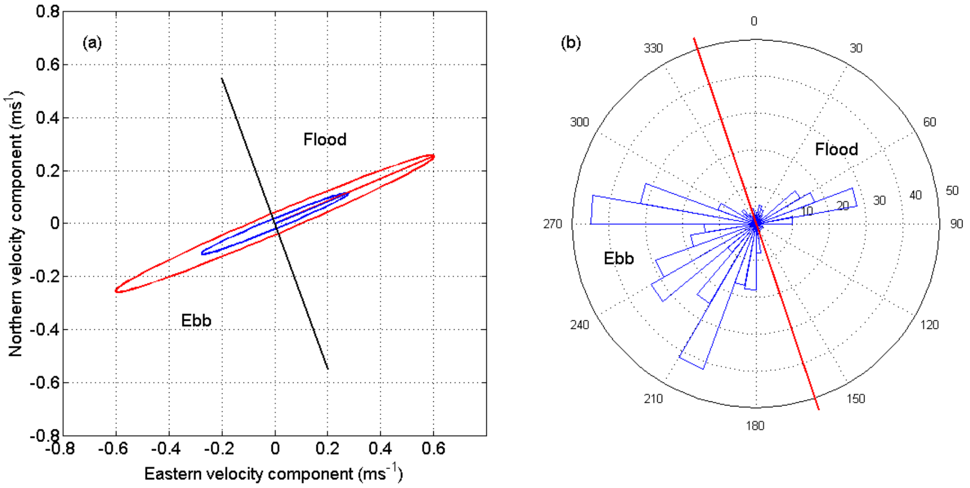

Figure 3.4 Left (a), the tidal ellipse generated from continuous current measurements from the moored ADCP (August to November 2012). Red shows the M_2 (semi-diurnal principle lunar) constituent, blue the S_2 (semi-diurnal principle solar) constituent and black the split between flood and ebb directions. Right (b), the distribution of sampled five minute observational segments from cross-front transect surveys relative to ebb and flood tidal phases. Uneven distribution is noted in the number of observations on either side of the red line that marks the split between flood and ebb directions. Departure times from the harbour were restricted to two hours either side of high tide and so sampling predominantly occurred during ebb tides.

3.2.3.2.5 Time of day and sea state

DecTime (decimal time of day) was included to account for any variation in abundance/presence attributable to individuals commuting between breeding colonies and/or foraging grounds, or in response to diel prey migrations (although surveys were mainly conducted from the late morning onwards and so would have missed a morning peak in activity, a late peak in abundance may still be present; Cleasby et al. 2015). *Seastate* (sea state corresponding to the Beaufort scale) was included in the dolphin analysis to account for a decrease in detection probability in rougher conditions (Barlow et al. 2001).

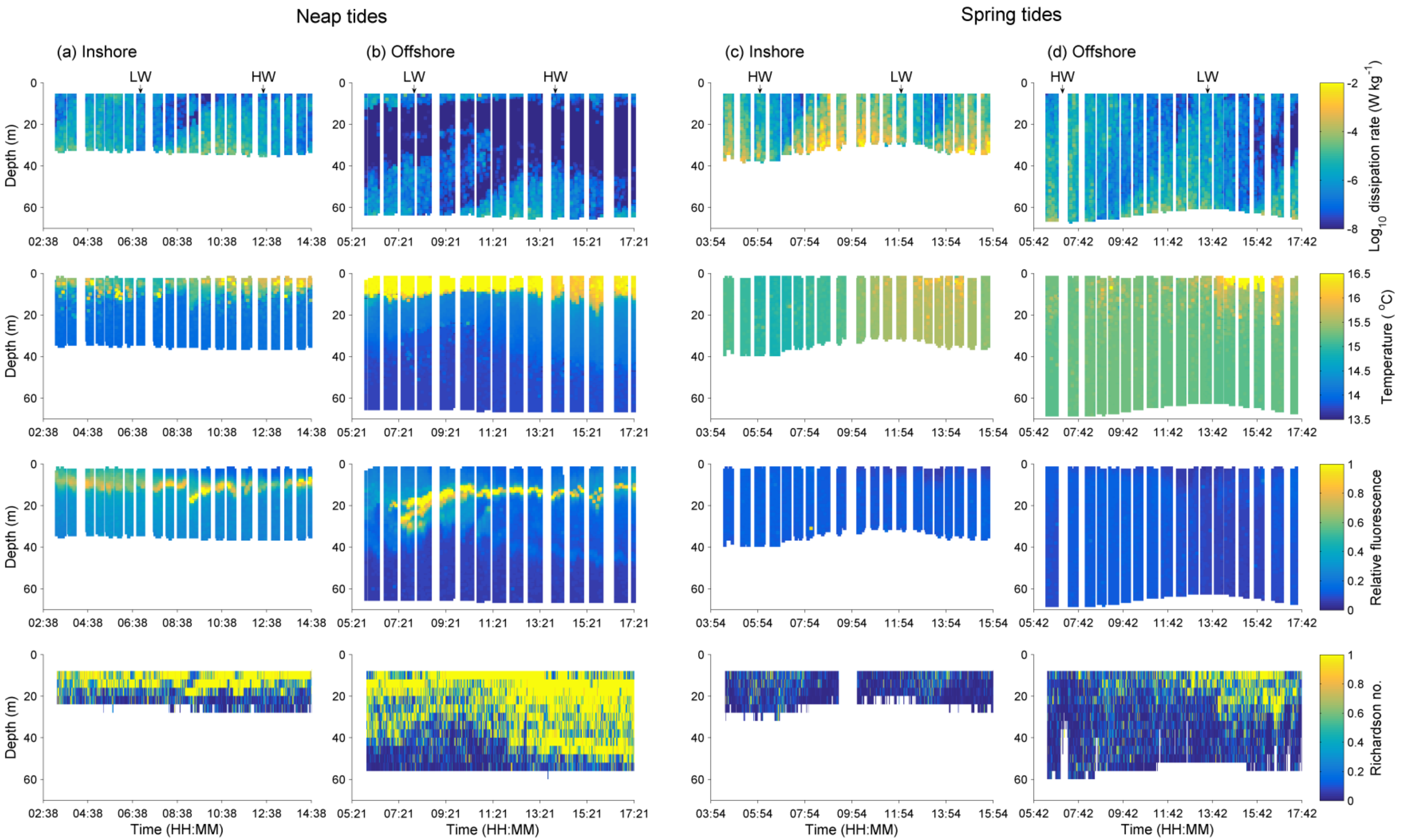

Figure 3.5 Oceanographic measurements taken during the oceanographic tidal stations. Rows from top to bottom show log turbulent dissipation, temperature, relative fluorescence, and Richardson numbers. Columns from left to right show measurements from the inshore neap (a; 12/08/2012), offshore neap (b; 13/08/2012), inshore spring (c; 19/08/2012) and offshore spring (d; 21/08/2012) tidal stations. The times of high water (HW) and low water (LW) are marked on the top row. Note that peaks in fluorescence generally occur above depths of 20m, making the use of the *MaxFluorescence* variable (which was calculated based on measurements taken from between 3-20m depth) in statistical modelling appropriate.

3.2.3.3 Statistical analysis

Data analysis was performed in R, version 3.0.2 (Copyright © 2013 The R Foundation for Statistical Computing). Two analyses were conducted to determine the influence of oceanographic conditions around the front on (1) variation in gannet absence/presence and abundance, and (2) variation in dolphin absence/presence.

Gannet abundance was modelled using a zero-inflated hurdle model, implemented through the R package pscl (Jackman 2011). This modelling framework was chosen over others (e.g. generalised linear models; GLM) due to a high prevalence of zero values (91%) which were driving over-dispersion. Hurdle models employ a two-step modelling approach. The first, binary component of the model estimates the Bernoulli probability of presence, whilst the second, count component of the model considers only the positive observations, and estimates expected abundance. In both cases, variation in the response variable (presence/absence or abundance of animals) is modelled with a number of explanatory variables which may be the same or differ in each stage of the model. The final output from the model is therefore determined, first, by the probability of presence in the binary component and, second, by predictions from the count component (Welsh et al. 1996, Zeileis et al. 2008, Zuur et al. 2009). In this analysis, the binary component of the model was fitted using a GLM with a binomial error structure and complementary log-log (clog-log) link, which is better suited to modelling binary data of asymmetric proportions (Aranda-Ordaz 1981, McCullagh & Nelder 1989). The count component was fitted using a zero-truncated GLM with a negative binomial error structure, which was chosen over a Poisson error structure to account for additional over-dispersion caused by a mixture of large and small observations. Analysis of dolphin sightings was limited to presence-absence data due to a positive observation rate of only 5.7%, which was deemed insufficient to additionally examine variation in abundance. A GLM with a binomial error structure and complementary log-log (clog-log) link was used.

All explanatory (environmental) variables were screened using histograms, box plots and univariate scatter plots to identify problematic distributions and the presence of extreme values or outliers (Zuur et al. 2010). *DepthChange* was logged (log [*DepthChange* + 1]) due to non-normality in distribution and some extreme values.

None of the variables displayed multi-collinearity, which was checked using pairs plots, correlation coefficients (r > 0.5) and variance inflation factors (VIF; VIF > 3).

All explanatory variables presented in Table 3.2 were included in both analyses, except for *SeaState*, which was not included in the gannet analysis because the detection rates of large airborne birds (gannets sitting on the water were not included in analyses; Table 3.1) would likely be unaffected by sea surface conditions. An interaction term was tested for between *CurrentSpeed* and *TideDir,* and an offset, *LogHundredMetresTravelled* (logged distance between the latitude/longitude taken at the beginning and end of each five minute segment), included to account for inconsistencies in the distance travelled within each five minute segment due to changes in vessel speed. Bivariate generalised additive models (GAMs) were used to identify potential non-linear relationships between response (animal sightings) and explanatory variables, and where indicated quadratic terms were included in the models (Crawley 2007). This applied to *LogMaxShear* and *MaxFluorescence* for both components of the gannet model. No quadratic terms were required for the dolphin analysis. The most parsimonious model was selected through forwards and backwards stepwise selection using Akaike's Information Criteria (AIC; Akaike 1973) and likelihood ratio tests (to compare nested models; Zuur et al. 2009).

Model fit was evaluated through observation of fitted versus observed values (Potts & Elith 2006) and, where appropriate (to evaluate binary models/components of models), by computing the area under the Receiving Operator Characteristic (ROC) curve (AUC; Zweig & Campbell 1993, Liu et al. 2005). Where extreme values were identified in the response variable (applicable only to the count component of the gannet hurdle model), models were fitted with both their inclusion and exclusion to determine their influence on results. Pearson residuals were extracted from each model and plotted against the fitted values of the model, the response variable, all explanatory variables (both those included and excluded after the model selection procedure), and space and time to identify any patterns that may indicate a violation of model assumptions (e.g. non-independence; Zuur et al. 2009). Semi-variograms and Moran's I statistic (using the 8 nearest neighbours) were generated from residuals to further test for spatial autocorrelation (Moran 1950, Zuur et al. 2009, Oppel et al. 2012). Temporal autocorrelation was additionally checked for through inspection of an auto-correlation function (ACF) plot of model residuals (Zuur et al. 2009).

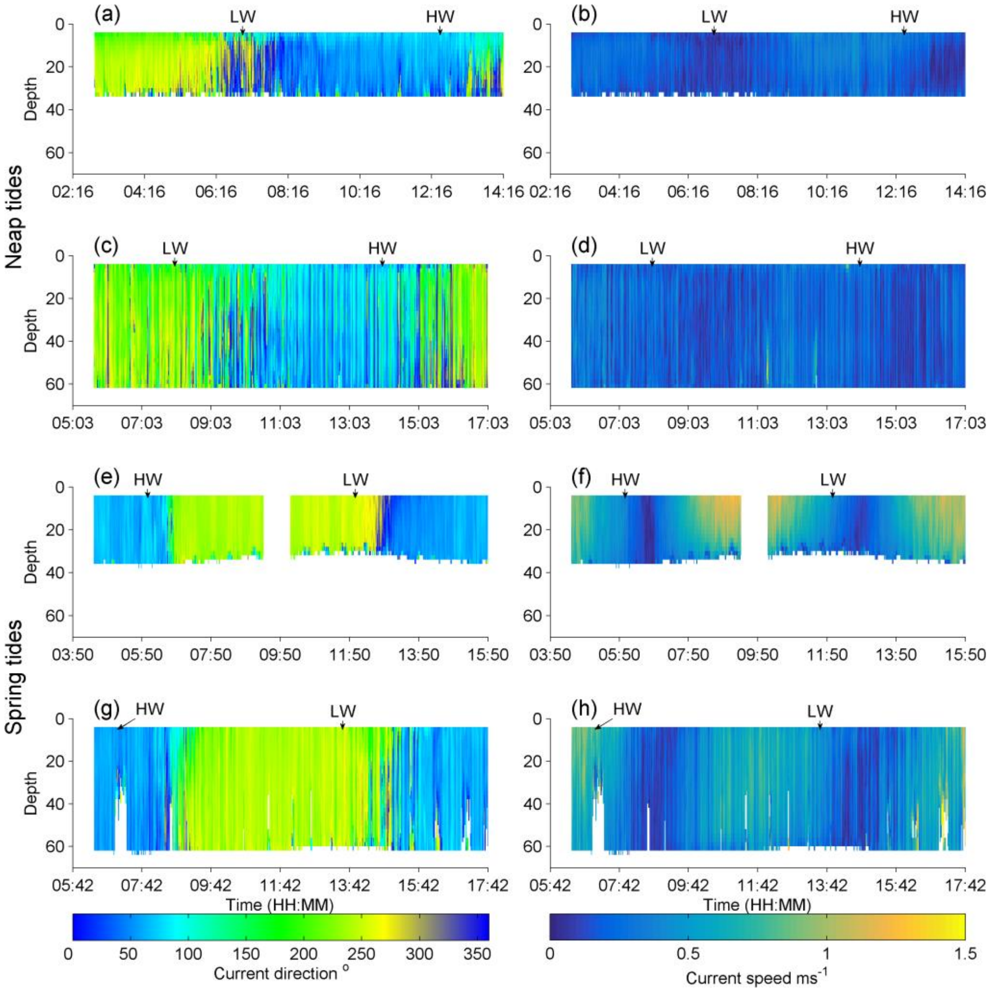

Figure 3.6 Current speeds and directions during oceanographic tidal stations measured via the hull mounted ADCP (acoustic Doppler current profiler) and averaged over one minute blocks. Columns from left to right show; (a), (c), (e) and (g) current directions, and (b), (d), (f), and (h) current speeds. Rows from top to bottom show; (a) and (b) inshore neap (12/08/2012), (c) and (d) offshore neap (13/08/2012), (e) and (f) inshore spring (19/08/2012) and (g) and (h) offshore spring (21/08/2012) surveys. The times of high (HW) and low water (LW) are indicated.

3.3 Results

3.3.1 Prevailing meteorological and oceanographic conditions

Tide, wave and wind conditions across and surrounding the entire surveying periods of 2012 and 2013 are presented in Figure 3.2. The inshore and offshore tidal stations were surveyed twice each, within three days of peak neap and spring conditions. Cross-front transect surveys were conducted within two days of neap and three days of spring conditions in 2012, and during the transition from spring to neap conditions in 2013 (three to seven days after peak spring tides; Figure 3.2). All surveying occurred in Beaufort sea states of four or less, and boat operations were paused when wave heights exceeded 2m and/or wind speeds reached 15ms^{-1} (30 knots). This happened once, between the 15th and 18th of August 2012 during a storm event that coincided with the transition from neap to spring conditions (Figure 3.2). Current speeds, as measured by the moored ADCP, increased, almost linearly, between the 12th and 21st of August from hourly peaks in depth mean averages of 0.3ms^{-1} to 1ms^{-1} (Figure 3.2.g). Residual current speeds across this period averaged 0.14ms^{-1} and ranged from 0.006 to 0.37ms^{-1}.

3.3.2 Characterisation of the front

The front orientated along a latitudinal axis in both 2012 and 2013 (Figure 3.3 and Appendix A1.1). Inshore waters were characterised by sea surface temperatures of between 13-15^{o}C dependent upon position in the spring-neap cycle. Offshore of the front, surface waters typically exceeded 16-17^{o}C and were at least 2^{o}C higher than inshore waters regardless of position in the spring-neap cycle.

3.3.2.1 Neap oceanographic tidal stations

During neap conditions the water column was thermally stratified at both the inshore and offshore stations, and characterised by top (5m) to bottom (30-60m) temperature differences exceeding 1.5-3^{o}C (Figure 3.5). Near-surface temperatures (at 5m) averaged 15.6^{o}C and 16.5^{o}C respectively. Bottom temperatures, across both stations, did not exceed 14.1^{o}C. There was a pronounced thermocline at a depth of roughly 10m, where vertical gradients in temperature (over a metre of depth) averaged 1.4^{o}C and 1.6^{o}C at the inshore and offshore sites respectively. Peak current speeds across both sites were around 0.5ms^{-1}, and occurred during the two hours preceding the times of low and high water (Figure 3.6). At the offshore site, turbulent dissipation rates in the upper two thirds of the water column (depths less than 40m) rarely exceeded 10^{-6}W kg^{-1} (Figure 3.5). Near the seabed, values peaked at 10^{-5}W kg^{-1} coinciding with the times of maximal current flows before high and low water. At the inshore station, turbulent dissipation rates were comparatively high, by several orders of magnitude, and typically exceeded 10^{-6}W kg^{-1} with peaks of 10^{-4}W kg^{-1} occurring again, in the lower half of the water column during maximal current flows. Richardson numbers were high (> 1) in the top 10m and 40m of the water column at the inshore and offshore stations respectively, and indicated that the stratified structures of both sites were stable (Figures 3.5 and 3.7).

Across both sites, peak measurements in fluorescence occurred at and around the thermocline (Figures 3.5 and 3.7) where Richardson numbers exceeded 0.25 (Figure 3.7). At the offshore site, pronounced thin layers of fluorescence (around 5m thick) formed between depths of around 10-20m (corresponding to the bottom of the thermocline), where measurements exceeded 3-5 times that of lower ambient background levels and N^2 peaked above $8e^{-4}s^{-2}$ (Figure 3.7). At the inshore site, the occurrence of fluorescence was shallower (at depths of less than 10m) and more diffuse (corresponding N^2 were around $4e^{-4}s^{-2}$). Ambient background levels were twice those measured at the offshore site. In the first half of the survey (until roughly 09:00), peak values were half those observed at the offshore site and spread across a thick depth band of around 10m. However, the latter half of the survey (09:00 onwards) saw the formation of thin layers that were similar in characteristic to those present at the offshore station (5m thick with values 3-5 times lower ambient background levels). This followed both a reduction in turbulent mixing during slack tide, and a 1^{o}C rise in near-surface temperatures (from 15^{o}C to 16^{o}C; Figure 3.5), both of which coincided with an increase in the strength of thermal stratification.

3.3.2.2 Spring oceanographic tidal stations

Top to bottom temperature differences were less than 0.5^{o}C during spring conditions across both the inshore and offshore stations. The erosion of the strong thermal stratification established during neap tides drove a northwards shift in the position of the front (Figure 3.3). This followed both a transition from neap to spring tidal conditions and the passing of a storm event (Figure 3.2). Depth mean temperatures across the day averaged 15.2^{o}C and 15.3^{o}C respectively. Peak current speeds occurred, again, during the two hours preceding high and low waters and exceeded $1ms^{-1}$, which was more than double those measured during neap conditions (Figure 3.6). Periods of maximal current flow coincided with turbulent dissipation values of more than 10^{-3}W kg^{-1} and 10^{-4}W kg^{-1} at the inshore and offshore stations respectively that extended the entire water column, and were at least an order of magnitude higher than peak measurements taken during neap conditions (10^{-4}W kg^{-1} and 10^{-5}W kg^{-1} respectively). Fluorescence was comparable to the ambient background levels measured at the offshore station during neap conditions (Figures 3.5 and 3.7). Low Richardson numbers (generally less than 0.25; Figures 3.5 and 3.7) reflected low buoyancy frequencies (Figure 3.7) following strong turbulent mixing and a break down in stratification.

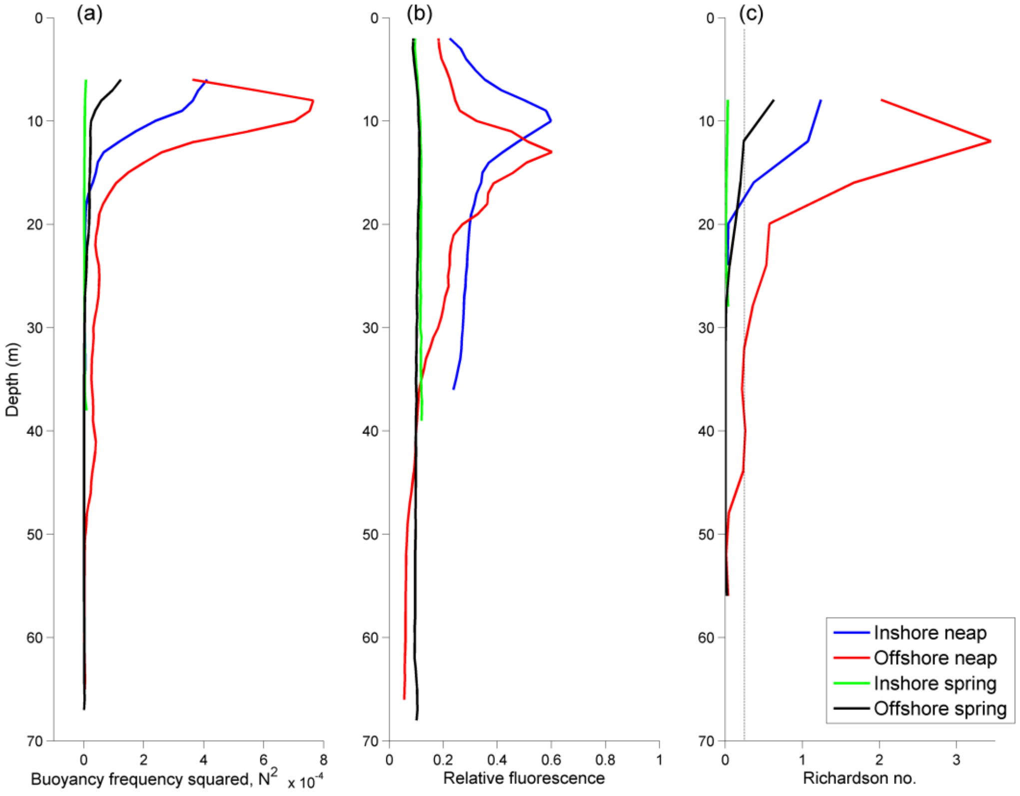

Figure 3.7 From left to right: daily averaged (a) buoyancy frequencies squared N^2 (indicating the strength of vertical density gradient) calculated over 1m intervals, (b) relative fluorescence over 1m intervals and (c) Richardson numbers (indicating the ability of shear instability to overcome water column stratification) calculated over 4m intervals. Colours indicate observations pertaining from the inshore neap (blue), offshore neap (red), inshore spring (green) and offshore spring (black) surveys. The dashed line in subplot (c) corresponds to Richardson values of 0.25 below which shear is sufficient to overcome density stratification and promote turbulent mixing. Low Richardson values below depths of 20m reflect the impact of weak stratification rather than strongly destabilising shear.

3.3.2.3 Oceanographic observations from cross-front transect surveys

Oceanographic measurements obtained during cross-front transect surveys reiterated observations from the tidal stations. The position of the front was variable and further offshore (by more than 10km) on days following spring conditions (Figure 3.8). Near-surface temperatures (at 3m) offshore of the front often reached 17°C. At times these were more than 2°C higher than those observed at 20m (that ranged from 13.5°C to 16.5°C). A pronounced yet shallow thermocline was detected in 2012, the depth of which rarely exceeded 15m (Figure 3.9 and Appendix A1.2). In 2013, the thermocline was deeper and at times exceeded depths of 15m (Figure 3.9 and Appendix A1.2). Across both years, peak fluorescence measurements were patchy and generally occurred at or around the thermocline on the stratified side of the front (Figure 3.9 and Appendix A1.2). Shear (S^2) values generally varied between $10^{-4}m^2s^{-2}$ and $10^{-3}m^2s^{-2}$. Peaks exceeding $10^{-3}m^2s^{-2}$ occurred near the seabed, or in shallow waters on the inshore side of the front (Appendix A1.2).

3.3.3 Links to large marine vertebrate predators

Over the seven cross-frontal transect surveys, 422 five minute observational segments were surveyed. A total of 223 foraging/searching gannets were seen in 38 (9%) of these, and 122 common dolphins in 24 (5.7%). The highest number of gannets and dolphins seen within one five minute segment was 60 and 12 respectively. General distributional patterns in relation to *ThermStrat* are shown in Figure 3.8.

Gannet presence was positively associated with *DecTime* ($p < 0.001$, $df = 1$, Table 3.3 & Figure 3.10). Variation in abundance was related to *Depth* ($p = 0.001$, $df = 1$, Table 3.3) and *MaxFluorescence* (p < 0.001, df = 2, Table 3.3). Areas of increased *Depth* and upper intermediate *MaxFluorescence* values (between 0.4 and 0.7) for the region were associated with increased foraging/searching activity (Figure 3.11). Dolphin presence was positively associated with *MaxFluorescence* ($p = 0.003$, $df = 1$, Table 3.4 & Figure 3.12) and negatively associated with *SeaState* ($p = 0.001$, $df = 1$, Table 3.4 & Figure 3.12) and *FrontIndex* ($p = 0.04$, $df = 1$, Table 3.4 & Figure 3.12).

Table 3.3 Explanatory variables retained by the binomial (π) and count (μ) components of the gannet *Morus bassanus* zero-inflated hurdle model. AIC (Akaike's Information Criterion) and degrees of freedom are given for the selected model (Gannets ~ *MaxFluorescence* + *MaxFluorescence*^{2} + *Depth*|*DecTime)*. AIC, degrees of freedom, likelihood ratio test results and percentage reduction in deviance explained are given for the removal of each variable from the selected model. A *p*-value of less than 0.05 from the likelihood ratio test indicates a variable is significant and should remain in the model (Zuur et al. 2009).

Dropped term	df	Δ AIC	Likelihood ratio test		Dev exp.
Selected model	380	0			
MaxFluorescence (quadratic) from μ	382	+13.05	$X^2 = 17.05$	(df = 2, $p < 0.001$)	4.45%
Depth from μ	381	+ 8.23	$X^2 = 10.23$	(df = 1, $p = 0.001$)	2.67%
DecTime from π	381	+12.54	$X^2 = 15.54$	(df = 1, $p < 0.001$)	3.79%

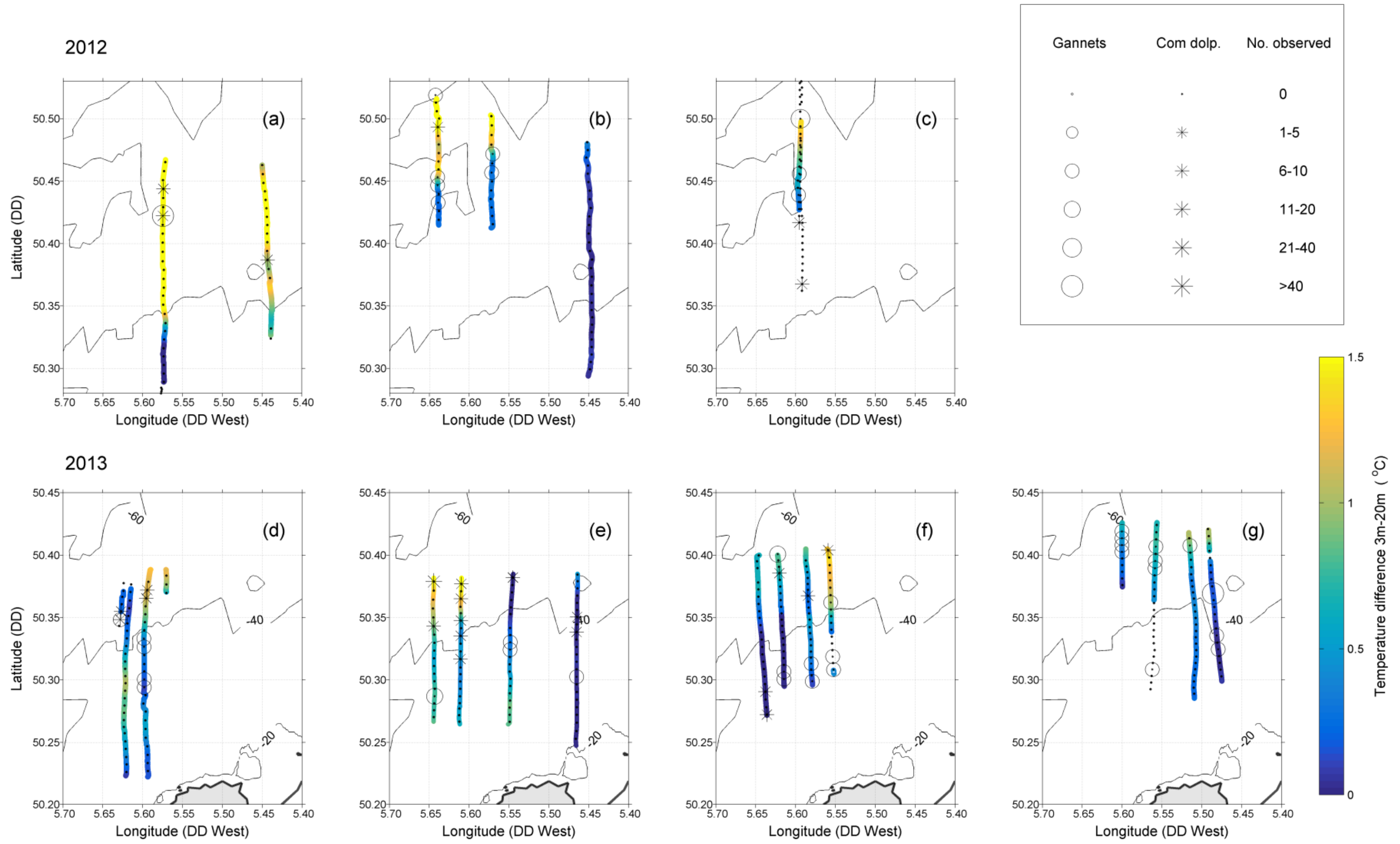

Figure 3.8 Spatial distributions of gannets *Morus bassanus* and common dolphins *Delphinus delphis* in relation to thermal water column structure *ThermStrat* (the temperature difference between 3m and 20m). Bathymetric contours for the region are marked in black. From the top left to bottom right: (a) Aug 14th 2012 (neap tide conditions), (b) Aug 20th 2012 (spring tide conditions), (c) Aug 22nd 2012 (spring tide conditions), (d) Aug 12th 2013 (spring tide conditions), (e) Aug 13th 2013 (spring tide conditions), (f) Aug 14th 2013 (midway between spring to neap tide conditions), and (g) Aug 15th, 2013 (midway between spring to neap tide conditions). Gaps in oceanographic measurements are due to malfunctions in equipment.

Forwards and backwards stepwise model selection gave consistent results for both the gannet and dolphin models, and model fit was deemed satisfactory (AUC for the binomial component of the gannet model was 0.7, and for the dolphin model was 0.8). The deviance explained by each model was 9.6% and 11.6% for gannets and dolphins respectively. Neither model was over-dispersed, and no substantial signs of spatial correlation (Moran's I statistic of 0.01, where values close to zero suggest observations are independent, and $p > 0.05$ for both gannets and dolphins) or temporal correlation were present.

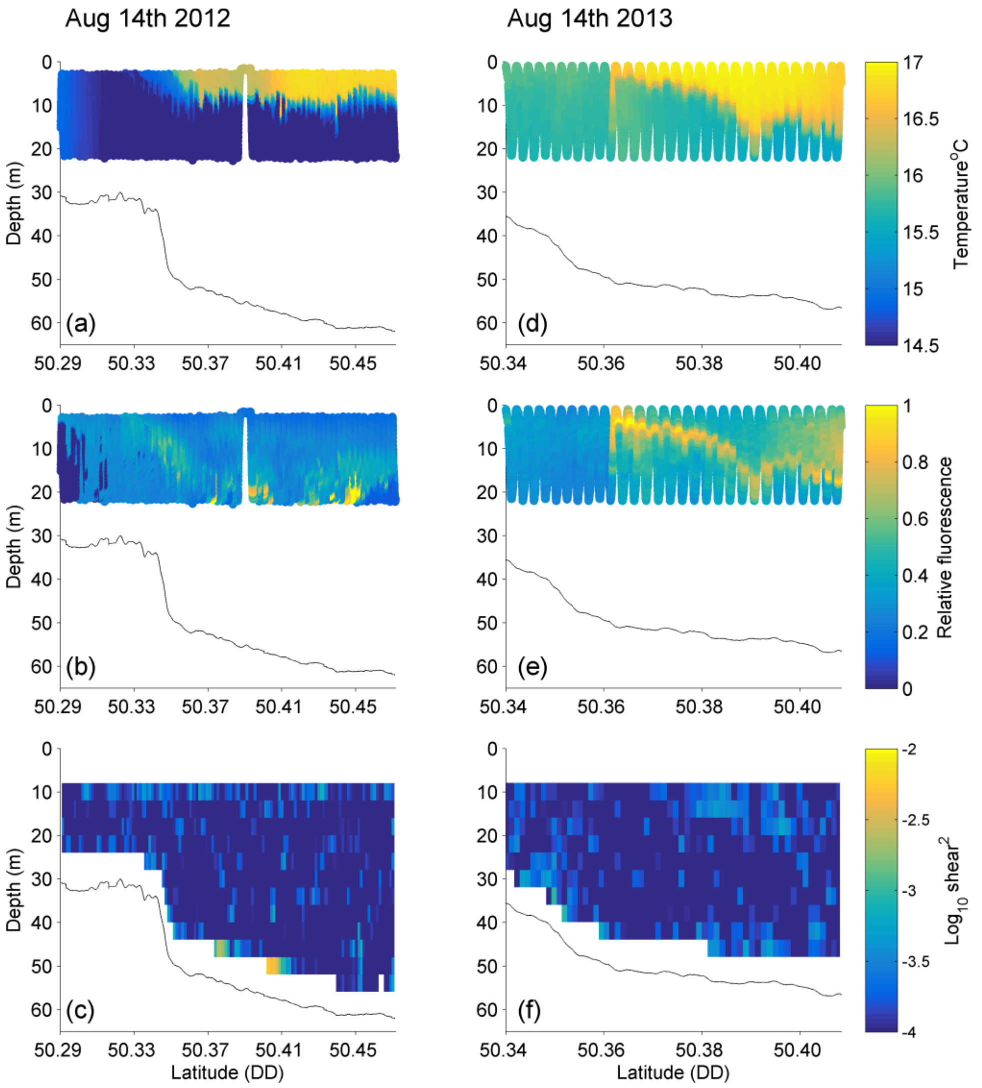

Figure 3.9 Oceanographic measurements from the undulating CTD for two sample cross-front transects from Aug 14th, 2012 (1st column; a:c) and Aug 14th, 2013 (2nd column; d:f). Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row (a & d) shows temperature, the middle row (b & e) relative fluorescence, and the bottom row (c & f) log shear S^2. The black line indicates the total water column depth. Peaks in fluorescence lie just below the thermocline on the stratified side of the front (b & e).

Table 3.4. Explanatory variables retained by the dolphin *Delphinus delphis* binomial GLM. AIC (Akaike's Information Criterion) and degrees of freedom are given for the selected model (Dolphin presence ~ *MaxFluorescence* + *FrontIndex* + *SeaState*). AIC, degrees of freedom, analysis of deviance test results and percentage reduction in deviance explained are given for the removal of each variable from the selected model. A *p*-value of less than 0.05 from the analysis of deviance test indicates a variable is significant and should remain in the model (Zuur et al. 2009).

Dropped term	df	Δ AIC	Analysis of deviance		Dev exp.
Selected model	383	0			
MaxFluorescence	384	+7.06	*Diff. deviance* = 9.06	(df = 1, *p* = 0.003)	6.33%
FrontIndex	384	+2.27	*Diff. deviance* = 4.27	(df = 1, *p* = 0.04)	2.64%
SeaState	384	+8.24	*Diff. deviance* = 10.24	(df = 1, *p* = 0.001)	5.60%

3.4 Discussion

This study provides insight of the fine-scale oceanographic conditions associated with the foraging habitats of large marine vertebrate predators around fronts. Fluorescence, indicative of chlorophyll production, was the most important environmental factor that influenced patterns in the occurrence of gannets and common dolphins. This supports a growing body of evidence that links large marine vertebrate predators to regions of increased surface (Louzao et al. 2006, Boersma et al. 2009, Sabarros et al. 2014) and sub-surface (Scott et al. 2010) productivity, and suggests this is a key component of foraging habitat. In addition to establishing links between marine predators and patches of increased primary productivity around fronts, this study also provides an in-depth overview of the physical processes that control the generation and distribution of this productivity, and hence localised availability of foraging habitat to marine predators around fronts.

3.4.1 Spatio-temporal variation in foraging habitat

Gannets and common dolphins occupied just 9% and 5.7% of surveyed segments respectively. The patchiness of these distributions reflected the limited availability of the bio-physical conditions that characterised foraging habitat. Only 17% of surveyed segments had *MaxFluorescence* values of between 0.4 and 0.7 which were identified as preferable conditions for gannets, and 23% had values greater than 0.6, representative of the upper values linked to dolphin presence. The occurrence of these patches of productivity was ephemeral and appeared dependent upon (1) episodic mixing and water column stability with the spring-neap cycle and (2) plankton entrainment in and around the thermocline.

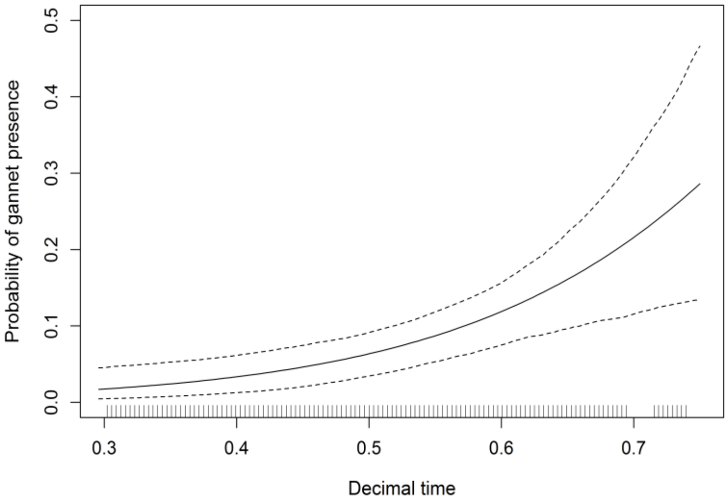

Figure 3.10. Gannet *Morus bassanus* presence. Outputs from the first, binomial component of the zero-inflated hurdle model. An increase in the probability of gannet presence (black line) corresponds to an increase in decimal time (time of day), possibly reflective of transit times between breeding colonies (likely at Grassholm, Wales; Wakefield et al. 2013) and foraging sites off the north Cornwall coast or diel migrations in prey (surveys here were mainly conducted in the late morning onwards so would have missed a morning peak in activity; Cleasby et al. 2015). Dashed lines show bootstrapped 95% confidence intervals. Plot produced using constants of *Depth* = 50 and *MaxFluorescence*= 0.5.

3.4.1.1 Episodic mixing and water column stability with the spring-neap cycle

Most of the study region experienced times when the water column was either fully mixing or thermally stratified (Figures 3.5, 3.8 and 3.9), and this coincided with an inshore-offshore shift in the position of the front with the spring-neap cycle. Storm-induced mixing between the 15th and 18th of August in 2012 may have additionally influenced this observation, although its contribution was likely small given that residual current speeds corresponding to this time period (around $0.35ms^{-1}$) were less than half the speed of those associated with the tide (Figure 3.2). Fluorescence peaked during neap conditions when turbulent mixing reduced and the water column was stable (Figures 3.5 and 3.7) suggesting these conditions are better suited for primary production. However, episodic bursts in nutrient supply which result from short term-mixing events are likely required to sustain this (Simpson et al. 1979, Ruardij et al. 1997). It was found that following a period of quiescence, increases in current speeds, predominantly due to a transition from neap to spring conditions, induced turbulent mixing which broke down previously established stratification and was likely sufficient to drive a redistribution of nutrients, both vertically from bottom layers and laterally from inshore mixing waters (Ruardij et al. 1997). During these times, an analogous dispersal of plankton away from well-lit surface waters temporarily reduces productivity (Cross et al. 2014), and this was evident in the overall low fluorescence levels measured during spring tides (Figures 3.5 and 3.7). Productivity resumes only when stratification has re-established and the water column is stable (Cloern 1991, Van Haren et al. 1998, Huisman et al. 1999). Along the cross-front surveys, regions of high productivity appeared to also be limited to stratified waters.

3.4.1.2 Plankton entrainment in and around the thermocline

The distribution and occurrence of productivity across the water column may be further influenced by turbulent flows that advect organisms into shear boundaries between opposing water currents at the thermocline. Resultant concentrations may exceed three times ambient background levels over depths of a couple of metres (Franks 1995, Durham et al. 2009, Cheriton et al. 2010), which when persistent over timespans of a few hours to several days are referred to as phytoplankton thin layers (Dekshenieks et al. 2001). Thin layers of fluorescence were evident, during neap conditions, at both the inshore and offshore sites (Figure 3.5). Although chlorophyll quenching (Dandonneau & Neveux 1997, Muller et al. 2001) may have influenced these observations, comparisons between measurements taken during daylight hours and night did not indicate this to be substantial (see Appendix A1.3). Layers occurred at and around the thermocline in regions of strong stratification and increased stability (as indicated by high buoyancy frequencies and Richardson numbers; Figure 3.7), and were particularly prominent at the offshore site. At the inshore site, thin layers were less distinguishable, probably due to differences in turbulent mixing (Ryan et al. 2008), which extended the entirety of the water column and were at least an order of magnitude more than that measured at the offshore site. Increases in zooplankton biomass have been observed in and around phytoplankton thin layers (McManus et al. 2003) suggesting accumulations may propagate across multiple trophic levels.

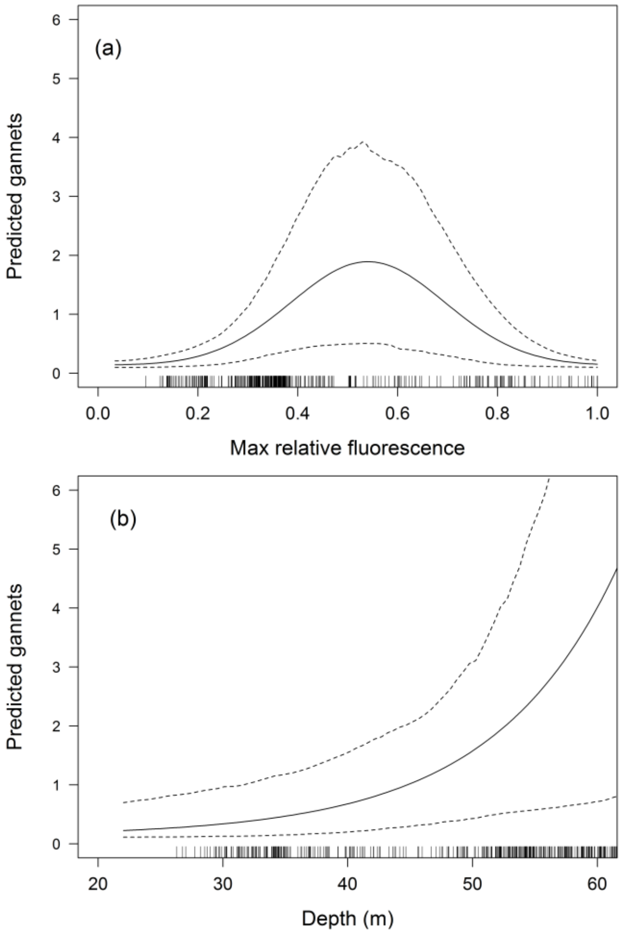

Figure 3.11 Gannet abundance *Morus bassanus* predicted (black line) from the second, count component of the zero-inflated model. Dashed lines show bootstrapped 95% confidence intervals. Intensified foraging is associated with regions of (a) intermediate fluorescence (relative values ranging from 0.4 to 0.7) and (b) increased water depth. Overall low expected counts are in part attributable to the high probability of a zero value as determined in the binomial component of the model. Plots produced using constants of *Depth* = 50, *MaxFluorescence* = 0.5 and *DecTime* = 0.6 for variables not included in a subplot.

3.4.2 Implications for marine predators

Gannets and common dolphins feed primarily on pelagic fish, and therefore direct correlations between patterns in their occurrence and a proxy of chlorophyll production, particularly in a highly variable region such as that surrounding the front, would not necessarily be anticipated. Previous links to sub-surface productivity have been characterised by its persistence and localised predictability (Bertrand et al. 2008, Scott et al. 2010, Embling et al. 2012). This is thought to attract planktivorous grazers, such as zooplankton, and so provides a predictable resource for forage and pelagic fish and their predators. However, my findings differ in that productivity was transient and dependent upon episodic periods of turbulent mixing and thermal stratification of the waters surrounding the front with the spring-neap cycle (Figures 3.5 and 3.7). As such, peaks in productivity were unlikely to be locally retained for timespans exceeding several days, suggesting predators were responding to tight coupling between lower and mid trophic levels. This raises questions regarding the lags and scales at which productivity propagates the food web, and suggests low trophic level planktivorous species are highly responsive to peaks in productivity, the effects of which appear to propagate across multiple trophic levels to create foraging opportunities for higher level consumers.

Tidal-mixing fronts form seasonally on a predictable yearly basis (Pingree 1975, Pingree & Griffiths 1978) and are an important resource for a number of large marine vertebrate predators (Scales et al. 2014b). I have shown that, within a season these fronts can be highly variable in their localised positions (Figure 3.5 and 3.8), and that this has concomitant consequences for ecological processes. Over the fine-scales surveyed (less than 1km), foraging habitat did not appear to be spatially predictable. Although the production of sub-surface fluorescence was, at least partially, controlled tidally, outside influences (such as weather and climatic variability) mean the precise locations at which the conditions required for the formation of associated foraging habitats converge are likely not consistent across weeks, months, seasons and years. As such, marine predators face substantial challenges when locating their prey. Evolved hierarchical movement patterns, where intensified searching is concentrated in regions where accessible prey resources are expected (Pinaud & Weimerskirch 2005, Sims et al. 2008), are probably a result of the varying predictability of foraging habitats with spatio-temporal scale (Fauchald 2009). Recent work has shown that rather than associating with the concurrent surface signature of a front, gannets preferentially target regions where fronts frequently manifest to perform intensive search behaviours (Scales et al. 2014a). My results indicate that within these regions, foraging habitat occurs as a result of the periodic break-down and re-establishment of stratification in waters surrounding a front which corresponds to a shift in its position with the spring-neap cycle. As such, whilst the availability of foraging habitats and their associated prey resources appear dependent upon the occurrence of a front, they may not reflect its instantaneous surface signature. Fronts and the waters immediately surrounding them likely represent predictable locations over coarse spatio-temporal scales around which localised ephemeral but reliable foraging opportunities can be found.

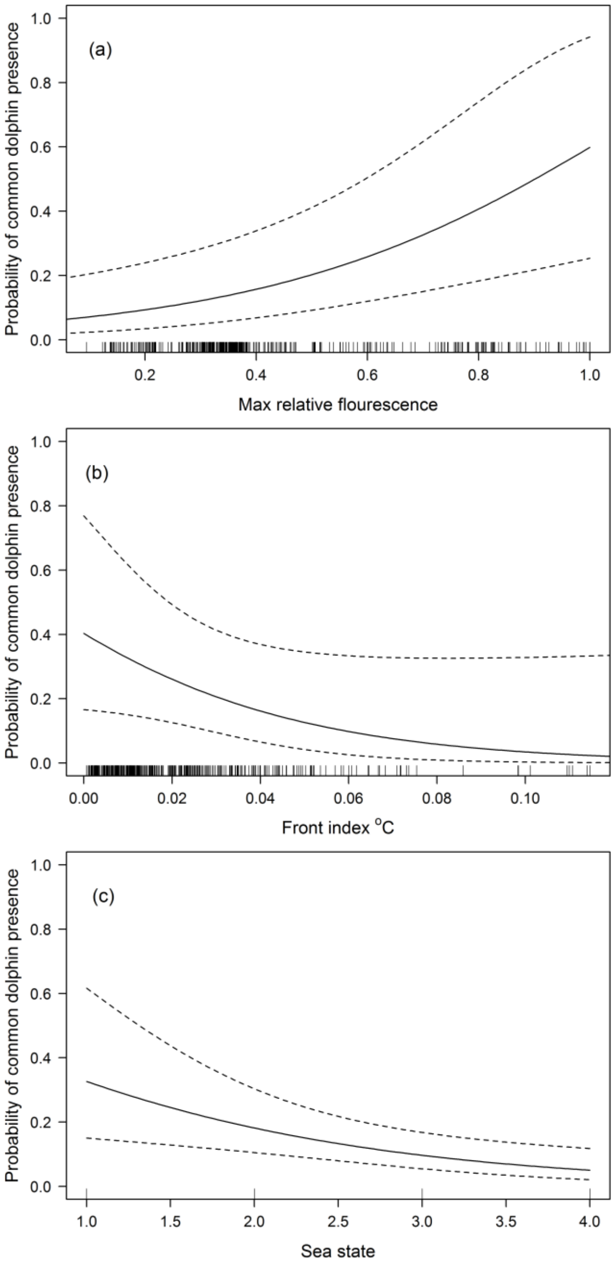

Figure 3.12 Dolphin *Delphinus delphis* presence (black line) from the binomial generalised linear model (GLM). Probabilities increase with maximum relative fluorescence (a) and decrease with front index (b) and sea state (c). Dashed lines show bootstrapped 95% confidence intervals. Plots produced using constants of *MaxFluorescence* = 0.7, *SeaState* = 1 and *FrontIndex* = 0.01 for variables not in a subplot.

3.4.3 Species specificity in habitat associations

There were noticeable differences in the relationships between gannets, dolphins and patches of increased productivity. Dolphin presence increased linearly with fluorescence, whilst gannet abundance peaked where production levels were intermediate for the region. All dolphin sightings were included in my analysis, and so this disparity could be because, in some instances, dolphins were engaged in non-foraging activities (e.g. socialising and travelling) and so the habitats they were occupying were coincidental. Alternatively, inconsistencies in the characteristics of the habitats targeted by these two species may arise from differences in foraging strategies and subsequent abilities to closely track prey movements.

First, current understanding suggests gannets rely predominantly on visual cues when searching for and capturing their prey (Machovsky-Capuska et al. 2012, Machovsky-Capuska et al. 2013). Visibility may be greatly reduced in areas of increased primary productivity (Jaud et al. 2012). As such, a preference for regions of intermediate productivity may reflect a threshold in the visibility levels required for prey detection. An additional ability to echolocate means dolphins are able to navigate such dark or murky waters (Wursig 1986) and so likely less influenced by this constraint.

Second, whilst in shallow regions (such as those surveyed in this study) dolphins can easily move throughout the water column, gannets dive from a typically air-borne position limiting their access to deeper depths (the dives of gannets in this region do not regularly exceed 8-10m; see Chapter V). Turbulent mixing may play an important role in making prey available at shallower depths (Embling et al. 2013, Scott et al. 2013), which may improve prey accessibility and foraging efficiency (Ropert-Coudert et al. 2004b, Green et al. 2009). However, this physical process may simultaneously disperse and/or disrupt productivity levels, and links between gannet abundance and intermediate fluorescence levels may reflect this. Indeed, at the inshore station during neap tides, increased turbulent mixing coincided with diffuse layers of fluorescence that were decreased in their values compared to those at the offshore site where turbulent mixing was comparatively low (by at least an order of magnitude).

3.5 Conclusions

The locations at which large marine vertebrate predators were observed around the front were spatio-temporally limited and correlated with regions of increased sub-surface fluorescence indicative of increased primary productivity. This productivity occurred at and around the thermocline, and appeared to be mediated by a bi-weekly cycle of stratification and episodic mixing of waters surrounding the front which coincided with a shift in its position with the spring-neap tidal cycle. This suggests the associated formation and occurrence of marine predator foraging opportunities around fronts is transient and controlled bottom up by complex oceanographic processes. As such, these habitats may not be predictable over localised spatio-temporal scales, and evolved hierarchical search strategies likely reflect this. Fronts and the waters immediately surrounding them represent coarse spatio-temporal locations within which localised ephemeral but reliable foraging opportunities can be found. As such, these structures are likely important habitat resources to a range of large marine vertebrate predators.

CHAPTER IV

Temporal patterns in habitat use by small cetaceans around a seasonally forming tidal-mixing front in the Celtic Sea

ABSTRACT

Understanding habitat use by large marine vertebrate predators, such as marine mammals, is essential for the effective conservation and management of shelf-seas. Typically these environments are highly dynamic, which likely influences the spatio-temporal distributions of high trophic level predators. This study uses a five year (2009-2013) passive acoustic data-set to examine temporal patterns in habitat use by small cetaceans, dolphins (unspecified *Delphinids*) and harbour porpoises *Phocoena phocoena*. CPODs were deployed at five locations across a seasonally stratifying shelf-sea site in the southern Celtic Sea, characterised by the presence of a tidal-mixing front during the summer months. To resolve patterns in site use over large seasonal and short (e.g. bi-weekly) temporal scales, two separate analyses were conducted using (1) daily detection rates of animals spanning the entire year and (2) daily detection rates taken only during the summer months (defined as June to mid-October). In both instances, generalised additive mixed effects models (GAMM) were used to relate detection rates to a suite of environmental variables representative of the oceanography of the region. I show that (1) increased harbour porpoise detection rates in the late winter/early spring (January-March) are associated with lower frontal activity, and (2) peaks in dolphin detection rates in the late summer (August-October) coincide with increased sea surface temperatures and high frontal activity. Together these findings suggest that habitat use by small cetaceans within shelf-seas is both temporally variable, species specific and possibly driven by complex bottom-up processes. As such, understanding the habitat needs of mobile large marine vertebrate predators in shelf-sea environments requires that we understand the dynamic complexities of these systems and the species that inhabit them.

4.1 Introduction

Mid to high latitude shelf-sea environments host high levels of biodiversity (Stone et al. 1995, Reid et al. 2003) yet are heavily impacted by anthropogenic activities (Frederiksen et al. 2004, Savenkoff et al. 2007, Lewison et al. 2014). Mitigating this depends upon effective conservation management for which integrative ecosystem based approaches are commonly proposed (Hyrenbach 2000, Frid et al. 2005, Crowder & Norse 2008, Game et al. 2009). However, for these to prove successful it is necessary to understand the habitat needs of marine animals in greater detail than is currently known (Taylor et al. 2005, Hooker et al. 2011, Waggitt & Scott 2014).

Large vertebrate marine predators, such as marine mammals, that occupy high trophic levels, play a vital role in marine ecosystem functioning (Heithaus et al. 2008, Baum & Worm 2009, Kiszka et al. 2015). However, understanding habitat use by these species is confounded by their often highly mobile nature and the dynamic structure of the systems they exploit. Mounting evidence suggests many marine predators concentrate in localised foraging regions (Hastie et al. 2004, Sydeman et al. 2006, Weimerskirch 2007), the situations of which are driven by bottom-up oceanographic processes that increase prey availability (Russell et al. 1999, Vlietstra et al. 2005, Embling et al. 2012). Specifically, within shelf-sea environments, marine predator habitat use has been linked to a number of oceanographic features including tidal-mixing fronts (Decker & Hunt 1996, Durazo et al. 1998, Scales et al. 2014b), regions of thermal stratification (Hunt & Harrison 1990, Scott et al. 2010, Cox et al. 2013), internal waves at offshore banks (Stevick et al. 2008, Scott et al. 2013) and tidally active topographic structures around the coast (Benjamins et al. 2015).

Many of the oceanographic features that marine predators forage at vary temporally in their occurrence. For example, regions of stratification develop seasonally during the spring and summer months, when increased solar irradiation heats surface waters sufficiently so as to overcome tidal and wind driven mixing (Pingree et al. 1976, Pingree & Griffiths 1978). This further drives the formation of tidal-mixing fronts that mark the transitional zones between resultant stratified offshore waters and permanently mixing inshore coastal waters. The position and strength of these features may additionally alter over shorter temporal scales in response to changes in turbulent mixing with the spring-neap tidal cycle and passing storm events (Nahas et al. 2005). Concomitant consequences on the availability of the associated prey resources that attract marine predators (Van der Kooij et al. 2008, Embling et al. 2012, Cox et al. 2013, Embling et al. 2013) mean the importance of an area where these oceanographic features regularly manifest will vary over both long (seasonal) and short (bi-weekly) temporal scales. As such, identifying when and why marine predators exploit specific sites can improve our understanding of their habitat requirements.

Studies of large marine vertebrate predators are often limited by the logistics and constraints of data collection. In particular, a number of challenges exist when attempting to examine habitat use by small cetaceans such as dolphins and porpoises, which are not only highly mobile but also inconspicuous in their behaviours (e.g. spending long periods of time diving; Barlow et al. 2001, Sveegaard et al. 2011). However, these species are often extremely vocal enabling passive acoustic techniques to offer effective alternatives (Philpott et al. 2007, Pirotta et al. 2014a, Pirotta et al. 2014b) to labour intensive observational methods such as boat and land based surveying. Whilst the spatial coverage of these moored devices is often limited, the ability to continuously log activity over deployments lasting several months make these instruments particularly well suited to long term studies at point locations.

The overall aim of this study was to examine temporal patterns in the use of an offshore topographically smooth shelf-sea site in the southern Celtic Sea (Figure 4.1) by harbour porpoises *Phocoena phocoena* and dolphins (unspecified *Delphinids*). This site was selected for the study because (1) it is subject to seasonal stratification and the formation of a dynamic tidal-mixing front in the summer (Chapter III) and (2) it is the location of a preoperational marine renewables wave energy test site. Passive acoustic monitoring devices were deployed over a five year period at five sites across an area of roughly 40km^2 (Figure 4.1, Table 4.1). Temporal variability in the daily detection rates of harbour porpoises and dolphins was examined in relation to a suite of environmental variables sourced via a combination of satellite remote-sensing and numerical modelling. To be able to resolve patterns in site use over both large seasonal and short (e.g. spring-neap tidal cycle) temporal scales, two analyses were conducted using data spanning (1) the entire year and (2) solely the summer months (defined as June to mid-October; Figure 4.2).

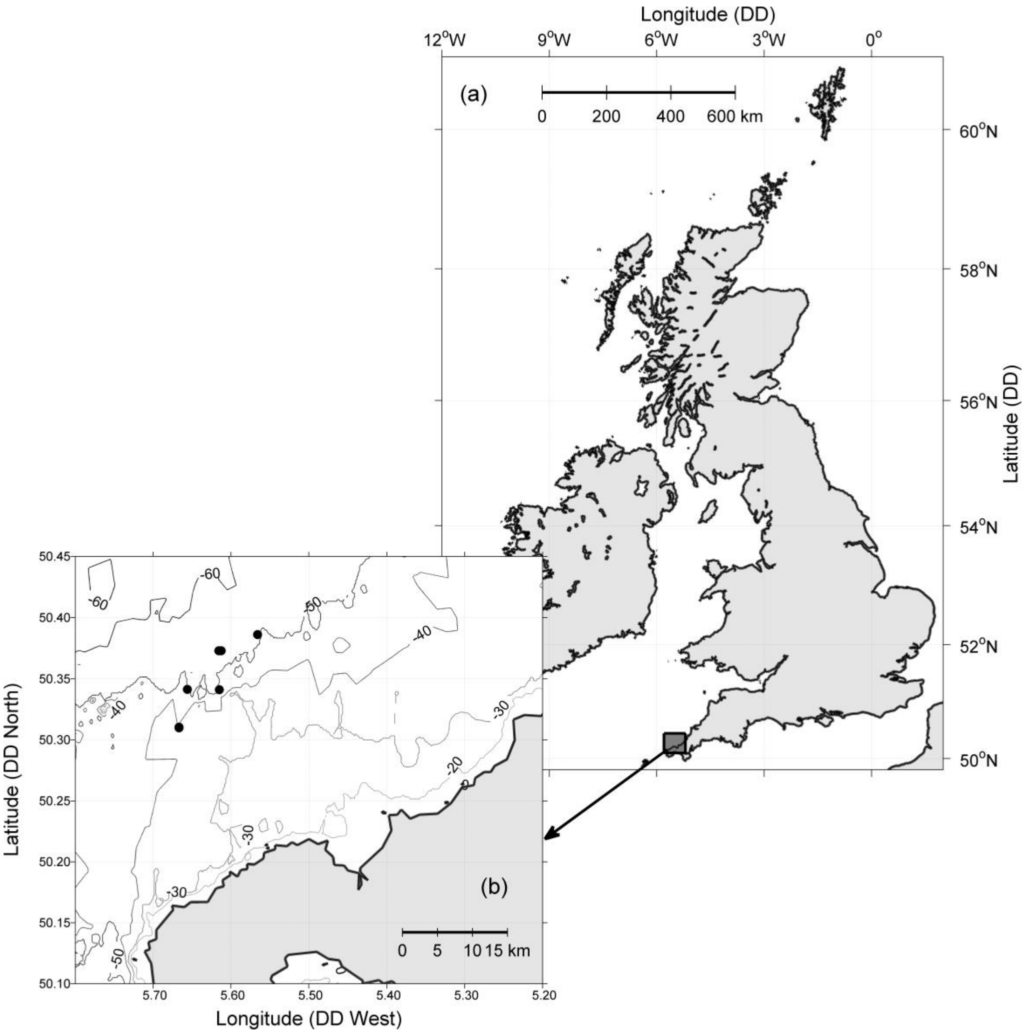

Figure 4.1 The deployment site: (a) in the context of the UK, and (b) with the positions of the CPODs (black filled circles) and bathymetric contours.

4.2 Methods

4.2.1 Passive acoustic monitoring

Acoustic loggers (CPODs, Chelonia Ltd, UK) were deployed off the north Cornwall coast (originally as part of a renewable energy impact assessment), at mid-water depths (~15m from the seabed) intermittently from September 2009 to December 2013 across an area of roughly 12km by 3km (Table 4.1, Figures 4.1 and 4.3). Devices were deployed at seven locations, however in two instances the CPOD detection range (omnidirectional ~400m for harbour porpoise and ~1km for dolphin species; www.chelonia.co.uk) overlapped two locations and so, to avoid sampling the same animals twice, devices deployed within 1km of one another were used interchangeably resulting in five discrete recording sites (Table 4.1, Figure 4.1).

CPODs continuously monitor the 20-160 kHz frequency range for potential cetacean echolocation clicks. For each click detected they log the centre frequency, frequency trend, duration, intensity and bandwidth. Once recovered, data were downloaded and processed using version 1.054 of the custom CPOD software (www.chelonia.co.uk). This software differentiates between dolphin and porpoise clicks as well as other noise sources, such as sonar, using the Kerno classifier (Chelonia Ltd 2013a) that assigns a level of confidence in the detection classification as low, medium or high. To ensure data quality, analyses only included click trains classified as medium or high, all of which were manually screened for false positives using the CPOD software (Chelonia Ltd 2013b).

Table 4.1 Locations of the five sites and deployment dates of devices.

Location	Latitude	Longitude	Deployment dates (inclusive; MM/YYYY)
Site 1	50.3862	-5.5661	09/2009 - 12/2009, 05/2010 - 10/2010 & 01/2011 - 03/2011
Site 2	50.3730	-5.6143	09/2009 - 12/2009 & 05/2010 - 01/2012
Site 3	50.3414	-5.6561	09/2009 - 10/2009 & 05/2010 - 02/2011
Site 4	50.3102	-5.6687	04/2010 - 03/2011
Site 5	50.3412	-5.6151	02/2012 - 04/2012, 08/2012 - 10/2012 & 03/2013 - 12/2013

Data were exported as the number of detection positive hours per day (DPH) for harbour porpoises and dolphins (unspecified *Delphinids*) separately. Whilst anecdotal dolphin observations in the area suggest common dolphins *Delphinus delphis* are the most common and predominant species present during the summer (Cox, unpublished data), Risso’s dolphins *Grampus griseus* and bottlenose dolphins *Tursiops truncatus* are occasionally sighted (Leeney et al. 2011, Pikesley et al. 2012). As it is not currently possible to distinguish between *Delphinid* species using CPODs, all dolphin species detected were grouped and referred to as ‘dolphins’. In addition to detection rates, details of the CPOD’s operating performance were also exported as the percentage logging time lost per day (to provide information of times when the CPOD stopped operating due to an overload of noise from tidally/weather generated turbulence) and the angle of the device in the water (that may vary with water current speeds), both of which can influence the detection rates recorded by a device.

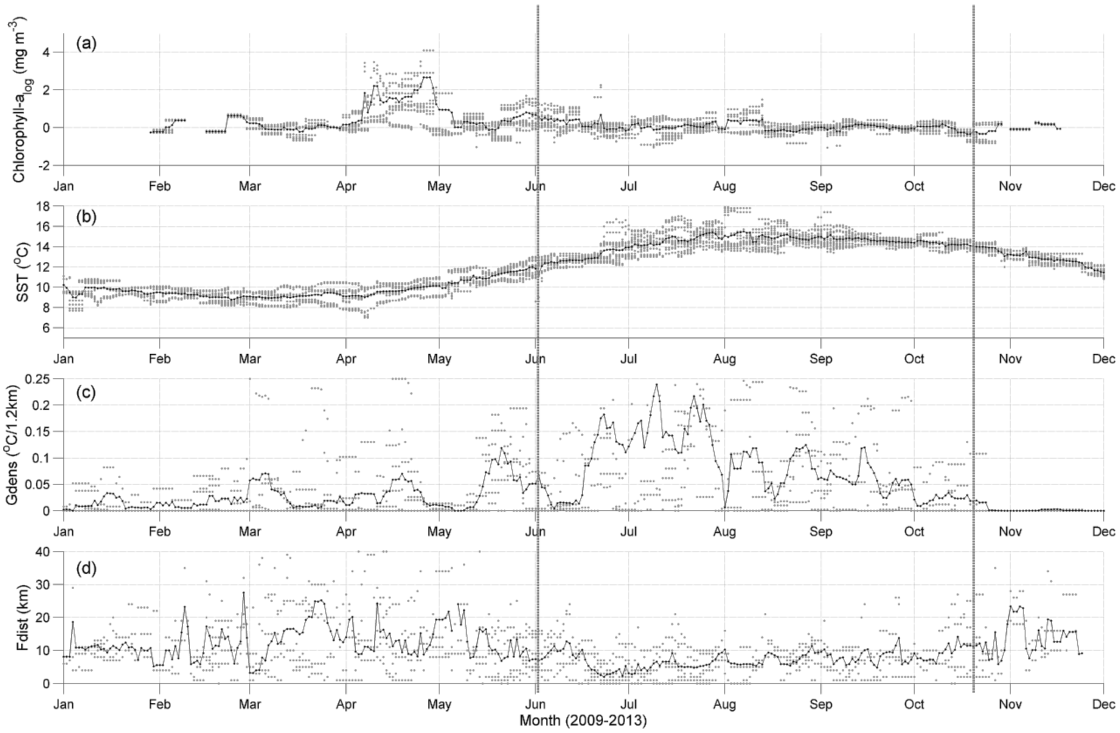

Figure 4.2 Variation in environmental conditions averaged across the five sites and years (raw values are plotted in light grey). From top to bottom: (a) surface chlorophyll-a *Chlorophyll*, (b) sea surface temperature *SST*, (c) front gradient *Gdens* and (d) distance to closest front *Fdist*. Seasonal variation is noted, with warmer temperatures and increased frontal activity during the summer months between June and October (marked with a dashed line). A peak in surface chlorophyll-*a* in late April indicates the occurrence of the annual spring bloom.

4.2.2 Environmental data

I explored relationships between cetacean occurrence and a suite of environmental variables that characterised the oceanographic variability of the region. These included sea surface temperature (SST), surface chlorophyll, distance to closest front, at-site frontal activity and relative time in the spring-neap cycle.

4.2.2.1 Sea surface temperature (SST) and chlorophyll

SST was included to determine how cetaceans respond to the seasonal warming and thermal stratification of the region (approximated by an increase in surface waters; Ropert-Coudert et al. 2009b). Moreover, a bi-weekly cycle of water mixing with the spring-neap cycle (Simpson & Sharples 2012) during the summer months (June-Oct) could alternate the locations of the CPODs between periods when the water column was stratified (approximated by high surface temperatures) or mixing (approximated by comparatively lower surface temperatures), and cetaceans may also respond to this

(Figure 4.3). Surface chlorophyll was included to investigate links between marine predators and primary productivity (Louzao et al. 2006, Scott et al. 2010) that could be indicative of tight coupling between trophic levels at the site.

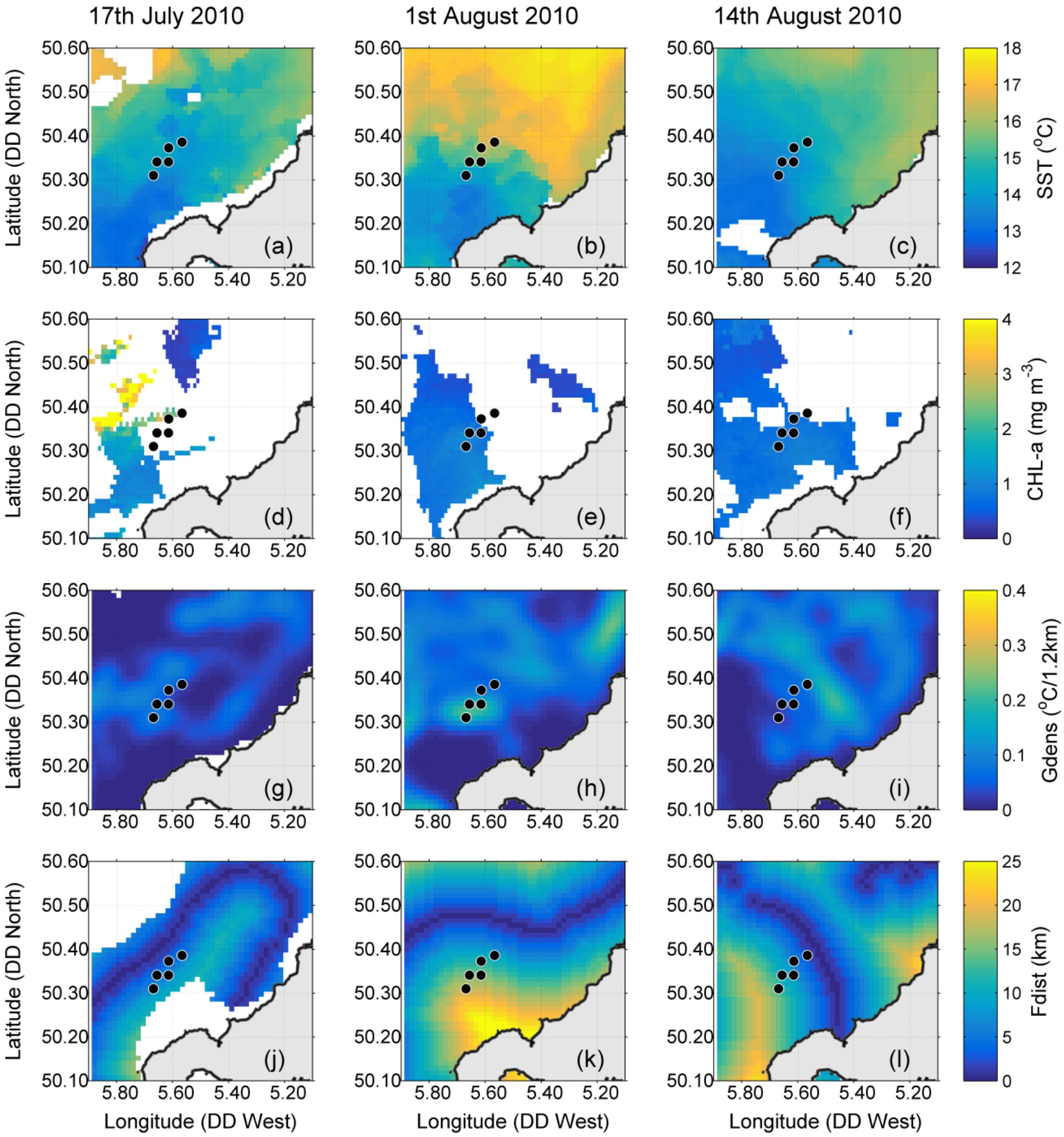

Figure 4.3 Across summer environmental variability in 2010. From the top to bottom rows: sea surface temperature *SST* (a:c), chl-a *Chlorophyll* (d:f), front gradient *Gdens* (g:i) and distance to closest front *Fdist* (j:l). Locations of CPOD deployment sites are shown by black dots with white outlines. Each column corresponds to a different date as indicated: 17th July (a, d, g & j), 1st August (b, e, h & k) and 14th August (c, f, i & l). A cycle of SST warming (approximate for thermal stratification) and cooling (approximate for water mixing) is noted between dates, and as such variation in the position and intensity of fronts is evident. Differences in the anticipated location of the front between subplots b (SST) and k (Fdist) are due to specifics of the compositing and smoothing processes used to generate the SST maps and front metrics.

SST, *SST*, was taken from advanced very high resolution radiometer (AVHRR) data and surface chlorophyll-a, *Chlorophyll*, from Aqua-MODIS standard chlorophyll (OC3) data. These data were provided as level 3 weekly composite maps at 1km and 4km for SST and chlorophyll respectively by the NERC Earth Observation Data Acquisition and Analysis Service (Figure 4.3; NEODAAS, Plymouth, UK). Weekly composites were selected to minimise the obfuscating effect of cloud cover. Data were sourced from the pixel corresponding to the location of each CPOD deployment. Each daily detection rate was matched to the corresponding central date of a seven day composite.

4.2.2.2 Front metrics

To determine the importance of the seasonally forming tidal-mixing front to small cetaceans in this area, thermal frontal activity across the five sites was summarised into two metrics: (1) front gradient intensity, *Gdens*, as a measure of the strength of frontal activity occurring directly at each of the five sites, and (2) distance to closest front, *Fdist*, as a measure of the distance between each of the five sites and the closest simplified front (Figure 4.3; Miller 2009, Scales et al. 2014a).

Raw (level 0) AVHRR infrared data were converted to an index of sea surface temperature (SST; level 2) and mapped across the Celtic Sea at a spatial resolution of approximately 1.2km/pixel. Thermal fronts were then detected in single scenes of 32 by 32 pixels using single image edge detection (SIED; Cayula & Cornillon 1992) with a temperature difference threshold of 0.4^{o}C across the front (Miller 2009). *Gdens* was taken as the spatially smoothed average temperature gradient across all frontal pixels detected over a seven day composite to give a continuous distribution of frontal intensity. A Gaussian filter with a width of five pixels was used for the spatial smoothing (Scales et al. 2014a). *Fdist* was taken as the distance from any point to the closest simplified front. Simplified fronts were defined using a clustering algorithm to identify continuous contours through the strongest frontal pixels on the spatially smoothed *Gdens* front map (Scales et al. 2014a). Data were sourced from the pixel corresponding to the location of each CPOD deployment. Each daily detection rate was matched to the corresponding central date of a seven day composite.

4.2.2.3 Relative position in the spring-neap cycle

Variation in the quality of a habitat may stem from changes in the strength of tidal currents associated with the spring-neap cycle (Embling et al. 2010, Embling et al. 2013). Moreover, at this study site, during the summer months it is expected that the oceanographic conditions at the locations of the CPODs cycle through periods when the water column is mixing (more probable during spring conditions; Chapter III) and periods when the water column is likely stratified (more probable during neap conditions; Chapter III). As such, a measure of relative position in the spring-neap cycle was included in analyses.

Tidal predictions were made using POLPRED offshore tidal computation software version 2.4.1.0 (National Oceanography Centre, Liverpool, UK). Offshore tidal elevations were predicted at a single central location of 50.36 N, 5.61 W at 10 minute intervals continuously from January 2009 to January 2015. A bespoke peak finding algorithm was then used to split predictions into complete neap-spring-neap cycles. An index of relative position in the spring-neap cycle, *SpringNeapCycle,* was then taken for each day as the time since the last neap tide (defined as a trough in the tidal elevations) divided by the total time between the neighbouring neap tides.

4.2.3 Statistical analysis

Analyses were conducted using (1) all daily measurements of animals and their environment spanning the entire year and (2) daily measurements taken only during the summer months (that ran from the 1st June until the 20th October; Figure 4.2). The beginning of summer (June 1st) was defined as when SST (averaged across the five sites and years) had begun to increase and frontal activity (as indicated by the two front metrics, also averaged across the five sites and years) intensified (Figure 4.2). The end of summer (20th October) was defined as when SST began to cool and frontal activity decreased (Figure 4.2).

For both analyses I used generalised additive mixed models (GAMMs) with a Poisson error structure from the mgcv package in R (Wood 2015). DPH (response variable) was modelled for dolphins and harbour porpoises against a number of selected environmental variables (explanatory variables): *SST, Chlorophyll, Gdens, Fdist* and

SpringNeapCycle. These were fitted using cubic regression splines, or for *SpringNeapCycle* cyclic splines, with a maximum of five knots. Scatterplots, histograms and boxplots were generated to check for extreme values and severe non-normality of explanatory variables which would violate model assumptions (Zuur et al. 2010). As GAMMs are sensitive to colinearity between explanatory variables, which can lead to unreliable parameter estimates (Zuur et al. 2009), I tested the influence of each explanatory variable on cetacean DPH in separate models. This also minimised the number of data rows lost due to missing data values, the locations of which were often not consistent between variables (e.g. between *Chlorophyll* and *Fdist*).

Strong water currents, attributable to large spring tides and passing weather events, can cause the CPOD to shut down temporarily to avoid overloading its memory with excessive noise recordings. As such, bias in detection rates may be introduced as a result of days when the CPOD was not fully operational. To minimise the effect of this, I excluded those days when the time lost (i.e. the time the device shut down) across a day was not equal to zero (‘time lost’ could not be included as a co-variate in the modelling process as it would have been co-linear with *SpringNeapcycle*). Across the entire year, this resulted in the removal of 26.6% of recordings taken during spring conditions (*SpringNeapCycle* > 0.25 and < 0.75) and 16.7% of recordings taken during neap conditions (*SpringNeapCycle* ≤ 0.25 and ≥ 0.75) leaving a total of 770 and 801 recording days during spring and neap conditions respectively. Of the summer observations, 15% of excluded recordings occurred during spring conditions and 2.8% during neap conditions leaving 397 and 462 recording days during spring and neap conditions respectively.

To account for differences in the detection capabilities between CPOD deployments, which may arise from inconsistencies in instrumentation and mooring configuration or differences in location specifics (Thomsen et al. 2005), I included a random effect of deployment ID. Exploratory analysis of the data showed distinct serial auto-correlation between observations and so a nested continuous temporal correlation structure was also included. Several correlation structures were tested (e.g. exponential, rational quadratic, autoregressive) and the most appropriate selected through inspection of residual plots (Zuur et al. 2009).

To ensure the data were not over-fitted, in addition to the use of *p*-values, conservative *k*-folds cross validation was used to compare between models including and excluding each explanatory variable (Hastie et al. 2008, Cleasby et al. 2015). Data were divided into five continuous segments for each device deployment. Four subsets were then used as a training dataset to which each model was fitted both with and without the inclusion of the explanatory variable being tested. The coefficients from these models were then used to make predictions on the remaining, validation, data subset. This process was repeated until all data subsets had, in turn, been used as the validation dataset. A *k*-fold cross-validation (KCV) statistic was then calculated for each model as the sum of the total difference squared between the observed and predicted values of each validation dataset. An explanatory variable was retained if its inclusion decreased the KCV statistic and it had a *p*-value < 0.05 (as estimated by the model fitted using the entire dataset).

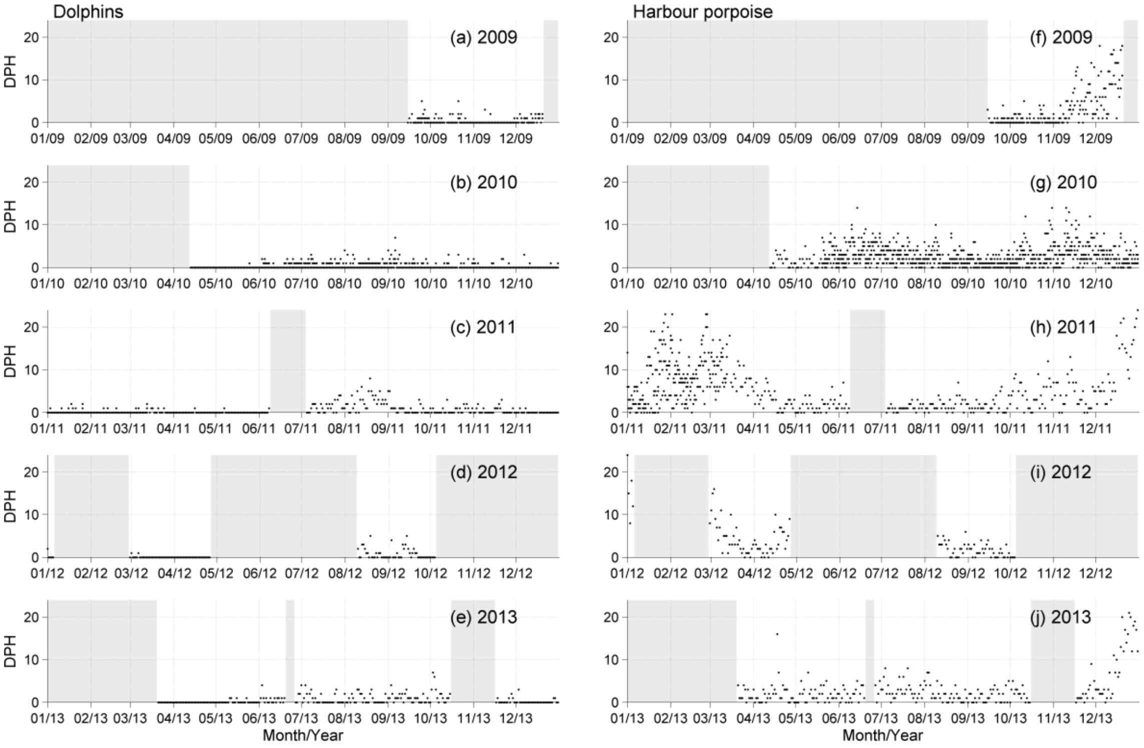

Figure 4.4 Patterns in the occurrence (detection positive hours per day; DPH) of dolphins (a:e) and harbour porpoises *Phocoena phocoena* (f:j) across all device deployments. From top to bottom: 2009 (a & f), 2010 (b & g), 2011 (c & h), 2012 (d & i) and 2013 (e & j). Dolphin detection rates peak in summer from around June to October, whilst, in contrast, peak harbour porpoise detection rates run from late December to March. Periods of no data are shaded grey.

Models were evaluated by plotting normalised residuals against all potential explanatory variables, day of year, month, year, angle of device, site ID, CPOD ID and deployment ID to check for any patterns indicative of a violation of model assumptions. Fitted versus predicted values were inspected to check for satisfactory model fit. Models were checked for over-dispersion and auto correlation (ACF) plots were generated to check that residual temporal auto-correlation had been accounted for (Zuur et al. 2009).

4.3 Results

Across the five sites, passive acoustic monitoring was carried out continuously from September 2009 to December 2013, with four gaps of greater than a month between (1) January to March, 2010, (2) January to March, 2012, (3) May to July, 2012, and (4) November, 2012 to February, 2013 (Table 4.1). This yielded a total of 2023 days (48,552 hours) of data, on 1062 unique dates. Dolphin and harbour porpoise presence was recorded on 20.7% and 81.1% of these days respectively (Figure 4.4).

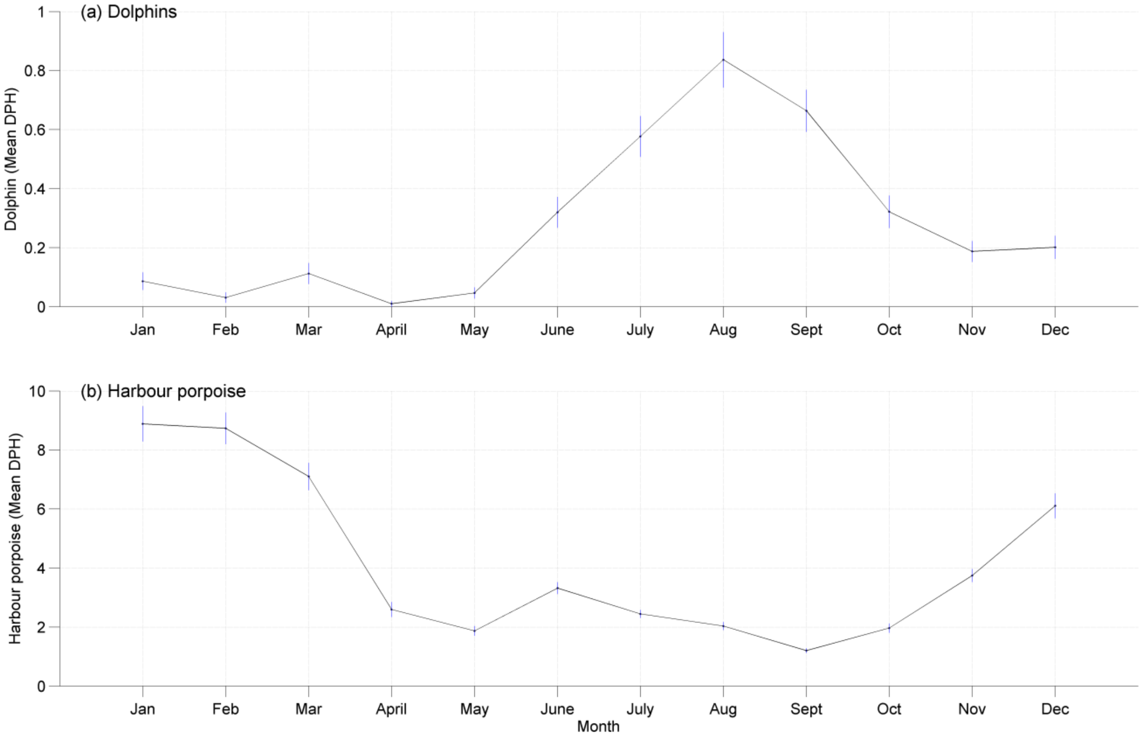

Figure 4.5 Monthly mean daily detection positive hours per day (DPH) of (a) dolphins and (b) harbour porpoises *Phocoena phocoena*. Dolphin occurrence peaks in summer from June to October, whilst in contrast, harbour porpoise occurrence peaks from December to March. Blue vertical lines indicate the standard error associated with each mean.

4.3.1 Seasonal variation in the occurrence of small cetaceans across the entire year

Dolphins were detected most frequently during the summer across all years (Figure 4.5). DPH was several times higher between June and November than during the remainder of the year (e.g. 0.8 in August vs 0.1 in January; Figure 4.5). This coincided with increased temperatures and frontal activity (Figure 4.6). DPH increased linearly with *Gdens* ($p < 0.05$, Table 4.2, Figure 4.6) and *SST* ($p < 0.001$, Table 4.2, Figure 4.6), which explained 2% and 15.5% of deviance respectively. A negative relationship was found with *Fdist* ($p < 0.01$, Table 4.2, Figure 4.6) which explained 3.8% of deviance.

Table 4.2 Results from yearly models for (a) dolphins (unspecified *Delphinids*) and (b) harbour porpoises *Phocoena phocoena*. Each term was tested in a standalone model as a single term alongside a random effect of deployment ID with a nested continuous auto-regressive temporal correlation structure. The models intercept (standard errors in brackets), estimated degrees of freedom (E.df), parameter coefficient (standard errors in brackets), deviance explained (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross validation (KCV) statistic on the inclusion of each term in the model is also indicated.

Environmental variable	Intercept	E.df.	Coefficient	Dev. exp.	*p*-value	Δ KCV
(a) Dolphin species						
Fdist	-1.37 (0.19)	1	-1.35 (0.52)	3.83%	0.0095	-9
Gdens	-1.51 (0.21)	1	0.66 (0.28)	1.96%	0.018	-7.5
SST	-1.50 (0.73)	1	2.39 (0.380)	15.5%	< 0.001	-64
(b) Harbour porpoise						
Fdist	0.97 (0.19)	1	0.39 (0.71)	2.03%	0.025	-140
SpringNeapCycle	1.11 (0.18)	1.9	NA	1.02%	0.011	-72

Across the entire year, the detection rates of harbour porpoises were generally higher than those observed for dolphins (monthly mean DPH of 2 to 9 vs 0 to 1 respectively; Figure 4.5). Occurrence peaked between December and March (Figure 4.4 & 4.5). No relationships were observed with *SST*, *Gdens* or *Chlorophyll*. There was a positive relationship with *Fdist* ($p < 0.05$, Table 4.2, Figure 4.7) that explained 2% of deviance (Table 4.2, Figure 4.7). DPH varied significantly with *SpringNeapCycle* ($p < 0.05$,

Table 4.2), although the deviance explained was low (1%). The rate of harbour porpoise detections increased during neap conditions (Figure 4.7).

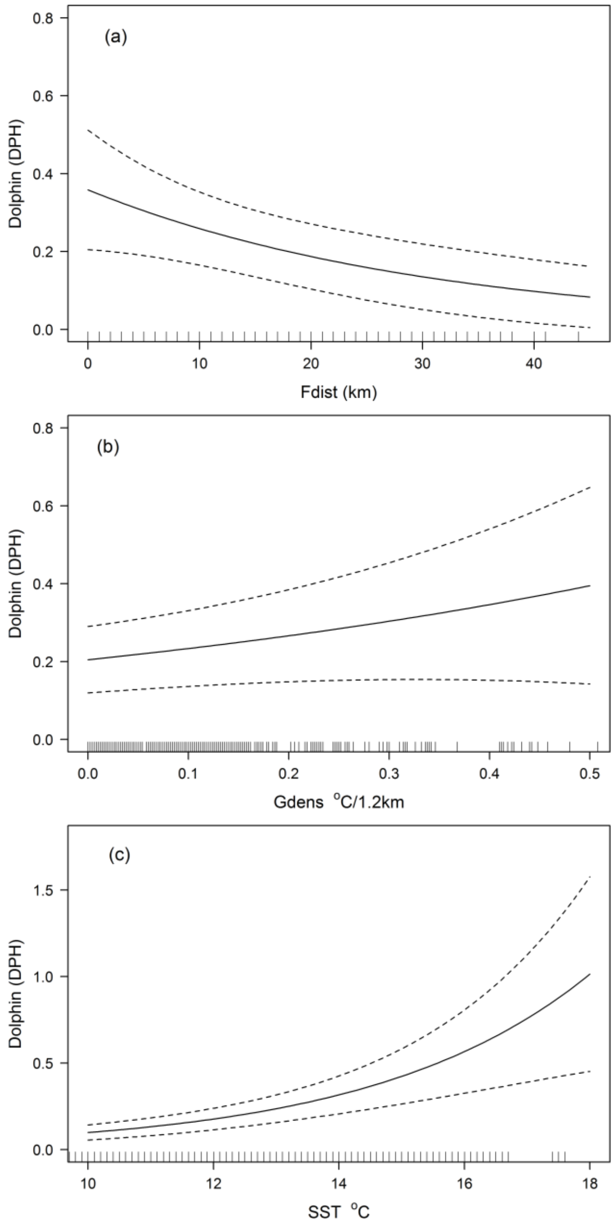

Figure 4.6 Predicated dolphin detection positive hours per day (DPH) from models fitted using data across the entirety of a year. From top to bottom: (a) distance to closest front *Fdist*, (b) front gradient *Gdens* and (c) sea surface temperature *SST*.

4.3.2 Temporal variation in the occurrence of cetaceans during the summer months

Temporal variation in the occurrence of both species was evident across the summer months (Figure 4.4), but was generally not well explained by any of the environmental variables, except, for dolphins where *SST* and *SpringNeapCycle* were both significant and decreased the KCV model selection score (Table 4.3). Dolphin detection rates increased, by almost double, when surface waters were warmer ($p < 0.01$, Table 4.3, Figure 4.8) explaining 5% of deviance. Detection rates also varied significantly with *SpringNeapCycle* ($p < 0.05$, Table 4.3) that explained 1.3% of deviance. Following neap conditions dolphin DPH increased (Figure 4.8).

4.4 Discussion

This study provides new insight toward the temporal use by small cetaceans of a dynamic shelf-sea site subject to thermal stratification and the manifestation of a tidal-mixing front across the summer months. Using a longitudinal dataset of continuous acoustic detections of cetaceans, a clear seasonal pattern in the use of the site was shown that differed between species/groups. Increased harbour porpoise detection rates in the late winter/early spring (January-March) were associated with lower frontal activity. In contrast, dolphin detection rates peaked in the late summer (August-October) and coincided with increased SST and high frontal activity. Together these findings suggest that habitat use by small cetaceans within shelf-seas is both temporally variable and species specific.

Table 4.3 Results from summer models for dolphins (unspecified *Delphinids*) which included observations between the 1st of June and 20th October only. Each term was tested in a standalone model as a single term alongside a random effect of deployment ID with a nested continuous auto-regressive temporal correlation structure. The models intercept (standard errors in brackets), estimated degrees of freedom (E.df), parameter coefficient (standard errors in brackets), deviance explained (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross validation (KCV) statistic on the inclusion of each term in the model is also indicated.

Environmental variable	Intercept	E.df.	Coefficient	Dev. exp.	*p*-value	Δ KCV
SST	-0.90 (0.19)	3.4	NA	4.93%	0.0074	-10
SpringNeapCycle	-0.86 (0.20)	1.69	NA	1.25%	0.018	-2.3

4.4.1 Seasonal fluctuations in habitat use, prey movements and frontal activity

Seasonality in site use by small cetaceans has been identified across a number of regions (Skov & Thomsen 2008, Simon et al. 2010, Sveegaard et al. 2011). For example, in the Baltic Sea populations of harbour porpoise are known to move between key sites (Sveegaard et al. 2011), the use of which varies between the summer and winter months (Sveegaard et al. 2012). My results support such observations and show that at one site, the occurrence and rate of both dolphin and harbour porpoise detections are also seasonally dependent. The high energetic demands of these species requires them to spend a large proportion of their time foraging (Williams et al. 2001, Lockyer et al. 2003), and this has been demonstrated in links between high use habitat and frequent foraging activity (Hastie et al. 2004). As such, temporal changes in their distributional patterns are likely to reflect those of their preferred prey.

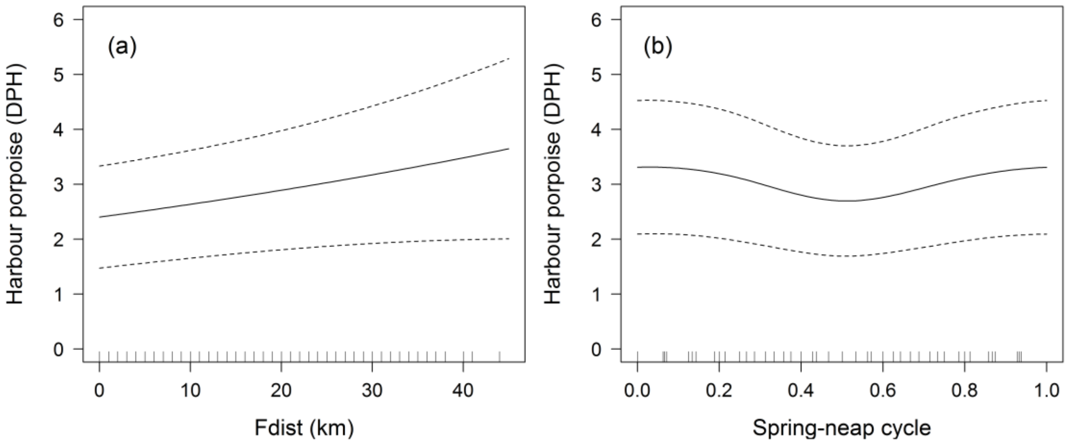

Figure 4.7 Predicted harbour porpoise *Phocoena phocoena* detection positive hours per day (DPH) from models fitted using data across the entirety of a year. From left to right: (a) distance to closest front *Fdist*, and (b) relative position in the spring-neap cycle *SpringNeapCycle*.

Large-scale seasonal migrations between spawning and feeding grounds are common in a number of fish species (Coull et al. 1998). In the Celtic Sea, few known studies exist on the prey distributions and preferences of cetaceans, however, of the species linked to harbour porpoise and dolphin diets elsewhere, the region is known as a spawning ground for cod *Gadus morhua* and whiting *Merlangius merlangus* during spring and sprat *Sprattus sprattus* during late spring/summer (Coull et al. 1998, Santos & Pierce 2003, Murphy et al. 2013). Additionally, the outer region of the continental shelf hosts spawning mackerel *Scomber scombrus* from May to August afterward of which, despite a mass population migration to northern North Sea feeding grounds, there is some limited evidence to suggest a partial movement into the waters around the south west of England in the summer/autumn (Coull et al. 1998, Iversen 2002, Jansen & Gislason 2013).

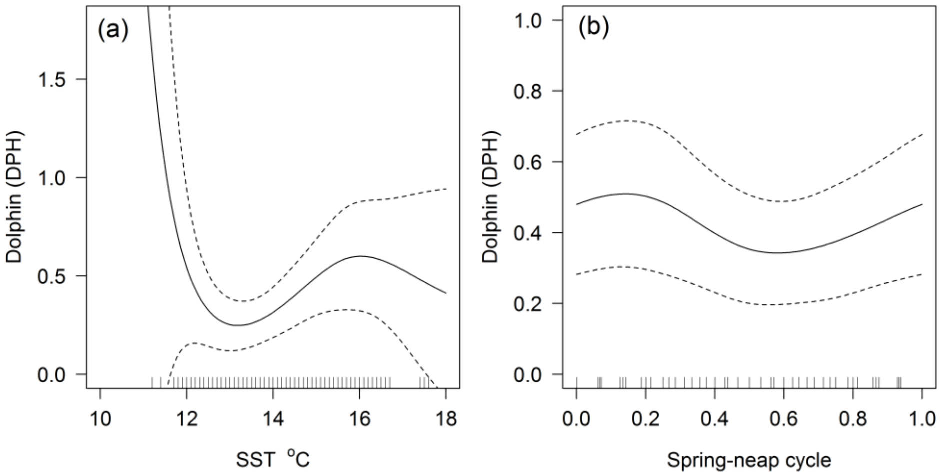

Figure 4.8 Predicated dolphin detection positive hours per day (DPH) in relation to (a) sea surface temperature *SST* and (b) relative position in the spring neap cycle *SpringNeapCycle.* Based on the summer only analysis. Note that although the response of dolphin DPH to SST takes an initial negative trend, the extensive range of the surrounding confidence intervals means this segment of the relationship is not interpreted. The same applies to the upper extent of the relationship above 16°C.

The harbour porpoise is particularly known to feed regularly due to its small size and high energetic requirements, which together reduce its ability to withstand periods of starvation (Kastelein et al. 1997). As such, it is often opportunistic in its foraging strategies and feeds on a wide range of both pelagic and demersal fish (Santos & Pierce 2003, Santos et al. 2004). This flexibility means a wide variety of habitats may be suitable for foraging, and at least low levels of occurrence in the area throughout the year (harbour porpoise detections were recorded on 81% of days) reflect this. However, although porpoises will feed on a wide variety of prey, higher densities are thought to correspond to periods when demersal fish are present suggesting these prey types are preferred (Sveegaard et al. 2012). Peaks in site use during early spring, when cod and whiting are known to spawn in the region, support this and suggest the tidal-mixing front is not a particularly important habitat feature for harbour porpoises in this area despite some limited evidence of linkages to tidal-mixing fronts elsewhere (Weir & O'Brien 2000). This may in part also be due to avoidance of, or competitive exclusion by, other species feeding at fronts (e.g. dolphins and specifically bottlenose dolphins; Spitz et al. 2006, MacLeod et al. 2007). However, it should be noted that harbour porpoise were still present, at least in low levels (averaging 2 to 3 DPH), on days when other species were present whilst bottlenose dolphins (that are known to attack harbour porpoises; Ross & Wilson 1996) are thought to occur only rarely in the region during the times when harbour porpoise detection rates were low (the summer months; Wood 1998).

In contrast, dolphins were found in the region almost exclusively during summer (on 21% of days across the year occurring primarily from June to October) when frontal activity and SST were high, reflective in part of the thermal preferences of the predominant species expected, common dolphins (Lambert et al. 2011). In comparison with harbour porpoises, common dolphins are thought to be more specialist in their diet (Spitz et al. 2010) and when a selection of prey resources are available will selectively target energy rich pelagic fish such as mackerel (Meynier et al. 2008), which are thought to be particularly well suited to front associated habitats that provide a rich source of zooplankton (Sims & Quayle 1998, Russell et al. 1999, Wall et al. 2009) which attracts the smaller forage fish these pelagic species feed on. As such, these mid-trophic level prey may seasonally target specific regions only when these features are present (Kaltenberg et al. 2010) which may provide prosperous feeding opportunities for dolphins. Both observations here and those made in Wales (Goold 1998), where changes from high to low dolphin abundances between September and December were attributed to the presence and break-up of a corresponding front, support this.

4.4.2 Temporal patterns in habitat use by dolphins during only the summer months

A large-scale seasonal change in dolphin habitat use with frontal activity was not reflected in the analysis that included data solely from the summer months. Regional changes in prey densities that coincide with, but are not definitively driven by, frontal activity mean dolphins may not track the exact position of the front in this region. Alternatively, the prey resources that large marine vertebrate predators are thought to exploit around fronts may not occur directly at the surface signatures of these features and instead be associated with transient physical processes that occur within a buffer zone surrounding the front. The front within the survey region is highly dynamic and shifts laterally upwards of 10km over a time period spanning several days (Figure 4.3). This has been shown to coincide with position in the spring-neap tidal cycle, which drives bi-weekly peaks in sub-surface primary productivity that correspond with periods of episodic stratification (Chapter III). These peaks in productivity have been linked to the fine-scale summer distributions of common dolphins in the region (Chapter III), and are generally found in waters with high SST on the stratified side of a front (Franks 1992a), the spatial occurrence of which extends further inshore during neap tides and so more likely encompasses the locations of the CPOD deployments (Figure 4.3). It was found that the occurrence of dolphin detections increased both with increased SST and during neap tides, which possibly reflects evidence suggesting that transient habitats generated around a front, rather than directly at it, are important (Chapter III).

4.4.3 The influence of tidal currents at an offshore shelf-sea site

Both species showed a weak but statistically significant response to position in the spring-neap tidal cycle, with habitat use peaking during neap conditions (although note that more spring than neap associated observations were excluded from analyses due to device shutdown). For harbour porpoises this relationship was present year round, whilst for dolphins linkages were only identified in the summer months. Generally, associations between cetaceans and specific tidal conditions have been reported in regions where currents interact with topographically complex structures creating either (1) a channel of fast moving water that predators use to ambush transported prey (Pierpoint 2008), (2) transient frontal and eddy structures that shift prey distributions (Johnston et al. 2005b, Bailey & Thompson 2010, Jones et al. 2014), or (3) internal waves and/or localised upwellings that may trap prey against the surface (Embling et al. 2012). However, this study region is located in a topographically smooth area within which water depth changes little (< 10m) and tidal flow occurs in parallel with, rather than against the topographic gradient. As such, interactions with tidal currents at this relatively flat offshore site likely differ to those observed around the coast and offshore banks.

Whilst the mechanisms driving these observations are currently unclear, differences in habitat use between neap and spring conditions, when there are peak current speeds of $0.5ms^{-1}$ versus $1.2ms^{-1}$ respectively, could be related to the energetics involved when swimming in faster moving waters, which may be particularly pertinent for harbour porpoises due to their high energetic requirements and small size (Embling et al. 2010). For dolphins, position in the spring-neap cycle was influential on detection rates solely during the summer and so may also relate to a coinciding cycle of stratification and water mixing (detailed above).

4.4.4 Technical limitations

Whilst this study has increased the current understanding of temporal patterns in habitat use by small cetaceans in shelf-seas it is of course, not without limitations. First, the spatial restriction of both the detection range of acoustic devices (~400m to 1km) and the extent of the deployment locations (~40km^2) meant I was unable to determine if the observed patterns in habitat use were unique to the site and linked to the seasonal manifestation of the front, or related to a broader regional trend. I was unable to address this and as such, future work in the region should aim to expand the spatial extent of device coverage (e.g. Pirotta et al. 2014b). Second, it was not possible to resolve dolphin detections beyond species group and whilst common dolphins were the predominant species expected in the region, the presence of other species such as bottlenose dolphins and Risso's dolphins cannot be ruled out. Third, I was also unable to include non-vocalising behaviours in analyses. However, small cetaceans, such as harbour porpoises and dolphins, tend to be highly vocal (Henderson et al. 2012, Pirotta et al. 2014a), and so the impact of this on my findings is likely negligible, especially since analyses were restricted to detection positive hours per day minimising the influence of silent periods (i.e. individuals present should vocalise at some point if not continuously). Fourth, although generally suitable within the context I have used, the spatio-temporal resolution of the remotely-sensed satellite data coupled to its restricted ability to detect conditions below the seas surface, mean relationships between patterns in cetacean site use and specific habitat descriptors, such as sub-surface primary productivity that have been shown important elsewhere (Scott et al. 2010, Embling et al. 2012, Chapter III), may have been missed. Finally, adverse weather conditions in the region (that caused some CPODs to be lost) meant that although measurements across all months were achieved and showed similar trends, continuous monitoring for the duration of an entire year occurred only in 2011.

4.5 Conclusions

This study presents evidence that the use of a dynamic shelf-sea site by small cetaceans is temporally variable over both short (days to weeks) and long (seasonal) timespans.

Patterns in habitat use were shown to be species specific and coincided with particular oceanographic conditions including changes in SST, frontal activity and tidal currents. Combined, these findings demonstrate that understanding the habitat needs of mobile marine predators in shelf-sea environments requires that we understand the dynamic complexities of these systems and the species that inhabit them. This is essential for the effective conservation and management of the marine environment.

CHAPTER V

Seabird diving behaviour reveals the functional significance of shelf-sea fronts as foraging hotspots

ABSTRACT

Oceanic fronts are key habitats for a diverse range of marine predators, yet how they influence fine-scale foraging behaviour is poorly understood. Here, I investigate the diving behaviour of a medium-ranging marine predator, the northern gannet *Morus bassanus*, in relation to shelf-sea fronts. I GPS tracked 53 breeding birds and examined the relationship between 1901 dives (from time-depth recorders) made during foraging trips and fronts in the Celtic Sea (identified via Earth Observation composite front mapping). I (1) used a habitat use-availability analysis to determine if gannets preferentially dived at fronts and (2) compared dive characteristics in the presence and absence of fronts to determine the functional significance of these oceanographic features. Gannets were more likely to dive in the presence than absence of fronts, although relationships varied between sex and with the physical characteristics of frontal activity. Specifically, females were linked to discretely defined, predictable fronts, whereas males were found to dive both at and away from such features. Correlations with transient ephemeral fronts showed contrasting patterns for both sexes. Two dive strategies were identified in females and males; shallow V-shaped dives with little active swim phase (92% of dives), and deeper U-shaped dives with an active pursuit phase of at least three seconds (8% of dives). When foraging around fronts, gannets were half as likely to engage in U-shaped dives as opposed to V-shaped dives. Moreover, the average duration of a V-shaped dive was significantly shortened. I suggest these behavioural responses stem from an increase in the accessibility and catchability of prey around fronts, due to associated changes in densities and depth distributions. Together these results highlight the importance of fronts as marine predator foraging habitat and indicate a mechanistic link between the two. This

research also emphasises the importance of cross-disciplinary research when attempting to understand how marine ecosystems function.

5.1 Introduction

Large marine vertebrate predators, such as marine mammals, seabirds and turtles, forage over long-distances in dynamic environments where prey are patchily distributed (Weimerskirch et al. 1994, Sims et al. 2008). Many of these predators display targeted and individually-consistent movement patterns (Pinaud & Weimerskirch 2005, Weimerskirch 2007, Hamer et al. 2009, Patrick et al. 2014), that are frequently linked to physical oceanographic features, including fronts (Bost et al. 2009, Scales et al. 2014b), eddies (Cotté et al. 2011), tidal flow fields (Bailey & Thompson 2010) and regions of stratification (Scott et al. 2010), where lower trophic-level prey accessibility and availability is thought to be enhanced.

Ocean fronts are particularly important habitats for a taxonomically diverse array of marine predators (see Bost et al. 2009, Scales et al. 2014b). Fronts are physical structures, occurring between adjacent water masses of differing properties that produce strong gradients in density, temperature and/or salinity (Simpson & Hunter 1974). Physical attributes of fronts promote enhanced primary productivity (Franks 1992a, Yoder et al. 1994) and biomass accumulation/redistribution (Genin et al. 2005), often in a predictable manner. This may have cascading effects across the food web to higher trophic levels resulting in the formation of dense, and sometimes shallow, aggregations of prey (Decker & Hunt 1996, Russell et al. 1999, Jahncke et al. 2005) that are highly accessible to large marine vertebrate predators (Vlietstra et al. 2005). However, while these mechanisms are regularly proposed to make fronts attractive as foraging habitat, to date, there is little empirical evidence to support this assertion. This is mostly due to the logistical challenges of simultaneously measuring oceanography, lower- to mid-trophic level prey and large marine vertebrate predators at appropriate spatio-temporal scales.

Interactions between predators and oceanography have been predominantly revealed through the analysis of two-dimensional horizontal animal movement data obtained either directly from shipboard observations (Ainley et al. 2012) or remotely through animal-borne telemetry devices (Wakefield et al. 2009). However, in many predators, an additional evolved capability to dive means that much can be learnt through understanding variation in their vertical movements, particularly in species that employ a number of contrasting dive strategies. Specifically, changes in three-dimensional predator behaviours may be coupled to the fine-scale horizontal and vertical distributions of their prey (Elliott et al. 2008, Boyd et al. 2015, Goldbogen et al. 2015). As such, understanding how marine predators respond to fronts in the vertical dimension may help resolve the functional mechanisms that link the two.

Advances in bio-logging technologies mean we are now able to observe animal movements over fine-scales in three dimensions across entire foraging trips (Bograd et al. 2010). These data can be easily supplemented with near real-time remotely-sensed information on biological and physical oceanography. However, the relevance of traditionally used measurements such as sea surface temperature (SST) and surface chlorophyll-*a* concentration has, at times, proved questionable (Burger 2003, Gremillet et al. 2008). Composite front mapping (Miller 2009, Miller & Christodoulou 2014, Scales et al. 2015) is a relatively new technique that attempts to address this by objectively identifying discrete oceanographic frontal features that are, a priori, thought to represent prosperous foraging habitats. In addition, features are quantified through the output of several front metric products, that can be derived over a number of spatiotemporal scales (Miller 2009, Miller & Christodoulou 2014) allowing the dynamic nature of a front to be characterised (Scales et al. 2014a, Scales et al. 2014b) whilst also overcoming problems of cloud obfuscating signal. This may be particularly useful in highly active and dynamic environments where passing ephemeral activity can weaken links to marine predators (Scales et al. 2014a).

In this study I use the northern gannet *Morus bassanus* to investigate the influence of shelf-sea fronts on the distributions and characteristics of dives. I used high resolution GPS tracking and time-depth recorder (TDR) data, from breeding birds constrained to forage from a large colony in the Celtic Sea (Grassholm, Wales, UK), to link dive events with multiple products derived from composite front maps generated over both weekly and seasonal temporal scales. Specifically I ask: (1) do gannets preferentially target fronts for foraging as indicated by the distribution of dive events, (2) do gannets change foraging strategy, as indicated by the shape of a dive profile, in relation to fronts, and (3) do the depths and durations of dives decrease around fronts?

The gannet is a large, medium ranging piscivorous marine predator (Hamer et al. 2007, 2009). It exhibits a nested search strategy, and dives infrequently, presumably only when prey have been located (Hamer et al. 2009, Ropert-Coudert et al. 2009a). Foraging strategies range from short shallow plunge dives, to longer and deeper wing-propelled active pursuit dives that can reach up to 25m in depth (Garthe et al. 2000, Ropert-Coudert et al. 2009a). Gannets in the Celtic Sea feed on a number of forage and pelagic fish such as mackerel *Scomber scombrus*, garfish *Belone belone*, herring *Clupea harengus* and sprat *Sprattus sprattus*, and a range of demersal fishes, scavenged from fishing boats (Votier et al. 2010, Votier et al. 2013, Patrick et al. 2015). Previous work has shown that in both the Celtic Sea and the Benguela upwelling region off western South Africa, gannets increase foraging effort within regions where fronts frequently manifest (Sabarros et al. 2014, Scales et al. 2014a). By examining their diving behaviour I will attempt to establish why.

5.2 Materials and methods

5.2.1 Device deployment

Fieldwork was conducted on Grassholm Island, Wales, UK (51^o 43’N, 5^o 28’W; Figure 5.1.c & e) during the breeding seasons of July 2012 and 2013. Chick rearing gannets were caught on the nest during changeover (to ensure chicks were not left unattended and so deployments began immediately with a foraging trip), using a brass crook attached to the end of a ~5m carbon fibre pole. Birds were selected opportunistically, away from the edge of the colony (under license from the Countryside Council of Wales and the British Trust for Ornithology). Upon capture, birds were weighed and 1-2ml of blood taken via the tarsal vein, which was later used for molecular sexing (AvianBiotech.com). Birds were then equipped, using Tesa© tape, with: (1) a 30g GPS logger (i-gotU GT-120, Mobile Active Technology Inc) attached to either the dorsal surface of the central pair of tail feathers (2012) or the central back feathers (2013), and (2) a 5.7g or 10.5g TDR (CEFAS G5 or LOTEK LAT 1810 respectively) attached to the ventral surface of the central pair of tail feathers. Total handling time was around 12 minutes. The maximum combined weight of deployed loggers (40.5g) was 1.37% the average bird body weight (2948.8g ± 33.0g). Deployment durations ranged from one to seven days.

5.2.2 Particulars of device data acquisition

The GPS recorder logged location at one minute intervals throughout foraging trips with an accuracy of +/- 4.4m (Vazquez-Prokopec et al. 2009). The G5 TDR logged pressure every 0.1 seconds (10Hz) during dives, defined as wet periods (detected via a wet/dry sensor) below a depth of 1.5m. Pressure resolution was 4cm of water column with an accuracy of +/- 1m. The LOTEK LAT1810 TDR logged pressure continuously at one second intervals (1Hz). Pressure resolution was 2.5cm of water column with an accuracy of +/- 1m.

5.2.3 Animal behaviour metrics

5.2.3.1 GPS tracks

GPS fixes at night (between the end of civil dusk to the beginning of civil dawn) were stripped from the dataset to eliminate periods when birds roost on the water (Garthe et al. 1999, Ropert-Coudert et al. 2004a). In addition, all activity within 2km of the breeding colony was removed to account for non-foraging associated behaviours such as bathing and rafting (Carter et al. *accepted*). Tracks were then split into individual foraging trips, divided by periods of greater than five minutes within 2km of the colony. This was a good indicator of whether a gannet had returned to its nest, or had just flown within close proximity to the colony during a trip. All trips were plotted and manually screened to identify non-foraging trips (i.e. instances where rafting behaviour had drifted or occurred outside the 2km buffer zone), which were excluded from further analyses. Some incomplete trips were identified where deployments had exceeded the battery life of the GPS logger and, unless otherwise stated, were included in analyses.

5.2.3.2 Dive events

A bespoke algorithm, written in MATLAB, was used to identify dive events by birds equipped with a LOTEK TDR. To be consistent with the technicalities of the CEFAS logger, dives were defined as periods where the registered depth was at least 1.5m. This also accounted for shallow sub-surface activity associated with non-foraging behaviours such as sitting on the water and bathing (Garthe et al. 2000, Lewis et al. 2002).

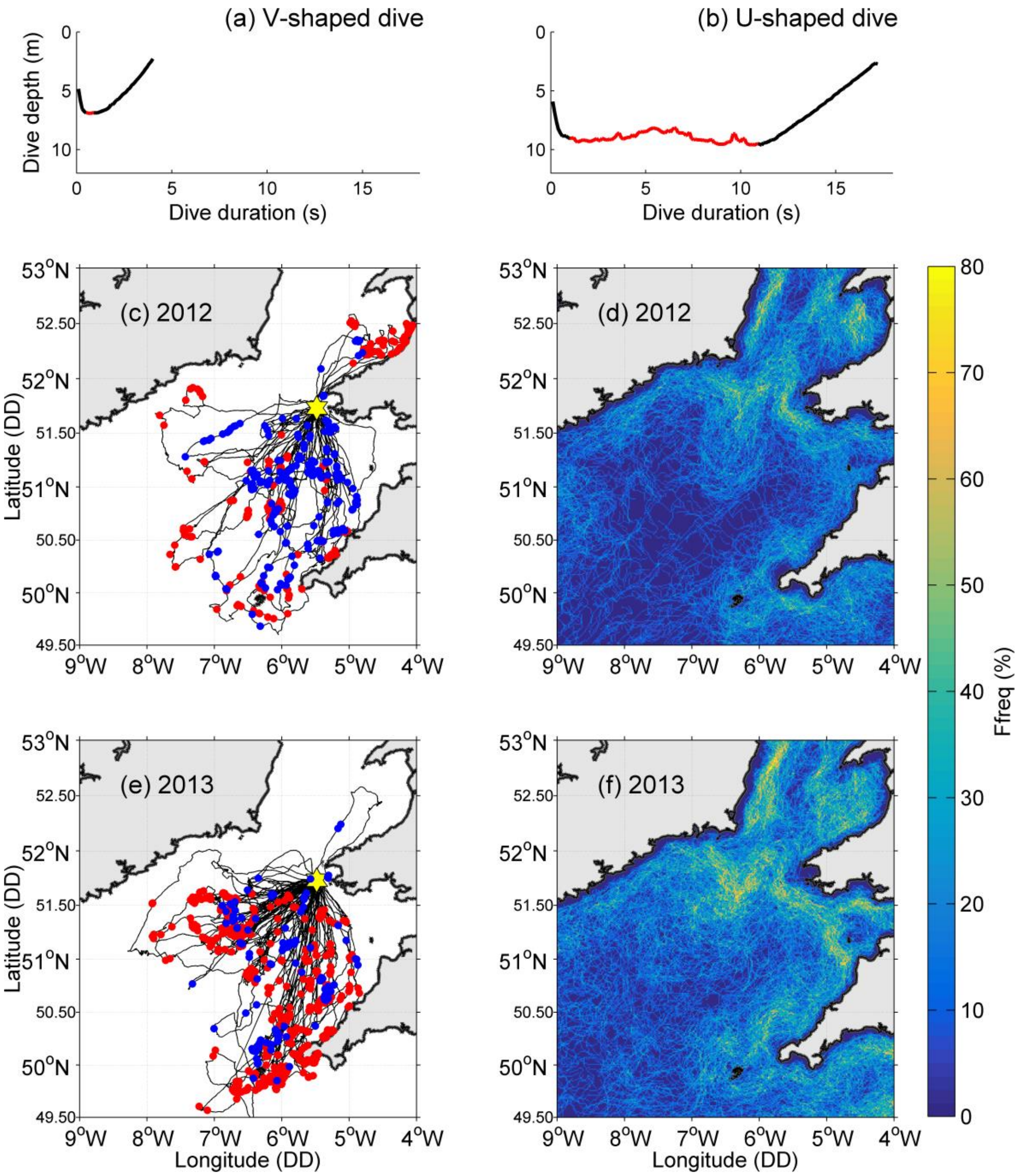

Figure 5.1 Rows show, from top to bottom: (a) typical V- and (b) U- shaped dive profiles with defined active swim phases highlighted in red, (c) 2012 GPS tracks and associated dives, (d) 2012 front frequency *Ffreq* map, (e) 2013 GPS tracks and associated dives and (f) 2013 front frequency *Ffreq* map. Blue and red dive markers (in subplots c & e) represent male and female dives respectively. The location of Grassholm is marked by the yellow star in subplots c & e.

To allocate each dive a location in space, GPS tracks were first interpolated to a resolution of one second (in time) using a cubic spline interpolation. The timestamp at the beginning of a dive event was then used to assign a corresponding location from the high-resolution interpolation. Allocations that were mismatched by more than a second (because the battery life of the GPS logger had been exceeded or a dive was within the 2km exclusion zone around the colony) were excluded from analyses. A small number of shallow dives (five in total) occurred around 40 minutes after the end of civil dusk. These were considered atypical and excluded from analyses (Garthe et al. 1999, Ropert-Coudert et al. 2004a).

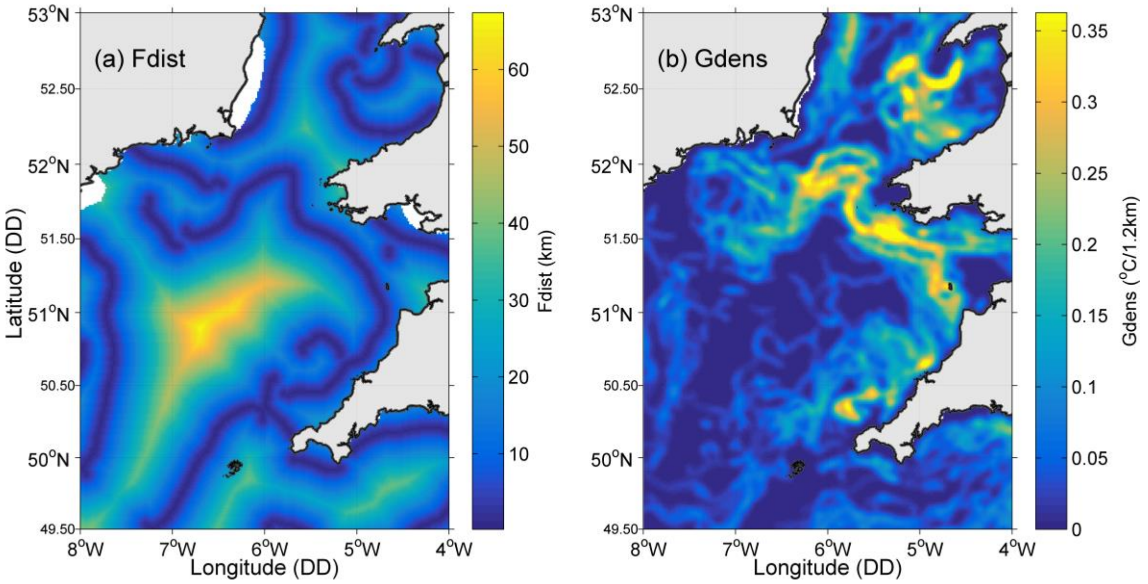

Figure 5.2 Front metrics derived for the Celtic Sea over seven day composites are shown for the 21st of July 2013. From left to right (a) *Fdist* (distance to closet front) and (b) *Gdens* (cross-front gradient strength).

5.2.3.3 Dive characteristics

For each dive I generated three variables: (1) maximum dive depth (metres), (2) total dive duration (seconds), and (3) dive shape (Figure 5.1.a & b). Dive shapes were classified as either V-shaped, with little or no active swim phase, or U-shaped, with an active swim phase of at least three or four seconds (dependent upon the sampling rate of the logger; one second and 10Hz respectively; Garthe et al. 2000). The start and end of the active swim phase was defined using gradients in the vertical change in depth (Appendix A2.1, Figure A2.1; Ropert-Coudert et al. 2009a, Cleasby et al. 2015).

5.2.4 Front metrics

Fronts vary in their strength, persistence and predictability (Scales et al. 2014b). To be able to determine the relative importance of these characteristics on foraging behaviour, thermal front activity across the Celtic Sea was summarised into three metrics: (1) front gradient intensity *Gdens*, (2) distance to closest front *Fdist*, and (3) seasonal front frequency *Ffreq*. These were produced over two temporal scales: (1) seven day composites (Miller 2009) and (2) seasonal composites (Miller & Christodoulou 2014), details of which are provided below. As the occurrences of thermal and chlorophyll fronts are typically linked across shelf-seas (e.g. at tidal-mixing fronts; Belkin et al. 2009, Miller et al. 2015) I did not include extra analyses using chlorophyll-*a* derived front metrics in this study.

5.2.4.1 Seven day composites

Gdens and *Fdist* (Figure 5.2) are based on seven day composites centred to the date of a GPS/TDR fix. First, 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 across the Celtic Sea with a spatial resolution of approximately 1.2km/pixel. Thermal fronts were detected over frames of 32 by 32 pixels using single image edge detection (SIED; Cayula & Cornillon 1992) with a temperature difference threshold of 0.4°C across the front (Miller 2009) comparable to Scales et al. (2014a).

Gdens was then taken as the spatially smoothed average temperature gradient across all frontal pixels detected over a seven day composite to give a continuous distribution of frontal intensity. A Gaussian filter with a width of five pixels was used for the spatial smoothing (Scales et al. 2014a, Miller et al. 2015). This metric indicates the intensity of contemporaneous frontal structures (cross-front gradient strength) that may be either transient or persistent in occurrence.

Fdist was taken as the distance from any point to the closest simplified front. Simplified fronts were defined using a clustering algorithm to identify continuous contours through the strongest frontal pixels on the spatially smoothed *Gdens* front map (Scales et al. 2014a). This metric quantifies the distance from each dive/pseudo-absence location to the continuous and discrete surface signature of a frontal system and generally excludes the small ephemeral features that are often picked up by the *Gdens* metric.

5.2.4.2 Seasonal composites

Ffreq is based on all composite front maps between June to August inclusive for each year (2012 and 2013) separately (Figure 5.1.d & f). Maps generated before spatial smoothing were used and *Ffreq* was taken as the percentage of total detections in which a frontal temperature gradient ≥0.04$^{\text{o}}$C was observed (see '*Average front gradient'* in

Miller 2009). This threshold reduced noise in front detections associated with minor discrepancies in temperature observations (Miller & Christodoulou 2014). This metric indicates areas where fronts frequently manifest across a season and so are highly predictable in occurrence.

Table 5.1 Overview of the three modelling approaches applied to determine the influence of frontal activity on (a) habitat use and the probability of a dive event, (b) dive shape (U versus V), and (c) depth and duration of U- and V- shaped dives. Terms between the curly brackets are interchangeable to represent where models were fitted separately to avoid issues associated with multi-collinearity. The initial fixed component with all potential explanatory variables (before model reduction/selection) is shown. The random component comprises a random intercept of *BirdID* and either (1) a nested spatial correlation structure *CorStructSp* (a) or (2) a nested continuous temporal correlation structure *CorStructTp* (b & c).

(a) Generalised linear mixed effects model (GLMM) with binomial error structure and complementary log-log (cloglog) link

$$Dive\ event\ (0/1) \sim \overbrace{\left\{\begin{matrix} Gdens \\ Fdist \\ Ffreq \end{matrix}\right\} \times Sex}^{Fixed\ component} + \overbrace{(1|BirdID) + (CorStructSp|BirdID)}^{Random\ component}$$

(b) GLMM with binomial error structure and complementary log-log (cloglog) link

$$Dive\ shape\ (0/1) \sim \overbrace{\left\{\begin{matrix} Gdens \\ Fdist \\ Ffreq \end{matrix}\right\} \times Sex + DecTime + DecTime^2}^{Fixed\ component} + \overbrace{(1|BirdID) + (CorStructTp\ |BirdID)}^{Random\ component}$$

(c) Linear mixed effects model (LMM)

$$\left\{\begin{matrix} U\ dive\ depth\ (m) \\ V\ dive\ depth\ (m) \\ U\ dive\ duration\ (s) \\ V\ dive\ duration\ (s) \end{matrix}\right\} \sim \overbrace{\left\{\begin{matrix} Gdens \\ Fdist \\ Ffreq \end{matrix}\right\} \times Sex + DecTime + DecTime^2}^{Fixed\ component} + \overbrace{(1|BirdID) + (CorStructTp\ |BirdID)}^{Random\ component}$$

5.2.5 Statistical analysis

Three modelling approaches were used to investigate the influence of frontal activity, as represented by the three front metrics (*Gdens*, *Fdist* and *Ffreq*), on gannet dive behaviour (Table 5.1). First, habitat use versus availability was modelled against frontal activity using generalised linear mixed effects models (GLMMs) from the MASS package in R (Ripley et al. 2014) with a binomial error structure and complementary log-log (clog-log) link (Zuur et al. 2009, Hamel et al. 2012). For each dive event, the locations of five pseudo-absences were randomly selected within the bounds of the 95% utilisation distribution of the population sample (see Appendix A2.2, Figure A2.2; Aarts et al. 2008). Second, dive shape was modelled against frontal activity using GLMMs, again, from the MASS package in R (Ripley et al. 2014) with a binomial error structure and complementary log-log (clog-log) link. Finally, the influence of frontal activity on dive depth and duration were modelled separately for U- and V- shaped dives using linear mixed effects models (LMMs) from the R package nlme (Pinheiro & Bates 2014).

Across the three modelling approaches, the *Gdens*, *Fdist* and *Ffreq* front metrics were tested separately to avoid issues pertaining from multi-collinearity. Sex was included as a fixed factor and in a two-way interaction with each front metric to allow for sexual segregation in foraging behaviour (Lewis et al. 2002, Stauss et al. 2012, Cleasby et al. 2015). Time of day (*DecTime*) was included in the dive shape, depth and duration models as a continuous quadratic function to account for potential changes in the profile of a dive in the middle of the day, possibly due to the diel migration of prey above and below the thermocline (Garthe et al. 2000, Garthe et al. 2007b). In all models, a random intercept of bird (*BirdID*) was included to avoid pseudo-replication and account for any individual differences in dive behaviour (Patrick et al. 2014). Where appropriate, a nested autocorrelation structure was also incorporated to allow for similarities between dives that occurred in temporal clusters. In the habitat use-availability analysis, this was fitted as a spatial correlation structure using the coordinates of each dive or pseudo-absence location on a UTM (Universal Transverse Mercator) projection, whilst for the dive shape, depth and duration analyses a continuous time correlation structure was used (Table 5.1).

As GLMMs from the MASS package are estimated using penalised quasi-likelihood, maximum likelihood (ML) selection techniques (e.g. Akaike's Information Criteria; AIC) were not available and so the best temporal correlation structure (e.g. exponential, rational quadratic, autoregressive) for the random component (Table 5.1) of the model was selected through inspection of residual plots. Model reduction of the fixed component (Table 5.1) was performed by removing variables with small parameter estimates, relative large standard errors, confidence intervals that passed through zero and large *p*-values ($p > 0.05$; Bolker et al. 2008, Murtaugh 2014, Stanton-Geddes et al. 2014).

For each LMM, the most appropriate random structure (Table 5.1) was determined via restricted maximum likelihood (REML) estimation (Zuur et al. 2009) and selected by comparison of AIC values and residual plots. Model selection of the fixed effects (Table 5.1) was conducted by backwards and forwards selection via ML estimation and the use of AIC and likelihood ratio tests. The most parsimonious model was then re-fitted using REML to obtain parameter estimates and *p*-values (Zuur et al. 2009).

Models were evaluated by plotting Pearson (GLMM) or normalised (LMM) residuals against all potential explanatory variables, bird ID, distance to colony, latitude, longitude, tag type, time and year to check for any patterns indicative of a violation of model assumptions. Fitted versus predicted values were inspected to check for satisfactory model fit and for the binomial GLMMs the area under the receiving operator characteristic (ROC) curve (AUC; Zweig & Campbell 1993, Liu et al. 2005) was calculated. Pseudo R^2 values were generated as an indication of variance explained as described by Nakagawa & Schielzeth (2013) using the MuMIn package in R (Barton 2014). All analyses were performed in R version 3.0.2 (R Development Core Team 2013) and MATLAB (R2011b).

5.3 Results

5.3.1 Gannet tracking data

All 53 birds equipped with GPS and TDR loggers yielded useable data: 11 males and 11 females in 2012 and 17 females and 14 males in 2013. This produced a total of 74 complete and 12 incomplete foraging trips. The number of complete foraging trips recorded per bird ranged from one to four, with an average of 1.4 ±0.08 (± standard error).

Gannet foraging tracks are shown in Figure 5.1.c & e. Maximum displacement (the furthest distance recorded from the colony during a trip) averaged 138.5 ±8.0km, ranging from 34.6km to 276.7km whilst trip track lengths ranged from 72.0km to 822.9km with an average of 424.0 ±25.8km. Foraging trip durations ranged from 2.7 to 50.6hrs with a mean of 23.2 ±1.5hrs.

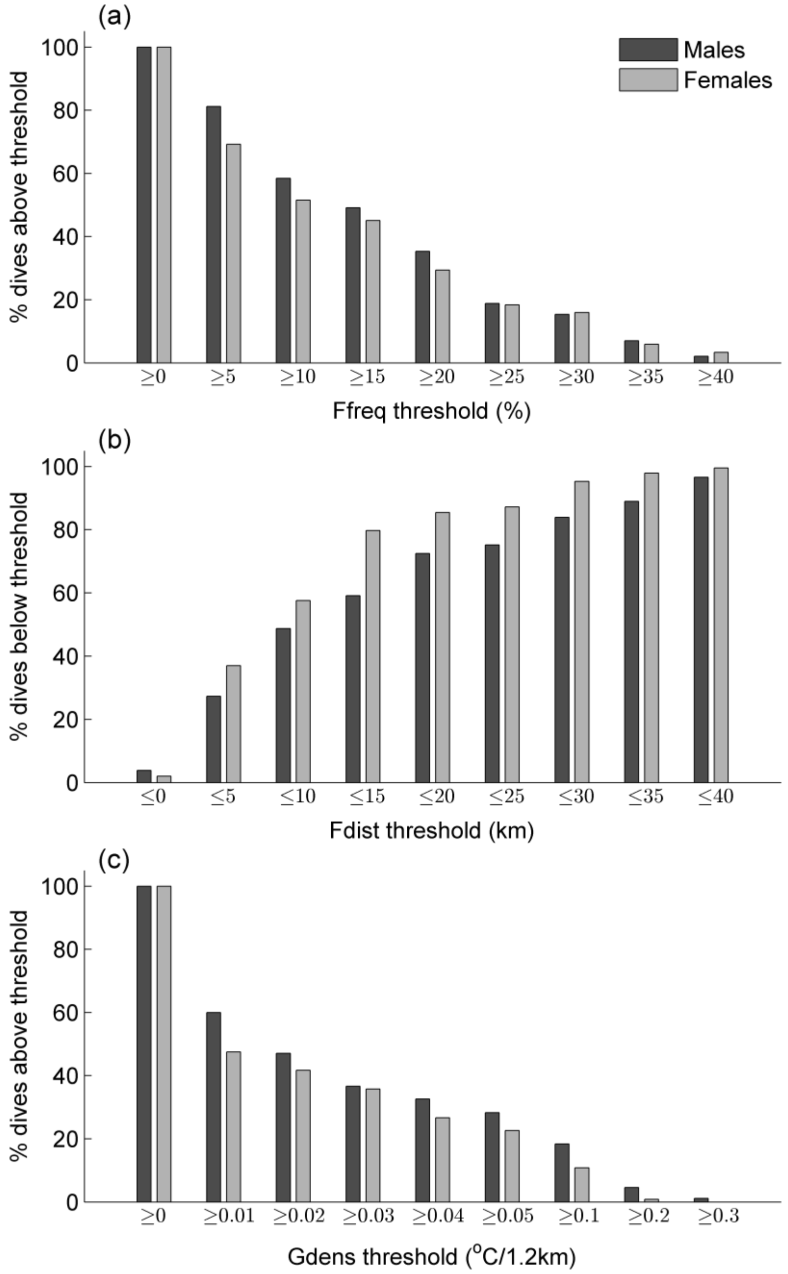

Figure 5.3 Percentage of total dives for males and females occurring within and around frontal regions as defined by varying thresholds of the three front metrics. From top to bottom: (a) the number of dives occurring at and above a range of *Ffreq* (seasonal front frequency) values, (b) the number of dives occurring at and below a range of *Fdist* (distance to closest front) values, and (c) the number of dives occurring at and above a range of *Gdens* (cross-front gradient strength) values.

5.3.2. Overview of gannet diving behaviour

The total number of dives made across all foraging trips was 1901 (Figure 5.1.c & e). Of these, 712 and 1189 were made by males and females respectively. The number of dives made per complete foraging trip averaged 22.2 ±3.8, although 17.6% of these trips had no dives. All incomplete foraging trips included dive events. Six birds did not dive at all during deployments.

Table 5.2 Parameter estimates, standard errors, lower (2.5%) and upper (97.5%) 95% confidence limits (CI) and *p*-values for the generalised linear mixed effects model fitted with a random intercept of *BirdID*, nested spatial correlation structure and binomial complementary log-log (cloglog) link for the habitat use models. Base level of the two-state factor for *Sex* is male. Models fitted, from top to bottom for: (a) *Gdens*, (b) *Fdist* and (c) *Ffreq*. The calculated area under the receiver operating characteristic (ROC) curve (AUC) is indicated. Pseudo-R^2 estimates are quoted as an indication of the variance explained by the fixed component of the model.

(a) *Gdens*: AUC = 0.53

Fixed effect	**Estimate**	**Std. error**	**Lower CI**	**Upper CI**	***p*-value**	**Pseudo R^2**
Intercept	-2.675	0.137	-2.944	-2.407	< 0.001	-
Sex (Female)	-0.133	0.178	-0.492	0.226	0.460	-
Gdens	2.402	1.273	-0.093	4.897	0.059	-
Sex (Female) Gdens*	-5.593	1.819	-9.159	-2.028	0.002	5.0%

(b) *Fdist*: AUC = 0.56

Fixed effect	**Estimate**	**Std. error**	**Lower CI**	**Upper CI**	***p*-value**	**Pseudo R^2**
Intercept	-2.745	0.171	-3.080	-2.411	< 0.001	-
Sex (F)	0.014	0.223	-0.436	0.464	0.949	-
Fdist	0.012	0.007	-0.001	0.026	0.077	-
*Sex (Female)*Fdist*	-0.027	0.011	-0.048	-0.006	0.013	3.37%

(b) *Ffreq*: AUC = 0.55

Fixed effect	**Estimate**	**Std. error**	**Lower CI**	**Upper CI**	***p*-value**	**Pseudo R^2**
Intercept	-2.745	0.167	-3.070	-2.417	< 0.001	-
Sex (F)	-0.620	0.203	-1.029	-0.212	0.004	-
Ffreq	0.006	0.006	-0.007	0.018	0.366	-
*Sex (Female)*Ffreq*	0.027	0.008	0.012	0.042	< 0.001	11.5%

Dives tended to occur in short bursts rather than being spread out equally over the foraging trip. 25.1%, 39.9% and 58.2% of all dives were followed by another dive within five, 10 and 20 minutes respectively and only 22.9% of dives were spaced more than one hour from the previous dive. Across complete foraging trips, the number of dives made per hour ranged from zero to 5.5 with an average of 0.9 ±0.13. The percentage of time spent underwater during a complete foraging trip was low and ranged from zero to 0.7% with an average of 0.1 ±0.02%.

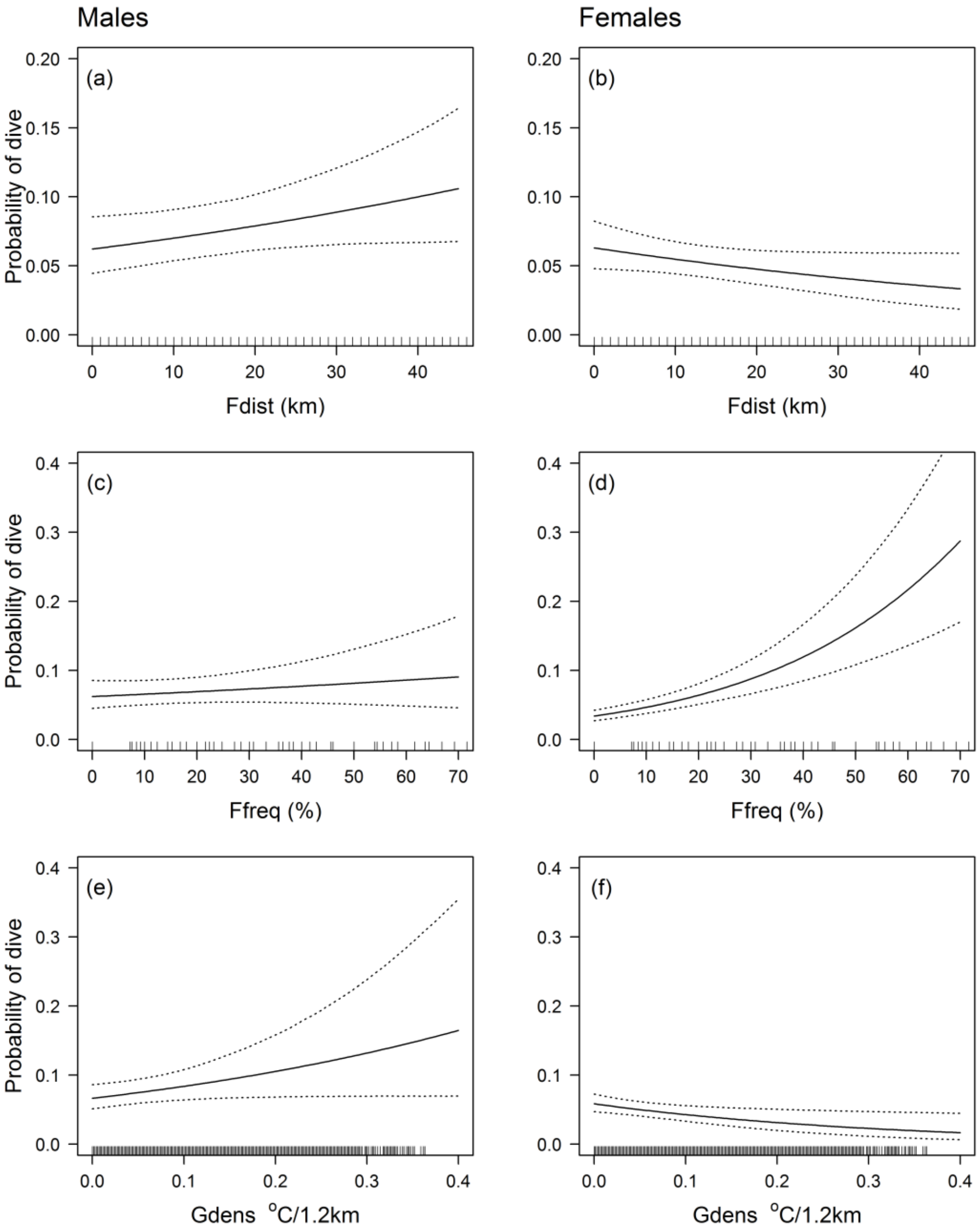

Figure 5.4 Habitat use as indicated by the probability of a dive event occurring within a specific habitat type relative to that available. From top to bottom: (a & b) *Fdist*, (c & d) *Ffreq* and (e & f) *Gdens*. The first column shows habitat preferences for males (a, c & e) and the second column for females (b, d & f). Filled lines show expected dive probabilities for an 'average' bird. Dotted lines show bootstrapped 95% confidence intervals. Note the change in y-axis extent between the top row and bottom two rows.

5.3.3 Dive behaviour at fronts

5.3.3.1 Dive events

Gannets dived in a wide range of oceanographic conditions including areas of high frontal activity (Figure 5.3). When compared to the available habitat types, dive distributions were significantly related to all three of the front metrics (*Fdist*, *Ffreq* and

Gdens), although relationships varied by sex (Figure 5.4, Table 5.2). Male dive probabilities were positively correlated with distance to front (*Fdist*), cross-front gradient strength (*Gdens*) and (weakly) with seasonal front frequency (*Ffreq*). Female dive probabilities were negatively correlated with distance to a front (*Fdist*) and cross-front gradient strength (*Gdens*) and positively correlated with seasonal front frequency (*Ffreq*).

5.3.3.2 Dive shape

V-shaped dives were more common than U-shaped dives (92.1% of dives were V-shaped; Figure 5.5). All birds performed V-shaped dives and 69.6% performed U-shaped dives. Dive shape varied significantly with frontal activity (Figure 5.6, Table 5.3). When diving in areas of high front frequency (*Ffreq*), the probability that a bird performed a U-shaped dive compared to a V-shaped dive halved. Dive shape did not change in response to any of the other front metrics (*Gdens* and *Fdist*), *DecTime* or sex. There was no interaction between sex and frontal activity.

Table 5.3 Parameter estimates, standard errors, lower (2.5%) and upper (97.5%) 95% confidence limits (CI) and *p*-values for the generalised linear mixed effects model fitted with a random intercept of *BirdID*, nested temporal correlation structure and binomial complementary log-log (cloglog) link for dive shape. The area under the receiver operating characteristic (ROC) curve (AUC) was calculated as 0.8. Pseudo-R^2 estimates are quoted as an indication of the variance explained by the fixed component of the model.

Fixed effect	**Estimate**	**Std. error**	**Lower CI**	**Upper CI**	***p*-value**	**Pseudo R^2**
Intercept	-1.981	0.180	-2.334	-1.627	< 0.001	-
Ffreq	-0.016	0.006	-0.028	-0.004	0.011	3.3%

5.3.3.3 Dive depth

Overall dive depths ranged from 1.6m to 14.9m and were greater when birds performed U-shaped as opposed to V-shaped dives (Figure 5.5.a:d). V- and U- shaped dive depths were not significantly related to any of the front metrics. Females consistently dived deeper than males when performing V-shaped dives (4.6 ±0.4m vs 3.4 ±0.3m; p = 0.003). U-shaped dive depths averaged 6.3 ±0.3m and did not differ between sexes. *DecTime* had no influence on dive depth for either strategy and there was no interaction between sex and frontal activity.

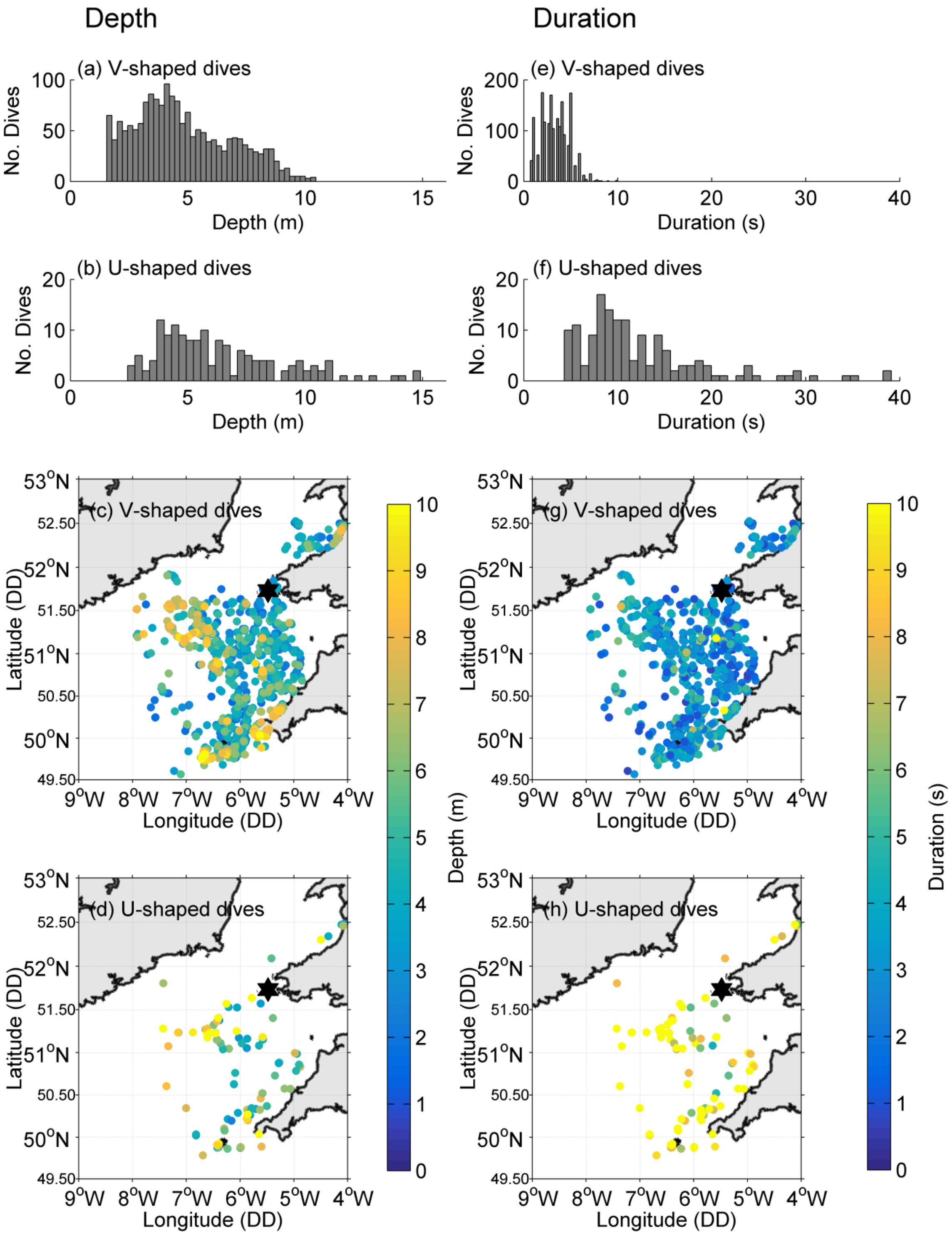

Figure 5.5 Distributions of gannet dive depths and durations during 2012 and 2013 combined. The left column, from top to bottom shows: frequency distribution of (a) V-shaped dive depths and (b) U-shaped dive depths, (c) the distribution of V-shaped dive depths across the Celtic Sea, and (d) the distribution of U-shaped dive depths across the Celtic Sea. The right column, from top to bottom shows: Frequency distribution of (e) V-shaped dive durations and (f) U-shaped dive durations, (g) the distribution of V-shaped dive durations across the Celtic Sea, and (h) the distribution of U-shaped dive durations across the Celtic Sea. The location of Grassholm Island is marked by the black star in subplots c, d, g & h.

5.3.3.4 Dive duration

Overall, dive durations ranged from 0.7 to 39.1s and were greater when birds engaged in a U-shaped strategy compared to a V-shaped strategy (Figure 5.5.e:h). V-shaped dives were significantly shorter in proximity to fronts (*Fdist*; Table 5.4, Figure 5.7). This response was more prominent in males (Table 5.4, Figure 5.7.a) which had significantly shorter dives than females (Table 5.4, Figure 5.7.b). Dive duration was not significantly related to any of the other front metrics. Dives were longer in the middle of the day (*DecTime*, Table 5.4; Appendix A2.3, Figure A2.3). U-shaped dive duration averaged 12.9 ±0.8s and did not vary with any of the front metrics, *DecTime*, or sex. There was no interaction between sex and frontal activity.

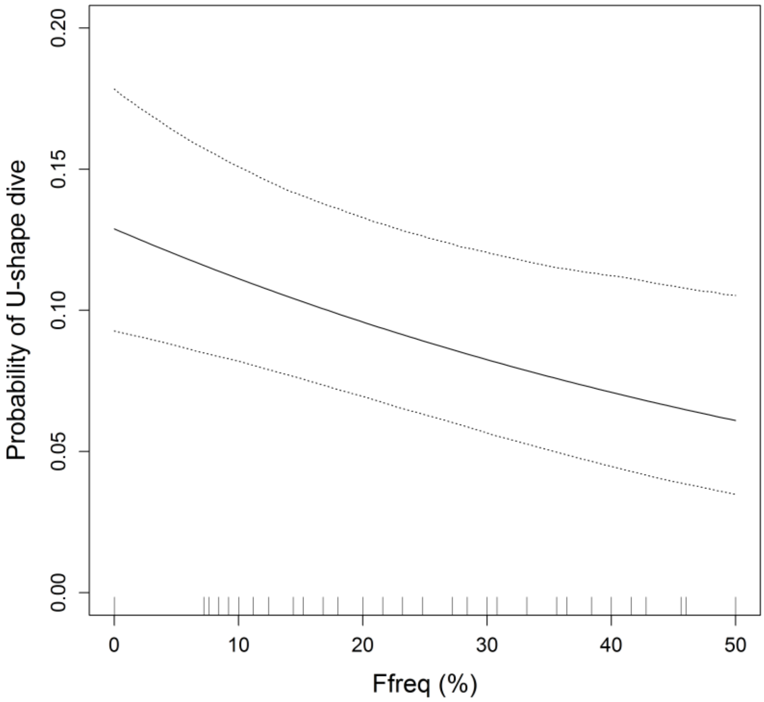

Figure 5.6 Probability of a U-shaped dive decreases in regions of enhanced frontal activity (*Ffreq*). Filled line shows expected dive shape probabilities for an 'average' bird. Dotted lines show bootstrapped 95% confidence intervals.

5.4 Discussion

This study provides a novel insight toward the influence of physical oceanography on the habitat use and dive behaviour of a medium-ranging piscivorous predator. I build upon prior observations that gannets intensify restricted search behaviours within regions where fronts frequently manifest across a season (Scales et al. 2014a) to show that these habitats are also favoured for diving. In addition, I also show that when diving around fronts, gannets are half as likely to engage in U-shaped as opposed to V-shaped dives and the average duration of a V-shaped dive is significantly shortened. Combined, these findings are of particular significance because, as well as confirming the importance of shelf-sea fronts as foraging habitat, they provide a functional mechanism underpinning the links between these physical features and large marine vertebrate predators. My suggestion is that around fronts, predators can minimise their foraging effort (in the case of gannets by exploiting shorter, V-shaped dives) while maintaining sufficient catches.

Table 5.4 Parameter estimates, standard errors, lower (2.5%) and upper (97.5%) 95% confidence limits (CI) and *p*-values for the linear mixed effects model fitted with a random intercept of *BirdID* for dive duration. Base level of the two-state factor for *Sex* is male. Pseudo-R^2 estimates are quoted as an indication of the variance explained by each explanatory variable within the fixed component of the model. These were generated as the difference in pseudo R^2 values of models with and without a specific term.

Fixed effect	**Estimate**	**Std. error**	**Lower CI**	**Upper CI**	***p*-value**	**Pseudo R^2**
Intercept	1.468	0.348	0.785	2.152	< 0.001	-
Sex (Female)	0.686	0.236	0.210	1.161	0.006	-
Fdist	0.027	0.007	0.014	0.040	< 0.001	-
DecTime	3.754	1.317	1.171	6.337	0.004	-
DecTime^2	-2.965	1.232	-5.381	-0.549	0.016	1.2%
*Sex (Female)*Fdist*	-0.021	0.009	-0.038	-0.003	0.020	2.8%

5.4.1 Dive distributions and fronts

Predictability and persistence are known to be important components of the habitats favoured by foraging marine predators (Gende & Sigler 2006, Davoren 2013). A use-availability analysis showed both females and, to a lesser extent, males preferentially dived in regions where fronts either predictably manifested across a season (*Ffreq*) or were discrete and clustered in occurrence (*Fdist*). Across shelf-seas, these physical features typically form as tidal-mixing fronts at the interface between seasonally stratifying offshore waters and permanently mixing inshore coastal waters, and the near coastal distributions of frequent frontal zones and, to a lesser extent, discrete and clustered frontal structures reflects this (Figures 5.1.d & f and 5.2.a respectively). Once established, tidal-mixing fronts are generally constant in their spatial positions with localised adjustments that typically do not exceed 20km. As such, associated prey resources are likely persistent and predictable in occurrence over at least coarse spatio-temporal scales, allowing marine predators to learn and remember their locations (Weimerskirch 2007, Pettex et al. 2010, Regular et al. 2013). Work in this study adds to a growing body of evidence documenting these seasonally occurring shelf-sea fronts as important foraging resources for a wide diversity of marine predators (Durazo et al. 1998, Jahncke et al. 2005, Doniol-Valcroze et al. 2007, Kokubun et al. 2008).

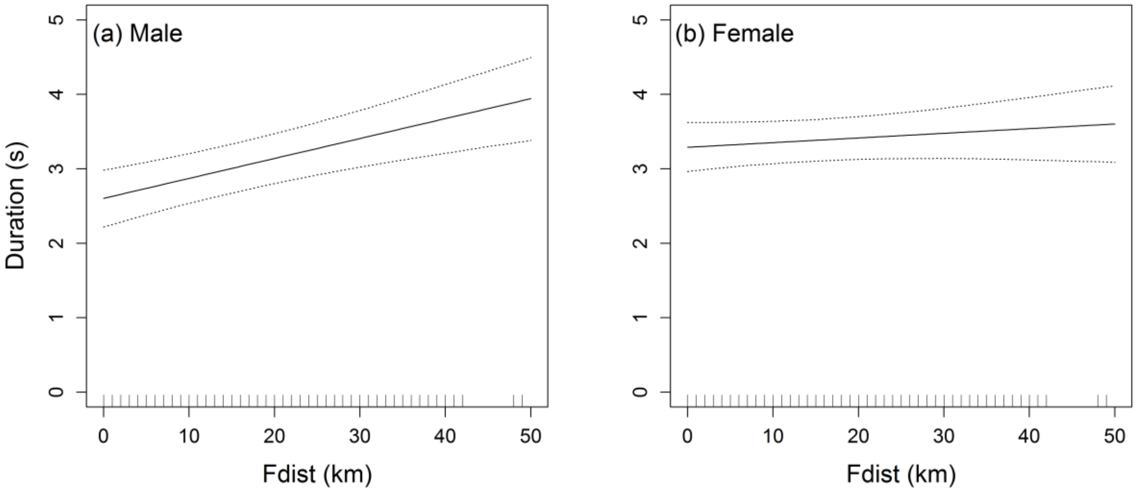

Figure 5.7 Predicted durations of V-shaped dives at varying proximity to fronts (*Fdist*). From left to right; (a) V-shaped dive duration of males increases with distance to nearest front, and (b) V-shaped dive duration of females increases with distance to nearest front, but not as markedly as observed in males. Filled lines show expected dive durations for an 'average' bird. Dotted lines show bootstrapped 95% confidence intervals.

5.4.2 Three-dimensional sub-surface characteristics of dives around fronts

The principal purpose of this study was to investigate the three-dimensional characteristics of dives performed by gannets in relation to shelf-sea fronts so as to be able to establish the functional mechanisms that link these features to marine predators. In addition to providing a persistent and predictable foraging resource, fronts are also thought to increase the accessibility and catchability of prey (Russell et al. 1999, Vlietstra et al. 2005). Gannet foraging strategies are known to be especially energetically expensive (Furness & Tasker 2000, Ropert-Coudert et al. 2004b, Green et al. 2009). As such, maximising efficiency is of high priority (Amelineau et al. 2014) and to achieve this, individuals are known to alter their behaviours in response to the behaviours and depth distributions of their prey (Garthe et al. 2007a, Garthe et al. 2011, Machovsky-Capuska et al. 2011, Machovsky-Capuska et al. 2013). I suggest that a decrease in both the use of U-shaped dive strategies and the duration of V-shaped dives around fronts reflects the improved accessibility and catchability of prey.

For example, around fronts, strong biophysical coupling is thought to attract large numbers of the energy rich pelagic fish (e.g. garfish, herring and mackerel) that gannets from this colony prey on (Votier et al. 2010 and unpublished data). Resultant aggregations may occur in high densities (Vlietstra et al. 2005) that aid in prey capture by increasing encounter probabilities (Enstipp et al. 2007). This is reflected both by a decrease in dive duration around fronts and a decrease in the frequency of U-shaped dives, that often appeared to represent the continued active pursuit of prey at a constant depth after, presumably, a failed initial capture attempt (Appendix A2.1, Figure A2.1; Ropert-Coudert et al. 2004a, Ropert-Coudert et al. 2009a). Moreover, at features such as shelf-sea fronts, where the thermocline reaches the surface, prey availability may also be increased at shallower depths. This is due both to the attraction of fish to near-surface primary productivity and small nekton accumulated in and around the thermocline (Franks 1992a, Franks 1992b, Russell et al. 1999), and because some fish may actively avoid cool bottom-boundary layer waters (e.g. mackerel; Grégoire 2006, Garthe et al. 2014). Air breathing marine predators, such as gannets, that are required to dive from the surface when foraging will benefit greatly from foraging around features that alter the depth distributions of prey to make them more available near the surface. V-shaped dives were shallower than U-shaped dives (3.4/4.6m versus 6.3m) and so an increase in the probability of their use around fronts likely reflects an increase in the availability of prey at shallower depths (Ropert-Coudert et al. 2009a, Machovsky-Capuska et al. 2011). In some instances, gannets may additionally cue in on other species such as cetaceans (Camphuysen & Webb 1999, Davoren et al. 2010, Tremblay et al. 2014) that also exploit the prosperous foraging opportunities associated with fronts (Goold 1998, Doniol-Valcroze et al. 2007, Dalla Rosa et al. 2012) and whose foraging strategies often prevent prey escaping to deeper waters when under attack (Vaughn et al. 2008). Decreased dive durations around fronts may also reflect shallower foraging behaviours although it should be noted that no direct relationship between the maximum depth of a dive and any of the front metrics was detected.

5.4.3 Identifying important habitat features for foraging marine predators in dynamic ecological systems

There was a high noise to signal ratio across all analyses and as such, the resultant variances explained were low (less than 12%) whilst model fits were sometimes poor (AUC of use-availability models less than 0.6; Zweig & Campbell 1993). This is likely a by-product of the highly dynamic nature of shelf-sea environments coupled to the multiple trophic linkages required to relate physical features to piscivorous marine predators. Moreover, individual and sex-specific foraging specialisation may obfuscate relationships between gannet distributions and oceanographic habitat descriptors (Stauss et al. 2012, Votier et al. 2013, Patrick et al. 2014, Cleasby et al. 2015). Nevertheless, that the relationships found were based upon a priori predictions gives weight to their validity.

Ephemeral features that were highly variable in their spatial occurrence (that the front metric *Gdens* would have been sensitive to) did not appear to elicit a change in the sub-surface dive behaviours of gannets in this region, and relationships to dive distributions were inconsistent with those observed with the other front metrics. The Celtic Sea is a highly dynamic, shallow, shelf-sea environment and fluctuations in surface temperatures can create transient frontal features that are characteristically dissimilar to the clustered and predictable tidal-mixing fronts that are thought to provide a highly accessible and available prey resource to marine predators. As such, being able to distinguish between the two is fundamental to identifying their relative importance to ecological processes in dynamic shelf-sea environments. Composite front mapping provides an invaluable technique for this by allowing frontal features to be objectively defined and identified across multiple spatio-temporal scales. Through its use I was able to identify the significant role shelf-sea fronts play in shaping the at-sea behaviours of a medium ranging piscivorous predator.

Correlations between the dive distributions of males and frequent frontal zones (Ffreq) were weaker than those observed with females (Figure 5.4.c & d), which was reiterated in the contrasting negative and positive relationships observed with distance to front

(*Fdist*; Figure 5.4.a & b). Such sex specificity in habitat use has also been observed in gannets foraging in the shelf-sea waters off the east coast of Scotland (Cleasby et al. 2015). Whilst relationships with fronts were not explicitly analysed, females in this region were shown to favour areas of intermediate SSTs, that were typical of those present at the interface between coastal mixing and offshore stratified waters where fronts would ordinarily manifest. In contrast, males preferentially foraged in near-shore coastal mixing waters of low SSTs, or strongly stratified offshore areas with high SSTs. My results substantiate these findings and, whilst the mechanisms driving these behaviours are unclear, I highlight the need for a comprehensive knowledge of species specific behaviours when investigating the drivers of habitat selection (Zavalaga et al. 2007, Wakefield et al. 2013, Patrick et al. 2014).

Gannets feed on discards from commercial fisheries and this may have explained the differences in habitat-use observed between sex whilst simultaneously introducing additional noise into an already highly variable system (Stauss et al. 2012, Votier et al. 2013, Patrick et al. 2015). However, previous investigations have indicated that this generally has little impact on relationships between foraging behaviours and fronts (Scales et al. 2014a). To confirm this, I ran an additional analysis that incorporated information on the presence of fishing boats greater than 15m in length within 10km (Bodey et al. 2014) and an hour of the location and timestamp of a dive (17.6% and 20.9% of female and male dives respectively as indicated by the UK vessel monitoring system provided by the centre for environment, fishes and aquaculture science; CEFAS). Habitat-use availability analyses were re-fitted excluding the locations of dive events and their associated pseudo-absences. No substantial differences in findings were noted and measures of model fit were consistent with those analyses including fisheries associated dives. I also re-fitted the two models that showed a change in dive duration and shape around fronts with the presence of fishing boats as a two stage factor, in and out-with an interaction with sex. This did not significantly impact dive behaviour ($p > 0.05$). Whilst commercial fishing boats less than 15m may still have impacted my findings, the effect of this is likely negligible.

5.5 Conclusions

Mounting evidence suggests shelf-sea fronts constitute key components in the functioning of marine ecosystems (Scales et al. 2014b). My work reveals the significant role these features play in shaping the at-sea foraging behaviours of a medium-ranging, piscivorous marine predator. In addition to providing a persistent and predictable foraging resource that diving gannets preferentially used, fronts also appeared to increase the accessibility and catchability of prey as indicated by an increase in the use of short V-shaped dive strategies. This study highlights the complexities of interactions between large marine vertebrate predators and their environment, and the subsequent importance of collaboration across disciplines (spatial ecology, oceanography and remote-sensing). I show that studies combining fine-scale foraging behaviours and remotely-sensed measurements of physical oceanography can provide valuable insights toward the mechanisms that drive the at-sea distributions of large marine vertebrate predators. As such, there is a pressing need for cross-disciplinary research when attempting to understand marine vertebrate ecology and how marine ecosystems function.

CHAPTER VI

The use of tidally driven hydrodynamic features by bottlenose dolphins in a topographically complex estuarine system

ABSTRACT

Understanding the distributions, movements and foraging behaviours of large coastal marine vertebrate predators, such as the bottlenose dolphin *Tursiops truncatus,* is critical for effective marine planning and conservation management. Here, I use 11 years (1997-2007) of bottlenose dolphin encounter data collected during standardised surveys of a tidally dominated system, the Shannon estuary (Ireland), to model animal distributions relative to tidal temporal variables as well as topographic descriptors. A GEE-GAM modelling framework is used to show that the spatial distributions of dolphins throughout the estuary are tidally mediated. This relationship was most prominent in a 5km section of a narrow scoured channel between the mouth and upper extent of the lower estuary, where concentrated foraging activity occurred almost exclusively during flood tides. I further investigated habitat use within this 5km section of the central channel using additional analyses that concentrated solely on observations taken within this site. In addition to responding to tidal state, dolphins were also found to respond to the strength of the tide, as determined by concurrent local changes in tidal height and daily maximum tidal ranges. To investigate the oceanography of this area, in 2014 repeat mini-survey circuits were conducted throughout a complete 12 hour tidal cycle across the site and, using an acoustic Doppler current profiler (ADCP), hydrodynamic features within and adjacent to the central channel were measured and characterised. Strong downwelling features were identified at the edge of the channel between convergent fast flowing waters. These features were most prominent during the flood tide at the times associated with increased dolphin foraging activity. I suggest the presence of these features aids animals in capturing their prey by either trapping and accumulating biomass or acting as a barrier against which prey are herded. As such,

these features constitute important foraging habitat locations within the estuary environment. I show that incorporating detailed measurements of the dynamic hydrography of a tidally active site with fine-scale animal distributions can provide new insight into the drivers of habitat selection and increase our understanding of potential interactions of coastal dolphins with human activities in tidally dominant coastal systems.

6.1 Introduction

Many large marine vertebrate predators, such as marine mammals, are capable of using vast areas of the ocean (Block et al. 2011) yet typically concentrate in localised regions resulting in the formation of discrete hotspots (Worm et al. 2003). The mechanisms driving these behaviours are likely based on foraging decisions (Fauchald & Tveraa 2003, Hastie et al. 2004, Weimerskirch 2007) and so understanding the habitat preferences of a species, both in space and time, can provide invaluable information for improving our understanding of how marine predators interact with their environment. Large marine vertebrate predators play a vital role in ecosystem functioning (Heithaus et al. 2008, Baum & Worm 2009), yet are highly susceptible to disturbance (Furness & Tasker 2000, Gremillet & Boulinier 2009). Understanding the processes that drive the habitat use and movement of mobile marine predators is fundamental to effective marine planning and conservation management. This may be particularly pertinent in regions where human activities are concentrated, such as estuaries that experience intense pressure from a number of anthropogenic stressors such as shipping (Lesage et al. 1999), marine renewable energy installations (MREIs; Frid et al. 2012) and recreational activities such as whale watching (Berrow & Holmes 1999).

In marine systems, heterogeneity is the result of complex and dynamic oceanographic interactions that often work to create predictable features that predators repeatedly target (Pettex et al. 2010, Patrick et al. 2014), presumably due to increases in prey availability that enhance foraging efficiency (Vlietstra et al. 2005, Gende & Sigler 2006). The spatio-temporal scales over which these features occur vary, dependent upon the mechanisms underlying their creation. In near-shore coastal regions, tidal currents and topography play a dominant role, and interactions between the two create a number of localised ephemeral features that may only persist for a couple of hours, but often occur on a regular basis in a highly predictable fashion. Growing evidence suggests that these features are of importance to a number of large marine vertebrate predators for foraging (Zamon 2003, Embling et al. 2010, Isojunno et al. 2012, De Boer et al. 2014, Waggitt & Scott 2014, Benjamins et al. 2015).

For example, headlands and islands may disrupt current flows at certain times in the tidal cycle to create wakes around which shear induced hydrographic fronts accumulate prey (Johnston et al. 2005a, Johnston et al. 2005b), whilst narrow channels are known to sometimes act as a bottleneck in which prey become concentrated during peak tidal flows (Zamon 2001, Pierpoint 2008). Moreover, their steep sloping banks can create a barrier to tidal current flows (when orientated in perpendicular manner) inducing the periodic formation of strong upwelling features which act to aggregate zooplankton and mid-trophic level prey (Cotté & Simard 2005, Rogachev et al. 2008). Finally, under specific tidal conditions current flows across complex reef systems may generate shear and shear-induced instabilities, which are thought to alter the distributions of prey in a manner that enhances their availability to large marine vertebrate predators (Skov & Thomsen 2008, Jones et al. 2014). Within estuarine environments a number of these features may occur (Wilson et al. 1997, Mendes et al. 2002, Bailey & Thompson 2010) and so understanding the associated habitat preferences of marine predators requires robust methodological designs that are both of high resolution and inclusive in their spatio-temporal extent (Pirotta et al. 2014b).

The bottlenose dolphin *Tursiops truncatus* is a species typically found in near-shore tidally dominated systems (Bailey & Thompson 2009), and whilst their habitat use within these environments has been previously examined (Wilson et al. 1997, Ingram & Rogan 2002, Mendes et al. 2002, Bailey & Thompson 2010), as of yet a fine-scale, fully encompassing study of a tidally dominated estuarine system has not been completed. Here I used observations of bottlenose dolphins, taken over 11 years during dedicated boat-based surveys (Figure 6.1) across the Shannon Estuary (Ireland), to examine patterns in habitat use in relation to a suite of topographic and tidal variables. I conducted a three-stage analysis where I: (1) examined patterns in dolphin habitat use across the entire lower estuary, (2) conducted a detailed investigation of the influence of tidal currents on temporal patterns in dolphin occurrence within the central channel of the estuary (as defined in Figure 6.1.b and hereafter referred to as the ‘central channel’) where this relationship appeared particularly pronounced, and (3) characterised the current regime in the central channel using *in-situ* current measurements collected during additional repeated oceanographic surveys of the area across an entire tidal cycle in 2014.

The Shannon estuary comprises a ~80km stretch of the longest river in the British Isles, which spans over 300km from its source. The estuary regularly surpasses 5km in width and measures over 10km wide at its mouth. A semi-diurnal tide occurs with average ranges of 2m and 4.3m during peak neap and spring tides respectively. On large spring tides, these can exceed 5.3m with current speeds that regularly surpass $2ms^{-2}$. The estuary is topographically complex (Figure 6.1.b) with depths ranging from less than 10m on the outer banks to more than 60m in a deep central channel that runs the extent of the system. The estuary hosts a resident population of bottlenose dolphins estimated to comprise around 115 individuals (Ingram 2000), which are protected under the Irish Wildlife Act 1976 and Wildlife (Amendment) Act 2000, and are included in Annex II of the EU Habitats Directive (Council Directive 92/43/EEC) as a priority species for conservation. As such the lower Shannon estuary is a special area of conservation (SAC). To ensure the habitat needs of this resident population of bottlenose dolphins are protected, a detailed knowledge of the physical mechanisms underlying their creation is required.

6.2 Methods

6.2.1 Boat-based dolphin surveying across the estuary

Boat based dolphin surveys were conducted between July 1997 and September 2007. Across the 11 years, 103 standardised surveys were conducted in Beaufort sea-states of three or lower using a rigid inflatable boat (RIB). Of these, 76 were conducted between May and September and 27 between October and April.

Surveys followed a predetermined route (Figure 6.1.b) designed to identify distributions and abundance estimates of bottlenose dolphins across the entire lower estuary (Ingram & Rogan 2002). On all surveys, positions were continuously logged by either a hand-held GPS at five minute intervals (1997-2001) or the boat’s GPS at one minute intervals (2001-2008). Surveys were conducted at a steady speed of around $20kmh^{-1}$ and a constant lookout for dolphins was maintained. Upon sighting a dolphin the boat was slowed to avoid disturbance and the individual/group (defined as all dolphins within a 100m radius of each other; Irvine et al. 1981) approached. During these encounters, individuals/groups were followed at a distance and attempts were made to take photographs of all individuals as part of a photo identification project (see Ingram & Rogan 2002). Encounters ended and surveying resumed once all individuals within a group had been photographed or 10 minutes had elapsed since the last dolphin sighting. For each encounter the start and end times were noted alongside an estimated group size. On completion of an encounter the survey was resumed until the route was completed and another individual/group encountered.

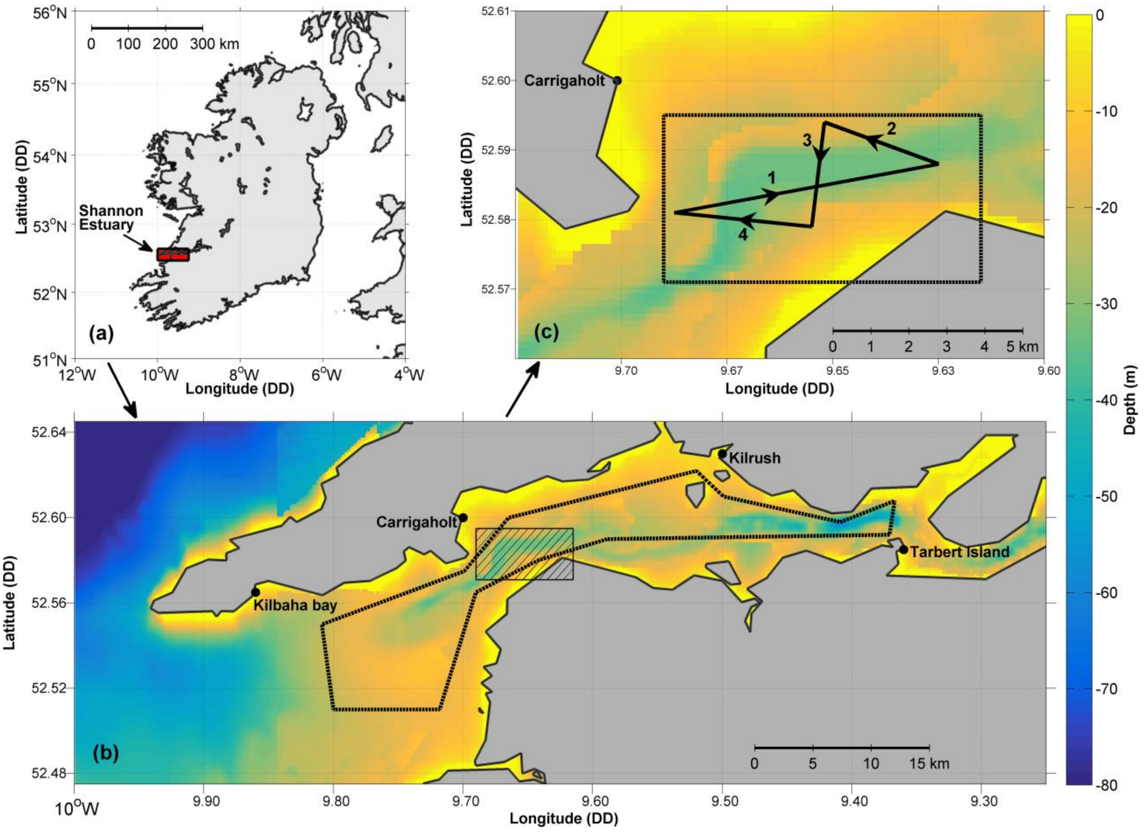

Figure 6.1 Anti-clockwise from top left: (a) map of Ireland with the location of the Shannon Estuary shown in the red box, (b) the Shannon Estuary with bathymetry as indicated by the colour bar (to the right), the route followed on dolphin surveys as indicated by the thick dashed line and the area selected for the nested channel survey as indicated by the hatched box, and (c) an overview of the nested channel survey (as indicated by the thick dashed line) with bathymetry (as indicated by the colour bar) and the route followed on the oceanographic survey with number corresponding to each repeat transect leg/section.

6.2.2 Survey standardisation

To create a unit for analysis, GPS locations from each survey were standardised to a common two minute time interval using a cubic spline interpolation. This time interval was chosen (1) to be able to resolve fine-scale patterns in habitat use and (2) for data management purposes to avoid long model runs and computer memory issues. Off-survey points (those GPS locations not associated with animal encounters or where the boat was not actively searching for animals) were those where the boat speed had dropped below 10kmph^{-1} and no encounter had been recorded. These were excluded from further analysis. The remaining survey points were (1) classified as zero if there were no animal encounters associated within one minute either side of a survey point's timestamp or (2) classified as one if an encounter had been recorded within one minute either side of a point's timestamp.

6.2.3 Bathymetric and tidal data

6.2.3.1 Bathymetric data

Multibeam bathymetric data for the central channel running through the estuary and surrounding waters (see Appendix A3.1, Figure A3.1 for exact spatial extents) was available at a spatial resolution of less than 5m from the integrated mapping for the sustainable development of Ireland's marine resource program (INFOMAR; www.infomar.ie). For the remainder of the estuary, data was downloaded from the British Oceanographic Data Centre (BODC) general bathymetric chart of the oceans at a spatial resolution of 30 arc seconds (The GEBCO_2014 Grid, version 20150318; www.gebco.net). For each of these datasets a measure of slope (^{o}km^{-1}) was generated using the SDMTools package in R (Van der Wal et al. 2014). The depths and slopes of the INFOMAR and BODC datasets were then each merged (for depth see Figure 6.1 and for slope see Appendix A3.2, Figure A3.2), giving preference to the INFOMAR high resolution multibeam data. Corresponding data were extracted from resultant maps for each survey point.

6.2.3.2 Tidal data

Tidal data was obtained from the admiralty Easytide tidal prediction model via the United Kingdom hydrographic office (UKHO; www.ukho.gov.uk). From this, for the full estuary analysis two variables were created: (1) tidal state (Table 6.1) and (2) spring-neap phase (Table 6.1), For the central channel, in addition to these two indices three further tidal variables were created: (1) relative position in the tidal cycle, (2) daily tidal height range, and (3) concurrent tidal height change.

Tidal states were assigned using the times of low and high water taken from four ports positioned at roughly 20km intervals through the estuary: (1) Tarbert Island, (2) Kilrush, (3) Carrigaholt and (4) Kilbaha Bay (Figure 6.1.b). A range of port locations was used to account for a lag of between 20 and 50 minutes in the times of low and high water between Kilbaha Bay and Tarbert Island. Each survey point was assigned a relative position in the tidal cycle taken as the time since the last low water divided by the time between the last low water and the next low water. Times from/to the last/next low waters were calculated in decimal hours using the times of low waters taken from the closest port to a survey point (Appendix A3.3, Figure A3.3). The relative position in the tidal cycle was then used to create a six-phase tidal factor, running at roughly two hour intervals from an hour before low water (Table 6.1).

The spring-neap phase of each survey point was determined from maximum changes in tidal heights (elevation above chart datum) for each day (daily tidal ranges), calculated using data from Carrigaholt (selected because of its central position in the estuary). A bespoke peak finding algorithm was used to split predictions into complete neap-spring-neap cycles based on an oscillation of these daily tidal ranges. For each day, the time since the last neap tide (defined as a trough in the daily tidal ranges) was divided by the total time between the neighbouring last/next neap tides to give an index of relative position in the spring-neap cycle. This was then used to assign each survey point a spring and neap two-phase factor where neaps were roughly three days either side of low peak tidal heights, and springs were three days either side of high peak tidal heights (Table 6.1).

Relative position in the tidal cycle and daily tidal height range were used as continuous variables to assign survey points tidal states and spring-neap phases. Concurrent tidal height change was calculated from 10 minute estimates of tidal elevation taken from Carrigaholt and was the difference between the tidal heights from the closet 10 minute interval after and before a survey point. Negative values correspond to ebb flows, and positive values to flood flows. Extreme negative or positive values represent times of large tidal height changes when tidal current flow was expected to be high, whilst values close to zero indicate times when the tide was changing.

Table 6.1 Specifications for the allocation of tidal phases and spring-neap phases to survey points. Relative position was used rather than time since low tide/neap tide as this allowed for variation in the length of the tidal/spring-neap cycles. Times since low tide (hours) and neap tide (days) are just a guide, and were calculated for a 12 hour and 14 day cycle respectively.

Tidal phase	**Relative position in tidal cycle**	**Time since low tide**
First half flood	> 0.0835 & ≤ 0.2499	> 1 hours & ≤ 3 hours
Second half flood	> 0.2499 & ≤ 0.4165	> 3 hours & ≤ 5 hours
High tide	> 0.4165 & ≤ 0.5831	> 5 hours & ≤ 7 hours
First half ebb	> 0.5831 & ≤ 0.7497	> 7 hours & ≤ 9 hours
Second half ebb	> 0.7497 & ≤ 0.9163	> 9 hours & ≤ 11 hours
Low tide	≤ 0.0833 or > 0.9163	≤ 1 hour or > 11 hours
Spring-neap phase	**Relative position in spring-neap cycle**	**Time since neap tide**
Neaps	< 0.25 or ≥ 0.75	≤ 3.5 days or > 10.5 days
Springs	≥ 0.25 & < 0.75	> 3.5 days & ≤ 10.5 days

6.2.4 ADCP (acoustic Doppler current profiler) survey of the central channel

To be able to describe tidal currents in detail, oceanographic surveys were run on the 28th May 2014 across a bow tie in the channel of the estuary (Figure 6.1.c) over a complete spring tidal cycle. Velocity speeds and directions were measured via a hull mounted 600kHz ADCP (acoustic Doppler current profiler) that operated over a vertical bin size of 1m with a ping frequency of 1.5 seconds. To reduce measurement error/noise, post-survey data processing was conducted across the eastern, northern and vertical velocity components using (1) a median filter of two standard deviations across 15 seconds of measurements horizontally and three bins vertically, and (2) a running average across 15 seconds of measurements horizontally and three bins vertically.

During the oceanographic survey a constant look out for dolphins was maintained and the times and positions of any sightings noted.

6.2.5 Statistical analysis

Two statistical analyses were conducted to (1) examine the spatio-temporal distributions of dolphins throughout the entire lower estuary, and (2) examine temporal interactions between dolphins and fine-scale descriptors of tidal currents in the central channel.

6.2.5.1 Modelling spatio-temporal changes in dolphin distributions through the estuary

The influences of environment (depth and slope), location and tidal phase on patterns in dolphin presence (0/1) through the entire lower estuary were modelled using GEE-GAMs (generalised additive estimating equations; Liang & Zeger 1986) in R (R Development Core Team 2014). GEE-GAMs were fitted via the geepack package (Hojsgaard et al. 2014) with a binomial error structure and logistic ('logit') link. A working independence structure was specified to account for autocorrelation between repeat observations of single dolphin encounters (Panigada et al. 2008, Pirotta et al. 2011). Under this approach, data are grouped into blocks within which autocorrelation between point observations is allowed (Hardin & Hilbe 2002). A combination of variance estimators are then used to produce realistic (inflated) standard errors thus enabling robust inference (Panigada et al. 2008, Pirotta et al. 2011). Point observations were grouped into blocks corresponding to either (1) a continuous segment of survey transect with no breaks of greater than 10 minutes where no animals had been recorded, or (2) an encounter or series of encounters with no breaks of greater than 10 minutes. Separate models were fitted for (1) all observations over spring and neap tidal phases, (2) observations made only during neap tidal phases, and (3) observations made only during spring tidal phases.

One-dimensional smooths were fitted for depth, slope and day of year (included to account for seasonal fluctuations in dolphin presence) using cubic *B*-splines from the splines library (R Development Core Team 2014). For each smooth, one internal knot was specified, the position of which was selected using an adaptive knot placement algorithm, SALSA (spatially adaptive local smoothing algorithm; Walker et al. 2011, Scott-Hayward et al. 2013), from the MRSea package (Scott-Hayward et al. 2015). For depth and slope an interaction term with tidal phase was also tested for.

Latitude and longitude, projected on a UTM (Universal Transverse Mercator) coordinate system, were included in the model as an interaction term with tidal phase using a complex region spatial smoother (CReSS; Scott-Hayward et al. 2013, Scott-Hayward et al. 2014) from the MRSea package in R. CReSS is a smoothing method where latitude and longitude are represented by a local radial basis function with a specified number of knots, around each of which a radius is drawn that encompasses a fixed proportion of the survey data as determined via estimated geodesic distances (Petersen et al. 2011, Scott-Hayward et al. 2014). The number and position of these knots is selected using SALSA which also allows the radii around the knots to vary so that data-rich areas exhibit smaller radii than data-sparse areas. This allows local patterns to be resolved without over-fitting noise, and so provides robust smoothing estimates over complex domains, such as an estuary.

6.2.5.2 Modelling interactions between dolphins and tide within the central channel

Temporal patterns in dolphin presence in the central channel were further examined in relation to tidal currents using three additional fine-scale descriptors: (1) relative position in the tidal cycle, (2) daily tidal height range, and (3) concurrent tidal height change. To avoid issues pertaining from multi-colinearity these indices were fitted in separate models. In all cases, GEE-GAMs were used with a binomial error structure and logistic (‘logit’) link, and a working independence correlation structure (as specified above). Additional explanatory variables (non-tidal) initially included (before model selection) were depth, slope and day of year. Interactions were tested for where specified.

First, spring-neap phase and relative position in the tidal cycle were modelled. An interaction between the two was tested for. Second, tidal phase and daily tidal height range were modelled. For this model, the six-level tidal state variable specified in Table 6.1 was collapsed into two phases: (1) ebb (first and second half ebb and low tide), and (2) flood (first and second half flood and high tide). This was because, during low tide, no animals were observed within the central channel which would have caused issues with model fit. Interaction terms were tested for between tide and each of daily tidal range, depth and slope. Finally, concurrent tidal height change was modelled. No interactions were tested for in this model. In all models, one-dimensional smooths were fitted for each continuous explanatory variable, using SALSA as previously specified.

6.2.5.3 Model selection and validation

Backwards manual stepwise model selection was performed on a full model (containing all potential explanatory variables, interactions and smooths) by removing those variables, interactions or smooths that were either deemed non-significant ($p \geq 0.05$) through repeated Wald's tests, or whose inclusion did not lower the model's $\mathrm{QIC_u}$ (quasi-likelihood criterion; Pan 2001) score. The inclusion of each smooth term was further evaluated through visualisation, to deem them biologically reasonable, and where appropriate smooths were removed as a conservative approach to avoid over-fitting (e.g. in the nested channel analysis the day of year smooth was removed and replaced with a linear term).

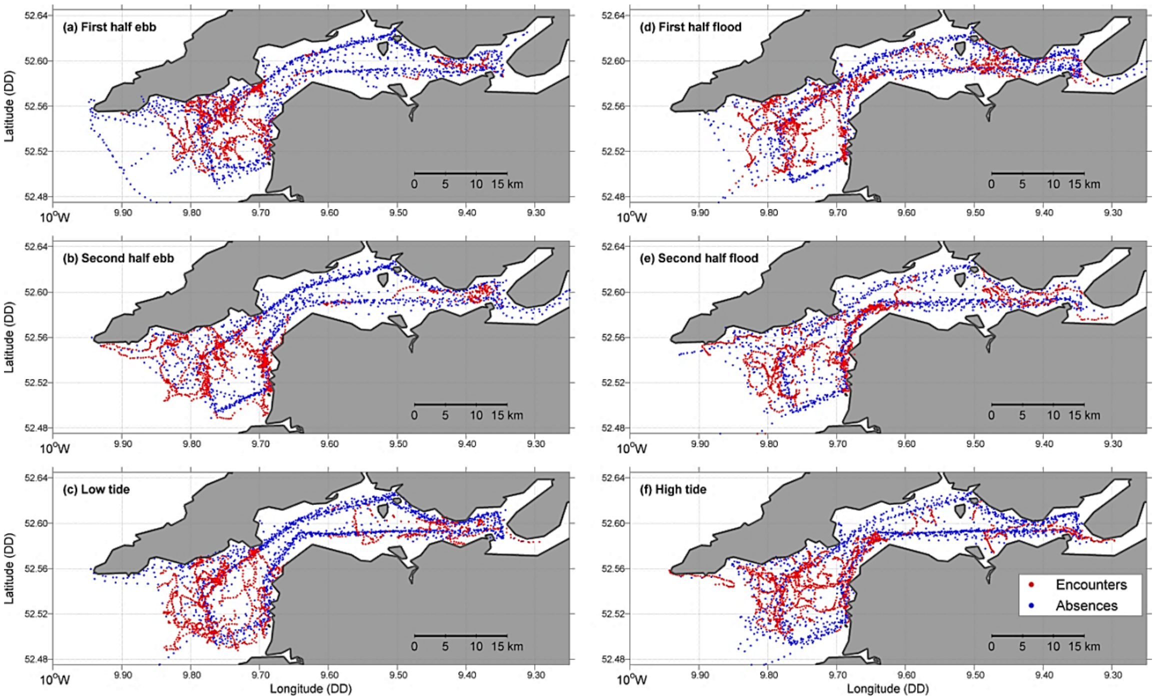

Figure 6.2 Survey observations (GPS points). Locations where dolphins were encountered are marked in red and those locations where no animals were sighted are marked in blue. The left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. The right column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

Pearson residuals were plotted against all potential explanatory variables, time, year, and survey ID to check for any patterns indicative of a violation of model assumptions.

Fitted versus predicted values were inspected and the area under the Receiving Operator Characteristic (ROC) curve (AUC; Zweig & Campbell 1993, Liu et al. 2005) computed to check for satisfactory model fit.

6.3 Results

A total of 578.5 hours of on-effort surveying, covering over 8564km, was procured from the 103 surveys conducted over the 11 years (1996-2007). Of these surveys, 50 (285.7 hours) were conducted in spring tides and 53 (292.9 hours) in neap tides. A total of 319 separate dolphin encounters were made over 1609km of the survey route, with dolphin sightings occurring on all bar four surveys. Survey coverage of the estuary and the locations of encounters across both neap and spring conditions at each tidal phase are shown in Figure 6.2 (see Appendix A3.4 for coverage across the estuary separated into spring and neap conditions).

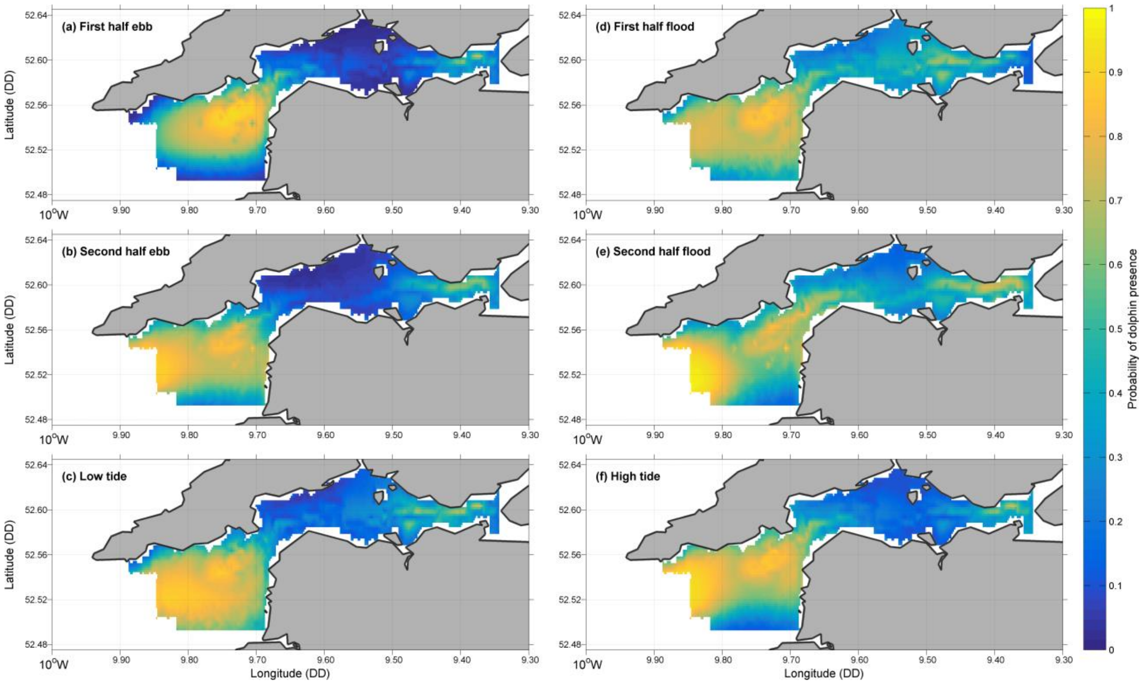

Figure 6.3 Predictions of the probability of dolphin presence encompassing depth and slope measurements for the entire estuary at all locations over all stages of the tide as determined via GEE-GAMs (generalised estimating additive models). Left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. Right column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

6.3.1 Spatio-temporal changes in dolphin distributions through the estuary

Dolphins concentrated in three core areas across the estuary: (1) Kilbaha bay and the outer estuary mouth, (2) the central channel near Carrigaholt and (3) the upper estuary near Tarbert (Figures 6.2 & 6.3). Patterns in presence varied with tide (Table 6.2.a, Figure 6.3), particularly within the central channel near Carrigaholt, and appeared to be predominantly driven by three topographically defined factors: depth, location and slope (Table 6.2.a, Figures 6.4, 6.5 & 6.6), the influences of which were consistent across both spring and neap tides (Table 6.2.b & c, Appendices A3.5 & A3.6). Figures and results presented here are from the GEE-GAM model encompassing data collected during both spring and neap conditions (see Appendices A3.5 & A3.6 for figures obtained from the neap and spring condition specific GEE-GAMs).

A smooth term for depth was retained by the model ($p < 0.001$, Table 6.2.a). The probability of encountering a dolphin was lowest between depths of 5m and 25m, with higher probabilities (by ~30%) occurring out-side this range (Figure 6.4). This relationship was consistent across all tidal states. Dolphin presence varied tidally with location ($p < 0.001$, Table 6.2.a, Figure 6.5). During the second half of ebb flow and low tide, dolphins were generally encountered in the outer mouth of the estuary (Figure 6.5.d:g). During the first half of the flood, encounter probabilities increased in the central channel of the estuary (Figure 6.5.j:l) and a second narrow channel further up the estuary by Tarbert. The use of both these regions by dolphins peaked during the second half of the flood (Figure 6.5.m:o), with predicted encounter probabilities of over 0.7. Use of the central channel continued to remain high through high water and partially in the first half of the ebb. During the second half of the ebb and low water, predicted encounter probabilities dropped to less than 0.2 (Figure 6.5.p:r & a:c). At the upper estuary channel by Tarbert, encounter probabilities decreased during high water to intermediate levels that remained constant across all tidal states (~0.5; Figure 6.5). A smooth term for slope was retained in an interaction with tidal state ($p = 0.02$, Table 6.2.a). During the second half of both the ebb and flood tides, intermediate slope values (between ~30^o and 70^o) were associated with a decreased probability of dolphin presence, whilst during low and high tides and the first half of ebb and flood flows, steeper slopes (of between ~60^o and 80^o) were favoured (Figure 6.6). Finally, a smooth term for year was retained by the model ($p = 0.03$, Table 6.2). Dolphins were more frequently encountered during the summer than at other times of the year (Appendix A3.7, Figure A3.14) although this trend was only evident in models encompassing surveys across both spring and neap conditions.

Table 6.2 Results from the GEE-GAMs run to examine the influences of environment (depth and slope), location and tide on dolphin distributions through the estuary. From top to bottom: (a) using all survey points taken during spring and neap conditions, (b) using only observations taken during neap conditions, and (c) using only observations taken during spring conditions.

(a) Neap and spring conditions combined: QIC$_u$ of full model = 19205; AUC = 0.78

Explanatory variable	**Removal of smooth ΔQIC$_u$**	**Removal of term ΔQIC$_u$**	***p*-value**
s(Depth)	+ 82	+ 317	**< 0.001**
s(Location (*X*, *Y*))	-	-	**< 0.001**
s(Slope)	+ 103	-	0.15
Tide	-	-	0.53
s(Day of year)	+ 261	+ 263	**0.03**
s(Location (*X*, *Y*)) * Tide	-	+ 706	**< 0.001**
s(Slope) * Tide	+ 103	+ 54	**0.02**

(b) Neap conditions: QIC$_u$ of full model = 9114; AUC = 0.81

Explanatory variable	**Removal of smooth ΔQIC$_u$**	**Removal of term ΔQIC$_u$**	***p*-value**
s(Depth)	+ 44	+ 134	**<0.001**
s(Location (*X*, *Y*))	-	-	**<0.001**
s(Slope)	+ 76	-	0.16
Tide	-	-	0.75
s(Location (*X*, *Y*)) * Tide	-	+ 798	**<0.001**
s(Slope) * Tide	+ 76	+ 48	**0.005**

(c) Spring conditions: QIC$_u$ of full model = 9383; AUC = 0.79

Explanatory variable	**Removal of smooth ΔQIC$_u$**	**Removal of term ΔQIC$_u$**	***p*-value**
s(Depth)	+ 40	+ 166	**< 0.001**
s(Location (*X*, *Y*))	-	-	**< 0.001**
s(Slope)	+ 44	-	0.09
Tide	-	-	0.52
s(Location (*X*, *Y*)) * Tide	-	+ 708	**< 0.001**
s(Slope) * Tide	+ 44	+ 27	**0.01**

6.3.2 Interactions between dolphins and tide within the central channel

Within the central channel of the estuary, dolphins were present predominantly only during flood tidal states ($p < 0.001$; Table 6.3.a:c, Figure 6.7). Dolphins were encountered only five times across the 63 surveys that passed through the estuary's central channel during ebb tidal states (first and second half ebb and low tide; Table 6.1), compared to 33 encounters made during flood tidal states across 71 surveys (first and second half flood and high tide; Table 6.1). Of the total surveying time spent in the central channel, dolphins were encountered 6.5% of the time during ebb tides and 59.1% of the time during flood tides.

Table 6.3 Results from the three GEE-GAMs run to examine interactions between dolphins and fine-scale tidal variables in the central channel of the estuary (a region characterised by a deep narrow scoured channel and strong tidal currents). From top to bottom: (a) using a spring-neap two-stage factor variable and a continuous tidal variable, relative position in the tidal cycle, (b) using a two-stage factor tidal variable alongside an index of the size of the tide as daily tidal range, and (c) using a continuous proxy for tidal flow as tidal height change.

(a) Channel analysis: Continuous temporal tidal variable: QIC_u of full model = 1426; AUC = 0.72

Explanatory variable	**Removal of smooth ΔQIC_u**	**Removal of term ΔQIC_u**	***P*-value**
s(Depth)	+ 10	+ 25	**0.02**
s(Relative position in tidal cycle)	+ 281	+ 380	**<0.001**

(b) Channel analysis: Factor tidal temporal variable: QIC_u of full model = 1477; AUC = 0.76

Explanatory variable	**Removal of smooth ΔQIC_u**	**Removal of term ΔQIC_u**	***P*-value**
Tide (2-stage factor)	-	-	**< 0.001**
Daily tidal range	-	-	0.40
Tide * Daily tidal range	-	+ 22	**0.003**

(c) Channel analysis: Continuous tidal height variable: QIC_u of full model = 1608; AUC = 0.80

Explanatory variable	**Removal of smooth ΔQIC_u**	**Removal of term ΔQIC_u**	***P*-value**
s(Concurrent tidal height change)	+ 24	+ 256	**< 0.001**

Fine-scale tidal descriptors were retained in each of the three models run to examine interactions between dolphins and tide in the central channel (Table 6.3), and identified relationships were consistent (Figure 6.7). The first model retained a smooth term for both relative position since low tide ($p < 0.001$; Table 6.3.a) and depth ($p = 0.02$; Table 6.3.a). Dolphin presence was increased from between ~1.5 hours after low water to ~7.5 hours after low water. Encounter probabilities rose from close to zero to over 0.4 and peaked just before high water at 0.7 (~4.5 hours after low tide; Figure 6.7.a). Depths shallower than 12m and deeper than 20m were preferred (Figure 6.7.b), which is consistent with results from the analysis of the full estuary. The second model retained a linear term for daily tidal range, a two-stage tidal state factor variable and an interaction term between the two (Table 6.3.b). Encounter probabilities significantly increased (almost five fold) during flood tides ($p < 0.001$; Table 6.3.b, Figure 6.7.c & d).

During these times there was a positive relationship between the probability of dolphin presence and the size of the tide ($p = 0.003$; Table 6.3.b, Figure 6.7.d). In contrast, on ebb tides a negative relationship with the size of the tide was observed (Figure 6.7.c). The third model retained solely a smooth term for concurrent tidal height change ($p < 0.001$; Table 6.3.c). The probability of dolphin presence increased with change in tidal height almost linearly until a threshold of around 12m, above which a levelling and subsequent drop off in encounter probabilities is observed (Figure 6.7.e). It is noted however that above this threshold there is limited available data, as evident in increased 95% confidence intervals.

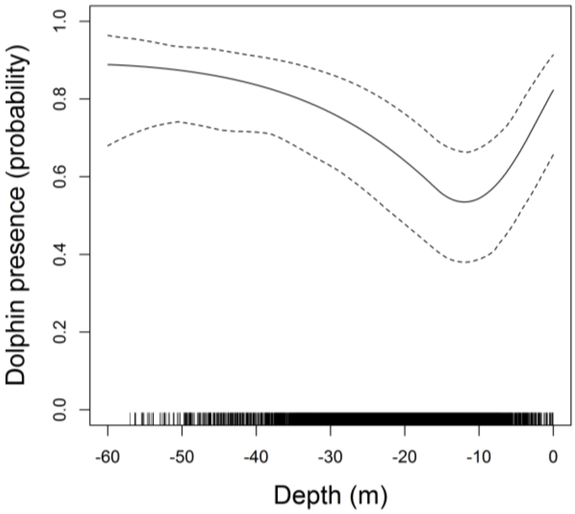

Figure 6.4 The influence of depth on the probability of dolphin presence as determined via GEE-GAMs (generalised estimating additive models) fitted using all survey observations across the entire estuary.

6.3.3 Observations from the ADCP survey of the central channel

The ADCP survey was conducted in conditions representative of peak spring tides with a daily tidal range of 4.09m. Wind speeds during the survey were essentially zero and the resultant sea state permitted extremely high quality current measurements due to minimal vessel movement, that otherwise would have increased noise in the ADCP measurements. Surveying commenced at 10:00 (40 minutes before low water that occurred at 10:40) and was continuous through to 22:00 (around an hour before the following low water at 23:06). High water was at 17:02. Dolphins were sighted six times at: (1) 15:08, (2) 15:57, (3) 16:06, (4) 16:22, (5) 17:08 and (6) 17:52 (Figures 6.8 & 6.9), which corresponded to the second half of flood flow and high tide tidal states (roughly three hours before high water to an hour after; Table 6.1). All times quoted are in GMT.

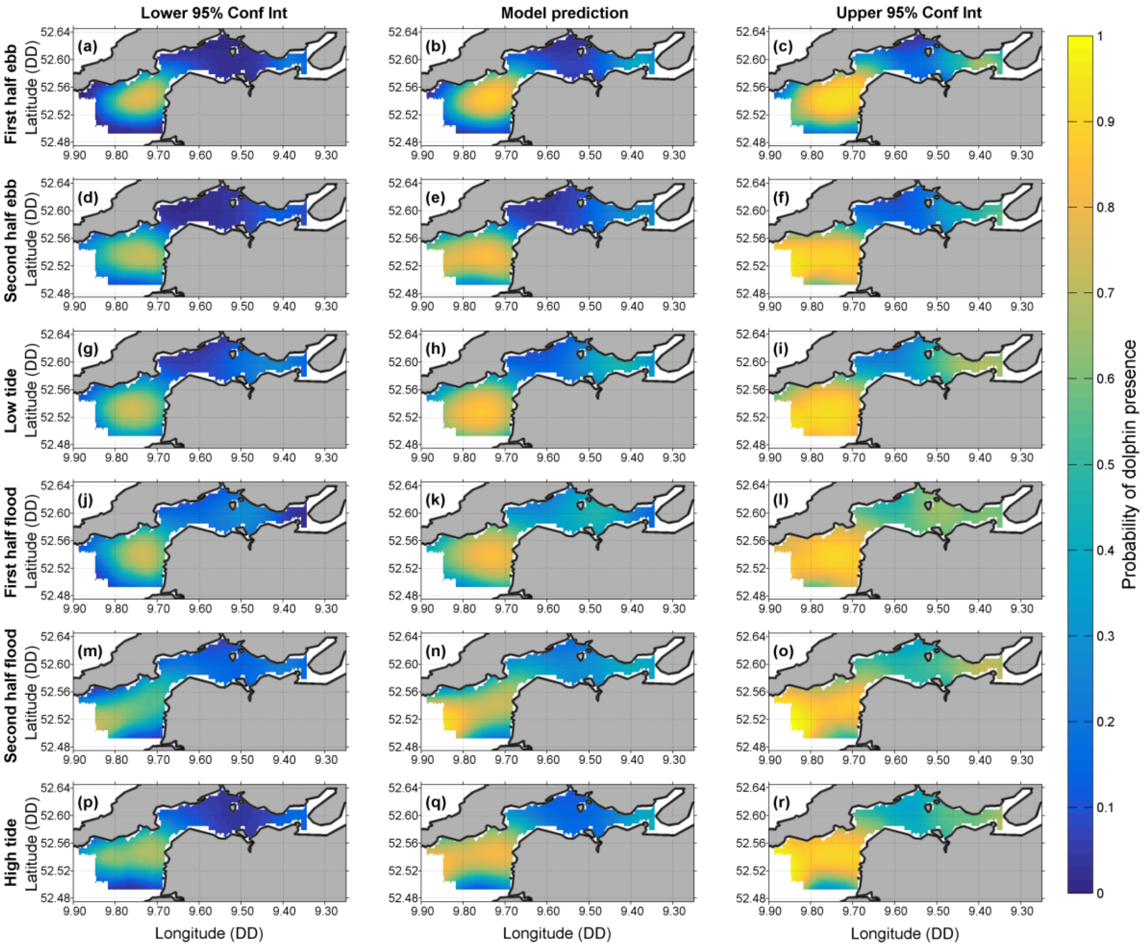

Figure 6.5 The influence of location and tide on the probability of dolphin presence as determined via GEE-GAMs (generalised estimating additive models) fitted using survey observations taken across the entire estuary during both neap and spring conditions. Columns from left to right show: (1) upper 95% confidence intervals (subplots a, d, g, j, m and p), (2) model predictions (subplots b, e, h, k, n and q), and (3) lower 95% confidence intervals (subplots c, f, i, l, o and r). Rows from top to bottom show: (1) first half ebb (subplots a, b and c), (2) second half ebb (subplots d, e and f), (3) low tide (subplots g, h and i), (4) first half flood (subplots j, k and l), (5) second half flood (m, n and o) and (6) high tide (subplots p, q and r).

During maximal ebb flows (defined as 2.52hr to 0.22hr before low tide; 10:00 to 10:20 and 20:35 to 22:00) current speeds in the central channel averaged 1.52 ±0.18ms^{-1} and ranged from 0.17ms^{-1} to peaks of 2.26ms^{-1} (Appendix A3.8). Average current speeds during maximal flood flows (defined as 3.2hr to 1.53hr before high tide; 14:25 to 15:30) were 1.33 ±0.16ms^{-1}, which was 0.9ms^{-1} weaker than those observed during maximal ebb flows. These ranged from 0.28ms^{-1} to peaks of 1.95ms^{-1} (0.31ms^{-1} weaker than peak speeds during maximal ebb flows). Current flows changed from ebb (a predominantly west-southwest direction with an average of 244^{o}) to flood (a predominantly east-northeast direction with an average of 60°) directions 1hr to 2.5hrs after low water (11:40 to 13:10; Appendix A3.8), and from flood to ebb directions 0.8hr to 2.63hrs after high water (17:50 to 19:40; Appendix A3.8). During these periods, current speeds averaged 0.45 ±0.19ms^{-1} and ranged from 0.0016ms^{-1} to 1.83ms^{-1}.

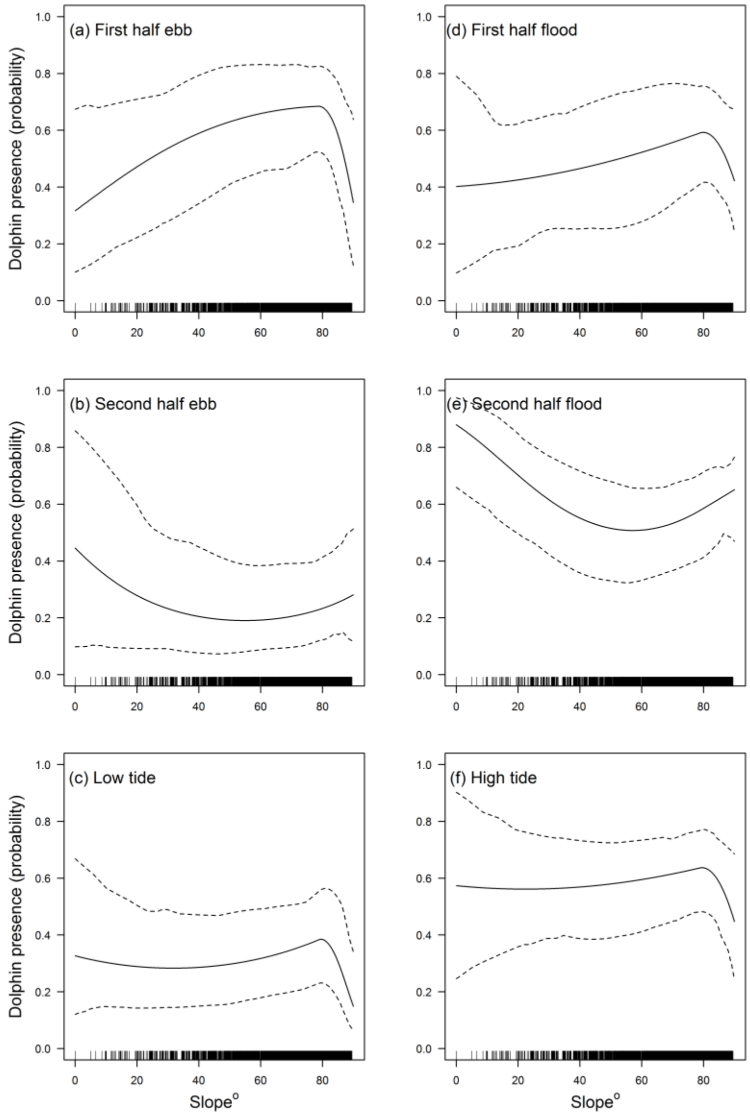

Figure 6.6 The influence of slope on the probability of dolphin presence as determined via GEE-GAMs (generalised estimating additive models) fitted using survey observations taken across the entire estuary during both neap and spring phases. Left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. Second column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

Current speeds during ebb flow, when water was exiting the estuary, were general constant across the channel and its surrounding banks (Appendix A3.8). In contrast, during flood tides, when water was entering the estuary, current speeds were asymmetric with lower speeds (< 0.5ms^{-1}) observed leeward (landward) of the shallow southern side banks of the central estuary, compared to the central deep channel (> 1.25 ms^{-1}; Figure 6.8.f & g). Along the edge of the bank where these waters converged, a hydrographic front manifested along which strong downwelling features, with vertical downward velocities exceeding 0.2ms^{-1}, were identified (Figure 6.9). The times at which these features were present coincided with the times at which dolphin sightings were made (the latter half of the flood tide).

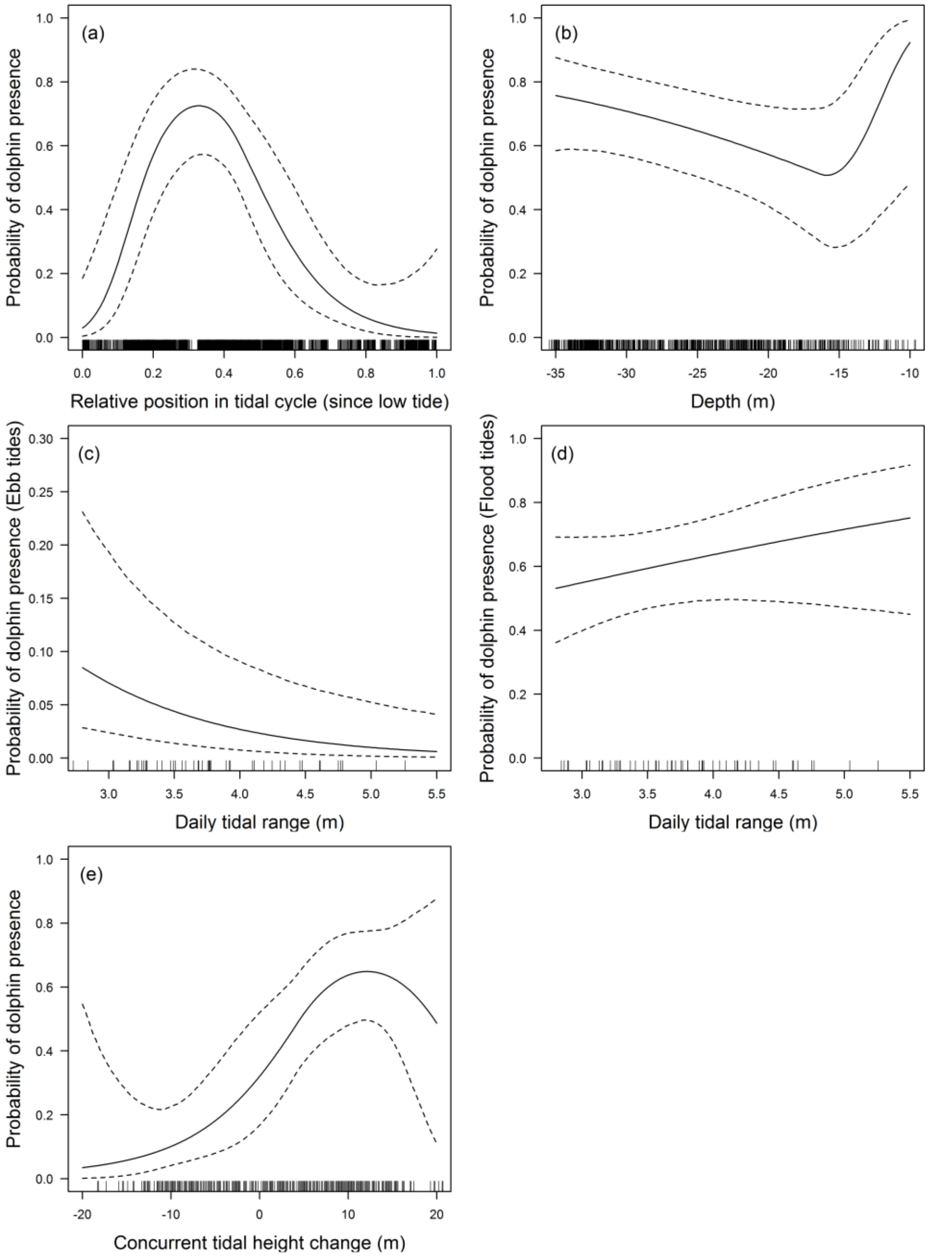

Figure 6.7 Probability of dolphin presence in the channel central as determined via GEE-GAMS (generalised additive models): (a) relative position in the tidal cycle (time since low tide), (b) depth, (c) daily tidal range during ebb tides, (d) daily tidal range during flood tides, and (e) tidal height change.

6.4 Discussion

This study provides a unique insight into the fine-scale physical processes that drive habitat use by a large coastal marine vertebrate predator. I show that the occurrence of dolphins across the estuary varied significantly, and was dependent on the state of the tide. During ebb phases, dolphins concentrated in the outer estuary mouth, and use of the central and upper estuary was comparatively low. During flood stages, occurrence increased further upstream, across both the central and upper estuary region, and peaked during maximal flood tidal flows. I identified two discrete areas within these regions where the influence of tide on dolphin presence was strongest: (1) the central channel near Carrigaholt, and (2) the upper estuary channel near Tarbert. A nested analysis of the former of these revealed that dolphin occurrence appeared to also be influenced by the strength of flood flow, with times associated with higher current speeds linked to higher levels of dolphin occurrence. During ebb flows the reverse was observed, with lower levels of occurrence when flow speeds were likely increased. ADCP surveys revealed that the times at which dolphin presence peaked in the central channel coincided with the manifestation of strong downwelling features in the area.

Whilst fish and plankton species are known to move with prevailing tidal currents (Olson & Quinn 1993, Simard et al. 2002), there is little or no evidence of similar patterns occurring in dolphins. Maximum current speeds in the central channel during spring tides were $2.25 ms^{-1}$, which is well below the maximum speeds that bottlenose dolphins are capable of swimming at ($8.2 ms^{-1}$; Rohr et al. 2002) and observations both here (Ingram 2000) and elsewhere (Pierpoint 2008, Bailey & Thompson 2010) show small cetaceans regularly moving against prominent current flows. Dolphin movements in the estuary are therefore likely independent of direct advection, and so tidally driven changes in habitat use are probably induced by corresponding changes in prey availability (Hastie et al. 2004). The highly dynamic characteristics of estuarine systems mean a number of mechanistic processes could underlie the distributions of prey and their availability to predators. My observations indicate these are likely related to interactions between tide and topography.

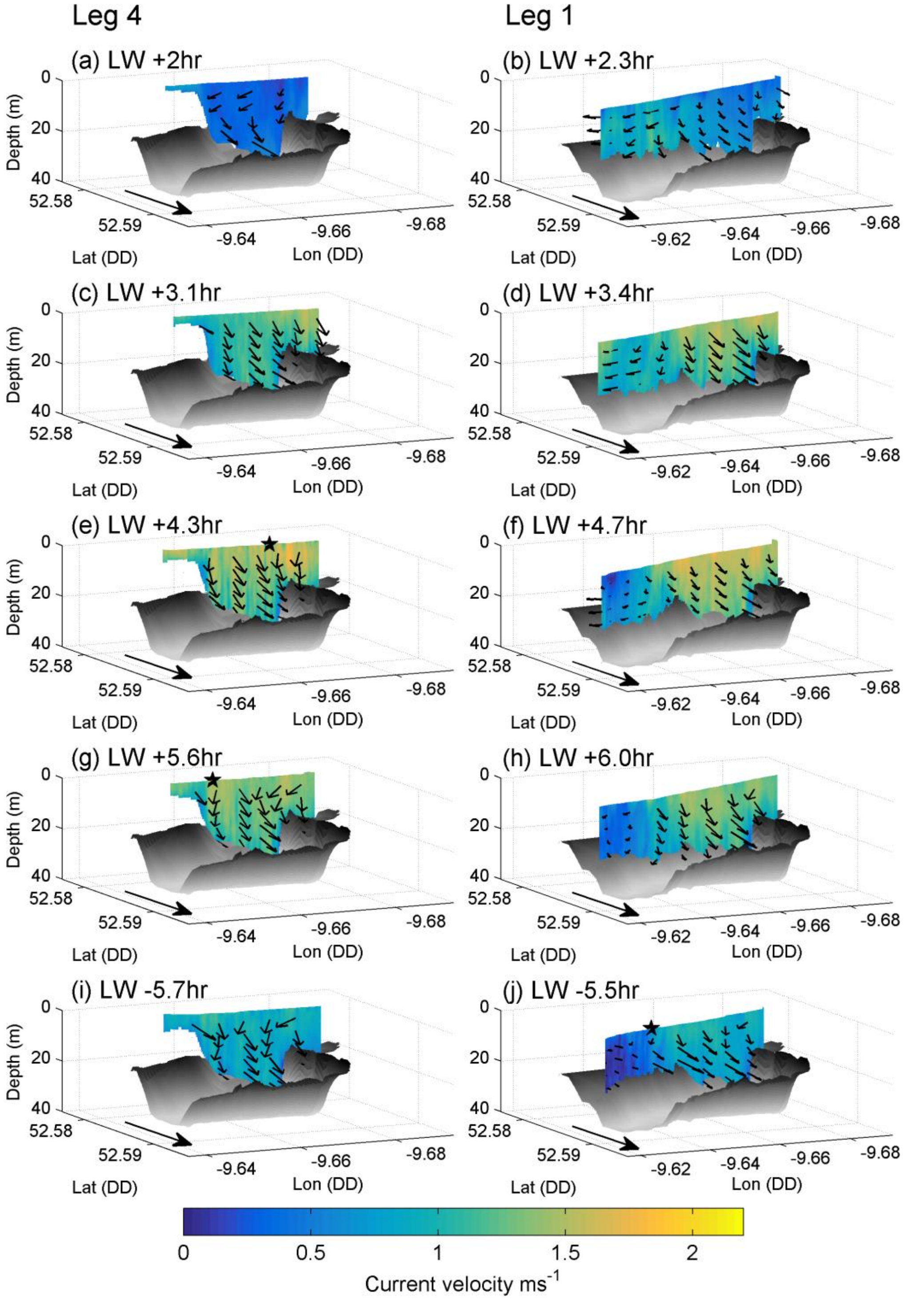

Figure 6.8. Current velocities and directions (small black arrows at 5m vertical depth intervals and 75 second horizontal time intervals) as measured by the acoustic Doppler current profiler (ADCP) during the oceanographic surveys in the central channel (Figure 6.1.c) on the 28th May 2014. The left hand column (a, c, e, g & i) shows leg four of the survey and the right hand column (b, d, f, h & j) leg one. Each row corresponds to a different circuit of the survey route. Relative time to low water (LW) is indicated in the top left of each subplot. Only circuits completed during the flood and high tide, when dolphin presence in the region was high, are shown. Multibeam bathymetry for the channel is shown in grey. The thick black arrow shows the orientation of the plot relative to north. Times of dolphin sightings (in subplots e, g and j) are marked with a black star. Legs two and three of surveying can be viewed in Appendix A3.9.

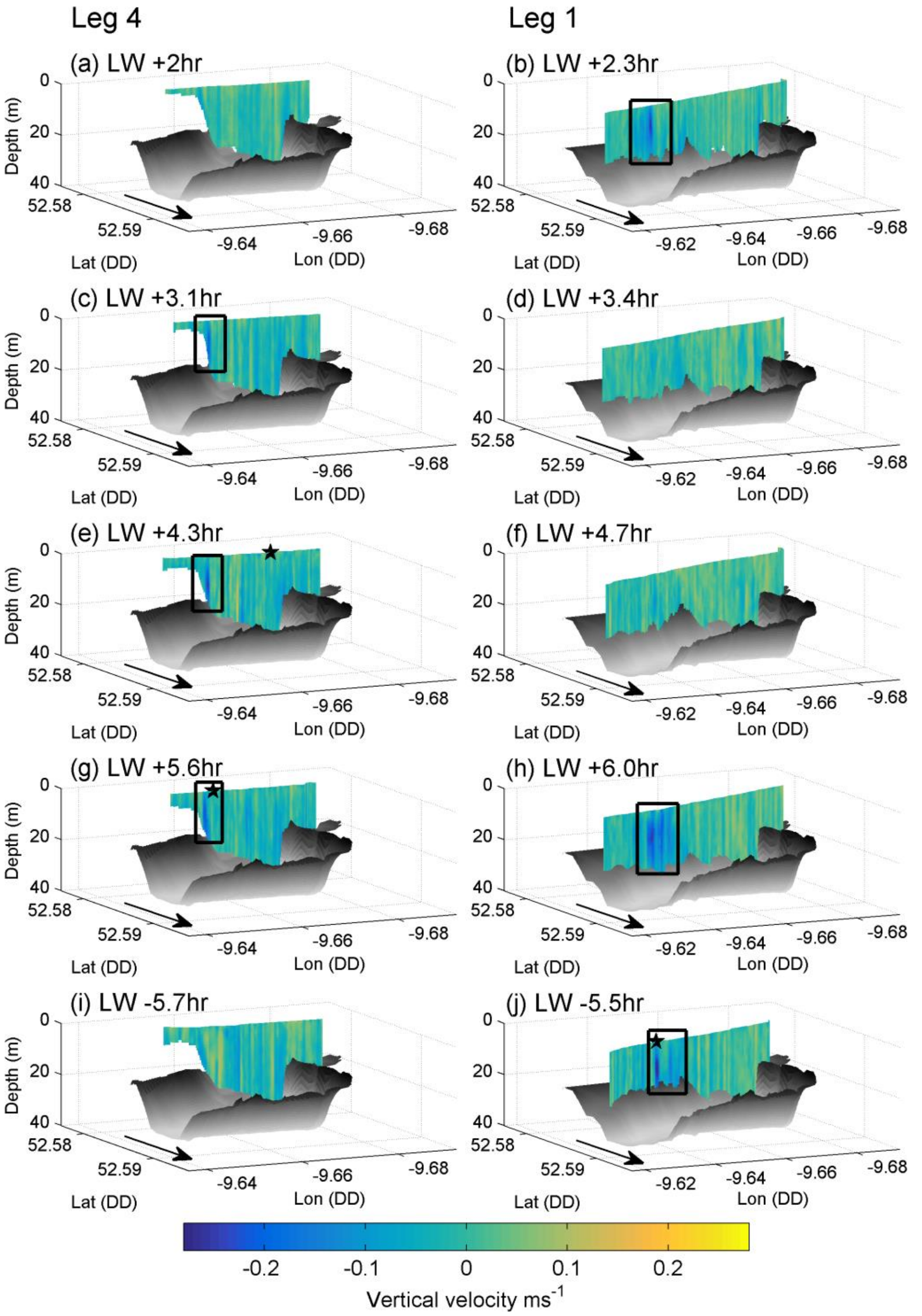

Figure 6.9 Vertical velocities as measured by the acoustic Doppler current profiler (ADCP) during the oceanographic surveys of the central channel (see Figure 6.1.c) on the 28th May 2014. Strong persistent downwelling features are highlighted by the black boxes that were also evident at the surface as lines of foam that reflected strong convergence. The left hand column (a, c, e, g & i) shows leg four of the survey and the right hand column (b, d, f, h & j) leg one. Each row corresponds to a different circuit of the survey route. Relative time to low water (LW) is indicated in the top left of each subplot. Only circuits completed during the flood and high tide, when dolphin presence in the region was high, are shown. Multibeam bathymetry for the channel is shown in grey. The thick black arrow shows the orientation of the plot relative to north. Times of dolphin sightings (in subplots e, g and j) are marked with a black star. Legs two and three of surveying can be viewed in Appendix A3.9.

6.4.1 Tidally mediated topographic foraging habitats

The two regions where dolphin occurrence was most tidally dependent were both characterised by the presence of narrow steep-sided topographic channels, where strong current flows were either expected or directly measured (Figure 6.1.b & 6.8). Dolphins in the Shannon estuary feed on a number of fish species that likely includes salmon *Salmo salar* (McDermott 1990, Janik 2000, Rogan et al. 2000). These fish are known to travel upstream with prevailing tidal currents during flood flows (Groot et al. 1975, Olson & Quinn 1993), and narrow topographic channels likely act as a bottleneck to these movements concentrating prey into densely packed aggregations (Zamon 2001, Bailey & Thompson 2010). As such, dolphins presumably concentrated within the central and upper channels during flood flows because these locations provided a predictable and prosperous foraging resource. The steep sides of these channels may also have provided dolphins with a barrier against which prey could be actively herded (Heimlich-Boran 1988), aiding in their successful capture. However, that individuals did not occupy these regions during ebb tidal floods (when it would be expected that prey advected out the estuary would be similarly concentrated) suggests additional processes may be at work.

The occurrence of dolphins in the central channel near Carrigaholt was greater, and more tidally dependent than at the upper estuary channel by Tarbert. Whilst this may be a by-product of overall distributional patterns in the estuary (i.e. great occupancy of the mouth of the estuary), there are further, distinguishing features at this site that may make it additionally attractive to dolphins. Unlike the upper estuary channel, the central channel occurs on the edge of a right-angled bend at which a shallow bank is located (Figure 6.1.b). This pronounced curvature in the profile of the channel drives a separation of flow on the flood tide, creating a leeward wake of slower moving water on the north-eastern edge of the southern bank (Figure 6.8.f, h & j). Water from the bank appears to pour downwards into this wake and, on convergence with the fast flowing water of the centre of the channel, forms a hydrographic front. Along the front, distinctive downwelling features were identified (Figure 6.9) that coincided with the locations and times at which dolphins were regularly present (Figure 6.2). Whilst the exact mechanisms that drive dolphin use of the central channel during flood tides cannot be definitively resolved without quantitative measurements of the distributions of plankton, fish prey, and the underwater movements of these predators, the hydrodynamic features described may attract dolphins because of their potential to increase foraging efficiency via (1) extending the barrier created by the steep slopes of the channel against which prey can be herded, and/or (2) mechanically accumulating prey that have been advected into the channel into densely packed aggregations.

Dolphins employ a number of complex foraging behaviours to aid in prey capture (Benoit-Bird & Au 2009). These range from the use of physical structures, such as the sea floor and surface, against which prey are herded (Fertl & Wursig 1995, Finn et al. 2009), to self-generated disturbance to the water column that disorientates and/or traps prey (Fertl & Wilson 1997, Lewis & Schroeder 2003). The strong downwelling features observed in the central channel of the estuary are likely capable of influencing prey behaviours, and dolphins may exploit this to manipulate prey prior to capture events. When forced into complex hydrographic structures prey can become disorientated and behave in a predictable fashion (Liao 2007) making them easier for dolphins to catch, whilst an avoidance of associated turbulent flows (Yousif & Aglen 1999, Nichol & Somerton 2002) may limit escape options during interactions with dolphins.

Alternatively, the convergent currents and downwelling features present during flood flows around the southern bank of the central channel may act to advect plankton and prey species into an associated leeward wake of calmer water where they become trapped (Farmer et al. 1995, Zamon 2002). In the St Lawrence estuary, upwelling induced by tidal flow against abrupt topographies has been shown to herd plankton and fish species into dense aggregations at a whale feeding hotspot (Simard et al. 2002, Cotté & Simard 2005), whilst in the Bay of Fundy, increased concentrations of plankton and fish species foraged upon by harbour porpoise *Phocoena phocoena*, minke *Balaenoptera acutotstrata* and fin *Balaenoptera physalus* whales (Johnston et al. 2005a, Johnston et al. 2005b) correspond to the periodic presence of shear induced hydrographic fronts, generated along the edge of a leeward wake that occurs when tidal flow is interrupted by an island (Johnston et al. 2005b, Johnston & Read 2007). Subsequently, these features appear capable of providing large marine vertebrate predators with a localised and predictable prey resource (Cotté & Simard 2005, Johnston et al. 2005a).

During ebb tide flows, dolphin occurrence in the central channel was low, especially on larger tides (Figure 6.7), suggesting that prey aggregations created during the flood tide are dispersed with the onset of ebb flow. Tidally dominated systems, where prey are aggregated during flood tides, often experience a flushing during ebb conditions (Simard et al. 2002), and a peak in dolphin occurrence at the mouth of the estuary during the first half of the ebb may reflect this.

6.4.2 Habitat predictability within an estuarine environment

Estuaries are highly complex and dynamic environments, yet interactions between tidal currents and topography appear to create predictable habitats that large marine vertebrate predators exploit. Predictability in foraging habitat is particularly important for marine predators, whose foraging efficiency is limited by their ability to search for and locate habitats where prey are available (Gende & Sigler 2006). As such, these habitats may represent critical areas within the range of a population.

The Shannon Estuary is a highly productive system (O'Boyle & Silke 2010) yet coupling between trophic levels appears to be constrained both spatially and temporally, suggesting prey are not randomly distributed and changes in distribution rather than overall abundance are important (Zamon 2003, Boyd et al. 2015). The dynamic nature of estuarine systems likely means they are energetically expensive for large marine vertebrate predators to inhabit. Measured current speeds in the Shannon estuary surpassed the energetically efficient swimming speed of bottlenose dolphins ($2.1ms^{-1}$; Williams et al. 1992), and individuals regularly sighted moving against prevalent tidal currents (Ingram 2000) would be required to swim at speeds exceeding this. Knowledge of the locations and times at which prey are available allows predators to adjust their movements in the estuary so as energy expended in moving through these environments is minimised, and offset by gains in foraging efficiency. This is reflected in the low occurrence of dolphins in the upper estuary during ebb tides, when currents are particularly strong and the features thought to increase prey availability absent.

The ADCP survey of the central channel was conducted during peak spring conditions on an above average sized tide (4.9m versus an average peak spring tide of 4.3m and overall average tide of 3.3m). Subsequently, the current regime identified may not be fully representative of those that occur during smaller tides. However, my analysis encompassing observations in the central channel across a range of spring-neap conditions found that the occurrence of dolphins during flood tides was increased when the size of the tide (as indicated by daily change in tidal height) was bigger (Figure 6.7.d). This suggests that the conditions during which the ADCP surveys were performed were representative of the conditions associated with high levels of bottlenose dolphin occurrence. Additional oceanographic surveys, alongside long-term moored deployments that encompass a variety of tidal ranges, would improve our understanding of how the current regimes of the estuary vary with the size of the tide and how this may impact upon the suitability of the area for dolphins.

6.4.3 Implications to conservation and management

The Shannon estuary is subject to intense anthropogenic pressure from a number of stressors. A deep water port at Foynes regularly caters for some 2000 commercial ships annually, with sizes of up to 289m by 17.4m (length by width) and a maximum dead weight tonnage of 200,000 (Anonymous 2012). During flood tides, dolphins concentrated in two core areas of the estuary, the locations of which likely coincide with the predominate routes followed by shipping traffic navigating the complex topographies of the region. Moreover, tourist boat operators run in excess of 200 dolphin watching trips annually that focus on the area of highest dolphin site use (Berrow & Holmes 1999). The likely significance of these sites as foraging hotspots means the potential for disturbance to bottlenose dolphins is high (Pirotta et al. 2015), and this should be considered in the management of the SAC. In addition, the Shannon estuary has been recently identified as a suitable site for the future development of MREIs (O'Rourke et al. 2010). Dolphin occurrence at core locations in the estuary was dependent on both tidal phase and the size of the tide. The potential for MREIs to impact the current regimes of the estuary (Shields et al. 2011), and as such alter the critical habitats of dolphins, should be carefully considered in their development and implementation across the SAC.

On a wider context, I have shown that within estuarine environments, habitat use by a large marine vertebrate predator is variable and dependent upon complex interactions between topography and tidal currents. The implications of this are far ranging, impacting both the methods used to assess the habitat use and population dynamics of coastal marine predators, and the strategies implemented in the management of associated ecosystems. Surveying of similar coastal systems, where the influence of tide and topography is prominent, will require sufficient spatio-temporal coverage so as to be able to identify core habitat locations that may occur periodically (e.g. Pirotta et al. 2014b). Moreover, failing to account for spatio-temporal variability in distributions can have significant impacts on population abundance estimates (Johnston et al. 2005b). Integrative management of these near-coastal tidal-topographic systems can benefit from the identification of important habitat locations. I show that the preferred habitats of bottlenose dolphins are highly predictable on localised spatio-temporal scales and so can be used to regulate overlap between marine predators and a number of concentrated, spatially explicit anthropogenic stressors. Moreover, my results suggest that the effective management of MREIs will require a good knowledge of the physical processes that underlie the formation of critical habitats so as to be able to minimise the potential impacts of this fast growing industry, that is particularly pronounced in near-coastal regions (Waggitt & Scott 2014).

6.5 Conclusions

This study provides evidence to suggest that complex coastal topographies can modify tidal current patterns and influence the structure of dynamic marine ecosystems. I have shown that the foraging habitats favoured by a resident population of bottlenose dolphins occur as a result of complex interactions between topography and tidal currents. I suggest tidal topographically mediated hydrodynamic features aid animals in capturing their prey, and so constitute important foraging habitat features within estuarine environments. Growing evidence suggests that within coastal regions, these types of features are important to a diverse range of large marine vertebrate predators. Incorporating quantitative measurements of the distributions of plankton, mid-trophic level prey, and the underwater movements of associated predators into future studies would add valuable insights toward the functional mechanisms that underlie the use of these habitat hotspots. Nevertheless, detailed measurements of the dynamic hydrography of a tidally active topographic site, alongside spatio-temporally comprehensive fine-scale observations of animal distributions, can provide new insight into the drivers of habitat selection and increase our understanding of potential interactions between coastal dolphins and anthropogenic activities in tidally dominant coastal systems.

CHAPTER VII

General discussion

7.1 Introduction

Together the main findings of this thesis indicate that physical processes play a fundamental role in the structuring of marine ecosystems. The at-sea behaviours and distributions of marine predators were linked to a number of oceanographic features, including tidal-mixing fronts and tidally-mediated topographic structures, which were often found to be persistent and/or predictable in occurrence (dependent on spatio-temporal scale). The characteristics of these associations were variable and regulated both by the bio-physical properties of a feature and species-specific aspects of foraging ecology. This was likely due to the attributes of corresponding prey resources (e.g. accessibility and availability).

This chapter examines how the studies presented in the thesis extend our current understanding of the physical processes that underlie the at-sea behaviours and distributions of large marine vertebrate predators in coastal and shelf-sea environments. The bio-physical properties of important habitat features are discussed alongside species specificity in marine predator associations and the implications of habitat heterogeneity on foraging strategies. Recommendations for future research are then highlighted. This chapter also discusses key methodological techniques available for these investigations, aiming to provide valuable insight towards corresponding considerations and limitations alongside possible solutions for recommended future research questions. Finally, the implications of the findings of the thesis to marine conservation and management are briefly considered.

7.2 The use of physical oceanographic habitats by marine predators in shelf-seas: main findings and future directions

Shelf-seas are vast, heterogeneous environments. The resultant patchy nature of prey distributions means large marine vertebrate predators face substantial challenges when foraging (Weimerskirch et al. 2005, Sims et al. 2006). The studies presented in this thesis, alongside those reviewed in Chapter II, show a number of key oceanographic features are preferentially foraged at by a diverse range of marine mammals and seabirds, which suggests that physical processes are capable of generating high quality habitats that aid marine predators in fulfilling their often considerable energetic requirements (Williams et al. 2001). Essential components of these habitats were the capacity to provide persistent and/or predictable foraging resources, which were highly accessible as defined by changes in the behaviours, densities and vertical distributions of associated prey aggregations.

7.2.1 Bio-physical dynamics of ecologically significant oceanographic features

Studies presented in this thesis suggest that intricate interactions between heat influx (that drives the seasonal stratification of offshore shelf-sea waters), tidal currents and shallow complex topography create a diversity of persistence and/or predictable oceanographic habitats that are regularly foraged at by a number of large marine vertebrate predators. The mechanisms by which these processes influenced the behaviours of marine predators appear to be dependent upon the individual characteristics of the physical feature involved and showed distinct site specificity.

In Chapters IV and V, the behaviours and distributions of marine predators were shown to correlate with the seasonal formation and occurrence of offshore oceanographic habitats generated at and around tidal-mixing fronts. The significance of tidal-mixing fronts is thought to stem from corresponding increases in primary productivity (Simpson et al. 1979, Holligan 1981, Franks 1992a, Boersma et al. 2009) that increase prey accessibility by attracting dense surface aggregations of forage and pelagic fish (Russell et al. 1999, Vlietstra et al. 2005). However, direct evidence of the bio-physical mechanisms that create these foraging opportunities is often lacking. Chapter III shows that episodic periods of turbulent mixing and stability (induced by the re-establishment of thermal stratification) with the spring-neap cycle were crucial to generating high levels of productivity in the late summer months. Moreover, piscivorous northern gannets *Morus bassanus* and common dolphins *Delphinus delphis* were directly linked to these patches of increased productivity suggesting these features drive tight coupling across multiple trophic levels. Together these findings demonstrate the crucial roles tidal currents and stratification play in the formation of marine predator foraging habitats around tidal-mixing fronts.

In Chapter VI, patterns in habitat use by bottlenose dolphins *Tursiops truncatus* residing in a nearshore, estuarine system were examined. This region was oceanographically distinct from the offshore habitats examined in Chapters III, IV and V in that it was both topographically complex, and regularly subjected to strong current flows that were at least double peak measurements acquired around the tidal-mixing front in Chapter III. Alongside distinct tidal periodicity in the use of key habitat sites by bottlenose dolphins throughout both spring and neap conditions, increased productivity levels, typically generated during prolonged periods of stratification (of at least three to seven days; Cloern 1991), were not expected to be the predominant drivers of habitat formation. Away from estuaries, large marine vertebrate predators are known to be attracted to nearshore coastal habitats because of corresponding changes in the behaviours and distributions of plankton and small prey (e.g. forage fish) in response to strong tidal currents (Simard et al. 2002, Cotté & Simard 2005, Johnston et al. 2005b) and complex topography (Zamon 2001). Moreover, tidal-topographic structures can also act as a barrier against which prey can be herded, and their occurrence may be incorporated into the complex foraging strategies often employed by species that hunt in groups (e.g. bottlenose dolphins). In Chapter VI, estuarine foraging habitats were characterised by the presence of transient but strong downwelling features that coincided in occurrence with the times when bottlenose dolphins were observed. This finding, in combination with previous work (Zamon 2001, Simard et al. 2002, Cotté & Simard 2005, Johnston et al. 2005b), suggests complex hydrodynamics, driven by intricate interactions between tidal currents and topography, play a crucial role in aiding marine predators to capture their prey.

Across the scientific literature, despite distinct site-specificity, the mechanisms by which interactions between tide, topography and stratification influence the behaviours of marine predators have been generally attributed to either (1) the presence of primary productivity at sufficient levels so as to attract high numbers of low to mid trophic level prey, (2) the mechanical accumulation and/or concentration of small nekton, or (3) the generation of a foraging aid against which prey can be herded. Studies presented in this thesis show stratification appears key to features where primary productivity is important, whilst intricate topography in areas subjected to convoluted current flows are essential for the generation of complex hydrodynamic features that accumulate biomass and/or act as a foraging aid. This likely has implications on both the suitability of a specific feature to a species and the susceptibility of an oceanographic habitat to anthropogenically induced disturbance.

7.2.2 Species specificity in habitat associations

The variable nature of associations between marine predators and physical oceanographic habitats did indeed also appear to be regulated by aspects of foraging ecology that included prey preference, physiological constraint and whether a species was opportunistic or specialist in its foraging strategy. In Chapter III, whilst both northern gannets and common dolphins were linked to patches of increased sub-surface productivity the specifics of correlations differed. Gannets foraged in areas of intermediate production whilst dolphins targeted areas where primary productivity was highest. These discrepancies were attributed to possible differences in foraging strategy driven by physiological constraint (near-surface feeders versus full water column access and/or visual forager versus ability to echolocate). In Chapter IV, contrasting patterns in habitat use were again observed, this time between two small cetaceans, dolphins (unspecified *Delphinid* species) and harbour porpoises *Phocoena phocoena*, with similar dive and prey detection capabilities. Alternating patterns in site use were accredited to disparities in habitat requirements stemming from differences in prey target and possibly foraging strategy (opportunistic versus specialist). This adds to a growing body of evidence that suggests species specificity plays a crucial role in the definition of a high quality foraging resource and so mediates the use of physical oceanographic features by foraging marine predators (Vilchis et al. 2006, Drew et al. 2013). In Chapter V, male and female gannets were shown to differ in their habitat preferences suggesting specificity may also exist between members of the same species. Together these findings highlight the need for a good understanding of a marine predators foraging ecology to be able to fully comprehend patterns in habitat use.

7.2.3 Implications for marine predator foraging

By targeting habitats where prey accessibility and availability is thought to be enhanced, marine predators have been shown to be able to optimise their foraging efficiency (Ropert-Coudert et al. 2009b, Borstad et al. 2011, Pelletier et al. 2012). Both the persistence and predictability of a foraging resource are known to play a key role in this (Gende & Sigler 2006, Davoren 2013) suggesting that memory is an important component to foraging (Weimerskirch 2007, Regular et al. 2013). As such, the spatio-temporal variability of an individual's preferred habitat likely drives the evolution of their specialised foraging strategies. For example, gannets foraging at shelf-sea fronts in the Celtic Sea have been shown to use restricted search patterns in areas of around 2 to 10km (Hamer et al. 2009, Scales et al. 2014a) reflective of the findings of Chapter III, that indicate a similarly scaled shift in the geographical position of a tidal-mixing front and the localised habitats surrounding it (increased sub-surface productivity) in response to episodic water mixing events. In contrast, bottlenose dolphins in tidally active estuarine habitats have been observed intensively searching in regions spanning only a few hundred metres (Bailey & Thompson 2010) that is reflective of the highly localised predictability of the tidally meditated topographic features identified in Chapter VI.

In addition to persistence and predictability, the accessibility of a prey resource is also known to depend upon its corresponding behaviour (Garthe et al. 2011, Crook & Davoren 2014), density (Enstipp et al. 2007, Benoit-Bird et al. 2013, Goldbogen et al. 2015), and vertical distribution through the water column (Friedlaender et al. 2006, Benoit-Bird et al. 2011, Boyd et al. 2015). In Chapter III, differences in the bio-physical properties of the localised habitats foraged at by gannets and common dolphins were suggested to possibly stem from differences in the required depth distributions of prey (although note this was also possibly attributable to differences in visibility requirements). Gannet foraging was thought to be limited to areas where prey were possibly available near the surface. Indeed the spatial distributions of closely related Peruvian boobies *Sula variegata* are known to be closely tied to the depth distributions of their prey (Boyd et al. 2015), and in Chapter V it was found that by foraging around fronts, gannets minimised the depths and durations of dives which may have reduced energetic expenditure. As such, by both providing a prey resource that can be exploited through less energetically costly behaviours, and whose location can be learnt and remembered, the physical oceanographic habitats used by marine predators likely represent critical locations within a population's range and foraging site fidelity across a number of species reflects this (Irons 1998, Pettex et al. 2010, Patrick et al. 2014).

7.2.4 Future directions

The main findings of the thesis show that, within shelf-seas, the distributions and foraging behaviours of marine predators are governed by a number of complex, variable and scale-dependent physical oceanographic processes, that are both region and species specific and likely have implications for the evolved foraging strategies of individuals. However, whilst these findings have contributed to furthering our understanding of the role physical processes play in habitat use by marine predators, studies were limited to only a few species and sites and this should be expanded upon. Moreover, a number of fundamental ecological questions remain which are highlighted below.

7.2.4.1 The trophic gap

The behaviours, distributions and movements of marine predators are likely driven by foraging decisions (Hastie et al. 2004, Warwick-Evans et al. 2015) that are ultimately motivated by the accessibility and availability of prey (Davoren 2013, Boyd et al. 2015). As such, marine predator responses to physical features imply these oceanographic habitats induce changes in the behaviours, densities, depth distributions and predictability of lower- to mid- trophic level prey. Direct links between piscivorous predators and patches of increased sub-surface primary productivity (Chapter III) suggest species from a number of trophic levels are attracted to these features whilst associated changes in the dive behaviours of gannets (Chapter V) indicate the accessibility and catchability of prey is likely increased. Accordingly, physical oceanographic habitats are often considered proxies for prey availability as other important aspects of a prey resource, beyond its simple presence, are represented (Torres et al. 2008, Benoit-Bird et al. 2011, Boyd et al. 2015). However, direct evidence is lacking, and few studies have examined how physical features impact the lower- to mid- trophic level species that many marine predators feed on (but see Bertrand et al. 2008, Stevick et al. 2008, Hazen et al. 2011, Embling et al. 2012, Cox et al. 2013, Embling et al. 2013). As such, our understanding of marine predator habitat use in shelf-seas is constrained by this trophic gap. Often, attempts to address this have been complicated by the fine spatio-temporal scales at which prey measurements are required so as to be meaningful which constrains the use of broad scale techniques such as stable isotope analysis (Inger & Bearhop 2008) and the mapping of fisheries hotspots (Witt & Godley 2007). Addressing this trophic gap will require novel technical and analytical approaches that ideally incorporate sub-surface prey behaviours, densities and distributions (both horizontal and vertically through the water column) simultaneous to oceanographic sampling and animal movement observations.

7.2.4.2 How do marine predators perceive their environment?

An increased knowledge of how predators perceive their surrounding environment would aid in furthering our understanding of how individuals identify and interact with their preferred foraging habitats. The oceanographic features identified as important foraging locations for marine predators in Chapter II were generally predictable in occurrence, as were the involved physical processes examined in Chapters III, IV, V and VI (although the spatio-temporal scales over which this occurred varied). As such, memory and learning capacity are likely important components in the ability of an individual to successfully find and exploit these habitats (Regular et al. 2013). Knowledge transfer between conspecifics may also be important in some species (Machovsky-Capuska et al. 2014). For example, bottlenose dolphins using the tidal features of the Shannon in Chapter VI belong to a small discrete population, and matrilineal cultural learning (Krutzen et al. 2005) is likely important in the fostering of the complex behavioural use of this dynamic habitat. However, marine predators are known to additionally use a range of other techniques to locate their prey, such as sight (Bodey et al. 2014, Tremblay et al. 2014, Bairos-Novak et al. 2015) and smell (Savoca & Nevitt 2014), and these should also be further investigated.

7.2.4.3 Is there an energetic advantage to exploiting oceanographic habitats?

The multiple links that have now been made between marine predators and a multitude of oceanographic habitats occurring across shelf-seas begs the question of whether there is an energetic advantage to foraging at and around these features. In Chapter V the dives of northern gannets foraging around shelf-sea fronts were shown to be shorter and shallower than those dives performed elsewhere, suggestive of an increase in efficiency.

However this could not be definitively ascertained. In some instances, comparative measures of fitness have been shown to vary between years of differing oceanographic regimes (e.g. reproductive output; Borstad et al. 2011) suggesting oceanographic influences on prey accessibility and availability impact foraging efficiency. Ideally future studies will incorporate measures of prey capture rates and energetic expenditure which would aid in elucidating this.

7.3 Linking habitat use by marine vertebrate predators to physical oceanographic processes: methodological approaches

To be able to adequately identify, describe and quantify the diverse nature of interactions occurring between marine predators and key physical habitat features, the studies presented in the thesis employed a range of methodological techniques including at-sea boat surveying, animal-borne telemetry and passive acoustic monitoring. These were then coupled to a number of oceanographic datasets sourced via *in-situ* sampling, remote-sensing and numerical modelling. For each chapter, the combination of approaches used was tailored relative to the corresponding aims and objectives of the work. This required careful consideration of the applicability of each of the available approaches alongside associated constraints and potential complications. In a number of cases, the nature of resultant datasets necessitated the use of specialised analytical and statistical techniques. Insight gained through this process is discussed below.

7.3.1 At-sea boat surveys

At-sea boat surveying allows direct observation of animals and the environmental conditions in which they are occupying to be made. Furthermore, oceanographic sampling can span the entire water column. As such, this approach is particularly useful for understanding the bio-physical dynamics of the habitats favoured by marine predators (Tremblay et al. 2009, Ainley et al. 2012). Indeed, in Chapter III the use of at-sea boat surveying provided valuable insights toward patterns in sub-surface primary productivity and its importance to marine predators, that would likely have been missed through the use of other methodological approaches (e.g. animal-borne biologging coupled to remote-sensing). Moreover, the *in-situ* nature of this type of sampling means information on prey behaviours and distributions can also be obtained (Embling et al. 2012, Cox et al. 2013). However, the underwater behaviours of predators are generally missed (which is particularly pertinent to cetacean sightings), although videography may be used to observe those individuals within the immediate vicinity of the boat (dependent on water clarity; Machovsky-Capuska et al. 2011).

Often identifying key habitat components for marine predators alongside the oceanographic processes that drive their production requires data of differing spatio-temporal scales. As such, in Chapters III and VI, a two-step surveying approach was employed that allowed habitat use over broader spatial extents to be examined whilst reserving localised intensive surveying for further investigation of the fine-scale dynamics of key features. This nested approach minimised the high cost and effort generally associated with these types of surveys. In some instances the two approaches can be combined (see Embling et al. 2012, Embling et al. 2013, Scott et al. 2013), although this is generally only suitable when features of interest are identified beforehand, and are highly localised and predictable in their spatio-temporal extent (e.g. offshore banks where internal waves propagate).

The predominant disadvantages of at-sea boat surveying are the costs and effort associated with obtaining sufficient spatio-temporal coverage of a region so as to be able to identify the key foraging locations of marine predators, alongside an inability to be able to operate during adverse weather conditions. As such, data are typically limited in either their spatial or temporal extent, which can be particularly problematic when animals are sparsely distributed (as was the case in Chapter III). Moreover, inconspicuous species (such as harbour porpoise) may be missed in less than perfect sea states (Embling et al. 2010). Ideally, standardised survey routes should be repeated during calm conditions across a number of months and years, and this approach proved successful in Chapter VI, where the tidal dependency of habitat use required observations across a range of hydrodynamic conditions so as to be adequately identified and observed. This was achievable, in part, due to the near-shore and discrete nature of the estuarine system, alongside the localised range and protected status of the animals that inhabited it, which together meant long-term data from previously funded projects were available for analysis. Indeed, few other studies exist that have had access to such a long-term dataset of repeat standardised surveying due to the logistical demands of building such a dataset. However, these types of studies are particularly useful in the conservation of vulnerable coastal animal populations that occupy discretely defined regions.

7.3.2 Animal-borne biologging

In the last 20 years, advancements in animal-borne biologging mean the three-dimensional movements of marine predators can now be observed across their entire range, providing unprecedented information on animal behaviours (Ropert-Coudert & Wilson 2005, Bograd et al. 2010, Costa et al. 2010, Hazen et al. 2012). As such, these techniques are particularly well suited to investigating the behavioural responses of individuals to habitat heterogeneity. Moreover, the individual based approach of these methods means additional information of condition (Borstad et al. 2011) and gender (Cleasby et al. 2015) can be incorporated into analyses. In Chapter V, GPS tracking and time-depth recorders (TDRs) were used in combination to log the geographical locations of gannet dive events and characterise their vertical profiles, providing valuable insight toward the functional mechanisms that link marine predators to shelf-sea fronts whilst also allowing for sex-segregation in habitat use.

Due to a paucity of *in-situ* oceanographic data at matching spatio-temporal scales, most studies that use tracking data to investigate the foraging behaviours and distributions of marine predators in relation to habitat heterogeneity use satellite derived broad-scale environmental descriptors such as sea surface temperature (SST) and ocean colour (Tremblay et al. 2009). However, this approach is somewhat questionable, often procuring variable results (Burger 2003, Gremillet et al. 2008, Suryan et al. 2012), that rather than identifying the processes that influence prey availability and drive habitat use, provide broad-scale descriptors of the oceanographic conditions experienced where individual marine predators are present (Tremblay et al. 2009). As such, in Chapter V composite front mapping techniques (Miller 2009, Miller & Christodoulou 2014) were used to identify and test the importance to foraging marine predators of discrete physical features that, a priori were expected to provide prosperous foraging opportunities by increasing prey availability. This proved successful, adding to a growing body of research that demonstrates front metrics can be used to further our understanding of habitat use by a number of marine predators (Scales et al. 2014b, Miller et al. 2015, Scales et al. 2015). However, these data are restricted to the sea surface, yet the foraging decisions made by marine predators are governed by three-dimensional sub-surface processes. Biologging can also provide information on *in-situ* oceanographic conditions (Daunt et al. 2003, Charrassin et al. 2008), the addition of which would provide valuable insight of the sub-surface conditions experienced by individuals around frontal features. Although the TDRs used in Chapter V were capable of recording temperature, on post-processing, the response times of the thermistors (3.8 to 28 seconds) lagged considerably behind the velocities of gannet movements both when transitioning between air and water and when submerged. As such, these outputs could not be used in analyses.

The predominant disadvantage of animal-borne biologging techniques stems from the limited number of animals that can logistically be equipped with devices. For example, in Chapter V, the proportion of individuals tagged represented less than 0.001% of the known population and was restricted to breeding individuals (to aid in tag retrieval). As such, although population level inferences are commonly made, relationships may be vulnerable to individually specialised behaviours (Patrick et al. 2014, Ceia & Ramos 2015), whilst information from core groups may be missing (e.g. immature individuals; Votier et al. 2011). In addition, whilst individuals can be tracked across vast distances, they are not directly observed and so advanced analytical techniques are often required to infer behavioural states (e.g. area restricted search and state-space modelling; Fauchald & Tveraa 2003, Patterson et al. 2008). The use of additional devices such as accelerometers, animal borne videography, TDRs (as demonstrated in Chapter V) and wet-dry sensors can aid in this (Votier et al. 2013, Warwick-Evans et al. 2015). Moreover, these devices can also be used to obtain information on prey fields, capture rates and energetic expenditure (Viviant et al. 2010, Watanabe & Takahashi 2013).

7.3.3 Passive acoustic monitoring

Passive acoustic monitoring (typically achieved through hydrophones and CPODs; Rayment et al. 2009, Thompson et al. 2010, Yurk et al. 2010, Kyhn et al. 2012) can be used to continuously log the activity of echolocating marine mammals over long temporal scales with minimal effort and cost (Philpott et al. 2007, Todd et al. 2009). As such, this approach is particularly suitable for linking patterns in site use to localised dynamic habitat features. Moreover, animals that are particularly inconspicuous in their behaviours (i.e. are shy and spend long periods of time submerged) can be detected, that may have otherwise been missed during boat or land based visual surveying. Ideally devices should be deployed at multiple locations across a site to be able to resolve localised versus regional patterns in species occurrence.

In Chapter IV, dolphin and harbour porpoise detections acquired from CPODs were coupled with remotely-sensed and numerically modelled environmental data to determine if site use was correlated with changes bio-physical oceanographic conditions. However, the localised nature of the data collected meant that, for fine-scale analyses the spatio-temporal scale of the remotely sensed data (1-4km over weekly composites) was too coarse and so investigations were constrained to broad-scale patterns in habitat use. Incorporating moored oceanographic sensors could have aided in addressing this. For example, temperature loggers positioned at regular intervals through the water column would have allowed the fine-scale movements of a tidal-mixing front with the spring-neap cycle across the site to be resolved.

The localised and remote nature of passive acoustic monitoring means several constraints are inherent with its use. It is difficult to distinguish between the vocalisations of closely related species (i.e. some *Delphinids*) whilst abundance estimations are rarely achieved. Moreover, non-vocalising behaviours may be missed and detection capabilities can vary with device configuration and deployment location (Thomsen et al. 2005) or during periods when background noise levels are increased (e.g. due to tidally induced turbulence or ship sonar). Coupled to the impracticality of mooring these instruments in areas exposed to extreme current velocities, passive acoustic monitoring approaches are generally not well suited to studies of tidally active areas (but see Wilson et al. 2013).

7.3.4 Modelling interactions between marine predators and physical oceanographic processes

The often large and complex datasets generated through at-sea surveying, animal-borne biologging and passive acoustics requires the use of sophisticated processing and analytical procedures. As such a number of both data processing and statistical techniques were demonstrated across the studies in Chapter III, IV, V and VI.

7.3.4.1 Data processing

Matching at-sea boat observations with *in-situ* oceanographic sampling requires that oceanographic data are summarised in a manner suitable for statistical comparisons with animal behaviours. Typically this involves creating a set of explanatory variables that represent the conditions sampled concurrent to the spatio-temporal location of an animal sighting. Chapter III (Table 3.2) demonstrates several techniques for achieving this, that have been applied across a number habitat selection studies (Scott et al. 2010, Embling et al. 2012, Cox et al. 2013, Scott et al. 2013). In some instances, animal observations may not have followed a predetermined sampling regime (e.g. Chapter VI) and so standardisation of the survey is required prior to the incorporation of information on oceanographic conditions. This can be achieved using standard interpolation techniques.

Understanding habitat-use by marine predators generally requires information both on where an animal was present and where it was absent. This can be problematic when using datasets obtained via animal-borne biologging, where information is available solely on locations an individual visited. A number of techniques are available to address this for which there are several comprehensive reviews (Aarts et al. 2008, Wakefield et al. 2009, Warton & Aarts 2013). In Chapter V, a habitat use-availability analysis was used to generate a series of pseudo absences against which dive events could be compared. The combined use of remote-sensing in this study meant that the oceanographic conditions at these locations could be easily obtained.

Passive acoustic monitoring typically generates large datasets of echolocation detections which require considerable processing to reach a format suitable for statistical analyses. For CPODs, accompanying software (www.chelonia.co.uk) can be used to automatically classify detections into probable groupings. Detection frequencies can then be extracted over a number of temporal extents. To minimise the effects of non-vocalising behaviours, in Chapter IV these were extracted as detection positive hours per day. Finer-scale analyses could be conducted using presence/absence over hourly intervals. In some cases detection positive minutes per hour may be used although this increases bias introduced from differences in the detection capabilities of devices, repeat observations of the same animal and the inability to detect non-vocalising behaviours.

7.3.4.2 Statistical analysis

Regression based statistical techniques are commonly employed when investigating habitat use by marine predators (Redfern et al. 2006, Fieberg et al. 2010) and were the predominant analytical methods used across the studies presented in this thesis. Sparsity in sightings is a common issue with animal observations made during at-sea boat surveying and typically results in zero-inflation that can lead to models that are over-dispersed, impeding statistical inference. To account for this, in Chapter III zero-inflated hurdle models were used (Zeileis et al. 2008, Zuur et al. 2012). In some instances zero-inflation may be so extreme that analyses are restricted to presence-absence models, and patterns in abundance cannot be investigated.

Often the way in which information is collected results in datasets that violate the assumption of independence between data points, a feature central to regression modelling frameworks (Zuur et al. 2009, Zuur et al. 2010, Fieberg et al. 2010). Data may be serially autocorrelated, spatially aggregated and/or pseudoreplicated (i.e. repeat observations from one individual). Ignoring such characteristics can result in parameter bias, underestimation of standard errors and artificially inflated significance values (Hamel et al. 2012). As such, in Chapter IV a mixed modelling framework was employed (Bolker et al. 2008, Zuur et al. 2009, Fieberg et al. 2010) to account for temporal auto-correlation in serial detection frequencies. This also allowed for variation in the detection capabilities of CPODs to be accounted for through the incorporation of a random effect. In Chapter V, gannet dive events were clustered, both by individual and through time. Again a mixed modelling framework proved successful at dealing with this and incorporated individual variation in behaviours between birds (Patrick et al. 2014). In Chapter VI, generalised estimating equations (Hardin & Hilbe 2002) allowed non-independence between data points resulting from photo-identification follows without the need for a random effect. These work by inflating the standard errors of associated parameter estimates resulting in adjusted and realistic *p*-values.

Relationships between the behaviours of marine predators and oceanographic conditions may not always be linear in their characteristics. Individuals may associate with a particular range of values presenting certain statistical challenges. Moreover, some explanatory variables may be circular with the minimum and maximum values representing identical conditions (e.g. directions and temporal tidal variables). Additive modelling techniques are a good tool for dealing with this and were used in Chapters IV and VI. In some cases, modelling the non-linearity of a relationship may be achieved through the incorporation of quadratic terms (Crawley 2007), which may be preferable when modelling frameworks are already complicated (e.g. zero-inflated models in Chapter III).

7.3.5 Future directions

A number of methodological techniques were employed across the various studies presented in the thesis, and their associated advantages and constraints have been discussed. At present there exists no 'one fit all' approach for investigating links between marine predators and the variable physical oceanographic habitats available across shelf-seas. As such, future research depends upon the adaptation and tailoring of current methodological techniques which, when used in combination, can provide valuable insight toward the functioning of marine ecosystems. New approaches to at-sea surveying are emerging that move away from the constraints of traditional strip-transect techniques. Two-step studies alongside repeat circuit designs have provided valuable insight of both habitat use by marine predators and involved bio-physical oceanographic processes (Chapters III and VI, Embling et al. 2012, Scott et al. 2013). Moreover the integration of underwater videography (Machovsky-Capuska et al. 2011, Crook & Davoren 2014) and active acoustical techniques (Benoit-Bird et al. 2011, Williamson et al. 2015) may add vital information of both associated prey resources and the underwater behaviours of marine predators. Submarine drones are an additional tool to this that can be equipped with an array of instrumentation, including passive acoustics, fisheries echosounders and undulating CTDs (conductivity-temperature-depth), to provide high resolution spatio-temporal data at minimal cost and effort (Suberg et al. 2014). Biologging technologies are also rapidly evolving and are now able to provide unprecedented levels of information about how an individual interacts with its environment. Information on oceanographic conditions can be obtained through remote-sensing and numerical modelling techniques which are fast improving in their ability to observe and predict the dynamic natures of the oceans. In some instances concurrent at-sea surveys have been used to also provide information on prey fields, and present the opportunity to sample sub-surface oceanographic conditions

(Gremillet et al. 2008, Boyd et al. 2015). As such, biologging will likely continue to play a key role in advancing the field of marine predator foraging ecology. In particular accelerometers and animal-borne videography appear to be especially promising avenues providing the opportunity to obtain information on the visual perception of an individual alongside fine-scale details of movements, allowing for encountered prey fields, capture attempts and energetic expenditures to be estimated (Viviant et al. 2010, Votier et al. 2013, Watanabe & Takahashi 2013, Tremblay et al. 2014).

7.4 Applications to conservation and management

Shelf-seas are subject to a number of anthropogenically induced pressures, including aquaculture, artisanal and commercial fishing, climate change, coastal development, marine renewable energy installations (MREIs), mineral resource extraction (i.e. gas and oil), pollution and recreational and industrial shipping. The effects of these stressors are far-reaching (Halpern et al. 2008) and as such, many marine predator populations have suffered severe declines in recent years (Croxall et al. 2012, McCauley et al. 2015) with concomitant consequences on ecosystem functioning (Heithaus et al. 2008, Baum & Worm 2009).

Studies in this thesis show that a number of physical oceanographic features in shelf-seas, including tidal-mixing fronts and tidal topographic structures, are important habitats for a range of large vertebrate marine predators. In many instances these habitats appear to represent critical locations within a species range by providing both a predictable and highly accessible foraging resource that allows for the use of efficient and effective behaviours. Protecting critical habitats has proved an important component in species conservation (Taylor et al. 2005) and so a good understanding of the oceanographic features favoured by marine predators is vital for the effective management of marine environments.

Marine predators spend large amounts of time within their preferred oceanographic habitats (Weimerskirch 2007) and so anthropogenically induced disturbance at these locations can have disproportionate effects on populations. This may occur as a result of direct increases in mortality through high levels of fisheries by-catch (Lewison et al. 2014) and collision with physical structures (e.g. MREIs and vessels; Laist et al. 2001), or displacement through avoidance induced behavioural changes (Pirotta et al. 2013, Chimienti et al. 2014). As such, reducing overlap between critical physical features and these spatially explicit anthropogenic activities/developments should be of high priority. The typically persistent and/or predictable nature of the oceanographic habitats favoured by marine predators makes conservational measures, such as marine protected areas (MPAs; Hyrenbach 2000, Hooker et al. 2011) and dynamic ocean management (DOM; Maxwell et al. 2015), particularly applicable.

A number of anthropogenically induced stressors have the potential to modify the physical structuring of marine ecosystems which may alter the dynamics of the oceanographic habitats that many marine predators are known to rely on (Ropert-Coudert et al. 2009b). Climate induced changes in the frequency and intensity of storm induced turbulent mixing (Young et al. 2011) may alter the spatio-temporal predictability of critical habitat locations (Hazen et al. 2013) whilst MREIs can modify the hydrodynamics of tidally-mediated topographic structures (Shields et al. 2011) with concomitant impacts on associated foraging opportunities. For example, the downwelling features associated with bottlenose dolphin foraging in Chapter VI may be particular vulnerable to disruption to the current regime of the estuary, which has received attention as a possible renewable energy resource (O'Rourke et al. 2010). Moreover, oceanographic features typically host individuals from multiple trophic levels and so a number of species may benefit from their preservation. In Chapter III, links between piscivorous marine predators and primary productivity suggested that tidal-mixing fronts are locations where high numbers of zooplankton and forage and pelagic fish are commonly found. A better understanding of the physical mechanisms that drive the creation of foraging habitat can aid in anticipating how marine ecosystems may respond to these changes, which will be useful in the development of precautionary conservation and management that is vital to achieving the objectives of ecosystem based management (Arkema et al. 2006, Crowder & Norse 2008).

7.5 Conclusions

In conclusion, this thesis shows that physical processes in shelf-seas create a number of oceanographic features that are key foraging habitats to large vertebrate predators such as marine mammals and seabirds. The thesis highlights the combined roles of tide, topography and thermal stratification in shaping the structures of shelf-sea ecosystems both offshore and around the coast. Specifically, marine predators were shown to forage at habitats generated at and around tidal-mixing fronts and tidally active coastal topographic structures. These features were characterised by the presence of either increases in sub-surface primary productivity or discrete hydrographic structures, that were thought to attract and accumulate mid-trophic level prey and aid in their capture. Moreover individuals exploiting these habitats were shown to alter their fine-scale vertical diving behaviours in a manner indicative of increased prey accessibility and availability. Together these findings highlight the important role physical oceanographic processes have in the provision of prosperous and reliable foraging resources that can be exploited by vulnerable marine predators in shelf-seas.

The studies presented in this thesis were completed through a combination of methodological techniques highlighting the need for adaptive and bespoke study designs that incorporate both continuous, fine-scale measurements of bio-physical conditions and the identification of discrete, physical oceanographic features. Future work should aim to further our current understanding of the functional mechanisms linking physical oceanography, prey and predators. Key to this is the additional incorporation of detailed three-dimensional measurements of prey behaviours, densities and distributions, and the addition of fine-scale predator movements that can be used to estimate foraging efficiencies. Identifying the physical oceanographic habitats used by marine predators and understanding the functional mechanisms that link the two can contribute towards achieving the objectives of ecosystem based management and marine conservation. It is hoped that the combined findings of this thesis encourage future studies aiming to understand the at-sea foraging ecology of marine predators to incorporate the fundamental role physical oceanography plays in shaping the ecosystems these animals inhabit.

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APPENDIX A1

Supplementary material for Chapter III

A1.1 Sea surface temperature (SST) maps for 2013

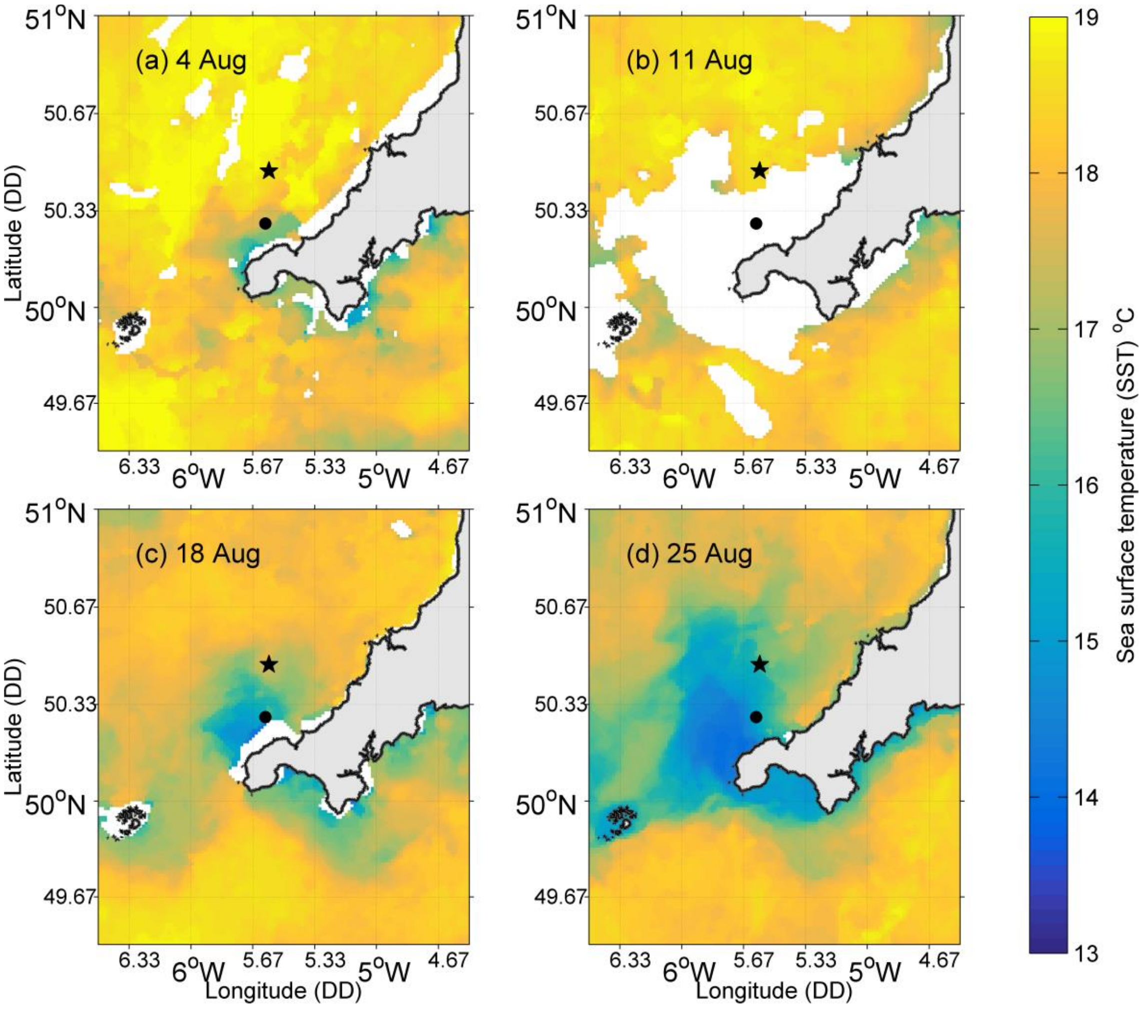

Figure A1.1 Seven-day composite sea surface temperature (SST) maps for the southeast Celtic Sea at weekly intervals through August 2013. From top left: (a) 04th August, (b) 11th August, (c) 18th August and (d) 25th August. The 4th August occurs within three days of peak neap tides. Offshore surface temperatures are around 19°C. Inshore waters are characterised by a small pool of cooler waters with temperatures of around 15°C. The 11th August occurs within two days of peak spring tides. The 18th of August occurs within two days of peak neap tides. Offshore water temperatures of around 18°C are 3°C higher than those observed in the inshore pool of cool waters which are between 14 °C and 15°C. The 25th of August occurs within two days of peak spring tides. The inshore pool of cool water has increased in size. Offshore waters in this instance are around 18°C and at least 4°C higher than those inshore that are around 14°C. The locations of the inshore and offshore tidal stations are indicated by the black filled circle and star respectively.

A1.2 Cross-front transect plots

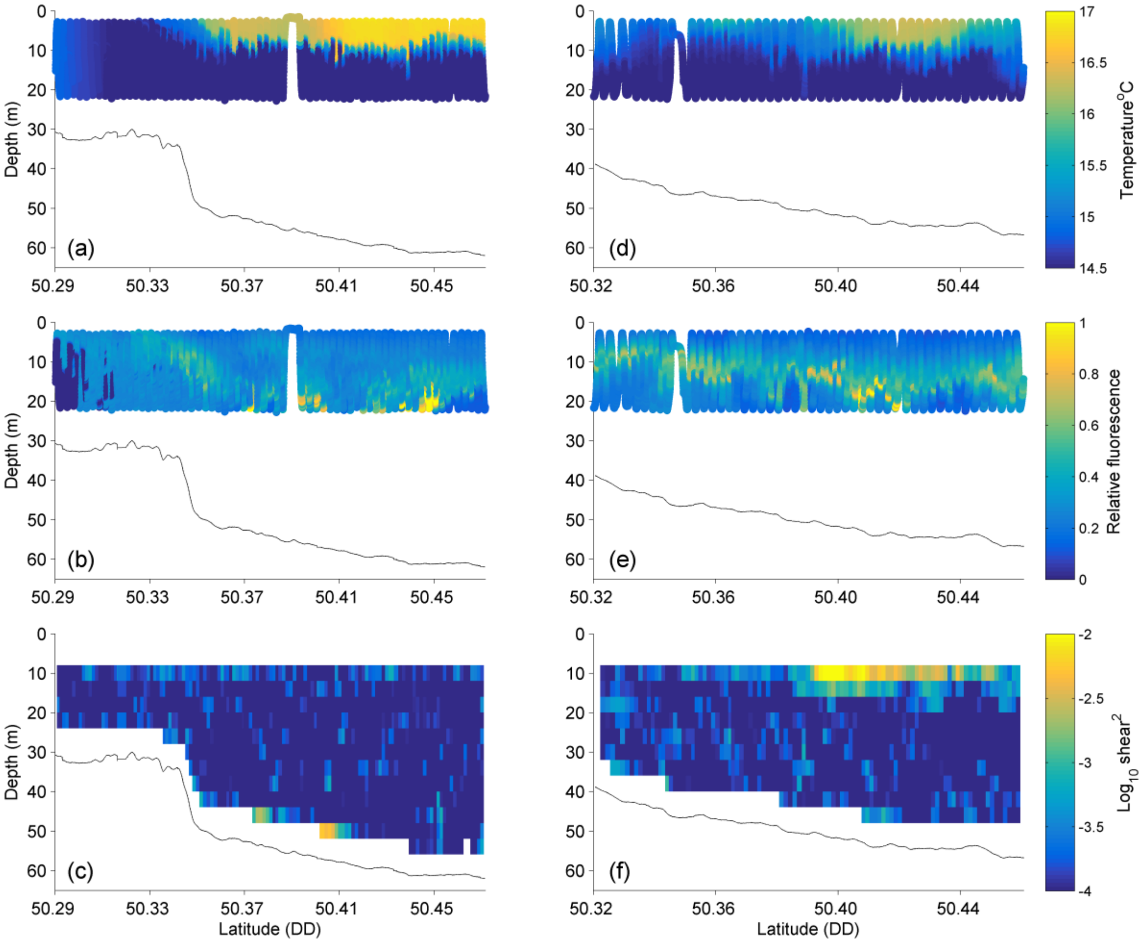

Figure A1.2 Oceanographic measurements from the undulating CTD for cross-front transects on Aug 14th 2012. Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row shows temperature (a & d), the middle row relative fluorescence (b & e), and the bottom row shear S^2 at 4m intervals (c & f). Each column (a:c and d:f) represents a separate transect leg. The black line indicates the total water column depth.

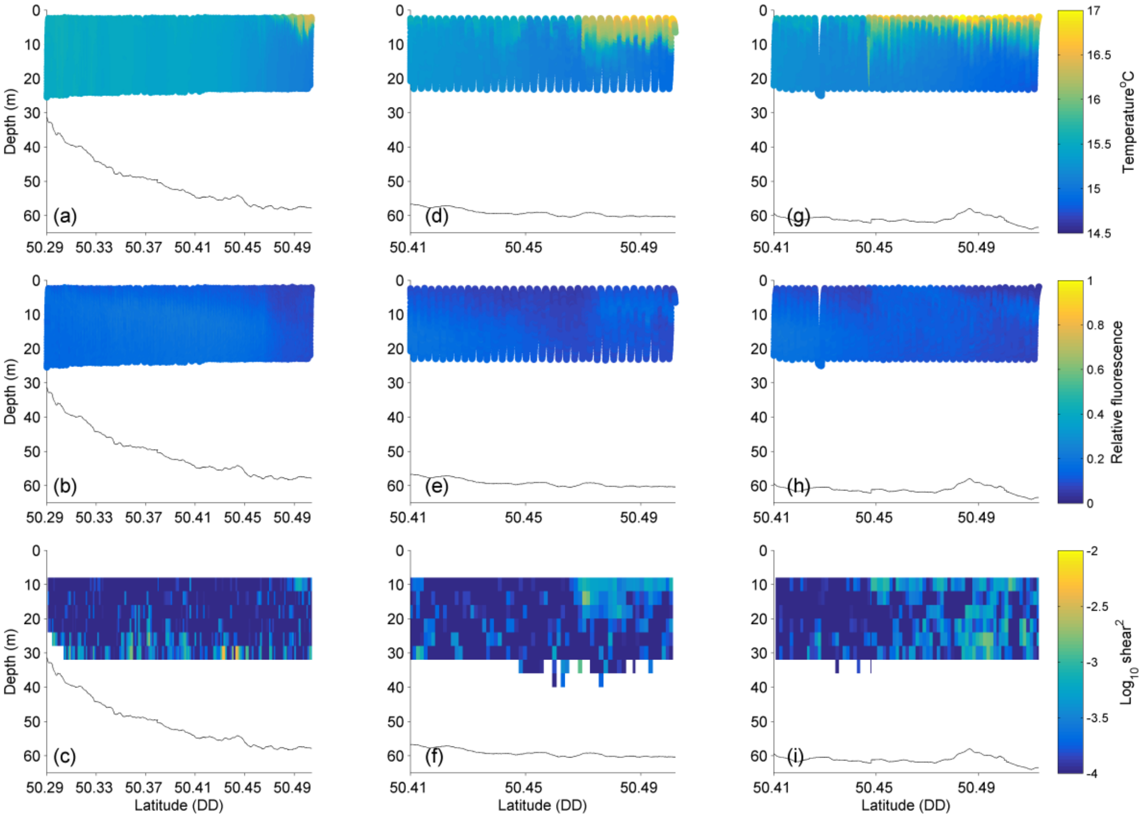

Figure A1.3 Oceanographic measurements from the undulating CTD for cross-front transects on Aug 20th 2012. Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row shows temperature (a, d & g), the middle row relative fluorescence (b, e & h), and the bottom row shear S^2 at 4m intervals (c, f & i). Each column (a:c, d:f and g:i) represents a separate transect leg. The black line indicates the total water column depth.

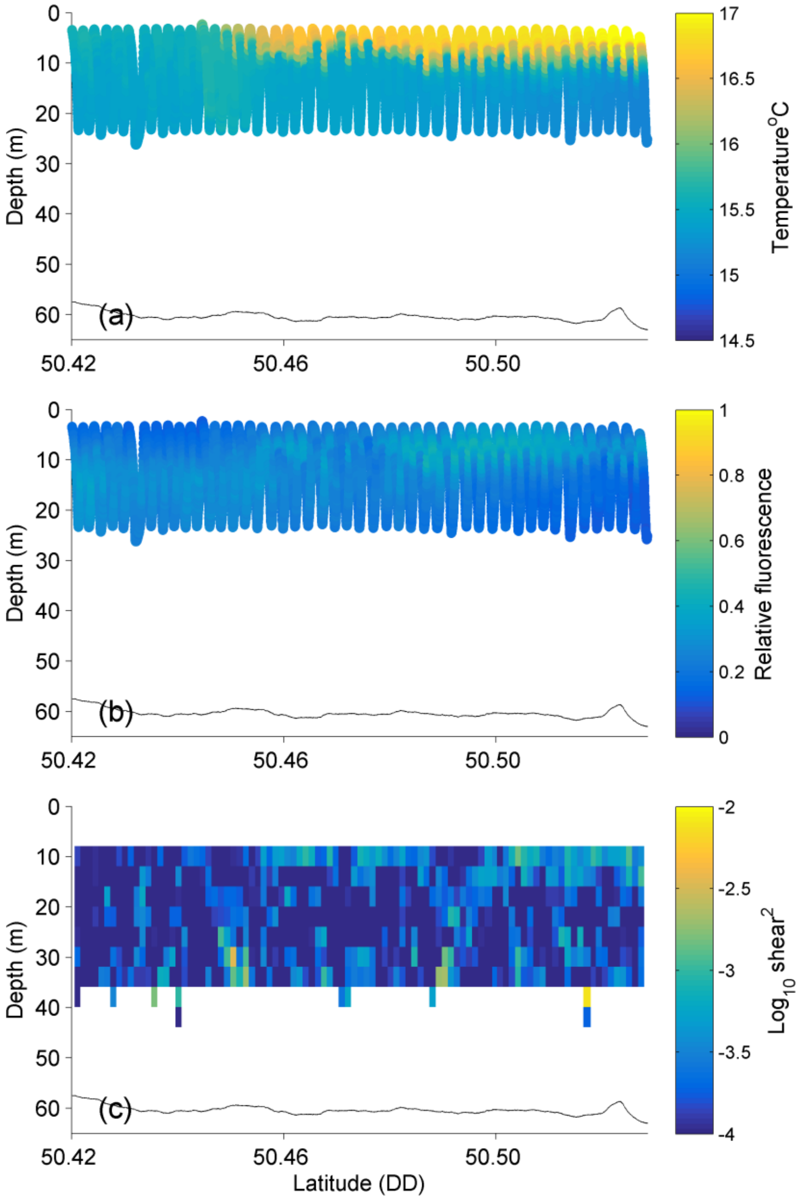

Figure A1.4 Oceanographic measurements from the undulating CTD for cross-front transect on Aug 22nd 2012. Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row shows temperature (a), the middle row relative fluorescence (b), and the bottom row shear S^2 at 4m intervals (c). The black line indicates the total water column depth.

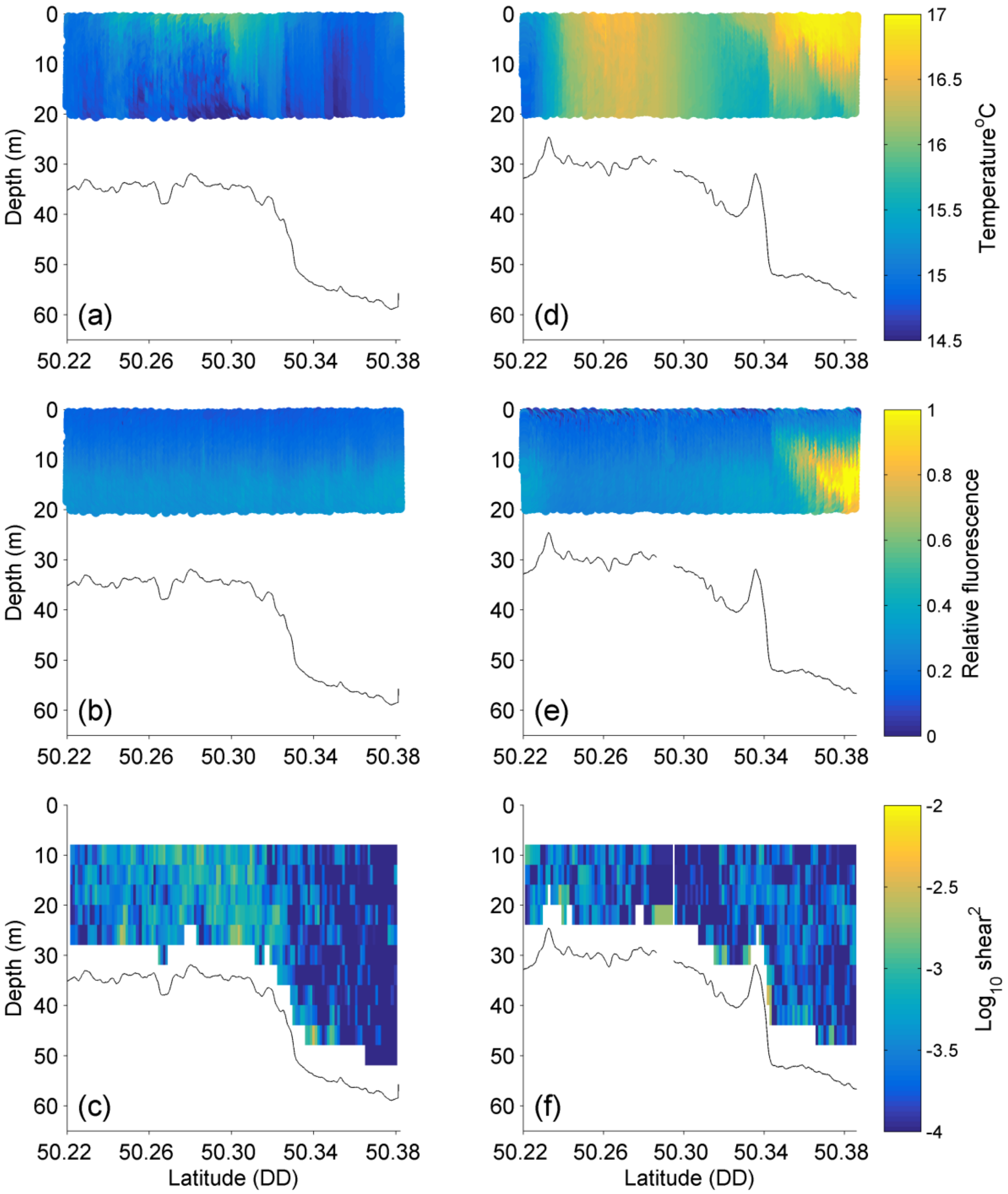

Figure A1.5 Oceanographic measurements from the undulating CTD for cross-front transects on Aug 12th 2013. Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row shows temperature (a & d), the middle row relative fluorescence (b & e), and the bottom row shear S^2 at 4m intervals (c & f). Each column (a:c and d:f) represents a separate transect leg. The black line indicates the total water column depth.

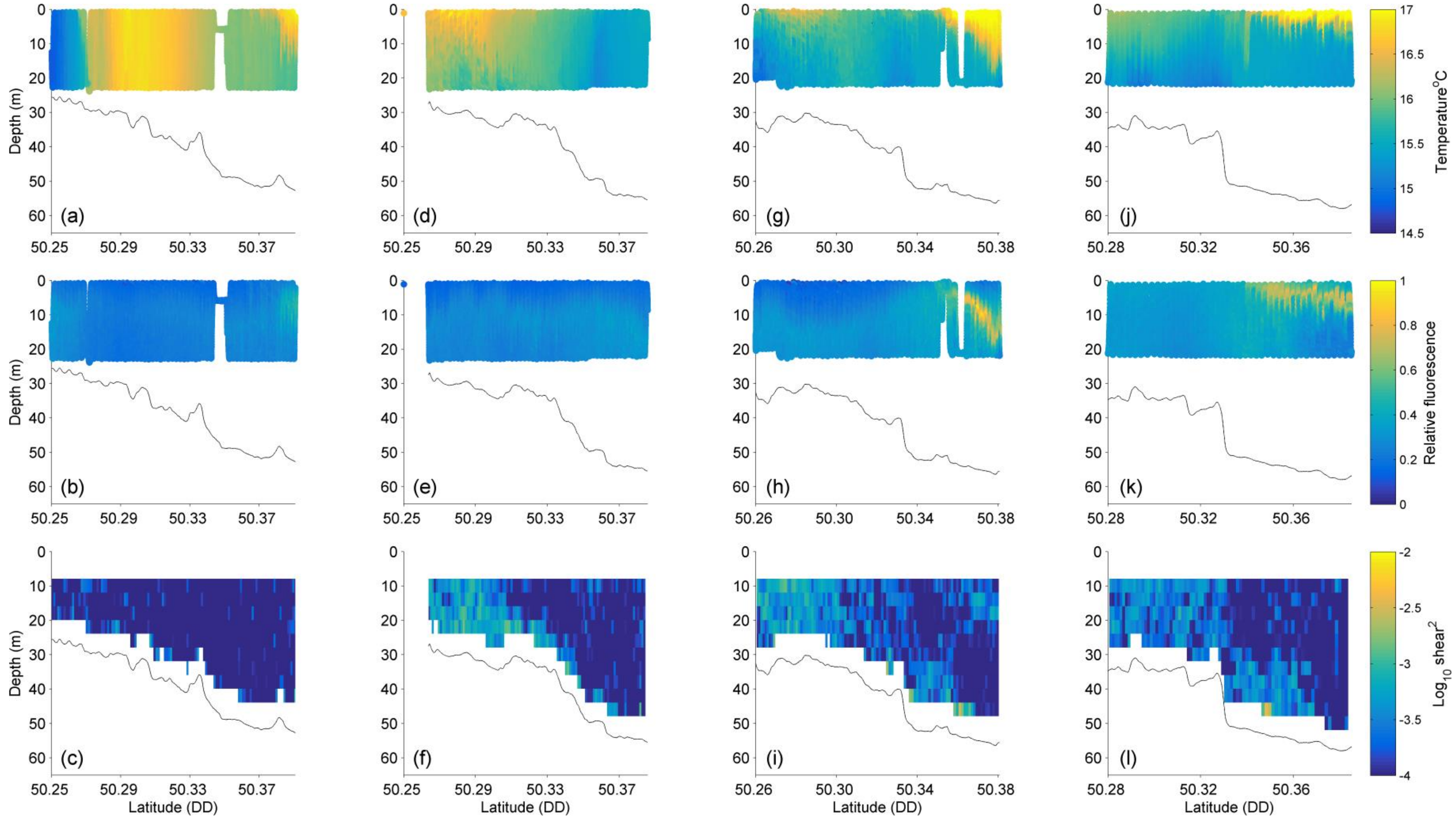

Figure A1.6 Oceanographic measurements from the undulating CTD for cross-front transects on Aug 13th 2013. Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row shows temperature (a, d, g & j), the middle row relative fluorescence (b, e, h, & k), and the bottom row shear S^2 at 4m intervals (c, f, I, & l). Each column (a:c, d:f, g:I and j:l) represents a separate transect leg. The black line indicates the total water column depth.

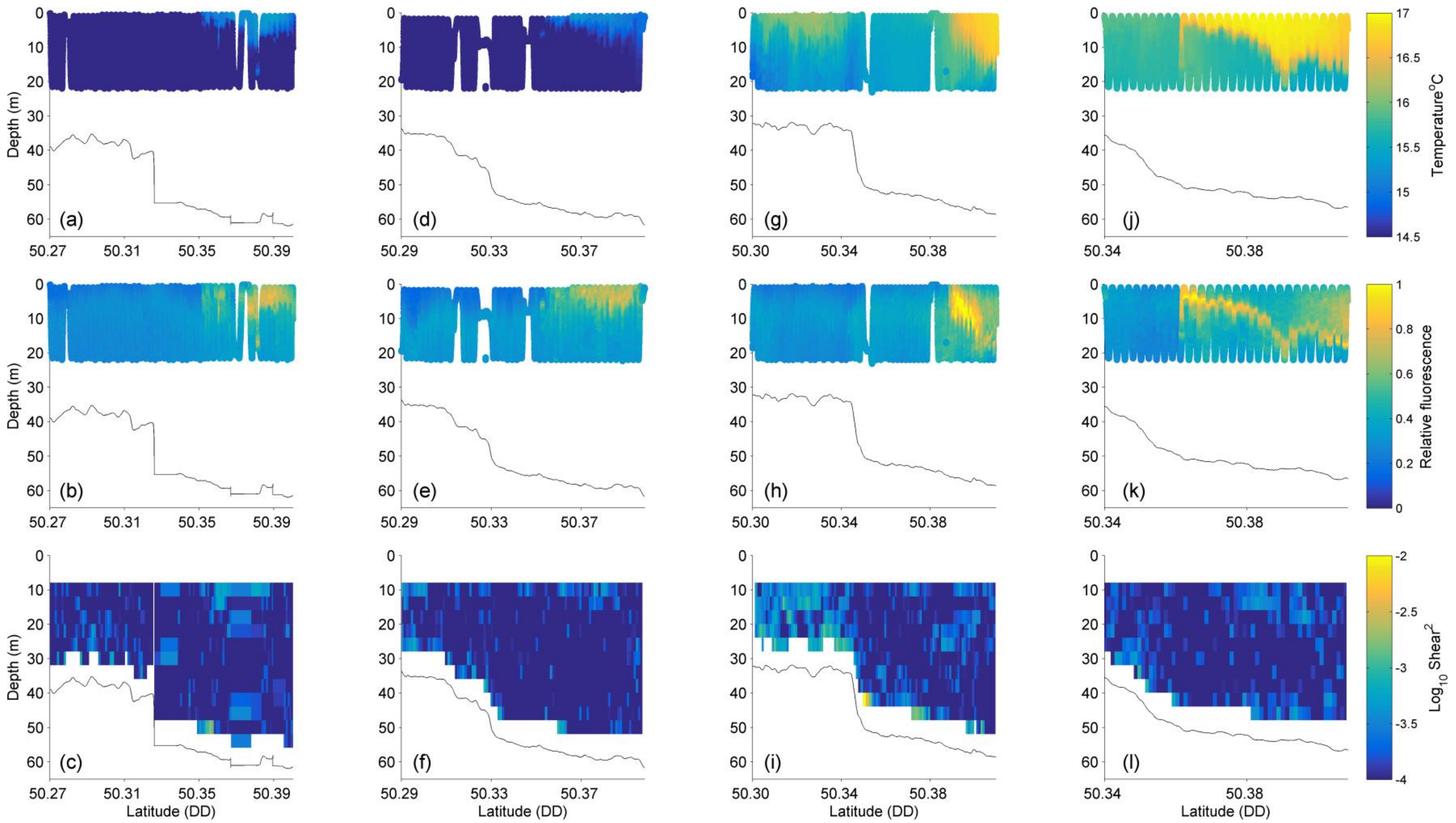

Figure A1.7 Oceanographic measurements from the undulating CTD for cross-front transects on Aug 14th 2013. Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row shows temperature (a, d, g & j), the middle row relative fluorescence (b, e, h, & k), and the bottom row shear S^2 at 4m intervals (c, f, I, & l). Each column (a:c, d:f, g:I and j:l) represents a separate transect leg. The black line indicates the total water column depth.

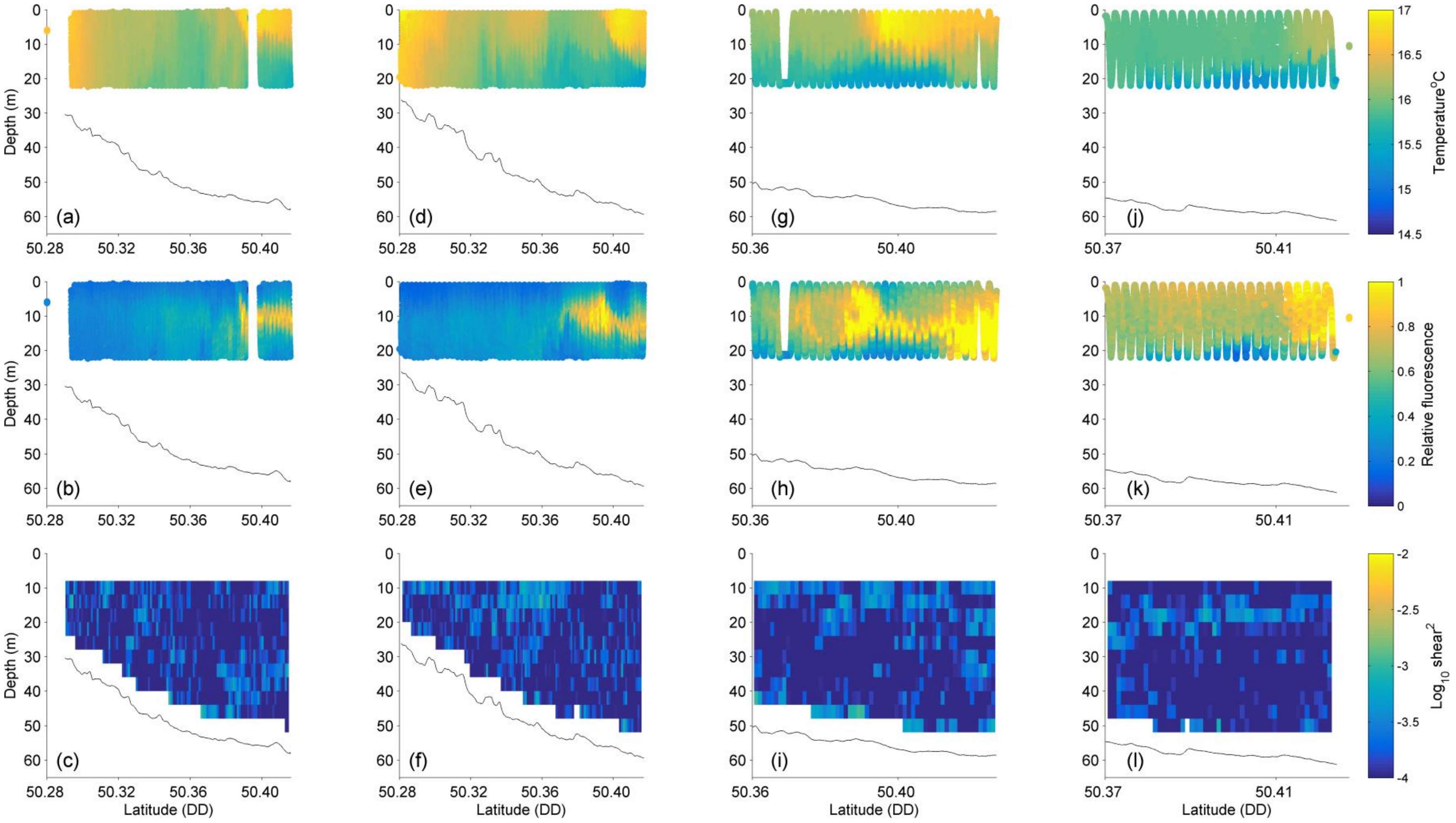

Figure A1.8 Oceanographic measurements from the undulating CTD for cross-front transects on Aug 15th 2013. Plots show measurements taken along each transect moving inshore (south) to offshore (north) with latitude (x-axis). The top row shows temperature (a, d, g & j), the middle row relative fluorescence (b, e, h, & k), and the bottom row shear S^2 at 4m intervals (c, f, I, & l). Each column (a:c, d:f, g:I and j:l) represents a separate transect leg. The black line indicates the total water column depth.

A1.3 Inspection of daylight and night fluorescence measurements

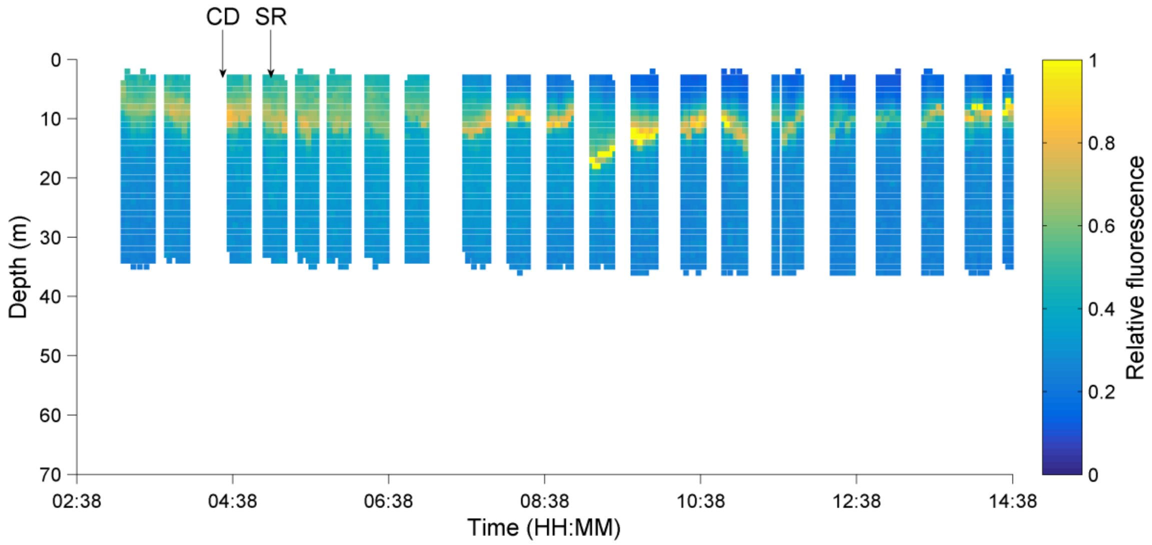

Figure A1.9 Fluorescence measurements taken during the inshore neap tidal station survey, which ran from 02:40 to 14:40, and so included observations representative of both daylight and night conditions. CD marks the beginning of civil dawn (04:31) and SR the time of sunrise (05:08). Visual comparisons between profiles taken before and after 06:00 (when daylight conditions established) do not show substantial differences suggesting that, at this location, chlorophyll quenching is not of great concern. Indeed, thin layers are still evident between the hours 03:00 and 05:00.

APPENDIX A2

Supplementary material for Chapter V

A2.1 Dive classification methods

To determine the length of the active swim phase, gradients in the vertical change in depth were used to split dives into three phases; unaided descent (plunge), active swim phase and ascent (Figure A2.1).

Using the depth data from the CEFAS tags, 100 dive profiles from a random sub-sample were allocated U- or V- shapes based on the length of the active swim phase, determined by visual inspection of dive profiles and changes in vertical descent gradient (change in depth/time to give ms^{-1} which was smoothed using a LOWESS smoother with f=0.125). The length of the active swim phase was based on the findings of Ropert-Coudert et al. (2009), and started at the end of the plunge phase of a dive and ended at the beginning of the final ascent of the dive. From these 100 sub-sampled dives, descent gradient thresholds were then estimated and used in an algorithm which was then applied across the whole dataset and validated against the manually determined dive shapes of the sub-sample. Additional visual inspection of the defined active swim phase for a number of further dives across the whole dataset was also performed to insure the selected thresholds were robust for a number of dive profile shapes (e.g. dives with an active swim phase encompassing a variety of depths, of which there were few in the randomly selected sub-sample). The active swim phase begun at the first point the vertical gradient of the dive fell below 1.05 and ended at the last point at which the vertical gradient rose above -0.2. U-shaped dives were defined as those with an active swim phase of at least four seconds (Garthe et al. 2000), which was also validated against the sub-sampled manually assigned dataset.

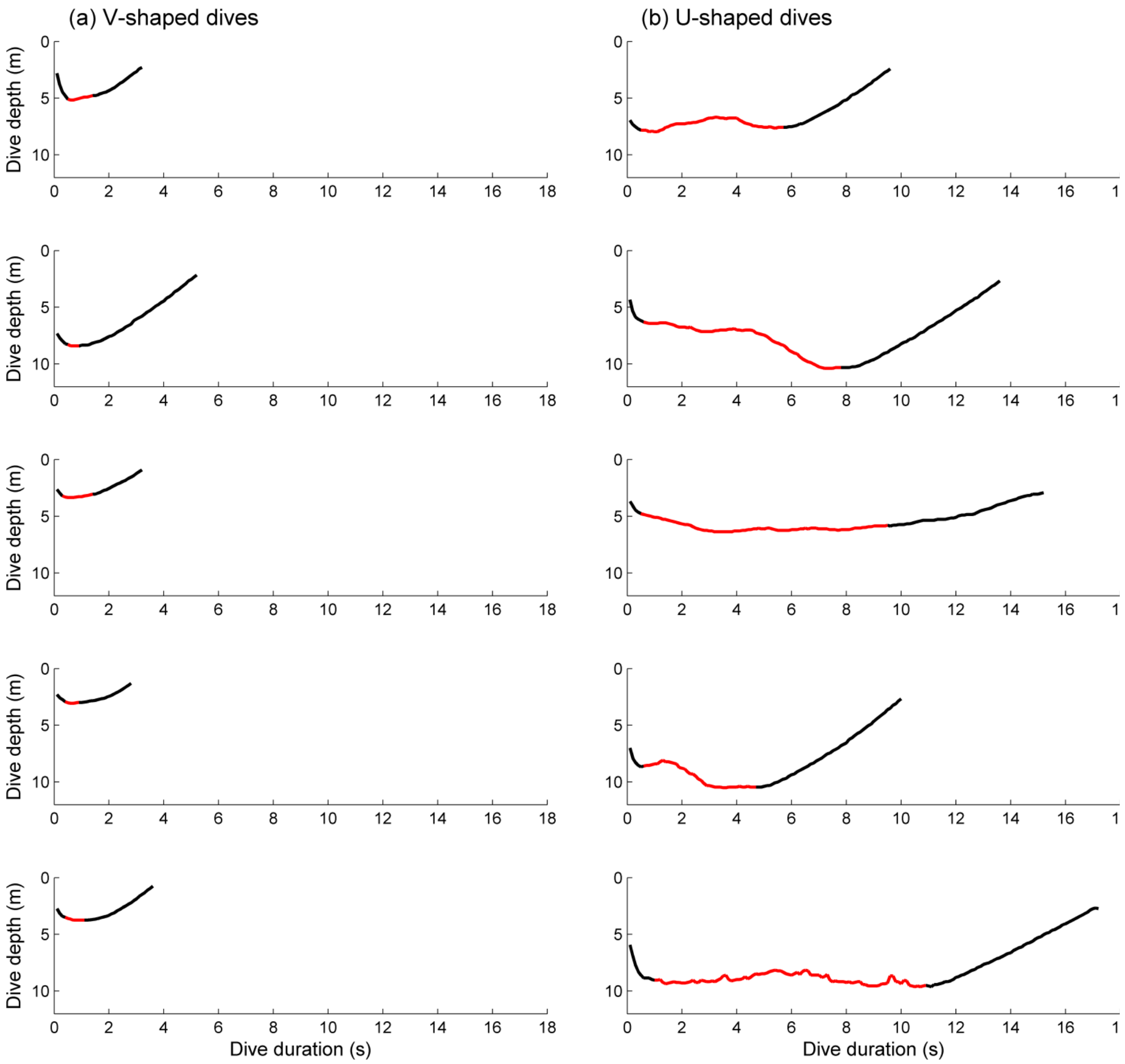

Figure A2.1 Examples of typical dive profiles form the CEFAS tags. Defined active swim phase is highlighted in red. From left to right: (a) dives classified as V-shaped and (b) dives classified as U-shaped.

To account for potential changes in gradient threshold because of sampling rate, and to keep allocations consistent between tag types, depth data from the CEFAS tags were resampled at a rate of one second, to give a dummy dataset representative of the sampling rate of the LOTEK loggers that could be directly compared to higher resolution data. These resampled profiles were then used to determine appropriate thresholds that gave similar allocations to those obtained using the higher resolution data. The active swim phase begun at the first point the vertical descent gradient of the bird fell below 1.05 and ended at the last point at which the vertical descent gradient was above -0.55. U-shaped dives were defined as those with an active swim phase exceeding three seconds which gave more consistent results with the higher resolution data than a four second threshold.

A2.2 Habitat use-availability analysis: generation of pseudo-absence locations

Habitat use was compared to habitat availability to determine if gannets preferentially targeted fronts for diving, and hence foraging (Aarts et al. 2008, Cleasby et al. 2015). The 95% utilisation distribution (UD) of the population sample was calculated using a kernel analysis conducted with the R package adehabitatHR (Calenge 2014) on the GPS locations of all individuals tracked across the two years (Figure A2.2.a). A binomial response variable (0/1) was then generated. For each dive event (coded as 1), the locations of five pseudo-absences (coded as 0) were randomly selected within the bounds of the 95% UD (Figure A2.2.b). To allocate front metrics generated using seven-day composites to each pseudo absence location, a date was assigned that corresponded to the date of the paired dive event.

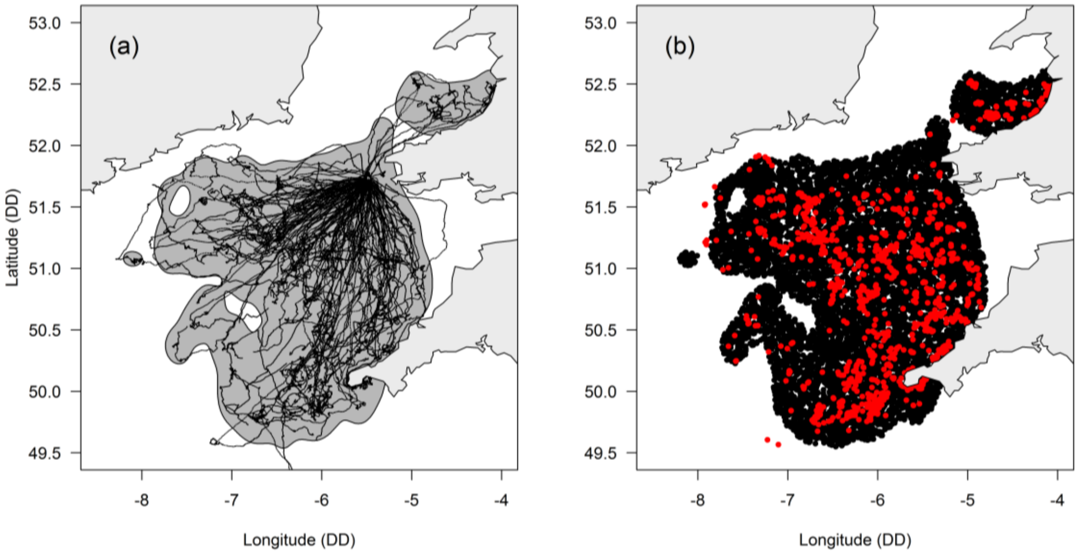

Figure A2.2 From left to right: (a) the 95% utilisation distribution (dark grey shaded area) as calculated using kernel analysis of all foraging trip tracks (indicated by black markers), and (b) the locations of randomly generated pseudo-absences (black markers) and recorded dive events (red markers).

A2.3 Dive durations

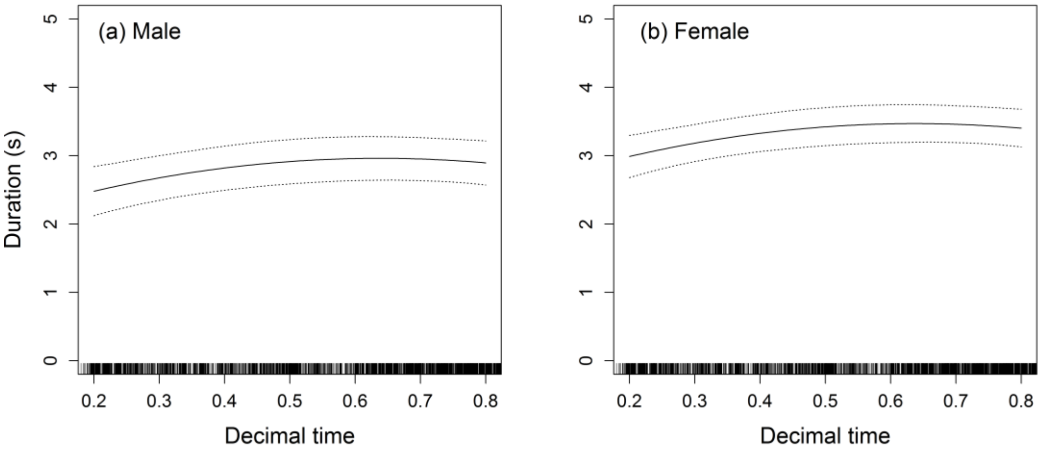

Figure A2.3 Predicted durations of V-shaped dives with time of day (*DecTime*). From left to right; (a) V-shaped dive duration of males and (b) V-shaped dive duration of females. Both show significant increases in dive duration around the middle of the day. Dives were shortest at dusk and dawn, which was possibly due to the diel migration of prey above and below the thermocline (Garthe et al. 2000, Garthe et al. 2007). The filled lines show expected dive durations for an 'average' bird. Dotted lines show bootstrapped 95% confidence intervals.

A2.4 References

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APPENDIX A3

Supplementary material for Chapter VI

A3.1 Spatial extent of bathymetric data

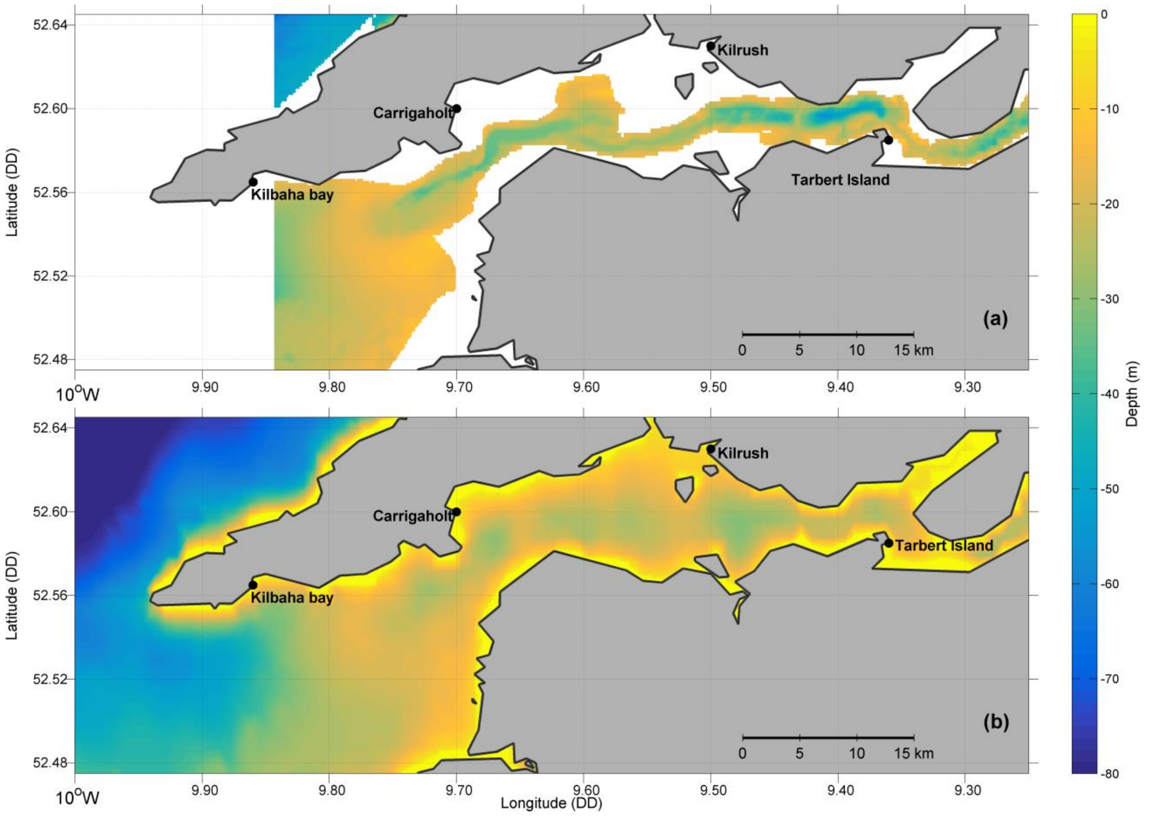

Figure A3.1 Spatial extent of the bathymetric data obtained from (a) the integrated mapping for the sustainable development of Ireland’s marine resource program (INFOMAR; www.infomar.ie) and (b) the British Oceanographic Data Centres (BODC) general bathymetric chart of the oceans (The GEBCO_2014 Grid, version 20150318; www.gebco.net).

A3.2 Slope estimates across the estuary

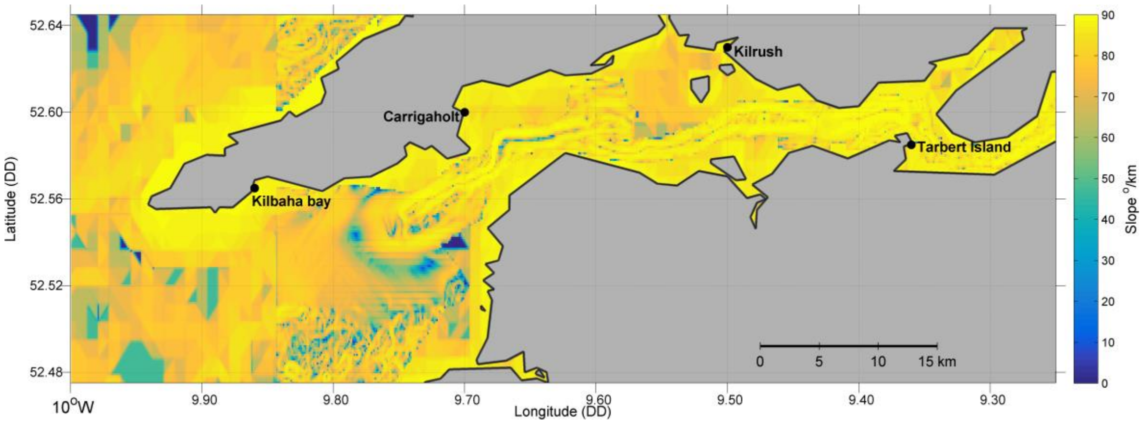

Figure A3.2 Slope derived using the R package SDMTools (Van der Wal et al. 2014) on bathymetric data obtained from (1) the integrated mapping for the sustainable development of Ireland's marine resource program (INFOMAR; www.infomar.ie) and (2) the British Oceanographic Data Centres (BODC) general bathymetric chart of the oceans (The GEBCO_2014 Grid, version 20150318; www.gebco.net).

A3.3 Origin of tidal data and matches to survey observations

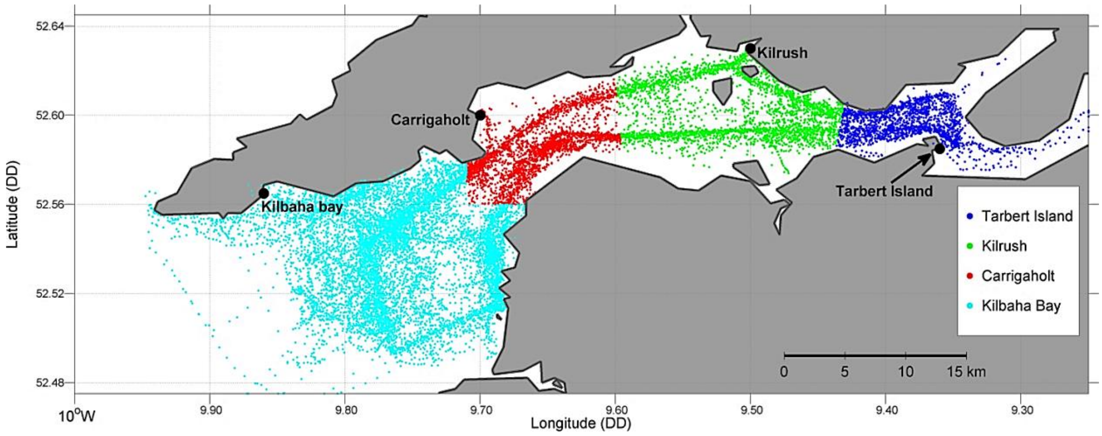

Figure A3.3 The origin of tidal data (sourced from admiralty Easytide tidal prediction model via the United Kingdom hydrographic office (UKHO); www.ukho.gov.uk) for each surveyed point in the estuary. Those surveyed points marked in blue were assigned tidal states using model data from Tarbert Island port, those marked in green using data from Kilrush port, those marked in red using data from Carrigaholt port and those marked in cyan using data from Kilbaha Bay port. This accounted for a lag of between 20 and 50 minutes in the times of low and high tide between Kilbaha Bay and Tarbert Island.

A3.4 Survey observations during neap and spring tide conditions

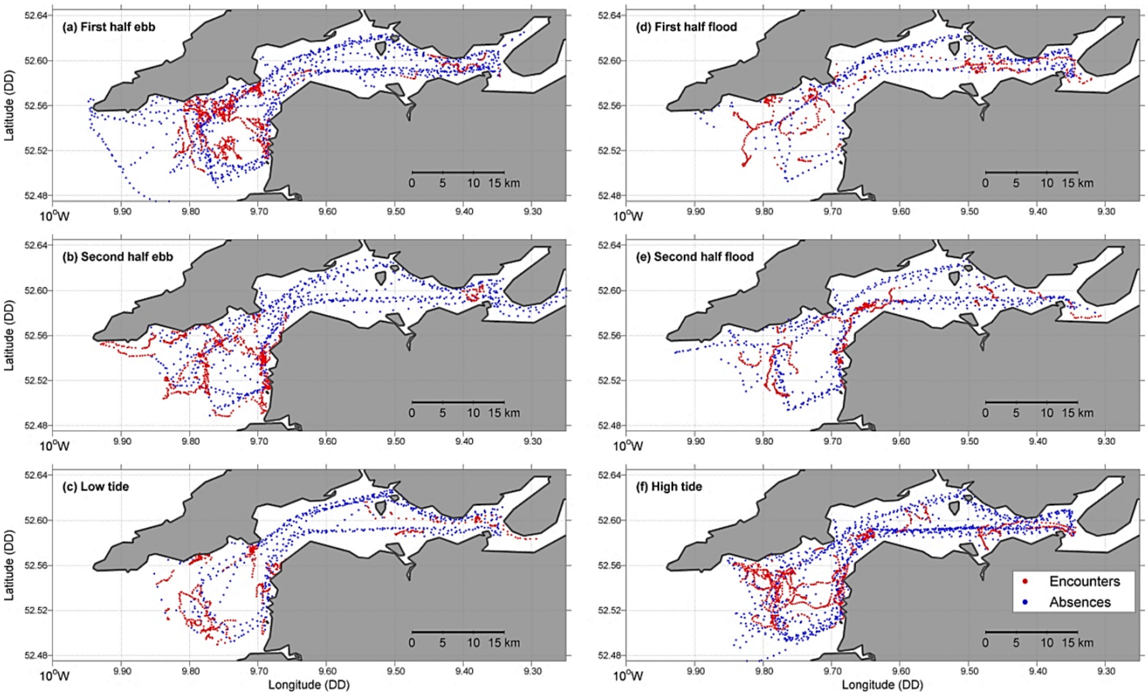

Figure A3.4 Survey observations (GPS points) associated with neaps conditions. Locations where dolphins were encountered are marked in red and those locations where no animals were sighted are marked in blue. The left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. The right column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

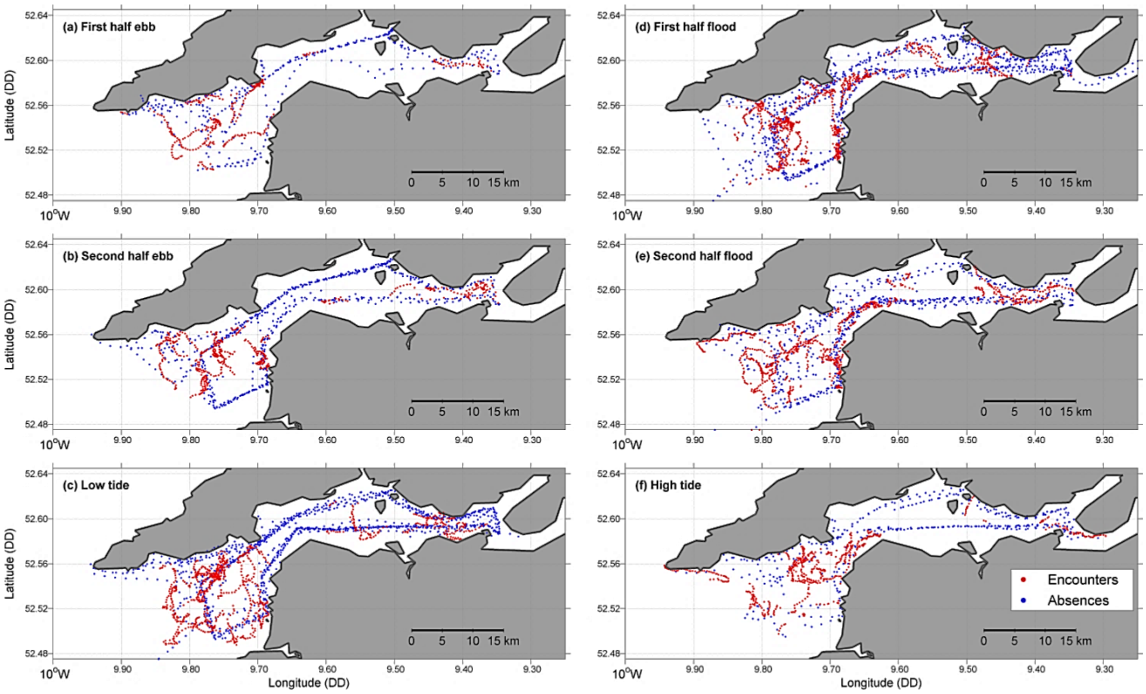

Figure A3.5 Survey observations (GPS points) associated with spring conditions. Locations where dolphins were encountered are marked in red and those locations where no animals were sighted are marked in blue. The left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. The right column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

A3.5 Model predictions for neap and spring tide conditions encompassing all variables

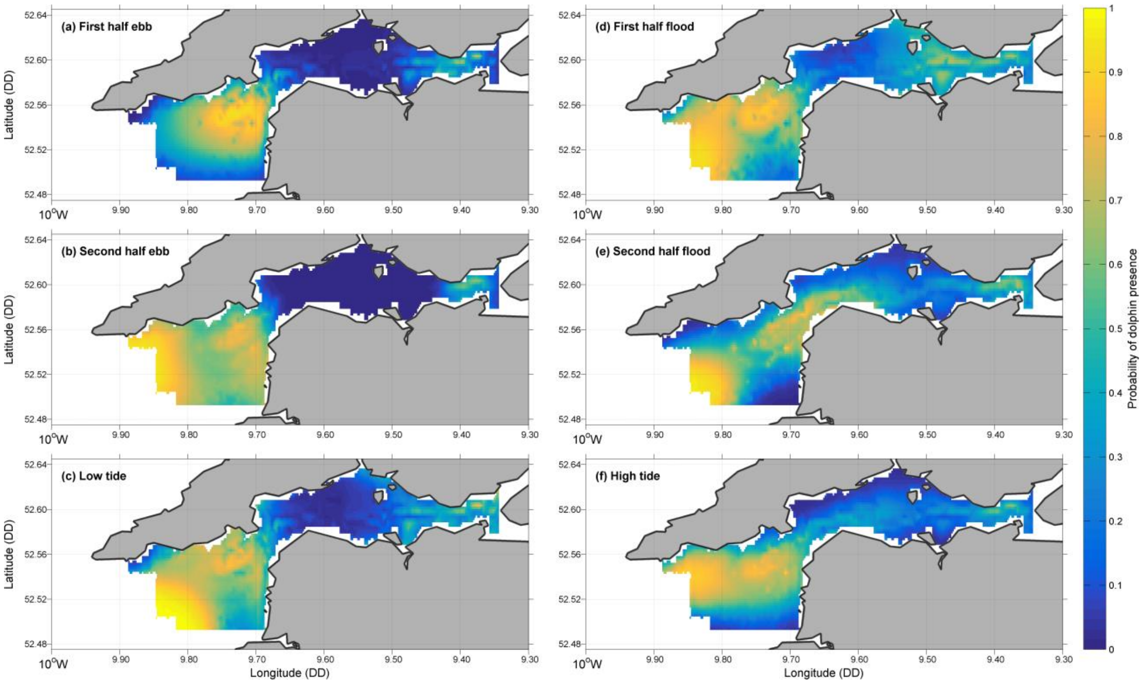

Figure A3.6 Predictions of the probability of dolphin presence encompassing depth and slope measurements for the entire estuary at all locations over all stages of the tide as determined via GEE-GAMs (generalised estimating additive models) during neap conditions. Left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. Second column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

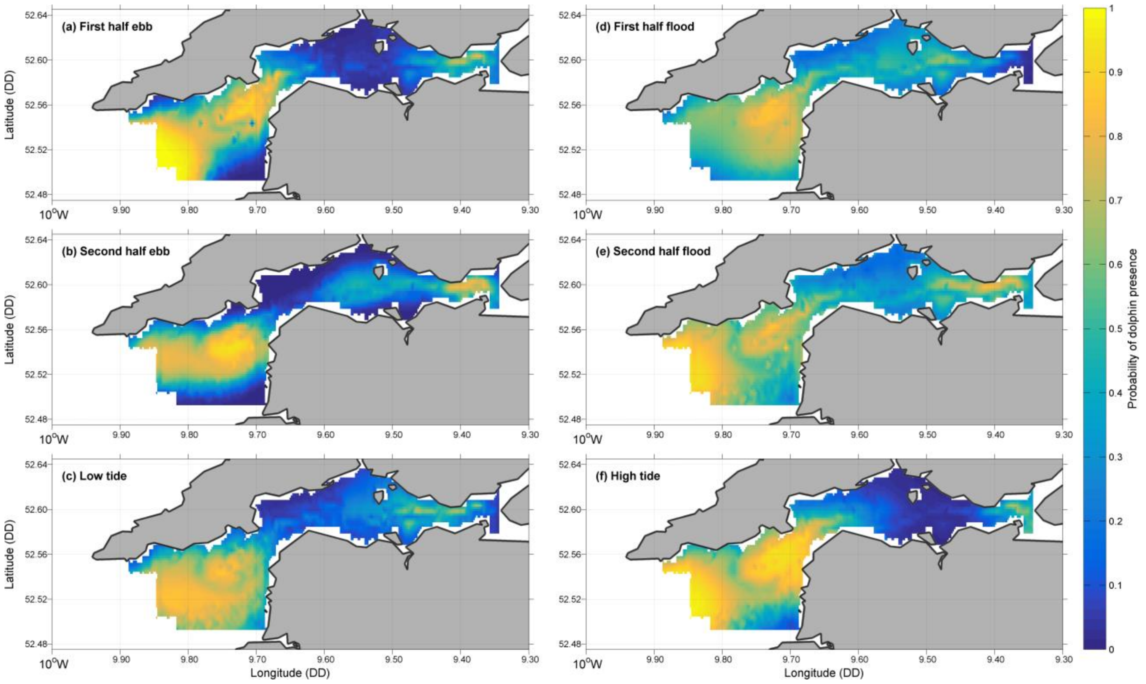

Figure A3.7 Predictions of the probability of dolphin presence encompassing depth and slope measurements for the entire estuary at all locations over all stages of the tide as determined via GEE-GAMs (generalised estimating additive models) during spring conditions. Left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. Second column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

A3.6 Influence of depth, slope, location and tide on dolphin presence in spring and neap conditions

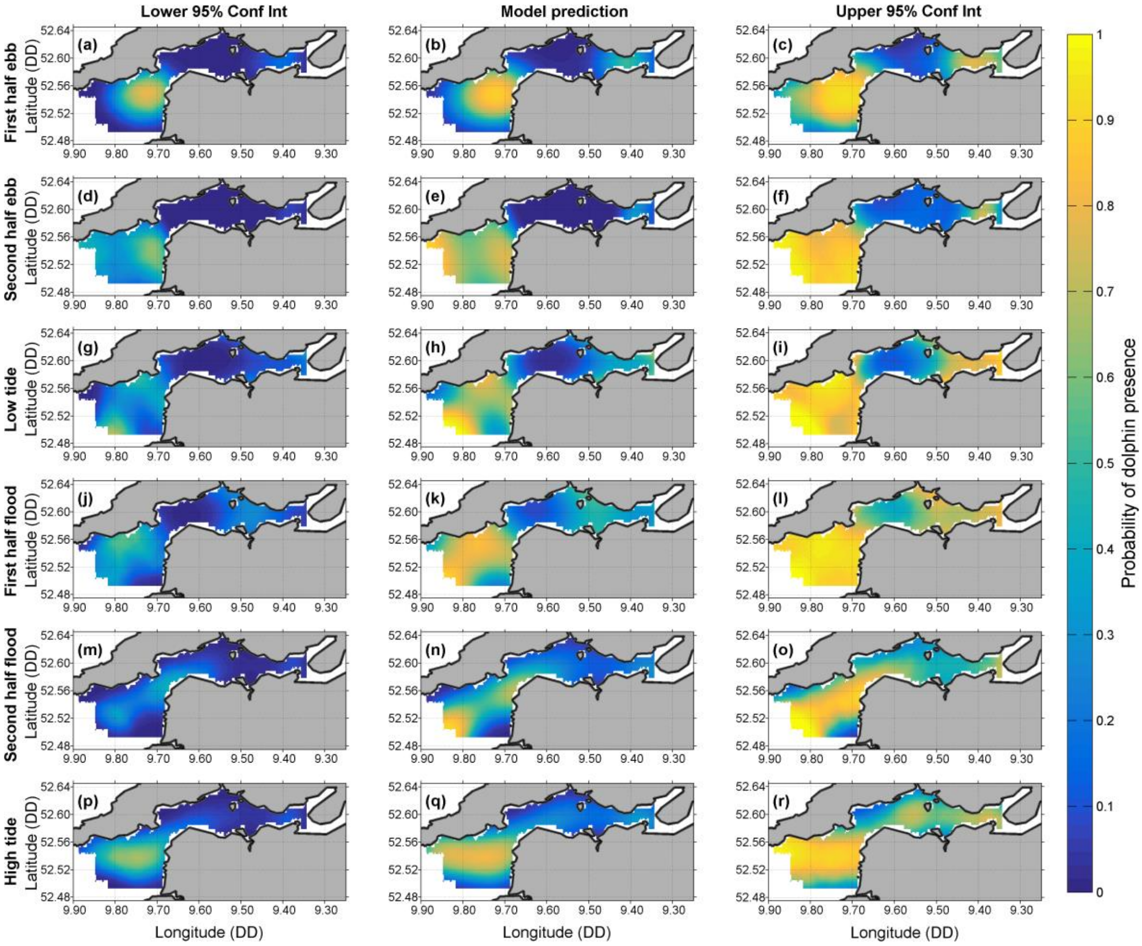

Figure A3.8 The influence of location and tide on the probability of dolphin presence during neap conditions as determined via GEE-GAMs (generalised estimating additive models). Columns from left to right show: (1) upper 95% confidence intervals (subplots a, d, g, j, m, and p), (2) model predictions (subplots b, e, h, k, n, and q), and (3) lower 95% confidence intervals (subplots c, f, i, l, o, and r). Rows from top to bottom show: (1) first half ebb (subplots a, b, and c), (2) second half ebb (subplots d, e and f), (3) low tide (subplots g, h and i), (4) first half flood (subplots j, k and l), (5) second half flood (m, n and o) and (6) high tide (subplots p, q and r).

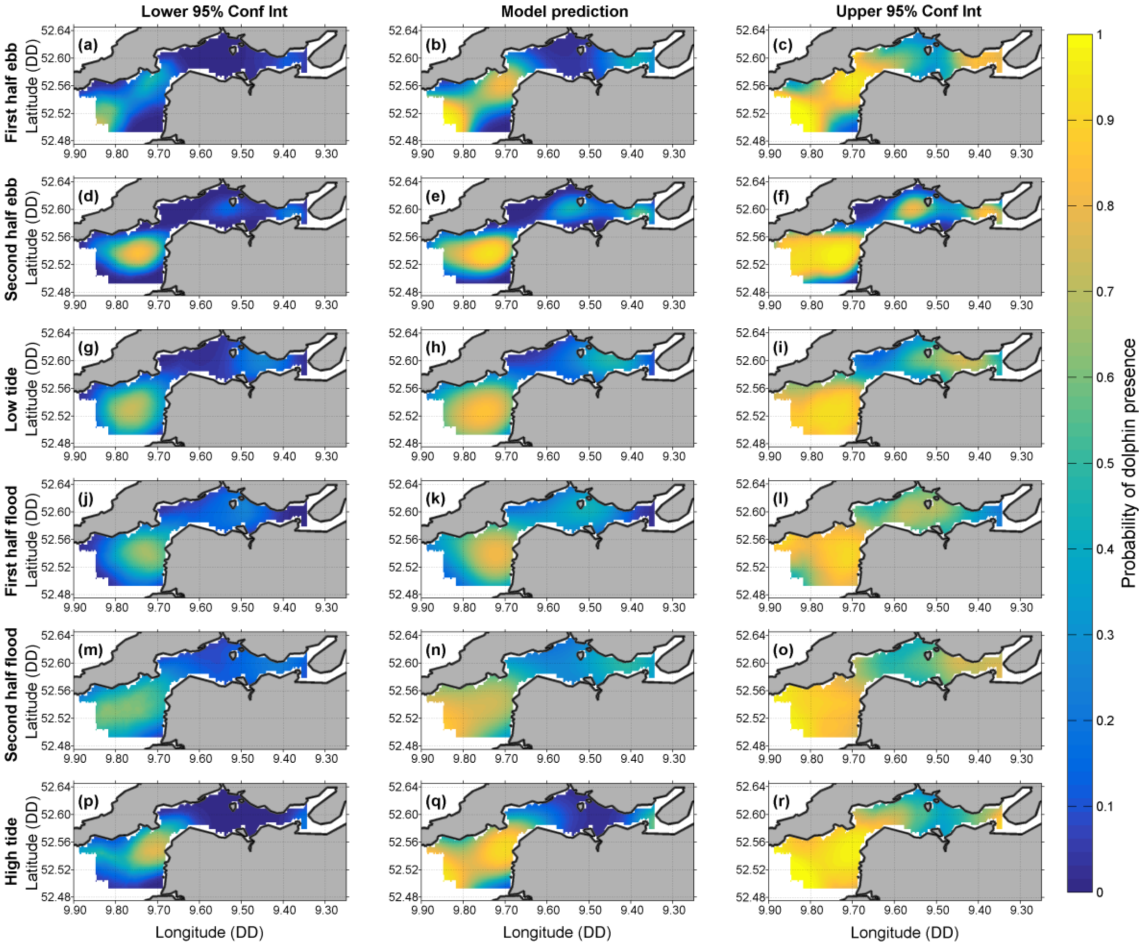

Figure A3.9 The influence of location and tide on the probability of dolphin presence during spring conditions as determined via GEE-GAMs (generalised estimating additive models). Columns from left to right show: (1) upper 95% confidence intervals (subplots a, d, g, j, m, and p), (2) model predictions (subplots b, e, h, k, n, and q), and (3) lower 95% confidence intervals (subplots c, f, i, l, o, and r). Rows from top to bottom show: (1) first half ebb (subplots a, b, and c), (2) second half ebb (subplots d, e and f), (3) low tide (subplots g, h and i), (4) first half flood (subplots j, k and l), (5) second half flood (m, n and o) and (6) high tide (subplots p, q and r).

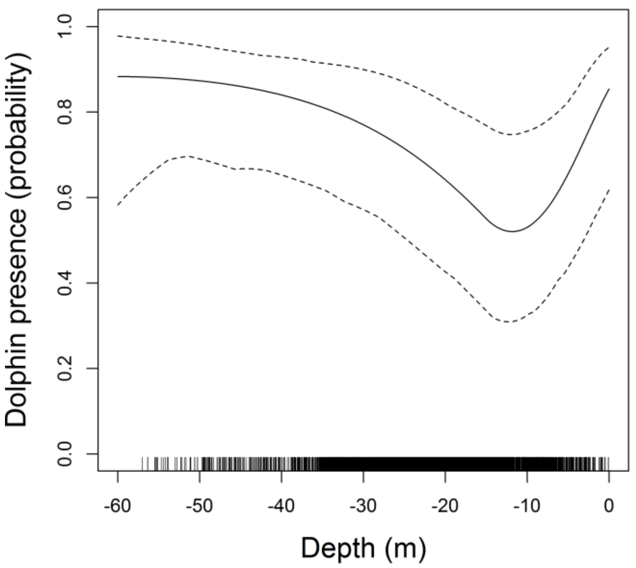

Figure A3.10 The influence of depth on the probability of dolphin presence during neap conditions as determined via GEE-GAMs (generalised estimating additive models) using survey observations from across the entire estuary.

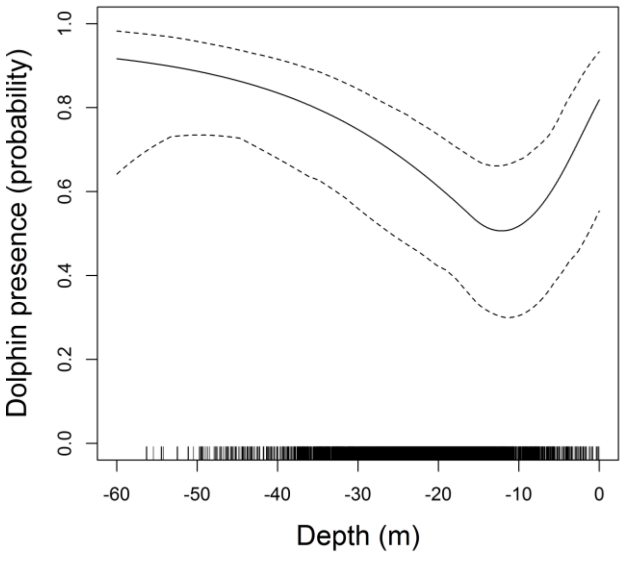

Figure A3.11 The influence of depth on the probability of dolphin presence during spring conditions as determined via GEE-GAMs (generalised estimating additive models) using survey observations from across the entire estuary.

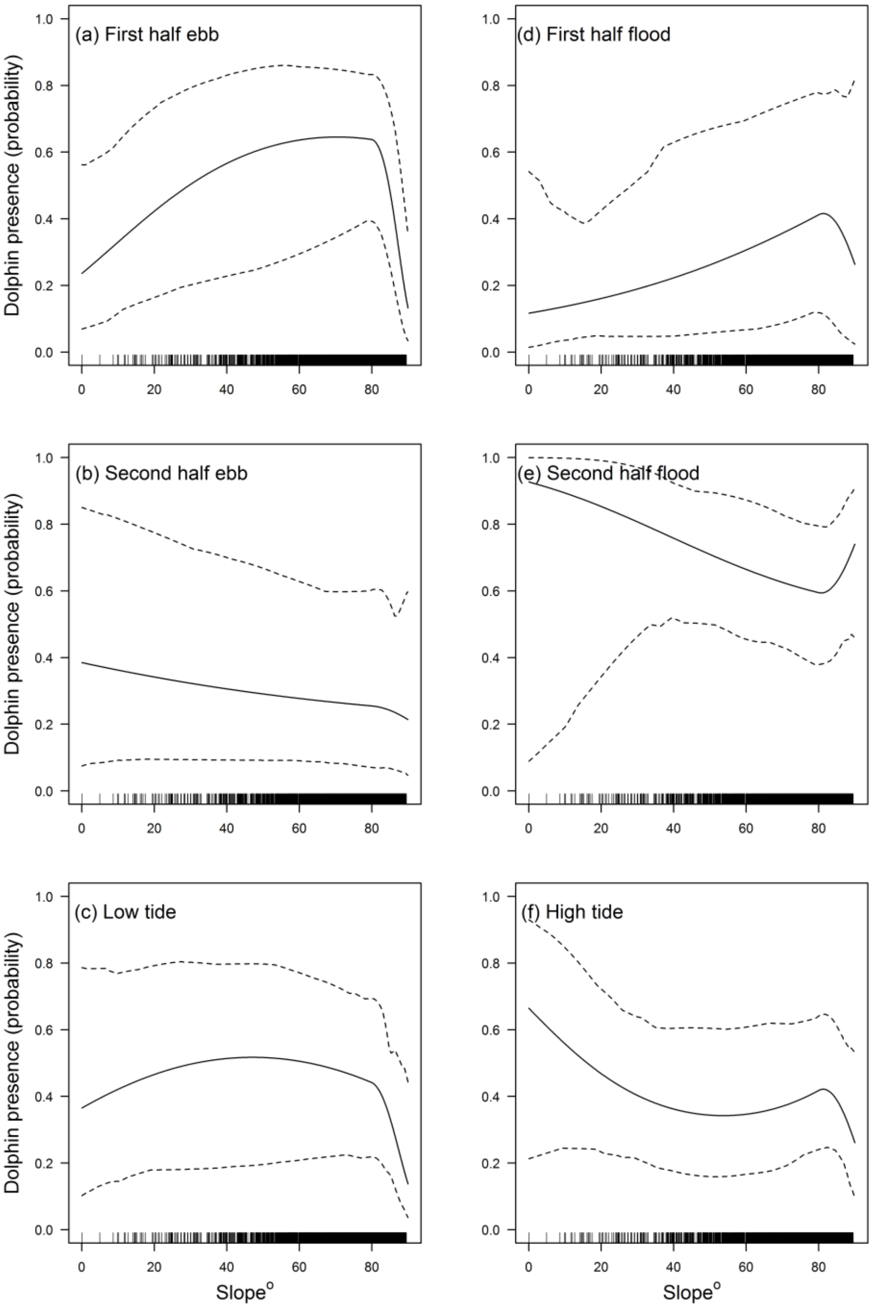

Figure A3.12 The influence of slope on the probability of dolphin presence as determined via GEE-GAMs (generalised estimating additive models) using survey observations from across the entire estuary during neap conditions. Left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. Second column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

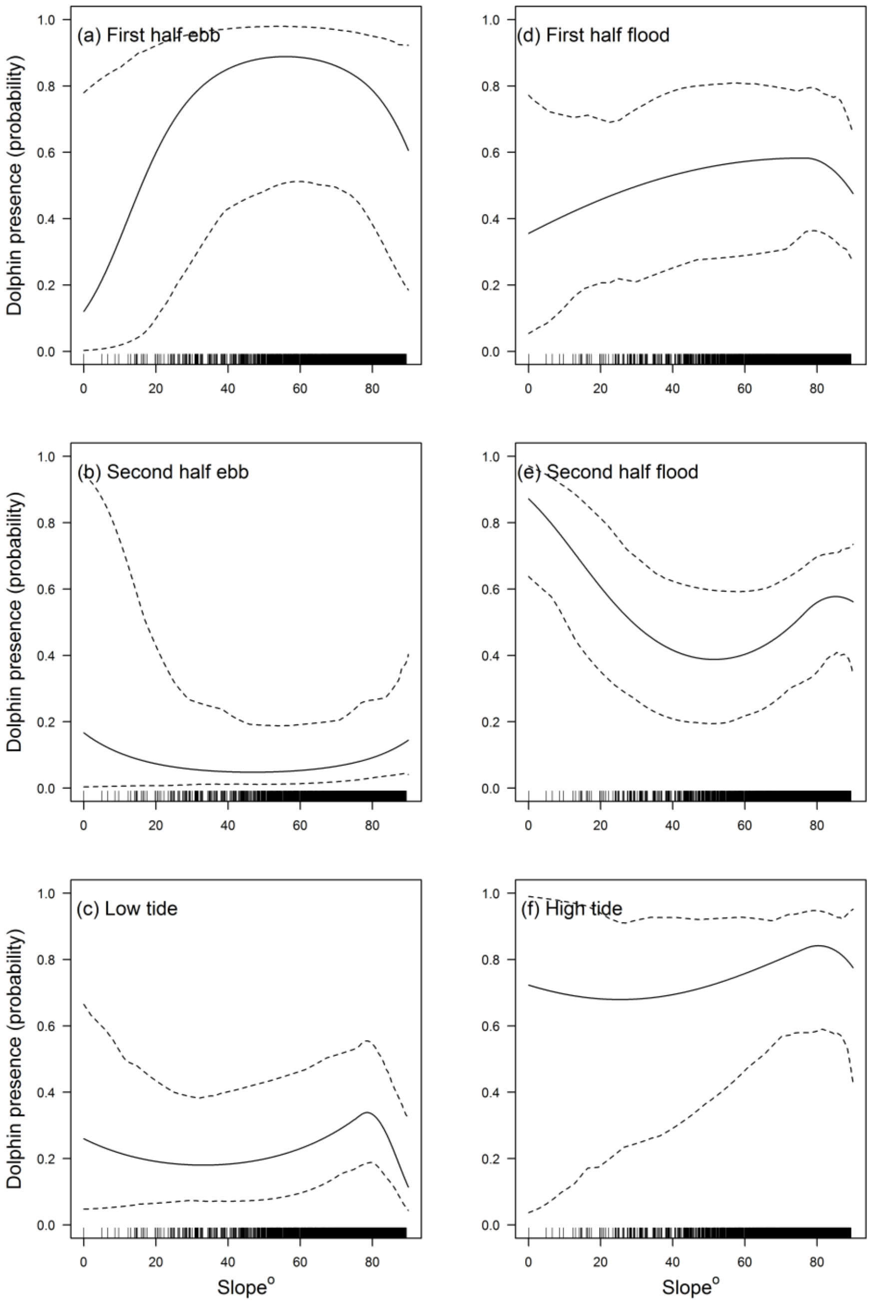

Figure A3.13 The influence of slope on the probability of dolphin presence as determined via GEE-GAMs (generalised estimating additive models) using survey observations from across the entire estuary during spring conditions. Left column from top to bottom: (a) first half ebb, (b) second half ebb and (c) low tide. Second column from top to bottom: (d) first half flood, (e) second half flood and (f) high tide.

A3.7 Influence of day of year on dolphin presence

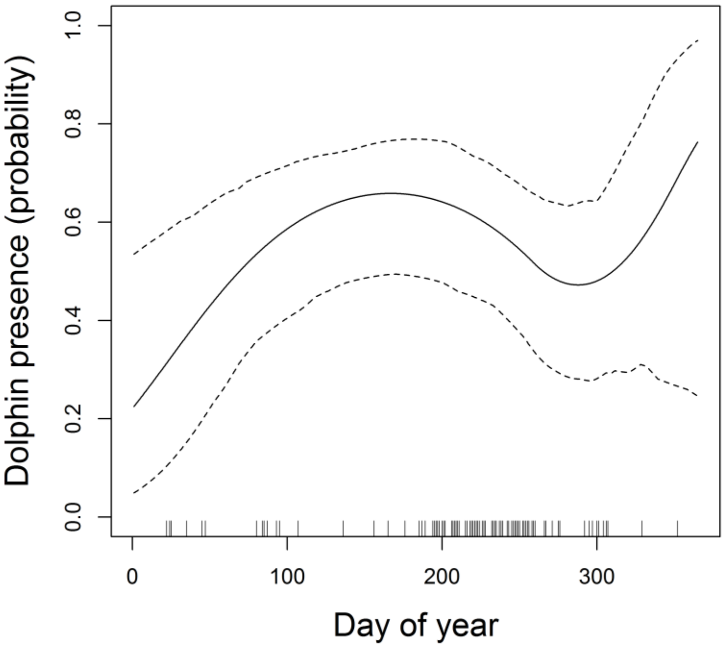

Figure A3.14 The influence of day of year on the probability of dolphin presence as determined via GEE-GAMs (generalised estimating additive models) using survey observations from across the entire estuary during both neap and spring tide conditions.

A3.8 Current speeds, directions and vertical velocities in the central channel

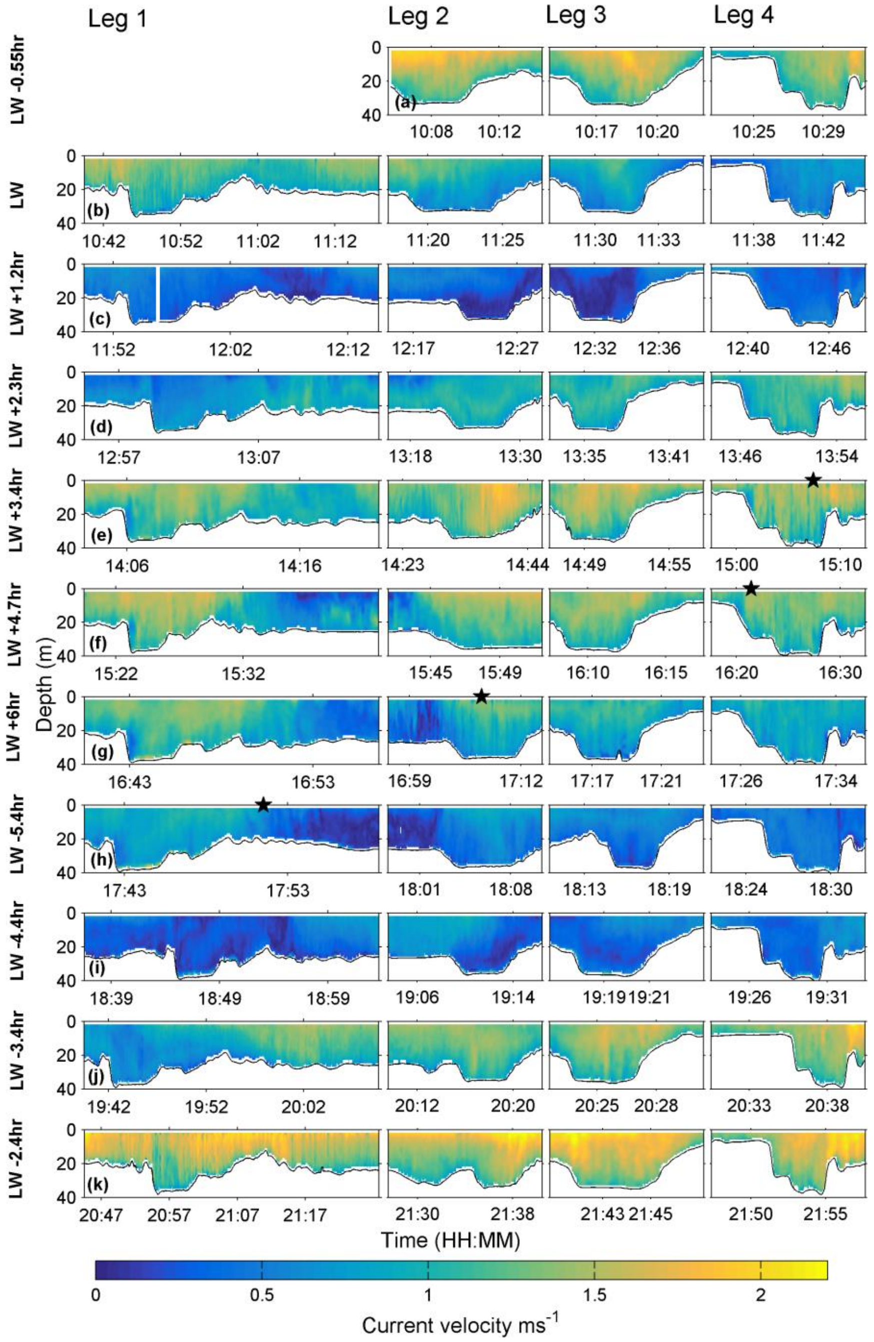

Figure A3.15 Current velocities as measured by the acoustic Doppler current profiler (ADCP) during oceanographic surveys of the central channel conducted on the 28th May 2014. Each column represents a leg (or transect) of the survey whilst each row corresponds to one repeat circuit of the survey route. The time since or to low water (LW) is indicated on the left. Rows b:g correspond to flood flows and rows a & h:k to ebb flows. The solid black line corresponds to the depth measured by the ADCP. Low water was at 10:40 and high water at 17:02 (GMT). Times of dolphin sightings (rows e:h) are marked with a black star.

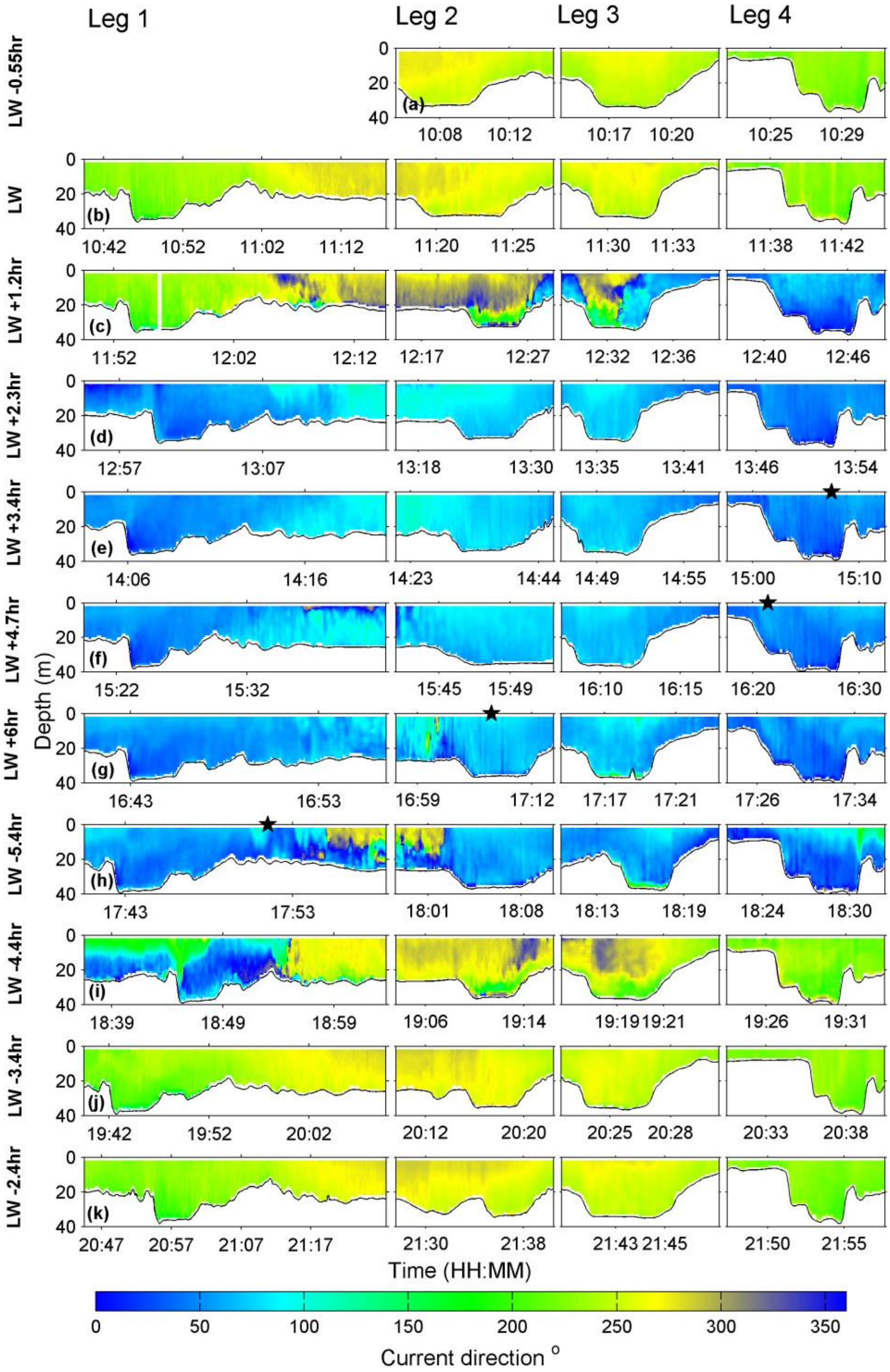

Figure A3.16 Current directions as measured by the acoustic Doppler current profiler (ADCP) during oceanographic surveys of the central channel conducted on the 28th May 2014. Each column represents a leg (or transect) of the survey whilst each row corresponds to one repeat circuit of the survey route. The time since or to low water (LW) is indicated on the left. Rows b:g correspond to flood flows and rows a & h:k to ebb flows. The solid black line corresponds to the depth measured by the ADCP. Low water was at 10:40 and high water at 17:02 (GMT). Times of dolphin sightings (rows e:h) are marked with a black star.

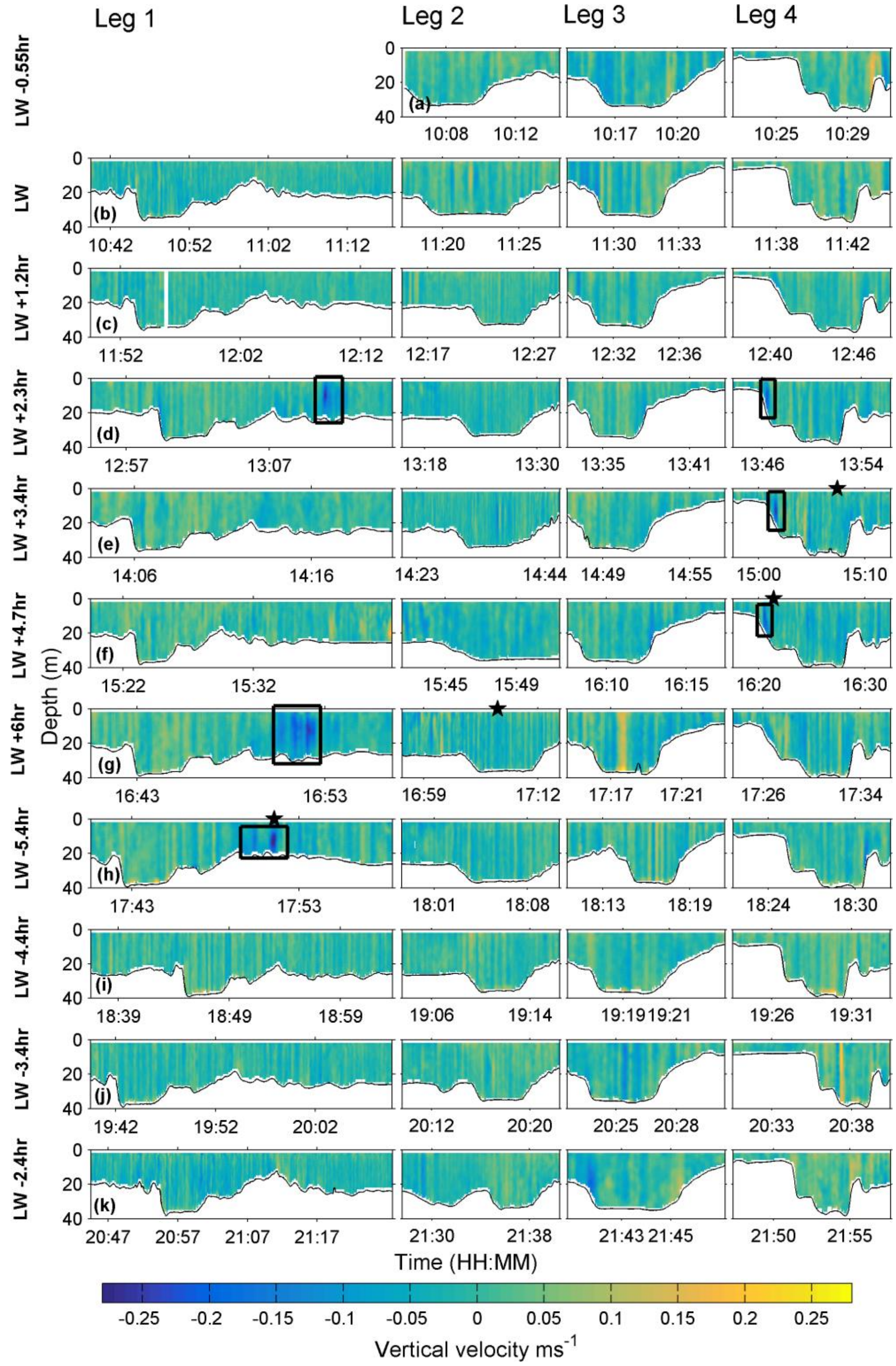

Figure A3.17 Vertical velocities as measured by the acoustic Doppler current profiler (ADCP) during oceanographic surveys of the central channel conducted on the 28th May 2014. Each column represents a leg (or transect) of the survey whilst each row corresponds to one repeat circuit of the survey route. The time since or to low water (LW) is indicated on the left. Rows b:g correspond to flood flows and rows a & h:k to ebb flows. The solid black line corresponds to the depth measured by the ADCP. Thick lined black boxes in rows d:h indicate identified strong persistent downwelling features. Low water was at 10:40 and high water at 17:02 (GMT). Times of dolphin sightings (rows e:h) are marked with a black star.

A3.9 Current speeds, directions and vertical velocities across the central channel during flood flows (legs two and three)

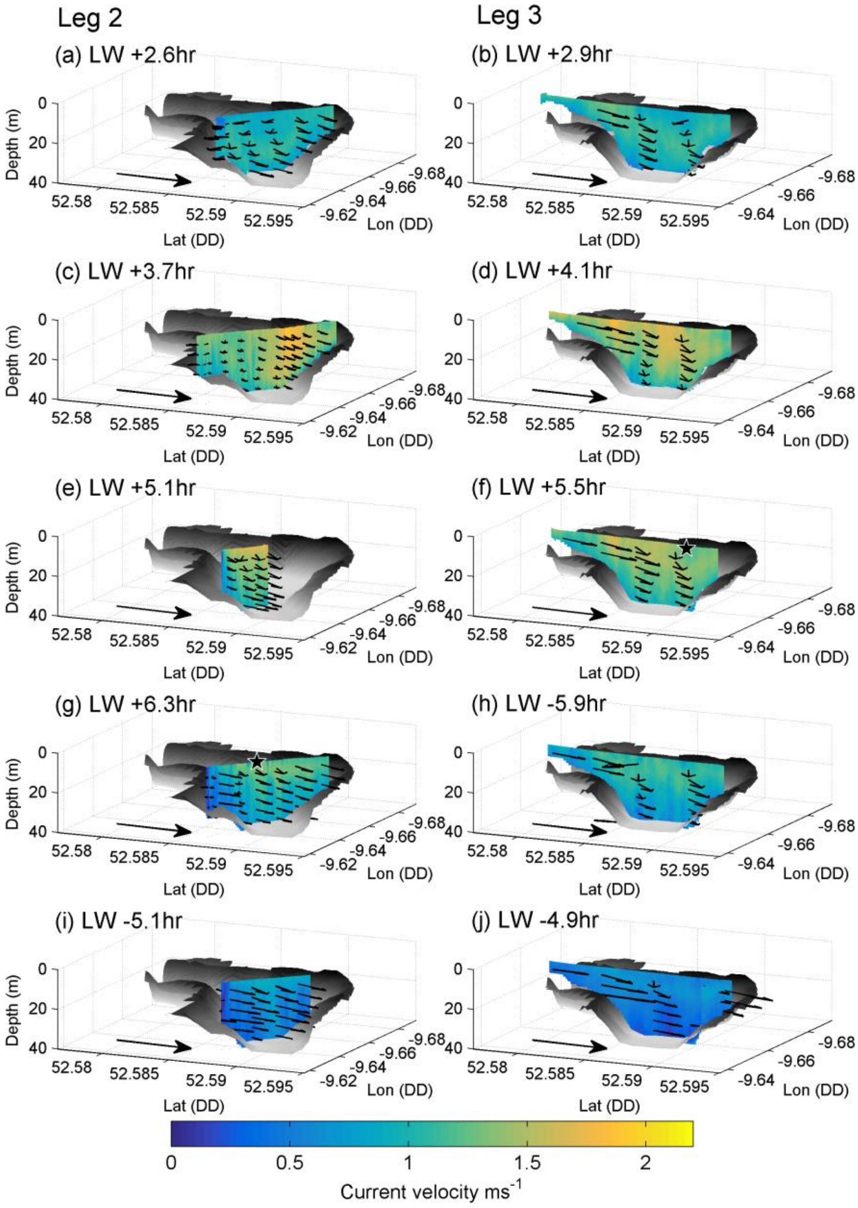

Figure A3.18 Current velocities and directions (small black arrows at 5m vertical depth intervals and 75 second horizontal time intervals) as measured by the acoustic Doppler current profiler (ADCP) during the oceanographic surveys of the central channel on the 28th May 2014. The left hand column (a, c, e, g & i) shows leg two of the survey and the right hand column (b, d, f, h & j) leg three. Each row corresponds to a different circuit of the survey route. Relative time to low water is indicated in the top left of each subplot. Only circuits completed during the flood and high tide, when dolphin presence in the region was high, are shown. Multibeam bathymetry for the channel is shown in grey. The thick black arrow shows the orientation of the plot relative to north. Times of dolphin sightings (in subplots f and g) are marked with a black star.

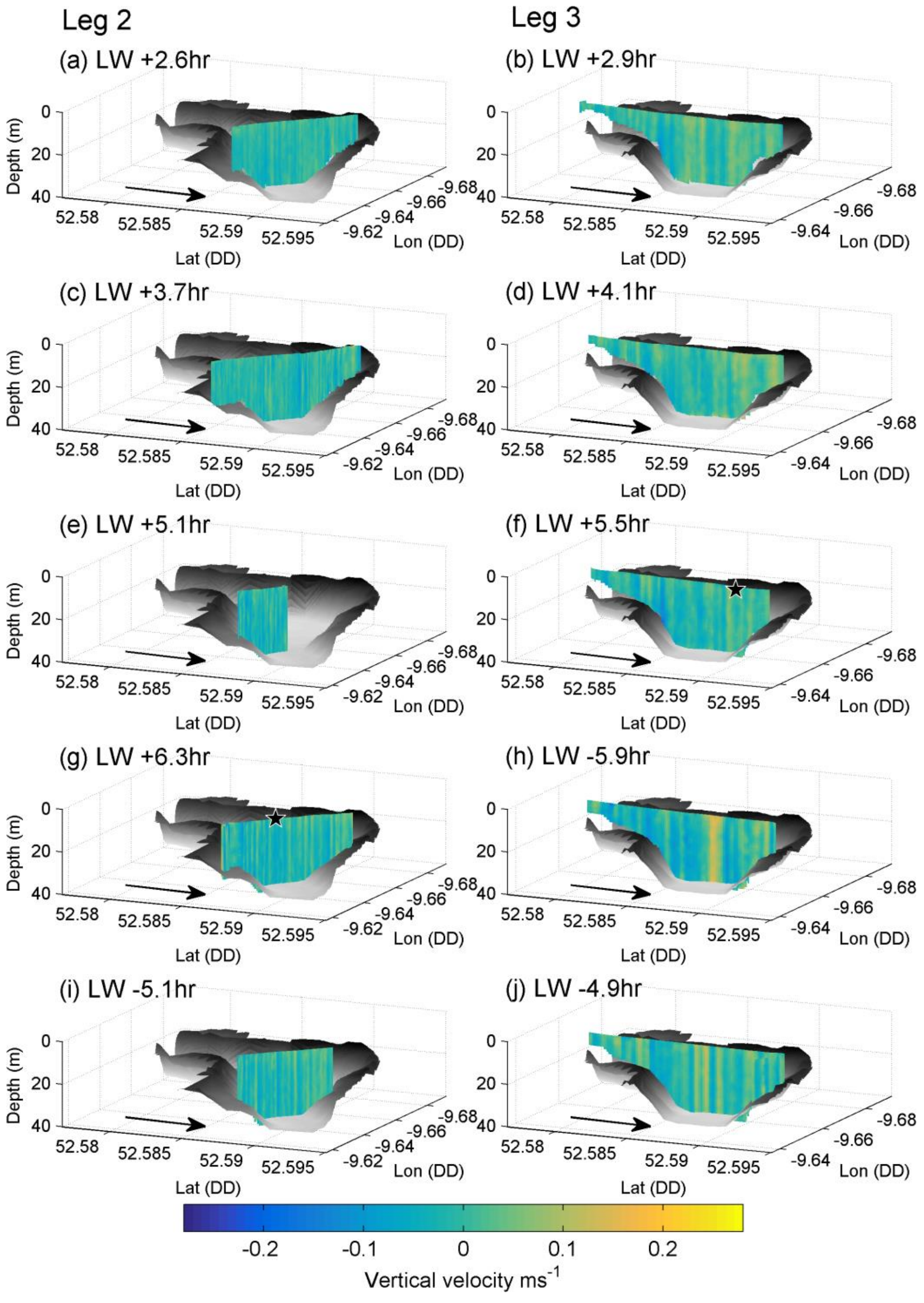

Figure A3.19 Vertical velocities as measured by the acoustic Doppler current profiler (ADCP) during the oceanographic surveys of the central channel on the 28th May 2014. The left hand column (a, c, e, g & i) shows leg two of the survey and the right hand column (b, d, f, h & j) leg three. Each row corresponds to a different circuit of the survey route. Relative time to low water is indicated in the top left of each subplot. Only circuits completed during the flood and high tide, when dolphin presence in the region was high, are shown. Multibeam bathymetry for the channel is shown in grey. The thick black arrow shows the orientation of the plot relative to north. Times of dolphin sightings (in subplots f and g) are marked with a black star.

A3.10 References

Wal J Van der, Falconi L, Januchowski S, Shoo L, Storlie C (2014) SDMTools.