UNIVERSITY OF Southampton

Faculty of Natural and Environmental Sciences

Ocean and Earth Science

The spatio-temporal distribution and habitat associations of marine mega-vertebrates off southwest UK

by

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ABSTRACT

Faculty of Natural and Environmental Sciences: Ocean and Earth Sciences

Doctor of Philosophy

THE SPATIO-TEMPORAL DISTRIBUTION AND HABITAT ASSOCIATIONS OF MARINE MEGA-VERTEBRATES OFF SOUTHWEST UK.

Alice R. Jones

This thesis uses data collected between 2007 and 2010 in an intensive, effort-based visual monitoring survey in southwest Cornwall, UK. The survey was carried out from a strategic watchpoint overlooking a regionally unique seabed feature, the Runnelstone Reef, which has previously been identified as key site for all three of the study's target species: harbour porpoise *Phocoena phocoena*, basking shark *Cetorhinus maximus* and Balearic shearwater *Puffinus mauretanicus.* The location of the survey site is perceived as a productive, coastal marine 'hotspot' by local wildlife observers, eco-tour companies, conservation bodies and commercial fishermen. The aim of the study was to use a multidisciplinary approach to investigate the drivers behind the increased abundance and diversity of mega-vertebrates at the site. A wide range of environmental data, from fine-scale bathymetry to remote-sensed oceanographic data, were utilised in an attempt understand the potential interactions between the target species and the environment at a variety of scales.

Although the target species have very different ecologies and each represent a different taxonomic Class; they each face significant threats throughout their range due to human impacts and are all listed as species of conservation concern on a number of UK, European and International Directives and Conventions. Therefore, improving our understanding of their distribution and highlighting interactions between the animals and their environment is an important objective, both for science and conservation.

Harbour porpoise sightings showed significant fine scale temporal clustering associated with tidal flow, as well as spatial clustering around parts of the survey area with steepest seafloor slopes. The timing and location of highest porpoise densities coincided with tidal-topographically controlled hydrodynamic features identified using fine-scale current profile data (ADCP). The sightings and acoustic monitoring (C-POD) data both showed a high amount of temporal variability at seasonal, daily and hourly scales, highlighting the complex nature of the fine scale animal-environment interactions.

Daily patterns in basking shark sightings data were investigated as a function of physical environmental covariates, with particular focus on the effect of meso-scale thermal fronts. In line with previous national scale studies of the species, shark sightings were significantly affected by sea surface temperature (SST) and there was evidence for a change in seasonal abundance compared to the long-term pattern. In addition, the variance of SST over the preceding weeks was identified as being a key predictor of the abundance of sharks in the survey area. Surprisingly, there was not a significant effect of the presence, persistence or thermal gradient strength of fronts on daily shark sightings. The implications of this result are discussed with reference to results of previous studies and the focus of marine protected area policy in the UK.

The broad scale spatio-temporal analyses of Balearic shearwater sightings data from the UK, Ireland and France indicate that the birds continue to be recorded in significant numbers throughout areas previously considered to be at the northernmost extent of their range. Record counts of passing birds were recorded off southwest UK in the last two years, along with unprecedented aggregations in bays along the Brittany coast, comprising approximately 20 % of the estimated global population. The data presented provide much-needed quantitative information on the at-sea distribution and behaviour of this Critically Endangered species during the interbreeding period, and support earlier studies suggesting a northwards shift in their migratory distribution.

“It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living“

David Attenborough

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Declaration of authorship.

I, Alice R. Jones declare that the thesis entitled '*The spatio-temporal distribution and habitat associations of marine mega-vertebrates off southwest UK*' and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
- where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help;
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
- none of this work has been published before submission

Signed: …………………………………………………………………………..

Date:………………………………………………………………………………

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Firstly I would like to thank my primary supervisor Dr. Russell Wynn who taught me everything I know about, in his words, 'field craft'. Long hours spent doing fieldwork together is certainly a good way to establish a productive and down-to-earth student-supervisor relationship and I do really feel lucky that I have had that. Thanks must also go to my co-supervisor at SAHFOS David Johns, who has been so supportive and always ready to lend an ear and give me a pep talk, which has been much appreciated. Also thank you to my co-supervisors at NOC, Prof. Simon Josey and Prof. Paul Tyler.

Other supervisory or collaborative support has come from a wide range of people who had no responsibility to me whatsoever, and I am extremely grateful to them. In particular to Clare Embling for her help and encouragement with statistical modelling, exemplified by agreeing to meet me and talk stats on the day before she gave birth to her second child and also a few months afterwards, with baby Poppy in tow. You are shining example to all of us up-and-coming female scientists! Thanks to Peter Miller at PML for the front data and for putting up patiently with all my questions; and to Simon Ingram, Phil Hosegood, Len Thomas, Marijke de Boer, Duncan and Hannah Jones, John Williams and Matt O'Shaughnessy for their help and comments over the last few years. Thanks to the crew of RV Callista (particularly Bill and Gary) and to Justin Dix for their help with planning and carrying out the physical oceanographic survey.

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I will always be grateful to Russ, Prof. Tim Guilford, Miguel McMinn and Ana Rodriguez for giving me the opportunity to be involved in the Balearic shearwater tracking work. It was such a fun and exciting adventure to go out to the colonies for the fieldwork. I will never forget the nights in the cave, playing cards (or attempting to in Russ' case!), drinking whiskey and later lying awake in the pitch black while the Balearic shearwaters scrambled all over me to get to their nests, calling in their peculiar way – what an experience! I think I want to be a seabird researcher….!

All my office mates have been great. I have seen a few come and go over the last 4 years. Lavinia and Sophia, things have certainly livened up in the office since you two arrived and thank you so much for your help with fieldwork, especially the boat surveys. Thank you both, and also Rhiannon – the newest recruit – for chats about data analysis. It has been really helpful to have people around to sound things out with. I am so glad that the office has been gradually taken over by biologists since I moved in, I don't think the geophysicists would have been much help! Matt, thanks for all the tea – even if you do leave the bag in!

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Chapter 1 Introduction to the thesis.

This thesis is the result of a 3-year PhD project at the National Oceanography Centre, Southampton. PhD funding was awarded by the Natural Environment Research Council (NERC), with additional support from the Sir Alistair Hardy Foundation for Ocean Science (SAHFOS). The Total Foundation supplied funding for key fieldwork packages.

The thesis is presented as 6 chapters, briefly outlined below:

1. Introductory chapter containing an overview of the research project with aims and objectives. This section also contains an introductory literature review focused on ecosystem dynamics and biophysical coupling in the marine environment.
2. An overview of the SeaWatch southwest (SWSW) survey including a description of the study site and survey methodology. This chapter also includes a detailed discussion of potential methodological limitations and actions that were taken to avoid introducing bias into the survey data. The information in this chapter is broadly relevant to all of the following science chapters. Methods specific to each of the following chapters are included therin.
3. The physical controls on the fine-scale distribution of the harbour porpoise. This chapter describes patterns in the spatio-temporal distribution of porpoises recorded in the SWSW effort-based survey study area and explores interactions between the animals and the fine scale physical habitat of the Runnelstone Reef.
4. Temporal variability in basking shark sightings: is there evidence for temporal coupling with meso-scale thermal ocean fronts? This chapter looks specifically at the temporal link between environmental variables and the timing of appearance of sightings of basking sharks in the effort-based SWSW monitoring survey.
5. Spatio-temporal distribution of the critically endangered Balearic shearwater in the UK, Ireland and NW France. This chapter is presented as a first authored paper (in review), which uses effort-based and opportunistic visual monitoring data to describe patterns in the appearance of the Balearic shearwater within the study area.
6. General conclusions: Synthesis of the key results from chapters 3, 4 and 5 and suggestions for future work.

1.1 Aims.

I. To describe baseline information on the abundance and distribution of harbour porpoise, basking shark and Balearic shearwater around the coast of southwest England.
II. To improve our understanding of the physical and biological controls on the spatio-temporal distribution of the target species listed above, in order to aid in their management and conservation.

1.2 Objectives.

i. Analyse data collected in a 4-year long effort-based visual monitoring scheme in SW Cornwall (UK) to describe the fine and meso-scale spatial and temporal distribution of the three target species.
ii. Collate and analyse local, regional and national data collected using alternative survey methods, in order to put the results of the small scale monitoring survey into a regional context. Additional data includes; local passive acoustic monitoring of porpoises, national public sightings records of Balearic shearwaters and basking sharks and regional boat-based visual surveys of all species.
iii. Collect and analyse a suite of biotic and abiotic data from the study area in order to provide evidence of the factors influencing the spatio-temporal distributions of harbour porpoise and basking shark.
iv. Interpret and disseminate the results of the study within the context of conservation management.

1.3 Context.

As the human population grows and development increases, there is intense pressure on the marine environment to provide resources. Fishing, oil and gas exploration, shipping, marine construction, waste disposal, renewable energy development and recreation all contribute to the exploitation of the seas. As the intensity of these activities increase, so do the negative impacts on the natural ecosystem and its ability to provide us with what we require.

Marine ecosystems are notoriously difficult to study due to their inaccessibility. Mobile marine species provide a particular challenge, as they are wide ranging and operate within enormous, complex, three-dimensional landscapes. As a result, there is a lack of medium- to long-term, effort-based datasets that report the effect of environmental variables on the distribution patterns of marine top predators. Due to this lack of data, many large marine species are at risk from no, or poor, management strategies that do not account for interactions between the animals and their environment.

This PhD research project is based around a visual monitoring dataset collected during the SeaWatch SW annual marine wildlife survey, which started in 2007 and was completed in 2011. Due to the large number of species monitored in the SWSW effort-based survey, and the wealth of data collected on each; it was not possible to use all of the data collected within the scope of this PhD research project, therefore it is focused on three of the survey's target species. All three of the target species were frequently recorded in the effort-based SWSW survey and are of conservation concern and listed under various national and international conservation policies and treaties. Although they have very different ecologies and each represent a different taxonomic Class; they each face significant threats throughout their range due to human impacts. For this reason, improving our understanding of their distribution, and highlighting habitat preferences and interactions is an important objective, both for science and conservation.

The target species are harbour porpoise (*Phocoena phocoena*, Linnaeus 1758), basking shark (*Cetorhinus maximus*, Gunnerus 1765) and Balearic shearwater (*Puffinus mauretanicus*, Lowe 1921). This research aims firstly to describe any patterns in spatial and temporal distribution of the target species and secondly to assess potential underlying influences of specific biotic and abiotic environmental parameters on their distribution at a variety of scales. It is worth noting from the outset that the studies of each of the three species were approached differently, both in terms of the context of the research questions and the types and scales of the analyses. Therefore, the results presented for each species should be considered separate and there is little opportunity for inferring common conclusions regarding all three species. The decision to approach the research in this way was made on the basis of the data available, the current level of knowledge regarding the distributions and habitat preferences of each species and the immediate information requirements from a conservation and management perspective.

For both harbour porpoise and basking shark there are numerous studies detailing distribution at regional, national and international scales (e.g. Hammond, 2006; Sims, 2008); therefore the focus was on improving the understanding of small-scale habitat interactions, in particular oceanographic and biophysical links. The extent of the effort based survey data available has allowed these interactions to be explored in a novel and robust manner. Conversely, there is little information regarding the migratory distribution of the Balearic shearwater and therefore a more descriptive and broader scale analysis was undertaken for this species; collating a broad range of data into a comprehensive overview. This information is extremely important to the management and conservation of this Critically Endangered species and invaluable at a time when there is increasing pressure on governments to monitor and protect the species when present in their waters.

The results of the research project provide valuable baseline data for the distribution of the three target species and improve our understanding of the drivers behind these patterns for porpoises and basking sharks, which will aid in the interpretation of long-term distribution patterns. The evidence presented for small and regional scale biophysical controls on the distribution of these species comes at a time when marine protected area policy is becoming increasingly focussed on highlighting sites where aggregations of vulnerable or priority species occur regularly. There is particular interest in development of predictive ecology, which associates quasi-stable topographic or oceanographic features with the appearance of vulnerable species.

1.4 Literature review on ecosystem dynamics and biophysical coupling.

Variability in the spatial and temporal distribution of marine megafauna in relation to ecosystem dynamics is an important research area in marine ecology (Ballance et al., 2006; Louzao et al., 2006a; Scott et al., 2010; Block et al., 2011; Camphuysen et al., 2012). The physical environment is a key control on many marine biological processes through biophysical coupling, where physical oceanographic conditions and processes affect a biological response. This principally occurs as a result of the impact that physical dynamics have on the distribution of nutrients and phytoplankton growth, which is at the root of all marine ecosystems. Although this interaction usually begins in lower trophic levels, its impacts commonly filter up through the marine food chain to the higher marine species such as fish, marine mammals and seabirds (Frederiksen et al., 2006).

Often the relationships between physical processes and higher trophic levels are inferred through proxies or described by coincidence in the distribution patterns of oceanographic conditions and species (e.g. Schneider, 1990; Worm et al., 2005; Wynn et al., 2007). The difficulty in making direct mechanistic associations comes with the need to track the effect of physical controls up through multiple trophic levels to apex predators at the top of the food chain (Scott et al., 2010; Luczak et al., 2011). The relationships between the trophic levels may be de-coupled or non-linear and therefore the greater the number of steps in the trophic system, the more complex the links between the bottom and the top.

At the largest scales, the effect of climate driven forcing on the marine environment is commonly reported (Stenseth et al., 2003; Stenseth et al., 2005) and the distribution of marine species is known to be highly dependent on the influence of ocean-climate variables, for example circulation patterns, gas/water exchange, temperature and salinity. These effects are mediated through the direct physiological tolerance limits of mega-fauna and their prey species. There is evidence of anthropogenic climate change effects in terms of both altered distributions (e.g. Hughes, 2000; Genner et al., 2004), phenological shifts and tropic mismatches (Edwards and Richardson, 2004; Thackeray et al., 2010). Yet there remain many uncertainties regarding the specific controls exerted by climatic parameters on particular ecosystems and species. Climate-linked distribution shifts that have been identified in lower trophic level groups (Beaugrand et al., 2002; Richardson and Schoeman, 2004) are predicted to filter up through ecosystems and impact predatory species including large fish, seabirds and cetaceans (Beaugrand and Reid, 2003; Frederiksen et al., 2006). There may also be direct responses from apex predators to environmental conditions, for example distributional ranges associated with thermal preferences (e.g. McMahon and Hays, 2006).

Hydrodynamic processes are also important factors in shaping marine ecosystems (Mann and Lazier, 2006). There are many ways in which the hydrodynamic environment can affect biological processes. Density gradients, wind and topographic features induce water movement, generating geographically distinct circulation patterns, which influence the structure of marine ecosystems (Lalli and Parsons, 1997). The biological impacts of these physical processes occur at a variety of scales, from the effect of micro-scale turbulence on planktonic organisms (MacKenzie and Leggett, 1991), to the influence of large-scale thermo-haline circulations on whole ecosystems (Ottersen et al., 2001). The resulting complex of interactions between physical and biological processes makes it important to look at the marine system as a whole, in order to better understand and interpret patterns in marine species distribution (Scott et al., 2010).

The physical processes underlying large-scale biological events are generally better studied than smaller scale interactions (Mann and Lazier, 2006). For example, the effect of the North Atlantic Oscillation (NAO) on the ecology of the North Atlantic marine system is well studied. References abound which detail mechanistic links between NAO controlled, low frequency, hydro-climatic processes and biological processes at variety of marine trophic levels (e.g. Beaugrand and Ibanez, 2002; Drinkwater et al., 2003; Stenseth et al., 2003). There is also an increasing amount of research documenting the effect of large-scale topographic and oceanographic features, such as shelf breaks and oceanic fronts, on trophic transfer and biodiversity (e.g. Schneider, 1990; Royer et al., 2004; Worm et al., 2005; Gannier and Praca, 2007).

Bio-physical processes also have important effects at meso- and fine-scales but significantly less is understood about these smaller-scale interactions, particularly in relation to their impacts on higher trophic level species (Mann and Lazier, 2006). Water column stability can influence the prey environment, and this effect can be scale dependent. At a large scale, high water column stability and reduced mixing/upwelling can reduce productivity as a result of low nutrient and oxygen levels. At a fine scale (metres in the vertical), the converse is true; high stability in the water column can be beneficial to foraging marine species as it leads to aggregations of plankton in the vertical plane, as proposed by Lasker's Stable Ocean Hypothesis (Lasker, 1978). Lasker's theory states that in calm water, a distinct vertical prey maxima (or 'thin layer') will form, which acts to concentrate plankton predators as a result of increased foraging success within this distinct depth band. Under turbulent conditions, which may occur due to wind- or tide-induced mixing, the prey field will become more dispersed as the prey maxima breaks down.

It is recognised that secondary flows and turbulence, commonly caused by wind, tide and topographic interactions, have impacts on prey encounter rates for planktonic organisms (Rothschild and Osborn, 1988). Medium to high levels of turbulence increase the probability of prey encounter and feeding rates for zooplankton and larval fish (MacKenzie and Leggett, 1991; Kiorboe and MacKenzie, 1995). These findings provide insight into the mechanisms responsible for the increased biomass and trophic transfer noted around key physical features such as fronts, upwellings, thermoclines and topographic features (MacKenzie and Leggett, 1991).

The open ocean can be viewed as a vast heterogeneous landscape, in which mobile species must forage effectively in order to increase prey encounter rates (Sims et al., 2006). Therefore distinct areas of high productivity are attractive to free-ranging higher predators, as they offer improved foraging opportunities (Block et al., 2011). These areas are often referred to as ‘hotspots’; defined by Sydeman *et al*. (2006) as “sites of critical ecosystem linkages between trophic levels”. There is growing interest in linking these biological ‘hotspot’ areas with the underlying physical oceanographic characteristics. The following sections will review two key types of physical habitat, which are often associated with significantly higher production, and denser aggregations of organisms, than the water surrounding them.

The research presented in this thesis is focused on scales of effect at spatial ranges of 100s to 1000s of metres and temporal ranges from hourly to yearly; for this reason, the next sections of the review cover key physical features which interact with the biological system at meso and fine scales.

1.4.1 Fronts

Fronts are hydrological features that mark the boundaries between water masses with different physical properties and are characterised by sharp transitional gradients in these properties (Le Fevre, 1986). Frontal features occur at a variety of different scales, they may be ephemeral or persistent and they can occur in either horizontal or vertical planes. Figure 1.1 is a summary diagram of the physical structure of a front between mixed and stratified water bodies.

Fronts are commonly associated with increased biomass and diversity and as such are key foraging environments for mobile marine species (Le Fevre, 1986). The mechanisms proposed for this increase in biomass are 1) increased in situ productivity due to favourable conditions for growth and 2) concentration of existing stock within a smaller area as a result of physical forcing (Holligan, 1981; Le Fevre, 1986) as illustrated in figure 1.2.

There is no definitive list of the different types of fronts that exist, but the main types outlined by Mann and Lazier (2006) include; shelf-break fronts, tidal-mixing (or shelf-sea) fronts, estuarine or plume fronts, upwelling fronts and topographic fronts.

Shelf-break fronts.

Shelf-break fronts are found at the edges of the continental shelves, where the bathymetry steepens to become the continental slope, leading down to the deeper open ocean. The water over the shelf is generally less saline due to the effects of coastal river and run-off inputs and is seasonally variable in temperature, being warmer in summer but colder in winter than the water off the shelf edge (Mann and Lazier, 2006). The resulting differences in density between the two water bodies create the shelf-break front, which is a persistent and large-scale transition boundary between the two water masses. Frontal features also occur at shelf-breaks due to upwelling of cold deep water from offshore onto the continental shelf (Owen, 1981).

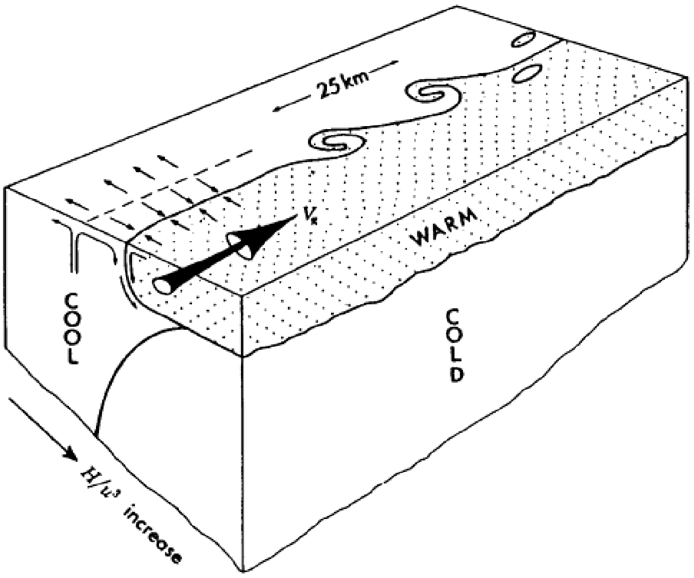


Figure 1.1 Schematic of the structure of a tidal front and its associated circulation patterns. The diagram shows that mean flow is parallel with the front (bold arrow) and there is surface convergence leading to downwelling at the frontal boundary, along with upwelling of cool water on the mixed side of the front. There are also some eddies forming, which can lead to exchange of water across the front. From Le Fevre (1986).

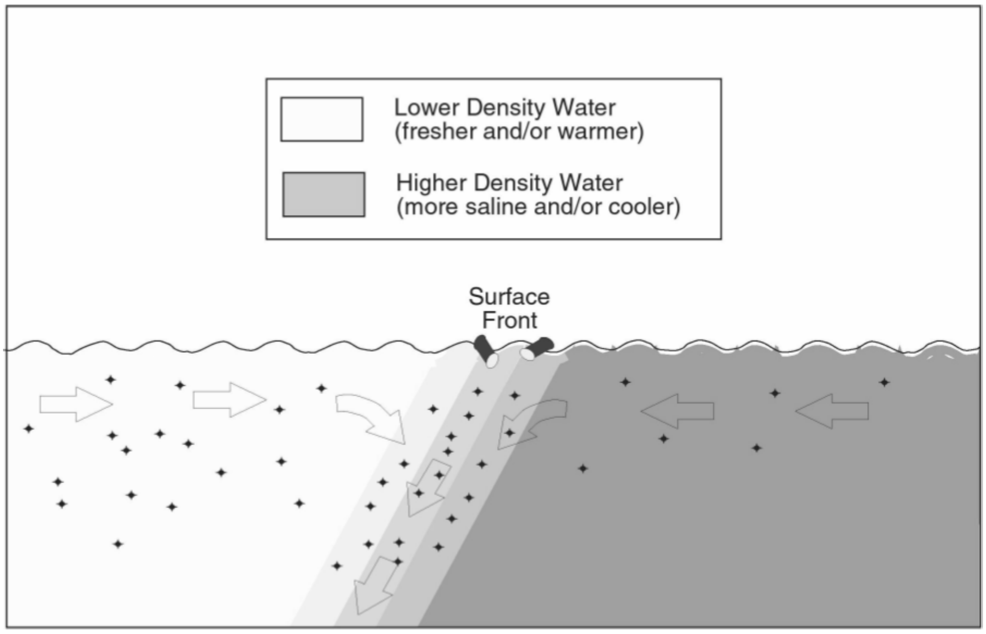


Figure 1.2: Diagram of a front formed between two bodies of water with different physical properties. The arrows show convergence towards the front due to density driven flows, which carry buoyant particles and planktonic organisms to the boundary where they accumulate. From Bakun (2006).

Shelf-break fronts are noted to be the most important type of front in terms of biological interactions and increased productivity (Le Fevre, 1986). It is likely that the persistence of these large-scale features at the shelf-edge means that both in situ augmentation of productivity due to increased nutrient input, as well as accumulation of buoyant particles, contribute to heightened biomass (Pingree and Mardell, 1981; Genin, 2004). Shelf-break fronts are commonly associated with important fishing grounds (e.g. Iverson et al., 1979; Podesta et al., 1993; Witt and Godley, 2007) and increased densities of other predatory marine species such as cetaceans (e.g. Kenney and Winn, 1987) and seabirds (e.g. Schneider, 1982).

Tidal-mixing fronts (shelf-sea fronts).

Tidal-mixing fronts are also sometimes referred to as shelf-sea fronts because they are restricted to the seas found over the continental shelves. In the shallow areas of the shelf, the frictional forces exerted by tidal flow over the seabed lead to turbulence, shear and subsequently vertical mixing of the water column (Simpson and Hunter, 1974). At a critical depth, the tides no longer generate enough turbulence to mix the water column through its full depth, and a thermocline develops as the upper most layers of water become warmed by the sun and stratification is achieved (Simpson and Hunter, 1974). Tidal-mixing fronts are therefore defined as the boundary between tidally mixed and stratified water bodies (Simpson, 1981).

Tidal fronts are ubiquitous on the continental shelf around northwest Europe, where tidal mixing is strong; the area was estimated by Miller (1966) to account for approximately one-eighth of the

World's tidal energy. In particular, tidal fronts around the UK are well documented and have been shown to be stable throughout most of the summer when the deeper shelf water is thermally stratified (Pingree et al., 1975). During the winter, when the seasonal thermocline has broken down due to the effect of wind and waves, these fronts are weaker, if present at all.

Figure 1.3 shows theoretically calculated locations for summer fronts between stratified deeper water and coastal mixed water for areas in the Western Approaches and Celtic Sea (Pingree and Griffiths, 1978). These theoretical predictions of summer front locations fit well with the location of fronts identified using measured temperature profiles collected by Pingree and Griffiths during research cruises on board the RV Sarsia (1978) (figure 1.4). Note the identification of a summer front around the southwest tip of England, close to the SWSW study area (marked with a red star on the map in figure 1.3 and 1.4).

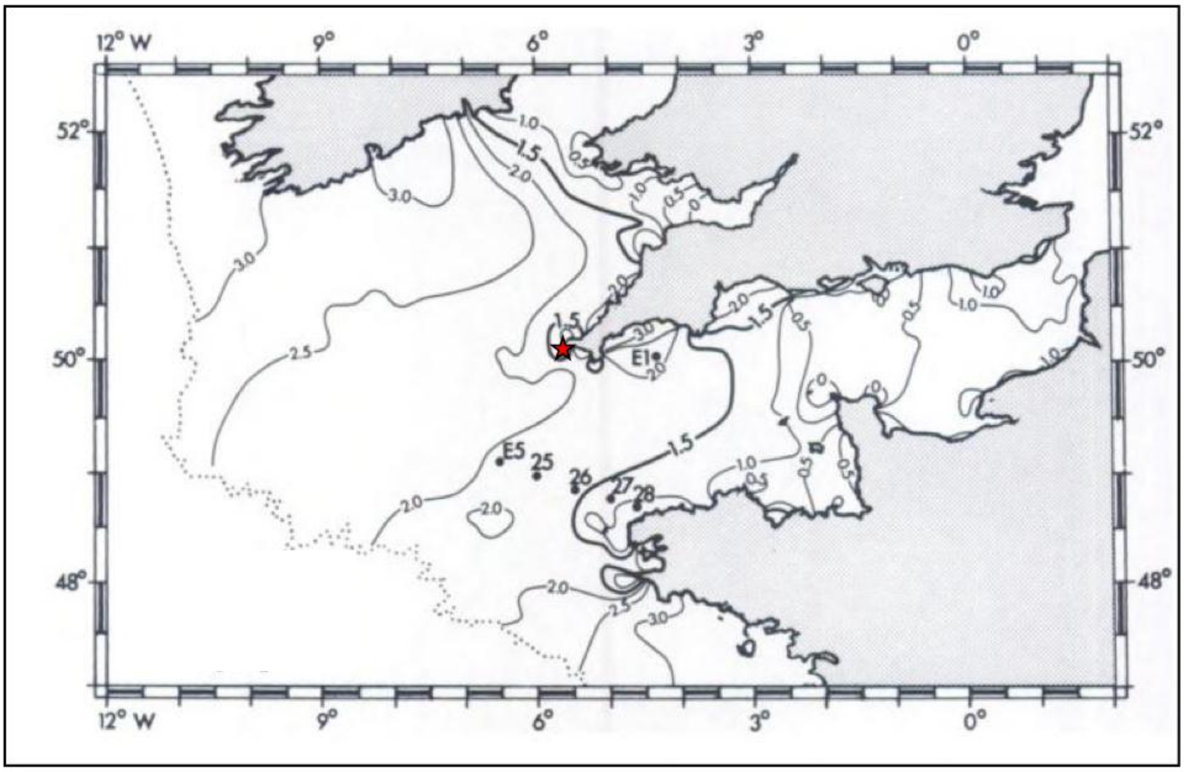


Figure 1.3: Stratification contours in the Celtic Sea and English Channel. The values represent *S*, the stratification parameter, which is calculated using data on water depth, tidal energy dissipation rate and sea temperature profiles. Low values of *S* are associated with well-mixed waters and high values with established summer thermoclines. The value of 1.5 (delineated in bold) represents transitional areas – or summer front locations - between mixed and stratified waters. From Pingree (1978). Red star in SW Cornwall indicates approximate position of the SWSW study site.

More recently, methods for identifying thermal fronts using satellite imagery have been developed. There is strong correspondence between the locations of tidal mixing fronts identified by early researchers (Fearnhead, 1975; Pingree et al., 1975; Pingree and Griffiths, 1978; Simpson,

1981) and those seen in recent analyses using satellite remote sensed sea surface temperature (SST) (figure 1.5). The satellite SST data again show that the water off the southwest tip of the UK is a key area for development of thermal fronts caused by tidal mixing (figure 1.5).

Tidal fronts have been shown to be important factors in the distribution of phytoplankton, particularly in relation to the spring and autumn plankton blooms associated with stratification of the shelf seas (Pingree et al., 1974; Pingree et al., 1976; Pingree and Griffiths, 1978). As with shelf-break fronts, the mechanism of this increased biomass in the vicinity of tidal mixing fronts remains unclear (Mann and Lazier, 2006). The fact that most tidal mixing fronts are seasonally stable and therefore persistent over periods of weeks to months makes it likely that a combination of both *in situ* enhanced productivity and accumulation mechanisms are responsible. Tidal fronts have also been identified as important habitat for some foraging necktonic species, indicating that they are key sites for trophic transfer (Pingree et al., 1974). Manx shearwaters *puffinus puffinus*, guillemots *Uria aalge* and razorbills *Alca torda* show positive associations with tidal mixing fronts in the Irish Sea (Begg and Reid, 1997) and various species of rorqual whale have been shown to associate with tidal-mixing fronts in the Gulf of St Lawrence, Canada (Doniol-Valcroze et al., 2007).

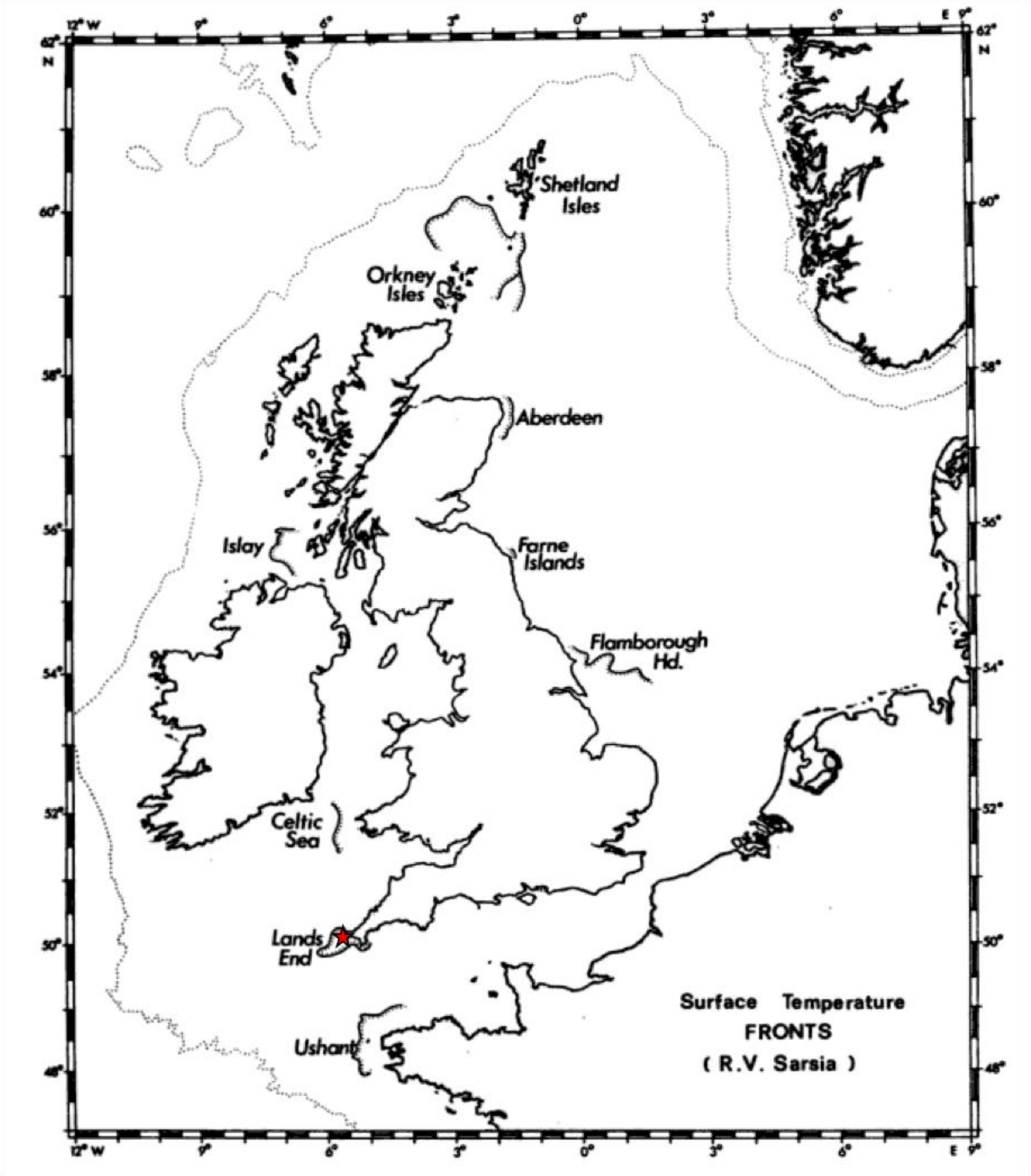


Figure 1.4: Position of tidal mixing fronts identified by data collected onboard the RV Sarsia. The solid side of each line represents the warmer, stratified side of the front and the dashed side represents the cooler, mixed side. From Pingree & Griffiths (1978). Red star in SW Cornwall indicates approximate position of the SWSW study site.

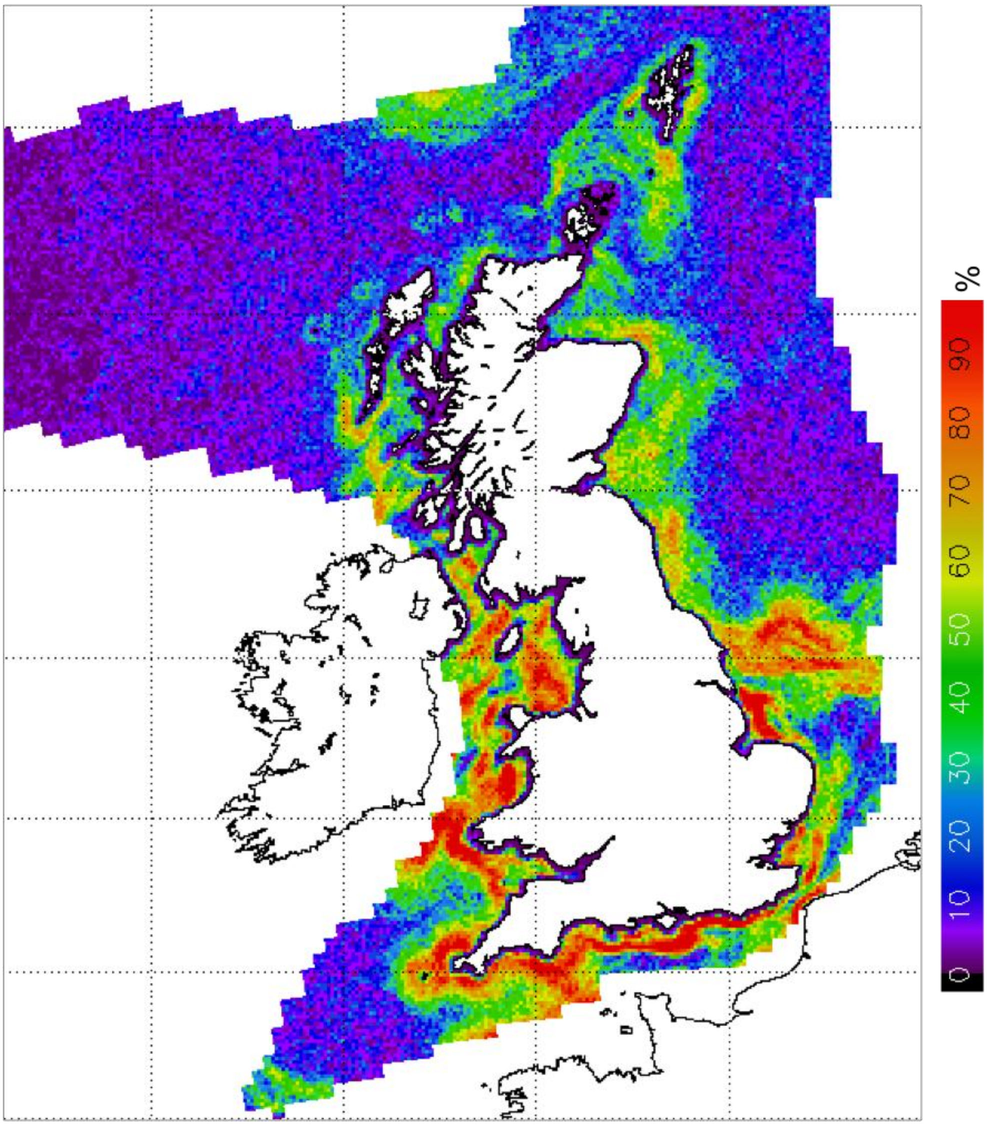


Figure 1.5: Map showing percentage of time for which a strong thermal front was observed in remote sensed SST data over a 10-year period from 1998 – 2008. A strong front is defined by a thermal gradient of 0.4 °C or more. Image courtesy of Dr. Peter Miller, Plymouth Marine Lab Remote Sensing Group.

1.4.2 Topographic features.

In coastal waters, around features such as headlands, reefs, bays and promontories; tide and topography may interact to form tidal-topographic fronts, generated under specific tidal flow conditions (Wolanski and Hamner, 1988). These tidally dominated features experience secondary flows and coupled increases in turbulence and mixing, which are often associated an increase in abundance and diversity of marine organisms (Alldredge and Hamner, 1990; Genin et al., 1994; Genin, 2004; Yen et al., 2004). As mentioned previously, the specific mechanisms for the increase in biomass are unclear, but there are broadly two main factors which control aggregations around topographic features; 1) enhanced local productivity as a result of increased nutrient input from upwelling and vertical transport, and 2) accumulation of biomass from elsewhere (Genin, 2004).

Upwelling-driven nutrient enhancement can only affect local productivity levels if the upwelled water is retained around the feature for periods long enough to increase local phytoplankton biomass (1 – 2 days) and, in turn, influence growth in local zooplankton populations (1-2 weeks) (Genin, 2004). This is unlikely to be the case at small coastal features, where upwelled water will be moved on by tidal and coastal currents before local productivity can be augmented (Genin, 2004).

Accumulation around complex or abrupt topographies may occur as a result of passive processes such as trapping of planktonic species by convergent flows and boundary mixing at tidal-topographic fronts (Wolanski and Hamner, 1988). The resulting high concentrations of plankton may then affect a behavioural response in larger organisms, who aggregate in the area because of the dependable resources provided by rich prey patches. Evidence of this effect on mobile marine predators is provided by Yen *et al*. (2004) who found that a variety of seabird and cetacean species were significantly associated with identifiable topographic features. Scott *et al*. (2010) investigated the effect of fine-scale controls on foraging by cetacean and seabird top predators in the North Sea and found that all seven of the species studied foraged preferentially in patches (2 – 10 km) associated with high concentrations of sub-surface chlorophyll and high variance in bottom topography. Further evidence supporting the theory of topographically controlled trophic transfer is given by Skov *et al*. (2008) for sei whales (*Balaenoptera borealis)* along the Mid-Atlantic ridge, Ingram *et al*. (2007) for fin (*B. physalus)* and minke whales (*B. acutorostrata*) in the Bay of Fundy, Bailey and Thompson (2010) for bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth and Piatt *et al*. (2006) for short-tailed albatrosses (*Phoebastria albatrus*) around the Aleutian Islands.

Chapter 2 The SeaWatch SW survey.

This chapter provides a detailed description of the main study site and the visual survey methodology including an in-depth discussion of methodological limitations. These sections are relevant to all of the following science chapters. Methods that are specific to each chapter are not included here, but can be found within each science chapter.

2.1 Overview.

The SeaWatch SW (SWSW) survey was an effort-based visual monitoring survey that recorded multiple species of marine wildlife from a single land-based watchpoint through the summer and autumn from 2007-2011 (although only 2007-2010 data were included in this thesis). The aim was not to census the target species, as the survey only covered a small part of their full distribution, but rather to monitor usage of the survey area by the target species and to better understand the effect of local static and dynamic habitat on the animal's behaviour and distribution.

The survey watchpoint is located on Gwennap Head, a strategic headland at the southwest tip of the UK mainland, which is an important flyway for migrating seabirds. Offshore is a tidally dominated topographic feature called the Runnelstone Reef, which is a regionally important site for small cetaceans and basking sharks (*Cetorhinus maximus*). The priority species of the monitoring survey was the Critically Endangered Balearic shearwater (*Puffinus mauretanicus*), but more than 30 other species of marine mammals, seabirds and large fish were also monitored during the intensive survey. Other target species included the basking shark, harbour porpoise (*Phocoena phocoena*), ocean sunfish (*Mola mola*), minke whale (*Balaenoptera acutorostrata*), sooty shearwater (*Puffinus griseus*) and Cory's shearwater (*Calonectris diomedea*).

The SWSW project was also responsible for collecting broader monitoring date for its primary target species, the Balearic shearwater. This was achieved through the collation of a national sightings database of all non-effort based public sightings for 2007 - 2010 from Great Britain and Ireland. The project also had a number of 'sister sites' within the southwest of the UK where regular seabird monitoring is carried out (figure 2.1), these data were useful for contextualising the results from the effort-based dataset collected at Gwennap Head. Additionally the project is involved in an ongoing research collaboration to collect multiple years of telemetry data for the species by tracking breeding adults at the colonies on the Balearic Islands.

2.2 The survey site

The SeaWatch SW survey was carried out from Gwennap Head, in southwest Cornwall, UK (figures 2.1 and 2.2). Gwennap Head is a south facing, strategic headland watchpoint at 30 m ASL, on the southwest tip of England (50° 02’ 06.29” N 005° 40’ 45.66” W) (SeaWatch SW 2012). The site is recognised as an important migratory fly-way for seabirds passing between the western Channel and the Celtic Sea (Wynn and Yésou, 2007) and is a regionally important site for basking sharks and cetaceans (Evans et al., 2003; Bloomfield and Solandt, 2007).

Figure 2.1: Location map of the SeaWatch SW effort-based monitoring site on Gwennap Head in southwest Cornwall. The location of the supporting 'sister sites' and also marked. Background bathymetry and topography is from GEBCO.

Figure 2.2: Google Earth image of the southwest tip of Cornwall with the survey watchpoint on Gwennap Head marked by red star.

2.2.1 Seafloor features within the study area

The watchpoint provides an almost 180˚ field of view from east to west and overlooks the Runnelstone Reef (figure 2.3). The reef is a horseshoe shaped rocky feature with an average depth of approximately 15 m out to 1.6 km, where at the southern edge it shallows to form pinnacles which come within a few metres of the waters surface, beyond which the depth drops down sharply to 60 + metres (figure 2.4). To the east and west sides of the reef the seafloor slopes away and depth increases gradually. High-resolution (1 m) multi-beam swath bathymetry data is available for the immediate coastal zone, up to approximately 2 km offshore (figure 2.4). This data were supplied courtesy of the Channel Coast observatory and was collected as part of the Maritime and Coastguard Agency's Civil Hydrography Programme. This 1-m resolution dataset was combined with lower resolution (10 m) data from the UK Hydrographic Office (UKHO), which extends further offshore, to create a bathymetric map covering the full extent of the survey area and beyond (figure 2.3).

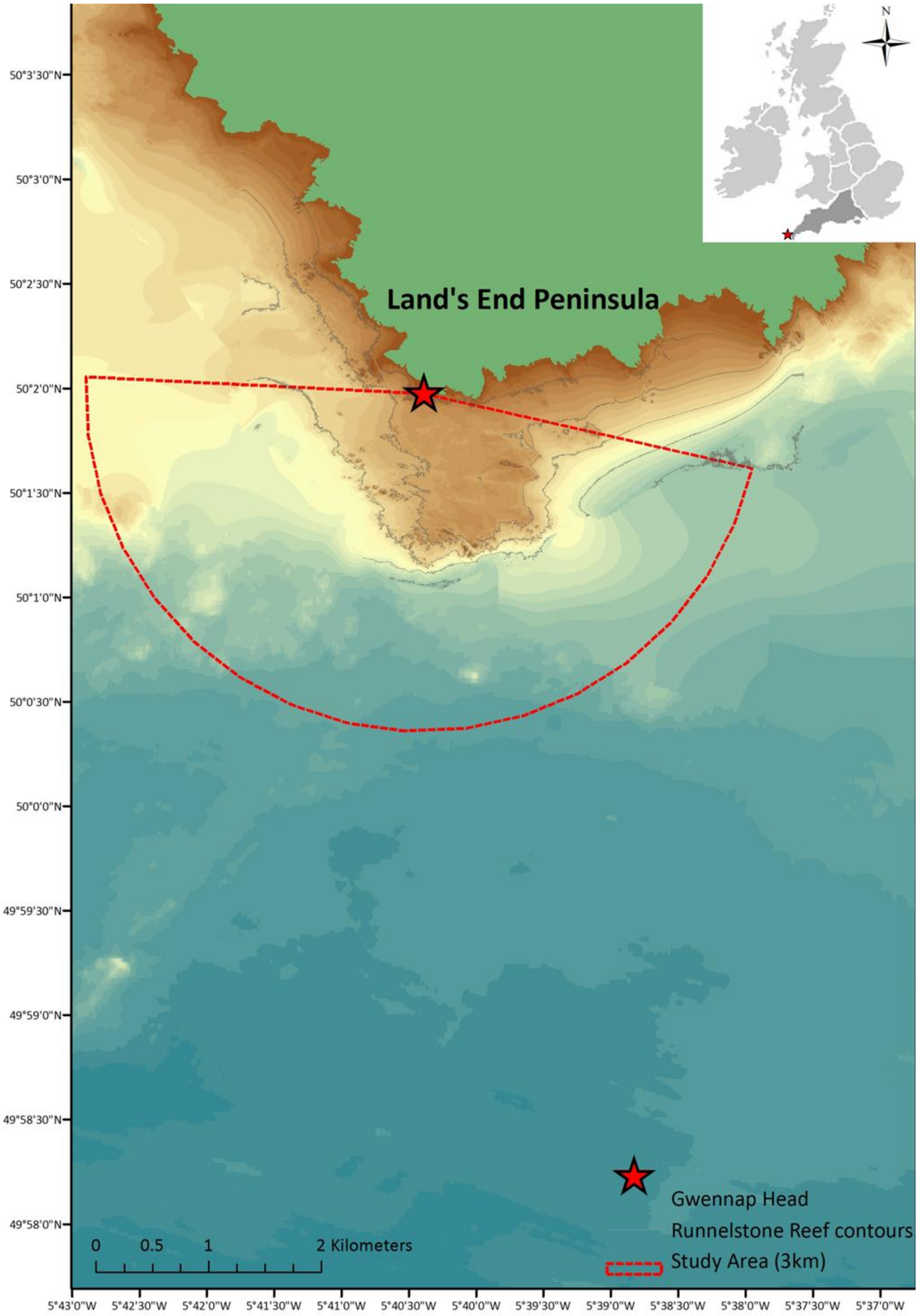


Figure 2.3: Overview map of the SeaWatch SW study area in southwest Cornwall, UK. A red star shows the watchpoint location and the field of view is indicated by dashed red line. The bathymetry is a combination of data supplied by the CCO/MCA and the UKHO and has a minimum resolution of 10-m.

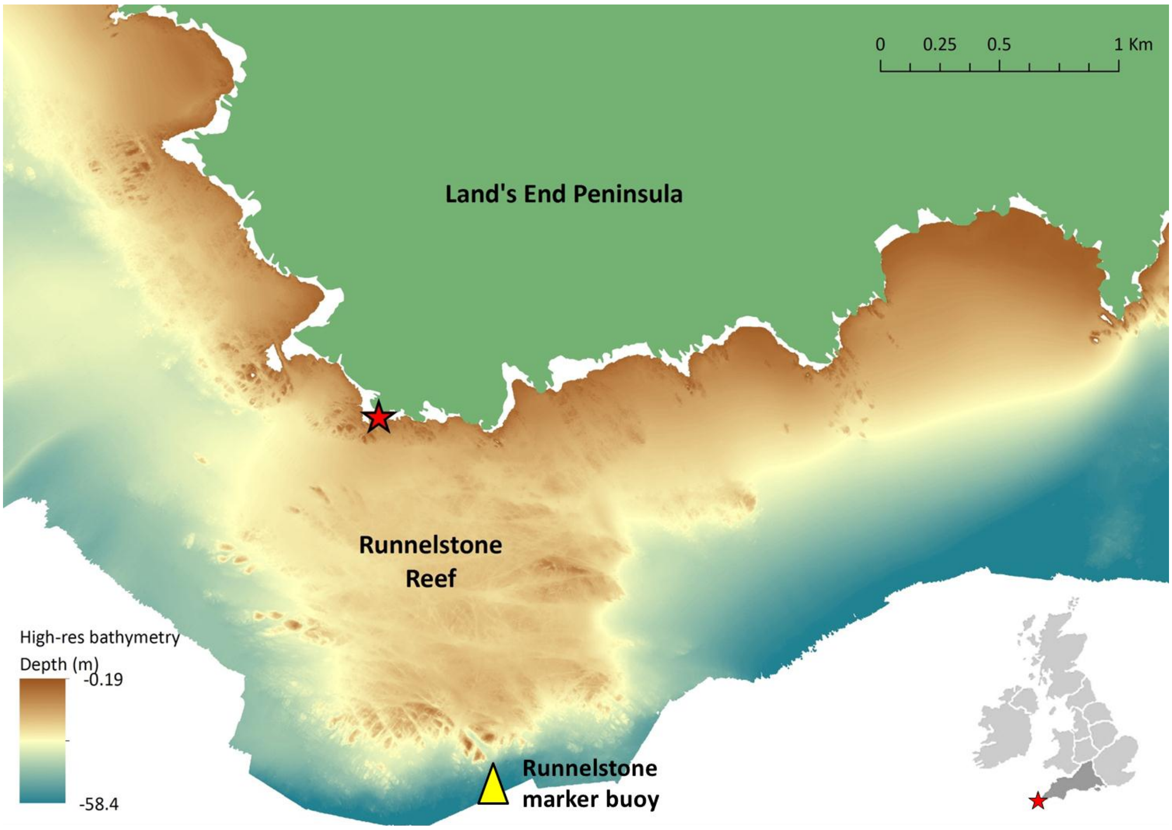


Figure 2.4: Bathymetry map of the Runnelstone Reef showing the high-resolution (1-m) multibeam swath data supplied by the Channel Coastal Observatory with the location of the SWSW watchpoint at Gwennap Head and the approximate location of the Runnelstone marker buoy, which is used by observers as an aid in distance estimation.

Depth profiles from across the reef are shown in figure 2.5 and illustrate the fairly constant depth across most the of the ‘reef top’ area (approximately 15 m) with a sharp drop off at the southern margin and more shallow depth gradients at the east and west reef margins. The colours on the depth profiles given in figure 2.5-b and c relate to depth values and match the scale in figure 2.5-a.

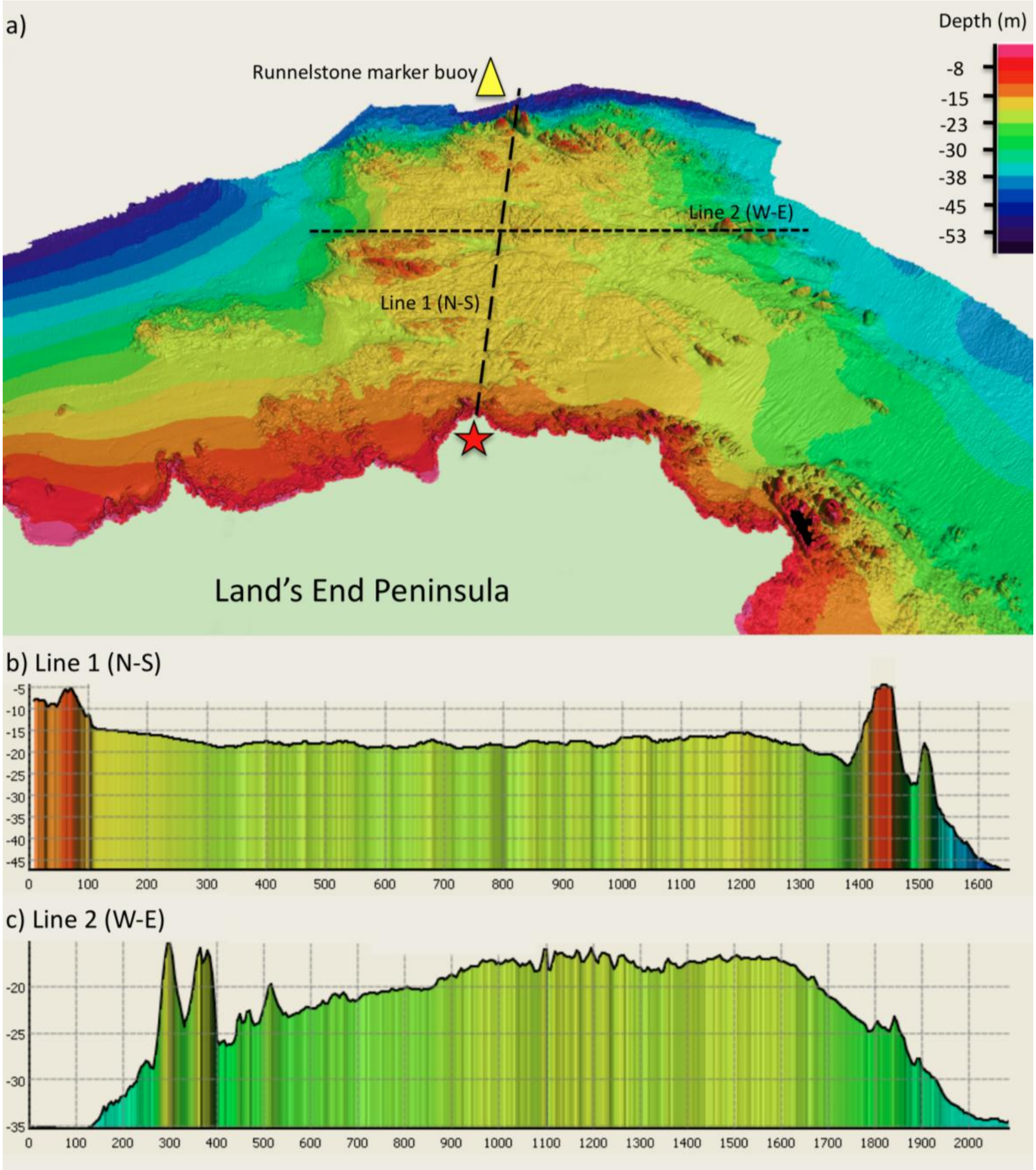


Figure 2.5: Detailed depth data for the Runnelstone Reef: (a) Runnelstone reef topography from the point of view of the SWSW watchpoint at Gwennap Head (red star), looking south towards the Runnelstone marker buoy (yellow triangle). (b) Depth profile from north to south across the reef along line 1 (long-dashed line) in (a). (c) Depth profile from east to west across the reef along line 2 (short-dashed line) in (a). The same colour scale of depth given in (a) is used in all parts of the figure.

2.2.2 Tidal flow

The site is exposed and tidally dominated, experiencing strong tidal flows and complex fine-scale flow patterns as a result of tidal-topographic interactions. Water flows around the headland reef as it enters and exits the western channel during the semi-diurnal tidal regime. The tidal current is westerly (i.e. flowing out of the Channel) for the majority of the semi-diurnal cycle, with eastwards flow (i.e. into the Channel) for only two hours per tidal cycle, at approximately an hour on either side of high water. Indications of the small-scale flow patterns around the survey area were visible at the surface as areas of turbulence and slick water, indicative of small-scale upwelling and downwelling respectively. The tidal complexities are illustrated in the hand-drawn images in figure 2.6, which were provided by local small-boat fishermen.

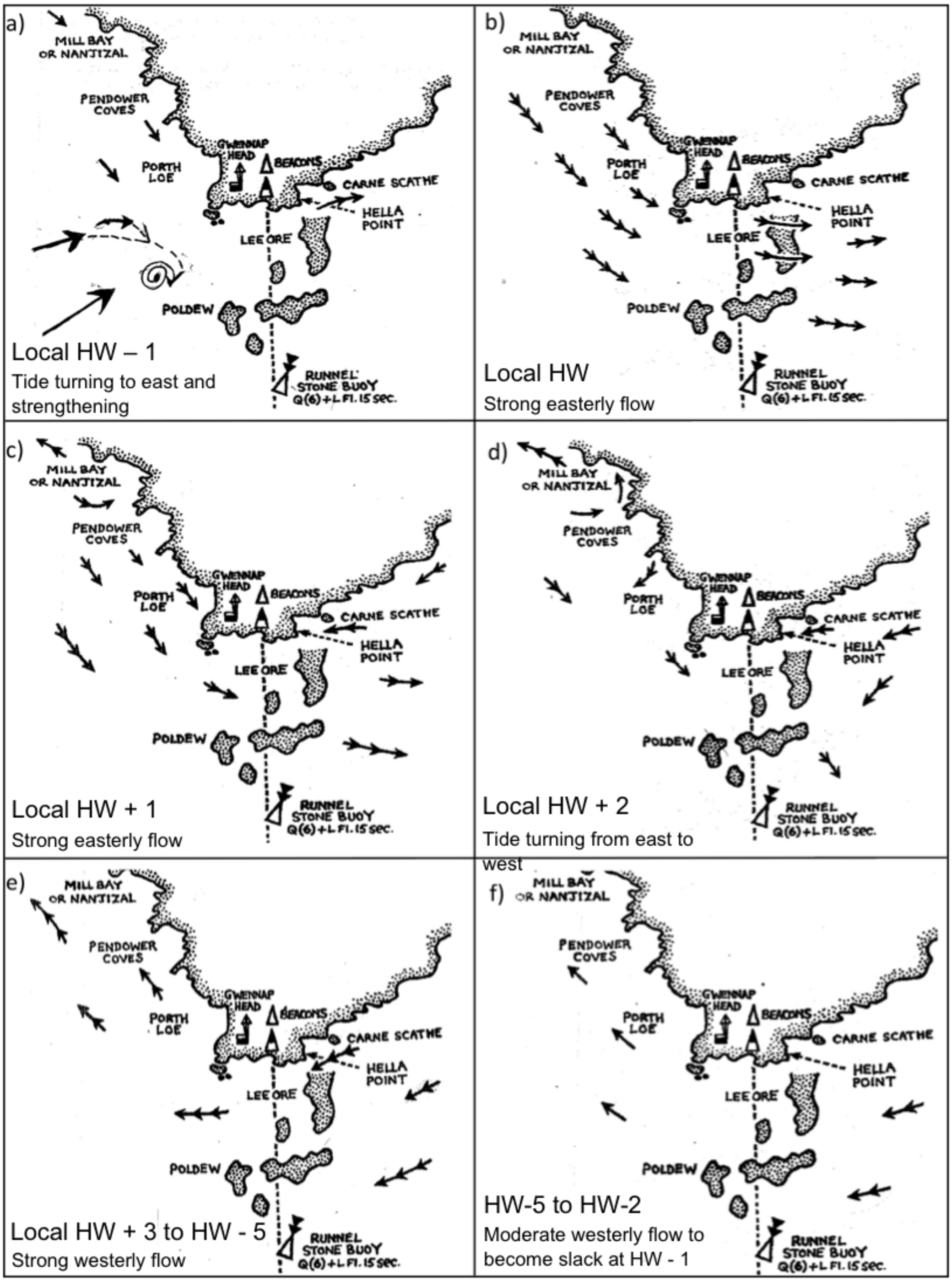


Figure 2.6: Fine-scale tidal flow diagrams for the Runnelstone Reef provided by the local National Coastwatch Institute (NCI) and local small boat fishermen. Tidal current direction indicated by arrows, where the number of arrow heads is indicative of relative speed (1 arrow head is approximately 1 knot).

2.3 Survey methodology

The survey was 'effort-based', with dawn to dusk observations carried out on each day of the 93-day period between 15th July and 15th Oct annually. Effort-based surveys are those that standardise survey effort, as opposed to ad-hoc or casual sightings surveys, where no control of survey effort is attempted. There are a number of benefits of this type of survey; primarily that absence data is collected as well as presences, because survey effort is continuous. Additionally, statistical analyses can be carried out on the data and the results are more robust because of the ability to create comparative metrics such as sightings per unit effort.

The timing of the annual survey was selected on the basis of the main period of passage of migratory seabirds passed southwest UK and the seasonal appearance period of many of the other target species. There were always at least two observers present at the watchpoint, one core observer and one supporting observer. On occasion there were also additional support observers present at the site. The core observers (n = 29 over the 4-year period) were skilled sea-watchers with prior experience of identifying the target species in the field. Selection priority was given to supporting observers who had previous marine wildlife survey experience, although this was not always the case.

Observers applied continuous search effort using telescope, binocular and naked eye scanning of the survey area, to ensure even surveillance of the near and far-fields. There was rotation of survey effort in the near and far fields between observers; with an effort to minimise the time spent continuously looking through optics. When more than two observers were present, each person was encouraged to take regular breaks, whilst always maintaining two observers 'on watch'. Although care was taken to reduce the biases introduced by varied survey conditions and the use of multiple observers, some important data limitations remain. The key limitations are; variation in observer ability, observer fatigue, variable quality of optical equipment and variable survey conditions such as the impact of glare and visibility on the detection of animals. It is also possible that there will be duplication due to animals repeatedly using the survey area on the same or subsequent dates.

Pre-printed recording forms were used to record data in the field (appendix 1) and comprehensive instructions were given to observers regarding the recording level of each species (appendix 2). The species included in this thesis (Balearic shearwater, harbour porpoise and basking shark) were all level-one target species, therefore records include date, time, number of animals and movement direction. The Balearic shearwater records also include an estimated distance from the watchpoint. The porpoise and shark records include a compass bearing and estimated distance from the watchpoint to the point of first sighting (with subsequent sighting positions also being recorded where possible).

2.3.1 Supporting environmental data.

Data on survey conditions was recorded each hour by observers at the watchpoint. These included visibility (km), sea state (Beaufort), wind speed (Beaufort), glare (% sea surface) and cloud cover (% visible sky). Guidelines on recording these environmental data were provided to observers and are given in appendix 2. Additional environmental data was collated from a variety of sources, detailed below.

Wave data.

Wave metrics and sea-surface temperature data were recorded at the Penzance wave buoy (Datawell BV Directional Waverider mark III) located at 50° 6.86232'N - 005° 30.18072', approximately 15 km to the northeast of the survey watchpoint. The wave buoy records *in situ* oceanographic metrics every 30 minutes and these data can be downloaded from the CCO website. The metrics that were used were H_s (significant wave height in metres), wave direction (degrees) and sea surface temperature (˚C).

Weather data.

Weather data were recorded at the Land’s End weather station and were supplied courtesy of John Chapell. The instrument is an Instromet weather station, which is located in Trebehor on a mast at approximately 100 m above sea level. The location is approximately 2 km from the survey watchpoint at Gwennap Head and collects data every minute on wind speed (mph), maximum wind speed (mph), wind direction (degrees) and air temperature (˚C) (CCO, 2012).

Remote sensed oceanographic data.

Thermal front maps (example images in figure 2.7) are created using processing algorithms designed by Dr. Peter Miller from the PML Remote Sensing Group (Miller, 2009). Thermal front locations are detected using Advanced Very High Resolution Radiometer (AVHRR) satellite remote sensed data. Fronts are detected where there is > 0.4 °C temperature difference between adjacent water masses. Data is processed using a compositing algorithm, which combines the location, strength and persistence of all fronts observed over several days/months/years into a single visual map or value (figure 2.7, left). Compositing reduces issues of cloud cover and highlights persistent or strong gradient fronts; providing a novel alternative to time averaging, which tends to blur dynamic features and lose mesoscale resolution (Miller, 2009). Quantitative time series data for front metrics were extracted from the data for a 5.5 km x 11 km box offshore of the survey watchpoint. The metrics are described in detail in chapter 4.

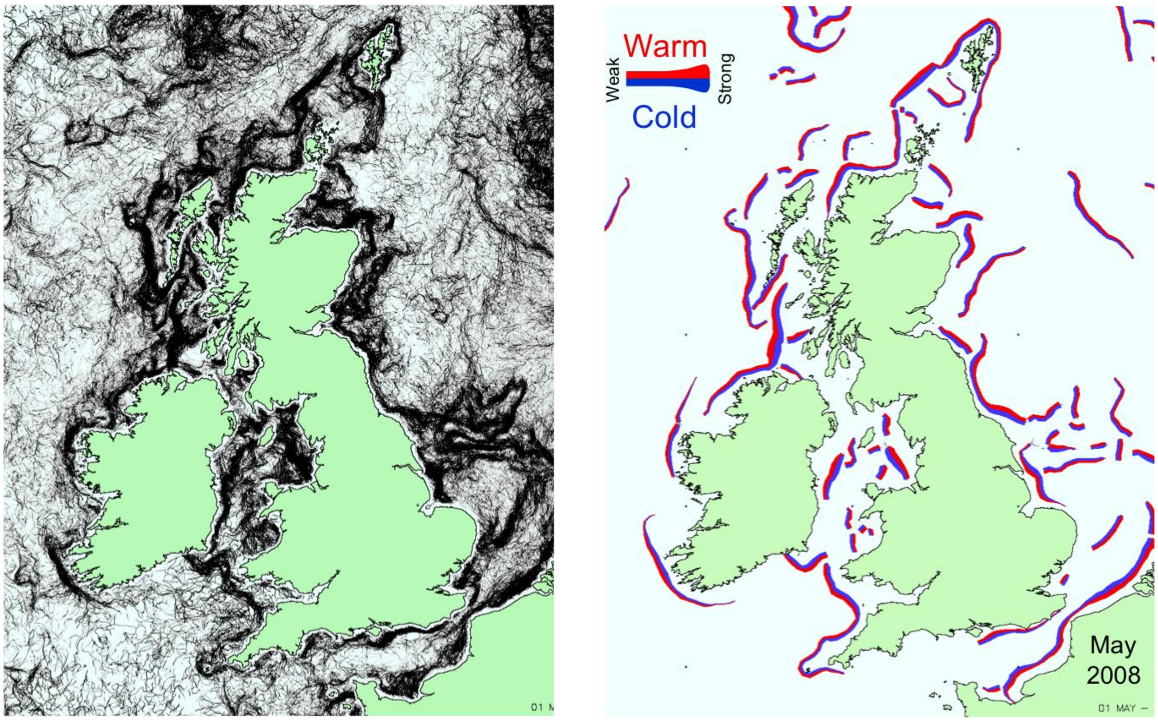


Figure 2.7: Thermal front images, May 2008. The left hand image is a composite front map showing all thermal fronts detected around the UK during May 2008. The darkness of the lines indicates the significance of the feature in terms of persistence and strength of temperature gradient. The right hand image shows improved visualisation of important frontal features, which was created using a line-clustering algorithm. This synoptic chart indicates the cold and warm sides of the front in blue and red respectively and the thickness of the line is related to the strength of the thermal gradient. Images are courtesy of Dr. Peter Miller at the Plymouth Marine Lab Remote Sensing Group.

Tidal data

Tidal data was extracted from the Proudman Oceanographic Laboratory (POL) High Resolution Continental Shelf Model (CS20) using POLPRED software. The model has a horizontal resolution of approximately 1 nm (1.8 km); which is the highest resolution tidal model available for the survey area. The resolution of the model is not high enough to use the data spatially to compare flows within different parts of the survey area, but the data are still valuable in a temporal sense to provide broader-scale tidal current flow patterns. The metrics extracted from the model were flow speed (m sec^{-1}), flow direction (degrees), tide height (m relative to mean sea level) and high-water times. A random selection of the high-water times and tide heights were compared to tide tables for the survey area and found to be in close agreement.

2.4 Constraining observer error on distance estimation

The SWSW survey required observers to make estimates of distance and take compass bearings to the position of marine wildlife sightings (cetaceans and fish). There will obviously be a level of inaccuracy associated with the estimates of each observer as well as variability in different observers' ability to correctly estimate distance and take an accurate compass bearing.

Observers looked out over an area of sea that encompasses the Runnelstone Reef and its marker buoy. The buoy is an obvious distance marker, being approximately 1.6 km from the observation watchpoint on Gwennap Head and on a bearing of 170°. Observers often used it as an aid in distance estimation and for quality control of bearing records. Training materials were provided to observers in advance of their shift to ensure that they were confident in using a compass and aware of the distances from the watchpoint to known visible features.

In order to be able to better understand how accurate the positional data were and to estimate an appropriate level of spatial error for the data; an attempt to constrain this error was made by testing two of the primary observers using the procedures outlined below. The aim of this exercise was both to better estimate observer error, but also investigate the consistency of estimates between observers. It was assumed that the level of error on position estimates would increase with distance.

2.4.1 Visual estimate error test 1: Boat position estimation.

2.4.1.1 Methods.

In October 2010, two regular observers (who between them have covered over 40 % of the entire 4-year survey period) were asked to take 30 bearing and distance estimates of a boat that was moving around over the survey area, within the field of view of observers on the watchpoint. Two-way radios were used to communicate between the boat and the observers. At designated times, the observers would take a bearing and distance estimate of the boat's position; whilst at the same time the true location of the boat was recorded using a GPS on board the vessel. Using the GPS position of the watchpoint, it was possible to convert the observers' distance and bearing estimates into co-ordinates using the method outlined by Veness (2012). Boat position and observer-estimated positions were plotted in a GIS, allowing errors to be calculated.

2.4.1.2 Results.

Error on boat position estimates:

The true boat positions were transformed into bearing and distance values from the watchpoint and these were compared to the observer estimates. The results showed a mean error of 320 m and 4.6° between the true position of the boat and the observer-estimated distance and bearing values (averaged over the 30 sites and from *both observer's* estimates).

The actual distance between the plotted positions of the boat and the observer-estimated positions was also measured in a GIS (using the spatial analyst: point distance tool). This data shows that the average distance between the exact location of the boat and where it was plotted according to the observer's estimates was 244 m (SD = 141 m). A single observer's test results are plotted in figure 2.8, which demonstrate that distances tended to be underestimated by the observer.

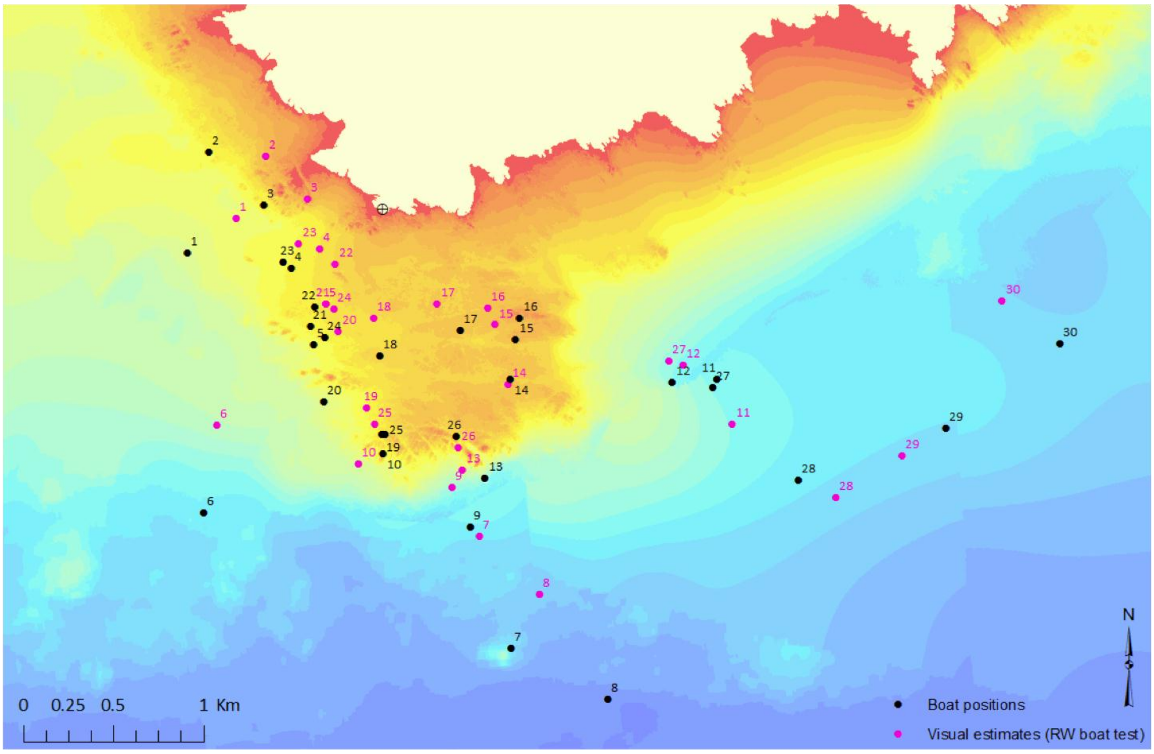


Figure 2.8: Results of visual error test one. True boat positions shown by black filled circles and observer-estimated positions shown by filled pink circles. The data shown are from one of the two observers who undertook the test in October 2009 (n = 30). The watchpoint location on Gwennap Head is indicated by the hatched circle. Bathymetry data supplied courtesy of the Channel Coastal Observatory.

The distance estimates were re-analysed after being grouped into distance bins of: 1 - 1000 m, 1001- 1500 m, 1501 – 2000 m and greater than 2000 m. The error was then averaged for all of the estimates within each distance bin. The results (table 2.1) show that distance error was highest in the furthest distance bin and lowest at distances between 1001 – 1500 m, likely as a result of the Runnelstone buoy marker at 1.6 km.

Table 2.1: Distance and bearing error on visual estimates of position during the boat position test. Data were averaged from 60 position estimates from two observers. The test was carried out in October 2010.

Distance band	Mean distance error	Mean bearing error
0 - 1000 m	0.25 km	4.8˚
1001 – 1500 m	0.13 km	4.7˚
1501 – 2000 m	0.32 km	4˚
> 2000 m	0.58 km	4.8˚
Overall	**0.32 km**	**4.58˚**

Variability between observers:

In a test of 30 locations; 28 out 30 of the bearings taken by the two observers were within 10° of each other and 20 out of 30 were within 5° of each other. The mean difference between the bearings taken by the two observers was 5.4°. When the positions were plotted in GIS, the average distance between the two observers estimate of the boat position was 250 m. Out of the 30 position estimates, 25 were less than 250 m apart. The distance estimates that were more than 250 m different were all outside the range of 1.5 km.

2.4.2 Visual estimate error test 2: Comparison with theodolite data.

2.4.2.1 Methods.

During a week of fieldwork in January 2011, data were collected to compare the visual estimation of position of porpoise sightings to accurate locations obtained using a theodolite. For each of 22 porpoise sightings a positional fix using a theodolite and a visual estimation of position (distance and bearing from watchpoint) was recorded. The observer who undertook this test was one of the observers who had previously taken part in the boat test (section 2.4.1). The data were compared using the position from the theodolite fix as the true location of the animal.

2.4.2.2 Results.

The points representing the true position of the animal and the visually estimated position were again plotted in a GIS (figure 2.9) and the mean error between them was 243 m (compared to a mean error of 320 m in the 2010 boat test, N= 60). When the data from the single observer who undertook both tests is compared, the error level is similar: test one error = 185 m (n = 30, SD = 207 m), test two error = 243 m (n = 22, SD = 158 m).

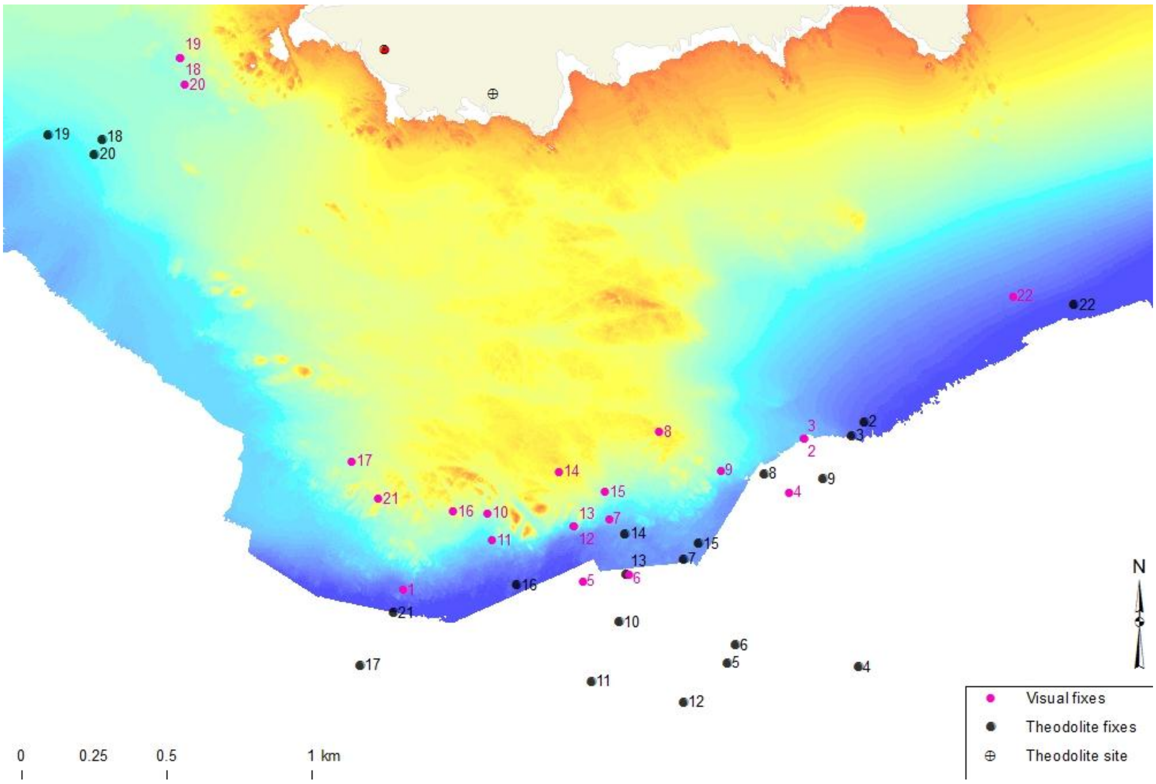


Figure 2.9: Results of visual error test two. True porpoise positions (theodolite fixes) shown by black filled circles and observer-estimated positions shown by filled pink circles (n = 22). The test was undertaken from watchpoint slightly to the east of the Gwennap Head watchpoint (hatched circle). Bathymetry data supplied courtesy of the Channel Coastal Observatory

Although these two tests were undertaken by only 2 of the SWSW observers, these two were involved in long periods of the fieldwork. Therefore, in the absence of data on the level of error for all individual observers, the mean error estimate from the tests was used to inform appropriate analyses of the spatial dataset, including smoothing bandwidth of kernel estimates (300-m) and grid cell size for spatial modelling (600-m).

2.5 Issues with detectability in the SeaWatch SW survey.

It is important to recognise that finding and counting all of the animals within a surveyed area is extremely unlikely (particularly when working in the marine environment). As a result, there is a need to attempt to account for the proportion of missed observations, or at least to reduce the biases associated with missed observations as much as possible when interpreting survey results.

Clearly, the availability of animals for inclusion in any survey is affected by the ability of an observer to see them; and this ability is reduced as distance between the animal and the observer increases. Typically, in the analysis of wildlife surveys, a 'detection function' is created from the survey data, using conventional Distance Sampling methods (Buckland et al., 2001). This 'detection function' can then be used to estimate the proportion of animals detected within distance bands from the observer compared to the theoretical 'true' underlying distribution of the animals. The 'detection function' therefore gives information about the probability of sighting or missing an animal at a specified distance from the observer and can be used to correct for the missed animals in density or abundance estimates made using the survey data.

Unfortunately, it is not possible to use conventional Distance Sampling methods for single land-based observation surveys. This is because undertaking continuous observations from a single point violates one of the main assumptions underlying Distance Sampling theory; that the animals are distributed randomly with reference to the observer (or alternatively, that the observer is distributed randomly with reference to the animals, as is the case in strategic monitoring surveys from multiple points or along transect-lines – based on stratified random sampling). Because of this violation of the random design assumption, there was no standard way to estimate a 'detection function' for sightings data collected in the SWSW single-point survey, and therefore no systematic way to correct for missed animals with increasing distance (Buckland et al., 2001).

However, it is possible to collect 'trials' data, using double-observer methods, which can then be used to create a 'detection function' for a single-point survey (Buckland et al., 2004). One-way or two-way independent observer trials are set up at the observation point. A successful trial involves both observers, independently, spotting the same animal and a failed trial involves only one observer spotting the animal. The proportion of successes and failures within specified distance bands from the observation point can be modelled using a logistic regression, and the results then used to estimate a 'detection function' (based on the proportions of successes and failures within each distance band). In a recorded conversation on 25th Jan 2012, Dr L. Thomas, a statistical ecologist at the Centre for Research into Ecological and Environmental Modelling (CREEM), confirmed that if double observations are not carried out throughout the entire period of the survey, it is valid to retrospectively apply a 'detection function' based on data collected later in double-observer trials from the same observation point and for the same species (see also Buckland et al., 2004; Thomas et al., 2010).

Very accurate distances must be associated with sightings made during double-observer trials, requiring the use of a theodolite. This ensures that the exact distance from the observer to the animal is measured accurately, so that the sighting can be attributed the correct distance for the 'detection function' modelling. Unfortunately, a theodolite was not available for use at the SWSW watchpoint until 2011, precluding double-observer trials being undertaken until this time, and therefore there were no data for estimating species-specific detection functions for data collected in SWSW 2007-2010. Double observer trials will be undertaken at the SWSW survey site during the 2012 survey season. The 'detection function' created using these data can then be retrospectively applied to the full SWSW dataset, for publication purposes.

In the absence of a 'detection function' and the associated ability to systematically correct for the effect of distance on the survey data, other measures have been used to reduce potential biases related to detectability and support the robustness of the dataset and analyses. These approaches are outlined below and although it is recognised that there are drawbacks to each of these methods, it is hoped that in combination they provide strong evidence for the chosen survey area delineation, with a reasonable level of detectability out to this boundary; supporting the results as genuine as opposed to an artefact of the survey methodology.

2.5.1 Exploring detection bias in the SWSW survey data.

Sightings of seabirds and marine wildlife were recorded from visually estimated distances of up to 8 km from the SWSW watchpoint. It is clear that identification of, and ability to detect animals (particularly smaller and less conspicuous species) will be adversely affected at longer distances, even when using optics.

Exploration of the data from single and multiple species was undertaken to identify whether there were patterns in the data that suggest the survey methodology is affecting the results, or if there was a systematic drop-off in all sightings recorded beyond a certain distance.

2.5.1.1 Inter-species comparison of distance-from-shore data.

The histograms in figure 2.10 show the distribution of visually estimated distances from the survey watchpoint for sightings of 4 different in-water species/groups; basking sharks (n = 529), dolphin species (n = 132), harbour porpoise (n = 563) and ocean sunfish (n = 109). These data will be used to explore the biases introduced by survey methodology and to define a sensible limit to the survey area, which delineates an area of the sea that is not obviously affected by decreased detectability. Note that the 'dolphin species' were grouped, due to their similar profile and visual cues at the sea surface and because there was not enough data to present individual histograms for each species (the group includes common dolphin, bottlenose dolphin and Risso's dolphin).

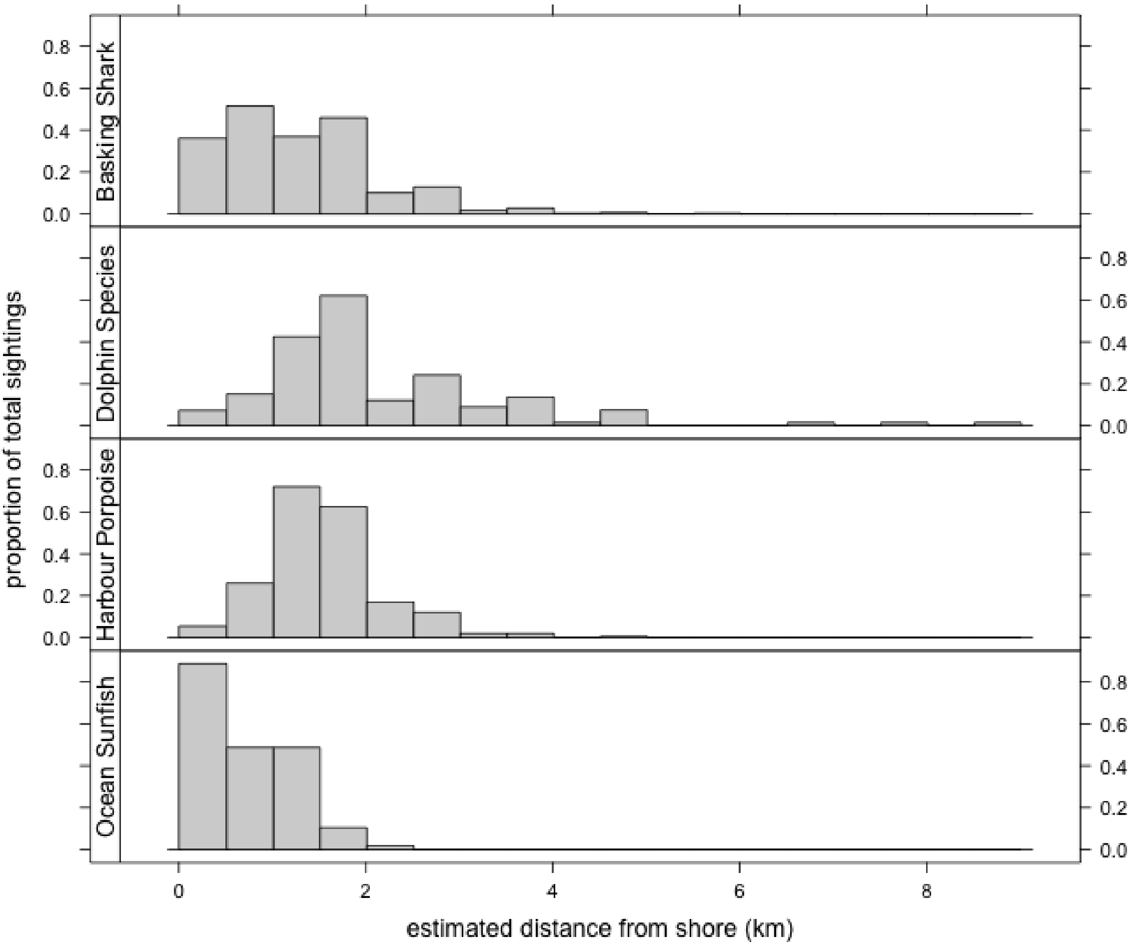


Figure 2.10: Density histograms of visually estimated distance-to-sightings for four species groups with different surface profiles, shape, size, and behaviour (i.e. different detectability). Data is from the SWSW effort-based survey. Harbour porpoise (N = 563), basking shark (N = 529) and ocean sunfish (N = 109) data are from 2007 – 2010; dolphin species (N = 132) data are from 2007-2009. No filtering for viewing conditions or sea state was carried out, but known or suspected re-sightings of the same individual/group were removed. Distance data is binned at 500 m in order to account for uncertainty in the visual distance estimates (which have an error of approximately 300 m, see section 2.4).

There were similarities in the distributions of distance-to-sightings for harbour porpoises and ‘dolphin species’ (figure 2 10), with very few sightings recorded inside 1 km and most sightings between 1 and 2 km; although sightings of ‘dolphin species’ were on occasion recorded much more distantly. It can be argued that this ‘humped’ distribution with distance might be expected in a ‘point’ survey, where the area of sea surveyed increases linearly with radial distance from the observer (Buckland et al., 2001) (Figure 2.11); but this same pattern is not seen in the data on basking sharks and sunfish (Figure 2.10), suggesting that survey methodology and pure detectability is not wholly controlling this pattern in the distance distribution of cetacean sightings.

The distribution of distances to sightings of basking shark (n = 529) and ocean sunfish (n = 109) were quite different to the cetaceans, with more sightings recorded closer to the shore (figure 2.10). The sharks have quite an even distribution within each of the 500-m distance bins up to 2 km, beyond which sightings drop off. The ocean sunfish were most frequently sighted within the first 0.5 km from shore and decrease steadily beyond that, with very few sightings recorded at distances of more than 1.5 km (figure 2.10).

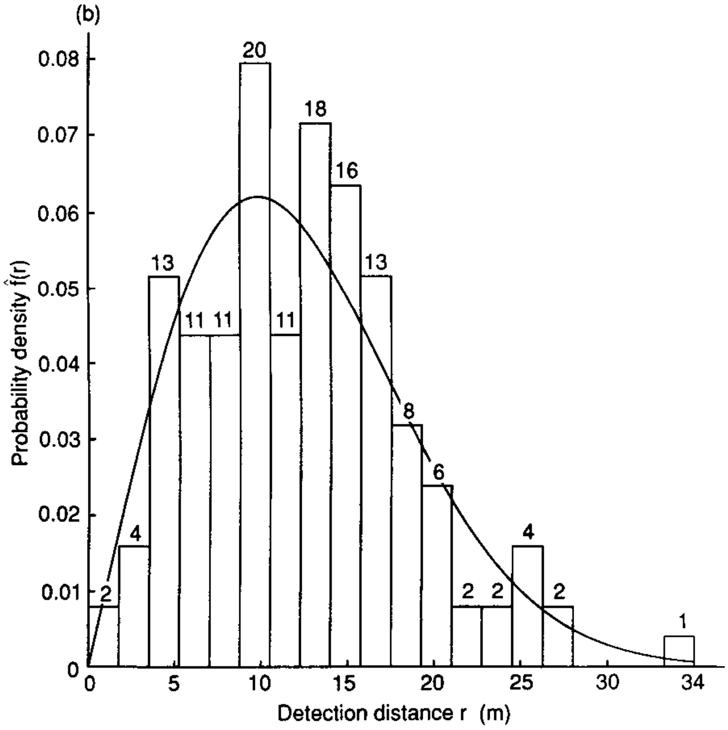


Figure 2.11: Density histogram of example point survey distance data presented by Buckland *et al.* in their book 'Introduction to Distance Sampling' (2001). The figure illustrates the expected 'humped' distribution of distances associated with point surveys, where area surveyed increases in radial bands with distance from the observer.

Variability in the distance distribution patterns of the different species (figure 2.10) counters the hypothesis that patterns in the distribution of sightings within the survey area result purely from detectability. The two species most similar in their surface profile are the ocean sunfish and the harbour porpoise; yet these show very different distance distributions (figure 2.10). The biggest and theoretically most 'detectable' of the four species is the basking shark, which spends long periods at the surface and has a very large, visible fin. Although there were sightings of sharks recorded out to 6 km, the majority sightings were within the first 2 km from the shore. Basking sharks are arguably easier to detect than dolphins and porpoises, yet these small cetaceans were seen more frequently seen at greater distances from the watchpoint than the sharks (figure 2.10). This may be as a result of detection cues associated with cetaceans such as circling seabirds above their location, or large groups of animals travelling together in pods.

2.5.1.2 Within species comparison of distance from the watchpoint.

Looking at the distribution of distance-from-shore data for the same species, but within different sections of the survey area potentially provides information about the effect of distance on detectability. The area surveyed from the SWSW watchpoint was divided up into 6 'sections' along different bearings from Gwennap Head (figure 2.12). The distance distribution of sightings recorded within each section was plotted as separate histograms in figures 2.13 (harbour porpoise) and 2.14 (basking shark).

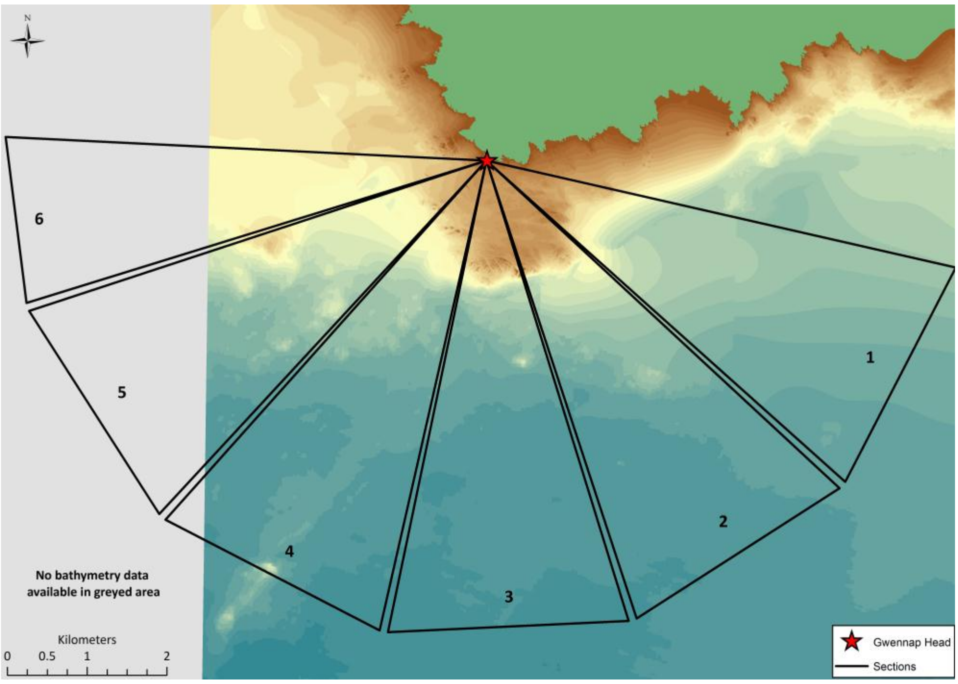


Figure 2.12: Map showing the delineation of six 30˚ bearing sections radiating out from the survey watchpoint at Gwennap Head (red star). The sections span an area from 100˚ to 270˚ (the field of view from the survey watchpoint) out to a distance of 6 km. Sections are numbered 1 to 6 and correspond to the histograms in figure 2.13 and 2.14.

The physical properties and habitat of the Runnelstone Reef survey area are variable in different directions from the watchpoint, with sloping sandy topography at the reef edges to the east and west and a more sudden rocky drop-off at the southern reef edge. If physical environmental factors were affecting the spatial distribution of porpoise sightings, we might expect to see some difference in the distance-distribution of sightings at different angles from the watchpoint (corresponding to different physical habitats along each section). Whereas a similar pattern in the distribution of sighting distances from each sector of the survey area would be expected if detection were the main controlling factor in the distribution of sightings of animals.

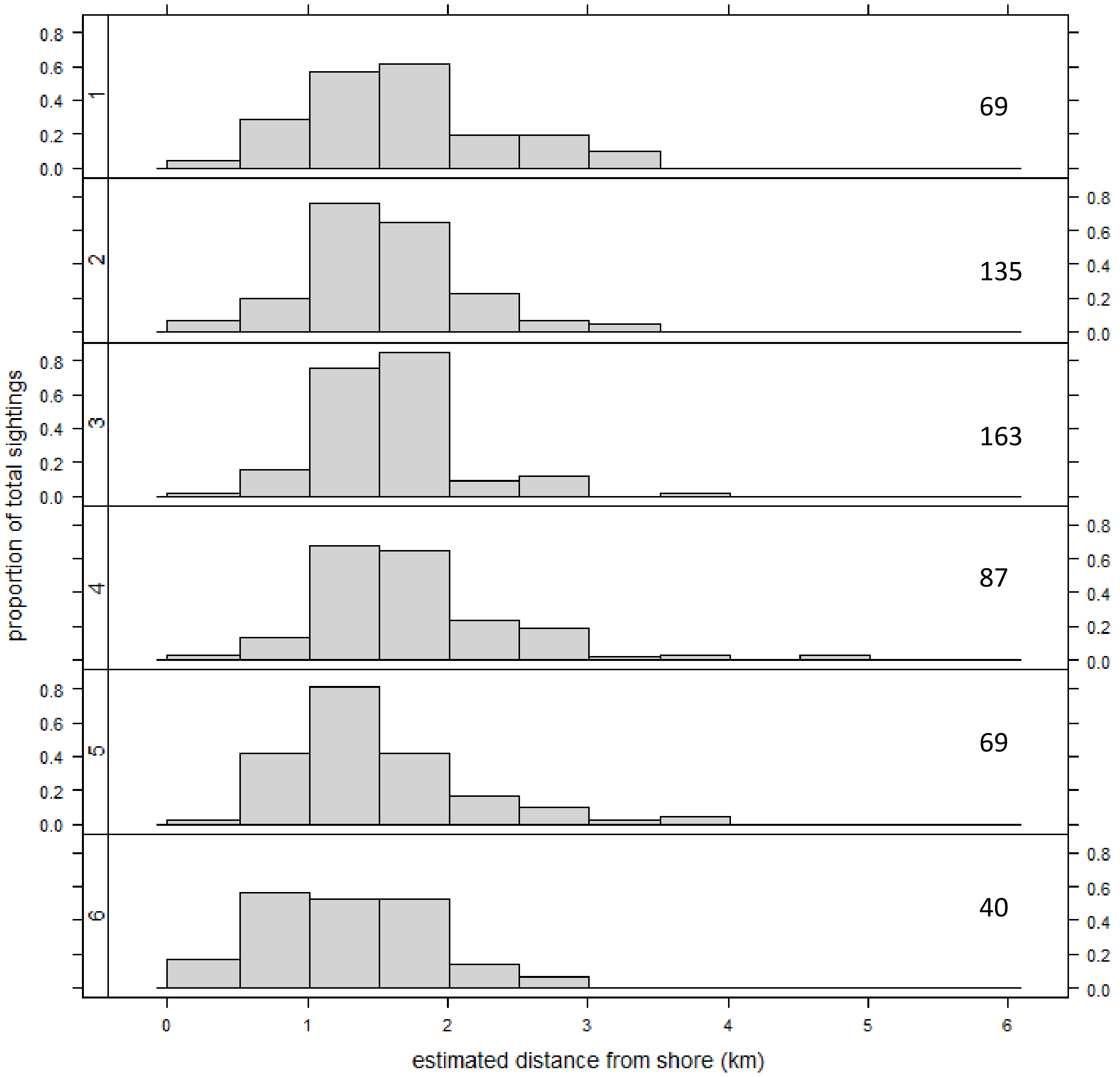


Figure 2.13: Density histograms of distance-from-shore data for sightings of harbour porpoise (n = 563) in the SWSW effort based survey from Gwennap Head (2007-2010). The numbered histograms correspond to sightings from within the number 'sections' of the survey area, shown in figure 2.12. The number of sightings within each distance band is indicated within each plot.

The histograms of distance density distribution for porpoise sightings within each sector (figure 2.13) generally show the 'typical' humped distribution that is expected from point transect surveys (figure 2.11), with peak sightings recorded at 1 -2 km from the watchpoint. There is slight variability in this pattern along some of the transect sections, for example section six shows a higher proportion of sightings closer to shore and generally a more even distribution of sightings between distance bands from 0.5 to 2 km. Section five also had higher numbers of sightings within the 0.5 – 1 km band than the other sections and a peak in sightings at 1 – 1.5 km followed by a steep decline. This is in contrast to the other sections where there were still high numbers of sightings from 1.5 – 2 km.

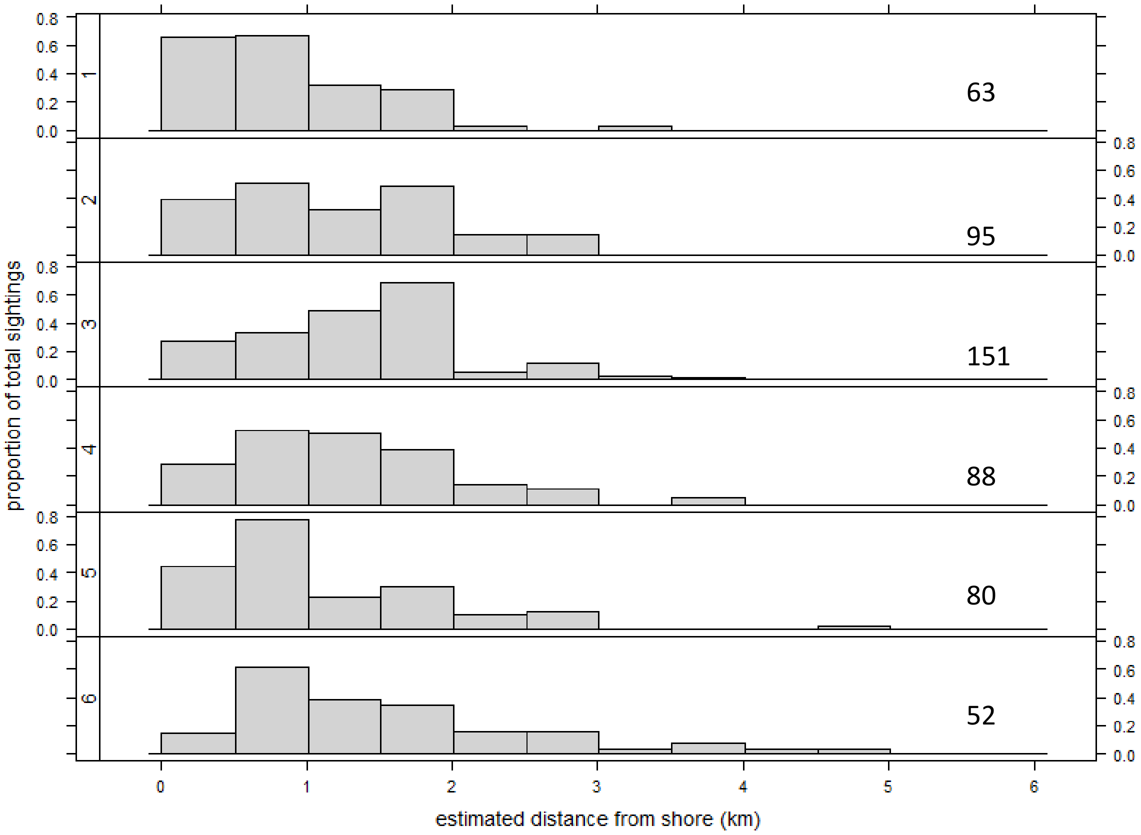


Figure 2.14: Density histograms of distance-from-shore data for sightings of basking shark (n = 529) in the SWSW effort-based survey from Gwennap Head (2007-2010). The numbered histograms correspond to sightings from within the numbered 'sections' of the survey area, shown in figure 2.12. The number of sightings within each distance band is indicated within each plot.

The basking shark sightings data in figure 2.14 show quite varied patterns of distribution with distance along each individual section of the survey area. In sections one and five, the sightings were primarily within the first km from shore, whereas in section three the number of sightings increased with distance to peak at 2 km, beyond which sightings decreased suddenly. Sections two, four and six show variability, with no clear trend in the relationship between the number of sightings and the distance from shore. It is notable that sightings in all six sections of the study area declined at distances of more than 2 km, but sightings were still being recorded in low numbers out to 5 km.

Overall the data from the SWSW survey show that there was generally a drop off in sightings beyond 2 km from shore. The porpoise sightings data show the 'expected' humped distribution of a survey affected by detectability issues; yet this is not obvious from the basking shark data. Looking only at the SWSW data, I would propose truncating the survey area at 2 km distance and excluding any sightings from beyond that, as I would not have high confidence in the ability to detect animals effectively at greater distances. The fact that there were different patterns in the porpoise and basking shark data within 2 km from the shore indicates that the sightings made *inside* 2-km were not significantly biased by the survey methodology.

2.5.1.3 Additional data from inshore boat surveys.

It is notable that although the SWSW data show variability between groups in the pattern of distance distribution within the first 2 km, beyond this distance, sightings of all species drop off (figure 2.10). It is easy to presume that this pattern results from sightings outside 2 km not being recorded reliably leading to a bias in the observed distribution of animals. But, it is possible that the drop off in sightings beyond 2 km is not an artefact of the survey method and is in fact a true pattern in the local distribution of the species, related to some environmental variable or common habitat preference.

In order to test this hypothesis and prevent a potentially un-necessary exclusion of 'good' sightings data from beyond 2 km; data from effort-corrected inshore boat surveys in the area have been examined. These data were collected on eco-tourism boat trips, run by Marine Discovery Penzance in conjunction with ecological researcher Marijke de Boer and have been made available for the purposes of investigating patterns in detectability in the SWSW survey.

The data were collected from the *MV Shearwater*, an ex-River Thames RIB (inboard 440 hp diesel). During passenger trips, systematic surveys were conducted following 'random transects', where the boat would stay on a randomly chosen straight line until the end of the transect section (usually determined by a sighting position). Whilst on this line, the following data was collected: position, course, speed and Beaufort sea state. GPS positions were obtained every minute and at sighting positions using a Garmin GPS. When a sighting was made (marking the end of a random transect section) the observers would go 'off-effort' and data would be collected on sighting position, species, heading of animal(s), behaviour and group composition. Effort would be resumed once the boat began travelling along the next randomly selected transect course.

These effort corrected boat data have reasonable coverage of the SWSW survey area (figure 2.15) and can be used to represent the 'underlying' distribution of harbour porpoises and basking sharks in the wider area around the Runnelstone Reef. The boat survey methods were not affected by the same detection issues as the single-point land-based survey, but some filtering for sea state was carried out to avoid biasing the data by including effort made in poor sighting conditions. Effort and sightings made in sea states above three and five have been removed from the porpoise and basking shark datasets respectively. Additionally, track sections at speeds below

4 knots have been removed as these represent periods when the boat was travelling very slowly, most likely ‘off-effort’ whilst observing animals in the water; therefore dedicated searching was unlikely to have been underway during these periods.

The data were supplied as gridded (500 m x 500 m) GIS layers of sightings and search effort (in km per grid cell), filtered for boat speed and sea-state, from which gridded maps of sightings per km search effort were created (figure 2.16). The pre-filtered, gridded data layers were queried in a GIS; extracting values from each grid cell within the field of view of the SWSW watchpoint (100 – 270°). The data extracted were the exact distance from the grid cell centre to Gwennap Head, the amount of pre-filtered effort (km) and the number of sightings for each grid cell. The grid cells were then attributed to the appropriate radial distance band from the SWSW watchpoint at Gwennap Head, out to a distance of 6.5 km, allowing effort-corrected sightings per distance band to be calculated for harbour porpoises and basking sharks (figures 2.17 and 2.18).

The difference in the amount and the pattern of search effort for the two species (figures 2.17 and 2.18) were as a result of the different sea state filters applied for each. The sea state conditions may also have affected the ‘behaviour’ of the boat, for example it is likely that the boat took a more in-shore track during higher sea states.

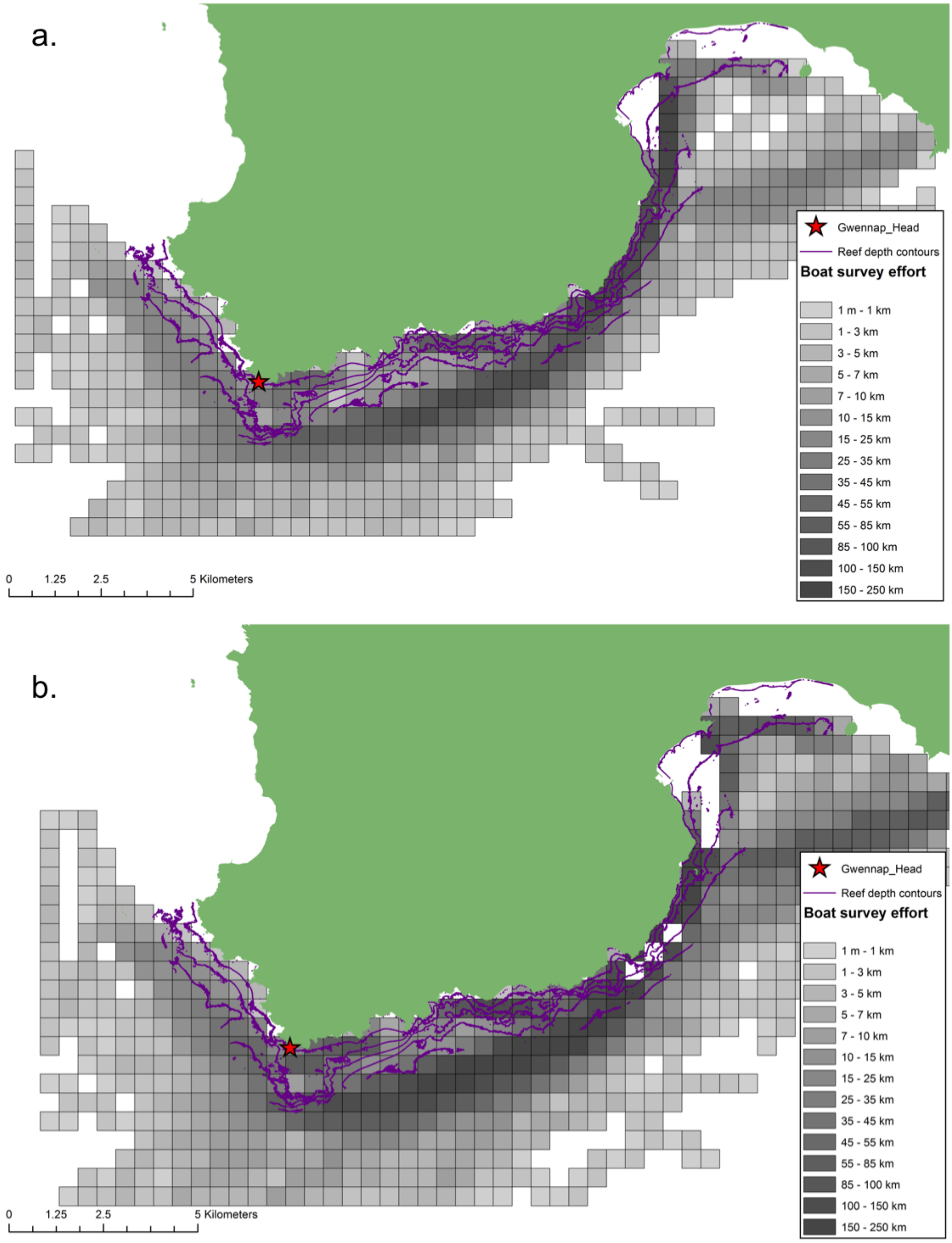


Figure 2.15: Marine Discovery boat survey gridded search effort maps for a) harbour porpoise and b) basking shark. Gridded into 500 x 500 m cells and displayed as km search effort per grid cell. Data supplied by Marijke de Boer and Marine Discovery Penzance, collected May to Oct 2008 - 2009. Search effort was filtered to remove effort at speeds below 4 knots and during sea states above Beaufort 3 for harbour porpoise (a) and above Beaufort 5 for basking sharks (b).

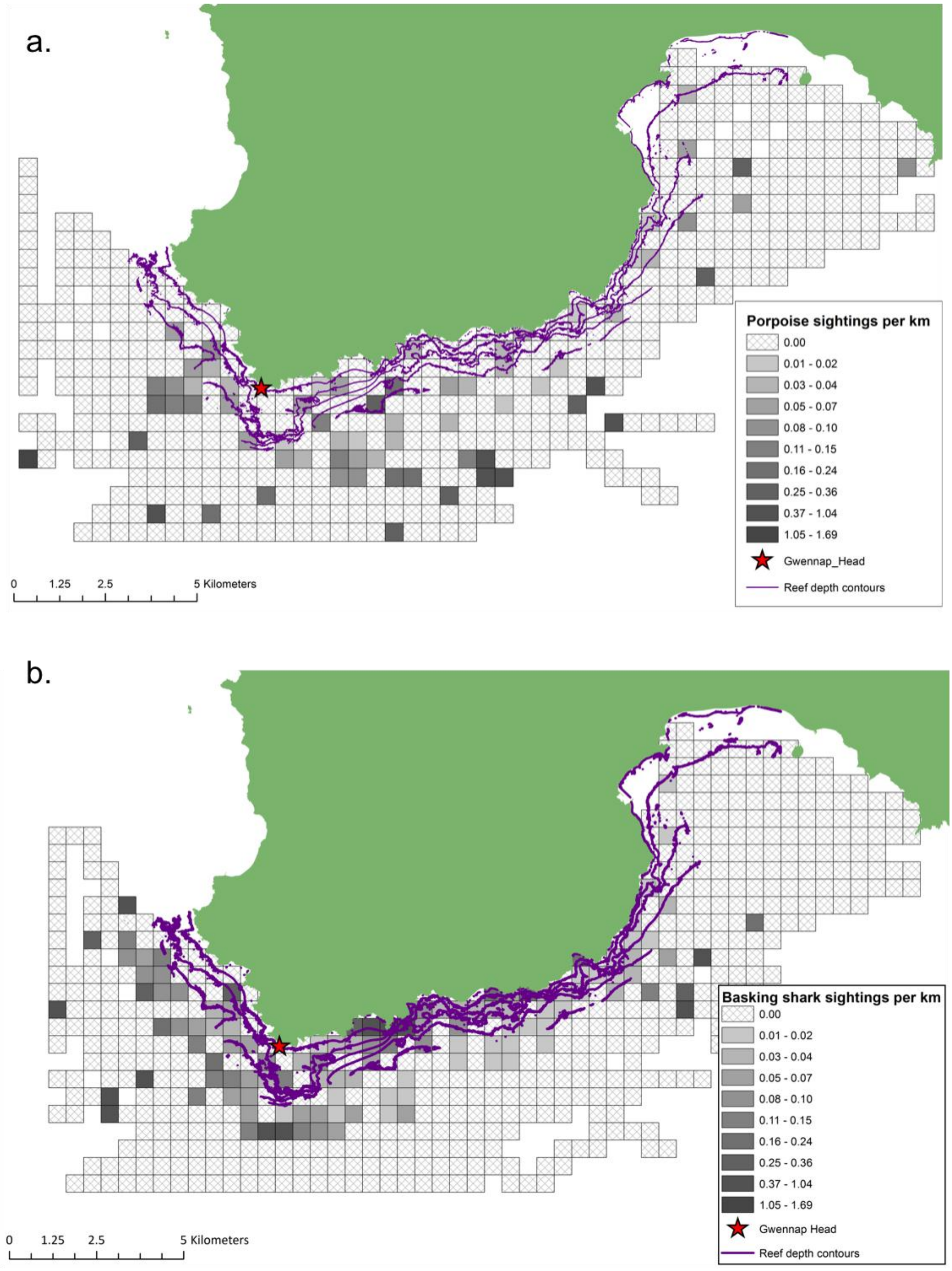


Figure 2.16: Marine Discovery boat survey gridded sightings per km search effort for a) harbour porpoise and b) basking shark. Grid cell size = 500 x 500 m. Data supplied by Marijke de Boer and Marine Discovery Penzance, collected May to Oct 2008 - 2009. Data were filtered to remove effort at speeds below 4 knots and during sea states above Beaufort 3 for porpoises and 5 for basking sharks. Cross-hatched fill shows grid cells where search effort was carried out, but no sightings were made.

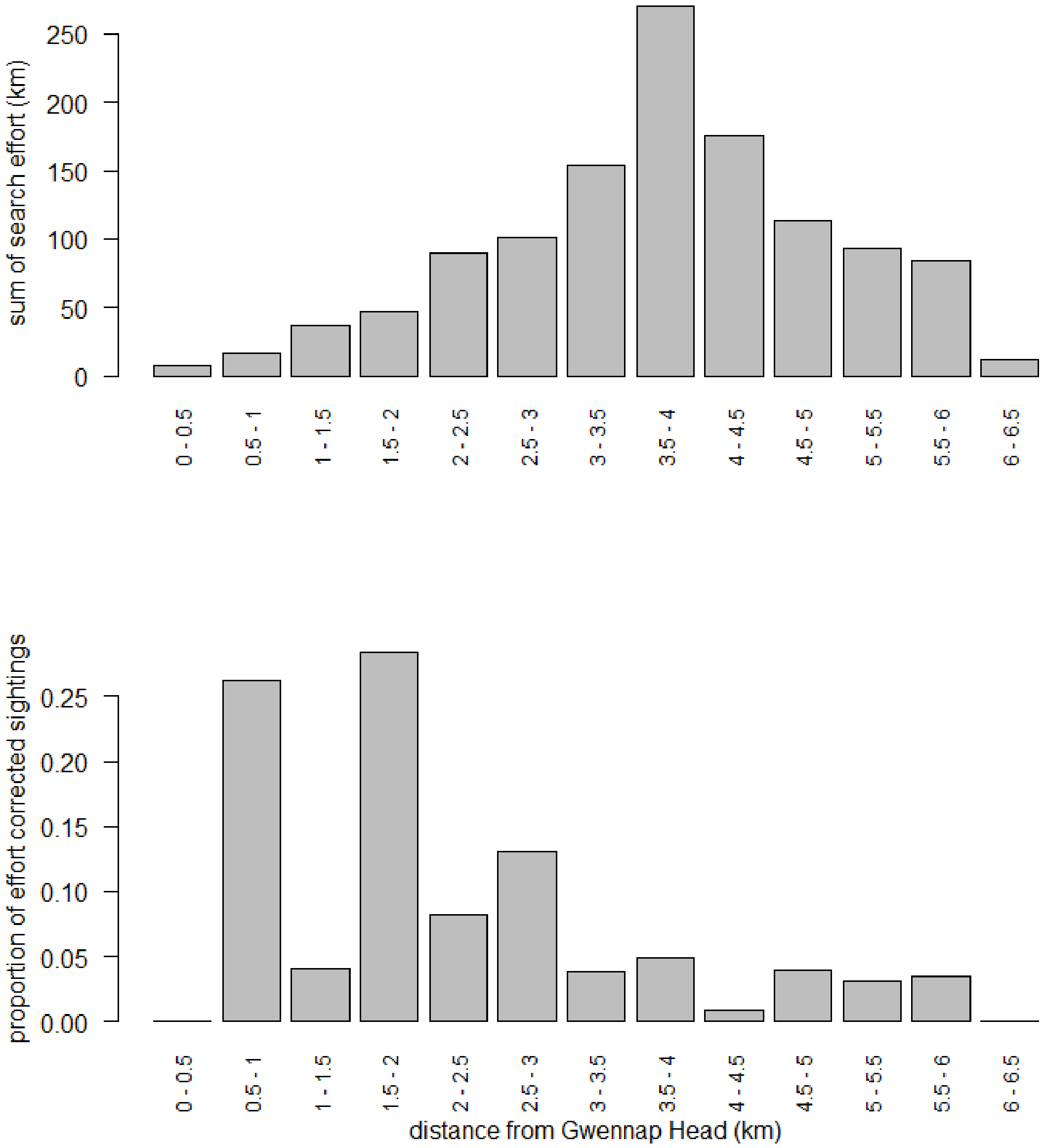


Figure 2.17: Distribution of boat search effort and sightings of harbour porpoise with reference to distance from the SWSW survey watchpoint at Gwennap Head. Top: total km of boat survey effort for harbour porpoise. Bottom: proportion of effort corrected sightings per km effort. Histograms were split into 500 m distance bands from Gwennap Head. Both plots exclude effort during speeds below 4 knots and in sea states above 3. Only data from grid cells within the field-of-view of the SWSW watchpoint were included. Total number of sightings = 48. Data were collected May - Oct 2008 – 2009 and supplied courtesy of Marijke de Boer and Marine Discovery Penzance.

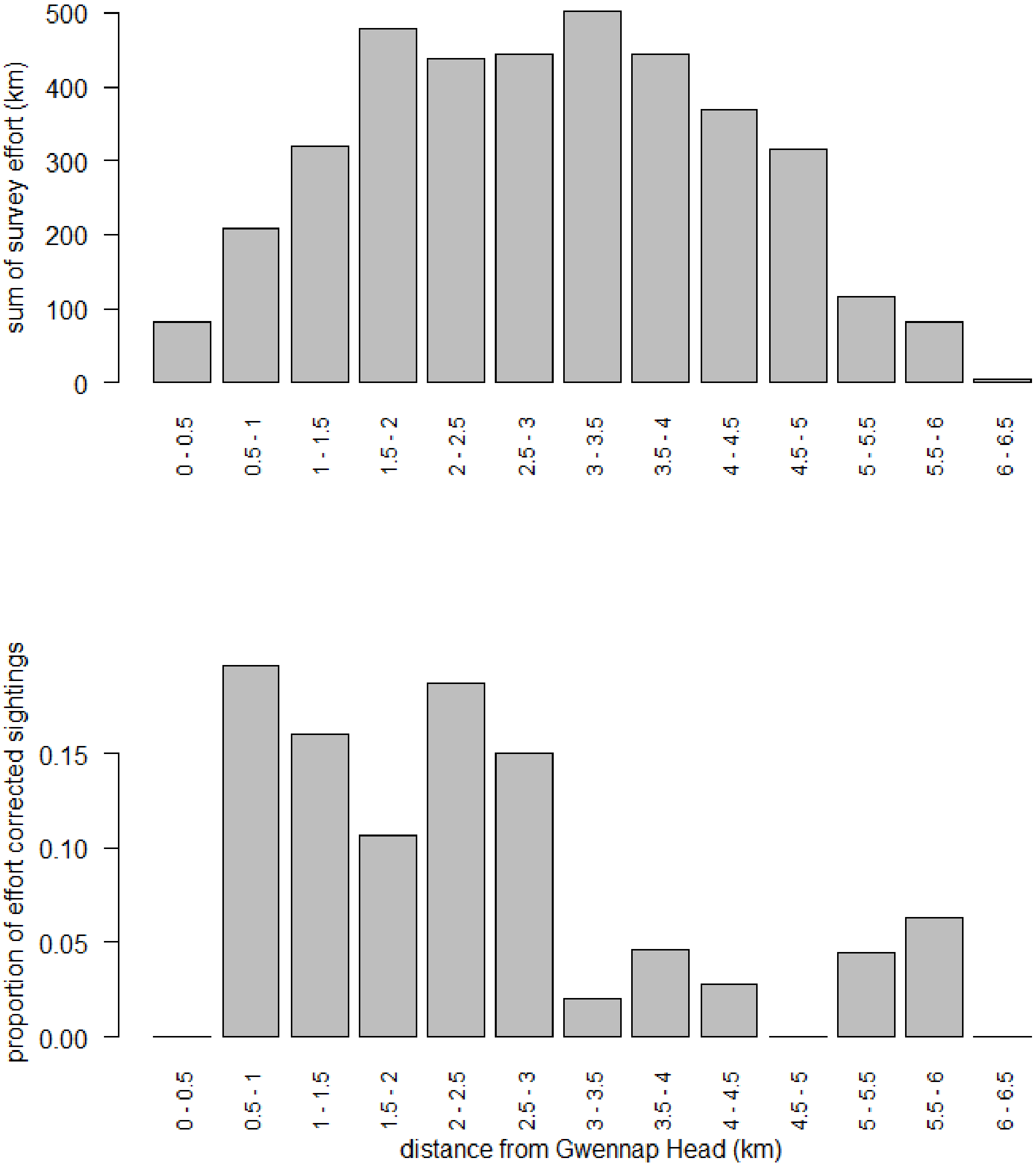


Figure 2.18: Distribution of boat survey effort and sightings of basking shark with reference to distance from the SWSW survey watchpoint at Gwennap Head. Top: total km of boat survey effort for basking sharks. Bottom: proportion of effort corrected sightings per km of effort. Histograms were split into 500 m distance bands from Gwennap Head. Both plots exclude effort during speeds below 4 knots and in sea states above 3. Only data from grid cells within the field-of-view of the SWSW watchpoint were included. Total number of sightings = 67. Data were collected May - Oct 2008 – 2009 and supplied courtesy of Marijke de Boer and Marine Discovery Penzance.

The fully effort corrected boat sightings grouped by distance-from-Gwennap Head suggest that, in the vicinity of the SWSW survey watch point, most porpoises were recorded within 3 km of the coast (figure 2.17, bottom). The peak in porpoise sightings, after correction for survey effort, occured inside grid cells whose centre point is 1.5 – 2 km from Gwennap Head, which supports the patterns in the data from the SWSW land-based survey (figures 2.10 and 2.13). Survey effort increased to a peak in the 4 km distance band, indicating that these results are not an artefact of the pattern in boat-survey effort (figure 2.17, top). The boat-based survey data provide evidence to support the SWSW survey methodology beyond 2 km and indicate that the 'humped' distance-distribution and the drop off at distances greater than 2 km (figures 2.10 and 2.13), is not simply a function of the survey methodology resulting from reduced detection at greater distances. The pattern in the boat-based survey data support the efficacy of the SWSW survey methods for porpoises and suggests that there were higher numbers of porpoises within 2km from the watchpoint than outside this distance. This result indicates that land-based sightings from beyond 2-km should be included in the SWSW porpoise data analysis. On the basis of these investigations, the harbour porpoise effective survey area delineation was made at 3 km distance from the watchpoint. Beyond 3-km distance there is lower confidence in being able to reliably detect porpoises.

The basking shark data collected in the boat surveys (figure 2.18) showed higher levels of sightings within grid cells that are 0.5 - 3 km from Gwennap Head. The pattern of distribution within 2 km distance from Gwennap Head was similar to that recorded in the SWSW survey (figures 2.10 and 2.14); but the boat data indicates that sharks remained present in high numbers beyond 2 km and therefore that the SWSW was underestimating their relative density at distances of 2 – 3 km. This result suggests that the drop off in sightings of basking sharks beyond 2 km in the SWSW survey was the result of decreased detection at further distances and supports the truncation of the basking shark data set at 2 km.

Chapter 3 The influence of physical habitat on the fine-scale distribution of harbour porpoises (*Phocoena phocoena*).

Most marine mega-vertebrates are noted for their wide-ranging behaviour, but are also known to concentrate within spatially constrained areas, associating with key species-specific habitats (e.g. Sims, 2003; Kai et al., 2009). The cues and controls on these space-use patterns are largely unknown, but are interpreted as being based on foraging decisions made at the meso and fine scale (Stephens and Krebs, 1986; Sims et al., 2008). For every species, there are a number of essential resources that are required by individuals in order to survive, or indeed to flourish, in an environment; at the most basic level these are appropriate physical conditions (for example temperature) and food. Looking at the distribution of an animal in time and space can therefore tell us a lot about its environmental requirements and preferences.

This chapter describes the fine-scale distribution of harbour porpoises observed in the SWSW effort-based marine wildlife survey between 2007 and 2010. Background information regarding the species' ecology and distribution is presented in order to contextualise the results. The analyses undertaken investigated links between static and dynamic physical habitat variables and the distribution of porpoise detections (visual and acoustic) within the survey area. The results are discussed with reference to existing research and current conservation and management objectives for the species.

3.1 Introduction – setting the scene

3.1.1 Biology and ecology of the harbour porpoise (*Phocoena phocoena,* Linnaeus, 1758*)*

Harbour porpoises are cetaceans; an Order of marine mammals that also includes the whales and dolphins. They are one of the smallest cetacean species and are considerably smaller than any other cetacean found in the waters of the northwest continental shelf (Read, 1999). They have teeth rather than baleen plates, and are capable of echolocation, which leads them to be grouped with all other toothed cetaceans in the Sub-Order Odonoceti.

There are currently four recognised geographically separated sub-species of *P. phocoena*, although their status remains in question. They are *P. p. phocoena* in the eastern North Atlantic, *P. p. vomerina* in the eastern North Pacific, and un-named sub-species in the western North Pacific and *P. p. relicta* in the Black Sea (Hammond et al., 2008). Genetic studies undertaken by Evans *et al*. (2009) indicate that the population in the North Atlantic could consist of up to 15 distinct sub-populations or stocks.

Harbour porpoises have small, rounded bodies with a blunt head and no obvious rostrum, unlike most dolphin species. Their stocky body shape helps reduce heat loss, which is critically important for such a small, warm-blooded marine animal. Size can vary depending on geographic location, with those from more southerly locations tending to be slightly larger (Santos and Pierce, 2003). Average sizes are 145 cm in males and 155 cm in females, but the maximum length and size recorded in porpoises found stranded around the UK are 153 cm/54 kg in males, and 189 cm/81 kg in females (Lockyer, 1995). Calves are approximately 70 – 80 cm long at birth (Reid et al., 2003). The body colour shows counter shading, with a dark grey dorsal surface and a paler underside that sweeps up onto the flanks in the central part of the body (figure 3.1). Harbour porpoises have a dark coloured, small triangular dorsal fin, which is very inconspicuous at the surface of the water and distinguishes them from most other small cetaceans in the field.

Harbour porpoises are generally seen individually or in small groups. There have been some reports of larger aggregations, but it is most likely that these occurred as a result of many small pods making use of the same habitat or prey source (Hoek, 1992). Porpoises do not whistle to communicate with each other as dolphins do, although the reason for this is unclear. As with all other toothed cetaceans, porpoises produce echolocation clicks, which are used for navigation and prey detection; there has been some suggestion that clicks may also be used to for communication with conspecifics in porpoise species (Clausen et al., 2010).

Figure 3.1: Illustration of a harbour porpoise (*Phocoena phocoena*) showing body shape, colouration and small triangular dorsal fin (Canada, 2011).

Because of their small size, harbour porpoises can only accumulate limited fat reserves and therefore do not have the same capabilities as some of the larger cetaceans for storing energy or heat (Brodie, 1995). As a result, they lose heat rapidly in cool temperate waters and have a high energy demand, leading to a requirement for regular feeding in order to fulfil their energetic requirements (Brodie, 1995). This means that they cannot stray too far from areas containing prey resources (Brodie, 1995; Santos et al., 2004; Lockyer, 2007).

Stomach content analyses on stranded or by-caught porpoises have contributed greatly to our understanding of the species' diet, and these studies have been reviewed by Santos and Pierce (2003). The review outlines primary prey items as being small fish from a variety of species, with small cephalopods and crustaceans also being eaten on occasion. Northeast Atlantic stomach content analyses have recorded whiting, herring, sprat, capelin, sole, mackerel, cod, poor cod, pout, sandeel, eel, gobies, blennies, shrimps and cuttlefish. Similar prey groups were found in Pacific specimens. Santos and Pierce (2003) also note a marked variability in the dominant prey species of animals living in different areas, as well as seasonal and inter-annual variability within the same populations, potentially as a result of differences in prey availability (Santos and Pierce, 2003; Santos et al., 2004).

It is still unclear whether porpoises are truly opportunistic or selective predators, but there is evidence to suggest that larger prey size classes are over-represented in the diet, indicating some selectivity in predation (MacLeod et al., 2006a). Even so, the level of selectivity is thought to be fairly low, with seasonal and inter-annual variability in stomach contents indicating that the species maintains a level of plasticity in their diet, which allows them to take advantage of changing abundances in prey resources (MacLeod et al., 2006a). This is evidenced by a general shift in the diet of the harbour porpoise in the North Atlantic from primarily clupeid fish prior to

1960, to a diet now based on gadoids and sandeels, presumably as a result of decreasing availability of clupeids within the porpoises range (Santos and Pierce, 2003).

Because of the physical properties of water, communication and prey location in marine animals are often undertaken in a different way to terrestrial animals. Porpoises, like all odonocete cetaceans, use echolocation when foraging. It is thought that this ability evolved as a result of the difficulties in locating prey in turbid or deep water, where light attenuation is high and therefore visual predation is far less effective than on land or in surface waters (Berta et al., 2006). Porpoises produce narrow band high frequency (NBHF) type echolocation clicks; conversely dolphin species and orcas produce broadband and lower frequency clicks. It is possible that evolution of NBHF echolocation in porpoise species, as well as their association with shallower coastal water may have been in response to top-down pressure from larger odontocetes (such as killer whales *Orcinus orca* and common dolphins *Delphinus delphis*) who may predate on, or show fatally aggressive behaviour towards porpoises (e.g. Morisaka and Connor, 2007).

Chemical and electrical cues are used by some marine species, but they have a more limited range than acoustic signals, which are transmitted rapidly and can cover large ranges as a result of the speed of sound through water being approximately five times faster than through air. These attributes make acoustic signalling the favoured method of navigation and communication in many cetaceans and also in other groups of marine mammals such as sirenians (Berta et al., 2006). In order to make use of echolocation in the marine environment, the toothed whales have evolved specialisations in vocal and auditory functional anatomy (figure 3.2).

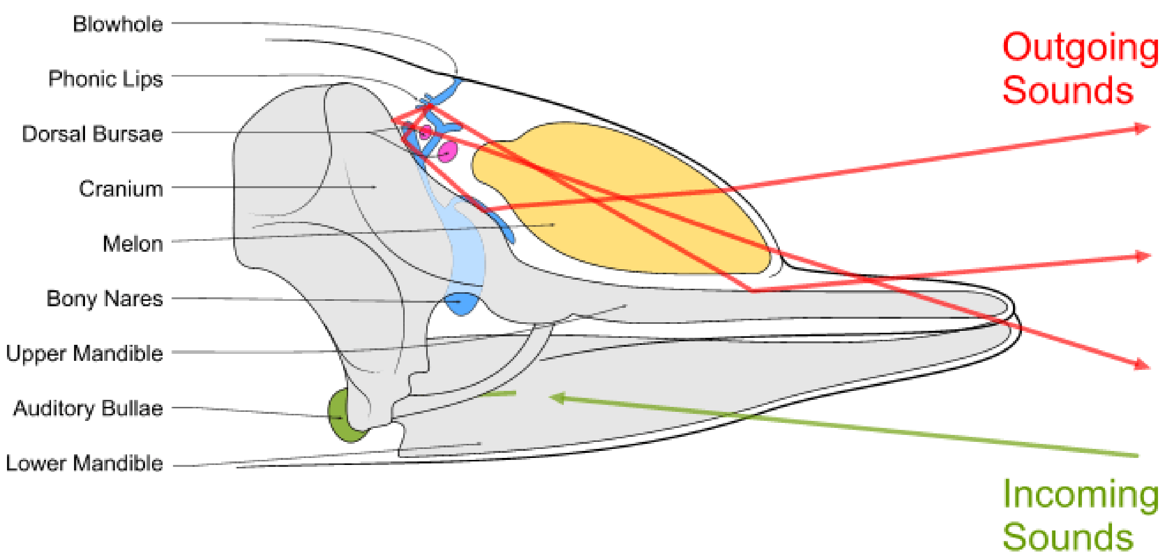


Figure 3.2: Schematic diagram showing the specialised functional anatomy of toothed cetaceans; illustrates the sound production and reception organs in the head (Anonymous, 2011).

Echolocation works by the animal emitting sonar calls (or ‘clicks’) into their surroundings, they then listen for echoes produced by the clicks reflecting back off objects in the environment. The attributes of the returning echoes build a ‘picture’ of the animal’s surroundings and can be used to locate and identify objects by providing information about their range and size (Tyack and Miller, 2002). In cetaceans, the sonar clicks are produced by forcing air from the nostrils through the ‘phonic lips’ in the top of the head. The clicks are modulated and focused in an organ called the melon, which is a large lipid-filled sac at the front of the head. The returning echoes are received in the jaw and transmitted through body fat channels to the ear (figure 3.2, Tyack and Miller, 2002).

Porpoise echolocation clicks have a narrow bandwidth and are therefore thought to be highly directional; they are also high frequency, usually falling within the range of 125 – 140 kHz (Hatakeyama and Soeda, 1990). The use of high frequencies means that porpoises can detect small objects, because echoes will be produced from any solid object with a circumference greater than or equal to the wavelength of the click. Using frequencies of 125 kHz, porpoises should be able to detect objects of ≥ 1.2 cm (Tyack and Miller, 2002).

Porpoises have been found to employ predictable echolocation phases during foraging, starting with the ‘search’ phase during which clicks are emitted less frequently and at equally spaced intervals. In the ‘approach’ phase, the inter click interval (ICI) shortens as the porpoise closes in on a prey item, and then immediately prior to attack a ‘buzz’ is emitted. The ‘buzz’ is the result of a steep increase in click rate and shortening of the ICI, so that many consecutive clicks are emitted in short succession (Verfuss et al., 2009). There is an inverse relationship between click rate and range-to-prey, so that porpoises tend to click slowly during ‘search’ and ‘approach’ and fast during the ‘buzz’ phase associated with prey capture and handling; resulting in more frequent updates about prey location, size and range (DeRuiter et al., 2009). In experiments using captive porpoises, median click rate outside ‘buzz’ phases was 25 clicks per second, but this was seen to rise to more than 300 clicks per second during the ‘buzz’ phase, which began when the animal was within one or two body lengths of the prey item (DeRuiter et al., 2009).

Researchers can take advantage of the echolocation behaviour of porpoises by collecting data using passive acoustic methods that detect and monitor their echolocation activity using hydrophones (e.g. Carstensen et al., 2006; Verfuss et al., 2007; Todd et al., 2009; Sveegaard, 2011). Clicks are usually produced in characteristic ‘trains’ or series, and the frequency and bandwidth of the clicks varies between odontocete species, meaning that it is possible to attribute clicks detected on passive monitoring systems to a group (e.g. dolphins) or even to a species (Tyack and Miller, 2002).

Porpoises are good targets for passive acoustic monitoring because they are rarely silent in the wild (Akamatsu et al., 2005; Akamatsu et al., 2007). Additionally, their narrow band, high frequency echolocation clicks mean that harbour porpoise acoustic signals are easier to identify and constrain using detection filtering software than dolphins and other odontocetes, who can rarely be identified to species level.

This thesis uses data collected by C-PODS, which are moored passive acoustic listening stations that collect information on cetacean activity over long periods by listening for cetacean click trains and logging data on their detection. C-PODS are automated, record 24-hours a day and only register the presence and length of click sounds matching pre- specified criteria, therefore saving battery and memory space and allowing longer deployments. Passive acoustic monitoring is especially useful for less conspicuous species, such as the harbour porpoise, whose detectability can be significantly affected by survey conditions and distance. Gillespie *et al* (2005) found that acoustic detection rates for harbour porpoise were over eight times higher than in visual surveys. Additionally acoustic detections do not suffer as much under poor survey conditions such as increased Beaufort sea state (Gillespie et al., 2005), whereas this is known to have a significant impact on visual detection of porpoises (Palka, 1996). In addition, passive acoustic surveys can be undertaken continuously (24-hr surveys) and do not need to be actively monitored whilst running. The main drawback is the detection range of acoustic methods for harbour porpoises, whose high frequency clicks attenuate over relatively short distances underwater; giving an estimated maximum detection range of 300 m (Urick, 1983).

3.1.2 Distribution and habitat associations.

3.1.2.1 Distribution.

Harbour porpoises are the most numerous cetaceans found in northwestern Europe. They have a wide coastal distribution throughout the northern hemisphere, being primarily found within temperate seas and only occasionally reported off the continental shelf in deeper water (Hammond et al., 2008) (figure 3.3). The most northerly records in the Atlantic come from the Russian White Sea (in summer) and 72° N in western Greenland. The species has been recorded from as far south as Cap Vert in Senegal (15 °S) (IWC, 1996).

Within the northeast Atlantic and North Sea there has been a large-scale coordinated cetacean monitoring study called ‘Small Cetaceans in the European Atlantic and North Sea’ (SCANS), which undertook visual boat-based and aerial surveys in 1995 (SCANS) and again in 2005 (SCANS-II). Outputs of the survey included stratified abundance estimates and modelled density estimates for harbour porpoise within the study region (figure 3.4). Comparison between the results of the two surveys did not show a significant change in the overall estimate of abundance of porpoises within the study area over the ten year period, but did find that the centre of gravity of the populations had shifted from the northern North Sea in the earlier study to the southerly part of the study area in the later study (figure 3.4, (SCANS-II, 2008).

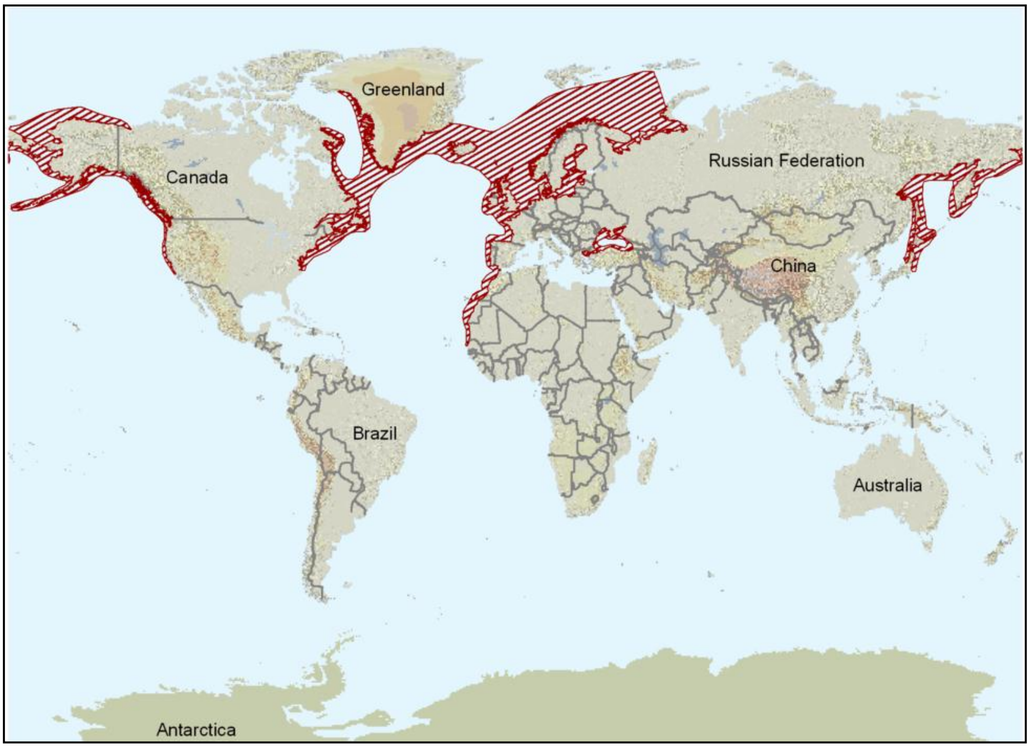


Figure 3.3: Worldwide distribution map of the harbour porpoise (*Phocoena phocoena*) from Hammond *et al*. (2008). Red shading indicates known global distribution.

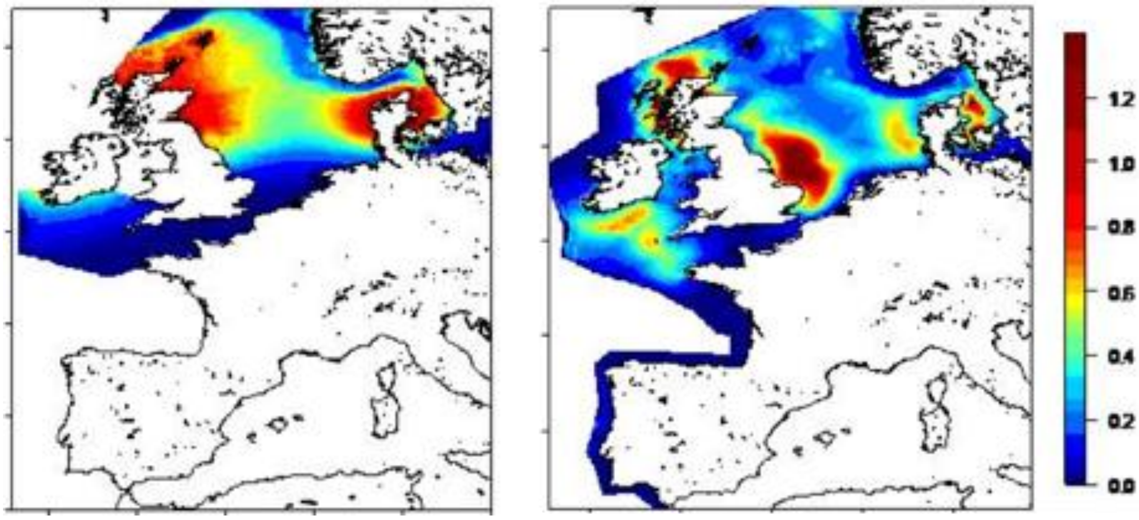


Figure 3.4: Harbour porpoise density estimations from the SCANS surveys: 1995 (left) and 2005 (right) showing a broad scale shift in abundance from north to south within the northwest European study region. Density scale is in animals per km^2 (SCANS-II, 2008).

Harbour porpoise are reported from all around the coast of the UK, but are less common in southeastern areas than around the other coastlines (Evans et al., 2003) (figure 3.5). Hotspot areas for harbour porpoises in the UK have been identified through various public sightings, opportunistic and effort based monitoring projects undertaken by the Seawatch Foundation/UK Cetacean Group (Evans et al., 2003) and other academic research groups. The key areas identified through these studies include southwest Ireland (Leopold et al., 1992), western Ireland (Rogan and Berrow, 1996), south and west Wales (Pierpoint, 2008), western Scotland (MacLeod et al., 2007; Weir et al., 2007; Marubini et al., 2009; Embling et al., 2010), eastern Scotland (Robinson et al., 2007) and southwest England (Northridge et al., 1995; Hammond, 2006; Brereton et al., 2007).

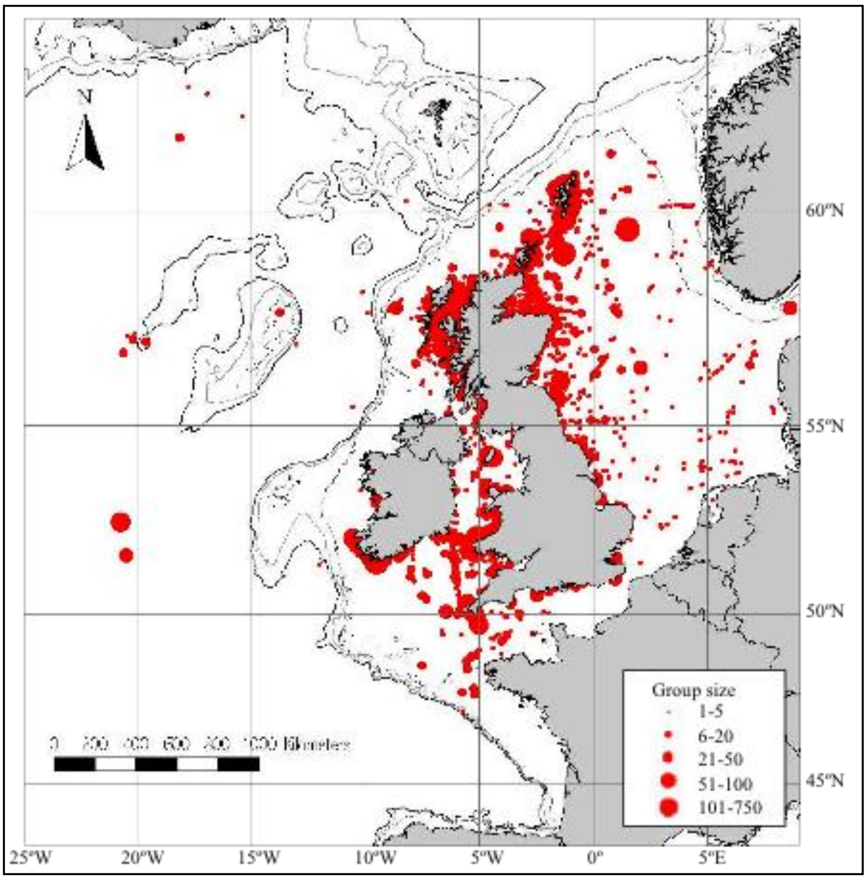


Figure 3.5: Map of UK and Irish harbour porpoise sightings collected by the Seawatch Foundation (effort-based and opportunistic) from 1992 – 2002 (Evans et al., 2003).

Harbour porpoise are present year-round in the key areas outlined above, although abundances tend to fluctuate seasonally, with highest densities usually recorded between July and October (Evans et al., 2003) (figure 3.6). It is not known whether there is a significant onshore-offshore movement associated with the seasonality seen in harbour porpoise distribution around the coast of the Britain and Ireland (Northridge et al., 1995). Seasonality in relative abundance has also been noted in the more northerly parts of the porpoises distribution. In the Baltic Sea and

Kattegat between Sweden and Denmark, there is a clear shift in winter distribution as the porpoises move into more southerly areas within the region (reviewed in Sveegaard, 2011). It may be that the porpoises inhabiting the coastal waters of the UK in summer move further south in the winter, but little survey and monitoring work has been carried out in the most southerly parts of the species' range.

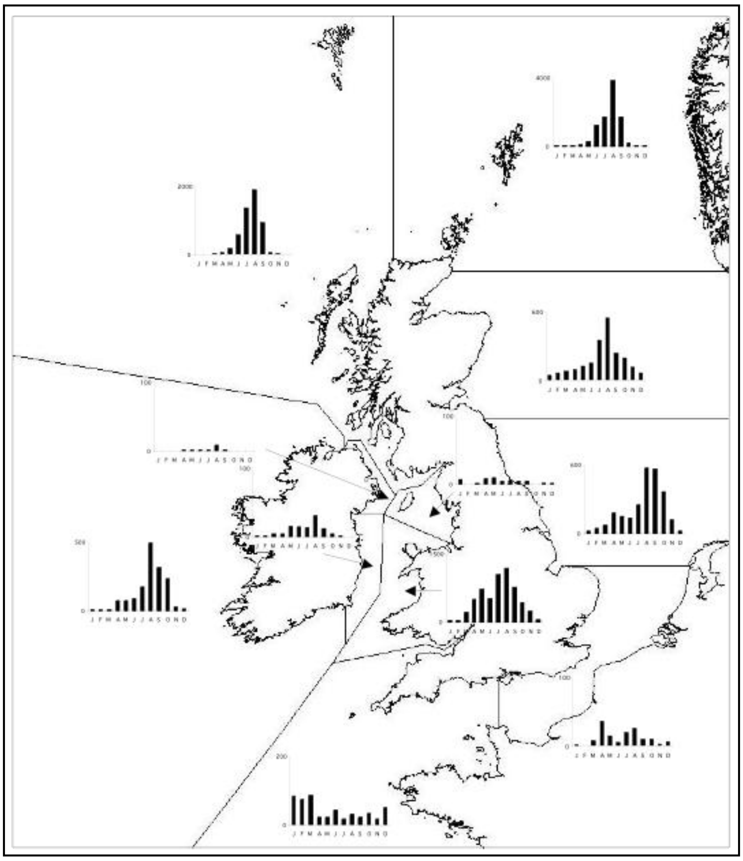


Figure 3.6: Seasonal distribution of Seawatch Foundation UK and Irish porpoise sightings from 1992 - 2002, grouped by region (opportunistic and effort-based data). From Evans *et al*. (2003).

A recent cetacean monitoring report by the Atlantic Research Coalition (ARC) describes a significant increase in harbour porpoise density within the western English Channel during the summer months between 1996 and 2006 (Brereton et al., 2007). This result is supported by the SCANS-II results (figure 3.4), which point towards a general southerly shift in the species distribution around the UK and an increasing importance of the Celtic Sea and Western Approaches to the Channel to the species (SCANS-II, 2008). The ARC research did not find a concurrent increase in porpoise abundance during the winter months (Brereton et al., 2007).

Our study site in southwest Cornwall has been highlighted as a particularly important area for harbour porpoises within the southwest English region (figures 3.4 and 3.5). Studies using data from public sightings, boats of opportunity and strandings have identified the Runnelstone Reef and surrounding areas as hotspots for the species (Leeney et al., 2008; Pikesley et al., 2011), not only in the summer months, but also throughout the winter (Evans et al., 2003; de Boer and Saulino, 2009).

3.1.2.2 Habitat associations

As with other marine megafauna, the broad-scale distribution of cetaceans is likely to be governed by prey availability (e.g. Pendleton et al., 2009; Certain et al., 2011) and thermal habitat requirements (e.g. Greene and Pershing, 2004). Changes in these parameters because of climate forcing have been found to impact on the spatio-temporal distribution of some cetacean species (Drinkwater et al., 2003; Greene and Pershing, 2004; MacLeod et al., 2005). Recent research has also found evidence of climate-controlled shifts in the relative abundance and range of a number of fish species around the British Isles (Genner et al., 2004; Genner et al., 2009; Simpson et al., 2011). These changes may have a knock-on effect on the distribution of predatory cetacean species like the harbour porpoise.

The specific environmental and biological controls on harbour porpoise distribution are not well understood, but as mentioned in section 3.1.1, the species have high energetic demands that are likely to create a particularly close spatial and temporal dependence on prey resources. This suggests that the species distribution is directly controlled by the distribution of prey or indirectly affected by biophysical factors that influence prey distribution or foraging efficiency (Brodie, 1995). Using data from 64 harbour porpoises satellite tracked in the eastern North Sea, Skagerrak and Kattegat, Sveegaard (2011) linked focal areas in the ranges of the tracked animals to the distribution of herring and mackerel, inferred from ICES acoustic fish survey data.

Prey distribution is generally patchy and controlled spatially by both stable and ephemeral environmental features such as water depth, topography, substrate, tidal flow, fronts, stratification and turbulence. Patchy distribution is often reported for schooling fish such as sandeel (van der Kooij et al., 2008) and clupeids (Haugland and Misund, 2004), and is also frequently true of demersal species. The foraging ecology of the harbour porpoise is poorly understood and the consequences of variation in feeding success because of altered distribution of prey have not been fully investigated. Due to their requirement for regular and frequent feeding, the ability to react to predictable oceanographic and hydrodynamic controls on prey location could greatly reduce foraging costs for the harbour porpoise.

A number of previous studies have suggested that harbour porpoise movement and distribution at small scales is linked to physical features such as depth, sediment type, slope, stratification and mixing, distance from land and tidal state. It is generally proposed that these key habitat characteristics influence porpoise distribution because they affect the distribution or availability of prey. An early study by Gaskin (1977) in the Bay of Fundy, Canada, found that depth and copepod density had positive relationships with porpoise sightings during boat transects. In the same study area, Watts & Gaskin (1985) also found positive links between porpoise sightings and physical features, which acted to concentrate Atlantic herring (*Clupea harengus*) close to the surface. More recent research in the area using remote sensing and satellite tracking technology has shown that tagged harbour porpoises ranged over large areas (7,738 – 11,289 km^2), but within these ranges tended to cluster around specific sites characterised by proximity to islands, headlands or channels (Johnston et al., 2005). In these specific physical habitats, enhanced turbulence and secondary flows created by tidal-topographic interactions were proposed to influence prey availability for the porpoises and thus provide important foraging sites (Johnston et al., 2005; Johnston and Read, 2007).

In their boat-based sightings study in western Scotland, Marubini *et al*. (2009) found significant preferences for areas within 15 km of the coast and depths of between 50 and 150 m. There was also an indication of tidally controlled habitat use, with more sightings in areas of highest tidal flow, and generally more sightings made during high tide (Marubini et al., 2009). Tidal currents were also found to influence the appearance of foraging harbour porpoises in a predictable manner in Ramsey Sound, southwest Wales. At this site, it was proposed that interactions between local topography and ebbing flows led to tide races, which provided beneficial foraging conditions for the porpoises. Tidal flow and state have also been correlated with sightings of other cetacean species (Sekiguchi, 1995; Sini et al., 2005). This relationship has been linked to tidal-topographic forcing of lower trophic level species during specific tidal states, leading to regular and predictable foraging opportunities (Baumgartner et al., 2003; Cotte and Simard, 2005; Johnston et al., 2005; Johnston and Read, 2007; Pierpoint, 2008).

3.1.3 Population status, exploitation, and threats.

There is a general lack of information on the size and status of most harbour porpoise sub-populations (Berggren and Arrhenius, 1995; Read, 1999) and there is currently no official estimate for the global abundance of the species. Some of the geographically distinct stocks have been estimated individually and when these separate estimates are summed they give a minimum value of 700,000 individuals globally (Hammond et al., 2008). The SCANS-II surveys estimated that there were a total of 315,027 harbour porpoises in the area encompassing the Western Baltic, North Sea, Celtic Sea and English Channel in 2005 (Hammond et al., 2002; SCANS-II, 2008).

The intrinsic population growth rate has been estimated to be between 5 % and 9.4 % (Barlow and Boveng, 1991; Woodley and Read, 1991) but the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) Working Group of the International Whaling Commission (IWC) uses the conservative estimate of 4% in its advice and analyses (IWC, 2000).

Historically, directed fishing for harbour porpoise was widespread throughout the northerly parts of its range, due to the species being sought for its blubber oil. Hunting occurred in both eastern and western North Atlantic areas including the Baltic and Black Seas, Iceland, Greenland, Bay of Fundy, Labrador and Newfoundland (Jefferson et al., 1993). Over 160,000 porpoises were taken in directed fisheries in the Black Sea between 1976 and 1983 (Hammond et al., 2008). Most of these fisheries are now closed, but there are still some areas where hunting for porpoises continues, with an annual catch of 2,563 individuals reported from Greenland as recently as 2006 (NAMMCO, 2009). Because of a scarcity of data on harbour porpoise population size and their genetic structure, the impact of contemporary fisheries has not been assessed, but there is clearly the potential for catches of this size to reduce local and regional populations (Hammond et al., 2008).

The population status of harbour porpoises is of concern throughout its range (Embling et al., 2010). Numbers in some parts of its distribution are thought to have have declined dramatically, particularly in the Black Sea, Baltic Sea and southern seas around the UK (eastern channel and southern North Sea), where porpoises appeared to be abundant until around the 1960s (Reid et al., 2003). The decrease in numbers in the southern North Sea has been linked to changes in prey availability as a result of both overfishing of herring and mackerel and a concurrent shift in the primary spawning areas of these species (Reijnders, 1992). These changes in prey availability affected a shift in harbour porpoise distribution out of the southern North Sea, which combined with incidental by-catch in fisheries to reduce overall abundance in the area.

During foraging and feeding, porpoises will encounter two key threats; fishing gear (figure 3.7) and persistent organic pollutants (see Santos and Pierce 2003). The main perceived threat to the species now comes from incidental by-catch in gillnets and tangle nets, although the impact of accumulated pollutants is potentially serious, and may pose a serious risk to the reproductive health and immune system function of many coastal porpoise populations (Antje and Prange, 2007; Pierce et al., 2008).

Jefferson and Curry (1994) found that by-catch in gillnet fisheries was the single most important threat to populations of all porpoise species worldwide and that harbour porpoise are taken in this manner throughout their range. In post mortem analyses on 176 harbour porpoises stranded around the coast of the UK, it was found that entanglement in fishing gear was the most frequent cause of death, and that the proportion of stranded porpoises with evidence of by-catch increased during every year of the survey (Kirkwood et al., 1997). Juveniles, particularly those who are immediately post-weaning and therefore recently independent, seem to be especially susceptible to by-catch, probably due to inexperience (Lockyer and Kinze, 2003).

Figure 3.7: Photograph of by-caught harbour porpoise tangled in a fishing net (by K. Skora)

Donovan and Bjorge (1995) reviewed available by-catch data and report minimum estimates for a number of key areas which together account for more than 10,000 harbour porpoises per year caught incidentally in fisheries in the North Atlantic. To aid in the conservation of the species, the ASCOBANS agreement for conservation of small cetaceans in the Baltic and North Seas requires all parties to reduce annual by-catch levels of harbour porpoises to below 1.7 % of the North Sea population (IWC, 2000). Monitoring and regulating this agreement is extremely challenging, particularly without reliable data on the levels of by-catch, the size of the population within the area or information on movement and dispersal between potential sub-populations (Hammond et al., 2008).

It is difficult to find up-to-date quantitative data on the number of porpoises caught in fishing gear around the UK, despite the introduction of compulsory monitoring under EC Regulation 812/2004 and the subsequent creation of the UK By-catch Monitoring Programme. The Regulation only requires monitoring to be undertaken in specific areas of the UK fisheries zones, therefore does not present a full picture of the extent of cetacean by-catch in fisheries (Northridge et al., 2010).

Additionally the Regulation does not require monitoring of static fisheries in the North Sea, where there are significant concerns about by-catch (Northridge et al., 2010). The UK By-catch Monitoring Programme found that pelagic trawls targeting herring and mackerel around the UK had no observed incidents of marine mammal by-catch over the period 2005 - 2009, indicating that they do not have significant impacts on any cetacean populations (Northridge et al., 2010). The 2009 annual report on the implementation of Regulation 812 estimated that 790 porpoises were caught in the set gillnet fisheries in the Western English Channel and Celtic Seas and suggests future monitoring effort be concentrated in the static gear fisheries, which are a principle area of concern due to evidence of high levels of cetacean by-catch (Northridge et al., 2010).

In addition to the threat of by-catch, harbour porpoises are at risk throughout many of the coastal areas they inhabit because of pollution and disturbance from boat and construction noise, and recreation. Noises associated with shipping, construction and seismic surveys have the potential to negatively affect porpoises through direct discomfort associated with high sound levels and through increases in ambient noise acting to mask returning echoes, affecting the animal's food detection capabilities (Gotz et al., 2009). Carstensen *et al*. (2006) used static acoustic monitoring to show that construction noises associated with the development of an offshore wind farm in the western Baltic Sea significantly reduced the porpoise activity within the surrounding area (up to a radius of 15 km from the site). This type of disturbance does not directly result in a reduction in the porpoise population, rather a spatial redistribution in response to disturbance. The study raises important questions about the recovery time of the local populations, and the long-term impact on the health and fitness of the animals that are excluded from potentially important foraging areas. There is also evidence that consistent exposure to shipping and construction noise can lead to hearing loss in porpoises, which will affect their echolocation capability and therefore their ability to hunt effectively (Gotz et al., 2009).

There is considerable evidence that harbour porpoises accumulate dangerous quantities of various types of pollutants that are discharged into the marine environment. Trace metals such as mercury, pesticides, flame-retardants and plasticisers are of particular concern, as they accumulate as opposed to being excreted, and they can disrupt endocrine processes. Pierce *et al*. (2008) found 74 % of porpoises sampled from the southern North Sea had concentrations of polychlorinated biphenyls (PCBs) in their blubber which were above the threshold level for negative effects on reproduction. There was also found to be a lower level of pregnant female porpoises in this area relative to that recorded in the West Atlantic population. Evidence has been found for links between high pollutant levels in the body and increased parasite burden and death associated with infectious disease, indicating a general loss of fitness and capability associated with high pollutant levels in the tissues (Pin et al., 2010)

The impacts of ongoing and future climate change on marine mammals are not fully understood. It is likely that changing temperatures and associated changes in weather patterns will affect the distribution of thermal habitat and key foraging areas such as thermal fronts (e.g. Cotton et al., 2005; Worm et al., 2005); thus potentially affecting the distribution of harbour porpoise habitat with their current range. There are also likely to be indirect effects of climate change, mediated through changing prey distribution and abundance (Edwards and Richardson, 2004; Genner et al., 2004; Perry et al., 2005; Simpson et al., 2011). At present there is little evidence for direct effects of climate change on harbour porpoises, perhaps as a result of the difficulties in separating short-term natural variability in their distribution and abundance from longer-term climate related shifts (see MacLeod et al., 2006b; and Thompson et al., 2007). The difficulties in observing and monitoring the species make these climate links even more problematic to establish.

In recognition of the declines in global harbour porpoise populations and the continued threats throughout much of the species' range, it is protected under a number of national and international policies and treaties. These include:

European and National:

- Appendix II of the Bern Convention (1982) for the Conservation of European Wildlife and Habitats, which designates strict protection and no direct exploitation of harbour porpoises.
- The UN Bonn Convention (1994) or Convention on the Conservation of Migratory Species, which encourages multilateral protection of the species within its range and promotes international research collaborations.
- Annex V of the OSPAR Agreement (Oslo Paris Convention 1998), which aims to protect and conserve the marine ecosystems of the Northeast Atlantic.
- ASCOBANS (1994), which requires conservation, research and management measures from all signatories to address issues of adequate monitoring, data sharing, by-catch reduction, pollution control and increasing public awareness. The aim of the agreement is to "restore and/or maintain biological or management stocks of small cetaceans at the level they would reach when there is the lowest possible anthropogenic influence".
- Annex II and IV of the EU Habitats Directive (92/43/EEC) (1992), which requires all member states to protect the species within the 200-mile nautical limits of their Economic Exclusion Zones (EEZ) and to designate Special Areas of Conservation (SAC) for the species

within their territorial waters by 2012. Designation of SAC requires initial identification of key sites for the species, which are chosen using a number of criteria relating to a high abundance of the species at the site, the regularity its use and the importance of the area for reproduction or nursing. Proposed SAC sites must be 'clearly identifiable areas representing the physical and biological factors essential to the species' life and reproduction'.

-

International:

- International Union on the Conservation of Nature (IUCN) Red List. The species has been monitored on the Red List since 1988, but until 1996 a lack of data prevented any designation. In 1996 the harbour porpoise was recognized as 'Vulnerable' by the IUCN, but this listing has since been reassessed and the species is now described as 'Least Concern' due to its widespread distribution and abundance in much of its range.
- Appendix II of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), which prevents international trade in the species without the granting of an export permit. The aim of Appendix II is to protect species which are not necessarily currently threatened, but that may become so if trade is not regulated.

Because they are a highly mobile species, harbour porpoise presents a serious challenge to monitoring, management, and conservation. This is a particularly important issue in the UK, where the Government is obliged to designate protected areas (SAC) for the species under the Habitats Directive. This requires the identification of important sites for the species, and therefore an increase in our knowledge of the ecology of the species and the controls on its behaviour and distribution.

3.1.4 Research objectives

In light of the previous studies and conservation and management policies described in this section, a research gap related to the interaction of harbour porpoises with their physical habitat at a fine scale was identified. The visual and acoustic data collected in the SeaWatch SW survey provided a unique opportunity to investigate the fine-scale spatial and temporal distribution of porpoises within the survey area in relation to high-resolution physical covariates such as bathymetric and other dynamic environmental variables. The main aims of this chapter were to describe the temporal and spatial patterns in sightings of porpoises as a function of the fine-scale habitat characteristics around the reef, by investigating associations between spatial clustering of sightings and identifiable reef features, and associations between temporal patterns in sightings and tidal flow features.

3.2 Methods

3.2.1 Visual monitoring data collection

Sightings data were collected during the effort-based SeaWatch SW wildlife monitoring survey 2007 – 2010. For details of survey methodology and methods for reducing error and detection bias see chapter 2.

The total number of harbour porpoise sightings collected in the survey over the four years was 736. Each of these records represents a harbour porpoise sighting from the survey watchpoint. Filtering of the dataset was undertaken in order to exclude known and suspected re-sightings of the same individuals/groups to avoid pseudo-replication. 'Known' re-sightings were classed as those where it was noted in the field at the time of observation that the same porpoise(s) had been tracked to a new position. 'Suspected' re-sightings were defined as those which occurred both within less than 30 minutes and ≤ 10° or ≤ 300 m of the previous sighting.

Additional filters were applied to remove sightings made during the 12:00 – 13:59 lunch break period (which was occasionally observed) and during poor survey conditions, defined as visibility less than 5 km and/or Beaufort sea-state of four or above. Sightings recorded as being outside the defined survey area (100˚ – 270˚ and out to 3 km) were also removed. Details of the number of sightings removed at each stage of this process are given in table 3.1, the final filtered-sightings dataset contains 418 records of harbour porpoise.

Table 3.1: Details of number of sightings removed from the dataset after each stage of filtering for survey conditions and quality control.

Filter applied	Number of sightings removed	Resulting dataset size
Re-sightings (known and suspected)	97	620
No survey conditions recorded	29	591
Sea state ≥ 4	84	507
Visibility less than 5 km	6	501
Sightings beyond 3 km	25	476
Sightings outside field of view (100° - 270°)	29	447
No distance/direction data recorded	29	418

This dataset (n = 418) was used for all analyses apart from the spatial analyses, where additional quality control filters, based on the confidence of the location estimate, were applied. This was done using a scoring system from 1 to 3, where only sightings with a position confidence score of 3 were included in the spatial analyses. The final spatial dataset included 255 records, the majority of which were sightings made in 2009 and 2010. This reflects an increased focus on the accurate recording of sighting locations over the duration of the project.

Temporal analyses were undertaken on an hourly time series of sightings. The hourly effort data included in this time-series have also undergone filtering, so as to only include effort undertaken in visibility of greater than 5 km and seas state 3 or less (table 3.2). There were 4020 hours observed over the 4-year survey period. 1623 (40 %) of these hours of effort could not be included in the final temporal analysis because of poor survey conditions for harbour porpoise.

Table 3.2: Details of survey condition filtering on the hourly effort data. Only effort collected during good survey conditions (visibility greater than 5 km and sea state of 3 or less) was included in the porpoise temporal data analysis.

Filter applied	Number of hours removed	Resulting dataset size
No survey conditions recorded	283	3737
Sea state ≥ 4	1122	2615
Visibility less than 5 km	202	2413

The remaining hours of effort were split relatively evenly between the 4 years of the survey with 608 hours in 2007, 538 hours in 2008, 569 hours in 2009 and 698 hours in 2010.

3.2.2 Acoustic monitoring data collection

Underwater passive-acoustic monitoring of harbour porpoises was undertaken during 2010 using moored passive acoustic devices called C-PODs. C-PODs are self-contained ultrasound monitors that contain a 20-160 kHz omni-directional hydrophone. The C-PODs detect tonal clicks and record the time and duration of each click to 5 µs resolution. 'Tonal' clicks are characterised by a narrow band of frequencies containing more energy than the rest of the frequency range. The C-PODs continuously search for sounds that are within the range 20 kHz to 160 kHz. CPOD detection range is a maximum of 300 m for detecting harbour porpoises (Urick, 1983). The data on the time, duration and click characteristics are stored on internal memory cards, which are downloaded upon recovery of the moored equipment.

The C-PODs were deployed in 3 locations in the vicinity of the survey area (figure 3.8). Two were closely associated with different bathymetric habitats around the Runnelstone Reef; one on a sloping sandy area of reef margin on the eastern edge in 30m depth ('eastern') and one in 41 m water depth, close to the rocky drop off where there is a large change in depth over a small distance ('reef margin'). These locations were based on areas of minimum ('eastern') and maximum ('reef margin') observations of porpoises in the visual survey (2007-2009). It was hoped that a C-POD could also be deployed on the western reef edge, but this area is much more tidally exposed and a previous attempt to moor a C-POD here had failed. Neither was it an option to deploy a C-POD on the reef-top (the area of ~ 15 m depth inside the horseshoe shaped margins) because of the importance of this part of the reef for local commercial fishing activity. Considering these issues, the third CPOD was deployed away from the reef, at a comparable depth (33 m) to the 'eastern' pod but further along the coast to the east, on a gently sloping area of sandy substrate ('control'). This 'control' C-POD was out of site of the SWSW watchpoint at Gwennap Head.

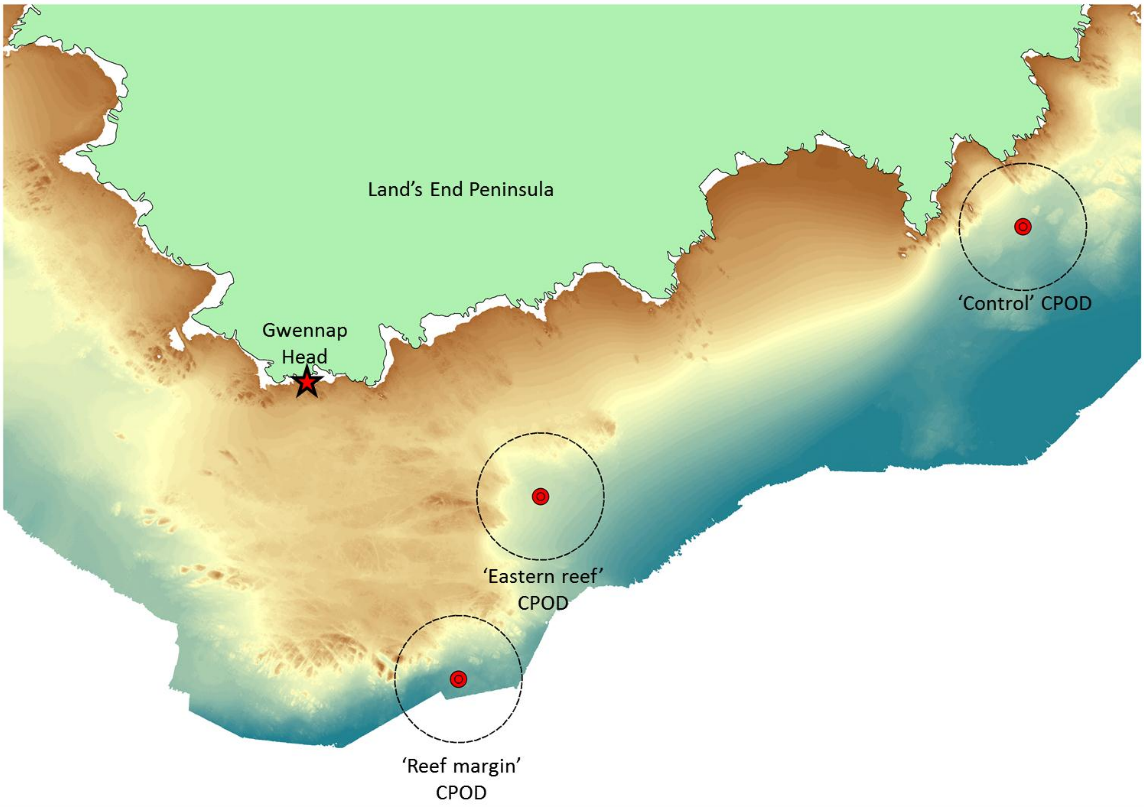


Figure 3.8: Location map showing the three CPODs (acoustic monitoring devices for porpoises). The dashed radius around each CPOD represents the approximate range of detection (300 m).

The C-PODs were moored on modified lobster pot moorings with the help of local fishermen Ted Chappell. The moorings were made of a length of ~ 30 m ground line with 30 kg chain-link anchors at either end. At one end there was a buoy line made of 12 mm leaded polypropylene rope with two deep-water trawl buoys connected to the top; one at low water depth and one at the end of the line. The buoy rope was approximately 1.5 times the water depth and leaded line was used to prevent excess line floating on the surface and becoming entangled in boat propellers. Each C-POD was connected to its buoy line at approximately half the water depth by a short tether attached with a swivel. The C-PODs are neutrally buoyant and therefore are self-righting and remain vertical in all but the strongest of tidal currents.

3.2.2.1 Statistical methods for analysis of harbour porpoise distribution.

This section provides an overview of the methods for statistical modelling of the spatial and temporal harbour porpoise sighting and acoustic detection data.

Generalised Additive Models (GAM) were used to model the porpoise sighting and acoustic data throughout this chapter. This is because the count data were not normally distributed and there were not necessarily linear or monotonic relationships between the response and predictor variables. Therefore a GAM model structure, that is generalised and has the option of fitting smooth functions, was most appropriate (Wood, 2006). The GAMs take the general structure specified by Hastie and Tibshirani (1990).

The statistical modelling was undertaken in "R" using the 'gam' function in the 'mgcv' package' (Wood, 2006), which contains integrated smoothness estimation, removing the subjectivity introduced by user-specified knot locations (join points in the smoothing splines). Smooth functions for model covariates were specified using thin plate regression splines with shrinkage. The 'shrinkage' smoothers are constructed to allow the effect of smooth terms to be shrunk to zero in cases where the optimal smoothing parameter is so large that it effectively represents zero effect (Wood, 2006). The dimension (maximum degrees of freedom) of the smoothers were manually limited by k = 4 for most variables (except where specified) to avoid excessive flexibility and model over-fitting.

The penalty (gamma) given to each degree of freedom in the automatic smoothing parameter (k) selection process was increased from the default of 1 to 1.4 as recommended by Wood (2006) to again reduce the potential for model over-fitting. Interactions between covariates were modelled using tensor product (te) smooths. Tensor product smooths are recommended by Wood (2006) for producing smooth functions of interactions between covariates with different units, or if different degrees of smoothness (k) are required for each of the interacting covariates. Circular variables, for example parameters with degrees as units, where 0 and 359 are adjacent values, were modelled with cyclic smooth terms that can account for their circular nature.

Predictor variables were selected through manual stepwise forwards selection, with the best model being selected at each step using the model fit score (estimated Akaike Information Criterion (AIC) for negative binomial models, Unbiased Risk Estimator (UBRE) transformed to AIC for binomial models, Generalised Cross Validation (GCV) transformed to AIC for quasi-Poisson models). Forwards stepwise selection involves the addition of single covariates to the null model and subsequent comparison of the resulting models on the basis of the AIC score and the amount of additional deviance explained by the model. At each step, the (significant) covariate that adds most explanatory power and results in the lowest model fit score (AIC/UBRE/GCV) is selected for inclusion in the model. This updated model is then taken forward into the next round of selection where the effect of adding the remaining predictor variables is tested again, and so on.

Predictor variables were only added to the model if:

i. The estimated AIC/AIC-equivalent score of the model by was reduced by a value of 2 or more, as recommended by Burnham and Anderson (2002).
ii. The variable was significant at $p < 0.05$.
iii. Addition of the variable to the model increased the amount of deviance explained by ≥1 %.

The importance of each selected predictor variable is described by the amount of deviance explained by the model (as a percentage). Deviance explained is the difference between the null model deviance and the current model deviance, where deviance is based on the residual sum of squares of each model. This metric represents the models ability to describe the variability in the data as a function of the covariates.

Prior to modelling, pairwise Spearman’s rank correlation tests and Variance inflation factors (VIF) (“R” ‘AED’ package, function ‘corvif’) were calculated for all of the candidate model covariates. Pairs of variables with high levels of correlation (Rho = ≥ 0.8) or VIF values exceeding the conservative threshold of 3 (Zuur et al., 2009) were identified. For significantly collinear pairs of variables, the one that was selected first during the stepwise covariate selection process was retained and the other was discarded, thus preventing the inflation of standard errors caused by inclusion of collinear pairs of variables.

3.2.2.2 Spatial analysis of visual monitoring data

The visually estimated locations of the pre-filtered spatial sightings data were transformed from bearing and distance to a lat and long coordinate and imported into an ArcGIS (v.10) layer file. The sightings were mapped over the high-resolution bathymetry data provided by the Marine and Coastal Authority (MCA), CCO and UKHO (figures 2.3 and 2.4).

<u>Tests for spatial clustering in the sightings data.</u>

A nearest neighbour spatial analysis was undertaken in ArcGIS using the Average Nearest Neighbour test in the Spatial Analyst Tools.

The visually estimated position of all harbour porpoise sightings and the extent of the 3-km survey area were imported as a point process pattern (ppp object) into the “R” package ‘spatstat’ (Baddeley and Turner, 2005). The distribution of the sightings within the survey area was explored using intensity images (function 'density') and a Ripley's *K* analysis (function 'kest') was carried out to test for non-random point processes. Ripley's K function is a second order analysis of spatial point processes that tests the distribution of points over various distances to look for scale dependent patterns. The test calculates distances from each point to all other points in the dataset, then summarises the average frequency of observations within distance bands (*d)* from each point. The cluster statistic, *K (d)*, represents the intensity of points within specified distances bands (*d*) from other points, and is compared to an expected *K* value based on simulations of complete spatial randomness (with the same number of points within the same survey area extent).

Kernel density analysis.

Utility distributions (UD) describe the pattern of use of an area by mapping animal intensity (probability of use), in this case porpoise sightings per unit area (Powell, 2000). Utility distributions (UD) were estimated for the porpoises observed within the study area using fixed kernel density estimation and derived kernel isopleths, which delineate areas dependent on probability of use. The 50 % density isopleth was selected to define a core-use area within the survey area as a whole. This selection was made on the basis that the 50 % isopleth will encompass an area that has a 50 % probability of sightings being made and contains approximately 50 % of the observations. Comparisons can then be made with the size and intensity of use of the remaining part of the survey area, where the other 50 % of the sightings were recorded. Use of a smaller core area (e.g. 25 % isopleth) is not recommended, as these tend to be more biased than the 50 % probability estimates (Borger et al., 2006).

The kernel estimate is considered one of the most accurate techniques currently available for representation of a probability density (Powell, 2000). The kernel estimated probability of an animal using the habitat at a specified location is a smoothed function of all sighting locations within a specified range (neighbourhood/bandwidth) around that location (Silverman, 1986). This method is therefore less affected by errors on the exact locations of an animal's position than some other space-use estimators (Millspaugh et al., 2006), although there is evidence that non-negligible errors can lead to biased UD estimates (Horne et al., 2007). The kernel density estimator is extremely sensitive to the choice of smoothing parameter (bandwidth or *h*) (Silverman, 1986; Powell, 2000). Intuitively, greater smoothing will consider the uncertainty in the UD estimate introduced by in-exact positional estimates (Millspaugh et al., 2006) although over-smoothing can produce biased estimates and the loss of fine scale space-use features. Powell (2000) recommends using a smoothing bandwidth that is at least equal to the uncertainty in the location estimates (which in this case has been investigated by the error tests presented in section 2.41).

The fixed kernel density estimate of the porpoise sighting locations was calculated in the Geospatial Modelling Environment software (GME, formerly Hawth's Tools) with the 'kde' and 'isopleth' commands (Beyer, 2012). The kernels were not weighted; therefore each sighting had a unit weight of 1 to represent only the presence of a sighting rather than a number giving the group size recorded at each sighting position. The X and Y coordinate data for the sightings were normally distributed; therefore a quartic approximation of the Gaussian kernel was used, which gives a uni-modal kernel that is symmetrical around the origin (the sighting position).

A number of potential bandwidth *(h)* values for the porpoise kernel density estimate were obtained using various estimation methods in the "R" 'sm' package (function 'h.select'), including cross validation, normal approximation and Sheather-Jones (Bowman and Azzalini, 2010). A visual comparison of the performance of these *h* values, and an evaluation on the basis of minimisation of the mean square error was undertaken (using the 'nmise' function in "R" 'sm'package). The smoothing parameter optimisation techniques suggested a value of 300 m (estimated using an un-weighted normal smoothing method) was most appropriate and so this was used in the kernel density and estimate calculations. The selected value of 300 m is also appropriate considering the error on the sighting position estimates (see chapter 2, section 2.4).

Gridded relative density analyses.

A radial grid was created, defined by the extent of the survey area, based on the field of view from the survey watchpoint (100° - 270° out to a distance of 3 km from the observer's location on Gwennap Head). The grid cells were divided along concentric distance bands from the watchpoint location that are 600-m apart and radial bearing lines that are 10 ° apart (based on plus/minus the mean error on visual estimations of position, see chapter 2, section 2.4) (figure 3.9).

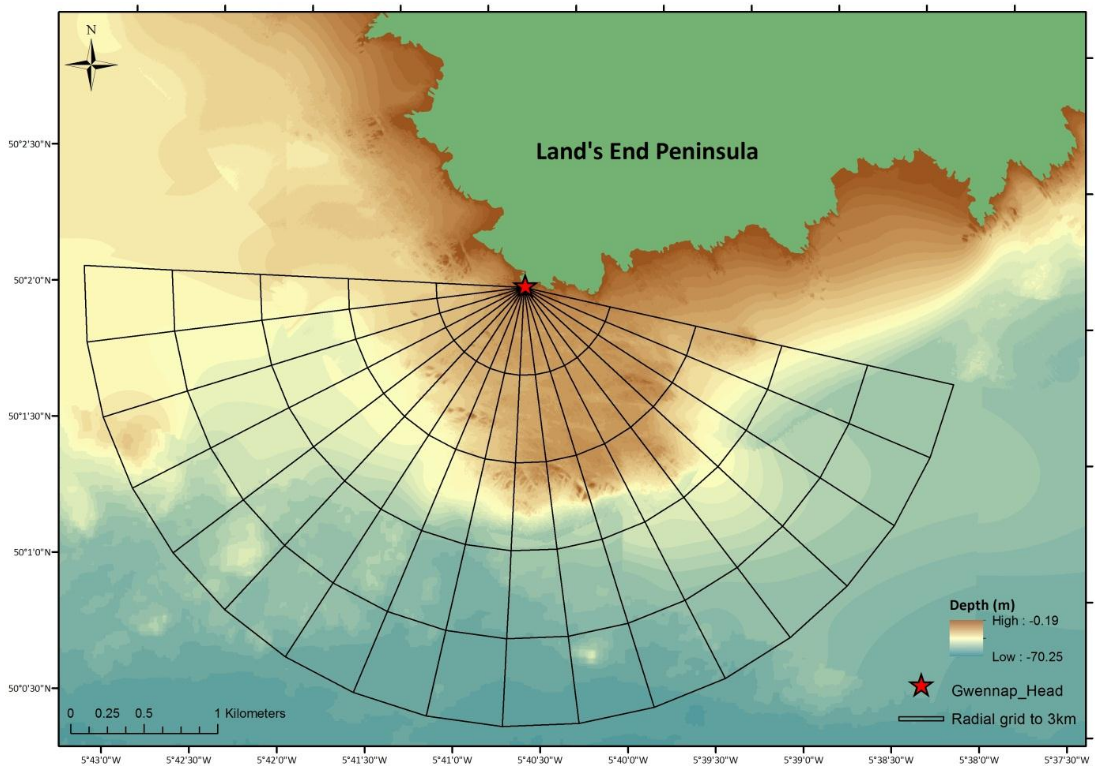


Figure 3.9: The radial grid used for gridded relative density analyses. The grid extends over the survey area, defined by the field of view from the watchpoint (100° – 270° and out to 3 km). To account for the error on visual estimation of sighting position, concentric distance bands are separated by a distance of 600 m and radial divisions are made at 10° intervals. The survey watchpoint at Gwennap Head is indicated by red star. High-resolution multi-beam bathymetry data is courtesy of the MCA/CCO and UKHO.

The porpoise sighting data and static bathymetric variables of depth, slope and aspect were summarised within each grid cell using the Spatial Joins and Zonal Statistics tools in ArcGIS v.10 (slope and aspect were first calculated from the depth data using the Spatial Analyst: Slope and Aspect tools in ArcGIS v.10). This produced mean and variance data for the bathymetric variables and mean and sum data for the sightings within each grid cell over the four-year survey period. The area of each grid cell is variable (because of the use of bearing sections, which widen with distance from the watchpoint); therefore an area-corrected value of sightings per km^2 was calculated for each grid cell.

Spatial model of harbour porpoise sightings per km^2 within each grid cell.

The influence of static bathymetric variables on the area-correct sightings of porpoises within each cell was modelled using a GAM with negative binomial error distribution and a logit-link function. An offset of grid cell area was included in the model to account for differences in the area of different cells. A cyclic cubic regression spline was used to represent aspect, which is a 'circular' variable, where the first (0°) and last (359°) values are adjacent.

The final model was used to predict the spatial distribution of porpoise sightings, for visual assessment of the model's ability to accurately reproduce the observed data.

3.2.2.3 Temporal analysis of visual monitoring data

The pre-filtered sightings-only and hourly presence-absence data were collated in Excel. Associated temporal environmental variables were linked to the time of each sighting and to the hour of the survey period. The environmental data available were sea-state, cloud cover, and glare from the observer record at Gwennap Head and tidal flow speed, direction, tide height and daily tide range from the POLPRED CS20 model.

For the sightings-only dataset the environmental variables were taken from as close to the exact time of the sighting as possible; for POLPRED data this was to the nearest 10-minute period and for the observer records of survey conditions this was to the nearest hour. For the hourly presence-absence dataset of filtered effort and sightings the environmental data were averaged where necessary (i.e. for the higher-resolution data-from POLPRED, the values are hourly averages).

Additional temporal covariates were created. These were 'Time of Day Index' (TODI), and 'Time to High Water' (TtHW). The Time of Day index is a value between 0 (sunrise) and 1 (sunset), which is a ratio of the time since sunrise relative to day length (using sunrise/set time for Penzance). This metric compensates for changing day length throughout the survey period. 'Time to High Water' is a measure of the time period to the nearest high water and ranges from -6.33 to 6.33, with 0 representing high water. This metric was calculated in MatLab using high water times from POLPRED (CS20 tidal model).

Analysis of the effect of dynamic variables on the presence or absence of porpoise sightings.

Pre-modelling data exploration was carried out on the sightings and hourly presence-absence data to investigate temporal patterns in the data and possible links between dynamic environmental conditions and the occurrence of sightings.

A GAM with binomial error structure and logit-link function was used to relate the presence or absence of porpoise sightings in each hour of survey effort to dynamic environmental variables. Candidate covariates were survey conditions (Beaufort sea state, glare and cloud cover), dynamic tidal variables (tide direction, tide speed, tide height, time to high water, tide flow group, tide range for the day of the sighting) and temporal variables (TODI, hour and week, month). 'Staged' forwards stepwise selection was carried out with significant survey variables being added to the model first (in order to initially account for biases introduced by varying survey conditions). The second stage of covariate selection was stepwise addition of significant dynamic environmental variables. Once all significant survey and environmental variables were selected, temporal variables were introduced as potential covariates. The idea behind this staged stepwise addition was to see whether the models containing only the environmental variables could adequately account for temporal changes in porpoise sightings.

Degrees of freedom (*k*) were limited to 4 for all survey and temporal variables. The tidal variables, which were expected to have a sinusoidal distribution, were allowed greater degrees of freedom (‘wigglyness’), being limited by k = 6. Note that this is still reduced compared to the default of k = 10. Tide direction is given in degrees, therefore was modelled using a cyclic smooth term.

In the case of binomial models, the model fit score is given as UBRE (UnBiased Risk Estimator). This is a linear transformation of the AIC model fit score and can be transformed back to AIC by UBRE x model *n*. This calculation was carried out for the binomial model UBRE scores so that AIC could be used for model selection purposes (outlined in 3.2.2.1).

Analysis of the effect of dynamic variables on the presence or absence of porpoises within and outside the 50 % UD area:

To investigate the effect of dynamic variables on the spatial pattern in porpoise sightings, the density of sightings under different tidal conditions was explored. Potential spatio-temporal interactions were further explored by separately modelling the effect of dynamic variables on the presence-absence of sightings per hour (1) inside and (2) outside the 50 % UD area calculated in the kernel density estimation analysis.

3.2.2.4 Analysis of acoustic monitoring data

Data processing and classification.

CPOD .exe V.2 software (supplied with the C-PODs) was used to extract and process the acoustic monitoring data. Version 2 of the software uses the KERNOW classifier, which first detects click trains and then classifies them (more information available at www.chelonia.co.uk). The classified click-trains are then saved to a filtered data file, on which further analysis can be undertaken.

Click trains are regular sequences of similar events and are characteristic of cetacean clicks. Other sources of click trains include boat sonars, clicking shrimps and Weak Unknown Train Sources (WUTS). The KERNOW click train detection algorithm is based on a probability model of whether a click is part of a train or is a chance event. Three main factors influence the probability of a click being ascribed as part of a train; (1) Coherence (whether similar characteristics are seen in successive clicks), (2) A quiet background (the likelihood of a chance train is reduced under low ambient noise), (3) Temporal association with other trains (when they are echolocating, cetaceans produce trains almost continuously).

The KERNOW classification algorithm ascribes click trains to a specific source based on their attributes, the groups are 'NBHF' (all species producing Narrow Band High Frequency clicks), 'Others' (all other odontocetes except sperm whales), 'Sonars', 'Unclassed' (almost all of these will be chance trains arising from ambient noise) and 'WUTS'. All of the click trains attributed to a specific source by the software are also given a confidence level (Hi, Mod, Lo and ?).

The data files for each C-POD from the two deployment periods (26/7/10 – 18/8/10 and 18/8/10 – 13/10/10) were joined and the data from each C-POD were then filtered for narrow band high frequency (NBHF) click trains using the Hi and Mod quality filters. The only cetacean in UK waters producing NBHF clicks is the harbour porpoise; so all clicks ascribed to this group can be interpreted as porpoise clicks. A random selection of 100 clicks from each data file were manually classified and checked against the classification by the software. The automated classification error level was found to be less than 5 % and this was deemed to be acceptable therefore no further manual quality control was carried out on the click data.

It is best to use the C-POD data as positive/negative detection periods rather than the absolute number of clicks recorded because this lessens the effect of potential false positives and false negatives, and also because a number of clicks may be produced by one animal (or echoed). This means that the absolute number of clicks detected is not necessarily representative of the density of animals within the recording area. The most widely used metric of acoustic detection from C-PODs is Detection Positive Minutes (DPM), which is a good indicator of relative density and habitat use and was used as the unit of detection in the analysis of the acoustic data.

Comparison of patterns in porpoise detection between C-PODs.

The numbers of detections and patterns in day-night distribution of detections at the three C-PODs is presented and compared. Encounter duration and movement between the C-POD detection areas were investigated using autocorrelation and cross correlation on the DPM time-series using the "R" functions 'acf' and 'ccf'.

Analysis of the effect of dynamic and temporal variables on the C-POD detections.

The data from each C-POD was modelled separately to look at the influence of time and tide conditions on porpoise detections. Two-stage models were used to analyse the detection data.

This method was used because of the excess of zeros in the dataset. Firstly the (binary) presence/absence of DPM in each hour of the data was modelled using a binomial GAM with logit-link function. Secondly the number of DPM per hour (during presence hours only) was modelled using a Poisson GAM with logit-link function. During the model fitting for the DPM per hour data, overdispersion was detected in the Poisson model and this was corrected using a quasi-GAM model where variance is given by dispersion parameter multiplied by the mean. This was specified in the model using a 'scale = -1' argument.

The potential model covariates for both stages were; wave height and direction (from the Penzance wave-rider buoy); tide direction, tidal flow speed, tide height, daily tidal range and time to high water (from the POLPRED CS20 model); tidal flow group (see table 3.7); hour and month.

The covariate selection was carried out in a staged fashion as described in 3.2.2.3, where significant wave variables were added first because these have the potential to affect background noise and therefore detection rates. The significant dynamic tidal variables were selected next, followed finally by the temporal variables.

3.2.3 Fine-scale oceanographic survey.

A fine-scale Acoustic Doppler Current Profile (ADCP) survey was undertaken within the survey area over a semi-diurnal tidal cycle on 11th July 2011. The aim of the survey was to better understand the hydrodynamics within the SWSW survey area across a tidal cycle, in particular to highlight any tidal-topographic flow features that may be relevant in the context of the SWSW marine wildlife sightings data. In order to build up a picture of the spatial variability of tidal flow over time, the transect route shown in figure 3.10 was repeated nine times over the 12.6 hour tidal cycle. The route was designed on the basis of the greatest possible coverage of distinct topographic regions of the reef, compromised with length, so that multiple (minimum of 8) repeats could be achieved over the tidal cycle.

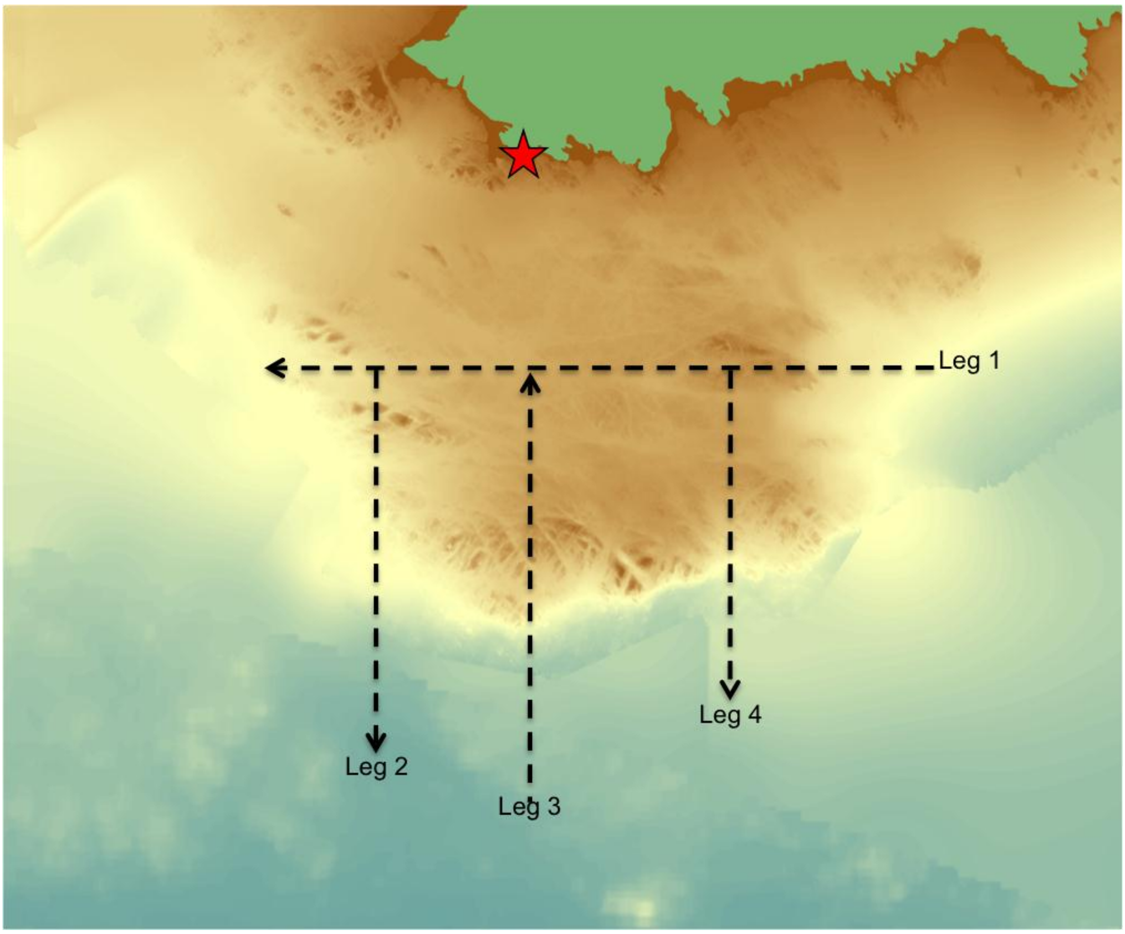


Figure 3.10: Map of ADCP survey transect route with each survey leg labelled. A red star shows the survey watchpoint at Gwennap Head. Bathymetry data supplied by the CCO and UKHO.

The survey was carried out from the University of Southampton inshore research vessel 'Callista', using a hull-mounted RDI Workhorse Mariner ADCP with data recorded by a linked computer running WinRiver v.2 software. The instrument was set at 600 kHz, giving a depth range of approximately 50 m (with 1-m vertical bins) and a ping rate of 2 Hz (2 cycles per second). The ADCP software recorded the latitude and longitude of the boat position from the boat GPS system and bottom tracking was used to determine speed and direction of travel.

The ADCP data was split into the four discreet transect line sections ('legs'), illustrated in figure 3.10, for comparison of current flow along each 'leg' during the repeats of the transect route. The data were processed and plotted by Dr Phil Hosegood at Plymouth University using WinADCP and MatLab.

3.3 Results.

3.3.1 Patterns in the spatial distribution of harbour porpoise sightings in the SWSW survey.

The positions of all harbour porpoise sightings in the spatial dataset (N = 255) are shown in figure 3.11, with the points scaled to indicate pod size. The concentric and radial banding pattern in the position of sightings is an artefact of rounding in the distance and bearing estimations made by observers. This is discussed further in the survey methods (chapter 2).

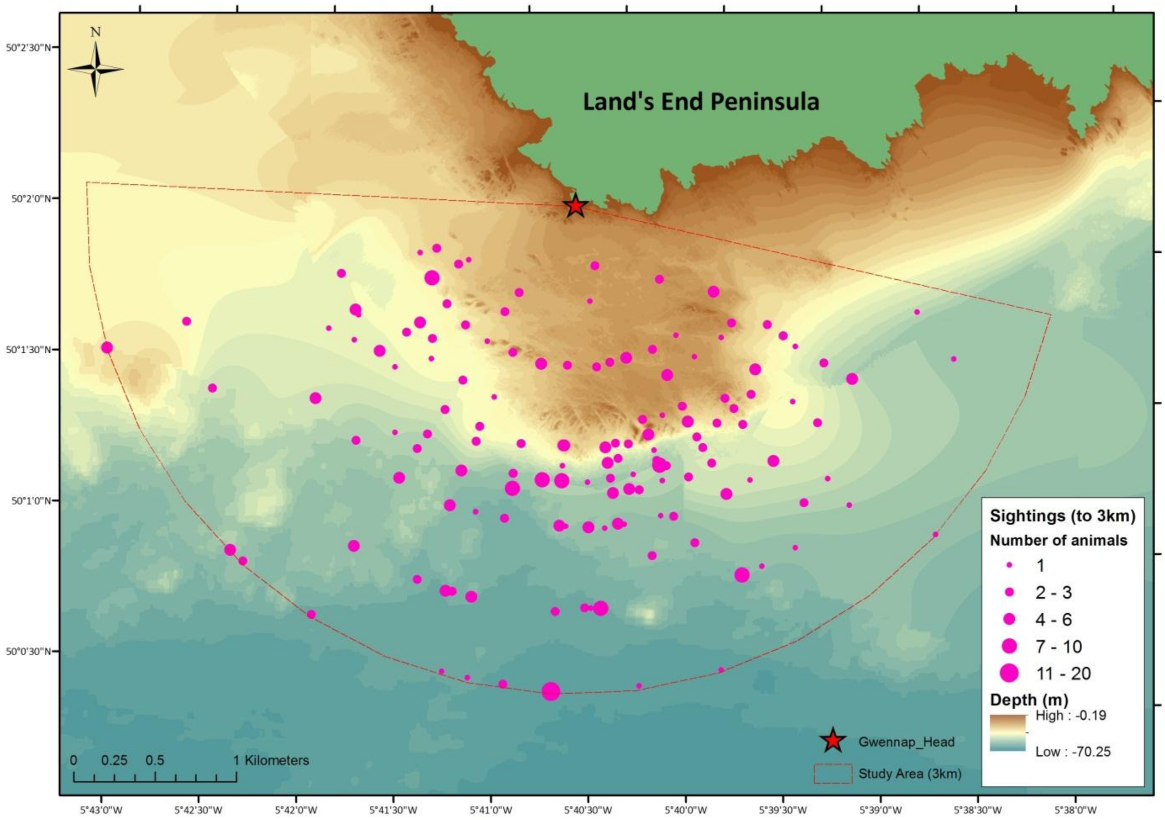


Figure 3.11: SeaWatch SW harbour porpoise sightings spatial dataset (pink dots) 2007 - 2010, symbols are scaled by size of pod (N = 255). Sightings were mapped over high- resolution multi-beam bathymetry data (courtesy of the Channel Coastal Observatory). The position of observers at the Gwennap Head watch point is shown by red a star. Survey area, delineated by dashed red line, indicates field of view.

In order to check for spatial bias introduced by survey conditions, the distance of sightings from the watchpoint was plotted against sea-state. The results showed that the distribution of distance data was not different under different sea-state conditions. There were generally fewer sightings reported under sea-state 0 and 3 than 1 and 2. In the case of sea state 0, this is probably because it was experienced very infrequently during the survey period (2 % of hours). Sea state 3 was experienced relatively frequently (33 % of hours), therefore the reduced sightings were likely a result of detection being reduced under these higher sea conditions; however, the distance distribution of the sightings that were made was not affected. The histograms are given in appendix 3.

3.3.1.1 Analysis of spatial clustering with spatial statistics.

The average point intensity within the 13.3 km^2 survey area is 1.92 x 10^{-5}. The average nearest neighbour test, a first order estimate for spatial pattern, shows that points are not randomly distributed within the survey area, but are clustered (table 3.3). The average distance between neighbouring points is significantly lower than would be expected under complete spatial randomness ($Z = 13.63$, $p = <0.0001$).

Table 3.3: Results of first order spatial process statistic; Average Nearest Neighbour. Area constrained by the border of the 3km survey area (figure 3.11). The expected mean distance is based on a pattern of complete spatial randomness with the same number of points within the same study area.

Spatial parameter	**Value**
Observed mean distance between points	63.1 m
Expected mean distance between points	113.1 m
Nearest neighbour ratio	0.5583
Z score	- 13.6268
P value	< 0.0001

The result of Ripley's *K* analysis (with edge correction) on the porpoise sightings data shows that the sightings were significantly ($p = <0.001$) clustered at all scales of analysis from 0 m to 800 m (figure 3.12). In figure 3.12, the black line, indicating the observed *K* values at specified distances (with CI indicated by dashed grey lines), lies above the line for expected *K* values under complete spatial randomness based on 999 simulations of randomly distributed points within the survey area (red dashed line, with variance of estimate indicated by shaded grey area).

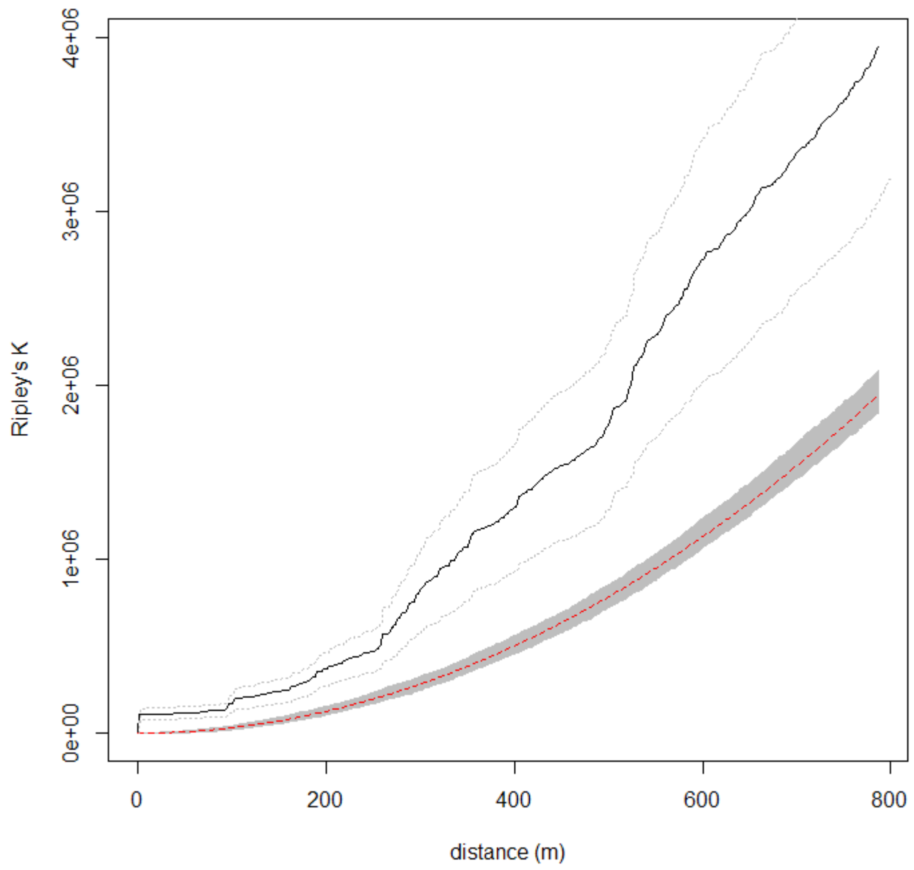


Figure 3.12: Ripley's K function test results for spatial intensity of porpoise sighting points within the survey area (N = 255). Black line indicates observed *K*(*d*), with upper and lower CI (grey dashed lines) based on variance of the observed *K* statistic at different locations in the survey area. The expected point intensity at each distance is shown by the dashed red line and was calculated using 999 simulations of Poisson point processes within the survey area (with minimum and maximum values from all simulations indicated by the grey shaded area around the line). Analysis carried out in "R", 'spatstat' (Kest) with edge correction.

Having established that the pattern in porpoise sightings over the survey area is not random, an investigation of patterns in the point intensity was undertaken using kernel density estimation. The kernel surface represents proportional utilisation of the survey area based on the probability density of porpoise sighting locations (figure 3.13). The 50 % UD isopleth is taken to represent the core area of use within the extent of the survey (figure 3.14) and has an area of 1.87 km^2, representing just 14 % of the full survey area (13.3 km^2) but containing approximately 50 % of the porpoise sightings. The position of the 50 % UD isopleth indicates that clustering of porpoise sightings occurs around the southern margins of the Runnelstone Reef (figure 3.14).

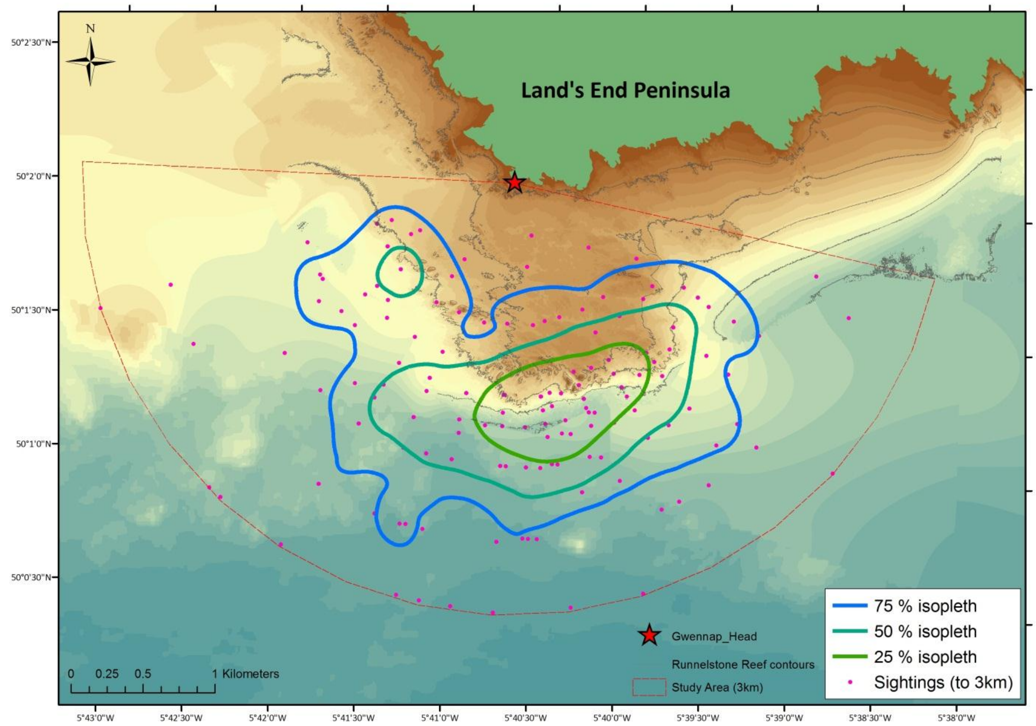


Figure 3.13: Filtered harbour porpoise sighting positions (2007 - 2010) and utilisation distribution (UD) calculated by kernel density estimation with bandwidth of 300 m. Location of sightings indicated by filled pink circles (N = 255) and kernel density estimated isopleths shown by coloured lines (75 %, 50 % and 25 %). High-resolution multi-beam bathymetry data is courtesy of the CCO and UKHO. The position of observers at the Gwennap Head watch point is indicated by red a star. Survey area, delineated by dashed red line, indicates field of view.

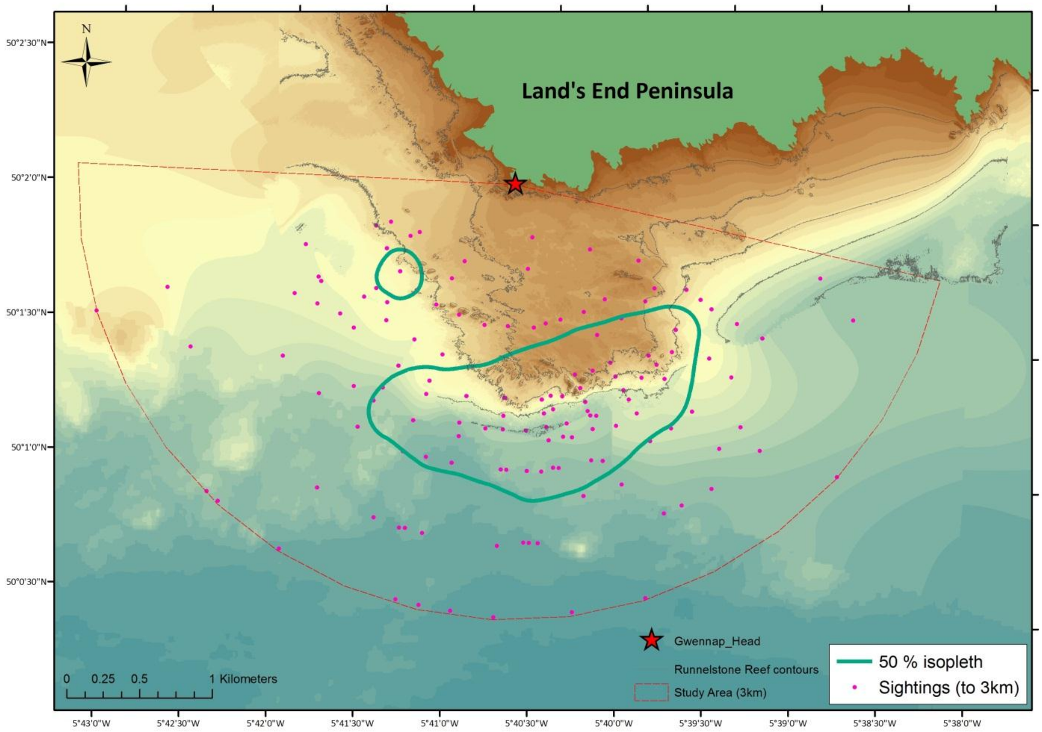


Figure 3.14: Filtered harbour porpoise sighting positions, 2007 – 2010, (pink filled circles) and kernel density estimated 50 % utilisation distribution isopleth (green line) with bandwidth of 300 m. High-resolution multi-beam bathymetry data is courtesy of the CCO and UKHO. The position of observers at the Gwennap Head watch point is indicated by red a star. Survey area, delineated by dashed red line, indicates field of view.

3.3.1.2 Habitat mapping: the effect of static physical variables on harbour porpoise distribution within the survey area.

Porpoise sightings per km^2 were calculated for each of the radial grid cells covering the survey area (figure 3.15). Data on the underlying bathymetric variables (depth, slope and aspect) have also been summarised by grid cell and are shown in figure 3.16 – 3.18. A summary of the sightings and static environmental variables used in the gridded analysis are given in table 3.4.

The maps show that grid cells with highest values for porpoise sightings per km^2 are located in a radial band along the reef edge, between 1.2 and 1.8 km from the watchpoint location (figure 3.15). Visually, there is good correspondence between these high relative density areas for porpoise sightings and parts of the reef with intermediate depths (pale brown areas on figure 3.16) as well as the steepest areas of slope (bright pink on figure 3.17). There does not appear to be an obvious influence of aspect on the location of cells with high relative density of porpoise sightings (figure 3.18), but there may be an interaction between aspect and the other bathymetric variables, such as slope that is not initially obvious and this will be investigated in the spatial model.

Table 3.4: Summary of the gridded porpoise sightings (2007 - 2010) and bathymetric variables averaged over each grid cell.

Parameter	Value
Number of grid cells	85
Number of sightings	255
Range of sightings per grid cell	0 – 28
Mean sightings per cell (std. dev)	3 (4.45)
Static physical variables	
Depth (m)	
Range	11.56 – 59.94
Mean (std. dev.)	34.4 (13.95)
Aspect (degrees)	
Range	91.4 – 220.5
Mean (std. dev.)	176.8 (27.8)
Slope (degrees)	
Range	0.19 – 14.48
Mean (std. dev.)	4.59 (3.6)
Distance from shore to centre of grid cell (m)	
Range	97.8 – 2719
Mean (std.dev)	1345 (784.8)
Grid cell area (km^2)	
Range	0.031 – 0.28
Mean (std. dev.)	0.16 (0.09)

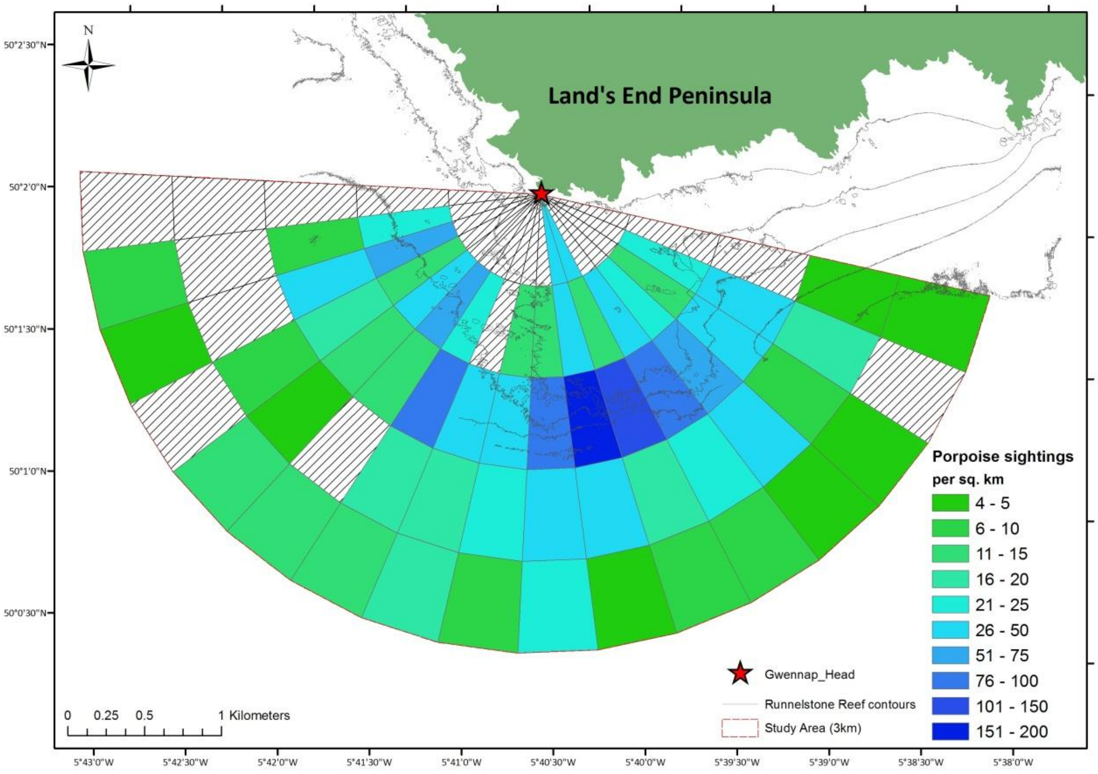


Figure 3.15: Filtered harbour porpoise sightings (N = 255) by grid cell (N = 85) corrected for cell area and presented as sightings per km^2. Hatched cells contain 0 sightings. Reef contours (10 m intervals) are shown (data courtesy of the CCO/MCA and UKHO). Position of observers at the Gwennap Head watchpoint is indicated by red star.

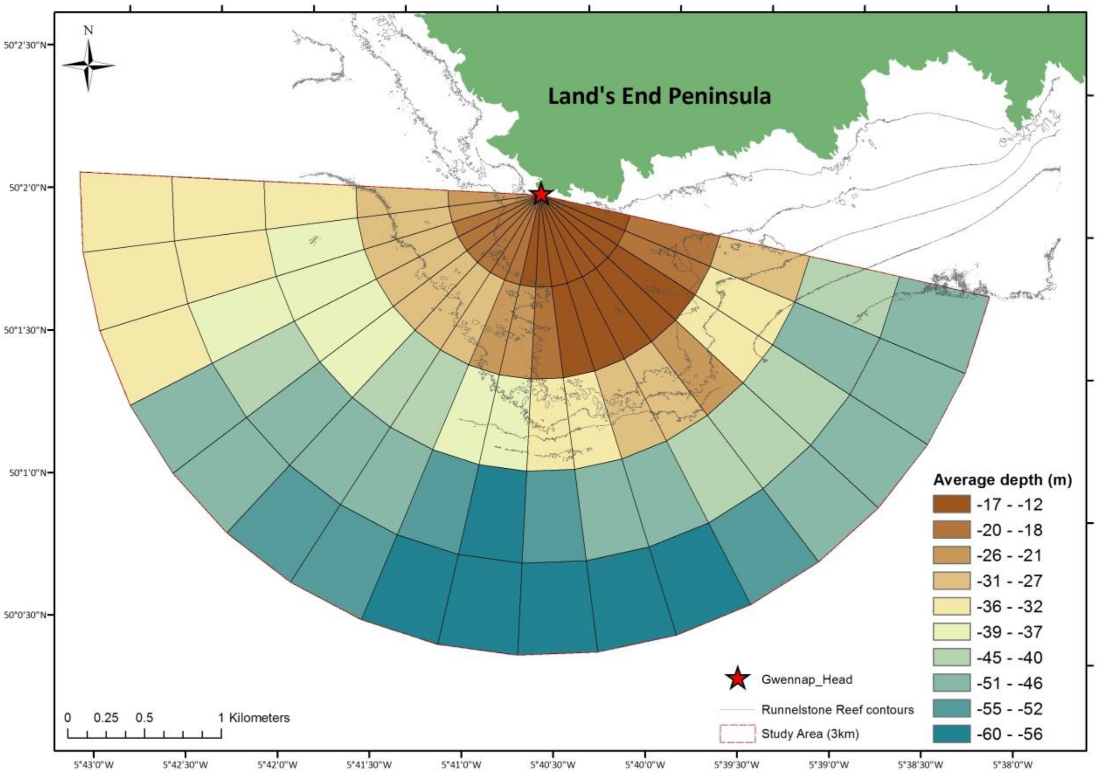


Figure 3.16: Average depth by grid cell (N = 85). Reef contours (10 m intervals) are shown. Position of observers at the Gwennap Head watchpoint is indicated by red star. Depth averages calculated from high-resolution multibeam bathymetry data, courtesy of the CCO/MCA and UKHO.

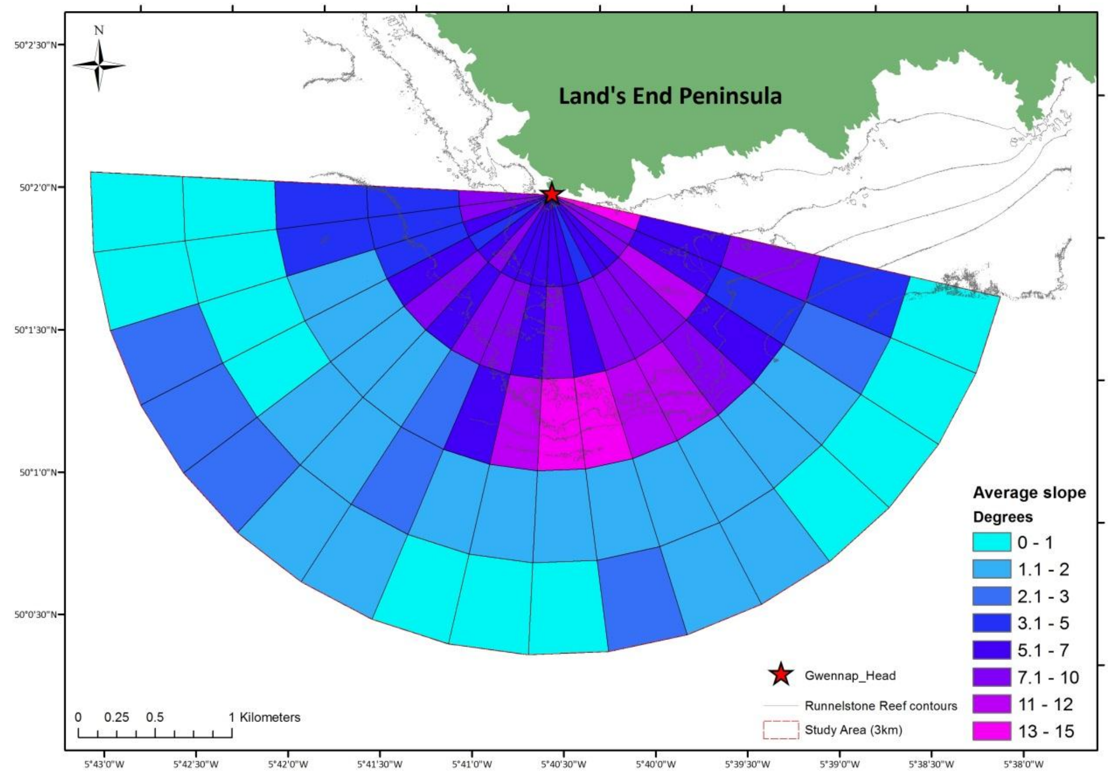


Figure 3.17: Average slope (degrees) by grid cell (N = 85). Reef contours (10 m intervals) are shown. Position of observers at the Gwennap Head watchpoint is indicated by red star. Slope averages calculated from high-resolution multibeam bathymetry data, courtesy of CCO/MCA and UKHO.

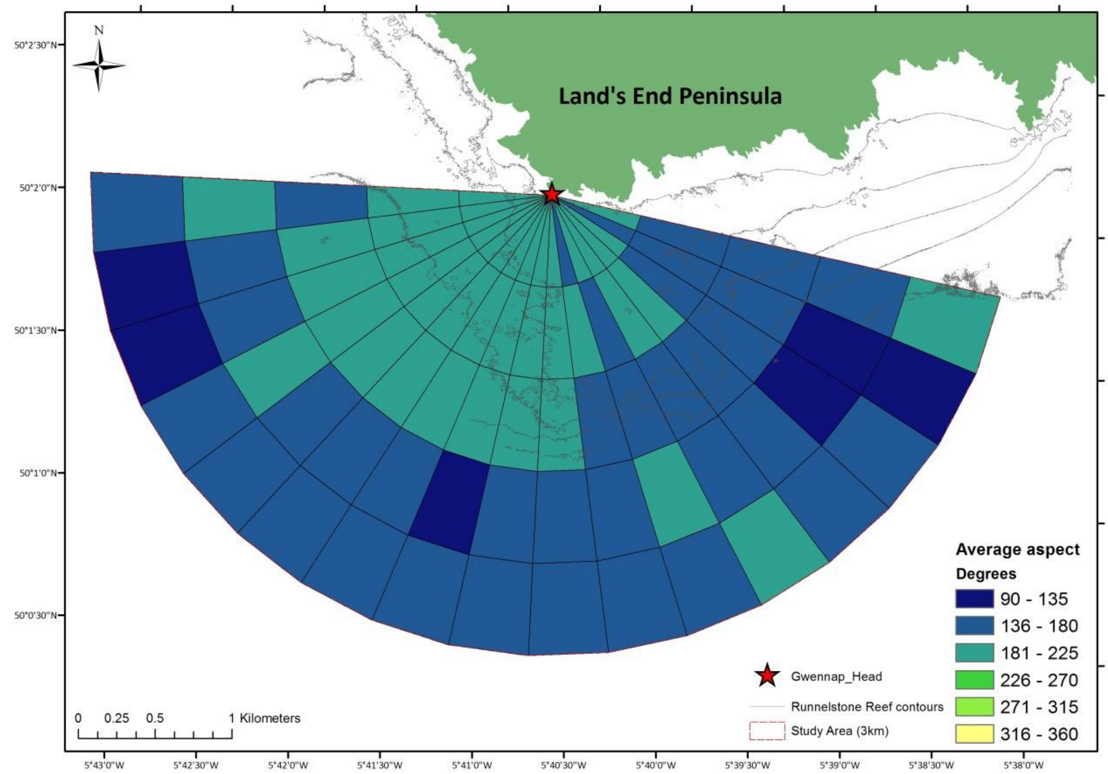


Figure 3.18: Average aspect (degrees) by grid cell (N = 85). Reef contours (10 m intervals) are shown. Position of observers at the Gwennap Head watchpoint is indicated by red star. Aspect averages calculated from high-resolution multibeam bathymetry data, courtesy of CCO/MCA and UKHO.

Grid cells with sightings recorded in them were in deeper water (median = -38.58 m) than cells with no sightings (median = -25.54 m) (figure 3.19-a). This relationship is also supported by the distance-from-shore boxplots, which indicate that cells that are further from shore were more likely to be positive for porpoise sightings than cells that are closer to shore (figure 3.19-d). There is a lower median value of slope within the presence cells than within the absence cells (2.6° and 5.2° respectively), which is likely due to the fact that the majority of cells were positive for sightings (figure 3.15) and therefore there is a much wider range of slope values in the cells with presences than in the absence cells (figure 3.19-b). There is an indication that absence cells have a more south-westerly aspect than cells where porpoises were recorded, but this difference is not clear-cut and the range of aspect values between the two groups overlap quite widely (figure 3.19-c and 3.20-b).

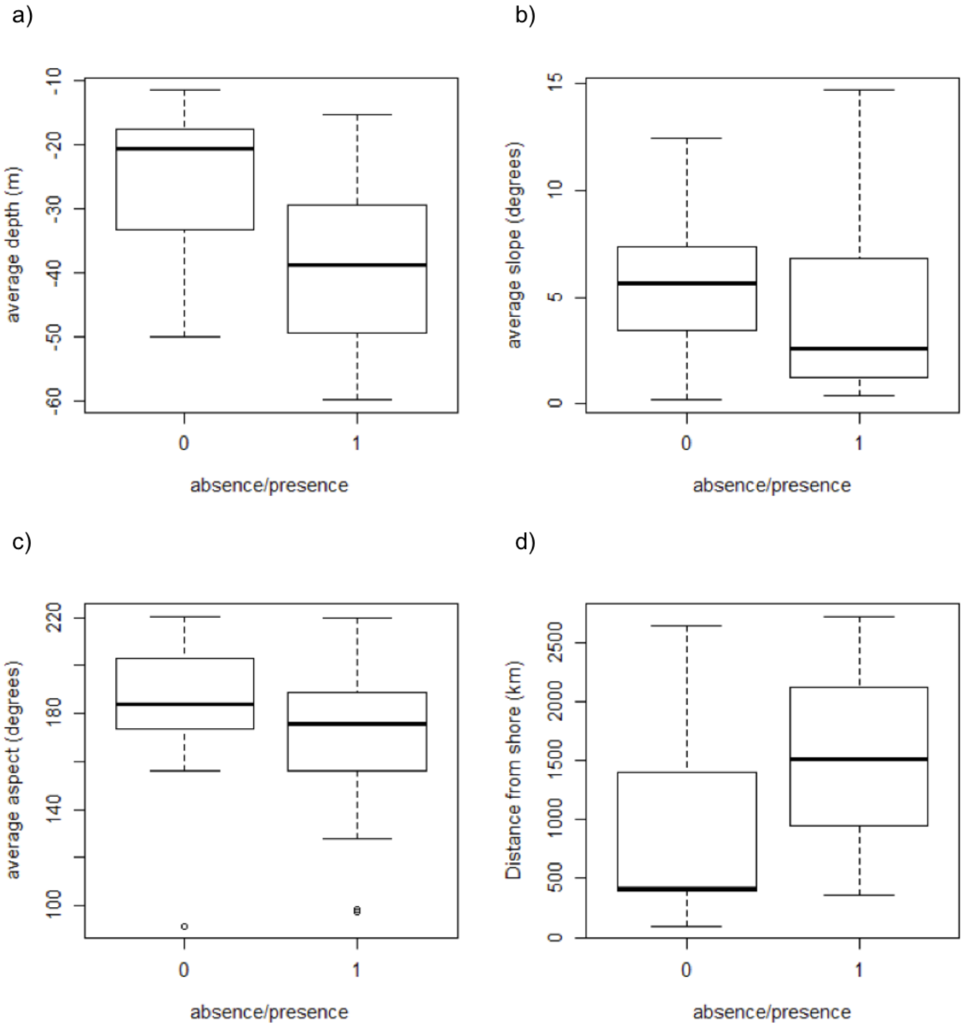


Figure 3.19: Exploratory boxplots showing median (black line), quantiles (box) and range (whiskers) of the (a) average depth, (b) slope, (c) aspect and (d) distance from shore for grid cells grouped by the absence (0) or presence (1) of porpoise sightings. Data from the SWSW effort based survey, 2007-2010.

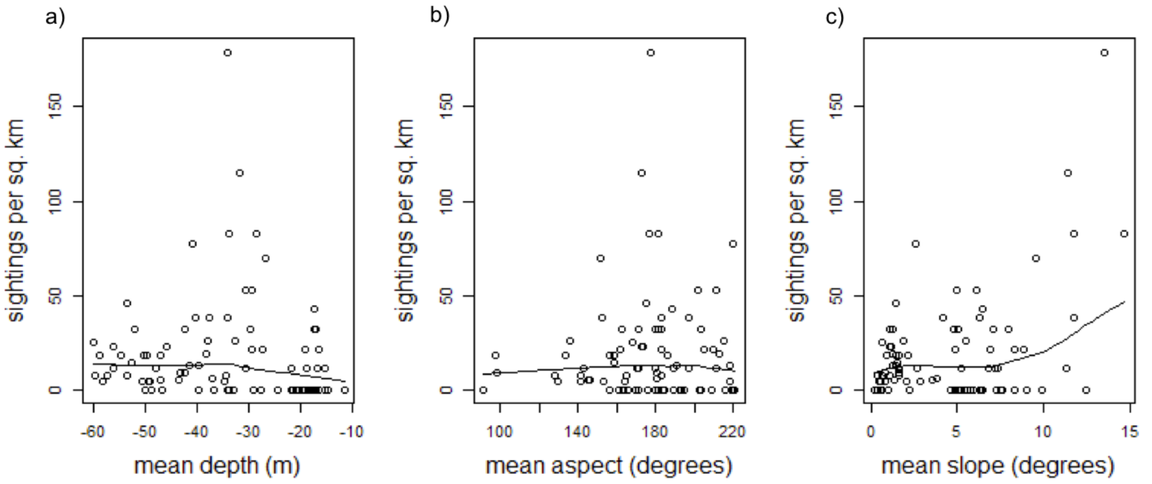


Figure 3.20: Exploratory scatterplots showing relationships between static bathymetric variables and sighting density of harbour porpoises with each grid cell (N = 85). LOESS smoothers, with default bandwidth, were added to enhance visual interpretation. Sighting data from the SWSW effort based survey, 2007-2010. Bathymetric data from the CCO and UKHO data.

The data on sightings per km^2 indicate that there were lower numbers of sightings in the shallowest depths (0 - -15 m) and highest numbers in depths between -20 – -40m (figure 3.20-a). Higher numbers of sightings per unit area were recorded in cells with steeper slopes (figure 3.20-c). The relationship with aspect is not obvious, but there may be a trend towards more sightings in cells with a more southerly aspect (figure 3.20-b).

Statistical modelling of gridded spatial data: Sightings per grid cell, corrected for area, with static physical covariates.

The effect of static bathymetric variables on the spatial distribution of porpoise sightings per grid cell (Jul – Oct, 2007-2010) was modelled using a GAM with negative binomial error distribution (logit-link) and an offset to correct for the different area within each grid cell. The variance in the sightings data is much greater than the mean value (19.79 and 3 respectively); therefore attempts to model the data with Poisson and quasi-Poisson distributions met problems due to overdispersion. As a result a negative binomial distribution was selected, which corrects the standard errors of the model to account for the heterogeneity of the data.

Initial exploration of co-linearity between the proposed model covariates showed that the average depth within each grid cell was highly co-linear with the cell's distance from shore (Rho = 0.90), so the predictor variable distance-from-shore was removed from the model covariates (as depth was considered to be the more biologically relevant variable). After removal of correlated variables, the remaining candidate covariates for model selection were average depth, average slope, and average aspect, with interaction terms specified for slope:depth and slope:aspect

The model selected through stepwise covariate addition retained only the slope and depth predictor variables (table 3.5). After the second round of covariate selection, no further terms were found to be significant. The model that was selected explains 42.5 % of the deviance in the relative density of harbour porpoise sightings within the SWSW survey area July-Oct, 2007-2010. Depth was the most significant predictor variable (p = <0.001), explaining 22.7 % of the deviance, with slope explaining an additional 19.8 % (p = 0.001) (table 3.5). The smooth functions for slope and depth from the final model indicate that porpoises were more frequently seen in grid cells with high average slope and intermediate to high average depth (figure 3.21).

Table 3.5: Results of stepwise forwards model selection on GAM for number of porpoise sightings per grid cell. Variables are shown in the order of selection, with terms being selected sequentially based on the amount of deviance explained and reduction in AIC score (AIC Δ) compared to the previous model (with the starting AIC score given in bold). All selected terms were significant to at least p = 0.05. The degrees of freedom of the estimated smooth functions are given in parentheses. Modelled data are 255 sightings of harbour porpoise made during the SWSW effort-based visual monitoring survey from 2007 – 2010; summarised over 85 grid cells.

Order	Smooth (df)	% Deviance	AIC Δ
1	s(Av_Depth, 1.92)	22.7	**360.98**
2	s(Av_Slope, 1.00)	+ 19.8	-23.32
Final	**s(Av_depth) + s(Av. Slope)**	**42.5**	**337.66**

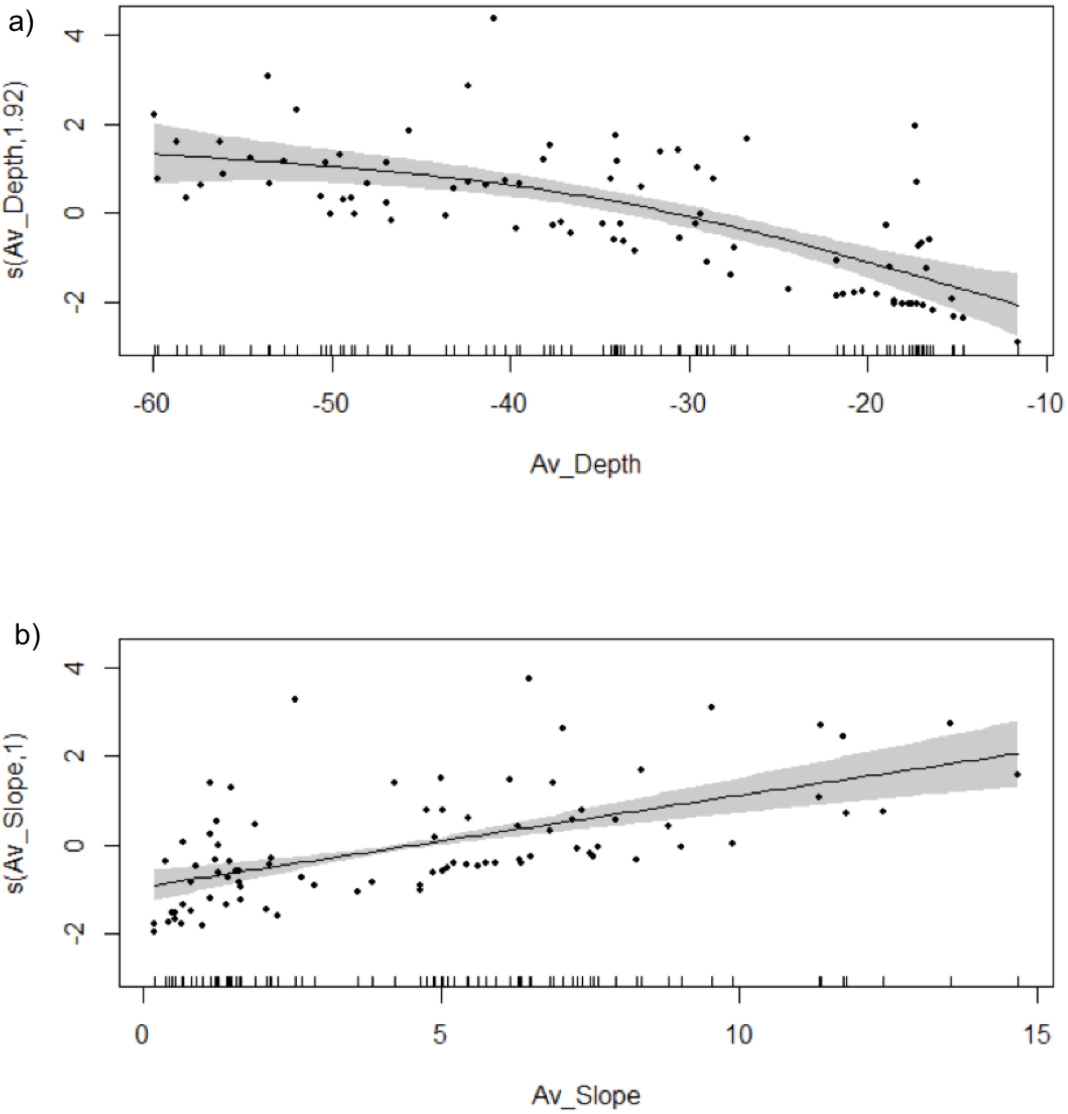


Figure 3.21: Harbour porpoise sightings modelled as (a) smooth function of average depth within grid cells and (b) average slope within grid cells. Shaded areas represent 95 % CIs. Residuals (Pearsons) are plotted as filled black circles. A rug plot with the actual data values is also shown.

Model checking plots are shown in figure 3.22; the quantile plot suggests that the negative binomial distribution is appropriate for the data because the deviance residuals lie close to the straight line of the expected quantiles. The residual plot shows that the variance structure of the model is accounting for heterogeneity in the data. The residual histogram is slightly bi-modal, which suggests that the model is both over and under-predicting response values more than would be expected, potentially because an important bimodal predictor variable was not included in the model. The response ‘vs’ predicted values of the response variable (sightings per grid square) show a positive linear relationship with some scatter, but nothing that is considered to be problematic.

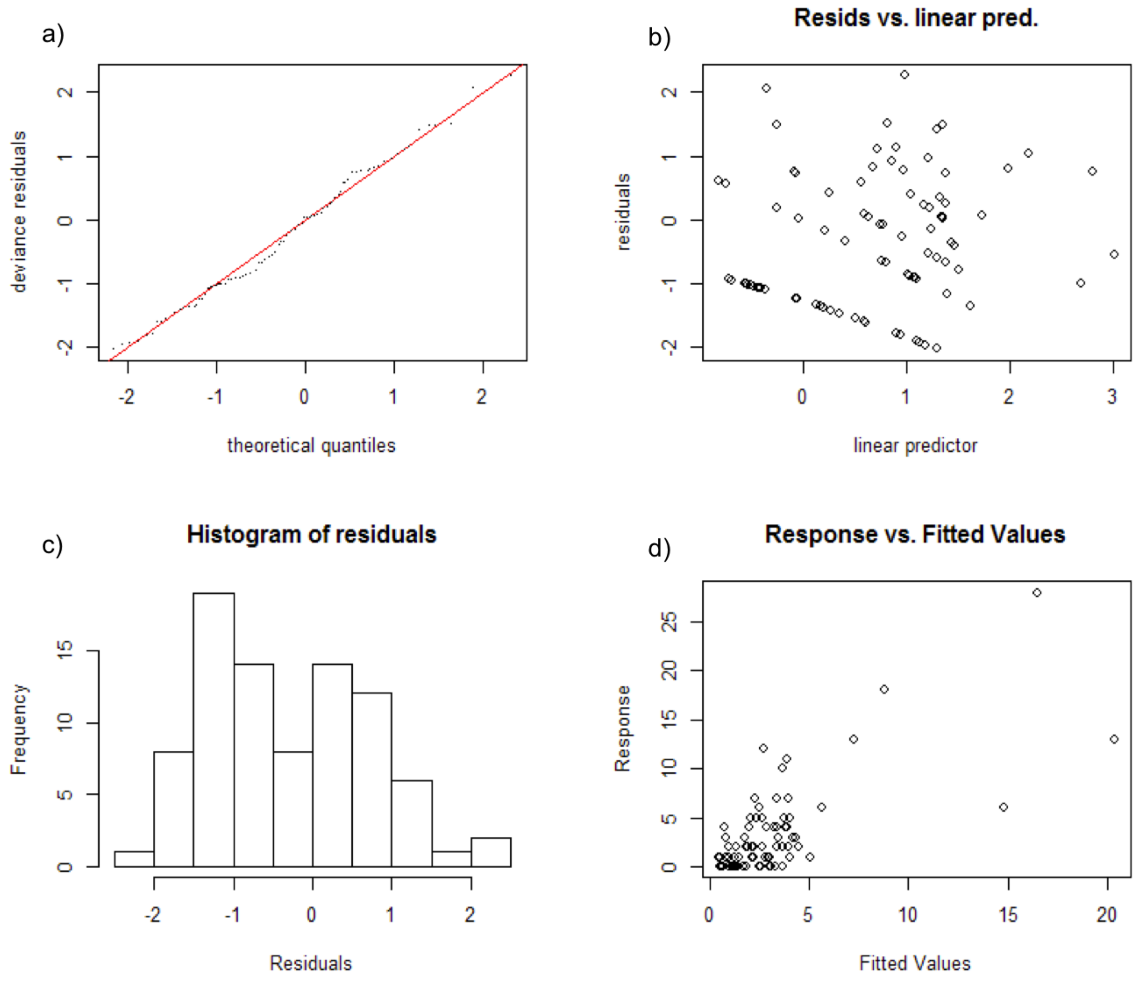


Figure 3.22: Model checking plots output from the final negative binomial GAM for harbour porpoise sightings modelled as a function of average depth and slope within grid cells. (a) Deviance residuals (black dots) plotted against theoretical quantiles for a negative binomial distribution (red line). (b) Pearson residuals against the linear predictor (on the log scale). (c) Frequency density of Pearson model residuals. (d) Observed response values (sightings per grid cell) against model predicted response values.

Model predictions of the density of porpoise sightings per grid cell (figures 3.23 and 3.24) follow the general pattern in the observed data (figure 3.15), with the poorest performance in cells with the highest and lowest sighting values. The maximum over prediction by the model for the sightings km^1 within a grid cell is + 13.9 and the maximum under prediction is - 6.7 sightings per km. The average difference between the model-predicted sightings and the observed sightings within each gird cell is 0.6 sightings.

Note the high predicted sighting values in the first band of the radial grid (closest to the survey watchpoint) in figure 3.24. These are likely to be as a result of the high slope in these cells (figure 3.17), which is clearly not being successfully offset by their shallow depth in the model prediction.

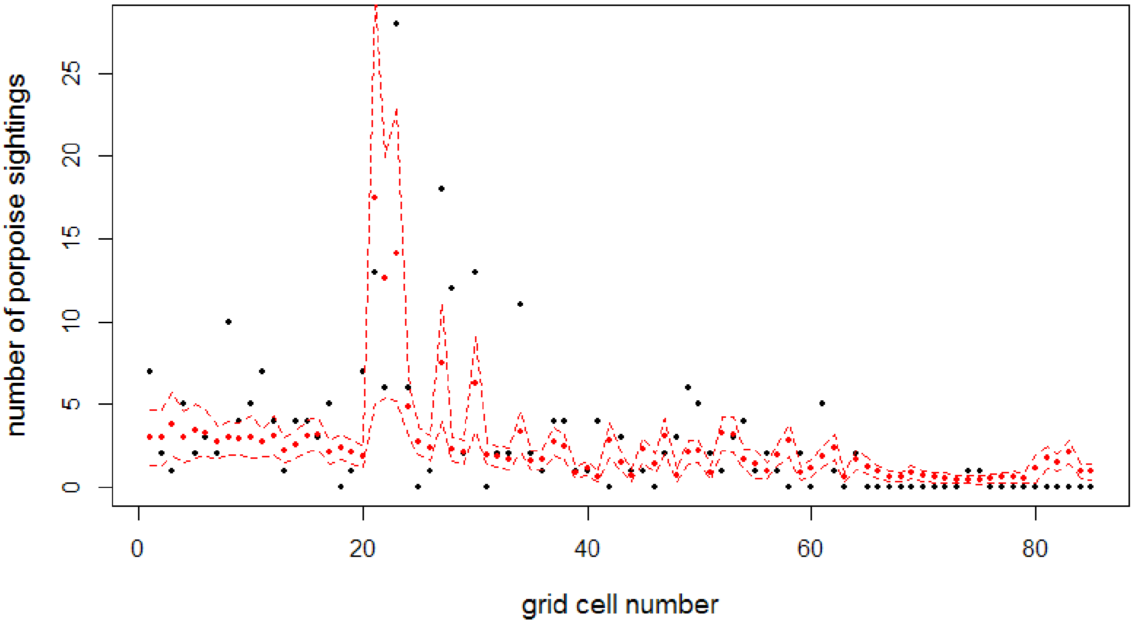


Figure 3.23: Negative binomial GAM model performance plot showing observed (black filled circles) and model predicted data (red filled circles) for area corrected sightings of harbour porpoise per grid cell. Red dashed lines indicate 95 % CIs for model predictions.

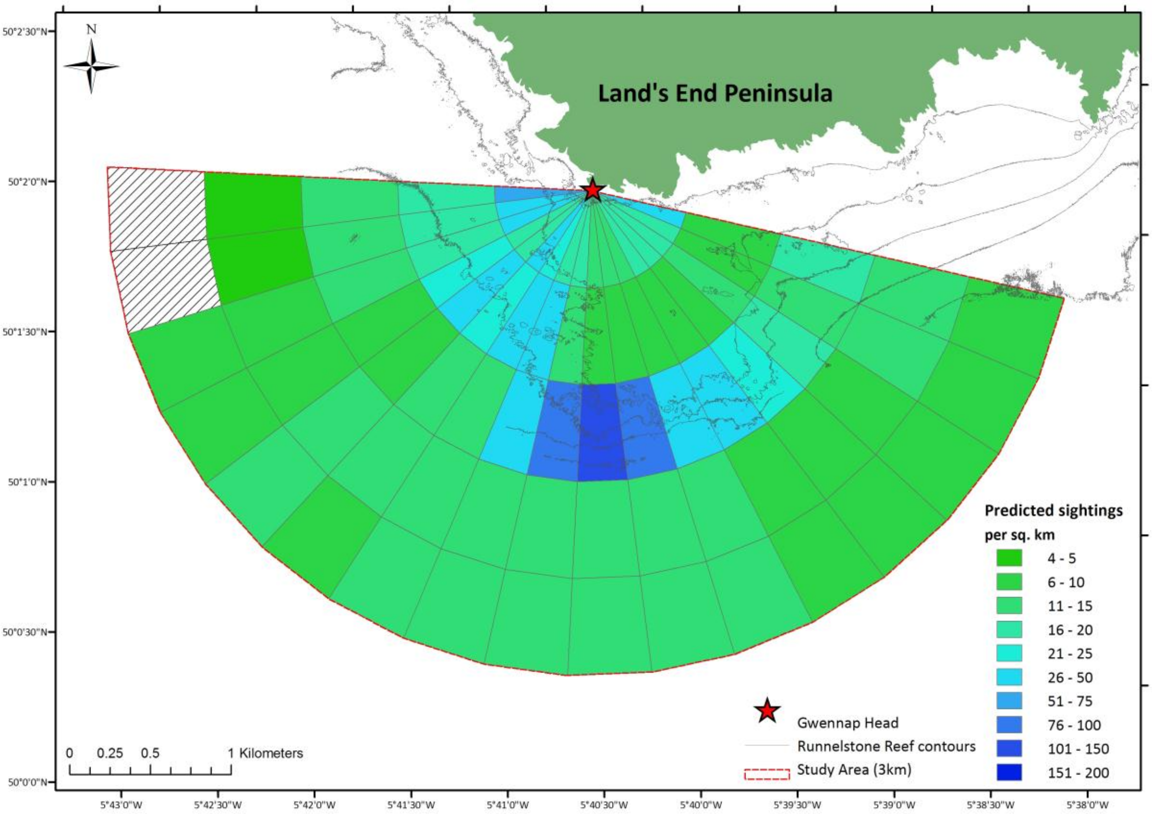


Figure 3.24: Negative binomial GAM model predictions of porpoise sightings per grid cell (corrected for area), based on the average depth and average slope values of each cell.

The performance of the model was further examined by mapping the difference between the observed data and the model predictions based on the static covariate values of depth and slope within each grid cell (figure 3.25). The difference was calculated by observed sighting values minus predicted sighting values for each grid cell. The model has a tendency to under-predict sightings in grid cells where the highest number of sightings were observed, indicating the high variance in the sightings data is not fully captured by the model.

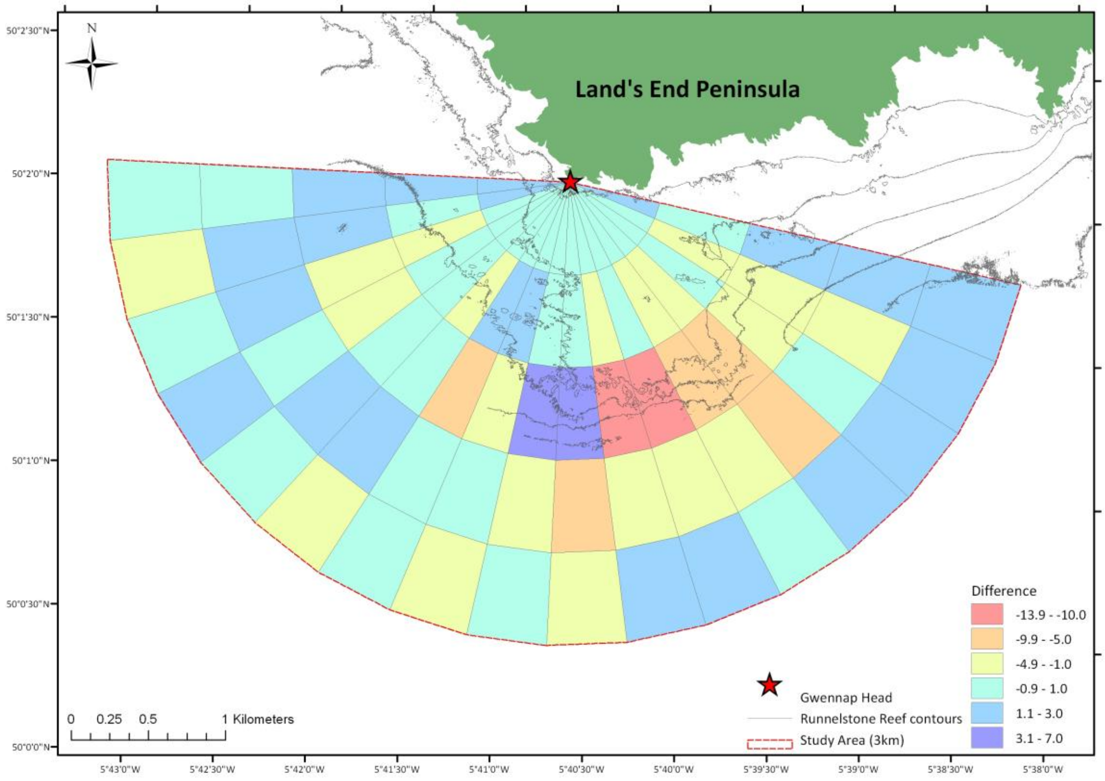


Figure 3.25: Model performance map showing the difference between observed and model predicted porpoise sightings within each grid cell (based on the predictions from negative binomial GAM with depth and slope covariates and an area offset). Blue cells represent model under-prediction; cream indicates approximately correct prediction (error of ± 1 sighting); red cells show where the model over predicts. Based on 255 harbour porpoise sightings, 2007 – 2010.

3.3.2 Temporal distribution of harbour porpoise sightings in the SWSW survey.

Harbour porpoises were sighted on 135 of the 372 days where survey effort was collected between 15th July and 15th Oct 2007-2010. The highest numbers of sightings and animals were recorded in 2009. This is also the year with the highest sighting rate, when amount of survey effort is taken into account (table 3.6).

Table 3.6: Summary of the filtered hourly harbour porpoise sightings from the SeaWatch SW survey, 2007-2010. 'Positive' hours/days are the periods during the survey when a harbour porpise was recorded.

Year	Hrs obs	Sightings	Animals	Positive hours	% positive hrs	% positive days
2007	608	86	202	69	11.35	35
2008	538	124	256	89	16.54	34
2009	569	128	306	103	18.10	42
2010	698	81	219	64	9.17	33
All Years	**2413**	**419**	**983**	**325**	**13.47**	**36**

Single animals were the most frequently observed (171 sightings out of a total of 419). The average pod size per sighting was 2.33 animals (SD = 2.02), with a maximum pod size of 20 animals, recorded on two dates, 08/09/2007 and 18/09/2010.

Sea state conditions, recorded hourly from the watchpoint, had a significant effect on the number of harbour porpoise sightings recorded. The survey data shows that as sea state increases, there is a corresponding decrease in the rate of sightings per hour of effort. The highest sighting rate was 0.48 porpoises per hour during in sea state 0. This reduced to 0.38 in sea state 1 and 0.15 in sea state 2. In sea state 3, the sighting rate was only 0.08, which represents a 6-fold decrease compared to sea state 0. These results indicate the importance of recording sea state and accounting for it in analyses of porpoise monitoring data.

3.3.2.1 Analysis of temporal patterns in the sightings data.

The survey runs for a 14-week period each year from 15th July to 15th October. The amount of effort during each week of the survey changes because of differences in day-length. After correction for effort (number of hours observed by week of the survey), late -September to mid-October (weeks 11 – 14) is the period with the highest number of harbour porpoise sightings (figure 3.26). This also corresponds with an increase in the number of animals per group seen later in the survey.

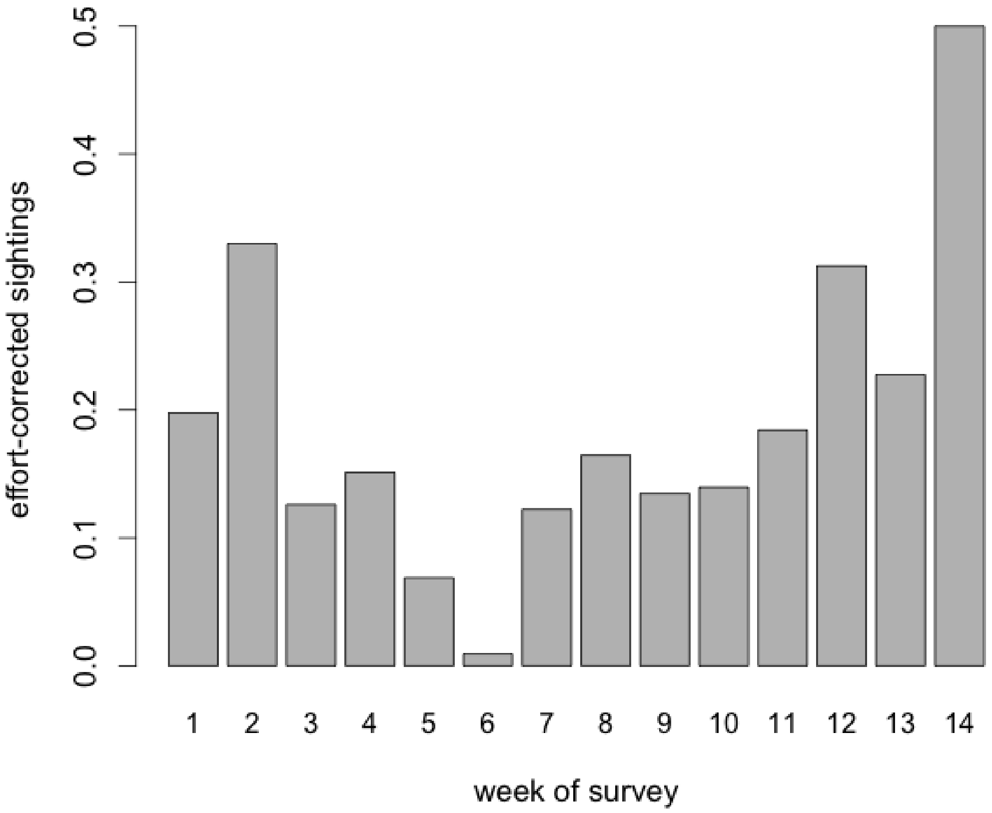


Figure 3.26: Number of harbour porpoise sightings by week of the SWSW survey (15th July - 15th Oct, 2007-2010). Sightings were effort-corrected by the number of hours observed in each week across all 4-years of the survey.

Sightings per day (corrected for the hours of effort each day) are shown in figure 3.27. The average number of effort-corrected sightings per day across all four years was 0.123 (SD = 0.25). There was significant autocorrelation in the raw daily sightings at a lag of two-days in 2007 and 2009 and one-day in 2008, indicating that the numbers of sightings made on consecutive days were generally not independent (figure 3.28).

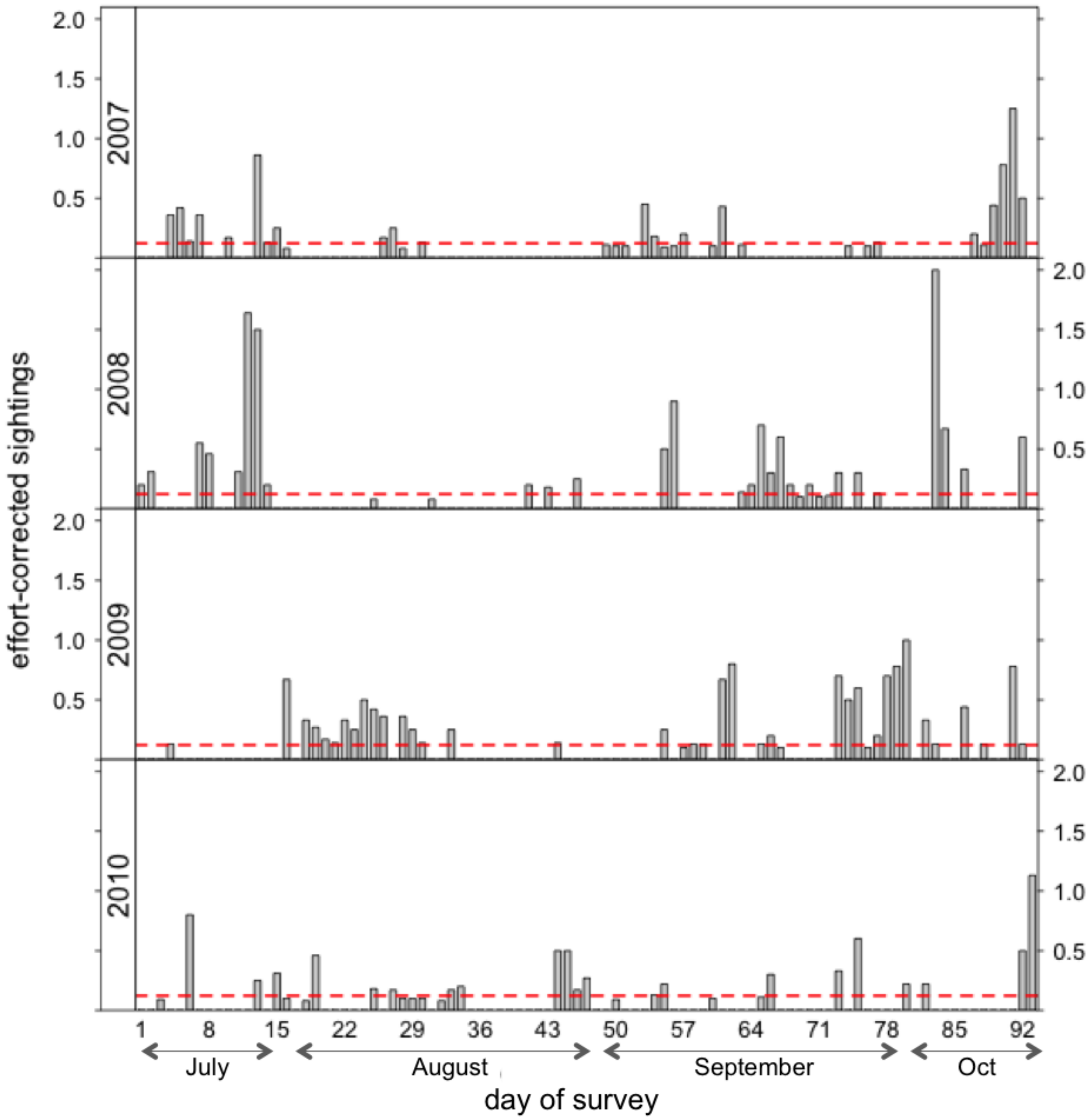


Figure 3.27: Harbour porpoise sightings per day, corrected for hours of survey effort. 93 days of data per year, from 15thJuly to 15th October 2007 - 2010. The red dashed line shows the multiyear mean value for daily effort-corrected sightings (0.123).

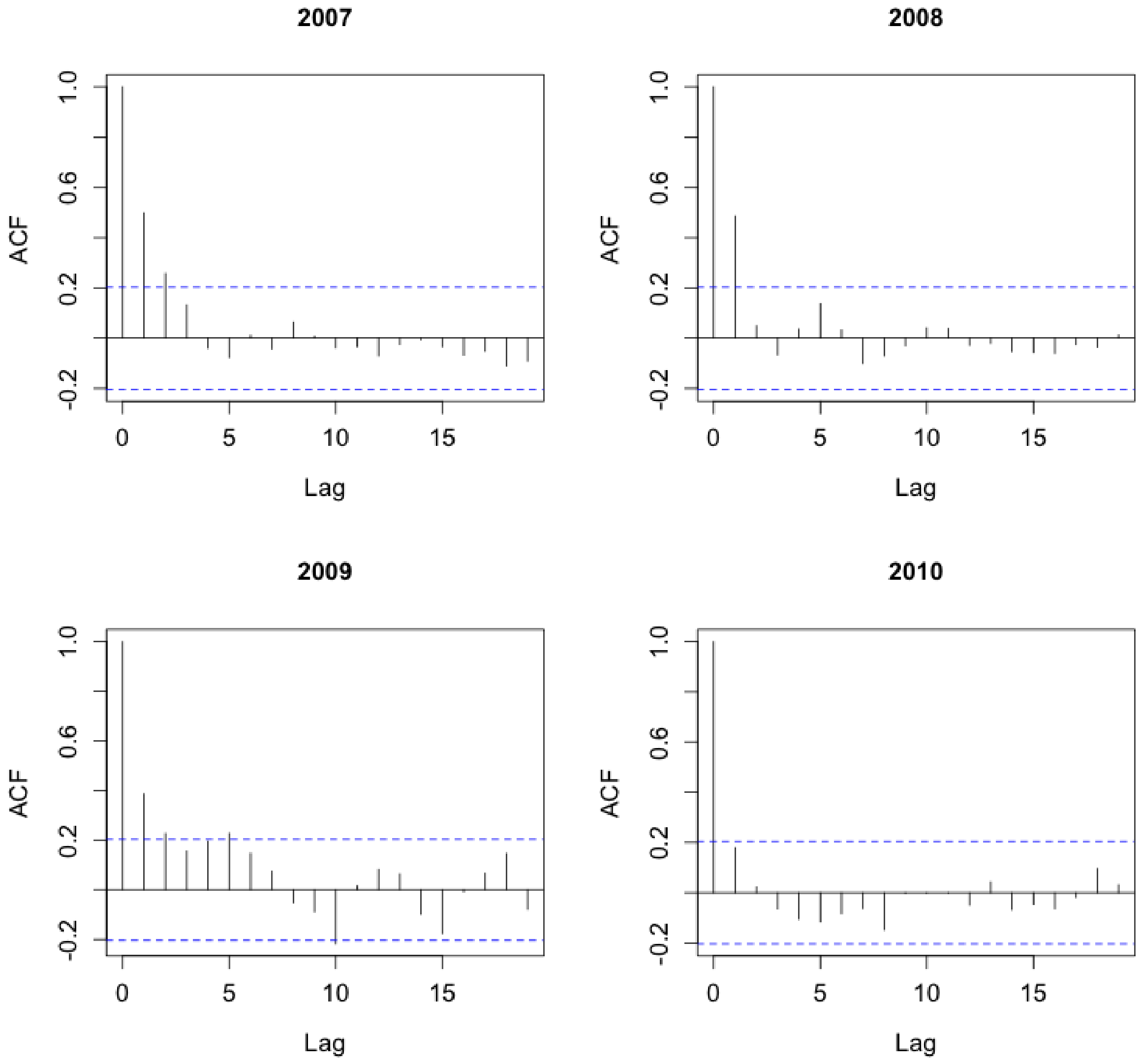


Figure 3.28: Daily sightings autocorrelation function (ACF) plots for each year of data (2007 - 2010), N = 93 days per year. Lag periods are days and significance limits (p = 0.05) are indicated by dashed blue lines.

Sightings data were summarised into an hourly dataset (N = 2413 hours) for the full survey period (15th July – 15th Oct 2007-2010), of which 325 hours were positive for porpoise sightings giving an overall probability of 0.135 of seeing a harbour porpoise during any hour of the filtered survey effort across the four-year survey period.

Harbour porpoise sightings plotted by hour of the day (figure 3.29) indicate that there is a higher chance of sighting a porpoise in the survey area during the morning session (prior to the 1200 – 1400 hrs break) than the afternoon session. The highest numbers of sightings were recorded between 0900 and 1200 hours (figure 3.29). The histogram of sightings by hour of the day includes only periods that were observed regularly (N > 100), therefore the results were not affected by reduced effort during early and late hours, which were only observed during the longest days in July.

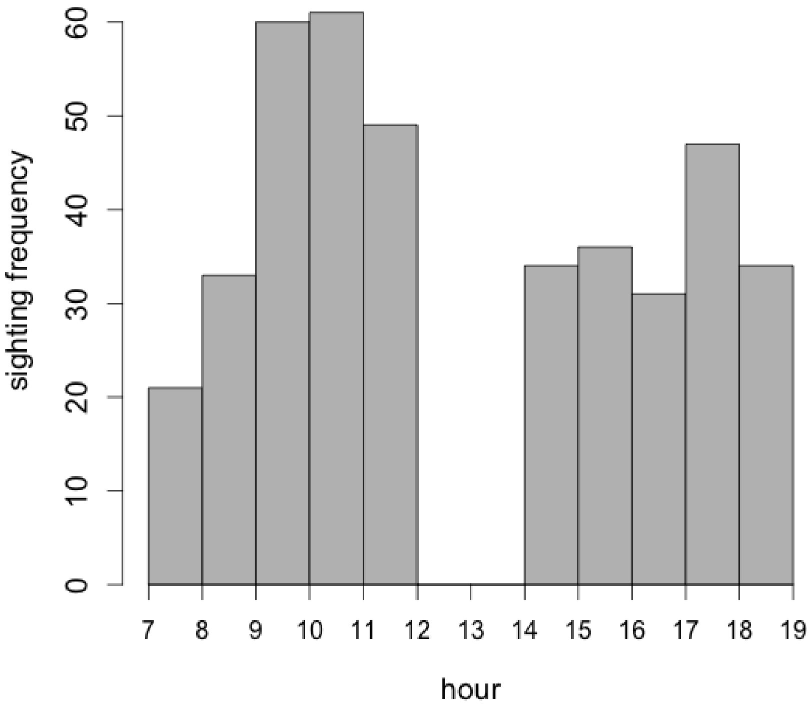


Figure 3.29: Harbour porpoise sighting frequency by hour of the day. Filtered SeaWatch SW data from 2007 - 2010 (N = 414 sightings). Only sightings made during hours with survey effort of N = >100 were included.

As mentioned in the methods, the tidal flow pattern at the study site is complex and although the tide rises and falls semi-diurnally, there are not equal periods of easterly (flood) and westerly (ebb) flow as may be expected in the Channel. The UKHO tidal charts are not accurate enough to indicate the very localised, topographically driven, flow patterns at the site, and there is some concern that the modelled data provided by the POLPRED CS20 model may also be too broad-scale to represent these patterns correctly. The information in table 3.7 describes the predominant direction of flow across the survey area for each hour of the tidal cycle and was derived from information provided by local fishermen and the National Coastwatch Institute (NCI) on Gwennap Head (see also figure 2.6). On the basis of this data, four groups representing the direction and speed of flow within the survey area were defined (table 3.7), and these were used to investigate possible tidal effects on the number of porpoises seen within the survey area.

The red line in figure 3.30 shows the smoothed frequency density of harbour porpoise sightings with respect to tidal period (hours relative to HW, where 0 = HW) and indicates a bimodal distribution, with lowest sightings associated with the time of HW (N = 419 sightings, 2007-2010). Higher numbers of sightings were generally recorded during westerly flows, which are experienced from 2 hours after HW until approximately 2 hours before the following high water. The blue line on figure 3.30 contextualises the pattern in the distribution of porpoise sightings by showing the smoothed frequency density of the full survey effort (hours observed) relative to HW. This indicates that the pattern in sightings (red line) is not simply a function of the survey effort, which is evenly spread across the tidal cycle (blue line). There were higher numbers of sightings than would be expected (according to the survey effort expended) in the period from two hours after HW until approximately low water (HW+6/-6 on figure 3.30). Between HW – 4 and HW + 2 the numbers of sightings were lower than would be expected if tide was not having any influence on the porpoise distribution and sightings were randomly distributed through the tidal cycle (figure 3.30, table 3.8).

When the binary presence-absence data for porpoises during each hour of survey effort are examined with respect to tidal flow conditions, the results support the porpoise abundance data shown in figure 3.30. Porpoise positive hours were more frequently recorded during westerly flows (groups 1 and 2 had sighting probabilities of 0.17 and 0.14 respectively) than in easterly or slack flows (groups 3 and 4, which both with a sighting probability of 0.11).

Table 3.7: Description of local flow pattern within the survey area over a full tidal cycle. These patterns have been inferred from local scale tidal flow schematics provided by the local National Coastwatch Institute (NCI); drawn originally by local fishermen (figure 2.6).

Tidal period	Flow characteristics	Flow group
HW-6 (LW) to HW-5	Strong westerly flow (full strength)	1
HW-5 to HW-4	Westerly flow gradually slowing down (moderate)	2
HW-4 to HW-3	Westerly flow gradually slowing down (moderate)	2
HW-3 to HW-2	Westerly flow gradually slowing down (moderate)	2
HW-2 to HW-1	Slackening flow, tide starting to turn from W to E	3
HW-1 to HW	Strengthening easterly flow	4
HW to HW+1	Strong easterly flow (full strength)	4
HW+1 to HW+2	Strong easterly flow (full strength)	4
HW+2 to HW+3	Slight slackening of flow speed and tide quickly turns	3
HW+3 to HW+4	Strong westerly flow (full strength)	1
HW+4 to HW+5	Strong westerly flow (full strength)	1
HW+5 to HW+6 (LW)	Strong westerly flow (full strength)	1

Table 3.8: Observed and expected harbour porpoise sighting frequencies for each of the four tidal flow groups (N = 419), with discrepancy given in brackets in final column. Expected values are based on the total number of sightings weighted by the period that each flow direction occurs within a tidal cycle.

Flow group	Flow direction	Hours of flow	Expected sightings	Observed sightings
1	West (strong)	4	139	173 (+ 34)
2	West (moderate)	3	105	98 (- 7)
3	Slack	2	70	73 (+ 3)
4	East (strong)	3	105	74 (- 31)

The data in table 3.8 shows that more sightings than expected were recorded under strong westerly flows and less sightings than expected under strong easterly flows. The discrepancy between the observed and expected number of sightings are given in parentheses in the last column of table 3.8. A Pearson's Chi-squared test for count data was carried out on the frequencies of sightings made during each of the 4 tidal flow groups (data in table 3.8). The test compared expected sighting frequencies under each flow against the observed frequencies (taking account of the period that each flow direction is experienced within each tidal cycle). The results show that there are significant differences between the observed and expected counts, indicating tidal flow has some influence on the temporal distribution of porpoise sightings (Chi-squared value = 18.27, *p*-value = >0.001).

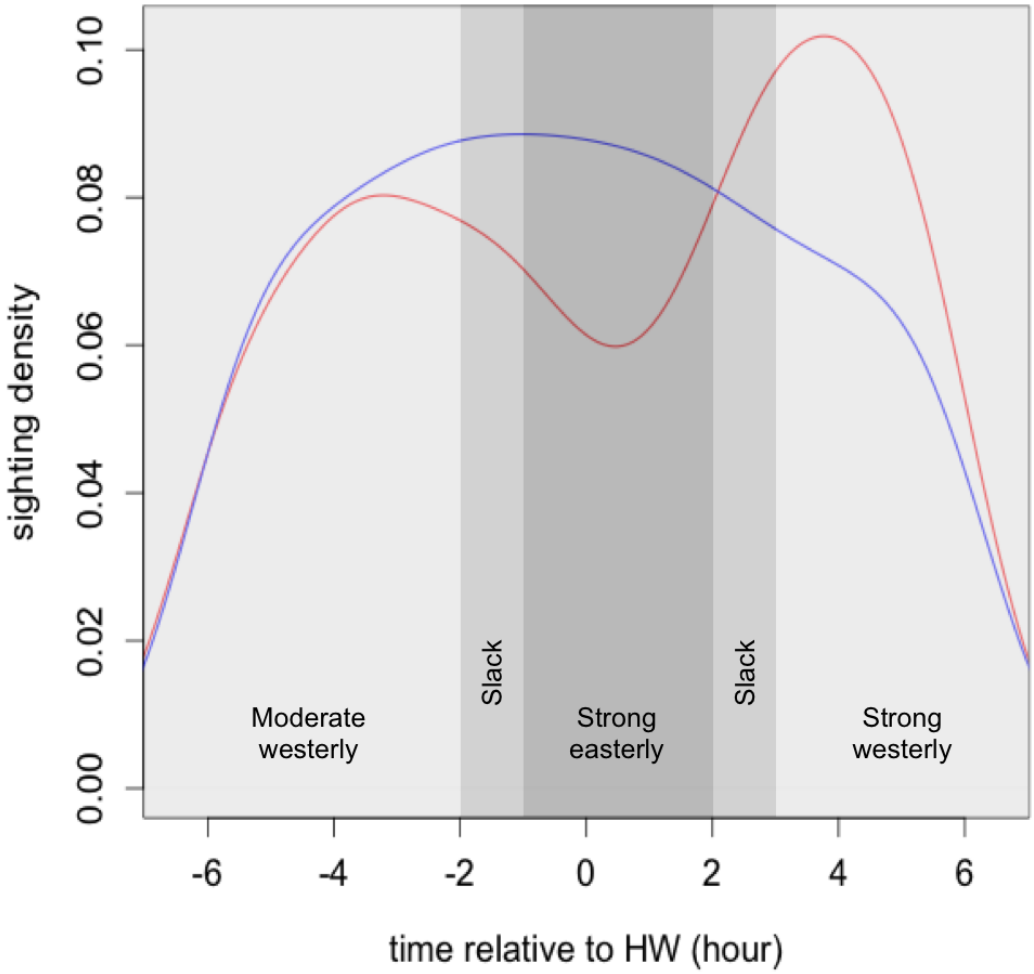


Figure 3.30: Smoothed frequency density of time of harbour porpoise sightings (red line, N = 419) and hours of survey effort (blue line, N = 2413) relative to high water time. Smoothing bandwidth = 1-hr. Shading indicates predominant flow direction within the survey area.

3.3.2.2 Modelling temporal patterns in the sightings data: the effect of dynamic oceanographic variables on the timing of harbour porpoise appearance.

The presence of porpoises within each hour of the filtered SWSW dataset was investigated using a binomial GAM with dynamic oceanographic and survey conditions included as model covariates. Initially the full four-year dataset was pooled and modelled together, but this was not very successful and the results suggested that year was a highly significant variable in the model. Therefore, each year of survey data was modelled separately to remove the additional noise introduced to the pooled sightings dataset as a result of inter-annual variation. A summary of the hourly presence/absence of harbour porpoises and the environmental variables used in the temporal model are given in table 3.9.

The data in table 3.9 show that there is high level of consistency in the average survey conditions across the four years of the survey. The tide direction data show some inter-annual variability, but the tidal flow speed is less variable through the years.

Boxplots for the effect of the continuous environmental variables on the presence-absence of porpoises per hour of the survey are shown in figure 3.31. These indicate that the average tide direction during absence hours is more easterly than in presence hours and the average tide speed is slightly lower, although both groups have similar variance (figure 3.31-a and b). The height of the tide is generally lower during presence hours than absence hours (figure 3.31-c) and the daily tidal range (m) for hours with presences is lower (figure 3.31–d). There is a high level of variability in the data associated with presence and absence hours, indicated by the wide and overlapping inter-quartile ranges of the two groups in the boxplots (figure 3.31).

Table 3.9: Summary table of environmental variables for each year of the hourly SWSW survey data, 2007 - 2010.

Parameter	2007	2008	2009	2010
Hours of effort	608	538	569	698
Number of sightings	86	124	128	81
Survey variables				
Glare (%)				
Range	0 - 100	0 - 100	0 - 100	0 - 100
Median (IQR)	10 (0-20)	10 (2-20)	10 (0-20)	10 (0-20)
Cloud cover (%)				
Range	0 - 100	0 - 100	0 - 100	0 - 100
Median (IQR)	30 (10-80)	60 (10-90)	60 (20-100)	60 (20-90)
Sea state (Beaufort)				
Range	0 - 3	0 - 3	0 - 3	0 - 3
Median (IQR)	2 (2-3)	2 (2-3)	2 (1-3)	2(2-3)
Tidal variables				
Tide direction (degrees)				
Range	2 - 358	7 - 357	6 - 358	1 - 356
Median (IQR)	142 (105 - 287)	169.5 (105 -287)	199 (106 - 286)	143 (105 - 286)
Tide speed (m sec^{-1})				
Range	0.06 - 1.39	0.06 - 1.34	0.06 - 0.76	0.07 - 1.46
Median (IQR)	0.53 (0.29 - 0.81)	0.5 (0.26 - 0.79)	0.49 (0.27 - 0.76))	0.51 (0.29 - 0.77)
Tide group				
Range	1 - 4	1 - 4	1 - 4	1 - 4
Median (IQR)	2 (1-4)	2 (1-4)	2 (1-4)	2 (1-4)
Tide Height (m from msl)				
Range	-2.54 - 2.83	-2.37 - 2.58	-2.57 - 2.77	-2.77 - 2.92
Median (IQR)	0.2 (-0.98 - 1.42)	0.14 (-0.98 - 1.37)	0.13 (-1.04 - 1.33)	0.18 (-1.03 - 1.32)
TtHW (hrs)				
Range	-6.17 - 6.33	-6.33 - 6.33	-6.25 - 6.33	-6.25 - 6.17
Median (IQR)	-0.25 (-3.0 - 2.91)	0.25 (-3.16 - 2.67)	-0.25 (-3.0 - 2.83)	-0.17 (-2.83 - 2.75)
Tide Range (m)				
Range	1.62 - 5.29	1.47 - 4.88	1.59 - 5.26	1.85 - 5.33
Median (IQR)	3.66 (2.92 - 4.12)	3.53 (2.89 - 4.25)	3.58 (2.62 - 4.13)	3.53 (2.78 - 4.09)
Temporal variables				
TODI				
Range	0.004 - 0.94	0.004 - 0.95	0 - 0.94	0 - 0.93
Median (IQR)	0.45 (0.3)	0.46 (0.3)	0.42 (0.3)	0.43 (0.3)
Hour (time)				
Range	0500 - 2000	0500 - 2000	0500 - 2000	0500 - 2000
Median (IQR)	1100 (0900 - 1600)	1100 (0900 - 1600)	1100 (0900 - 1600)	1100 (0800 - 1600)
Week (numeric)				
Range	1 - 14	1 - 14	1 - 14	1 - 14
Month (as factor)				
Range	7 - 10	7 - 10	7 - 10	7 - 10

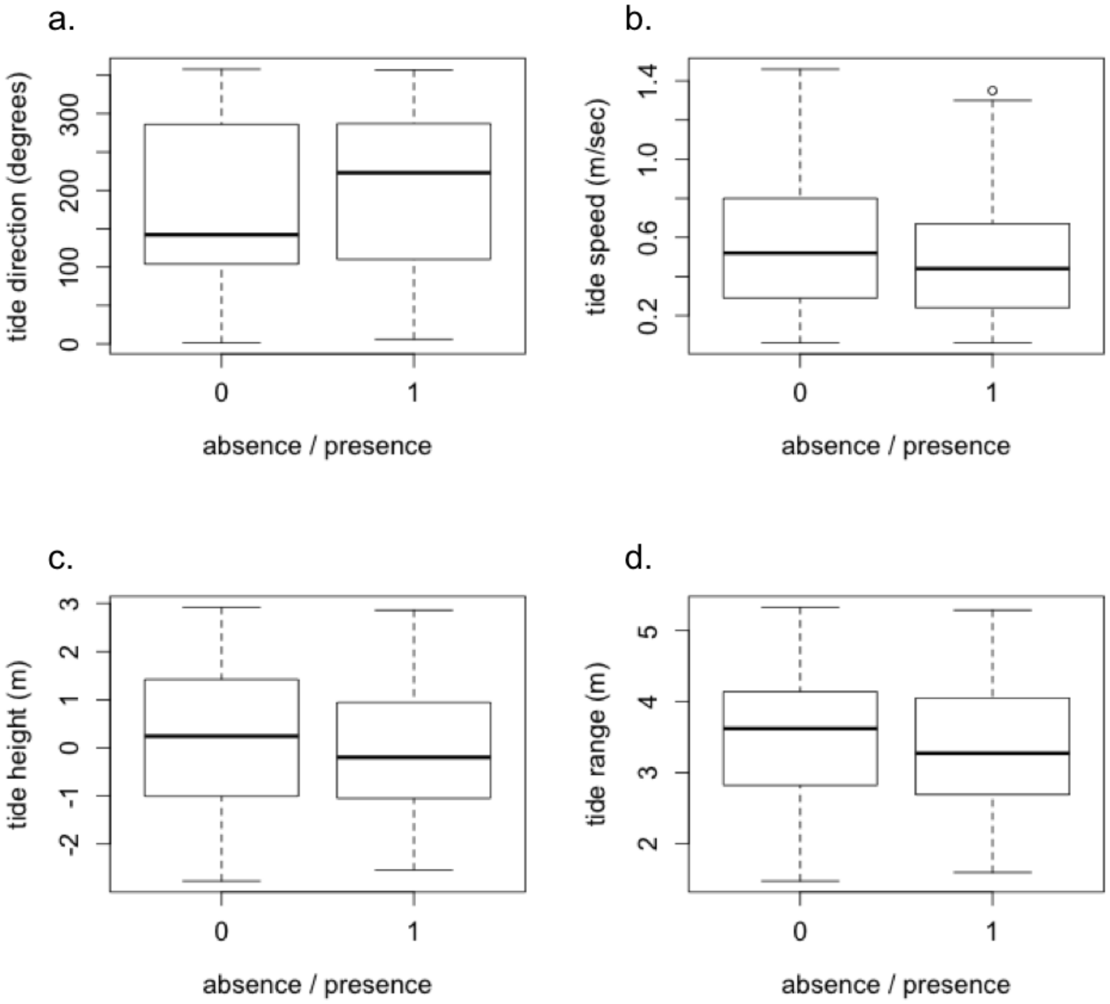


Figure 3.31: Boxplots for effect of continuous covariates on the presence and absence of harbour porpoise sightings in the SWSW dataset (2007-2010, N=2413 hours of effort): (a) tide direction, (b) tide speed, (c) tide height, (d) daily tide range. Thick dark lines show median values and box extents are the 25th – 75th quartiles. The full range of the data is indicated by the whiskers.

Temporal model results

The best models for each year of hourly presence-absence data are indicated in table 3.10, which gives the model-selected significant variables for each model.

The specific terms selected by each model are described in the following paragraphs, but in general there was little consistency between the covariates that were selected by GAMs for the individual years of sightings data (table 3.10). The most important predictor variable through all years was sea state, which was selected in the model containing all years of data and by three out the four annual data models. The seasonality in the sightings through the survey period is shown by the fact that all models containing either week or month (no models could contain both of these covariates as they were collinear, so after selection of one, the other was discarded).

Despite the evidence for an effect of hour of day, presented in figure 3.29, it seems that the inter-annual variability in the data overrides this signal; although is it shown to be significant when all years were modelled together (table 3.10).

Table 3.10: Summary of hourly porpoise presence-absence binomial GAMs for each year of the SWSW sightings data (2007 - 2010), and for all years of data combined. Parametric fits for factor variables (F) are represented by 'L' and smooth terms are represented by 'S (#)', where the number in parentheses is the degrees of freedom of the term. The superscripted numbers indicate the order of importance of the model terms, based on % deviance. Abbreviation definitions: BSS = Beaufort sea state; TtHW = time to HW; TODI = time of day index.

	Predictor variables												
	Survey variables			***Tidal variables***						***Temporal variables***			
Model	**BSS (F – 3)**	**Cloud (%)**	**Glare (%)**	**Tide dir.**	**Tide spd.**	**Tide height**	**TtHW**	**Flow group (F -4)**	**Tide range**	**Hour**	**TODI**	**Week**	**Month (F-4)**
2007	L^2	S^3 (2.53)										S^1 (2.78)	
2008								L^3	S^2 (3.43)				L^1
2009	L^1						S^3 (3.65)			S^2 (2.83)		S^4 (2.93)	
2010	L^1					S^4 (2.36)					S^4 (0.88)		L^2
All yrs	L^1					S^2 (1.8)				S^3 (2.8)			L^2

The best model for the 2007 porpoise presence-absence data explained 19.3 % of the deviance and contained 3 covariates, none of which were dynamic tidal variables. The most significant covariate was week of the survey (9 %), followed by sea state (6.33 %) and cloud cover (3.97 %). The smooth terms and model checking plots are shown in figure 3.32-a to d. The smooth for the effect of week on the presence of porpoises per hour shows the lowest sighting rates in weeks 4-10 (August and September) and the highest in July and Oct (figure 3.32-b). Moderate levels of cloud seemed to reduce the probability of sighting porpoises (figure 3.32-a) and hours when sea state was 0 had a significantly higher probability of being positive for porpoise sightings (figure 3.32-c). The model residuals did not show significant autocorrelation (figure 3.32-d).

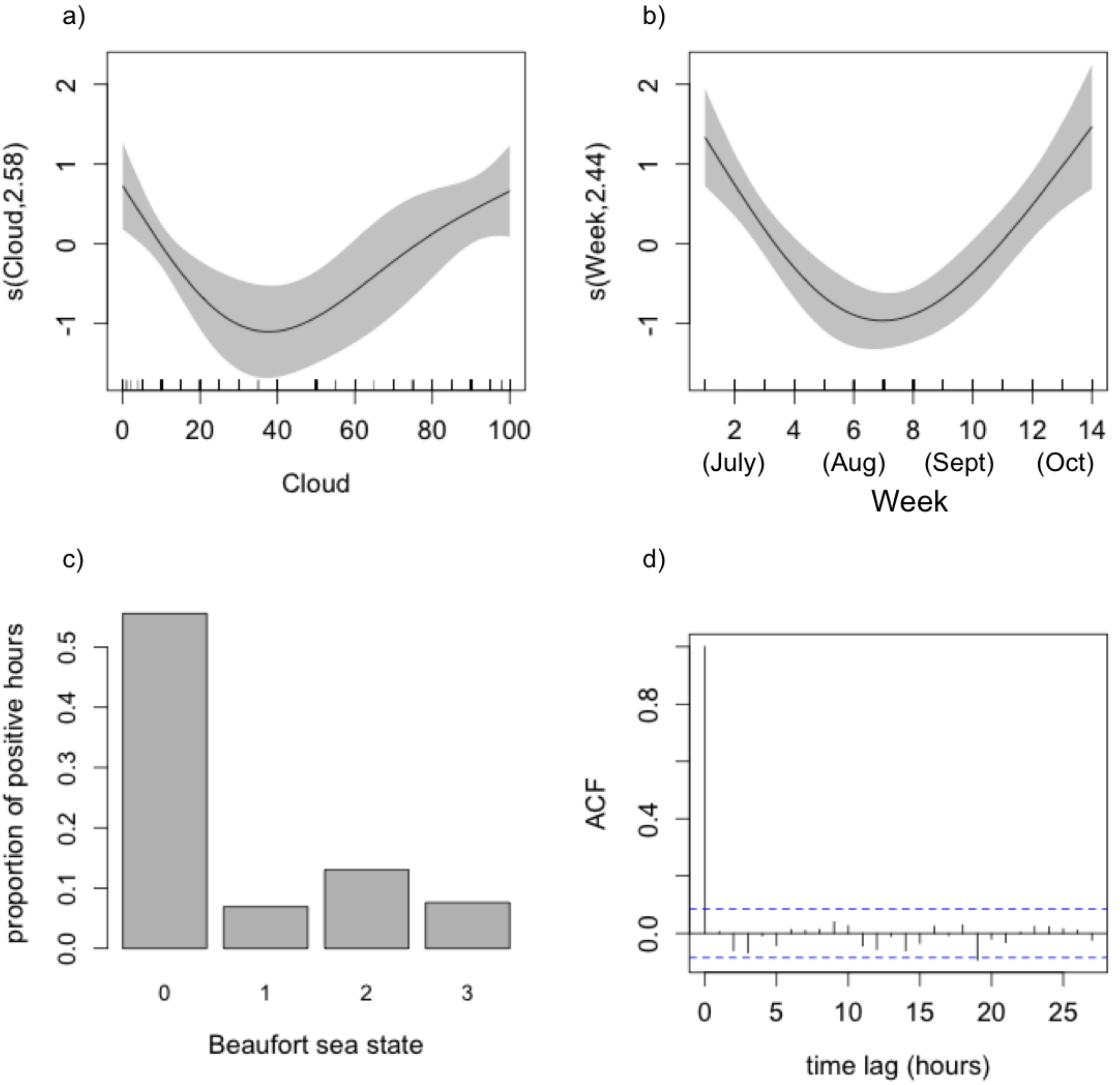


Figure 3.32: Porpoise presence-absence per hour of survey effort 2007 (N = 608) modelled as a GAM smooth function of (a) percentage cloud cover, (b) week of the survey. (c) Barplot of the proportion of positive hours recorded by the significant factor variable, sea state. The autocorrelation function plot for the binomial model residuals is given in (c), with significance thresholds (95 % CI) shown by dashed blue lines.

The model for the 2008 data on hourly presence-absence of porpoise sightings explained 19.4 % of the deviance and contained three covariates; month (13.6 %), tide range (4.2 %) and flow group (1.6 %). No survey variables were found to be significant predictors of porpoise presence. The smooth term for the modelled effect of tide range (the daily tide range in m) indicates that there were more presence hours in 2008 when the tidal cycle was nearing a spring (maximum range) or a neap (minimum range), with fewer presences in the middle of the spring-neap cycle (figure 3.33-a). Significantly lower numbers of porpoise-positive hours were associated with flow groups 3 (slack; model estimate 3 = -0.78, *p* = 0.05) and 4 (strong easterly; model estimate = -0.87, *p* = 0.05) than flow group 1 (strong westerly) (figure 3.33-b). The effect of month was significant, with higher probabilities of sightings in hours during July compared to August (model estimate = -3.1, p = < 0.001), September (model estimate = -1.34, p = <0.001) and October (model estimate = -1.1, p = 0.05) (figure 3.33-c). The residuals of the model do not show significant autocorrelation (figure 3.33-d).

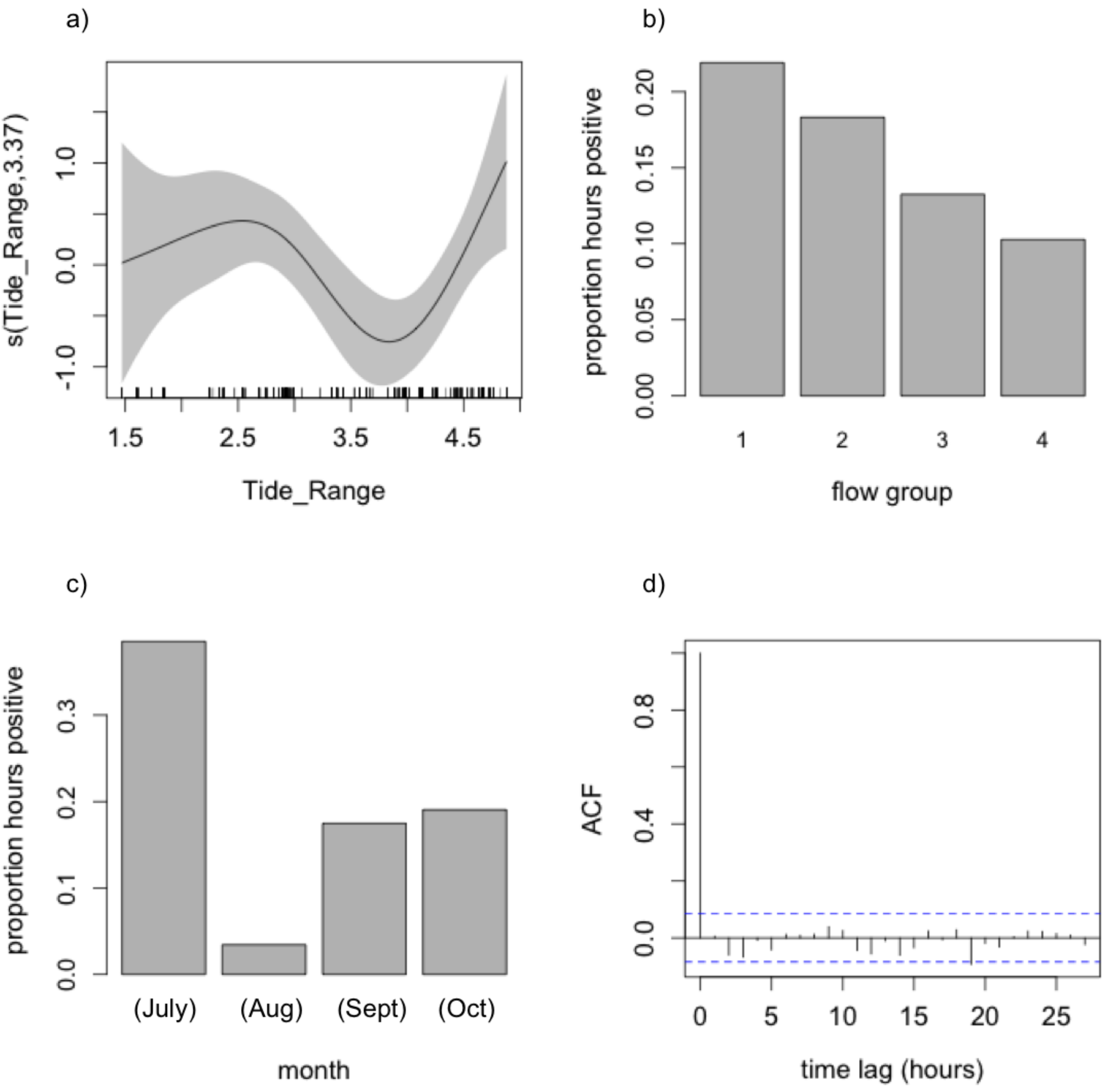


Figure 3.33: Porpoise presence-absence per hour of survey effort 2008 (N = 538) modelled as a GAM smooth function of (a) daily tide range in metres. Barplots of proportion of porpoise-positive hours recorded by the significant factor variables (b) flow group and (c) month of the survey. The autocorrelation function plot for the binomial model residuals is given in (d), with significance thresholds (95 % CI) shown by dashed blue lines.

The 2009 model for hourly porpoise presence/absence explains 20.7 % of the deviance and contains four covariates; sea state (8 %), hour (6 %), time to high water (TtHW) (3.7 %) and week (3 %). The smooth terms are shown in figure 3.34-a to c) and indicate a peak in presence hours between approximately 2-6 hours after high water, a trough in presences in the earliest hours of the survey (0600-0800) and highest probabilities of sightings in hours of effort in July/early August and October. There were significantly higher probabilities of sightings during hours when sea state was 0 or 1, than hours when sea state was 2 or 3 (figure 3.34-d). There is not significant auto-correlation in the model residuals (figure 3.34-e).

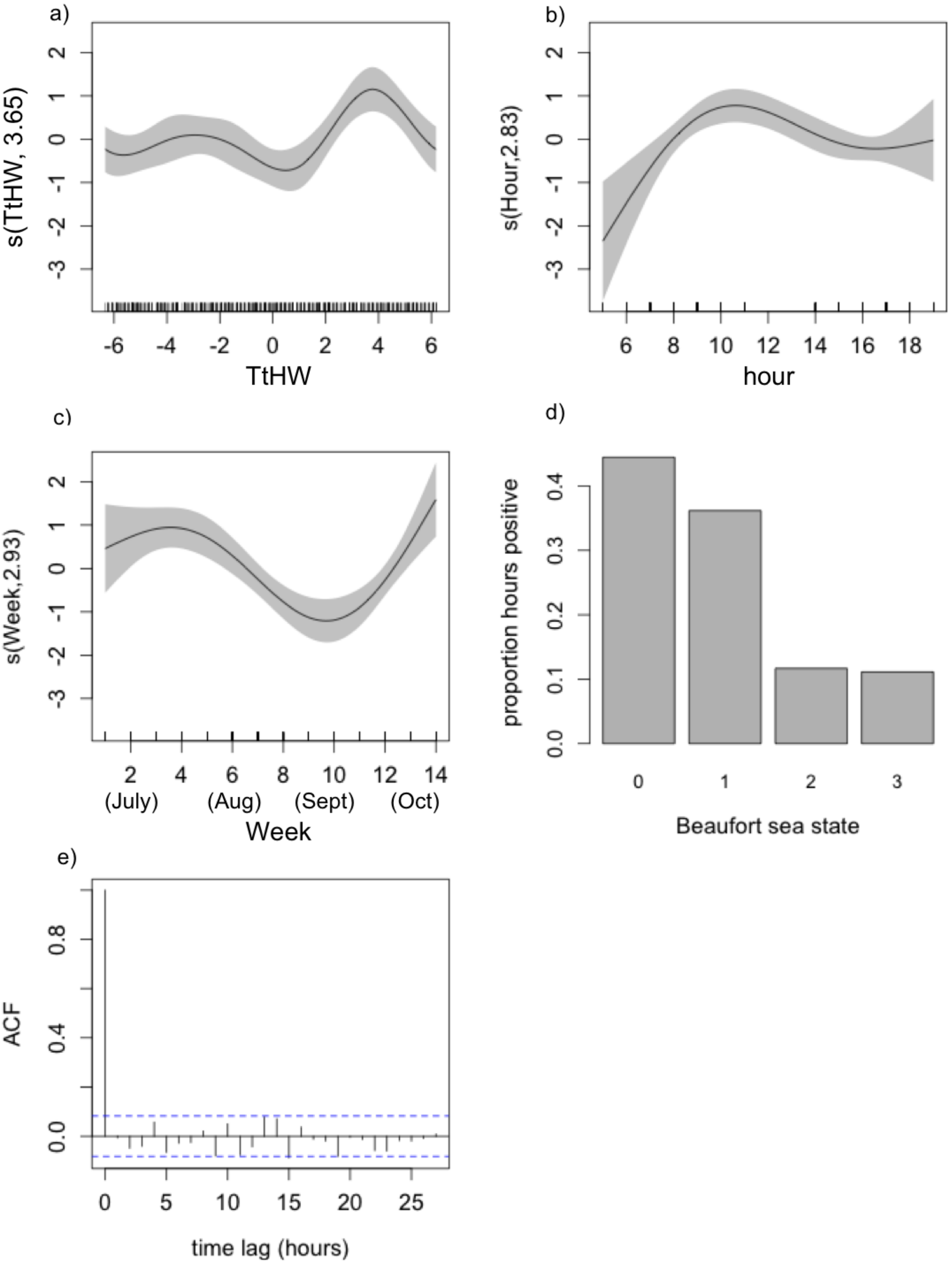


Figure 3.34: Porpoise presence-absence per hour of effort 2009 (N = 569) modelled as a GAM smooth function of (a) time to high water (TtHW), (b) hour and (c) week of the survey. (d) Barplot of the proportion of presence hours recorded by the significant factor variable sea state. The autocorrelation plot for the binomial model residuals is given in (e) with significance thresholds (95 % CI) shown by dashed blue lines.

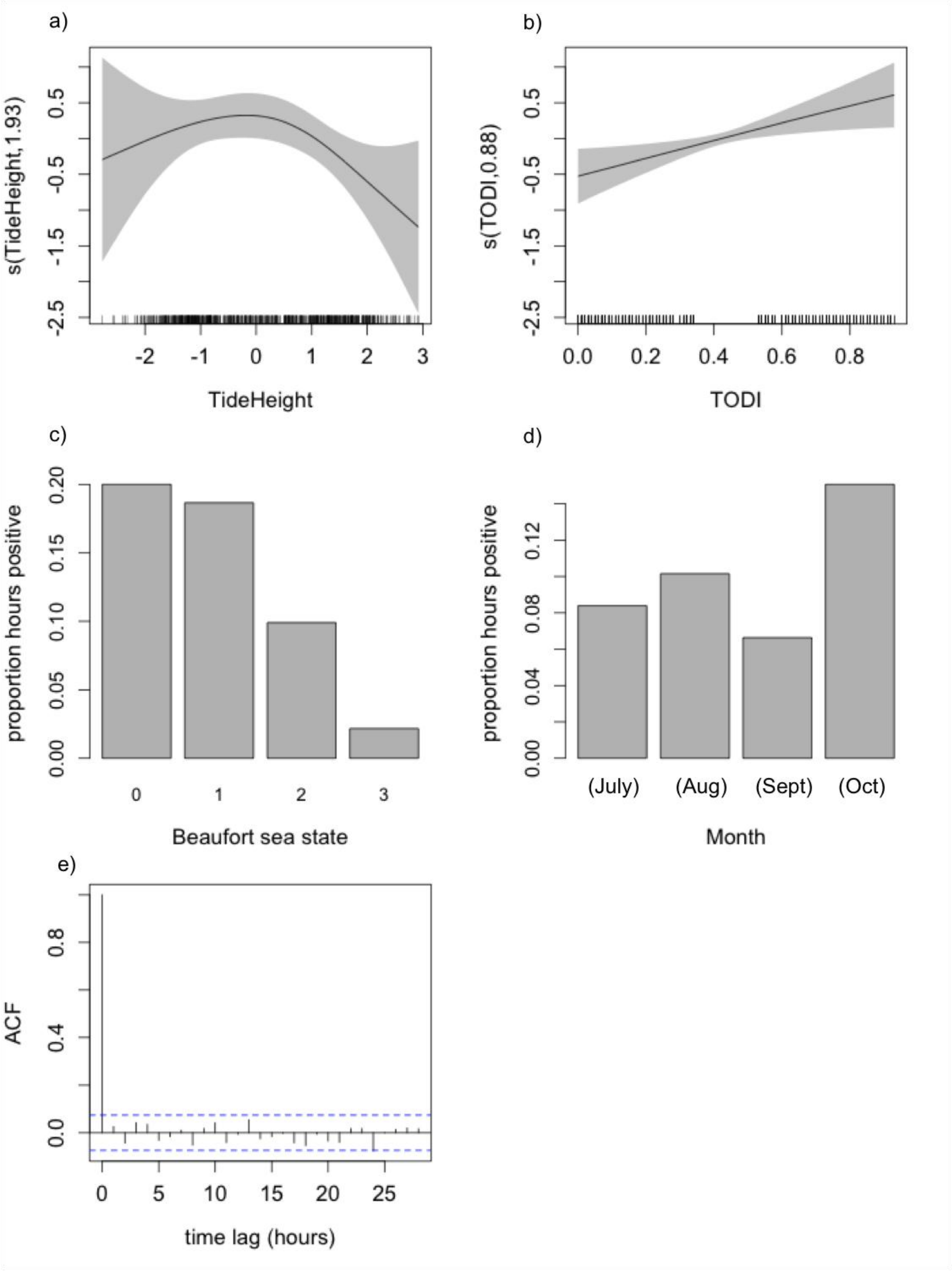


Figure 3.35: Porpoise presence-absence per hour of survey effort 2010 (N = 698) modelled as GAM smooth function of (a) tide height in metres and (b) time of day index (TODI). Barplots showing the proportion of presence hours recorded by the significant factor variables of (c) sea state and (d) month. The autocorrelation function plot for the binomial model residuals is given in (e), with significance thresholds (95 % CI) shown by dashed blue lines.

The GAM for the 2010 hourly presence-absence data explains 14.9 % of the deviance and contains 4 covariates; sea state (7.46 %), month (3 %), tide height (2.36 %) and TODI (2.08 %). The smooth term for tide height (figure 3.35-a) shows that porpoise positive hours were most likely to be recorded during mid-tide periods. There were also more presences recorded in hours later in the day (figure 3.35-b). Hours with sightings recorded were more likely during sea states 0 and 1 (figure 3.35-c) and more frequently in October than in other months of the survey (figure 3.35-d). The model residuals are not significantly auto-correlated (figure 3.35-e).

3.3.2.3 The effect of dynamic variables on the spatial distribution of harbour porpoise sightings data.

The maps in figure 3.36 show the relative density of harbour porpoise sightings by tidal flow group (as defined in table 3.7). Although there is a significant effect of flow on the density distribution of porpoise sightings (table 3.7 and figure 3.30), the pattern in the distribution of sightings recorded across the survey area does not show a clear change in the core density area as flow conditions change, with the highest relative sightings density being consistently concentrated around the southern and south-eastern reef edge (figure 3.36).

To further investigate the potential effects of dynamic variables on spatial distribution, the hourly time series of presence-absence of sightings from inside and outside the 50 % UD area were modelled separately using binomial GAMs (with logit-link function). The idea behind this comparative analysis was that the timing of sightings inside the 50 % UD area, where steep topographical features are present (figure 3.14), might show a stronger link with dynamic tidal variables because of tidal-topographic interactions. The results from the inside and outside kernel models are given in table 3.11 and do not indicate notable differences in the dynamic controls on sightings in the two sections of the survey area.

The majority of deviance in both modelled datasets was explained by the year of the survey (6.29 % and 6.72 % for inside and outside respectively) and survey condition variables (8.23 % and 5 % for inside and outside respectively). Tide height was the only tidal variable that was selected as significant, but was selected by both models, therefore doesn’t indicate a difference in the dynamic controls on porpoise sightings from inside and outside the kernel area. In addition, the variable explained only a small amount of the variance in both models (table 3.11).

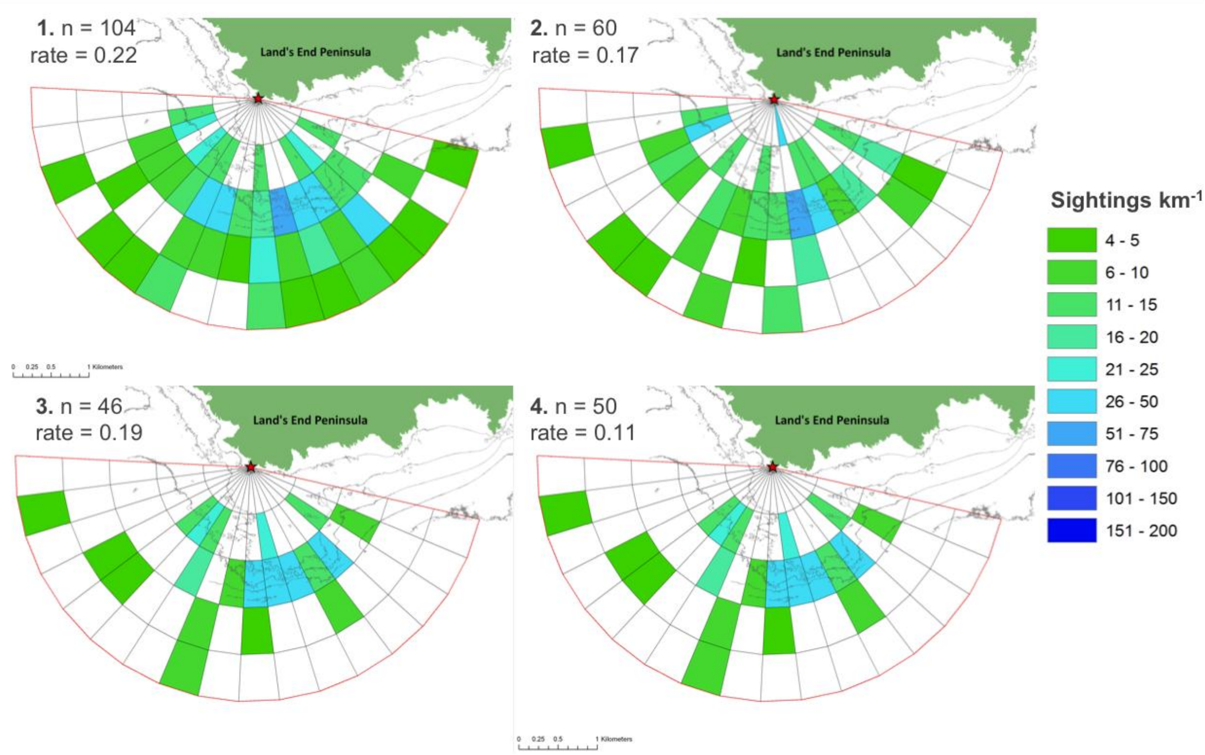


Figure 3.36: Area corrected harbour porpoise sighting density from the SWSW survey 2007 – 2010, separated by tidal flow group defined by flow speed and direction, described in table 3.7. Number of sightings per flow group and corrected sighting rate are given in each plot.

Table 3.11: Summary of GAMs for presence of harbour porpoise sightings inside and outside the 50 % UD area. Parametric fits for factor variables (month and sea state) are represented by 'L', and smooth terms are represented by 'S (#)', where the number in parentheses is the degrees of freedom of the term. The superscript numbers indicate the order of importance of the model terms, based on % deviance. Acronym definitions: BSS = Beaufort sea state; TtHW = time to HW; TODI = time of day index.

	Predictor variables													
	Survey variables			***Tidal variables***			***Temporal variables***							
Model	**BSS (F – 3)**	**Cloud (%)**	**Glare (%)**	**Tide dir.**	**Tide spd.**	**Tide height**	**TtHW**	**Flow group (F -4)**	**Tide range**	**Hour**	**TODI**	**Week**	**Month (F-4)**	**Year**
Inside	L^2	S^4 (0.75)				S^5 (1.08)					S^3 (2.51)			L^1
Outside	L^2					S^4 (2.95)						S^3 (2.15)		L^1

3.3.3 Spatial and temporal patterns in the acoustic monitoring data.

All C-PODs were deployed on the afternoon of the 26/7/2010. A mid-survey data download was carried out *in situ* on the 18/08/2010 when it was discovered that the 'reef margin' C-POD had failed due to disconnection of the battery spring. The three C-PODs were redeployed on the 18/8/2010, with only a very short interruption in recording whilst the memory cards were changed over. The 'eastern' and 'control' C-PODs were finally retrieved on the 13/10/2010 and the 'reef margin' on the 14/10/2010. All C-PODs successfully collected data for the full period of the second deployment.

The eastern and control C-PODs collected a total of 80 days of data (1896 hrs 27 min and 1899 hrs 7 min respectively). The reef margin C-POD collected 56 days of data (1365 hrs 33 min). A summary of the data recovered from each C-POD is given in table 3.12.

Table 3.12: Summary of acoustic detection data collected from three passive acoustic monitoring devices (C-PODs) deployed in the SWSW survey region (July - Oct, 2010). Acronym definitions: DPM = detection positive minutes; DPH = detection positive hours.

	Eastern C-POD	**Reef margin C-POD**	**Control C-POD**
Hours of effort	1896	1365	1899
DPM	742	818	693
Average DPM hr^{-1} (SD)	0.4 (1.7)	0.6 (2.0)	0.4 (1.8)
Average DPM $24\text{-}hr^{-1}$ (SD)	9.3 (13.4)	14.4 (14.7)	8.7 (13.4)
DPH	226	254	196
Average DPH $24\text{-}hr^{-1}$ (SD	2.8 (2.4)	4.5 (2.7)	2.5 (2.1)
% DPM day time	37	35	20
% DPM night time	63	65	80

Although the reef margin C-POD (located within the 50 % UD area defined by the sightings data, see figures 3.8 and 3.14) was only operational for the second deployment period (56-days from 18/8/10 to 14/10/2010), the total number of detection positive minutes recorded was higher than at the other C-PODs, which were deployed for the full 80-day period. Once the amount of 'effort' was taken into account, the margin C-POD has highest average hourly and daily detection rates (respectively 0.6 and 14.4 DPM) (table 3.12). The lowest number of detections was recorded on the control C-POD, located to the east of the SWSW survey area (figure 3.8).

3.3.3.1 Analysis of temporal patterns in the C-POD porpoise detection data

The daily DPM time-series data from the three C-PODs indicate a consistent level of porpoise activity at all sites (between 10 – 15 DPM per day), interspersed with higher numbers of detections over single and multiple days (figure 3.37). Note that because of the failure of the reef margin C-POD for the first period of deployment, the time-series shows 0 detections until the 24th day (figure 3.37). There were peaks in activity at all three sites between 30 and 40 days into the 80-day data collection period, and similar concurrent peaks in DPM per day recorded at the end of the period, between 70 and 80 days (figure 3.37).

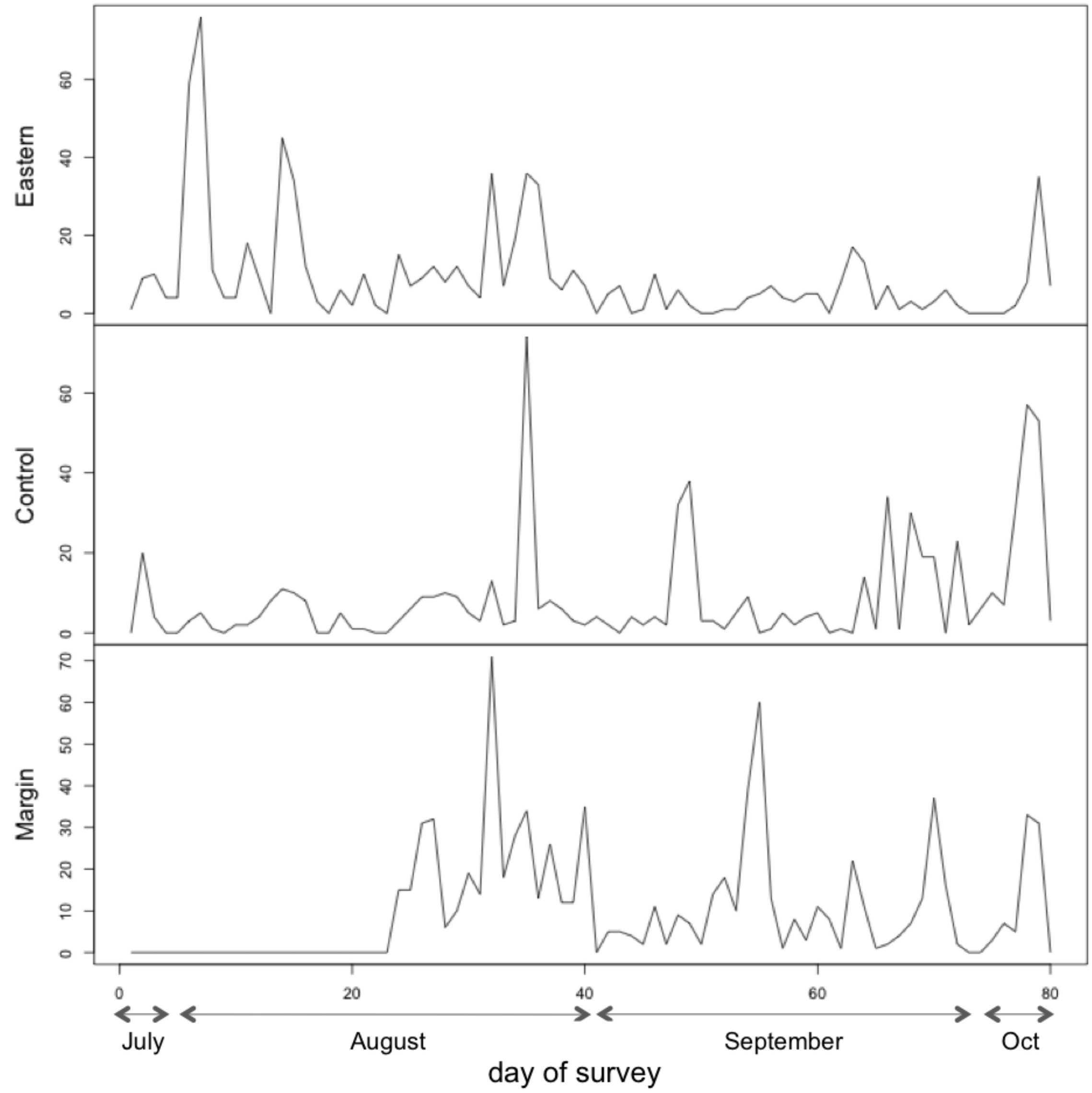


Figure 3.37: Time series of detection positive minutes (DPM) per day recorded at each of the three C-PODs over the duration of the 80-day deployment period (26/7/2010 - 13/10/2010). Note that no data was collected from the reef margin C-POD for the first 24 days due to equipment failure.

Autocorrelation functions show that the total daily DPM data are significantly correlated to a lag of 1-day at all three C-PODs (figure 3.38). This suggests a tendency for clustering of activity/non-activity periods over subsequent days.

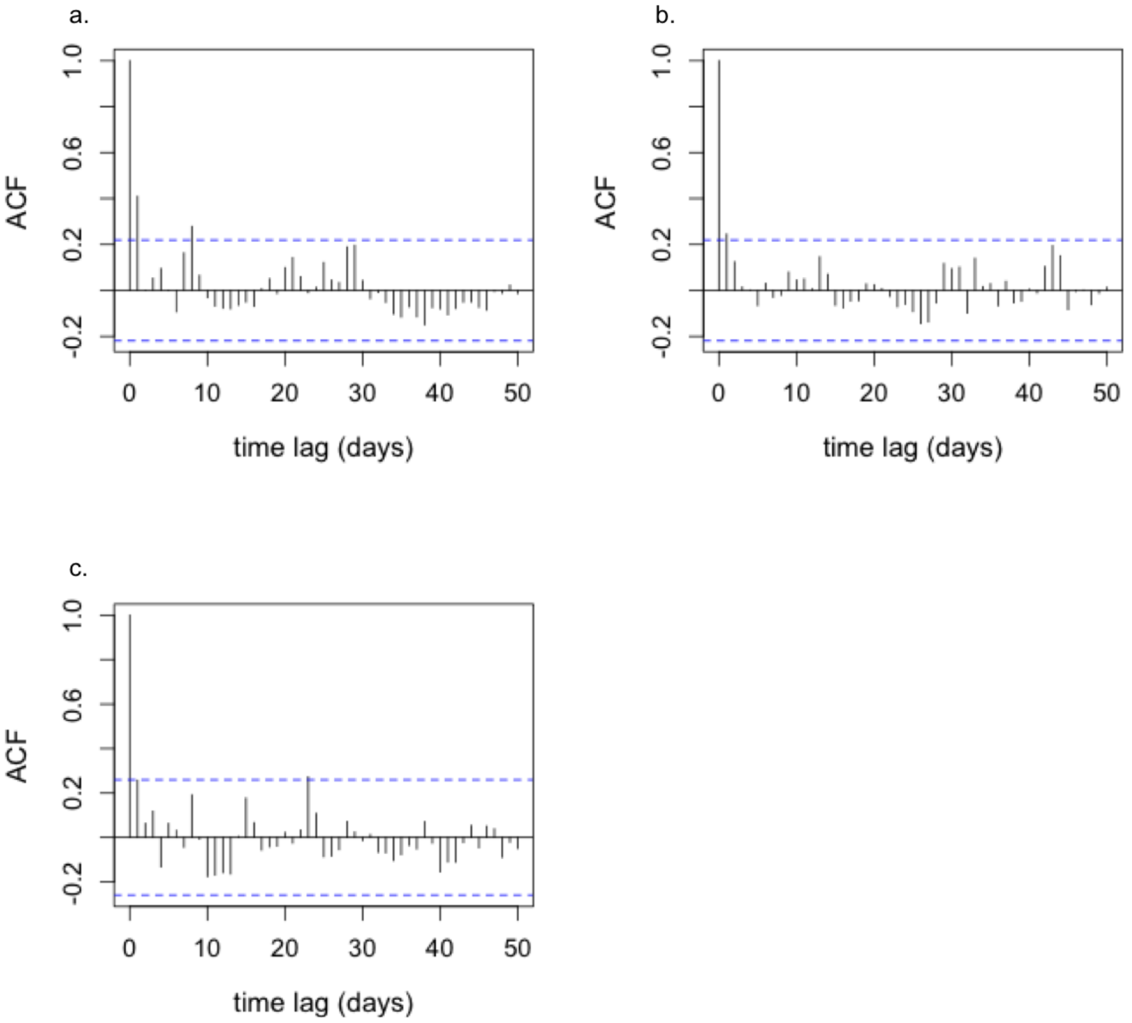
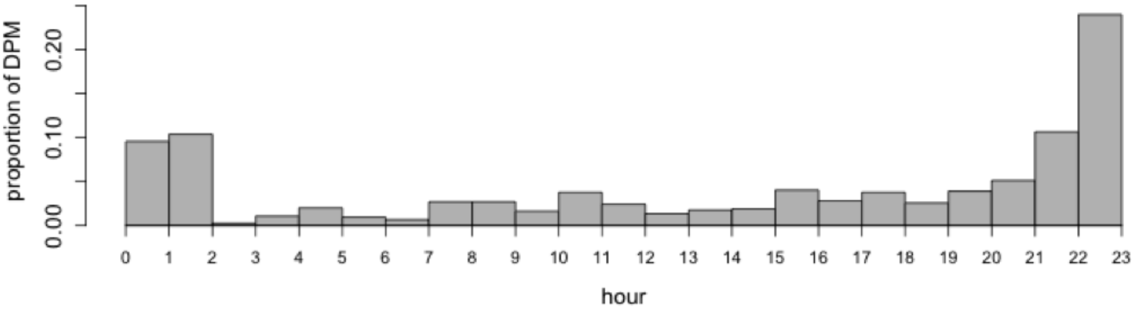


Figure 3.38: Auto-correlation functions for the daily DPM totals from the three C-PODs deployed July to Oct 2010. (a) eastern (N = 80 days); (b) control (N = 80 days); (c) reef margin (N = 56 days).

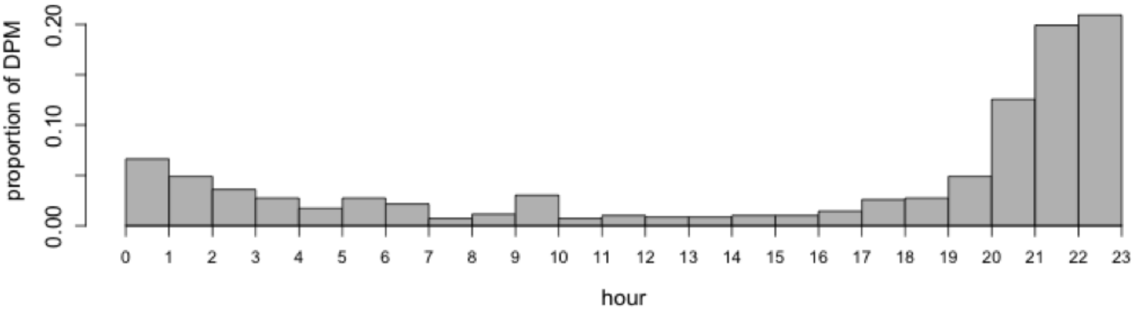
All three of the C-PODs recorded higher numbers of detections during the night than during the day (table 3.12) with an increase in detections notable from 1900 hrs until midnight at all locations (figure 3.39). The day-night split in DPM is most marked at the control site where 80 % of the detections occured during the night. This is compared to 63 % at the eastern reef pod and 65 % at the reef margin pod (table 3.12).

The reef margin C-POD shows more variability in the distribution of DPM throughout the 24-hr period (figure 3.39-c) and the pattern of detections during the daytime hours reflects what is seen in the visual monitoring data, with an increase in detection in the late morning (figures 3.39-c and 3.29).

a. eastern C-POD



b. control C-POD



c. Reef margin C-POD

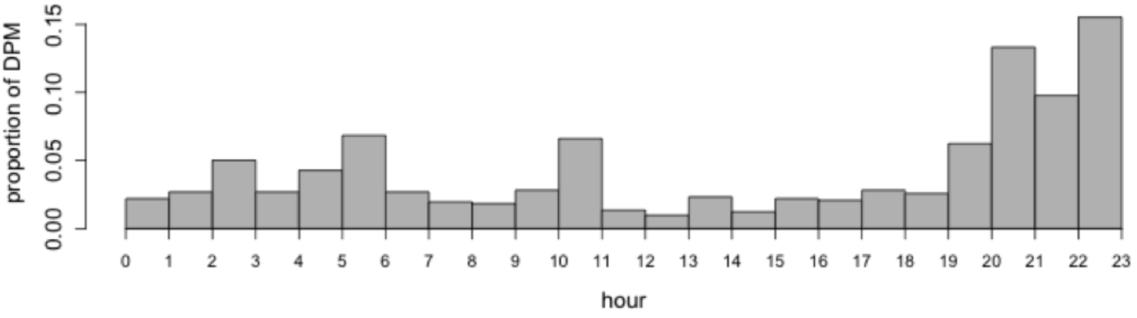


Figure 3.39: Density distribution of detection positive minutes recorded at the three C-PODs. C-PODs deployed July - Oct 2010 for periods of (a) eastern = 1896 hrs, (b) control = 1899 hrs, (c) margin = 1365 hrs.

The pattern in the total detection positive minutes recorded by each C-POD per day through the deployment period (figure 3.37) does not seem to show similarity with the effort corrected sightings per day for the same period in 2010, shown in figure 3.27. To investigate whether this negative result was heavily influenced by the night time detections at the C-PODs, the daytime only detections (0700 to 1900) from each of the CPOD were selected and plotted against the visual monitoring data (figure 3.40). Again there is very little correspondence between the pattern in the number of sightings and the number of DPM recorded each day during daylight hours.

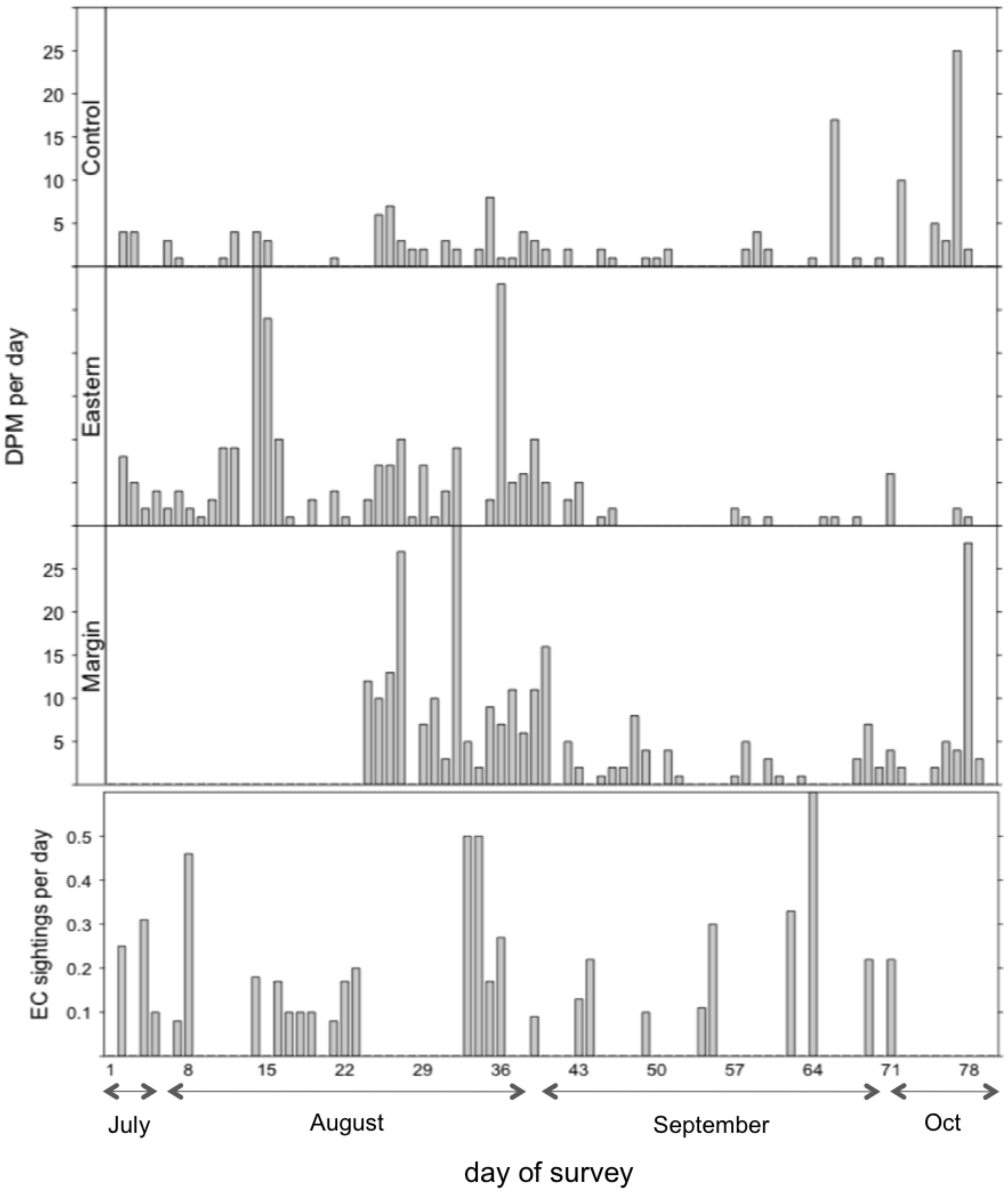


Figure 3.40: Daytime only (0700 – 1900 hrs) Detection Positive Minutes (DPM) by day of deployment from each of the three C-PODs, effort corrected sightings from the SWSW visual survey are also shown for the same period for direct comparison.

Autocorrelation functions for the presence or absence of detections per minute on each C-POD provide information about the average encounter duration. These data show that, on average, the longest encounters were recorded at the control site (max lag = 54 min, acf = 0.06, p = 0.05) followed by the eastern site (max lag = 25 min, acf = 0.055, p = 0.05) and then the reef margin site (max lag = 14 min. acf = 0.06, p = 0.05). These results suggest that although there were highest detection rates on the reef margin C-POD, this site may be used in a different way to the eastern and control sites, where the animals appear to remain for longer periods.

Pairwise cross correlations of the hourly DPM data show significant positive correlation between the detections recorded at all three C-PODs at and around time 0 (this analysis was only undertaken on the data from the second deployment period, so as to be directly comparable at all three C-PODs). High numbers of detections at one C-POD were indicative of high numbers of detections at the other C-PODs (figure 3.41). The periodicity of the significant correlations reflects the overall increase in activity around each C-POD during the night (recurrence at approximately 24 –hr periods).

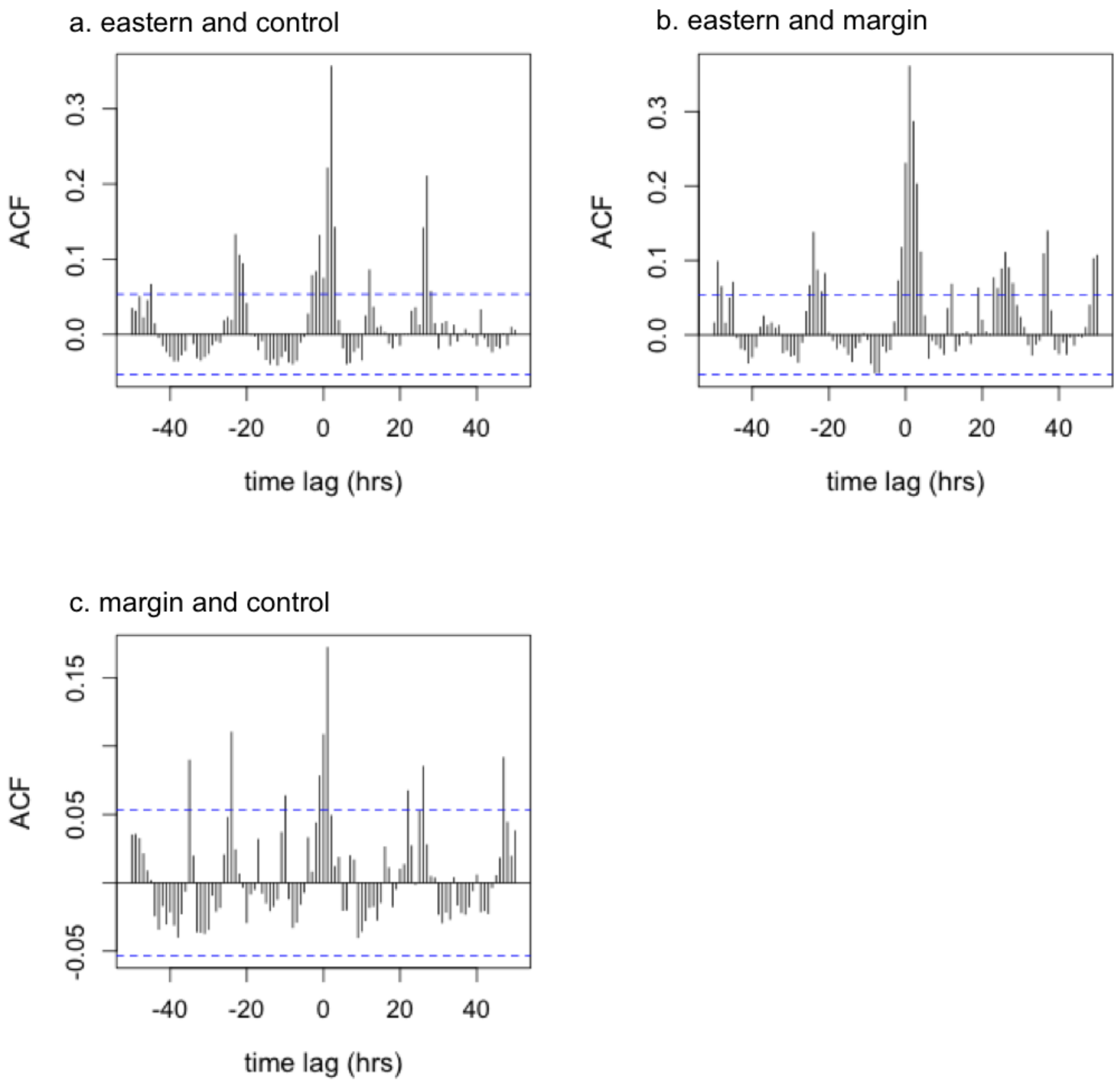


Figure 3.41: Cross-correlation functions for hourly DPM data from the three C-PODs for the second deployment period (56 days from 18/8/10 to 13/10/10): (a) CCF for eastern and control C-PODs, (b) CCF for eastern and margin C-PODs, (c) CCF for margin and control C-PODs.

3.3.3.2 Modelling temporal patterns in the porpoise acoustic detection data: The effect of dynamic oceanographic variables on the timing of harbour porpoise detections.

The presence-absence of detection and the frequency of DPM per hour from each C-POD were modelled using binomial and Poisson GAMs respectively; with tidal and temporal predictor variables. A summary of the environmental data available is given in table 3.13.

Table 3.13: Summary table of environmental conditions experienced during C-POD deployment and available for use in the models of acoustic detection. Left: summary of conditions during the full deployment period for each C-POD (Jul-Oct 2010 for eastern and control, Aug – Oct 2010 for margin). Right: summary of conditions experienced only during hours when detections were recorded on each C-POD.

	Hourly presence-absence model		**Presence only dataset**		
Parameter	**East and control**	**Margin**	**Eastern**	**Control**	**Margin**
Hours of data	1894	1347	226	196	254
Number of DPM	742/693	818	742	693	818
Survey variables					
Wave direction (°)					
Range	8.5 - 350	135 - 308.5	137 – 333.5	149 - 308	135 - 308.5
Median (IQR)	184 (177 - 190)	185 (179 - 190)	183.2 (175 - 189)	185 (177 - 189)	185 (178 - 190)
Wave height (m)					
Range	0.1 - 1.83	0.13 - 1.83	0.12 - 1.7	0.1 - 1.59	0.13 - 1.75
Median (IQR)	0.39 (0.22 - 0.65)	0.50 (0.34 - 0.81)	0.33 (0.21 - 0.54)	0.46 (0.25 - 0.77)	0.51 (0.31 - 0.82)
Tidal variables					
Tide direction (°)					
Range	0 - 359	0 - 359	7 - 359	1 - 359	1 - 359
Median (IQR)	168 (102 - 292)	167 (102 - 291)	156 (116 - 270)	160 (92 - 287)	153 (112 - 274)
Tide speed (m sec^{-1})					
Range	0.06 - 0.85	0.06 - 0.85	0.07 - 0.84	0.1 - 0.82	0.07 - 0.85
Median (IQR)	0.39 (0.27 - 0.52)	0.39 (0.27 - 0.51)	0.39 (0.28 - 0.5)	0.39 (0.28 - 0.5)	0.34 (0.23 - 0.52)
Tide group					
Range	1 - 4	1 - 4	1 - 4	1 - 4	1 - 4
Median (IQR)	2 (1 – 3)	2 (1 – 3)	2 (1 – 3)	2 (1 – 3)	2 (1 – 3)
Tide Height (m from msl)					
Range	-2.66 - 2.83	-2.66 - 2.83	-1.95 - 2.55	-2.49 - 2.74	-2.28 - 2.42
Median (IQR)	0.04 (-1.1 - 1.05)	-0.04 (-0.1.06 - 1.04)	0.165 (-0.93 - 1.22)	3.8 (3.053 - 4.255)	0.35 (-0.88 - 1.13)
TtHW (hrs)					
Range	-6.27 - 6.32	-6.27 - 6.3	-6.1 - 6.15	-6.18 - 6.07	-6.18 - 6.23
Median (IQR)	0.02 (-3.1 - 3.07)	0.02 (-3.1 - 3.07)	1.19 (-2.43 - 3.4)	0.1 (-3.6 - 2.25)	0.9 (-2.68 - 3.32)
Tide Range (m)					
Range	1.85 - 5.49	1.85 - 5.49	1.85 - 5.49	1.85 - 5.49	1.85 - 5.49
Median (IQR)	3.7 (2.84 - 4.23)	3.64 (2.78 - 4.16)	3.62 (2.86 - 4.04)	3.8 (3.1 - 3.7)	3.31 (2.4 - 4.0)
Temporal variables					
Hour (time)					
Range	00:00 – 23:00	00:00 – 23:00	00:00 – 23:00	00:00 – 23:00	00:00 – 23:00
Month (as factor)					
Range	7 - 10	7 - 10	7 - 10	7 - 10	7 - 10

Temporal model results

Details of the final two-stage GAMs for each C-POD, selected through step-wise forwards covariate addition, are given in table 3.14. The binomial models represent the variables that significantly influence the hourly presence or absence of detections on each C-POD. The Poisson models use the presence-only data and contain environmental variables that influence the frequency of DPM during presence periods.

Table 3.14: Summary of GAMs for presence-absence and presence-only (DPM per hour) at each of the three C-PODs. Linear fits for factor variables (month and sea state) are represented by 'L', and smooth terms are represented by 'S (#)', where the number in parentheses is the degrees of freedom of the term. The superscript numbers indicate the order of importance of the model terms, based on % deviance. Acronym definitions: BSS = Beaufort sea state; TtHW = time to HW; TODI = time of day index.

	Survey variables		***Tidal variables***						***Temporal variables***	
Model	**Wave dir.**	**Wave height**	**Tide dir.**	**Tide spd.**	**Tide height**	**TtHW**	**Flow group (F -4)**	**Tide range**	**Hour**	**Month (F-4)**
Eastern binomial								S^2 (2.6)	S^1 (1.84)	L^3
Eastern Poisson	S^5 (1.31)	S^2 (0.71)				S^2 (2.93)			S^4 (1.67)	L^3
Control binomial					S^3 (3.8)				S^1 (1.9)	L^2
Control Poisson					S^2 (0.9)			S^3 (0.57)	S^1 (1.82)	
Margin binomial				S^5 (4.2)	S^2 (3.76)	S^3 (4.42)			S^4 (1.82)	L^1
Margin Poisson		S^3 (0.77)				S^2 (3.72)		S^1 (3.82)		

The effect of hour of the day is clearly important at all C-POD locations, as are measures of the height and range of the tide, which will be linked to the position in the spring-neap cycle (table 3.14). There is also an effect of the semi-diurnal tidal pattern, indicated by the selection of tide height and time to HW (TtHW) as significant environmental predictors for presence and frequency of detections in five of the models (table 3.14). 'Survey' conditions of wave height and wave direction do not seem to have a notable influence across all of the detection data, but were picked up by two of the models (table 3.14)

The model selected for the presence-absence of DPM per hour of deployment at the eastern C-POD explains 6.24 % of the deviance and includes predictor variables hour (2.21 %), daily tide range (2.19 %) and month (1.84 %). The model estimated smooth terms are shown in figure 3.42 (a and b) and indicate that hours positive for detections occurred more frequently during the evening and night and on days with moderate tide range. A barplot of detection rate at the eastern C-POD by month is given in figure 3.42-c. The model found that hours recorded during October had significantly lower detection probabilities than other months (model estimate = -7.5, p = 0.05). Wave variables were not found to have a significant effect on the detection of porpoises by the C-POD. The model residuals remained auto-correlated to a lag of 2-hrs (figure 3.42-d).

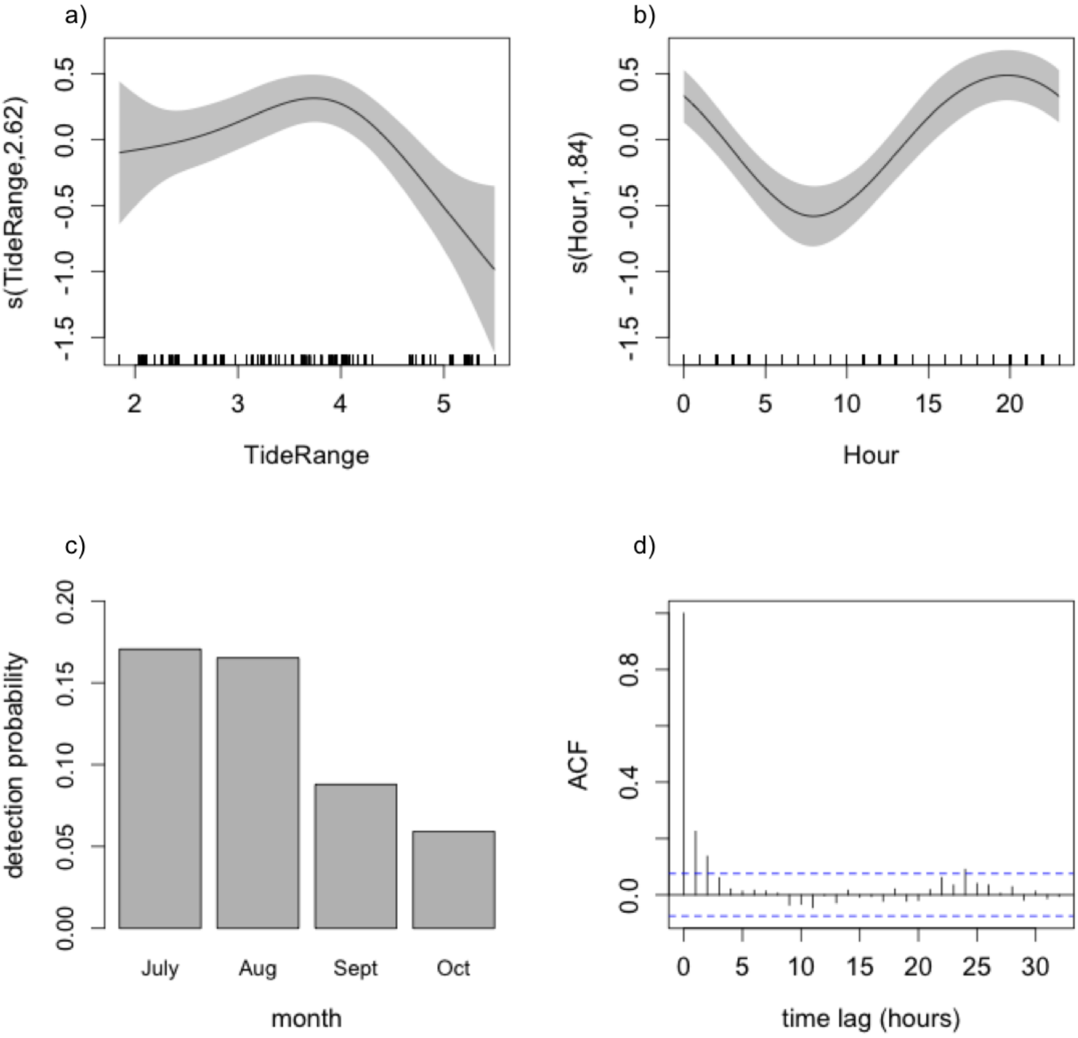


Figure 3.42: Eastern C-POD: presence-absence of porpoise detections per hour modelled by binomial GAM smooth functions of (a) tide range and (b) hour, with confidence intervals shown by grey shading. (c) Barplot of detection probability by the significant factor variable of month. Auto-correlation function of the binomial GAM residuals given in (d) with significance threshold shown by dashed lines.

The GAM for number of DPM per hour (during presence hours only) recorded at the eastern C-POD explains 34.6 % of the deviance and contains predictor variables wave height (8.09 %), time to HW (9.3 %), month (6.9 %), hour (5.7 %) and wave direction (4.61 %). The model estimated smooth terms are shown in figure 3.43-a to d and indicate that higher numbers of detections per hour were recorded when wave height is lower and wave direction is from the south. There were also higher numbers of detections on the falling tide and during hours between 2000 – 0500 (figure 3.43-c and d). A barplot of the average number of detections recorded during presence hours in each month is given in figure 3.43-e. Month was identified as having a significant effect on the number of DPM recorded each hour, with significantly lower detections in September (model estimate = -0.5, p = 0.05). The model residuals are significantly auto-correlated to a lag period of 1-hr.

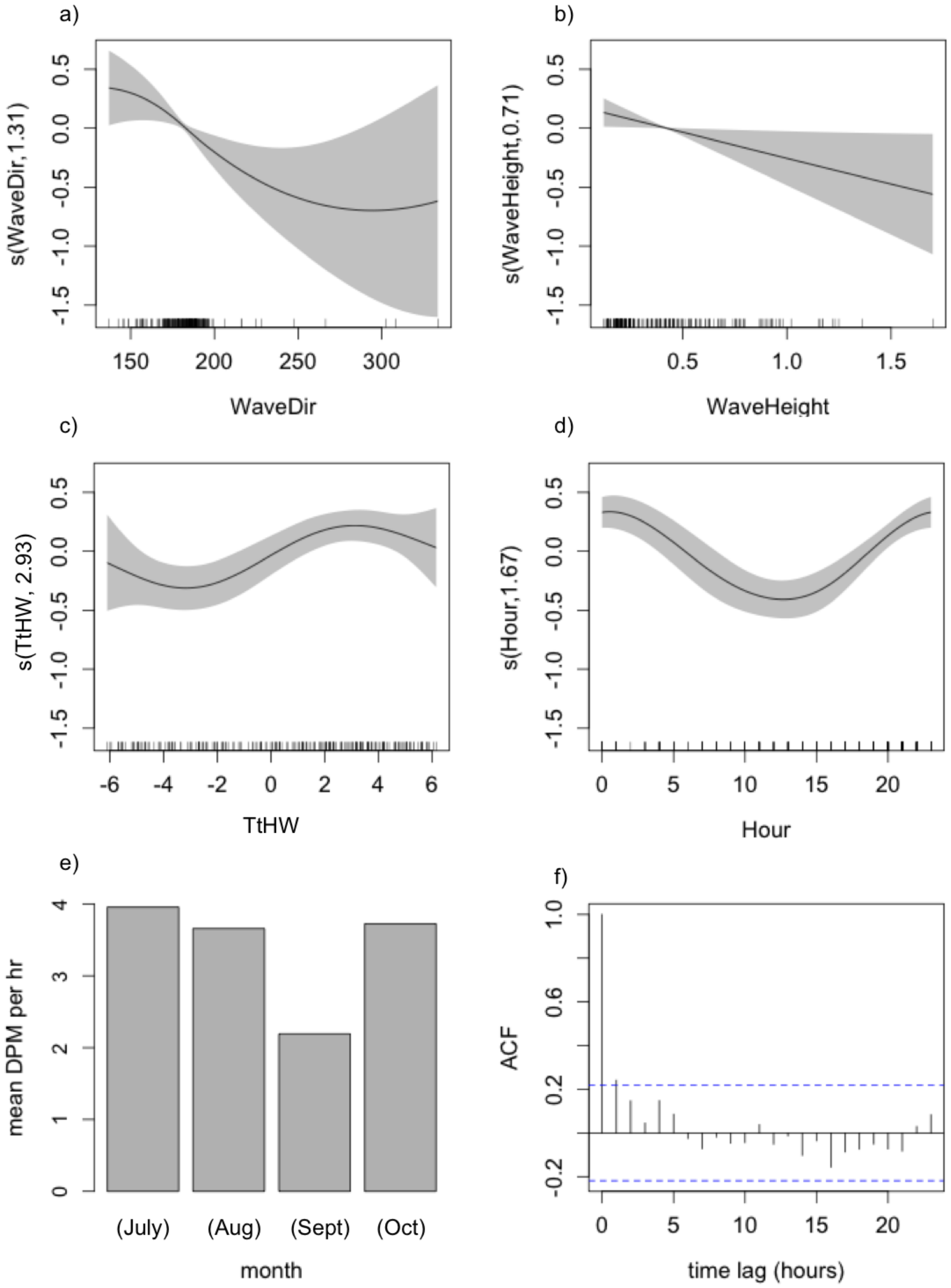


Figure 3.43: Eastern C-POD: Presence only, DPM hr^{-1} modelled by Poisson GAM smooth functions of (a) wave direction, (b) wave height, (c) time to HW and (d) hour, with CI shown by grey shading. (e) Barplot of mean DPM per hour by the significant factor variable of month. Auto-correlation plot for Poisson model residuals given in (f), with significance threshold shown by dashed lines.

The binomial GAM selected for the presence-absence of porpoise acoustic detections per hour at the control C-POD explains 6.88 % of deviance. The model estimated smooth terms are provided in figure 3.44 and show that the presence of detections was affected by tide height with fewer positive hours recorded around mid tides; but this variable explained very little of the deviance in the data (1 %) (figure 3.44-a). Hour explained 4.64 % of the deviance with presence hours associated with evening and night hours and few detection positive hours were recorded during the middle of the 24-hr period (figure 3.44-b). Month was identified as a significant predictor by the model, explaining 1.19 % of the deviance (figure 3.44-c); specifically, October was estimated to have the highest number of positive hours (model estimate = 0.85, *p* = 0.05). There was significant auto-correlation in the binomial GAM residuals to a lag of 1-hr (figure 3.44-d).

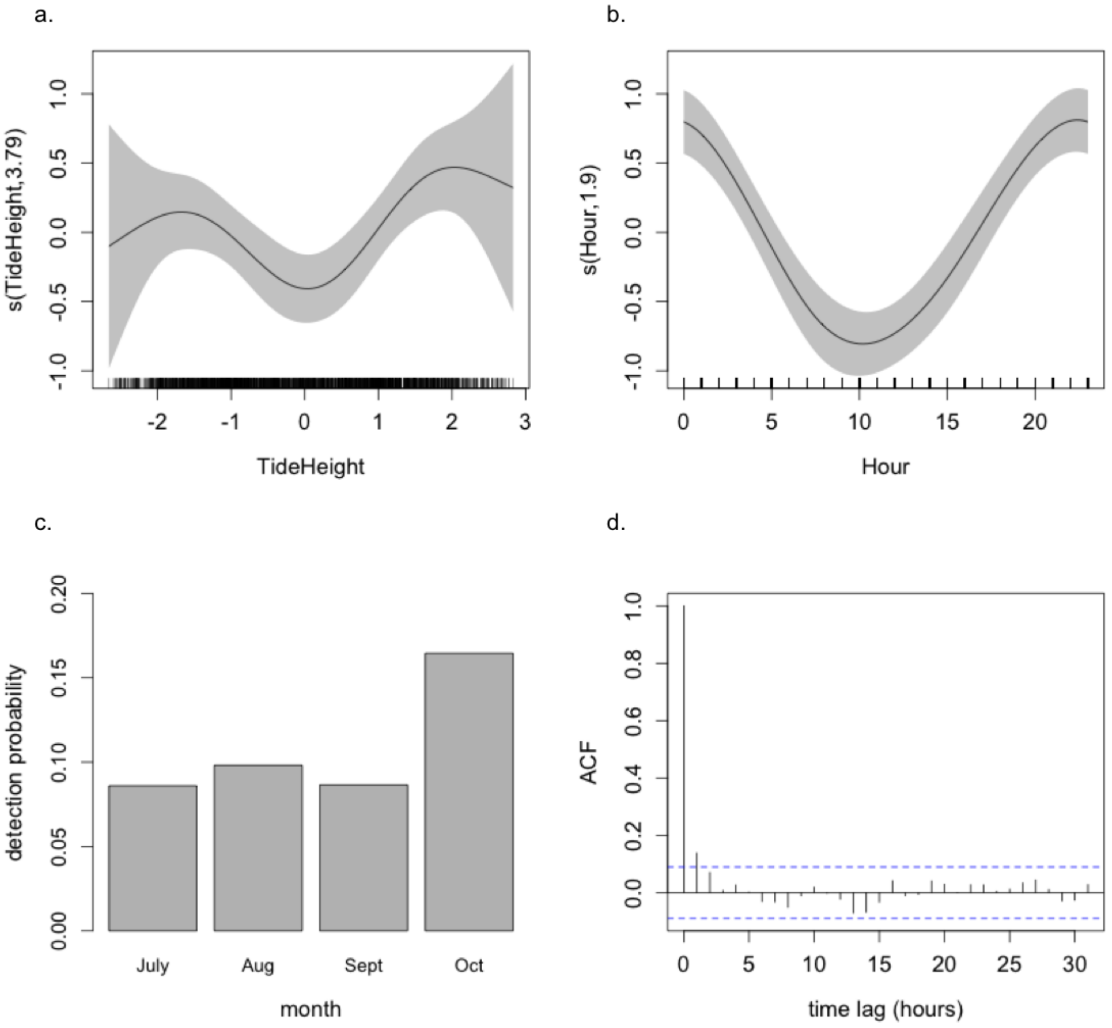


Figure 3.44: Control C-POD: presence-absence of porpoise detections per hour, modelled by binomial smooth functions of (a) tide height and (b) hour, with confidence intervals shown by grey shading. (c) Barplot of detection probability by the significant factor variable of month and (d) auto-correlation function of binomial GAM residuals, with significance threshold given by dashed lines.

The Poisson GAM of the presence only DPM per hour data from the control C-POD explains 18.5 % of the deviance in the data and contains the predictor variables; hour (13.59 %), tide height (3.25 %) and tide range (1.66 %). The smooth terms show that the number of DPM per hour was positively correlated with tide height and daily tide range (figures 3.45 a and b) and that more activity was recorded around the control C-POD during the night than during the day (figure 3.45-c). The model residuals were auto-correlated to a lag period of 1-hr (figure 3.45-d).

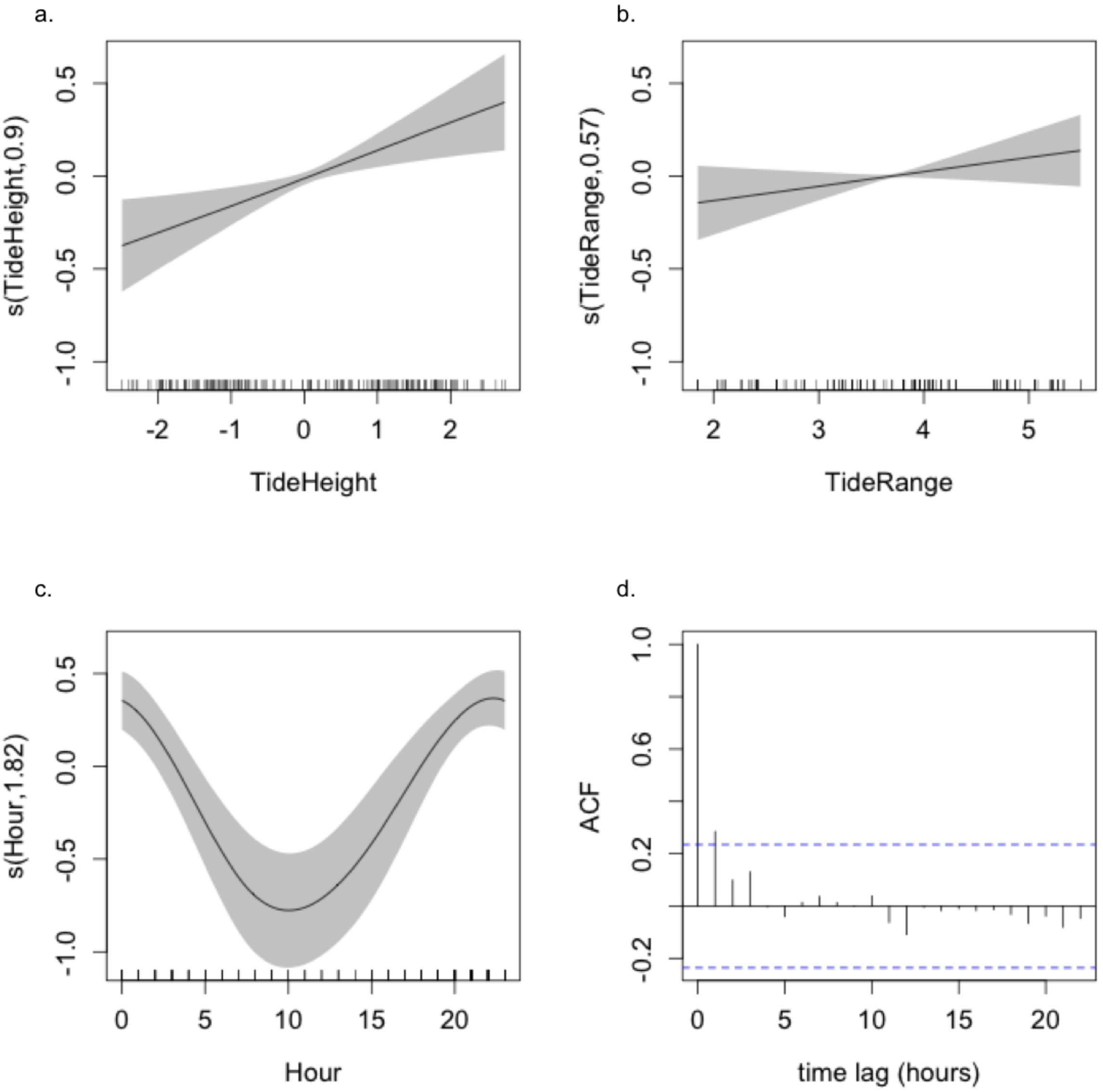


Figure 3.45: Control C-POD: Presence only, DPM hr^{-1} modelled by Poisson GAM smooth functions of (a) tide height, (b) tide range and (c) hour, with confidence intervals shown by grey shading. Auto-correlation plot for Poisson model residuals given in (d), with significance thresholds indicated by dashed blue lines.

The binomial GAM for presence-absence of porpoise detections on the reef margin C-POD explains 11.6 % of the deviance and includes month (2.87 %), tide height (2.78 %), time to HW (2.32 %), hour (2.3 %) and tide speed (1.33 %). The model estimated smooth terms are shown in figure 3.46. There was a positive relationship between presence hours and tide height and the highest likelihood of detections were in hours from 2 - 6 hours after high water (figure 3.46-a and b). There is evidence for higher presences recorded in low and high tide speeds over moderate speeds, but this variable only explained a small amount of the variability in the data and has wide confidence intervals at the extreme high and low values (figure 3.46-c). The effect of hour was found to be significant, with increased presence hours from 1500 – 0500, but the effect of time is much less pronounced than at the other C-POD locations (figure 3.46-d). There was a higher probability of detection during August on the reef margin C-POD (figure 3.46-e), with September and October having significantly lower numbers of detections (respective model estimates = -1.04, *p* = <0.001 and -0.87 *p* = <0.001). The binomial model residuals were significantly auto-correlated to a lag period of 1-hr (figure 3.46-f).

The GAM for DPM per hour (presence-only) from the reef margin C-POD explains 17.1. % of the deviance and includes the predictor variables daily tide range (7.57 %), time to HW (7.18 %) and wave height (2.35 %). The amount of DPM recorded per hour during presence hours has a slight negative relationship with wave height (figure 3.47-a). Higher numbers of DPM were recorded per hour on days with low (~ 2 m) and intermediate to high (~ 4 – 4.5 m) tidal ranges (figure 3.47-b). The effect of the tidal cycle is significant, with the period before and at HW having lower numbers of porpoise detections (figure 3.47-c). The model residuals are not significantly auto-correlated.

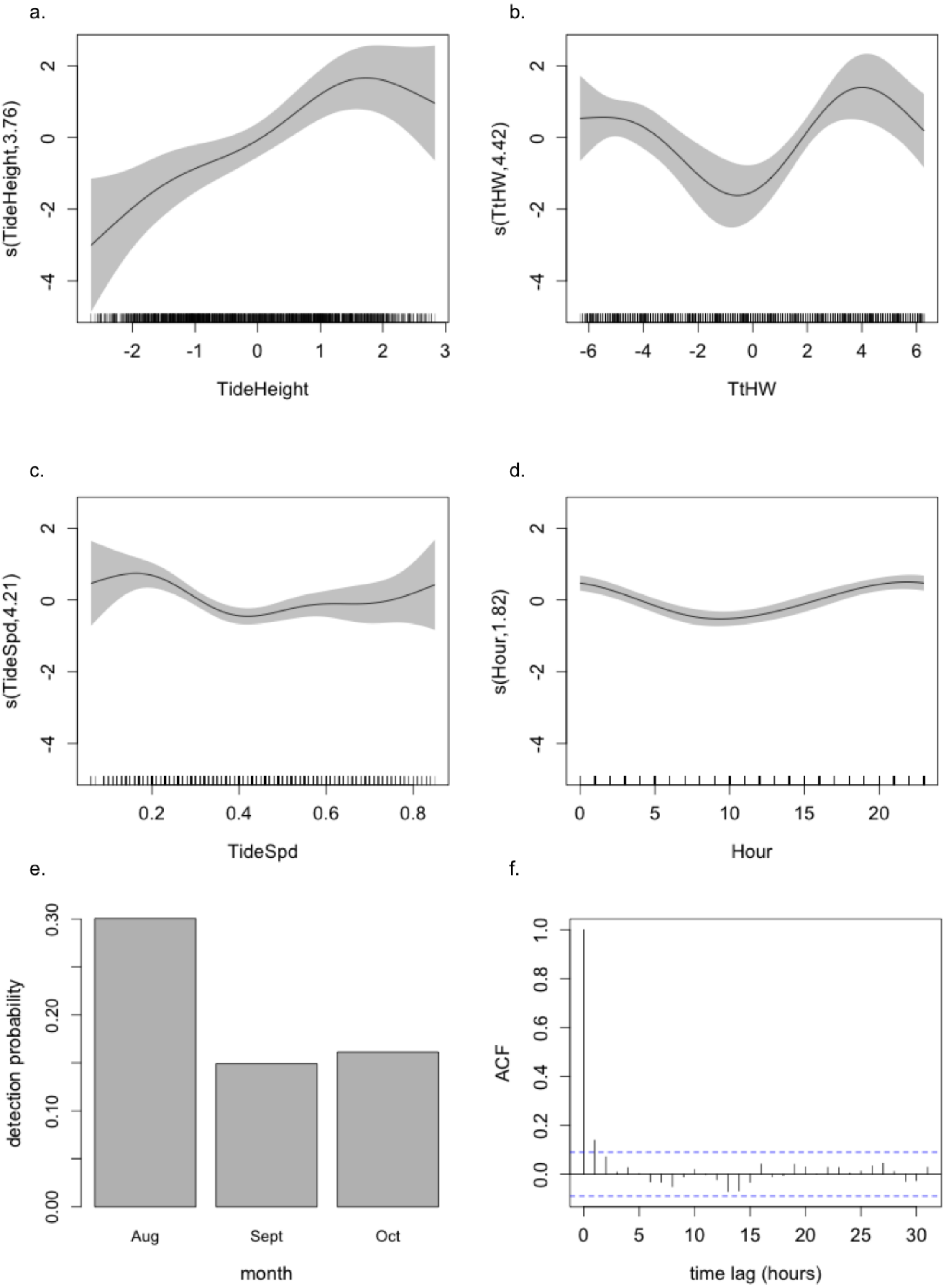


Figure 3.46: Margin C-POD: presence-absence of porpoise detections per hour, modelled by binomial smooth functions of (a) tide height, (b) time to HW, (c) tide speed and (d) hour, with confidence intervals shown by grey shading. (e) Barplot of detection probability by the significant factor variable; month of survey. (f) auto-correlation plot of binomial model residuals with significance threshold shown by dashed blue lines.

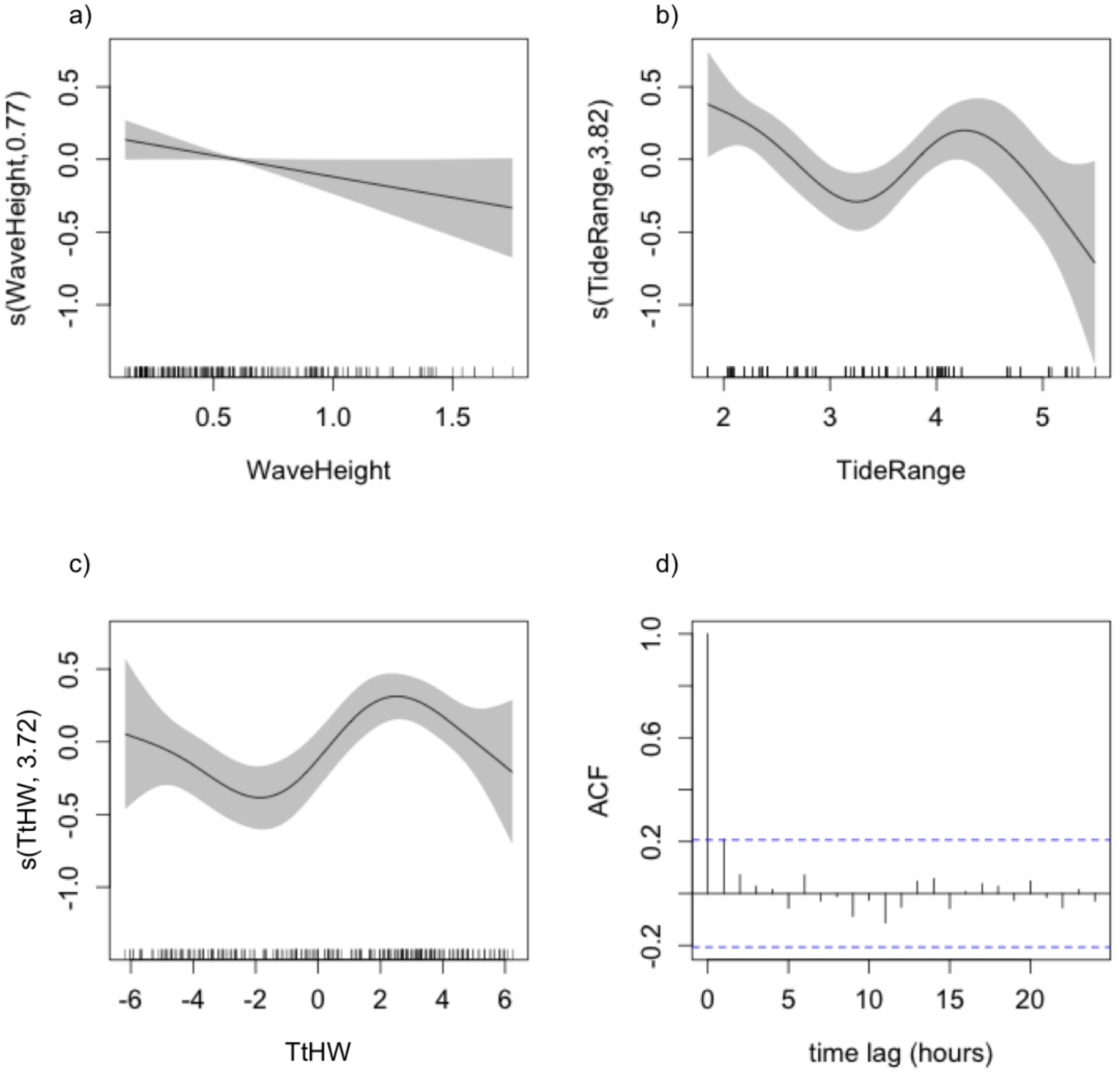


Figure 3.47: Margin C-POD: presence only, DPM hr^{-1} modelled by Poisson GAM smooth functions of (a) wave height, (b) daily tide range and (c) time to HW, with confidence intervals shown by grey shading. Auto-correlation plot for Poisson model residuals given in (d), with significance threshold shown by dashed lines.

3.3.4 Acoustic Doppler Current Profile (ADCP) survey results.

A total of nine transect repeats were carried out during the ADCP survey on the 11th July 2011, with an interval period of approximately 1.25 hrs between the start of each run. The survey started at 07:12 GMT and ended at 20:04 GMT. Local high water was at 12:51 (t = 0.5) and low water at 19:12 (t = 0.8) GMT. The survey was carried out 2 days after the neap tide. The sea state did not exceed Beaufort 2 during the survey; therefore the data are unlikely to have been affected by excess turbulence caused by rough conditions. The boat travelled at an average of 5 knots (~ 2.5 m per second) during the survey, giving an approximate raw data resolution of one ping per 1.25 m of horizontal distance travelled.

The repeated transects across the Runnelstone Reef study area demonstrate the complexity of the spatial and temporal variability in the flow field across and around the reef. Flow is predominately oriented along the reef edge, in the east-west direction. In line with the information received from the local scale tide charts (figure 2.6), current velocity is shown to be directed primarily to the west, reaching a maximum of > 1 ms^{-1} during two 2-hour periods before and after low water. The current flows eastward for just over two hours, coinciding with approximately hourly periods on either side of high water, when eastwards velocity also reaches 1 ms^{-1}. The strongest easterly flow is found over the shallower 'reef top' area, during the hour after HW. There is a clear slack water period observed one hour prior to HW, and another brief period of reduced flow as the tide turns rapidly around two hours after HW.

Data on the speed of flow around the reef are presented as the eastward (U) and northward (V) velocity components of the current flow. Plots of the full ADCP current velocity and shear data from the survey (all legs for all transects) are provided in appendix 4. The plots given in the results are a selection of the data based on the key findings of the survey.

The velocity profiles in figure 3.48 (a and b) show velocity data from leg 1 of the transect route, which ran from east to west across the reef (see figure 3.10 for transect route). The data show that in the east-west component (U), there is generally a higher flow speed over the reef-top area (the central, shallower part of the study area), than at the reef edges and the deeper water beyond (figure 3.48-a). This is likely to be as a result of the predominantly east-west flow component of the tide being pushed up over the reef where it is spatially constrained. This increase in flow speed and depth restriction also leads to a more turbulent flow over the top of the reef, as indicated in the shear data (figure 3.48-c).

There is also evidence from leg 1 of stronger flow in the north-south component (*V*) at the western side of the reef than at the east throughout much of the tidal period (figure 3.48-b). There is also some deflection of flow around the reef in the north-south component (*V*), evidenced by different *V* flow patterns on the east and west sides of the reef (figure 3.48-b). This suggests that during the westerly (ebbing) flow (see profiles 1-4, 8 and 9 on figure 3.48-a), water 'wraps round' the semi-circular reef feature, being deflected south-westerly on the eastern side of the reef and north-westerly on the western side of the reef. There is also evidence that this flow is reversed when the main tidal current is flooding to the east, but the pattern is less clear during these periods (profiles 5, 6 and 7 on figure 3.48-b).

Figure 3.49 shows shear squared (S^2) computed over 1-m vertical intervals for all four legs of the eighth transect run, carried out between HW+4 to HW+5; corresponding to the highest relative density period for porpoise sightings (figure 3.30). Topographic steering of the deeper flow around the reef is illustrated by velocity vectors (arrows) plotted at depths of 5, 15 and 30 m. The black velocity vector arrows on figure 3.49 provide evidence that the tidal current near the surface is able to flow over the reef, but offshore of the reef edge there is tidal-topographic interaction and the deeper flow is deflected to flow around the topography; indicated by the orange (15-m) and red (30-m) arrows in figure 3.49.

Current velocity data from the repeated transect along legs 3 and 4 are given in figures 3.50 and 3.51. These legs of the transect route were selected because they cross north-south through the porpoise 50 % kernel estimated UD (see inset map in figure 3.49), therefore flow features here may be particularly important with respect to temporal patterns in the porpoise sightings data.

The plots of eastward flow velocity (*U*) from leg 4 indicate that during periods of the strongest westward flow (dark blue), which correspond to expected and high amounts of sightings, there is an approximately 5-m thick layer immediately above the seabed on the sloping reef edge where flow is much slower (around 0.4 ms^1, lighter blue on figure 3.50-a, profiles 1, 2, 7, 8 and 9). This indicates the presence of a strongly sheared frictional bottom boundary layer, where turbulence is likely to be enhanced compared to in the interior of the main flow higher in the water column. The north component of the flow (*V*) for leg 4 (figure 3.50-b) is considerably weaker than the eastward component (*U*), remaining < 0.4 ms^{-1} throughout the tidal cycle, and is predominantly oriented to the south (blues on figure 3.50-b), as would be expected due to the topographical constraint of the reef and land to the north. In the leg 4 data there is a particularly interesting distinct two-layered flow recorded during many of the transect runs (figure 3.50-b, see profiles 1-4, 6, 8 and 9). This feature occurs where the flow intersects with the reef slope and separates a layer of northward flow in the top 20-m, from southward flow layer in the deeper water (figure

3.50-b); light blue bottom layer and yellow top layer). The split orientation of the flow is likely to be a result of topographic steering of the lower layer of water, which is deflected by the reef edge, whilst the water in the upper layer is able to flow largely unconstrained over the reef. This split layered flow is present through much of the period of westerly flow and breaks down during the easterly flood tide.

The flow data recorded along leg 3 of the repeated transects are given in figure 3.51-a and b. There is evidence of further shear features in both the U and V flow components during the periods corresponding to the times of highest sightings, which were not present at other times during the tidal cycle (figure 3.51, profiles 7 and 8). These mid-depth boundaries separate water moving in different directions and can also be seen in the shear data for legs 3 and 4 (figure 3.49). It is likely that the destabilising effect of the sheared frictional bottom layer and the mid depth boundary layers that have been discussed, will promote localised turbulence.

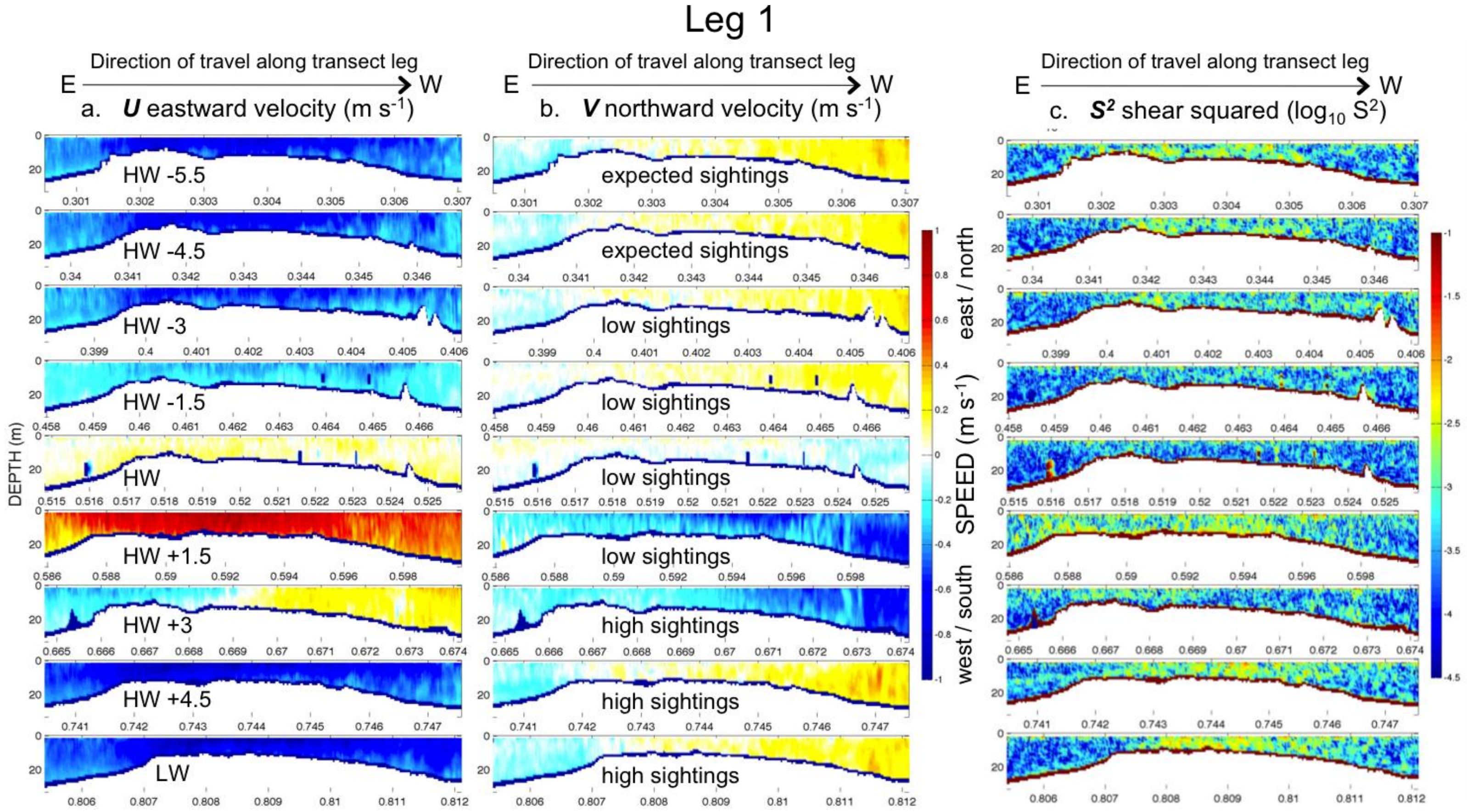


Figure 3.48: Current velocity and shear profiles from leg 1 (travelling east to west) of the ADCP survey of the SWSW survey area, carried out 11th July 2011 from the RV Callista. Data are from a full tidal cycle. Decimal time relative to HW (0 and 0.54) is given along the x axes and water depth along the y axes. Current velocity is colour scaled with a) the eastward velocity component scaled from east in red to west in dark blue and b) the northward velocity component, colour scaled from north in red to south in dark blue. Shear colour scale shows $\log_{10}$ shear squared, with red showing highest shear and blue showing lowest. The timing of each profile relative to HW and to relative density of porpoise sightings is labeled. ADCP data processed by Dr. P. Hosegood, Plymouth University.

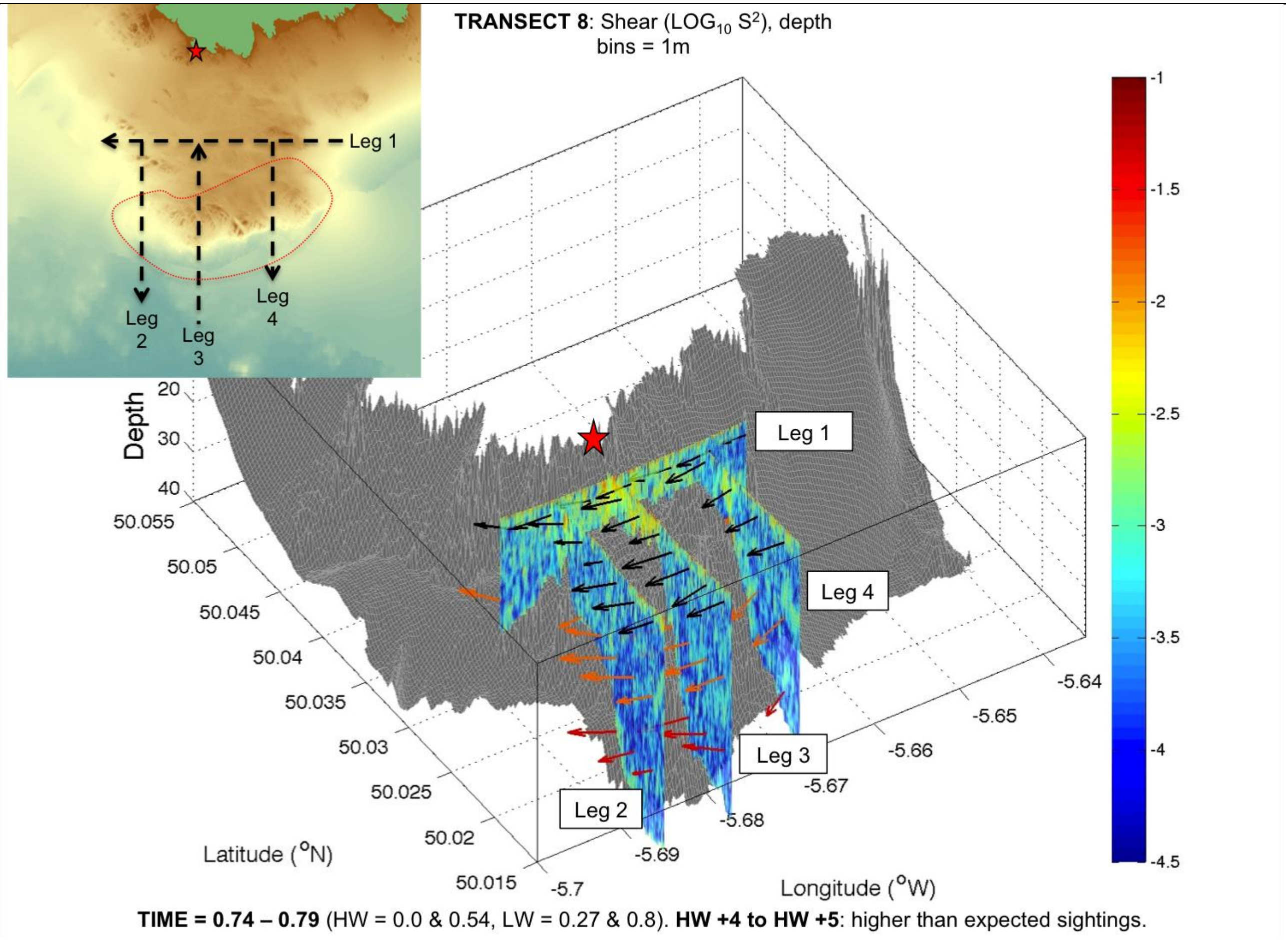


Figure 3.49: Shear squared ($\log_{10} S^2$) computed over 1-m vertical intervals for the eighth transect run (approximately HW +4 to HW +5). Velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (black), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. ADCP data processed by Dr. P. Hosegood, Plymouth University.

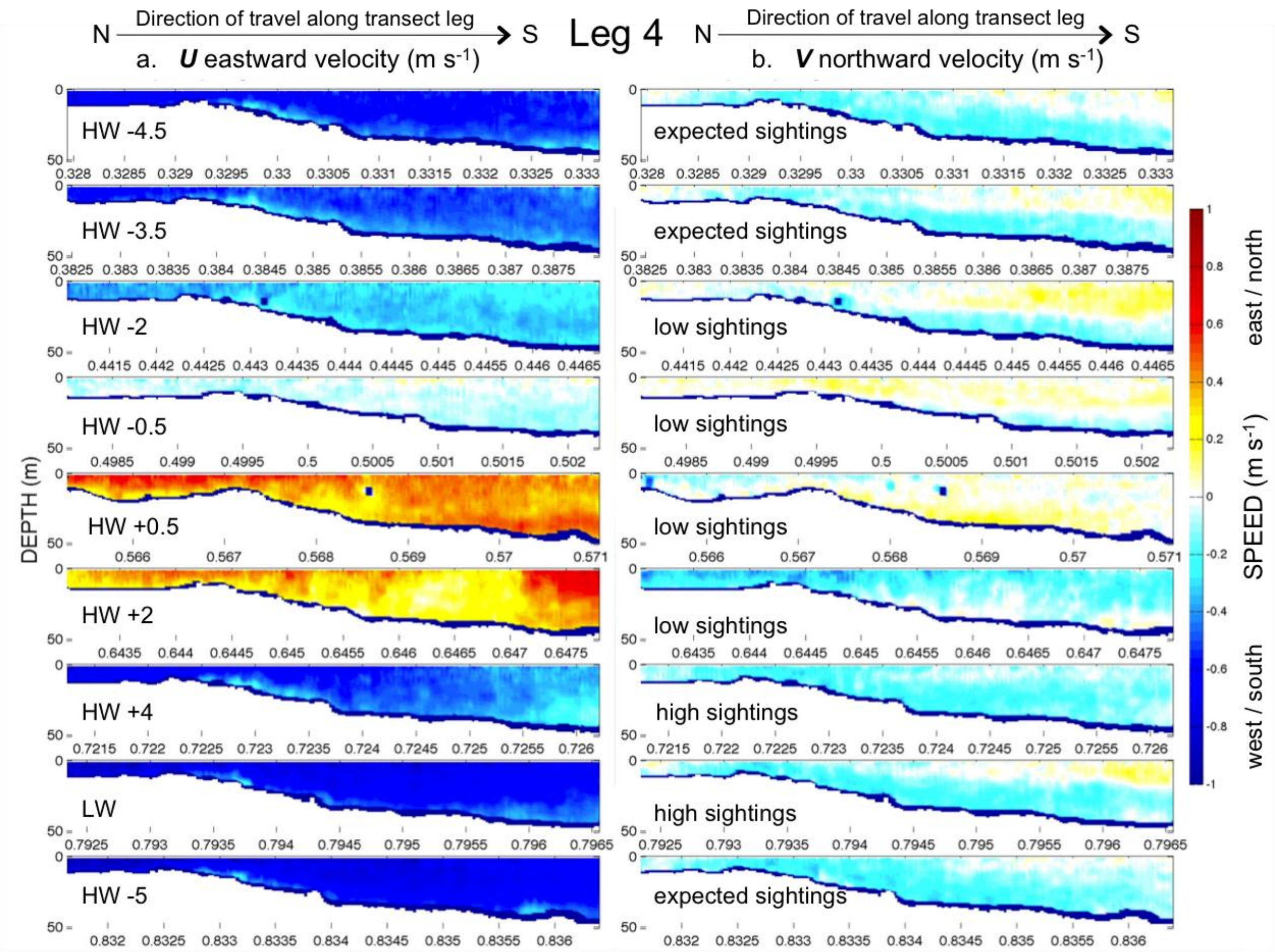


Figure 3.50: Current velocity profiles from leg 4 (travelling north to south) of the ADCP survey of the SWSW survey area, carried out 11th July 2011 from the RV Callista. Data are from a full tidal cycle. Decimal time relative to HW (0 and 0.5) is given along the x axes and water depth along the y axes. Current velocity is colour scaled with a) the eastward velocity component scaled from east in red to west in dark blue and b) the northward velocity component, colour scaled from north in red to south in dark blue. The timing of each profile relative to HW and to relative density of porpoise sightings is labeled. ADCP data processed by Dr. P. Hosegood, Plymouth University.

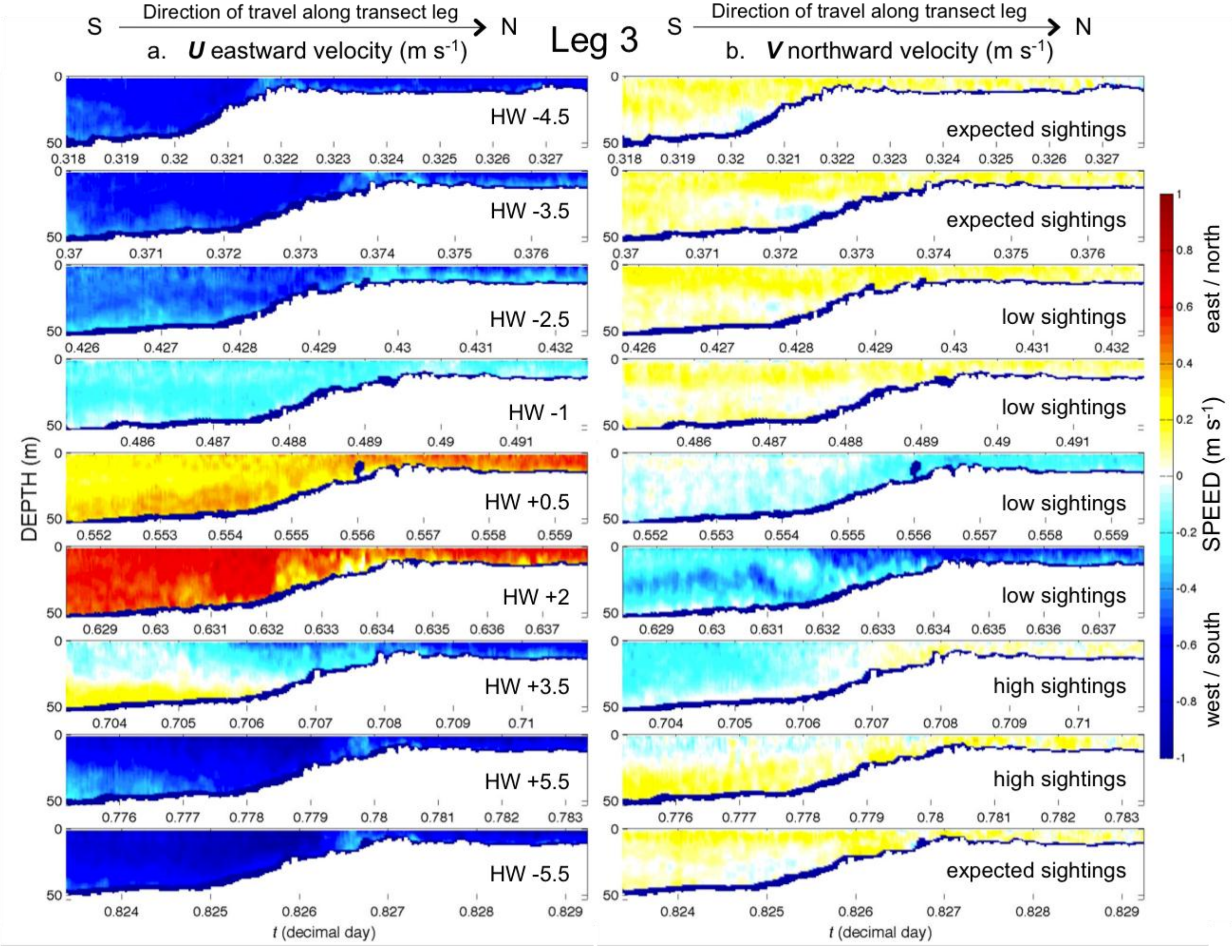


Figure 3.5132: Current veolcity profiles from leg 3 (travelling south to north) of the ADCP survey of the SWSW survey area, carried out 11th July 2011 from the RV Callista. Data are from a full tidal cycle. Decimal time relative to HW (0 and 0.5) is given along the x axes and water depth along the y axes. Current velocity is colour scaled with a) the eastward velocity component scaled from east in red to west in dark blue and b) the northward velocity component, colour scaled from north in red to south in dark blue. The timing of each profile relative to HW and to relative density of porpoise sightings is labeled. ADCP data processed by Dr. P. Hosegood, Plymouth University.

3.4 Discussion

3.4.1 Temporal patterns

There is temporal clustering in the porpoise sightings data at a number of scales. Seasonality in the sightings of porpoises within the survey area is indicated by lowest sightings during August and early September and an increase from then onwards (figure 3.27). This is consistent with other visual surveys, whose results indicate the local area is important for porpoises throughout the year, with an increase in numbers in autumn and winter (de Boer and Saulino, 2009; Pikesley et al., 2011; Leeney et al., in press, N. Tregenza pers. comm).

It is important to note that the C-POD data did not show as consistent a pattern in seasonality as the sightings data (figure 3.37). The models of the presence-absence and presence only (DPM per hour) acoustic data from the three C-PODs found different months to be most important (figures 3.42, 3.43, 3.44 and 3.46). This discrepancy between the seasonal patterns suggested by the visual monitoring and the acoustic monitoring data is a key finding and has serious implications for single method surveys. This issue was also noted by Embling (2008) who found that, even after including survey effects that ought to account for differences between acoustic and visual methods, models of data from the two sources found different environmental variables to be important. It is possible that the differences between the two datasets may be due to increased visibility under particular environmental conditions, for example if there were seasonal changes in foraging behaviour associated with differential prey availability, these may cause different behaviour at the surface that give more obvious cues and increase the availability of porpoises for inclusion in the visual survey.

The inability of the two monitoring methods to consistently capture patterns in temporal distribution is also shown by comparison of the effort-corrected sightings per day and DPM per day (daytime only, 0700 – 1900, figure 3.40). These two measures are not directly comparable, but it would be assumed that their levels ought to be related, as they are both taken to represent relative use of the survey area by porpoises. The mismatch in this comparison is likely to be as a result of both the C-POD's ability to detect animals under the surface and also their limited range; which effectively means the availability of porpoises for detection with the two methods is likely to be different; one is surveying porpoises at the surface within the entire study area and the other is surveying porpoises under the surface within a very small proportion of the survey area. In addition the 'control' C-POD is not within view from the SWSW watchpoint, therefore there is no reason to assume that the patterns of detection there would match those in the visual survey.

At a finer temporal scale, hour of the day was found to be a significant predictor of both porpoise sightings and acoustic detections, with the middle of the day having the lowest proportion of sighting/detection positive hours. The acoustic data consistently shows strong evidence for high levels of nocturnal porpoise activity in the survey area, a finding which is supported by Todd *et al* (2009) and Carlstrom (2005), who also found higher levels of acoustic detections during the night.

Although all three of the CPODs recorded more detection positive minutes during the night than during the day, the amount of deviance explained by time was less in the reef margin models of the acoustic data, where there was more variation in activity with time of day compared to the other two C-PODs. These results may reflect a difference in the way the porpoises use the more tidally dominated reef margin area and the 'eastern' and 'control' C-POD locations, where there is less complex topography, which presumably affects current flows. The longer encounter duration at the eastern (25 min) and control (54 min) C-PODs compared to the reef margin (14 min) also suggests a different pattern of use of these physically distinct areas, but it is not possible to tell from the data presented here whether specific behaviours such as foraging or resting were more frequent in one or other location.

The diel patterns in the porpoise acoustic activity recorded at the C-PODs may simply be the result of an increase in echolocation for navigation and exploration of the environment in poor light. It may alternatively represent an innate circadian rhythm, or be a response to external factors such as activity of prey species. Carlstrom (2005) and Todd (2009) examined and compared the porpoise click characteristics recorded during the day and night and both suggest that the night time activity was associated with foraging, indicated by the specific click characteristics recorded (buzz clicking identified by low inter-click- intervals). It will be possible to interrogate the acoustic data collected in this study in this way too, but was not feasible in the timescale of this thesis.

Studies reporting the distribution and behaviour patterns of lesser sandeel (*Ammodytes marinus*), which is an identified porpoise prey species (Santos and Pierce, 2003), suggest that they prefer areas with depths between 20 – 100 m that have coarse to medium grained sandy substrate (Wright et al., 2000; van der Kooij et al., 2008). These criteria are fulfilled at the eastern and control C-POD locations and are also found offshore of the reef margin in the deeper water beyond the rocky topography (Connor et al., 2006); suggesting a good likelihood of sandeels around the survey area. Although sandeels are known be most active in the water column during the day, and buried in the sand at night (Freeman et al., 2004), they may be more vulnerable to porpoise predation when buried because of the porpoise's echolocation ability, which allows them to detect and capture buried prey (Kastelein et al., 1997). It may be that this feeding mechanism is more efficient than pursuing the fish in the water column during the day.

Atlantic mackerel (*Scomber scombrus*) are another potential porpoise prey species (Santos and Pierce, 2003) that are known to inhabit the survey area. Although particulate (active pursuit) feeding by mackerel is dependent on light level, it is unlikely that light levels affect their ability to filter feed and they are therefore able to school and feed through the night (Macy et al., 1998). As a result of their echolocation abilities, the porpoises are not dependent on vision for prey capture, and may therefore find it easier to forage during the night, not only in response to the nocturnal behaviour of their prey, but also due to the reduced ability of their prey to detect them under low light conditions.

3.4.2 Spatial patterns

There is strong evidence for spatial clustering in the harbour porpoise sightings data from the SeaWatch SW visual survey. The highest areas of porpoise relative density were significantly associated with deeper parts of the survey area where the steepest slopes are found, in particular at the reef margins to the south and southeast. The importance of this part of the survey area is also identified in the C-POD acoustic detection data, with highest detection rates recorded by the C-POD located at the southern reef margin.

Although broader scale analyses have found positive links with porpoise sightings and areas of specific bathymetric habitat, such as moderate depth (Goodwin and Speedie, 2008; Marubini et al., 2009) and high slope (Pierpoint, 2008; Skov and Thomsen, 2008) few of these studies have been able to provide quantitative data on the physical mechanisms that may be at the root of this association. In a satellite tracking study of porpoises in the Bay of Fundy it was found that the core utilisation areas of the tracked animals did not overlap, and that different individuals associated with *different* types of bathymetric features (Johnston et al., 2005). On further investigation there were found to be oceanographic similarities between the core areas, resulting from tidal-topographic interactions. This suggests that sole reliance on static physical features for the identification of key habitats may not accurately capture the complexities of the biophysical interactions and individual decisions involved in habitat selection (Johnston et al., 2005).

The spatial GAM for harbour porpoise relative densities within the gridded survey area performed reasonably well, explaining over 40 % of the variability in the sightings, but the model over-predicted densities in areas with high slope and depth. This is likely to be because dynamic variables were not included in the model, and therefore the fine-scale tidal topographic interactions at the site could not be accounted for in the predictions. Additionally, the residuals from the spatial model show evidence of bimodality, which suggests that a variable affecting sightings in a bimodal fashion was omitted from the model (figure 3.22-c). These results highlight the importance of combining static and dynamic habitat variables (and if possible data on fine-scale prey distribution) in predictive models of porpoise distribution.

In this case, it was not thought appropriate to include dynamic variables in the spatial model of relative density, due to there being multiple sightings within some cells and no sightings within others. The dynamic variables (such as tidal flow metrics) are linked to the time of sightings, therefore, for cells with multiple sightings it would have been necessary to calculate a grid cell average for the conditions under which sightings were made; and this average value may not appropriately represent the favoured conditions and may introduce noise and uncertainty into the model. For the same reason, it was not felt that survey-period-averaged conditions should be used to represent dynamic variables for the absence data (i.e. within the cells with no sightings). This approach may have been considered if the spatial dataset were larger and contained fewer zeros values.

3.4.3 Evidence for tidal-topographic controls

Tidal flow group, based on the general flow direction and speed, was shown to significantly influence the timing of porpoise sightings when tested independently, but this was not consistently supported by the GAMs for the sightings or the acoustic data. When all years of sightings data were pooled, there were shown to be significantly higher than expected numbers of sightings in strong westerly flows (HW +2 to LW) than during the strong easterly flow periods and slack water (table 3.7). This same falling-tide period was identified by the binomial GAMs as having a positive influence on the presence of porpoises in the visual surveys from 2009 and 2010. In addition, time to high water was significant in predicting the frequency of acoustic detections on the eastern and reef margin C-PODs, with this same period in the tidal cycle associated with higher numbers of detections per hour. The GAMs for the data from the control C-POD show a different relationship between porpoise presence and tidal height, with a higher probability of detection around low and high water, but not during mid-tide periods (when the porpoises were more likely to be detected visually and acoustically at the reef itself). This could potentially indicate a movement between the two sites, with preferences for each during different tidal states.

Although the rate of sightings and acoustic detections is significantly influenced by tidal period (tables 3.7and 3.14), there is no indication of a shift in the core density within the survey area as tidal conditions change (figure 3.36 and table 3.11). This may be the result of a loss of power in the statistical analysis when the sightings data are split across the four tidal groups or between the inside and outside kernel areas, which results in relatively small sample sizes, and in the case of the presence-absence kernel models, a serious level of zero-inflation. Alternatively, this result may simply represent an overall preference for the deeper water off the reef margin, or an overriding tendency to avoid the faster flowing and more turbulent areas on the ‘reef flat’. Avoidance of this part of the reef is supported by the paucity of harbour porpoise sightings within the shallower part of the reef (figures 3.11 and 3.15); despite a theoretically higher visual detectability in this section of the survey area, which is closer to the observers at Gwennap Head. The porpoises were clearly not reacting to the time in the tidal cycle itself, they were presumably responding to some aspect of the speed and direction of current flow. Yet, the modelled speed and direction data from POLPRED (CS20) were not found to be significant predictors of porpoise activity in either the models of sightings or acoustic detections. It is considered that this is an issue of resolution, where the modelled data is not accurately predicting the very localised flow conditions at the reef.

Embling *et al* (2010) found similar results to those reported above in their study of harbour porpoise distribution in western Scotland. They report that dynamic tidal variables did not significantly affect the location of core use areas, but did affect the density of sightings within them. The study found that higher densities of porpoises were recorded around spring tides and during the slack tide period, with a notable reduction in density associated with the areas and periods of strongest tidal flows, which was around 2 knots (~ 1 ms^{-1}) (Embling et al., 2010). Our study has identified a negative relationship between frequency of sightings and strong easterly flows within the study area, which occur during the flood tide, and can reach more than 1 ms^{-1} (2 knots) particularly over the shallower the reef top (figure 3.48-a and b). Even so, the situation in this case does not seem to simply relate to flow speeds, as the data suggest that highest presences and relative density of porpoises were recorded during equally strong westerly flows.

There is some indication of an effect of position in the spring-neap cycle, highlighted by the selection of tide-height and tide range in the acoustic detection models, although the effect of tide range and height were not uniform between C-POD sites, with a higher likelihood of detection in low to moderate tidal range periods at the eastern (figure 3.42-a) and reef margin (figure 3.47-b) sites and a positive relationship with tide range at the control site (figure 3.45-a). This result suggests that tidal dynamics around the reef margin are likely to be different than at the control site. Unfortunately the ADCP transect did not extend to the control C-POD position due to time constraints, therefore there is no evidence of different flow patterns at the C-POD control site, but it seems likely that an area of shallow-sloping, sandy seabed would be less tidally dominated and presumably have fewer fine scale flow features than the topographically complex Runnelstone Reef.

Previous studies have found various associations between tidal flow speed and direction and porpoise presence in an area. It is expected though, that this relationship is extremely difficult to generalise, as it will be mediated through local tidal patterns and absolute speeds in an area, as well as the effect of flow on the behaviour of local prey species and site-specific tidal-topographic interactions. Embling *et al* (2010) describe a preference for slack period and slowest flow speeds (although even slow flow in their study area is considerably faster than the maximum flow reported in other studies), whereas Pierpoint (2008) and Marubini (2009) show evidence for a preference of high flow speeds and tide races in their respective study areas of Ramsey Sound (Wales, UK) and the Greater Minch (northwest Scotland UK). It is particularly notable that the studies of Marubini (2009) and Embling (2010) show different tidal flow preferences, even though their study areas were closely associated and even overlap in places.

There are a multitude of studies that report associations between meso to large-scale oceanographic features and productivity; noting evidence of trophic cascades and increases in the densities of megafauna (e.g. Holligan, 1981; Schneider, 1982; Ryan et al., 2005; Worm et al., 2005; Palacios et al., 2006; Doniol-Valcroze et al., 2007; Kai et al., 2009). Although the increase in primary productivity and the attraction of larger predators to these features is reasonably well documented, there is generally a lack of understanding of the physical or biological mechanisms that lead to these features being attractive areas to remain in for higher predators, and surveys have not been able to consistently show that the areas support increased zooplankton concentrations (Simpson and Sharples, 2012b). This is an important finding, as zooplankton is generally regarded as a key trophic link in the marine ecosystem between primary production and higher predators. In addition, the processes that may be involved with bio-physical coupling at fine scales are extremely complex and not well understood.

This study is one of few to investigate very fine-scale (100’s of m) habitat associations of cetaceans within a relatively small survey area. The constant effort survey data and highly resolved supporting environmental data represent an advance on some of the previous studies (Mendes et al., 2002; e.g. Ingram et al., 2007; Pierpoint, 2008; Skov and Thomsen, 2008; Bailey and Thompson, 2010) and mean that we can attempt to better understand the fine-scale functional mechanisms that are the basis of the apparent habitat associations often reported in studies on this species. Hastie *et al* (2003) had a similar aim for their study of the behaviour of bottlenose dolphin (*Tursiops truncatus*) in a coastal monitoring survey in NW Scotland. They successfully identified that “submarine habitat characteristics may be a significant factor in the foraging efficiency of dolphins”, but were not able to provide evidence of the physical features, which enable this improved foraging.

Recent works by Scott *et al* (2010) and Embling *et al* (2012) have made an effort to elucidate the biophysical links between current flow and biological systems at a small-scale in shallow coastal areas. Their studies provide empirical evidence of links between tidal forcing, chlorophyll, fish and seabirds. At these small temporal and spatial scales it is extremely unlikely that in situ enhancement of productivity is occurring, therefore evidence points towards accumulation of plankton as a result of physical forcing and swimming behaviour (dependent on species ability and buoyancy), and the subsequent attraction of predatory species (Genin et al., 1994; Genin, 2004). How the higher predators key into these aggregations is again, not well understood; but is assumed to be associated with optimal foraging behaviour, which has been shown to be similar in a wide range of marine groups and species (Sims et al., 2008).

Johnston *et al* (2005) highlighted key oceanographic features in the Bay of Fundy (Canada) that were found to be associated with core use areas of satellite-tracked and visually-monitored harbour porpoises. Their results suggest that island wakes created by tidal-topographic interaction lead to aggregations of passively transported zooplankton species, supporting the hypothesis of Hastie el al (2004) that the link between static bathymetric features and cetaceans is mediated through oceanographic processes that affect foraging success. The Canadian group initially used remote sensed synthetic aperture radar (SAR) data to visualise oceanographic features (Johnston et al., 2005), this method is beneficial in that it can pick up meso-scale features (100’s to 1000’s of metres), which *in situ* surveys may not detect; but it relies on there being a surface expression of the feature and therefore may not identify very fine-scale flow patterns at depth.

The ADCP survey data presented here (section 3.3.4) provides some interesting insights into tidal-topographic flow features that may be influencing harbour porpoise activity at a fine-scale within the SWSW survey area. The current flow data shows that there were tidally constrained hydrodynamic features associated with periods of the tidal cycle that had higher than expected porpoise sightings and acoustic detection rates at the reef margin C-POD. These features include frictional bottom boundary layers along leg 4, which form in the *U* (easterly) component during westerly flows only (figure 3.50-a), and periods of two-layered flow in the *U* and *V* components along leg 3 that were only present during periods of the tidal cycle associated with the highest sightings (figure 3.51-a & b, profiles 7 and 8). Both of these feature types were associated with higher than background levels of turbulence and were in the vicinity of the reef margin (within the 50 % UD delineation, figure 3.49).

A link between elevated turbulence and increased porpoise sighting and detection rates may be expected, given the causative link between shear and the generation of turbulence (Simpson and Sharples, 2012c) and the coupling of turbulence and the distribution and abundance of marine productivity and species (Mann and Lazier, 2006). But it should be noted that there were also shear boundaries and turbulent features present in the ADCP data during other periods of the tidal cycle too (particularly in the *V* component along leg 4, figure 3.50), when porpoise sighting rates were lower; suggesting that the situation is extremely complex and there may be specific characteristics of the shear features that cause either attraction or avoidance by the porpoises.

Shear and turbulence were highlighted as important hydrodynamic controls of both phytoplankton and zooplankton distribution, whose effects are mediated at very small scales, but which can influence the marine environment at large scales (Genin, 2004; Johnston et al., 2009). Shear boundaries can lead to the formation of phytoplankton ‘thin layers’, where the organisms are stretched out along spatially and temporally limited shear zones, identified by peaks in fluorescence, most likely as a result of being advected by turbulent processes and then ‘trapped’ between opposing flows (Johnston et al., 2009). These ‘thin layers’ may be detectable and attractive to predators such as zooplankton because of chemical cues that are smeared along the shear boundary (Jenkinson, 1995).

It is established that shear and the resulting turbulence have a dome-shaped impact on predation/prey encounter rates for zooplankton. Moderate levels of turbulence act to increase the likelihood of planktonic prey moving into a predators’ ‘perceptive range’ (Jenkinson, 1995). Extreme turbulence can have a negative effect on capture efficiency, as a result of prey being advected into, and out of, a predators ‘perceptive range’ before it has the chance to react (Kiorboe and MacKenzie, 1995). Clearly the exact effect of turbulence will be species-specific and will depend not only on the amount of turbulence and the specific animals’ turbulence thresholds; but also the predators’ perceptive range, its reaction time and its feeding mechanism. Nevertheless there is evidence to suggest that shear zones affect the fine scale foraging opportunities of zooplankters and therefore that they may selectively forage in these areas (Mann and Lazier, 2006). It is worth noting here that it is has been shown that larger zooplankton and meroplankton are independent of turbulent flow in terms of their movement (e.g. Yamazaki and Squires, 1996), therefore they are likely to be able to actively move into areas of optimal turbulence in order to increase foraging opportunities (McManus and Woodson, 2012)

Based on the spatio-temporal distribution of porpoise sightings and acoustic detection data, and the ADCP data presented in this work, it is possible that the porpoises were exploiting those periods during which bottom boundary layers and specific mid-depth shear layers present. These turbulent features may lead to physically aggregated or constrained phytoplankton, which lead to aggregations of grazing zooplankton and their fish predators (e.g. sandeels and mackerel); in turn affecting porpoise foraging due to the tidally predictable and enhanced feeding opportunities created by fine-scale elevated shear and turbulence. This hypothesis is supported by Johnston and Read's (2007) follow-on study to their earlier investigations in the Bay of Fundy. ADCP surveys were undertaken to better understand the oceanographic processes associated with the island wake previously reported (Johnston et al., 2005). The results showed the evolution of tidally induced vertical shear boundaries around small eddies created by the island wake and identified high concentrations of sound-scatterers (zooplankton and fish) in the acoustic data along these shear boundaries. Thus providing direct evidence of increased foraging opportunities for porpoises and other large marine species along associated with the shear (Johnston and Read, 2007).

The spatial and temporal consistency of the flow features identified in the SWSW ADCP survey and the causative biophysical links between them and the porpoises will clearly require further investigation. Characterisation of the ecological significance of the identified hydrographic features will necessitate concurrent collection of physical and biological measurements at fine temporal and spatial scales. A repeated ADCP survey over the transect route, perhaps extended to encompass the 'control' C-POD site, and carried out at a variety of periods within the spring-neap cycle will provide more robust evidence for tidal-topographically control flows and potentially enable a local scale tidal model to be created (e.g. Skov et al., 2008). Collection of biological acoustic backscatter data using an EK-60 fish-finder and the collection of plankton samples during the ADCP transect would add valuable direct biological evidence of spatial and/or temporal concentration of prey. Salinity, temperature and fluorescence data were collected at regular positions along the ADCP transect routes in July 2011, but these have not yet been analysed. The preliminary results indicate the development of spatially and temporally restricted deep chlorophyll maxima around the reef under specific flow conditions. This data will need to be analysed in-detail and may provide more information about the physical effect of the flow regime on phytoplankton and suggest links between the trophic levels.

3.4.4 Conservation and management context

Increasing the understanding of habitat associations of marine mega-vertebrates and, perhaps more importantly the mechanisms behind these perceived preferences, is a key research area within the context of protection of vulnerable species. Recent studies indicate that simply identifying appropriate static habitat for a species, using density and occupancy data, may not be sufficient and that there are complex interactions between static and dynamic variables in the marine environment (e.g. Johnston et al., 2005; Scott et al., 2010; Embling et al., 2012). As discussed previously, it is difficult to understand these interactions fully and it would be much easier to protect identifiable static environments as opposed to dynamic features; but without an appreciation of the complex systems that control an animal's habitat choices and the scales of these effects, protection measures are unlikely to be optimally effective.

The EU Habitats Directive requires active protection for the harbour porpoise by all member states within their Exclusive Economic Zones (EEZs) and the specific designation of Special Areas of Conservation (SACs) for the species (EU Habitats Directive 92/43/EEC 1992); a network of these sites was due to have been created in the UK by 2012. The guidelines for site selection of proposed porpoise SACs states that the area should contain key sites, that are used regularly by high numbers of the species and they 'must be clearly identifiable areas representing the physical and biological factors essential to the species life and reproduction'. In order for these sites to be identified, the species' interactions with their physical and biological environment must be better understood.

UK waters are home to a significant number of Europe's harbour porpoises (Hammond et al., 1995; 2002; Hammond, 2006), but very few SACs have been proposed and there is currently only a single protected site designated for the species within UK waters. This is likely to be a result of the clear difficulties in the identification of key sites for mobile marine species, in particular one, like the harbour porpoise, that is difficult to monitor as a result of its size, shape and surface behaviour. The Skerries and Causeway coastal SAC is in the waters of County Antrim in Northern Ireland and was announced on the 27th July 2010 (nidirect, 2012). The site's specification for porpoises has been based on high densities compared to other surveyed sites in Northern Ireland, the year-round presence of the species and the importance of the site to mother and calf/juvenile pairs (N.I.E.A., 2010). The proposal documents specifically mention key oceanographic features within the area of the SAC as a basis for designation (N.I.E.A., 2011). These features (including coastal headlands, strong tidal currents, tidal races and eddies) are understood to "provide enhanced foraging opportunities for feeding on aggregations of prey items", and as a result, provide key habitat for porpoises, although no direct evidence of a mechanistic link between the mentioned features and the porpoises is provided (N.I.E.A., 2010, 2011).

The harbour porpoise is also a target species for the Marine Strategy Framework Directive (MSFD) (2008/56/EC), listed within the 'mobile species' functional group. The Directive requires a baseline assessment of their status in UK waters (for which the results of the 2005 SCANS II survey will be used) and regular monitoring and assessment in order to achieve 'Good Environmental Status' (GES). The aim of the Directive is to achieve GES for all target indicators by July 2014. The criterion targets for marine mammals under the MSFD state that 75 – 90 % of the indicator species must be monitored and there must be no statistically significant contraction in range or reduction in abundance. It is acknowledged by the scientific advisory group that there are not sufficient monitoring programmes in place to be able to assess these criteria for cetaceans in UK waters, and they suggest that these programmes are unlikely to be in place until 2018 (Moffat et al., 2011). This highlights the need for ongoing monitoring programmes, such as SeaWatch SW, and an improvement in our understanding of the best practice for monitoring surveys and the habitat drivers for harbour porpoise distribution.

Although there are not deemed to be direct threats to the porpoises recorded within our study area, the Runnelstone reef has been proposed as a Marine Conservation Zone within the network of marine reserves that are to be created under the Marine and Coastal Access Act 2009 (aka 'The Marine Bill'). The proposal for the designation of the survey is on the basis of benthic and water column features, with specific mention of the importance of the area for harbour porpoises. A map of the proposed 'Land's End MCZ' is given in appendix 5.

There is an argument that small, static marine protected areas can do little to protect mobile marine species. At the least, sites designated for the protection of wide-ranging species need to be strategically placed in order to either protect a significant proportion of the habitat of a vulnerable species' or provide networks/corridors for movement along known routes (Roberts et al., 2001). Marine reserves are often the go-to solution for marine protection, and have been widely designated for cetaceans (Hoyt, 2005), with sites most commonly selected on the basis of 'critical habitat' focussed on important feeding and or calving grounds. It is clearly very important to protect these key areas, but the effectiveness of the overall protection that these measures provide may be limited because the animals are offered little protection over the remainder of their range. There is also very little evidence that fixed marine protected areas are successful tools for the effective conservation of mobile species, although this may be as a result of their relatively recent designation and therefore not enough time having passed for a fair assessment of their efficacy. The first empirical evidence for the success of marine protected areas for cetaceans was reported recently for Hector's dolphin (*Cephalorhynchus hectori*) in the Banks Peninsula Marine Mammal Sanctuary (New Zealand); a protected area that has been in place for over 15 years (Gormley et al., 2012). This is a promising result and indicates that for certain cetacean species, with limited range and high site fidelity (Rayment et al., 2009), marine protected areas can be a successful management tool.

It is likely, considering the time-pressure on SAC designation in Europe, that sites will be identified and designated based solely on occupancy and density of harbour porpoise, without understanding the habitat interactions behind the high densities. This approach is likely to identify areas where the most information is available (monitoring sites and coastal areas) and these may not necessarily represent the best habitat for the species, instead they represent the most accessible and well-recorded sites. An alternative approach to SAC site selection is predictive habitat modelling, which has been presented here at a fine spatial scale, but would clearly need to be extended to be useful at a national protection level. Although this approach, at least, allows areas beyond those directly monitored to be considered as potential SACs (e.g. Embling et al., 2010); without a better understanding of the functional mechanisms of observed and predicted habitat associations, we will lack an understanding about how changes in the environment may affect the way that porpoises use the sites.

It is hoped that the data presented in this chapter will help to improve harbour porpoise monitoring methods and direct future research focussed on the fine-scale hydrodynamic controls of porpoises within hot-spot areas, in order to better understand the attraction of some sites over others. In addition, the open discussion of land-based monitoring methods presented in chapter 2 can be of use to others designing monitoring surveys. The results also identify a potential issue with using single survey methods (visual/acoustic) and highlight the short and medium term variability in porpoise presence, which again has implications for the design of monitoring studies.

3.4.5 Limitations

Some limitations were addressed as part of the main discussion, but other noteworthy points are listed below.

3.4.5.1 Survey limitations (see also chapter 2)

Visual monitoring can only ever record the surface activity of the porpoises and is also significantly affected by sea state as detailed by (Palka, 1996) and indicated by the reduction found in sighting rates in the SWSW survey with increasing sea state. Sea state was found to be the most significant predictor of presence-absence in the visual survey data for all years apart from 2008, explaining between 6 and 8 % of the deviance in the models. This is an issue with all visual monitoring surveys of cetaceans, but in particular the harbour porpoise due to its small size and inconspicuous behaviour at the surface. The ability to account for this effect is limited to the inclusion of the sea state as a variable in models, as it is really not practical to use only data collected in sea-states 0 and 1, as these conditions were rarely recorded at our survey site. This is most likely as a result of the exposed and tidally dominated environment in which the survey is based, and the effect of tidal flow and related turbulence on the surface of the water within the survey area.

The C-PODs are range limited, therefore can only survey a small area of the sea; even so they have the benefit of recording throughout the day and night and can be good indicators of relative activity levels and habitat use (Gillespie et al., 2005; Bailey et al., 2010). Wave height and direction can potentially affect acoustic detection of cetaceans (Urick, 1983; Au and Hastings, 2010), but were not found to have a significant impact on the presence of detection in the binomial models of presence-absence of detection per hour of deployment (table 3.14). In hours when detections were recorded, wave height was found to have a negative correlation with the number of detections recorded per hour at the reef margin and the eastern C-PODs, but this was not the case at the control C-POD (table 3.14). This may reflect the different effects of increased wave height on wave-related noise around the Runnelstone reef and at the control site. It seems likely that the interaction between waves and topography at the reef may increase ambient noise levels, potentially impacting on the reliability of the C-POD's to detect porpoise click trains; but not so much that they remain totally undetected within hourly time periods if the animals remain within the vicinity of the C-POD.

The ADCP data presented can only be used in a descriptive way. It is not valid to attempt to interpolate temporally or spatially between the transect runs or legs due to the fine-scale complexity of the flow regime at the study site. The data are also only directly relevant to the time in the lunar spring-neap cycle that they were collected, although they are likely to be indicative of the patterns in flow experienced at other times.

The results from both the C-POD and visual monitoring results are related only to the July-Oct period and may not be representative of the patterns in porpoise density and distribution during spring and winter. In fact, it is understood from personal communication with Dr. Nick Tregenza (of Chelonia ltd. who manufacture the C-PODs), that data collected year-round at our site indicate higher porpoise activity during the late autumn and winter.

3.4.5.2 Analyses and statistical model limitations

Observations in space or time cannot generally be thought of as independent of each other and observations that are close to one another are likely to be similar (autocorrelated). This patterning can provide useful information about the influences underlying the observations, but it challenges the independence assumption of many statistical methods (Dormann et al., 2007). The models for the C-POD data showed significant residual auto-correlation to a maximum lag period of 1-hr. This non-independence in the model residuals undermines the model results to some degree, as it can lead to inflation of standard errors and increase the potential of finding significance where there is none (Dormann et al., 2007; Zuur et al., 2009). Dependence in model residuals may be indicative of a missing predictor covariate. To deal with the problem the model should be re-run with a structure that allows for dependence or accounts for it (for example Generalised Additive Mixed Models (GAMMs) or generalised estimating equations, (GEEs).

In all cases the binomial model for hourly presence-absence of porpoise detections perform less well than the Poisson model of frequency of DPM per hour (using presence only data). This is likely to be as a result of the 0-inflation in the binomial data due to much higher numbers of absence hours than presence hours. This is also an issue that affected the sightings dataset. Zero-inflated models have been much developed in the last 10-years, but packages have only relatively recently become available for statistical programmes such as “R”. Zero-inflated binomial GAMs were run on the survey data using the ‘zigam’ and ‘cozigam’ “R” packages (Lui and Chan, 2010), but the lack of documentation for, and model checking abilities of, these new packages meant that the resulting models were hard to validate and interpret and were not used.

Kernel methods were used to analyse spatial clustering in the sightings data and the resulting 50 % density isopleth was selected to define a core use area. Although bandwidth optimisation was used and the final bandwidth selected does account somewhat for the level of error on the positional estimates, it would be an improvement in the analysis method to deal with the error in a more quantitative way. This can be achieved by using de-convoluted kernel density estimates, which allow propagation of the error on the locations of points into the kernel density surface. It would be interesting to compare the kernel estimates created when the error is directly accounted for, with those based on the original dataset. Another possible method for this comparison would be to use bootstrapping methods with point ‘jittering’. This would create multiple replicate datasets where points are located randomly within the average error of their original position and kernel density estimates could then be calculated and compared using these (jittered) bootstrap replicate datasets.

3.5 Conclusions.

In line with the aims and objectives of this chapter, the fine-scale spatial and temporal patterns in the porpoise sightings data from the SWSW survey were explored and modelled as a function of a suite of environmental variables. The results highlight a clear diel pattern in activity around the survey area in both the visual and acoustic survey data, which is supported by other acoustic detection studies. This pattern is likely to be related to the availability of prey within the survey area, such as mackerel and sand eel, whose diel behaviour patterns may lead to improved foraging opportunities for porpoises during the night.

Spatial clustering is evident in the location of porpoise sightings around the reef margin, and is significantly associated with areas of steep topography and moderate depths. Similar associations with bathymetric features have been identified in previous studies of porpoise and other cetacean species; but this study goes one step further by identifying possible mechanisms for this relationship, using fine scale current profiling data. The ADCP data identify tidal flow features such as bottom boundary layers and topographically driven shear boundaries, which were spatially and temporally constrained to the periods and locations of highest porpoise sighting densities. These fine-scale oceanographic features may be important in aggregating planktonic organisms, leading to improved foraging opportunities for fish and subsequently porpoises, at specific areas within the Runnelstone Reef survey site at scales of hours to days.

The inclusion of different data collection methods in the porpoise survey (visual and acoustic), and the differences in the seasonal pattern of distribution from the resulting datasets provide important methodological information and suggests that serious consideration should be given before undertaking single-method surveys when assessing seasonal variability in relative densities.

Description of fine scale species distribution can provide important information on key habitats, trends in variation of habitat use (e.g. day and night) and animal-environment interactions that give insight into potential drivers of distribution. The data presented in this chapter build on the little research available about the key physical drivers of fine-scale porpoise distribution and provide new insights into specific hydrodynamic features created through tidal forcing that may be important for creating foraging opportunities at a local scale. These spatially and temporally predictable dynamic habitats are likely to be especially important for porpoises due to their small size, high metabolism and requirement for regular feeding. Although many aspects of the biophysical interactions between harbour porpoises and their immediate environment remain unanswered, the data presented represent an increase in knowledge and highlight the complexities of the relationship between the animals and their physical habitat.

Chapter 4 Temporal variability in basking shark (*Cetorhinus maximus*) sightings: Is there evidence for temporal coupling with meso-scale thermal ocean fronts?

The distribution patterns of marine mega-vertebrates and their prey are fundamentally linked, but the relationships underlying this association are extremely complex and have proven difficult to predict (Certain et al., 2011). There are likely to be many factors influencing an animal's distribution, each potentially acting at different spatial and temporal scales and having a level of associated variability. The strongest identified links between predators and prey are locations or periods of predictable increases in prey availability (Mendes et al., 2002; Royer et al., 2004; Worm et al., 2005; Palacios et al., 2006; Kai et al., 2009). For this reason, there has recently been an increased focus on the influence of thermal fronts in the marine environment, which are widely recognised as being areas of increased productivity and have been shown to attract and aggregate predatory species (Bakun, 2006; Etnoyer et al., 2006; O'Hara et al., 2006; Doniol-Valcroze et al., 2007; Gannier and Praca, 2007; Priede and Miller, 2009).

The impact of fronts on basking shark distribution is a question of particular interest because of the link suggested by a number of previous studies, but which has not so far been examined quantitatively. The aim of this research chapter was to investigate whether there is evidence for links between dynamic environmental covariates and the timing of shark peak counts recorded in the effort-based SeaWatch SW survey, at both real-time and lagged periods. The analyses used quantitative data relating to thermal front density and strength around the survey area. The results show no evidence for real-time effects of thermal fronts on the number of sharks sighted. There is tentative evidence that lagged or longer-term cumulative effects of frontal intensity may have had a positive effect on shark sightings during years when high numbers of sharks are present in the southwest region. The results are discussed with reference to conservation management policies.

4.1 Introduction.

4.1.1 Biology and ecology of the basking shark, *Cetorhinus maximus (Gunnerus, 1765)*

The basking shark is one of only three extant planktivorous sharks, the other two being the whale shark (*Rhincodon typus*) and megamouth shark (*Megachasma pelagios*). The basking shark and megamouth shark are both classified as Lamniformes, but each occupies their own family within the Order. The whale shark is in a different Order, the Orectolobiformes or carpet sharks, and it too is the only species within its family. The systematic separation of these three species indicates that the filter feeding traits they share evolved independently on at least three occasions. This theory is supported by genetic studies (Martin and Naylor, 1997).

The basking shark is the second largest fish in the world with a maximum-recorded length of 12.2 m and weight of 4 tonnes (Compagno, 1984; Lien and Fawcett, 1986). Matthews and Parker (1950) first described the anatomy and morphology of the basking shark and noted that the species has a large fusiform body which varies in colour from black, to various shades of grey and brown. The fins are correspondingly large and in adults, the first dorsal and pectoral fins are commonly over one metre in height with the caudal fin often being twice this size, although variability in relative fin sizes exists with age, size and sex of individuals (Sims, 2008). The head and huge cavernous mouth make up a large proportion of the front of the animal, with the large gill slits running almost the full circumference of the head, as shown in the photo in figure 4.1.

Figure 4.1: Photo of basking shark illustrating fusiform body shape, large mouth and long gill slits (photo by Dan Burton).

The large gill arches house the gill rakers, which are brush-like processes that emerge from the lateral edges of the gill arch (figure 4.2). Feeding occurs during forward swimming when the mouth and gill arches are held open, which acts to erect the gill rakers so that they can filter particles from the flow of water passing over them (Matthews and Parker, 1950). This mechanism of feeding is known as ram filtering.

Figure 4.2: Photograph of basking shark gill rakers (photo by Dan Burton).

The lack of gill rakers in some basking sharks caught during autumn and winter led early researchers to believe that the structures were shed during the winter months with an associated cessation in feeding until the spring, when new rakers were grown to coincide with seasonal plankton blooms (Parker and Boeseman, 1954). Further investigation discovered that many sharks captured or observed during winter retained their gill rakers and were found to have food in their stomachs. Observations of feeding sharks in the latter part of the year support this theory, as do more recent tracking studies, which indicate foraging behaviour occurs throughout the year (Sims, 1999; Weihs, 1999).

There is surprisingly little information available regarding basking shark biology and life history. Anatomical studies show that the basking shark is ovoviviparous (Matthews, 1950), meaning internal fertilisation takes place and embryos develop within egg sacs that are retained inside the body of the female until live birth occurs at full gestation. Gestation period is unknown but estimates vary from 1 year to 3.5 years (Sims, 2008). The developing fetuses are thought to be oophagous; feeding on unfertilised eggs supplied from the ovaries (Matthews, 1950). Despite the species being commercially harvested across its distribution for centuries (e.g. Matthews and

Parker, 1950; McNally, 1976; Sims and Reid, 2002), there is only one record of a 'pregnant' female, which delivered 6 pups after being caught by fishermen (Sund, 1943). If this record is accurate and representative of an average litter size, it indicates that the species has lower fecundity than other large shark species (Compagno, 1984). There have been no observations of reproductive behaviour or discovery of nursery areas, and only very few observational records of young basking sharks. Very little is known about age-growth relationships or age at maturity, although size of maturity is estimated to be at 5 - 7 m for males and 8.1 – 9.8 m for females, corresponding to estimated ages of 12-16 years and 16 – 20 years respectively (Compagno, 1984).

Basking sharks are planktivores, feeding primarily on zooplankton that is caught on the filtering apparatus attached to the gill rakers during forward swimming with the mouth open(Matthews and Parker, 1950). This ram filter feeding mechanism differs from that employed by both the megamouth and whale sharks, which use suction and gulping to force water from the mouth out through the gills (Clark and Nelson, 1997). The exact mechanism of trapping particulates on the gill rakers and subsequent transfer to the mouth has not been proven and it has been suggested that the rakers may not actually be responsible for capturing the prey, but instead create secondary flows within the oral cavity which cause concentration of particulates at the back of the throat (Sanderson et al., 2001; Sims, 2008). Using data collected on shark swimming speeds during feeding and mean zooplankton biomass in food patches, Sims and Merrett (1997) estimated that basking sharks could consume up to 30.7 kg day^{-1} if feeding constantly in productive areas.

Basking sharks, like many other large migratory species, manage to locate patchily distributed sources of prey over large distances. Sims *et al* (2006) compared tagged basking shark tracks with random-walk models within a heterogeneous prey field created using Continuous Plankton Recorder (CPR) data. Results showed the sharks had a considerably more successful prey-encounter rate than that yielded by the random-walk model (Sims et al., 2006). It is not known what mechanism allows the sharks to achieve this, but it is likely to involve some awareness of seasonal food availability (Sims et al., 2006) combined with proximal sensory cues (Sims and Quayle, 1998) and a probabilistic (Lévy walk) foraging pattern made up of a sequence of long straight movements interspersed by area restricted searches (Sims et al., 2008; Humphries et al., 2010).

There is also evidence that foraging strategy is altered in different habitats in response to changes in zooplankton vertical migration (Sims et al., 2005b). Data from archival tagging studies consistently show sharks undertaking vertical foraging movements in order to locate and exploit dense prey patches at depth (Sims et al., 2003b; Shepard et al., 2006; Gore et al., 2008; Skomal et al., 2009). The vertical diving behaviour of sharks seems to change according to the surrounding habitat (Shepard et al., 2006). This is potentially a reflection of different vertical migrations undertaken by their zooplankton prey in stratified versus mixed water bodies (Sims et al., 2005b). Alternatively, this behavioural change may be a response to more dispersed prey in turbulent environments as suggested by Lasker (Lasker, 1978), which is likely to influence foraging strategy (Humphries et al., 2010; Lundy et al., 2012).

On a local scale, basking shark feeding behaviour is influenced by zooplankton density (Sims et al., 1997; Sims and Merrett, 1997), with orientation towards concentrated food patches, containing greater numbers of larger prey items (Sims and Quayle, 1998). Sharks spend significantly more time in areas with zooplankton densities of > 3 g m^{-3} than those with < 1 g m^{-3} (Sims and Quayle, 1998), and have been shown to cease feeding at densities between 0.48 - 0.80 g m^{-3}, indicating the existence of a threshold, below which feeding is not profitable (Sims, 1999). Various post mortems and plankton sampling studies have shown that basking sharks primarily consume calanoid copepods (Matthews and Parker, 1950; Sims and Merrett, 1997), although whether this is simply a function of the dominance of calanoids within the plankton community composition in productive patches, or as a result of selective feeding by the sharks is unclear.

4.1.2 Distribution and habitat associations.

4.1.2.1 Distribution.

Basking sharks are found globally within boreal, temperate and, rarely, tropical seas. They are known to inhabit both coastal and pelagic environments. Figure 4.3 shows the established known range of basking sharks (shaded in red) along with recent satellite tracking data, which indicate their presence in the tropics (Skomal et al., 2009). Interestingly, during their time in the tropical seas around the Bahamas, the sharks mostly remained at depth, presumably preferring to stay in the cooler bottom water (Skomal et al., 2009). This may go some way to explaining why they were not previously reported from these areas.

Observations of basking sharks are highly seasonal throughout their range, with most sightings reported in coastal seas during summer months, associated with increased productivity (Sims and Quayle, 1998). Because of the basking sharks apparent disappearance during winter, a theory of deep-water hibernation was proposed by Matthews (1962) but has since been disproved (Sims et al., 2003b).

Satellite tagging studies have been invaluable in elucidating the broad-scale movement patterns of the species. Early tracking studies in the North Atlantic provided the first evidence that sharks remained active throughout the winter and associated with both shelf and shelf edge habitats (Sims et al., 2003b; Skomal et al., 2004). During winter the sharks were recorded utilising deeper water and areas further from the coast compared to the habitat occupied in the summer, but did not move into the open ocean (Sims et al., 2003b; Sims et al., 2005a).

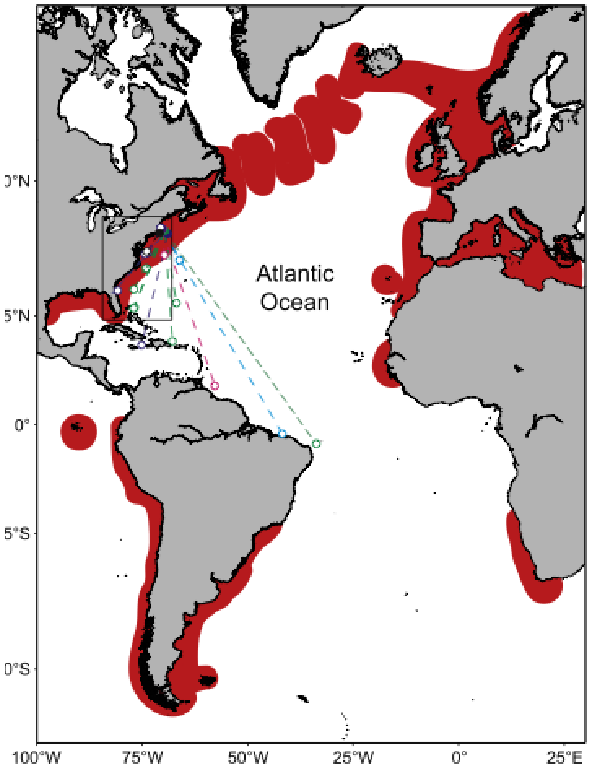


Figure 4.3: Known distribution of basking sharks indicated by red shading and new insights into range and distribution are revealed by tracks (dashed coloured lines) of individual sharks tracked during a study by Skomal *et al* (2009). Image from Skomal *et al* (2009).

More recent tag tracks returned some unexpected results (e.g. figure 4.3). In 2008 an 8 m female basking shark was tracked by Gore at al. (2008) moving west from the Isle of Man across the Atlantic to Newfoundland, Canada. The shark covered 9589 km in 81 days and exhibited regular deep diving (max. 1264 m) in the open ocean. This was the first evidence of Trans-Atlantic migration in the species and indicates a critical link between UK and North American populations. The Skomal *et al*. (2009) study tracked sharks tagged off the coast of Cape Cod in the western North Atlantic as they moved south into the Caribbean Sea and continued across the equator into Brazil. Over half of the 18 tagged sharks moved into tropical regions previously thought to be outside the species' range, indicating this migration route is relatively common (Skomal et al., 2009). Depth profiles from the study showed one shark remaining continuously at depths of 250-1000 m for 5 months. These recent studies have implications for conservation management as they indicate that the distribution and migration patterns of the species may not be as expected and that genetic mixing between ocean basin populations is likely to occur.

Using public sightings records and scientific surveys, three major basking shark 'hotspots' have been identified in British waters: The Isle of Man, northwest Scotland and southwest England; particularly Lands End and Lizard Peninsulas (Doyle et al., 2005; Sims et al., 2005a; Witt et al., 2012). Figure 4.4-a to d show density maps and kernel density estimations of long-term public sightings records of basking sharks submitted to the Marine Conservation Society (MCS) Basking Shark Watch. The data clearly show that sighting densities are highest around the three UK hotspots areas.

The SeaWatch SW project study site, at the southwest tip of the Lands End Pennisula, has been identified as a key site for basking shark sightings within the southwest regional hotspot, having very high sighting densities relative to surrounding coastal areas. This is evidenced by both public sightings data and effort-corrected boat based sightings data (figure 4.4) (Witt et al., 2012).

The southwest 'hotspot' accounted for more than 45 % of the public sightings records over a 20 year period from 1987 to 2006 (Bloomfield and Solandt, 2007). Analysis of the MCS public sightings data since 2006 indicates a shift in the importance of each of the hotspot areas, shown by a decrease in the proportion and number of sightings reported from the southwest of England and a corresponding increase in reports from Scotland and the Isle of Man; although the increase in reports from the Isle of Man may in part be due to the launch of the Manx Basking Shark Watch in 2005. The graph in figure 4.5 shows this changing pattern emerging in the spatial distribution of the public sightings records from the early 2000s. Subsequent MCS reports indicate that a higher proportion of sightings have continued to be reported from the Isle of Man, with a reduction in sightings from Scotland through 2007 – 2009 (no later data available); both in terms of absolute numbers of sightings and the proportion that these contribute to the annual UK sightings overall (Solandt and Ricks, 2009). Since the early 2000s and there has been a consistently lower level of reports from the southwest of the UK compared to the long-term average (with the exception of 2006, which was a year of high numbers in all hotspot regions). Although the overall numbers of sightings reported to the MCS project have remained high (over 1,000 records per year since 2006); the percentage contribution to the national sightings from the SW region has decreased from the long-term average of 45%, to 29% (N = 458) in 2007, 24% (N = 210) in 2008 and 18% (N = 213) in 2009 (Parker and Solandt, 2007; Morgan and Solandt, 2008; Solandt and Ricks, 2009; Witt et al., 2012).

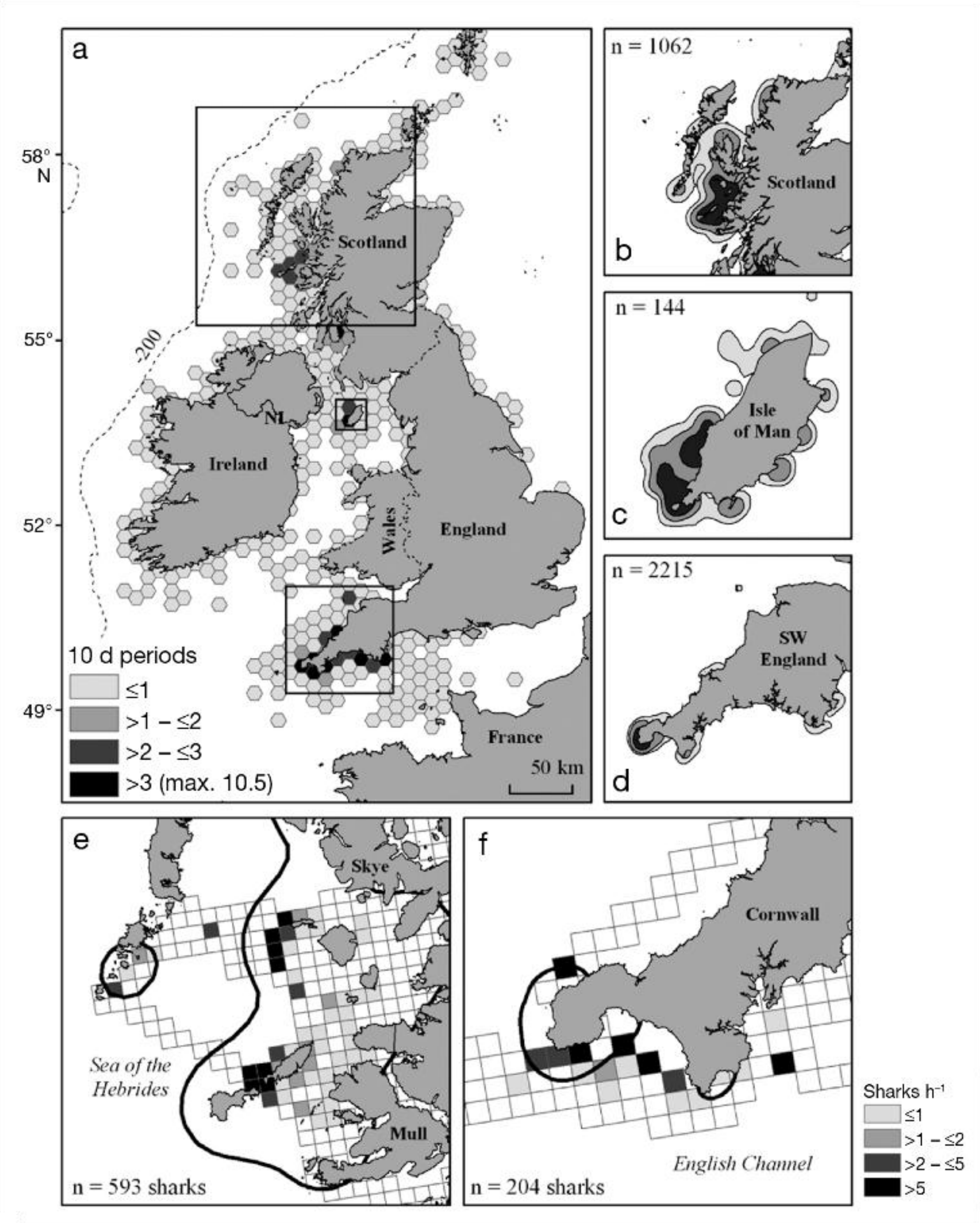


Figure 4.4: Map of basking shark regional sighting hotspots (Witt et al., 2012). (a) Mean annual sighting density, given as the number of 10-day periods containing sightings (1988 – 2008). (b – d) kernel smoothed distribution of basking shark sightings in western Scotland (b), Isle of Man (c) and SW England (d), with 25 %, 50 % and 75 % of records represented by shading. Basking shark sightings h-^{1} in western Scotland (e) and SW England (f) from boat transect surveys, with superimposed 50 % kernel isopleths (black line).

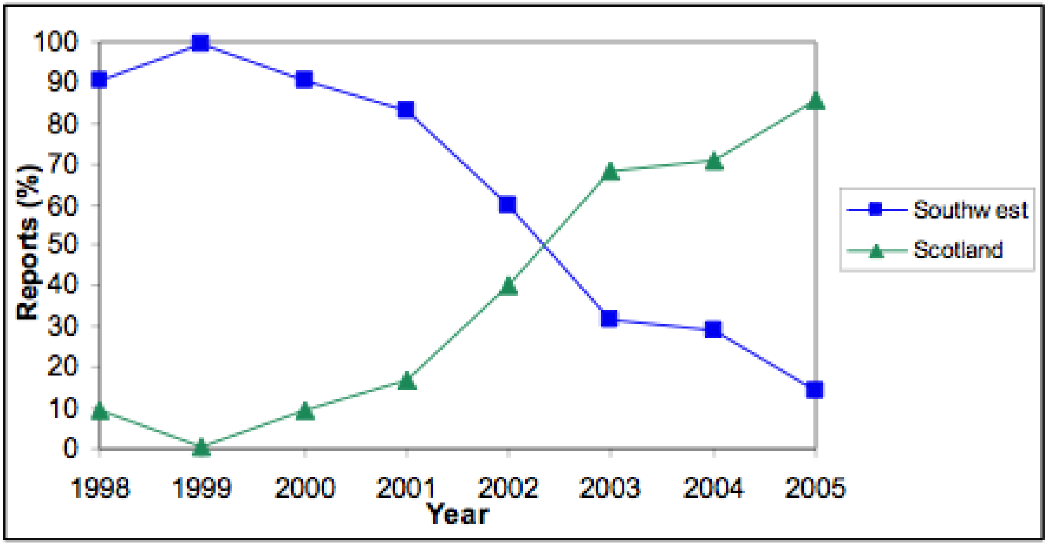


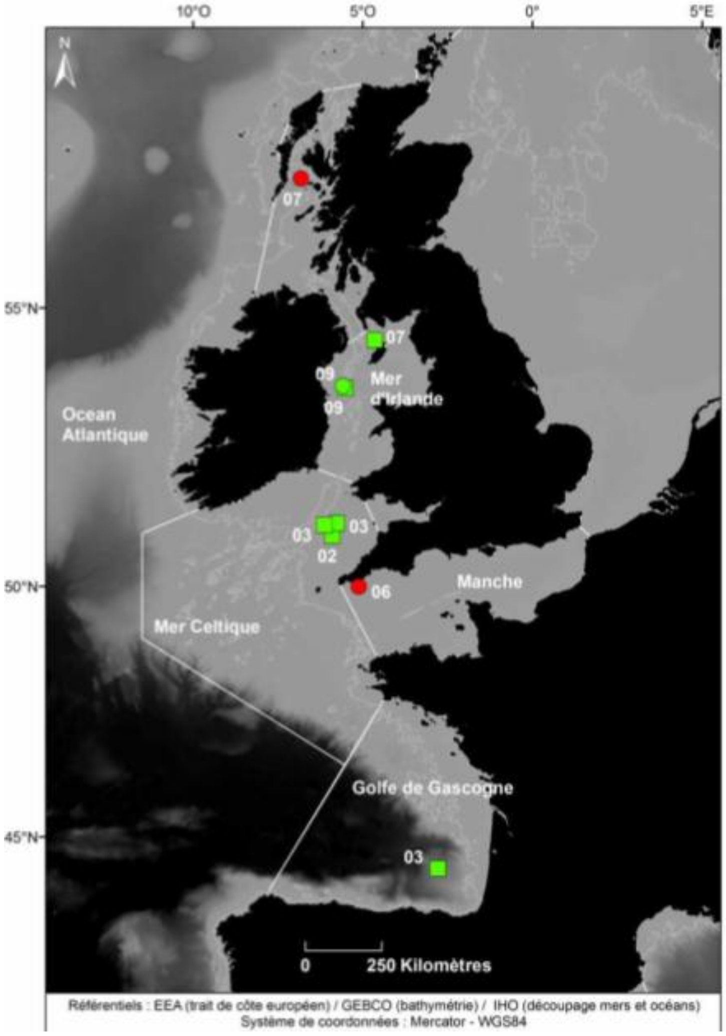
Figure 4.5: Proportion of basking shark sighting reports from two hotspot areas over time (1998 - 2005). Note the increase in sightings from Scotland (green triangles) and the decrease in sightings from southwest England (blue squares) (Bloomfield and Solandt, 2007).

It is important to remember that visual monitoring can only provide data on sharks at the surface and is generally limited to a coastal perspective of shark distribution. Detection of sharks through visual monitoring requires sharks to exhibit surfacing behaviour. Therefore, relying solely on visual monitoring data, whether it is collected during land-based, boat-based or aerial surveys, leads to a bias in shark distribution data because only areas where sharks are at the surface will be represented. Bias may also be introduced by the ad-hoc and non-effort based data collection methods of 'citizen-science' monitoring surveys, such as the MCS basking shark watch project.

There is clearly a requirement for non-visual monitoring, which can only be provided through remote methods such as telemetry and archival tracking. The data that these monitoring methods collect gives a somewhat different picture of the distribution and habits of basking sharks in areas of the sea that are effectively invisible to visual monitoring methods due to their depth or offshore locations (Sims et al., 2003b; Southall et al., 2005; Gore et al., 2008; Skomal et al., 2009). Southall *et al*. (2005) compared distribution patterns of sharks from visual and satellite tracking studies around the UK and found that satellite-tracking studies identified two new hotspot locations where basking sharks spent significant amounts of time; these are the Celtic Sea and Western Approaches. The results demonstrate that visual monitoring does not reliably report the full extent of basking shark distribution or habitat use.

Differences in shark feeding and surfacing behaviour according to the type of environment they are occupying may also lead to bias in distribution data. It was reported by Sims *et al*. (2005b) that increases in surface feeding associated with frontal zones on the continental shelf could lead to sharks being 60 times more likely to be seen in these areas than in stratified waters where they are more likely to be feeding at depth during the daytime. These results reveal the importance of combining data from more than one monitoring method wherever possible in order to prevent misleading reports of basking shark distribution (Southall et al., 2005).

Satellite tracking studies are also very important for investigating the movement of individuals within and between known hotspot areas. Basking sharks have been shown to move up and down the west coast of Great Britain, indicating that there are not separate populations resident at each hotspot (Sims et al., 2003b; Sims et al., 2005a). Additionally, sharks from the French side of the channel have been found to utilise hotspots in the UK. A recent French satellite tracking study found that sharks tagged off the tip of Brittany in the Iroise Sea moved up to the southwest UK hotspot area and north as far as the Hebrides (Stephan et al., 2011), see figure 4.6.



Référentiels : EEA (trait de côte européen) / GEBCO (bathymétrie) / IHO (découpage mers et océans)
Système de coordonnées : Mercator - WGS84

Figure 4.6: Tag release positions for satellite tracking study of basking sharks. Square symbols indicate male sharks, circles represent females; red coloured symbols show tags that were attached off Brittany and green symbols show tags that were attached around the Isle of Man. From Stephan *et al*. (2011).

Long-term monitoring through public sightings shows that basking sharks are conspicuous in British 'hotspot' locations between May and October and are rarely seen during winter (figure 4.7, shaded area indicates period encompassing the peak periods from all three regions) (Doyle et al., 2005), associated with seasonal increases in surface zooplankton stocks (Sims et al., 1997; Sims, 1999; Southall et al., 2005) and the location of known shelf-sea fronts (Sims et al., 2006; Priede and Miller, 2009). During peak periods, aggregations frequently occur in productive areas, with often more than 10 sharks in a group and occasionally over 100 (Doyle et al., 2005; Wynn and Brereton, 2009).

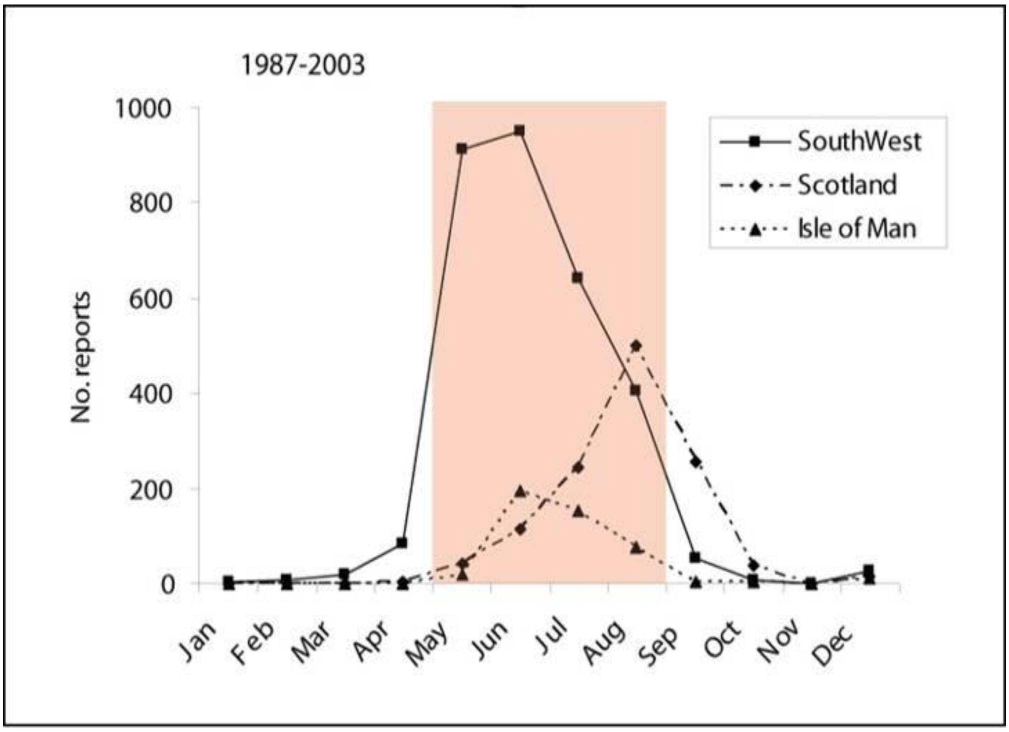


Figure 4.7: Long term temporal trends in basking shark sightings at the three UK hotspots (Southwest UK, Isle of Man and Scotland), 1987 - 2003. Based on public sighting data collected through the Marine Conservation Society Basking Shark Watch (Doyle et al., 2005). Shaded area indicates the period of peak sightings through the UK.

The southwest hotspot has traditionally had its peak number of sightings in the early part of the season, around May and June, with a drop in reports as summer progresses to autumn (figure 4.7). Since 2005 this trend seems to have been altered, with high inter-annual variability becoming evident in the peak sightings month and an overall trend towards a later influx of shark sightings in the region (Bloomfield and Solandt, 2006; Parker and Solandt, 2007; Morgan and Solandt, 2008; Solandt and Ricks, 2009).

4.1.2.2 Habitat associations

Increasing amounts of data are available on basking shark movement and distribution patterns, but much uncertainty remains regarding cues and controls on their broad-scale migratory movements and small-scale foraging behaviour. There are two major obstacles to determining connections between environmental factors and shark distribution. The first problem is the non-effort based nature of the majority of shark sighting data, which renders it difficult to use for this type of analysis. The second problem is that, although satellite tracking can provide extremely accurate data on distribution, the number of individuals that are tracked is very low and their behaviour may not be representative of the population as a whole. Even so, both methods have provided important insights into associations between basking sharks and their environments.

The peak month for shark sightings at the 'hotspots' varies geographically (figure 4.7). Tracking data indicates northerly movements early in the season are followed by southerly retreat in the early autumn (Sims et al., 2003b; Sims et al., 2005a), suggesting thermal preferences may be important in habitat selection during the summer/autumn sightings season (Sims et al., 2003b; Skomal et al., 2004). Results from the northwest Atlantic research group also found similar late summer southerly movements (Skomal et al., 2004). There is also evidence for movement into deeper water, indicating that the north-south migration is not the whole story and that a larger sample of tracking data will be required to better constrain seasonal movement patterns (Gore et al., 2008). Cotton *et al* (2005) showed NAO index and lagged mean monthly SST were primary controls on relative abundance of basking shark sightings in southwest UK from 1988 – 2001; although the results may have been influenced by bias in the public sightings data associated with weather and seasonality. Witt *et al*. (2012) found a significant positive influence of winter time NAO index on the duration of the subsequent basking shark sightings season and reasoned that this link is mediated through westward wind stress associated with positive NAO indices, and the impact of this on nutrient mixing and increased productivity. It is likely that regional prey availability is also a dominant control on broad scale movement patterns (Cotton et al., 2005). Sims and Reid (2002) found correlation between a shift in the distribution of copepods and a reduction in catches in a targeted basking shark fishery off west Ireland. A coincident increase was found in the number of basking sharks caught by the Norwegian fishery in an area where copepod abundance had increased, indicating a northwards dstribution shift of both prey and predator (Sims and Reid, 2002).

Basking sharks are commonly reported in the proximity of known frontal features, e.g. Ushant Front (Sims and Quayle, 1998), and have also been shown to forage specifically along defined fronts (Priede and Miller, 2009), indicating that these oceanographic features may provide key feeding habitat for the species (Sims, 2008). Each of the three UK hotspots are associated with well defined seasonal tidal-mixing fronts (Sims, 2008). At a local scale features such as Lands End and the Lizard Peninsulas may provide key hydrodynamic controls through tidal-topographic interactions. Feeding groups are commonly noted in areas with oceanographic or topographic features that affect productivity or zooplankton density (Sims and Quayle, 1998). The ensuing aggregations of mature sharks may have important implications for social behaviour, courtship, reproduction (Sims et al., 2000), and conservation.

4.1.3 Population status, exploitation and threats.

Fisheries derived data show that around the UK, female sharks were much more likely than males to be captured in directed shark fisheries (Maxwell, 1952; Watkins, 1958). By-catch data from Canadian (non-targeted) fisheries show the opposite pattern (Lien and Fawcett, 1986). This may indicate sexual segregation of the population, either seasonally or spatially (Compagno, 1984). Conversely, it might be the result of behavioural differences between the sexes, for example females may be more available to targeted fisheries due to increased surfacing behaviour (Sims, 2008).

Sharks tracked in the seas around the UK were shown to move freely along the coast between hotspot areas (Sims et al., 2003b; Sims et al., 2005a), and sharks tagged on the French coast have been tracked moving between France and the UK (Stephan et al., 2011); indicating a single population exists within the northeastern Atlantic range of the species. However, it was generally assumed that populations divided by ocean basins were likely to retain some genetic separation (Sims, 2008).

Genetic studies undertaken in 2006 by two different research groups provide interesting, but conflicting results. Hoelzel *et al*. (2006) used mitochondrial DNA and markers to analyse connectivity between the global basking shark populations. Their first key finding was that there was very little differentiation between distinct geographical populations found within the same ocean basin. They suggested that it would require only one migrant between these populations per generation to maintain this genetic link, and this type of cross-basin migration has been exemplified in tracking studies by both Gore *et al*. (2008) and Skomal *et al*. (2009). On the basis of their initial results, Hoelzel *et al*. (2006) grouped the sharks into assumed basin-scale populations from the Atlantic and the Pacific. Comparisons were then made between these groups and results showed no differences between the Atlantic and Pacific basking shark genetic samples; indicating no population structure at any spatial scale (Hoelzel et al., 2006). Conflicting results were found by Noble *et al*. (2006), who compared 18 microsatellite loci in basking shark tissues collected from global populations. Their results did show some structure in global populations, leading them to conclude that there was little gene flow between the populations in the northern and southern hemispheres. Since this study was published, tracking data have shown that there is movement of individuals between the northern and southern populations of basking sharks in the western Atlantic (Skomal et al., 2009); but this does not necessarily mean that gene flow occurs. Although further genetic studies are required to clarify the situation, the tracking studies indicate there is potential for migration between ocean basin populations, and it is likely that the population is panmictic.

There is no official basking shark census, and too little is known about their movements and behaviour to attempt to estimate overall population sizes using satellite tagging or sightings records. The genetic study by Hoelzel *et al*. (2006) produced a very rough population estimate of 8200, based on mitochondrial DNA samples. This result is certainly not conclusive; even so, the number is extremely low considering the species has a global distribution. Additional evidence for a larger global population comes from large counts of aggregating basking sharks made recently in UK coastal waters: >900 individuals in Aug 2012 off NW Scotland and >400 individuals off Land's End in September 2007.

Historically there were targeted basking shark fisheries in Norway, UK, Ireland, United States, Canada, Japan and New Zealand. Fisheries catch records indicate that the species used to be much more abundant throughout its distribution (e.g. McNally, 1976). An analysis of northeast Atlantic fishing records by Sims and Reid (2002) found that between 1946 and 1997 over 105,000 basking sharks were caught in the region. Global populations are thought to have declined dramatically over the last century as a result of large catches in fisheries combined with low fecundity, slow maturation of 12-20 years (Pauly, 1997) and a long gestation; estimated at 1-3 years (Parker and Stott, 1965; Holden, 1974). This leaves the species vulnerable to further over-exploitation and less resilient to environmental changes (Compagno, 2001).

Under the EC Common Fisheries Policy, the Total Allowable Catch quota for basking sharks in EC waters has been set at zero since 2007. This policy prevents the landing, trade, and shipment of all basking shark parts in European waters. There are now few targeted fisheries for the species anywhere in the world, but bycatch and illegal finning are still considered threats to the species (Sims, 2008). Unfortunately, sharks are still unintentionally captured in trawls (Francis and Duffy, 2002) and static fishing gear such as pots, creels, tangle and gill-nets throughout their range (figure 4.8), although the extent of this by-catch is not well reported in any region of the sharks distribution (Bloomfield and Solandt, 2007; Sims, 2008).

Additional, but arguably less significant threats to the species come from the potential for boat strikes as a result of the species' coastal surfacing behaviour as well as disturbance by recreational users of the marine environment including harassment through ecotourism (Kelly et al., 2004). There is also an increasing desire for the large fins in the shark finning industry (Sims, 2008) and although all legal trade in basking shark products must be licensed through the Convention on the International Trade in Endangered Species (CITES), there are numerous reports of illegal trade in fins (Magnussen et al., 2007).

Figure 4.8: Photograph of dead, by-caught basking shark in Sennen Cove, Cornwall, UK (June 2007). The shark was landed after becoming entangled in lobster pot ropes. Photo by Andrew Carn, from Bloomfield *et al*. (2007).

The added question of possible impacts of climate change on the species has also been raised. Future climate change may impact basking sharks via shifts in thermal habitat availability, particularly the formation and distribution of fronts, due to changes in SST, stratification regimes and storminess (Sims, 2008; Speedie and Johnson, 2008). This may have implications on foraging as a result of distributional shifts of prey species or trophic mismatch due to climate-mediated phenological changes in zooplankton abundance (Edwards and Richardson, 2004).

The basking shark is listed on the International Union for Conservation of Nature (IUCN) Red List as globally Vulnerable (Appendix 1a, d & 2d), and Endangered (EN Appendix A1a, d) within the northeast Atlantic (IUCN, 2011). Trade in basking shark products has been controlled through CITES since 2000 when it was listed on Appendix III of the convention; this listing was later upgraded to Appendix II, which requires licensing for all trade in the species. In British waters the species is protected under the Wildlife and Countryside Act and is a Biodiversity Action Plan (BAP) species. In other parts of its range the species is protected under various national and international treaties, including the Bonn Convention (or Conservation of Migratory Species), which requires international collaboration on the protection of the species due to its proven wide ranging migrations.

The range of protection offered to the species under various national and international policies is a reflection of the apparently dramatic decrease in numbers due to centuries of targeted fishing throughout its range.

4.1.4 Research objectives

The basking shark study presented in the following sections is the first quantitative analysis of the effect of fine- to meso-scale environmental variables on surface sightings of the species collected through an effort-based survey. The extensive effort of the visual survey enabled a hypothesis testing approach to be taken, which aimed to investigate temporal patterns in the basking shark sightings; in particular whether there was evidence to support a real-time, fine-scale effect of thermal ocean fronts on the surface foraging behaviour of basking sharks. Such a relationship is suggested widely in the literature, but has not previously been tested empirically. It was felt that this research question was timely, in light of recent conservation policies, which are beginning to focus on the effect of seasonal tidal-mixing fronts within waters surrounding the UK because of their apparent importance as foraging areas for basking shark and other marine mega-fauna.

4.2 Methods

4.2.1 Visual monitoring data collection.

Sightings of basking sharks were collected in the effort-based SeaWatch-SW wildlife monitoring survey 2007 – 2010. For details of general survey methodology and methods for reducing error and detection bias, see chapter 2. Further details on methodologies specific to the basking shark data are given below.

In 2007, basking sharks were surveyed in the same continuous search method as other marine wildlife and were recorded on the general marine wildlife survey forms (appendix 1). From 2008 onwards, the number of basking sharks visible at the surface was recorded in half-hourly scans of the survey area, with additional notes being made about other sightings outside of these periods (see basking shark survey forms in appendix 1). The different recording methods used in 2007, and a general improvement in the recording of accurate positional information as the survey progressed has meant that the data from earlier years can be difficult to filter for re-sightings of the same individuals and groups of sharks. The sharks often remained present at the surface in the survey area for long periods and although observers attempted, where possible, to keep track of individual sharks; during periods when multiple sharks were present in the survey area (which occurred most frequently in 2007 and 2008), this was very difficult.

This has led to some difficulties in interpreting the shark sighting records, as it is likely that the same animals may have been recorded on multiple occasions, causing problems when attempting to define fine-scale temporal (hourly) and spatial sightings datasets. Whereas with the harbour porpoise dataset, a filter was applied to attempt to remove 'likely' re-sightings, this was not possible for the shark data from 2007 and 2008, because of the lack of accurate positional information. Neither was discarding all ambiguous sightings an option, as this would have meant losing most of the data from 2007 and 2008; when the vast majority of basking shark sightings were recorded.

The unit of analysis that has been selected to be both most unbiased and most representative of the relative density of sharks is the 'peak day count'. This is the maximum number of sharks that were recorded at the surface at any one time during each day of the survey. Using this measure ensures that, at least within a single day of the survey, bias is not introduced by re-recording the same animals. However, using this metric also means that it is not possible to undertake any quantitative analyses of the spatial or fine-scale temporal (i.e. hourly) patterns in the shark sighting data.

According to the detection investigations undertaken and presented in chapter 2 (section 2.5), the basking shark sightings data should be truncated at a maximum distance of 2 km from the survey watchpoint, to ensure a reasonable level of detection within the full survey area. Again, there were some issues with filtering on this basis, because when large counts were made (for example a single count of 72 sharks at the surface at once on 5/09/07) the position of all of the individual animals was not recorded.

There is a tendency for the larger peak counts to be missing position data because of the difficulty in recording the location of all individuals simultaneously when multiple animals were present. This is indicated by a much lower average sharks per sighting value for the sightings where distance was recorded (average = 1.97, N = 1216) than for the sightings where distance was not recorded (average = 9.99, N = 68). It was felt that excluding the large counts because of the lack of location information would introduce significant bias towards lower peak day counts, during which it would have been easier to keep track of and record the position of all sharks. It is worth noting here that the majority of sightings did have information on distance from the watchpoint recorded (95 %) and that out of these sightings, more than 80 % were estimated to be within 2-km of the watchpoint. For these reasons, it was felt that there was justification not to use a distance filter for the shark sightings data and thereby prevent the biased exclusion of the larger counts, which may not have associated distance data. Quantitative analyses of the spatial distribution of basking shark sightings have not been undertaken, therefore it was not considered imperative that distance based truncation was carried out, although the drawbacks of this decision are acknowledged.

The full basking shark sightings dataset contained 1549 records of sightings, relating to a cumulative total of 3582 animals (July 15th to October 15th, 2007 – 2010). This did not include any records from the 12:00 – 13:59 lunch break period (which was occasionally observed). The sightings were then filtered to remove sightings made during poor survey conditions, defined as visibility less than 5 km and/or Beaufort sea state above 4. Sightings for which no sea state or visibility data were recorded have also been removed. These filters removed a total of 265 sighting records. The final dataset contains 1284 sightings relating to a cumulative total of 3069 basking sharks counted during the survey 2007 - 2010.

4.2.2 Thermal front data.

Quantitative data on the thermal fronts present in a 5.5 x 11 km (5 x 10 pixel) area offshore of the SWSW survey watchpoint were supplied by Dr. Peter Miller from the Plymouth Marine Laboratory Remote Sensing Group. The size of the box area was initially based on the area of sea visible from the watchpoint (approximately 5 x 5 km), but was extended seawards so as to reduce the effect of coastal smoothing which can lead to 'blank' pixels closest to the coast. A 5 x 5 pixel (5.5 x 5.5 km) box would also have suffered more from issues with cloud masking, due to the smaller number of pixels involved.

The front data are a spatially constrained quantitative representation of the front maps shown in figure 4.9-a. The front maps are created using Advanced Very High Resolution Radiometer (AVHRR) satellite remote sensed SST data. Thermal boundaries are detected in the SST images using the single image edge-detection algorithm (SIED) by Cayula and Cornillion (1992). The black lines on the maps (figure 4.9-a) identify the location of temperature gradients of ≥ 0.4 °C between two bodies of water. Each line, or part of a line represents the information from one pass of a satellite (which, on average, pass over the UK five times per day).

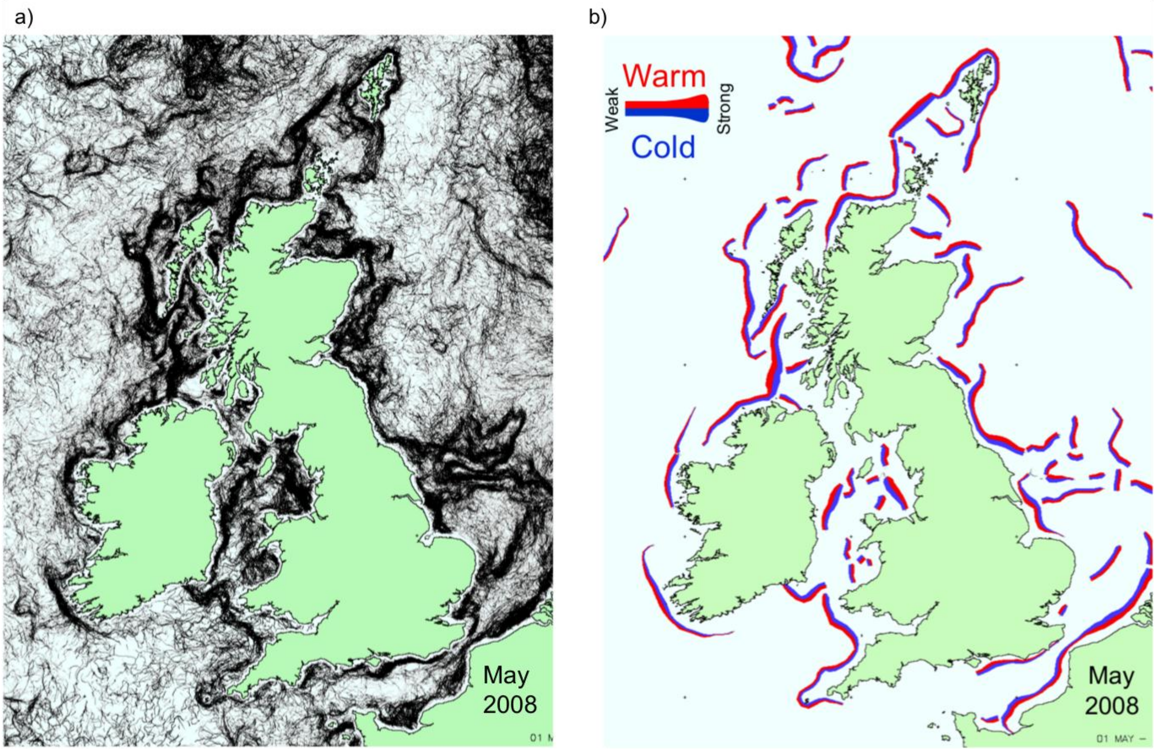


Figure 4.9: Examples of thermal ocean front maps, automatically generated from all cloud-free AVHRR sea-surface temperature data from the period 1st – 31st May 2008. (a) Composite front map, indicating the location, strength and persistence of all fronts observed during May 2008 around the British Isles. (b) Synoptic thermal front map that shows the position and strength of all main fronts detected during May 2008. Each front is coloured to indicate the warm and cold side (red = warm, blue = cold) and the width shows the strength of the front

Rather than averaging over a given set of images (as done in the past), Dr. Miller's approach accumulates a series of satellite images into a single map, resulting in enhanced highlighting and detection of persistent fronts. In addition, weighting factors are applied that remove noise introduced by single and transient frontal segments identified in a single pixel only, and produce maps like the one given in figure 4.9-a. The algorithm used to identify persistent frontal features and create the composite maps from multiple satellite images includes three weighting factors:

(1) The mean temperature gradient of each front.
(2) The persistence of a front through time (persistence = the probability of observing a front in a given pixel over a given sequence of images/satellite passes).
(3) Evidence of a feature in the proximity of another (allows for some movement of features over time as a result of tidal advection).

Details of the methodology and the processing algorithm are available in Dr. Miller's (2009) paper. The major benefits of the compositing method are that cloudy satellite images are less of a problem (because multiple images are combined) and the blurring of dynamic features does not occur; which can be the case with simpler SST time-averaging techniques. Additionally, more persistent fronts, or those with stronger gradients, are highlighted (figure 4.9-a). Dr. Miller has also developed a new line-clustering algorithm to simplify the composite front maps (in prep.). The resulting maps show only the main fronts and allow easier interpretation (figure 4.9-b). These maps also aid quantitative analyses, because the data are not affected by multiple observations of the same front over time and scattered, unimportant lines representing ephemeral fronts.

The quantitative metrics used in this chapter were extracted from 7-day composite front data for a 5 x 10 pixel box offshore of the SWSW watchpoint (pixel size = 1.1 x 1.1 km). Weekly composite data from weeks when over half of the 50 pixels in the box were obscured by cloud were omitted from the analysis. The position of the box relative to the watchpoint is shown in figures 4.10-a and b. The front data used in the analyses have had additional processing applied in order to reduce the effect of the coastal smoothing algorithm, which can affect data close to the coast, leading to a gap between the land and the sea (this effect can be seen in figure 4.9-a as a thin, white outline around the land).

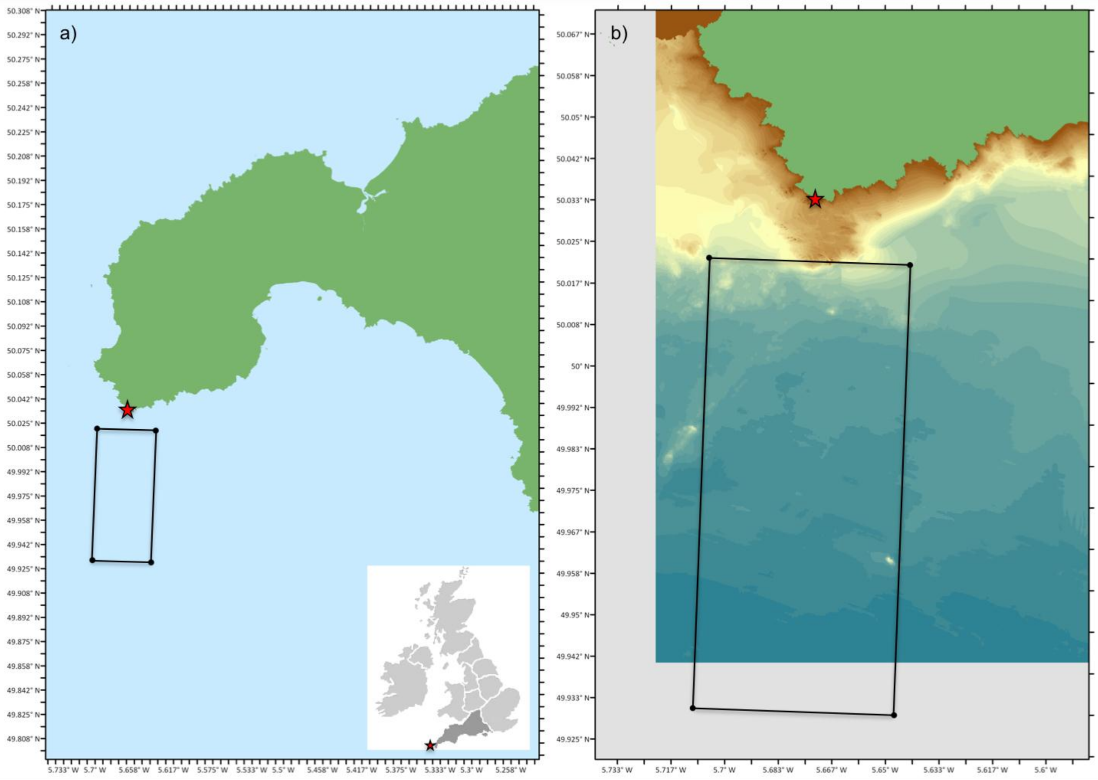


Figure 4.10: Location maps showing the position of the 5.5 x 11 km box area offshore of the SW tip of the UK from which averaged thermal ocean front metrics were taken. In all maps, a red star indicates the position of the SWSW watchpoint at Gwennap Head. The overview map in (a) indicates the position of the box within the southwest region as a whole, with a national scale map inset. The smaller scale map in (b) shows the position of the box with reference to the Runnelstone Reef and surrounding bathymetry (no bathymetric data are available for the greyed-out areas).

There were four different quantitative front metrics used to investigate the link between effort-based surface sightings of sharks in the SWSW survey and the frontal activity in the vicinity of the survey area; these are defined below. For each metric, the mean was taken from all cloud free pixels within the 5 x 10 pixel box.

'just fronts' is a metric that represents the mean strength of all fronts present in the box area. It is calculated as the thermal gradient magnitude (i.e. based on the difference in temperature between the colder water on one side of the frontal boundary and the warmer water on the other) from all fronts observed at the same pixel over the compositing period (7-days), weighted for persistence (repeated detection over time). The metric is given in arbitrary units ranging from > 0 to 0.254. The mean value for the box is calculated *only from pixels where a front was detected* and does not include 'sea' pixels where the sea surface was seen (cloud-free) but no front was present.

'f.mean' is the overall frontal gradient strength weighted by persistence (as described for 'just fronts') for all the cloud free pixels within the box area. This differs from 'just fronts' because the mean calculation *includes pixels where no front was detected* ('sea' pixels). This is therefore a representation of the overall extent of frontal activity in the box area through the 7-day compositing period. The values are again given as arbitrary units, but this time they range from 0 – 0.254, where 'sea' is given as 0 (i.e. no fronts detected) and fronts as a value of > 0 – 0.254. Note that the values will generally be lower than for 'just fronts', because the box averaged value for 'f.mean' takes account of 0 values returned from (cloud-free) pixels where no fronts were detected.

'**f.density**' is a simple statistic which represents the proportion of cloud-free pixels within the box that contained a front detection over the 7-day period. This was calculated by dividing the number of pixels that were positive for fronts by the overall number of cloud-free pixels. This is a measure of the density of fronts within the cloud-free pixels of the box area, but it does not include any information about the gradient strength of the features.

'**f.distance**' makes use of the newer, synoptic front detection methods described earlier, which use a line-clustering algorithm to define 'major' fronts. The 'f.distance' metric gives the mean distance from a point in the box area to the nearest major front (based on thermal gradient magnitude and persistence). Hence lower values would be expected when a major front is close to, or within, the box. The raw units of measurement were pixels, but this was transformed to km by multiplying the values by 1.1 (pixel size = 1.1 x 1.1 km), so data are presented as distance in km.

4.2.2.1 Long-term sea surface temperature records.

Data on average SST conditions in the southwest UK region for the last 50 years were used to compare the four years of the SWSW survey to the long-term average conditions. The data were sourced from the 'NOAA NCEP EMC CMB GLOBAL Reyn_SmithOLv.2 climatology sea surface temperature' dataset (Reynolds and Smith, 1995; Reynolds et al., 2002), downloaded from the International Research Institute data archive (IRI, 2012). The data come from a combination of sources including *in situ* data collected by ships and buoys, as well as (bias-corrected) satellite remote sensed data (only available since the 1990s). The data were combined in an averaging programme to produce a monthly-averaged long-term dataset with a resolution of 1° x 1° (Reynolds et al., 2002). Monthly average SST data were extracted from the archive for an area of sea around the SW tip of the UK, within a box with top left corner coordinates of 51°N and 6°W bottom right corner coordinates of 49°N and 4°W.

4.2.2.2 Spatial analyses of basking shark sightings data

All of the sightings in the (unfiltered) basking shark sightings dataset that had accurate location information for both distance and bearing from the watchpoint (n = 575) were mapped over the high-resolution bathymetry data.

4.2.2.3 Temporal analyses of basking shark sightings data

The sightings data (already filtered by survey conditions as described in section 4.2.1) were collated in Excel and associated environmental variables were linked to the time of each sighting. Two main datasets were created; these were a sightings-only dataset, containing only the sightings relating to the peak day count for each day of the survey (N = 162) and a daily dataset of peak-day counts, which also includes days when no sharks were recorded (N = 295 after filtering for daily averaged survey conditions). Weekly measures of shark counts have also been used in some analyses, for a direct comparison with front data at the same temporal resolution (from 7-day composites). The weekly sightings data are given as the average daily peak count for each week. This measure is indicative of the overall relative density of sharks in the survey area throughout the full weekly period.

The times of the peak shark sightings were examined with reference to hour of the day; tidal flow group (from the information in table 3.7); and time of sighting relative to high water (to the nearest hour). A chi-squared test for count data was used to test whether the expected numbers of sightings were recorded under each tidal flow condition.

The daily and weekly shark count data were used to explore temporal patterns in peak sightings across the full survey period and investigate the effect of daily and weekly averaged SST, tide height range and thermal ocean front metrics on shark sightings in the SWSW survey. Cross correlations were carried out to look for significant real-time and lagged effects between shark sightings and environmental conditions at daily and weekly temporal scales.

Analysis of the effect of dynamic environmental variables on peak counts of basking sharks through time.

Generalised additive models (GAMs) were used to model the temporal patterns in the distribution of shark sightings in relation to survey conditions, environmental and temporal variables. The general GAM structure and model fitting procedure is given in detail in chapter 3, section 3.2.2.1. The relative abundance of basking sharks (represented by the daily peak count) was modelled using negative binomial-based GAMs (with log link function), including an offset for the (logged) hours of effort per day. A negative binomial model structure was used to allow for the large variance in the count data, which led to problems with overdispersion when Poisson and quasi-Poisson model structures were attempted. Overdispersion in the models was detected using the ratio of the sum of squared Pearson residuals to the residual degrees of freedom; if this is larger than 1, it indicates overdispersion (Hilbe, 2011). Overdispersion can be caused by zero-inflation, outliers, poorly specified models, missing predictor variables, or by ‘real’ data variance. Modelling significantly overdispersed data using a Poisson error distribution is likely to be misleading, because it does not effectively account for the variability (overdispersion) in the data. In the negative binomial case, a random parameter is included in the model, which reflects unexplained variance between the counts.

Pearson correlation coefficients and variance inflation factors (VIFs) were examined for all pair-wise combinations of model covariates, and highly correlated pairs were not permitted to be included in the same model. Using stepwise forward-selection of covariates ensured this, by allowing only the first variable selected in the process to be included and discarding any strongly correlated variables from subsequent rounds of covariate selection.

A combined model (for all years of data) was carried out on the daily peak shark count data. It was felt that using the daily shark data was preferable to using weekly summaries of shark counts, as the sample size was greater. Negative binomial models can be particularly sensitive to lower sample sizes, which may lead to convergence problems, especially in models containing multiple predictor variables.

Environmental covariates

The candidate predictor variables included in the model selection stages for the GAM of shark daily abundance were; daily averaged survey conditions (sea state, visibility, cloud cover and glare); daily average SST, SST standard deviation (from half hourly data points) and SST anomaly (compared to the NCEP long term monthly averages); daily tide range (from POLPRED CS20 model); weekly resolution front metrics (weekly ‘just fronts’, ‘f.mean’, ‘f.density’ and f.distance); and 2-week moving averages of SST, SST standard deviation and SST anomaly (from the 14-day period prior to each observation). In order to assess the effect of seasonal and inter-annual variability in the abundance of basking sharks in the survey area, year and week of the survey were also included as potential model covariates. The variables included in the final model were selected through ‘staged’ forwards step-wise model selection, as described in chapter 3, section 3.2.2.3.

4.3 Results

4.3.1 Overview of the dataset and the spatial distribution of sightings.

Over the 4-year survey period, sharks were recorded on 162 dates (after filtering the sightings for survey conditions as described in the methods). The details of the peak counts from each year are given in table 4.1 and show clearly that 2007, and to some degree 2008, were better years for shark sightings than 2009 and 2010. Overall, 2009 and 2010 had fewer days with shark sightings and the maximum peak counts were lower in the latter two years than in 2007 by an order of magnitude (table 4.1). The number of days when peak counts of more than 10 animals were recorded was much lower in 2009 and 2010 (0 occasions in 2009/10, compared to 12 occasions in 2007).

Table 4.1: Summary of the basking shark peak day counts from the SeaWatch SW survey, 2007 - 2010. Peak day count is defined as the highest number of sharks visible simultaneously at the surface on each day of the survey and is a reliable measure of the minimum number of sharks in the survey area per day.

Year	Positive days (%)	Max. peak count	Sum of peak counts	Peak counts > 10
2007	71	71	444	12
2008	62	20	172	8
2009	46	3	38	0
2010	41	8	44	0

The location map of basking shark sightings shows that sightings were recorded in all parts of the survey area, with no clear clustering or spatial patterns in the overall distribution pattern (figure 4.11). Note that the data in figure 4.11 represent approximately 30 % (N = 575) of the total number of sightings made, due to many of the earlier records (2007 and 2008) not having accurate enough positional information and/or being suspected re-sightings. The data are considered qualitative and are only presented in order to give the reader an idea of the general spatial distribution of the sightings; with the assumption that the sub-sample of sightings shown are representative of the distribution of sharks in the study area over the survey period.

Considering the full sightings dataset (this has not been filtered for re-sightings, and therefore will contain some replication), there is a clear effect of sea state on the number of sightings recorded (figure 4.12). Using only the peak day counts (which were pre- filtered for survey conditions), there also appears to be an effect of sea-state on the value of peak counts made each day, with lower counts being associated with higher sea states (figure 4.13).

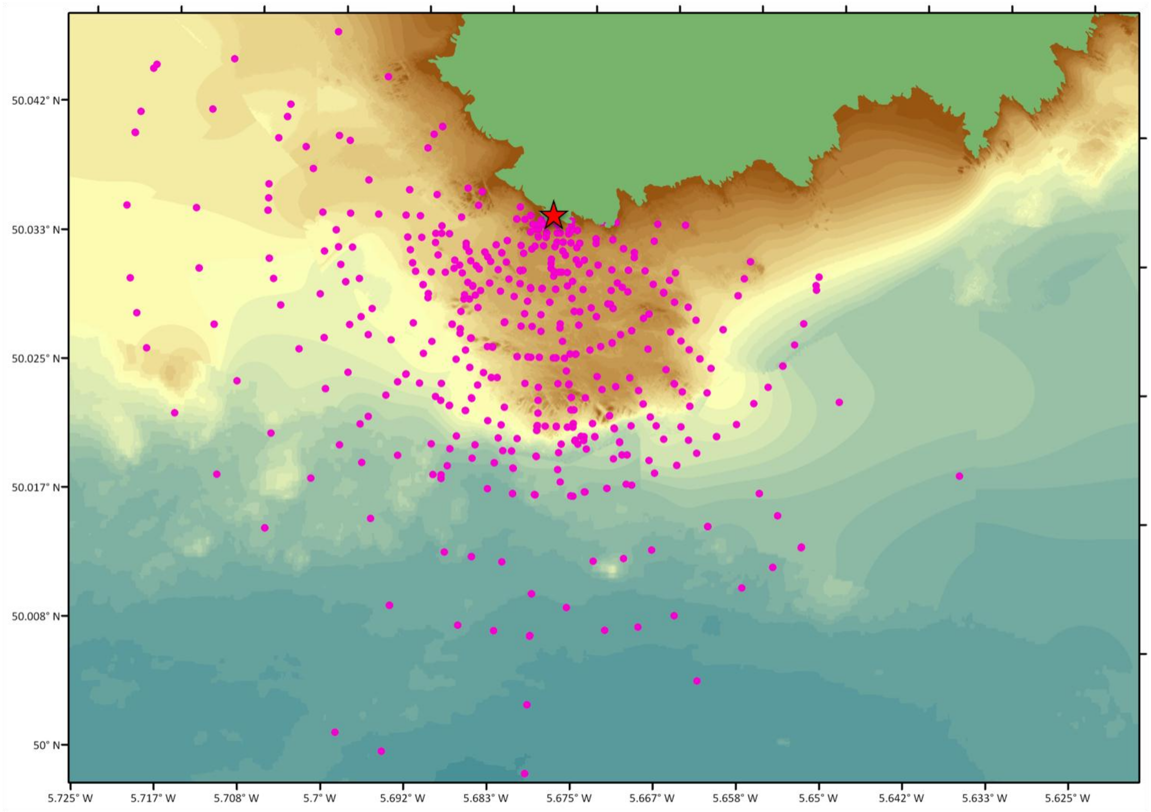


Figure 4.11: SeaWatch SW basking shark sightings map (pink dots) 2007 – 2010 (N = 575). Sightings are mapped over high-resolution multibeam bathymetry data (courtesy of the CCO/MCA and UKHO). The position of observers at the Gwennap Head watchpoint is shown by a red star.

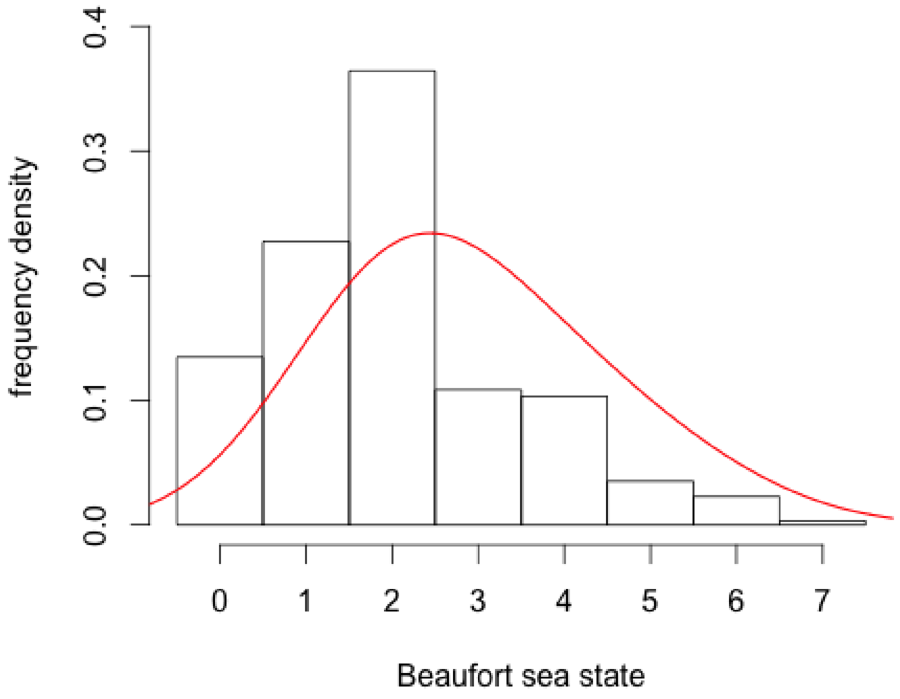


Figure 4.12: Frequency density of sea state conditions during all (unfiltered) basking shark sightings made in the SeaWatch SW survey, 2007 - 2010. The red line indicates the frequency density of the overall sea state conditions experienced across the full effort of the survey.

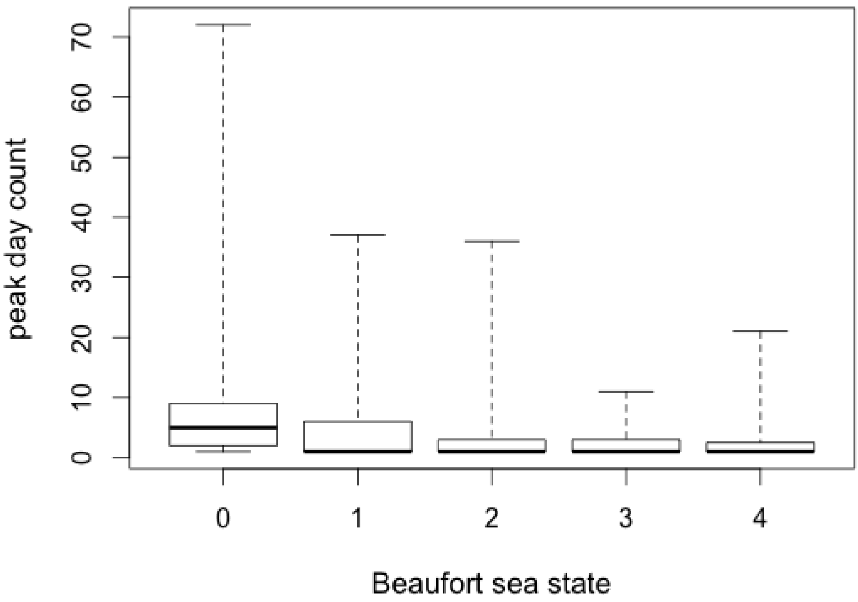


Figure 4.13: Boxplots of the peak day counts of basking sharks in the SeaWatch SW survey, by sea state conditions (N = 162). The dark line is the median; the upper and lower box extents are the 25th and 75th quartiles respectively; and the whiskers show the full range of the data for each sea state.

4.3.2 Analysis of fine-scale (hourly) patterns in the shark peak count data.

The timing of the peak day count of basking sharks shows a pattern with reference to both the time of day and the time relative to high water. There were more peak counts made between 0800 and 1200 hrs than later in the day (figure 4.14). It is probable that the spike in sightings at 14:00 may be anomalous (possibly as a result of this period being directly after the observer break period); therefore this peak should be disregarded. These data were corrected using the amount of survey effort expended by hour of the day, therefore the results were not affected by low effort during the earliest and latest hours. Even so, the hours of 0500-0600 and 2000-2100 were excluded due to the very low effort associated with these periods.

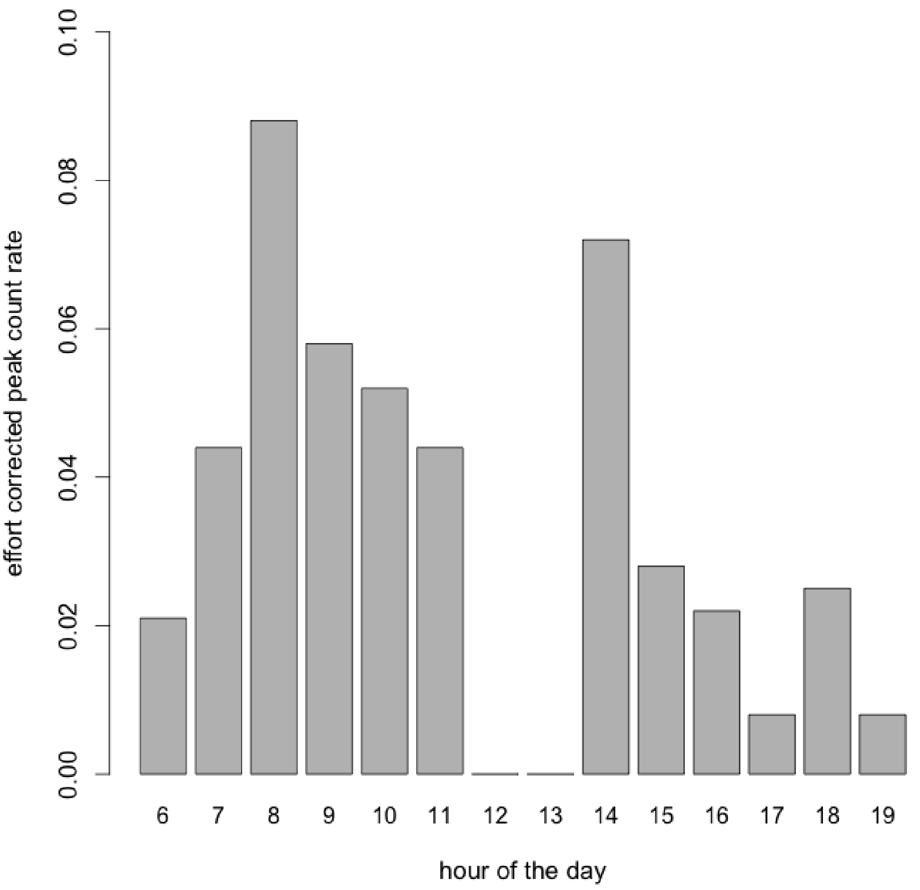


Figure 4.14: Effort corrected basking shark peak counts by hour of the day (N= 162). The frequencies of peak counts were corrected by the amount of survey effort for each hour. Data are from the SWSW effort based survey, 2007 – 2010.

There were higher shark peak count values recorded on the falling tide, under strong easterly and strong westerly flows, than at other times in the semi-diurnal tidal period (see red line in figure 4.15), despite an even distribution of survey effort with reference to the tidal cycle (blue line in figure 4.15). The numbers of peak counts made during each of the four flow groups, which are indicated by the shading in figure 4.15, are given in table 4.2.

A Pearson's Chi-squared test for count data was carried out on these data, comparing the expected peak count frequencies under each flow group with the observed peak count frequencies; taking account of the period that each flow direction is experienced within a tidal cycle (table 4.2). The results show that there were significant differences between the observed and expected counts, which suggests that tidal flow has some influence on the temporal distribution of basking shark peak counts (Chi-squared value = 9.64, df = 3, *p* value = 0.02).

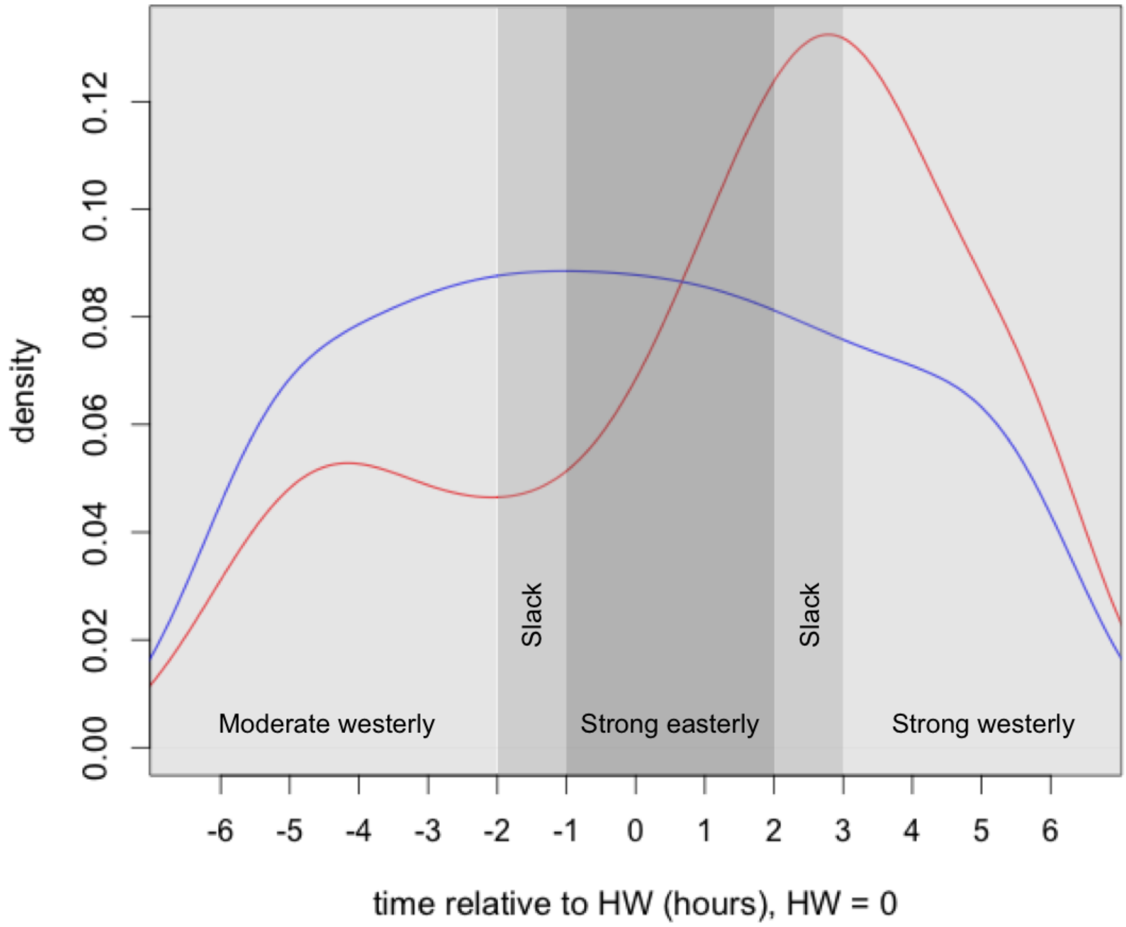


Figure 4.15: Smoothed frequency density of peak basking shark sightings (red line, N = 162) and hours of survey effort (blue line, N = 2413) relative to high water time. Smoothing bandwidth = 1-hr. Shading indicates predominant flow direction within the survey area based on the local tidal flow information provided by the National Coastwatch Institute on Gwennap Head.

Table 4.2: Observed and expected basking shark peak day count frequencies (N = 162) for each of the four tidal flow groups, with discrepancy given in parentheses in final column. Expected values are based on the total number of peak counts and the period that each flow condition is experienced within a tidal cycle.

Flow group	Flow direction	Hours of flow	Expected sightings	Observed sightings
1	West (strong)	4	54	67 (+13)
2	West (moderate)	3	40	26 (-14)
3	Slack	2	28	32 (-4)
4	East (strong)	3	40	37 (-3)

4.3.3 Exploration of patterns in the shark peak counts at daily and weekly scales.

After filtering for the average survey conditions experienced during each day of the SWSW survey (removing days with average sea state above 4 and average visibility less than 5 km), a total of 295 days remained in the dataset (2007 = 77, 2008 = 69, 2009 = 70, 2010 = 79). The peak day counts of basking sharks from all days of the filtered SWSW effort dataset are shown in figure 4.16. There is a striking difference between 2007/2008 and 2009/2010 in that there were fewer days when sharks were recorded and peak sightings were generally much lower in the latter two years of the survey. The dashed line on the plots indicates the multiyear mean peak count value (2 sharks), and the text in each plot gives the percentage of counts in each year that exceeded this value.

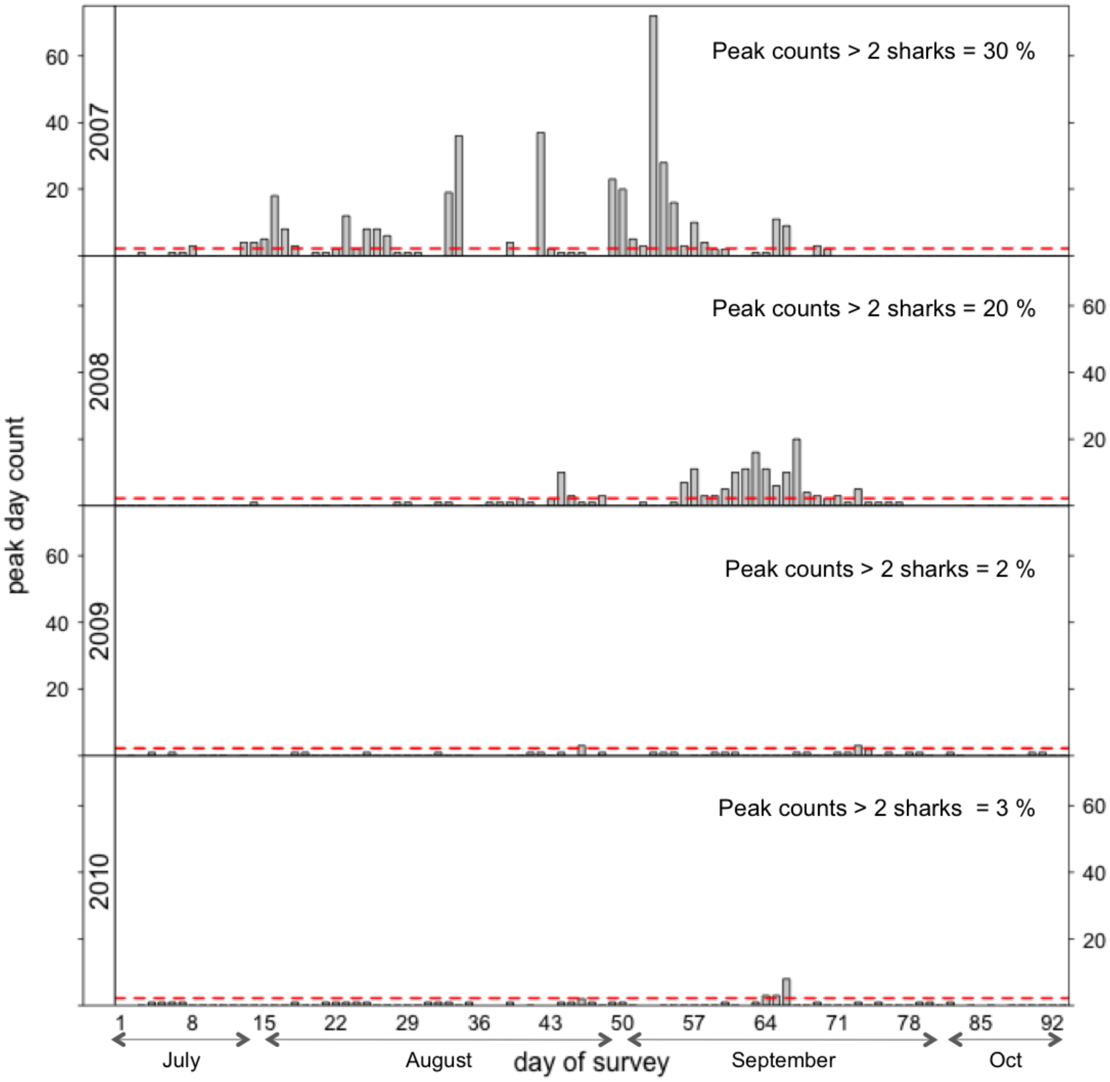


Figure 4.16: Peak day counts of basking sharks recorded in the SeaWatch SW survey, 2007 - 2010. The survey covered a 93-day long period from 15th July to 15th October each year. Red dashed line indicates multi-year mean peak day count value (2.21 sharks) and text inside plots gives the percentage of days when the multiyear mean peak count was exceeded.

4.3.3.1 Exploring relationships between the daily peak count of basking sharks and daily resolution environmental conditions.

The daily shark peak count data were log transformed because of the wide range of values and the presence of a few large outlying counts, which caused problems when undertaking exploratory analyses against environmental variables. A $\log_{10}$ transformation was used, but all values had 1 added to them prior to transformation to avoid problems with zero values.

The (logged) daily peak count from each year of the SWSW survey were plotted against mean daily SST (°C) and tide height range (m) in figure 4.17. There is some indication of a negative relationship between tide range and peak shark count value (although less clear in 2008); suggesting a preference for neap tide periods (figure 4.17, right hand column). It is unclear how reliable this result is, particularly in the 2009 and 2010 data when many peak count values were zero or one, and outliers (larger peak counts) seem to be having a significant effect on this correlation (figure 4.17 f and h). The value of peak day counts with reference to SST is more variable, with a positive relationship indicated in 2007, and in 2008 up to a point, from where the peak count values drop off again (figure 4.17-a and c). In 2009 and 2010 the peak counts seem to show a negative relationship with SST (figure 4.17-e and g).

Cross correlations were undertaken to further investigate the effect of SST and tide range on daily peak basking shark counts (using the un-logged raw data). The resulting correlograms are given in figure 4.18 and show that there is a negative effect of large tidal range on peak shark counts in 2007, 2009 and 2010. This indicates that higher peak counts were recorded when the tide was at or close to neap (smallest tide range values). This is further supported by the positive correlation between peak shark counts at time 0 and tide range at lags of 5-7, by which time the tide would have moved from neaps to springs (a change that occurs approximately weekly). In 2008 the peak shark sightings were positively correlated with spring tides at lags of -2 and -3, indicating that highest counts occurred in between spring and neap tides.

The shark ‘vs’ SST correlograms (figure 4.18) show that, in 2007, the daily peak counts were correlated with the average SST conditions from t_0 up to 13 days previously (figure 4.18- b). This positive relationship with SST from the preceding days is also suggested in 2010 (figure 4.18-h). This relationship is reversed in the data from 2009, where shark peak counts show negative correlations with the SST values from the preceding couple of weeks (figure 4.18-f). There were also positive correlations between shark counts and future SST conditions in 2009 and 2010 (figure 4.18-f and h), however there is low confidence in these results, because of the low frequency of sightings and lower counts during these two years of the survey.

There were no significant correlations between SST and shark peak counts in 2008 (figure 4.18-d), although the significance of any results in these analyses should be interpreted with caution as the data are likely to break some of the key assumptions of the test, such as normality and constant variance.

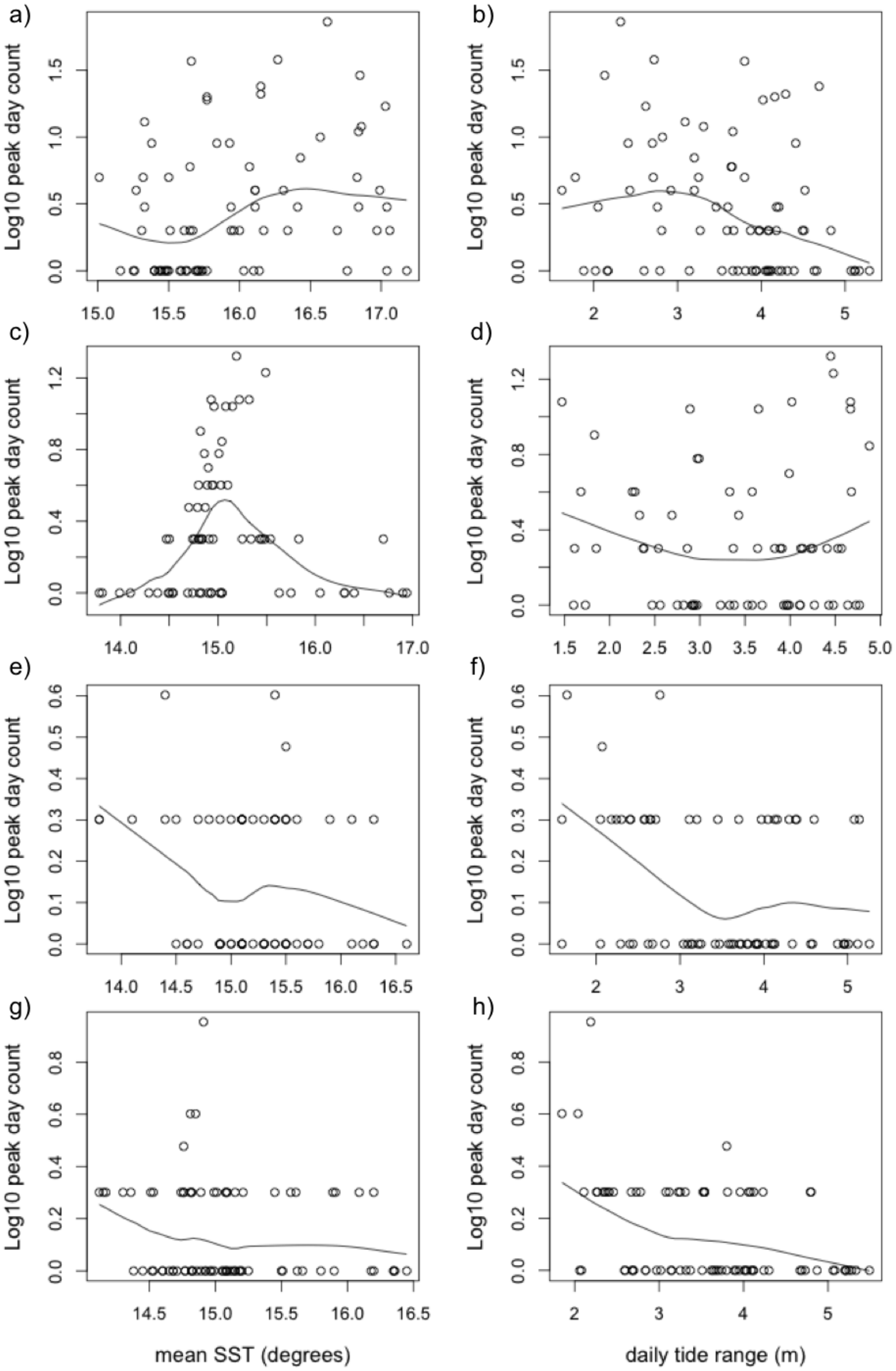


Figure 4.17: Exploratory scatterplots of the (Log$_{10}$ +1) peak day count of basking sharks and daily average SST (°C, left column) and daily tide range (m, right column). (a) & (b) 2007. (c) & (d) 2008. (e) & (f) 2009. (g) & (h) 2010. LOESS smoothers, with default bandwidth, were added to enhance visual interpretation.

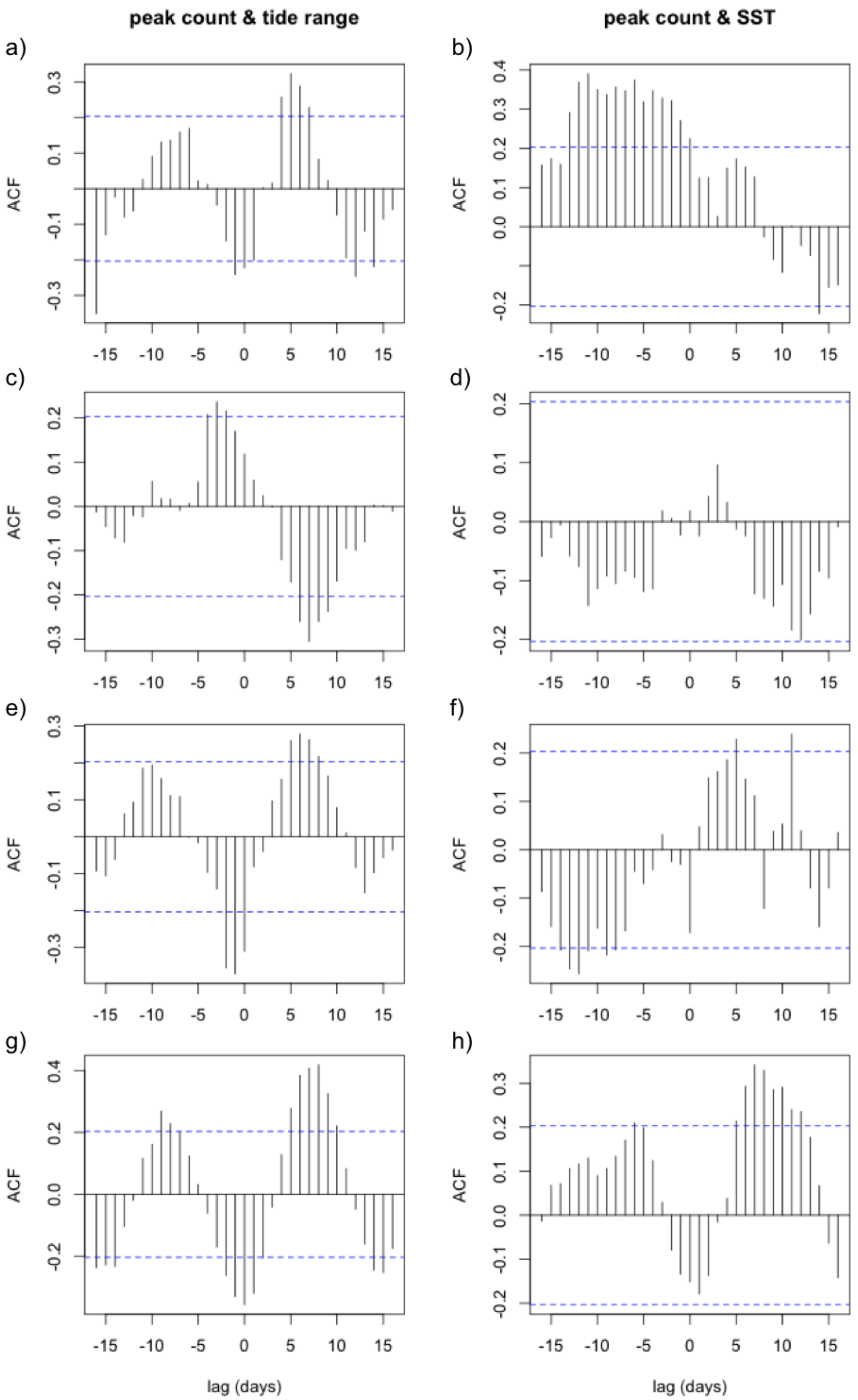


Figure 4.18: Correlograms showing the Pearson cross-correlation coefficients (ACF) between daily shark peak counts at time-0 and the daily tide height range (m, left column) and average SST (right column) at a variety of lag periods. (a) & (b) 2007. (c) & (d) 2008. (e) & (f) 2009. (g) & (h) 2010. Significance indicated by dashed blue lines, which represent the 95 % confidence intervals of the Pearson correlation test.

The SST range during each of the four years of the SWSW survey was variable, with 2007 having higher average temperatures throughout the season than the other three years. Anomalies were calculated between the SST for each day of the SWSW survey and the monthly average from the long-term regional data (NCEP). The daily anomalies were then averaged for each month of the survey (figure 4.19) and show that all four months of the 2007 survey season had higher SST than the long term mean for the region. In the remaining three years of the survey (2008-2010), the months of July to September had lower than average, and October had higher than average SST (figure 4.19). August 2010 was over one degree cooler than the long-term average for that month (figure 4.19).

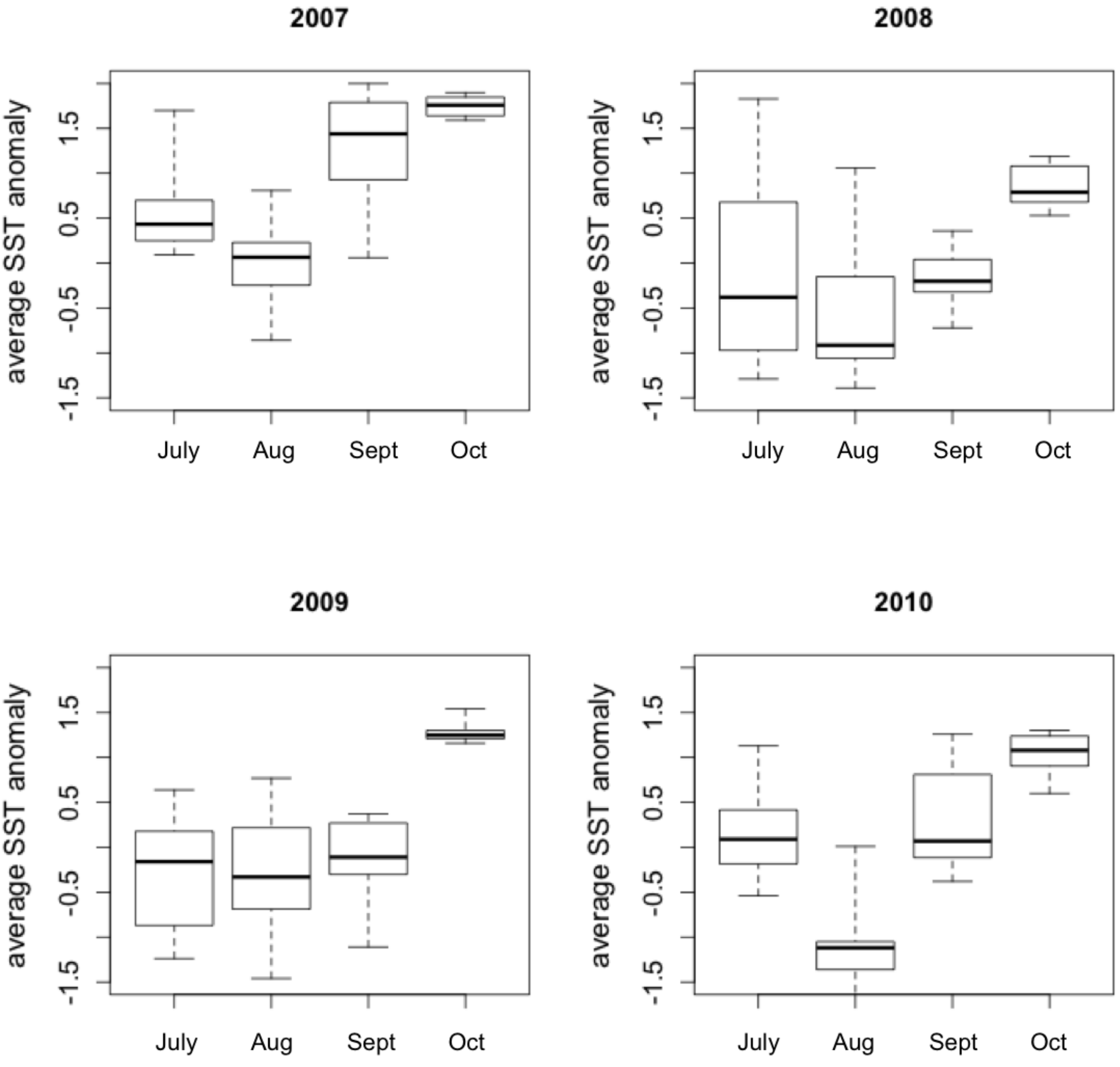


Figure 4.19: Boxplots of monthly sea surface temperature anomaly during the SeaWatch SW season (2007 - 2010). Anomaly is calculated against long-term monthly mean temperatures for the SW UK region (1949 – 2010). The dark horizontal lines show median values; the upper and lower box extents are the 25th and 75th quartiles respectively; and the whiskers show the full range of the anomaly data for each month.

4.3.3.2 Exploring relationships between the weekly average peak count of basking sharks and weekly resolution environmental conditions.

The (pre-filtered) daily basking shark survey data were averaged for each week of the SWSW survey (N = 14 weeks per year). This approach creates a weekly measure of shark presence, which takes account of the number of days per week that remained in the dataset after filtering by average daily survey conditions. The weekly metrics were logged for some of the exploratory analyses presented, so as to account for the wide variance in the numbers of sharks recorded within and between years.

Exploratory plots of weekly basking shark data, with reference to weekly average SST, tide height and thermal front presence and strength are shown in figure 4.20. When data from all years were combined, there are indications of positive relationships between logged basking shark sightings and the average weekly SST (figure 4.20-a) and the density of fronts (proportion of pixels in the box where a front was detected) (figure 4.20-c). There is also indication of a negative relationship with average weekly tide range (figure 4.20-b, suggesting higher average day counts during weeks associated with neap tides) and a negative relationship with the distance of major fronts from the watchpoint (figure 4.20-f).

When the data were split by year, the patterns described above hold for 2007 and 2008, but the relationships between the environmental variables and average weekly peak day counts were more variable in the 2009 and 2010 data. This is likely to be a result of the lower numbers of sightings (higher proportion of zeros in the data) and the lower average peak day counts recorded in weeks surveyed during 2009 and 2010 (figure 4.16). In addition, the fact that there are only 14 data points (weeks) per year makes these weekly scale analyses less robust than the daily scale analyses, which have a larger sample size.

The front data for each annual SWSW survey period (July to October, 2007 – 2010) were summarised in the boxplots in figure 4.21, which show that over the whole season, 2010 had the highest ‘f.mean’ and ‘just fronts’ values, which are measures of the average thermal front gradient strength within the box area. In addition, major fronts were generally closer the box area during the 2007 and 2010 SWSW survey periods. The gradient strength of fronts detected in the box area was comparable during 2007 – 2009 (figure 4.21-a and b). The year with the highest median value for the density of fronts within the box area (average proportion of cloud-free pixels where a front was detected) was 2007, but this was only marginally higher than in 2009, and both these years had much larger variability in this metric than either 2008 or 2010 (figure 4.21-c).

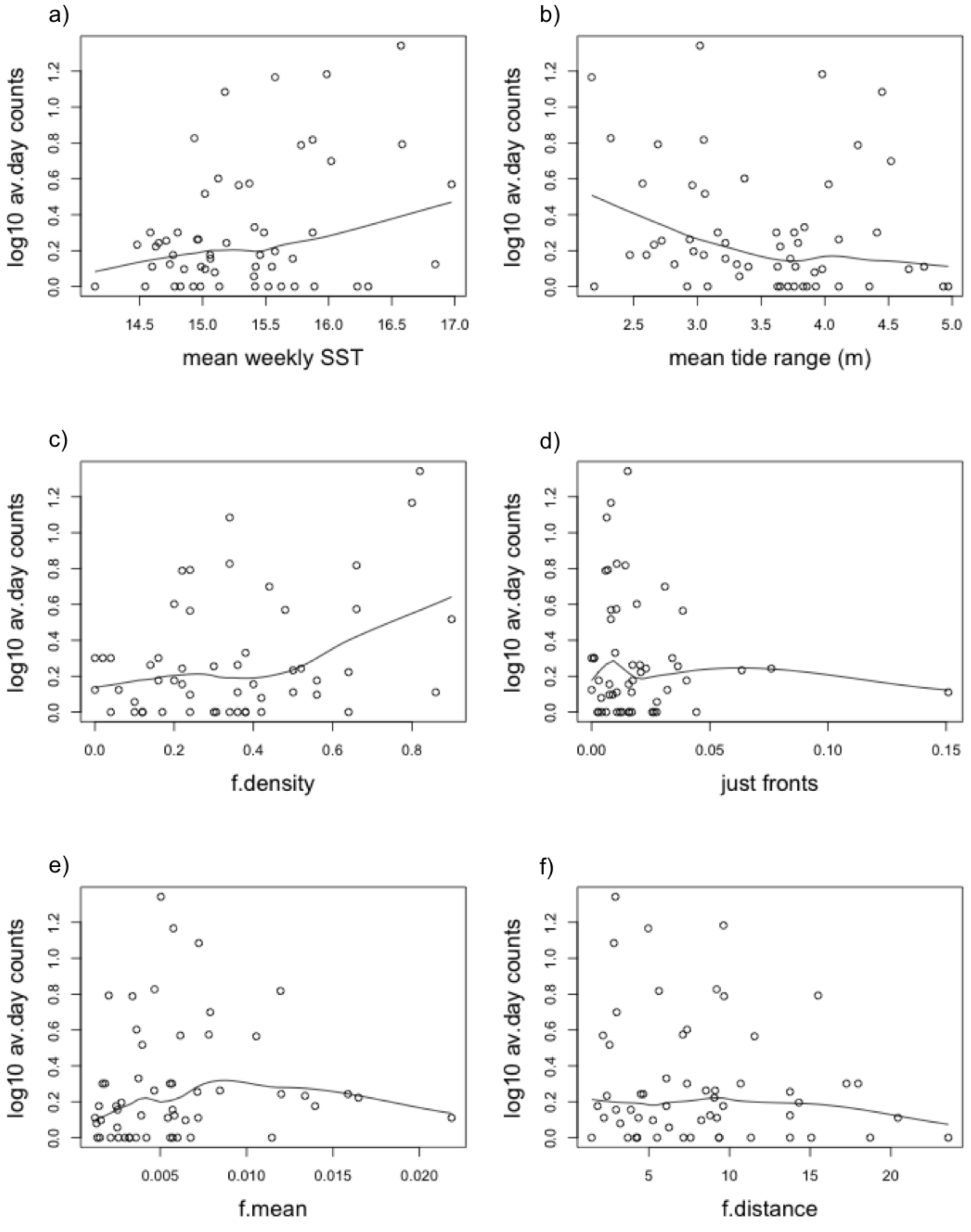


Figure 4.20: Exploratory scatterplots for data from all four years of the SeaWatch SW survey (2007 – 2010, N = 56 weeks), showing relationships between the (Log_{10}+1) weekly average basking shark peak count and weekly averaged environmental variables: (a) SST (°C) (b) tide range (m) (c) front 'density' (proportion of positive pixels) (d) 'just fronts' (pixel gradient strength) (e) f.mean (pixel gradient strength) and (f) 'f.distance (mean distance to nearest major front in km). LOESS smoothers, with default bandwidth, have been added to enhance visual interpretation.

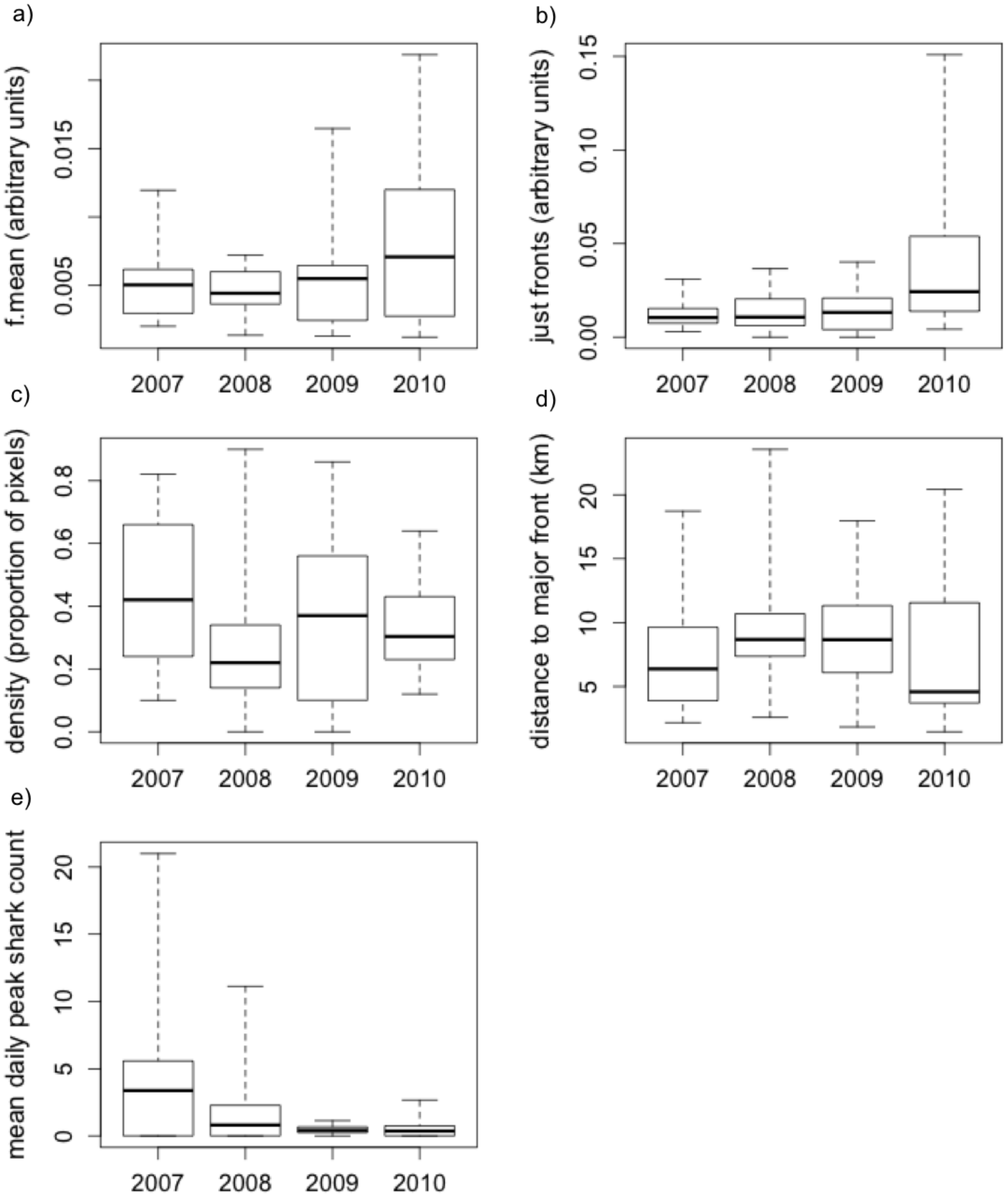


Figure 4.21: Annual boxplots of seasonal frontal metrics (a-d) and average day peak counts of basking sharks (e) in the SWSW survey. The data shown are for the SWSW survey period only (15th July – 15th October). The dark horizontal lines represent the median value and the 25th and 75th percentiles are shown by the lower and upper box extents respectively. The whiskers indicate the full range of the data from each year.

The correlation between the weekly averaged peak-day-count of basking sharks and the weekly averaged environmental variables was explored using cross-correlation analyses. These show inter-annual variability in the relationships between shark counts and SST, tide range and front gradient metrics (‘just fronts’ and ‘f.mean’). There is some consistency in the relationship between front metrics that refer to occupancy rates and proximity of thermal fronts (f.density and f.distance). There is positive correlation between peak shark counts from 2007-2009 and front density (at lags from 0 to 2-weeks, figure 4.22), but the significance of these results is questionable (even though the values exceed the significance threshold), because of the small sample size and therefore the low power of the cross correlation coefficient tests. Additionally, it is likely that the assumptions of normality and constant variance in the data were violated with this data set.

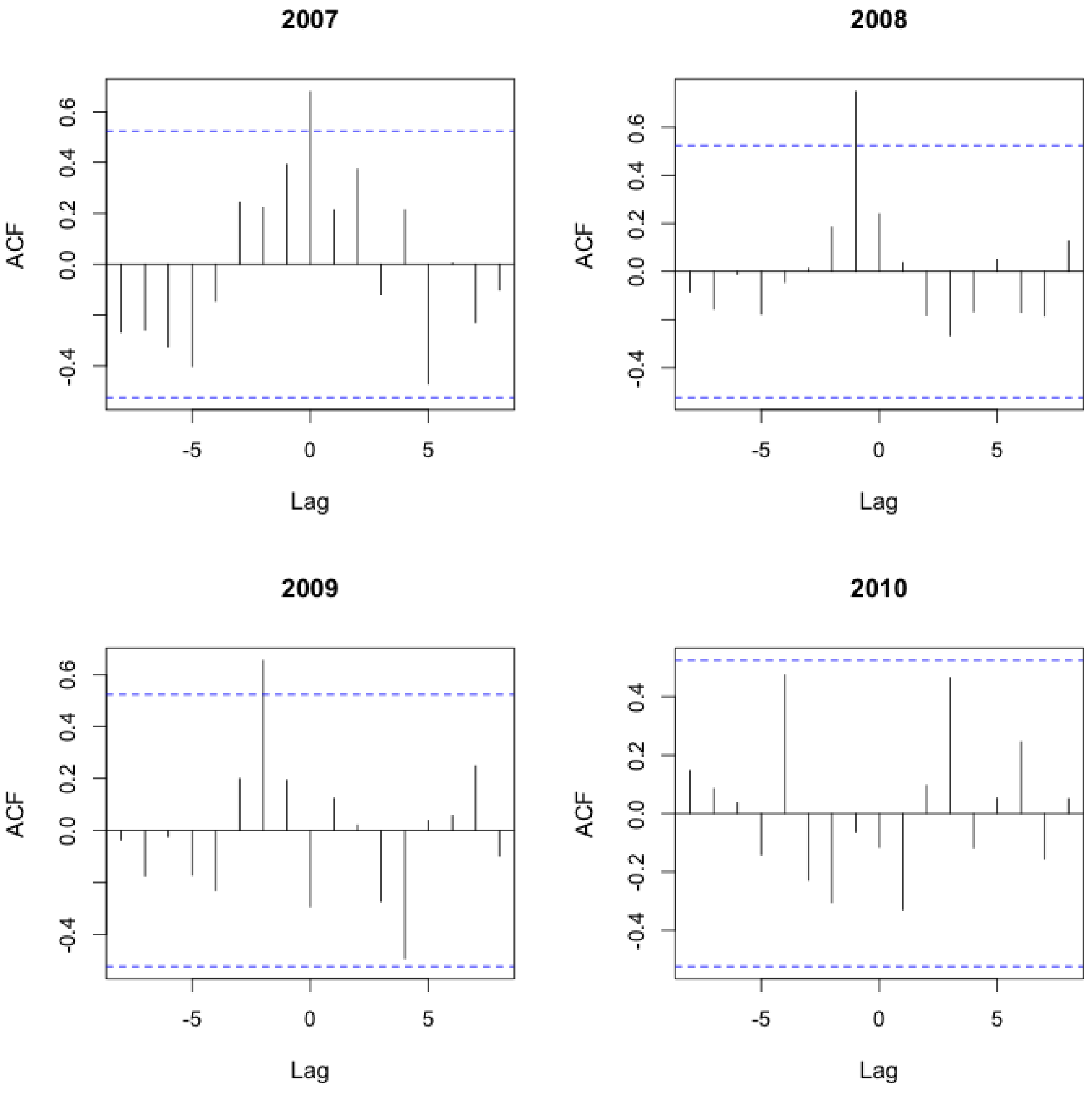


Figure 4.22: Correlograms showing the Pearson cross-correlation coefficients (ACF) between weekly averaged shark peak counts at time-0 and the lagged weekly front metric 'f-density', which indicates the proportion of cloud free pixels where a front was detected during each week of the survey (2007 – 2010). Significance threshold is indicated by the dashed blue lines, which represent the 95 % confidence intervals of the Pearson correlation test.

The weekly data from 2007-2009 also show a negative correlation at lags of 0 to 2 weeks between shark numbers and the mean distance from any point in the box area to the nearest major front (although this correlation does not quite exceed the significance threshold in 2008, figure 4.23).

This result implies that there were more sharks observed in the visual survey within two weeks of a major front approaching the box area. In 2007 and 2008 there is also a ‘significant’ positive correlation between the distance to main fronts at longer lag periods (from 3 – 5 weeks) and shark counts at time-0 (figure 4.23). This result suggests that the lack of a major front close to the survey area is related to increased shark sightings more than a month later, but the caveats associated with the significance of these results, mentioned on page 181, should be considered when interpreting the findings.

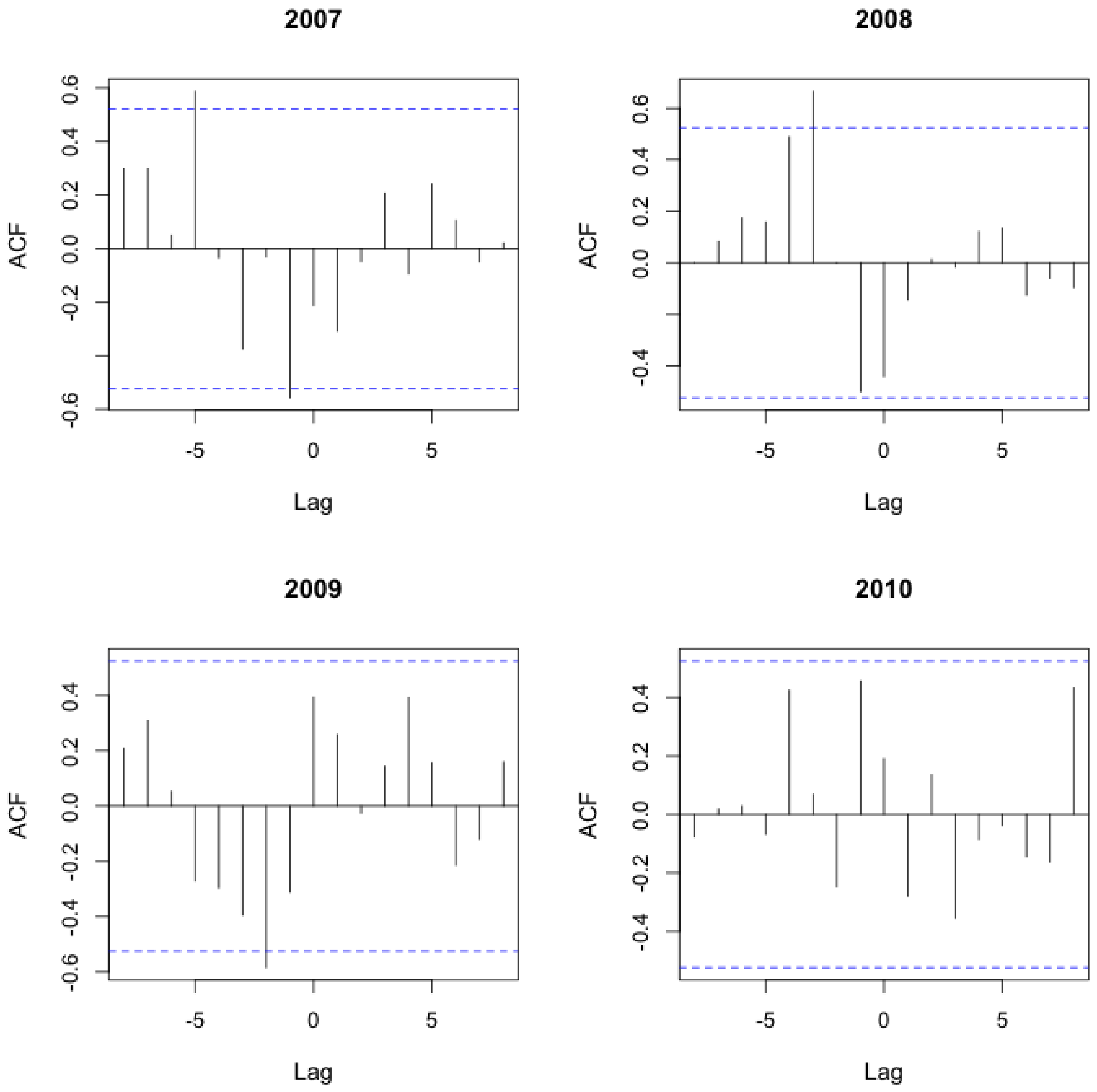


Figure 4.23: Correlograms showing the Pearson cross-correlation coefficients (ACF) between weekly averaged shark peak counts at time-0 and the weekly front metric 'f.distance', which indicates the average distance from any point in the box area to the nearest major front (in km) during each week of the survey (2007 – 2010). Significance threhold is indicated by the dashed blue lines, which represent the 95 % confidence intervals of the Pearson correlation test.

4.3.4 Modelling the effect of environmental variables at a variety of scales on the daily peak basking shark counts.

There was a large amount of variance in the daily shark peak count values (figure 4.24) therefore a negative binomial model was used, which effectively captured the dispersion in the data. Daily observations without a full complement of environmental data variables were removed from the daily dataset in order to achieve a balanced model and allow comparison between models using AIC scores (this can only be done if the models are based on the same data). This left 271 daily peak count observations in the dataset used in the GAM.

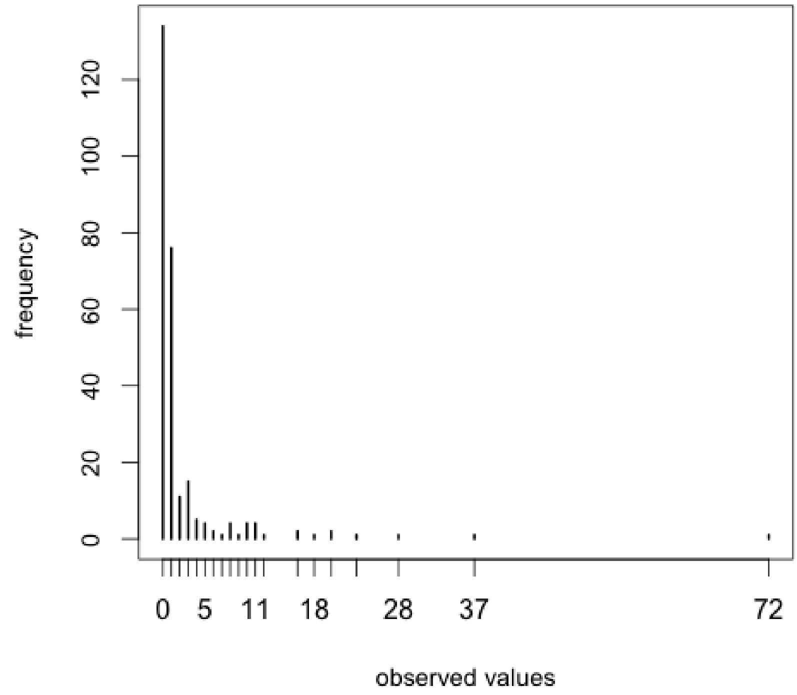


Figure 4.24: Frequency plot of pre-filtered shark peak day counts from the SeaWatch SW survey, 2007 - 2010 (N = 271).

All environmental covariates were considered in staged forwards step-wise selection. VIFs and pairsplots showed that both the real-time and the 2-week moving averages of SST and SST anomaly were co-linear and were therefore not permitted to be in the same model.

After covariate selection, the final model contained the predictor variables sea state (linear), 2-week moving average of SST variance (smoother), average daily tidal range (smoother), 2-week moving average of SST (smoother), year of survey (as factor) and week of the survey (smoother). The model explained 63.5 % of deviance in the daily peak shark counts. A summary of the model is presented in table 4.3. Notably, none of the weekly front metrics were selected as significant model covariates.

Table 4.3: Results of stepwise forwards model selection on GAM of peak day counts of basking shark recorded in the SeaWatch SW survey, 2007 - 2010 (N = 271). Variables are shown in the order of selection, with terms being selected sequentially based on the amount of deviance explained and reduction in AIC score compared to the previous model (with the null model AIC score given in bold). All selected terms were significant to at least $p = 0.05$. Estimated coefficients of linear terms are on the scale of the link function (logit) and degrees of freedom of the estimated smooth functions are given in parentheses.

Parameter	**Estimated coefficient / smooth d.f.**	**Deviance explained (%)**	***z* - value / *Chi sq*.**	**AIC**	***p* - value**
Intercept	-0.4887	0	-1.577	**962**	0.115
Average sea state	-0.4804	13.6	-4.439	929	< 0.001
2-week moving average SST SD (C)	s (1.896)	20.5	8.45	922	0.0198
Tide range (m)	s (4.545)	8.8	26.68	868	< 0.001
2-week moving average SST	s (2.694)	5.5	22.75	847	< 0.001
Year (baseline = 2007)	-	8.6	-	805	-
2008	-0.7052	-	-2.405	-	0.0162
2009	-1.9108	-	-5.822	-	< 0.001
2010	-1.9129	-	-6.064	-	< 0.001
Survey week number	s. (2.903)	6.5	41.55	799	< 0.001
Total deviance explained:	63.5 %				
N:	271 (day counts)				
Theta estimate:	1.299				
Dispersion:	0.969				

Model checking plots are shown in figure 4.25; the Q-Q plot suggests that the negative binomial distribution is appropriate for the data because the deviance residuals lie close to the straight line of the expected quantiles (figure 4.25-a). The residual plot shows that there is higher variance associated with larger peak counts (figure 4.25-b), but the negative binomial model does not assume a specific structure for the mean-variance relationship, so this is not an issue. The residual histogram is relatively normally distributed (figure 4.25-c) and the response ‘vs’ predicted values of the response variable (sightings per grid square) show a positive linear relationship with some scatter (figure 4.25-d), but nothing that is considered to be problematic.

All plots of model terms are shown in figure 4.26. The coefficient for the linear (parametric) predictor of sea state suggests that higher sea states had a negative effect on the daily peak count of basking sharks (table 4.3, figure 4.26-a). The year of the survey also had a negative relationship to basking shark peak counts; with significantly lower peak counts in 2008, 2009 and 2010, compared to 2007 (figure 4.26-b). High amounts of variance in SST in the preceding two weeks act to negatively affect the daily peak counts of basking sharks (figure 4.26-c). There were higher peak counts associated with low and moderate tide ranges, with a steep decrease at the highest tide ranges (more than 4.5 m) (figure 4.26-d). Low SST averages in the two weeks prior to each day of the survey were associated with low peaks shark counts (figure 4.26-e), as were weeks of the survey in late September and early October (figure 4.26-f).

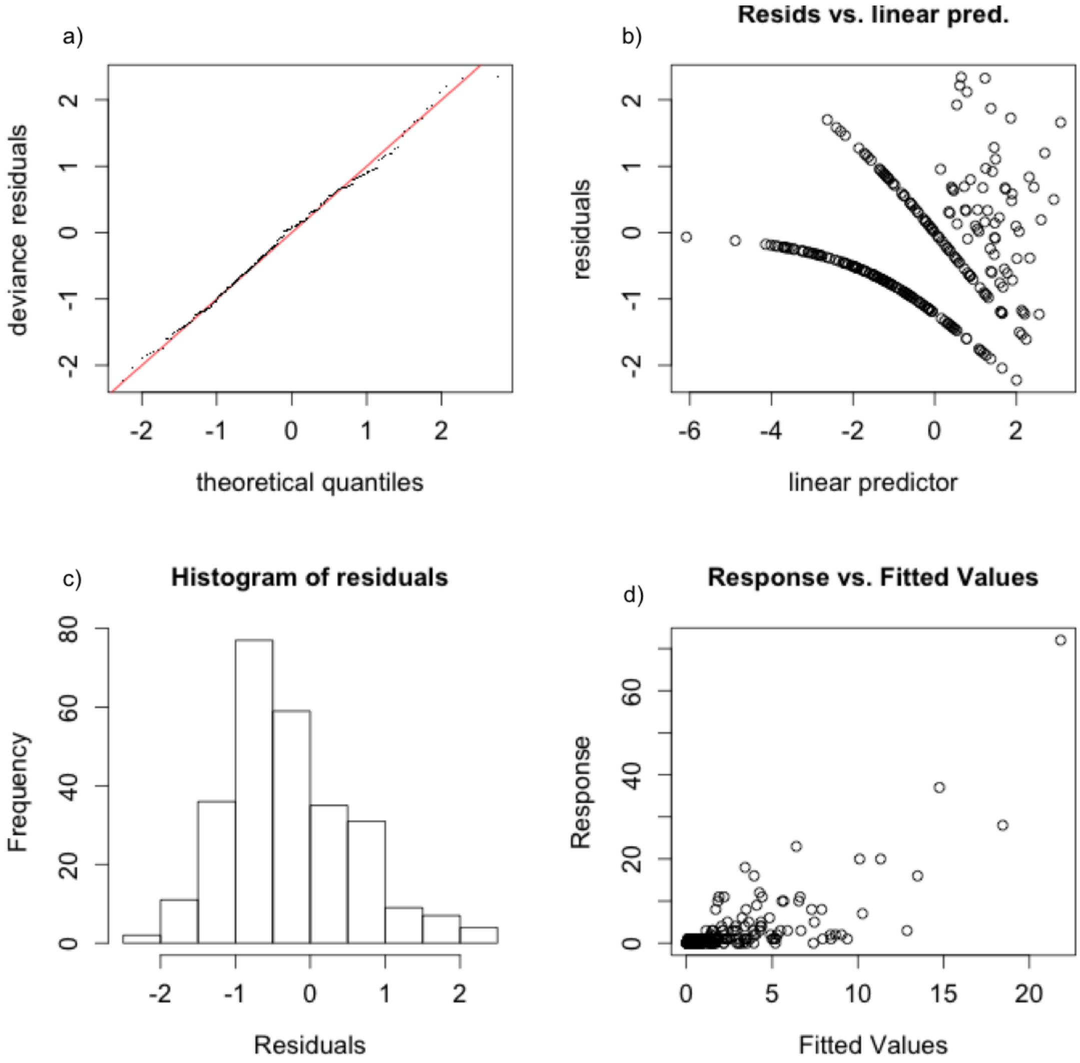


Figure 4.25: Model checking plots for the negative binomial GAM of daily basking shark peak counts modelled as a function of survey, environmental and temporal variables. (a) Deviance residuals (black dots) plotted against theoretical quantiles for a negative binomial distribution (red line). (b) Pearson residuals against the linear predictor (on the log scale). (c) Frequency density of Pearson model residuals. (d) Observed response values (daily peak counts) against model predicted response values.

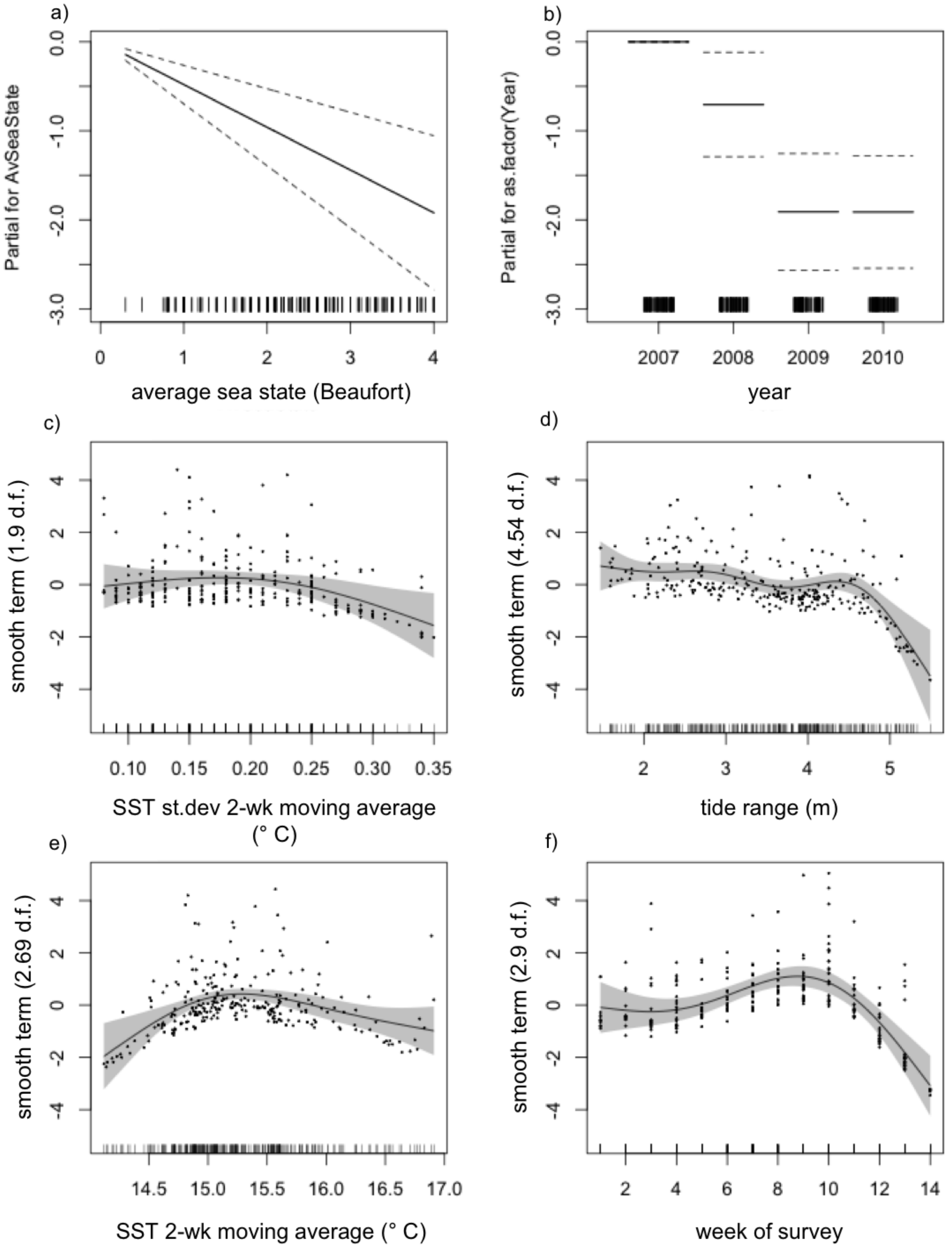


Figure 4.26: Parameter estimates from negative binomial GAM of daily peak counts of basking sharks in the SeaWatch SW survey (2007 - 2010), modelled as a function of environmental variables: (a) linear effect of daily average sea state (b) estimated effect of year of survey (as a factor) (c) smooth function of the standard deviation in SST over the preceding 2-weeks (d) smooth function of tide range (m) per day (e) smooth function of average SST over the preceding 2-weeks and (f) smooth term of week of survey. Shaded areas on the smooth plots and dashed lines in (b) represent 95 % CIs. Residuals (Pearson) are plotted as filled black circles. A rug plot with the actual data values is also shown.

The model residuals are correlated to a lag period of 1-day (figure 4.27), which may be leading to inflation of the significance of covariates.

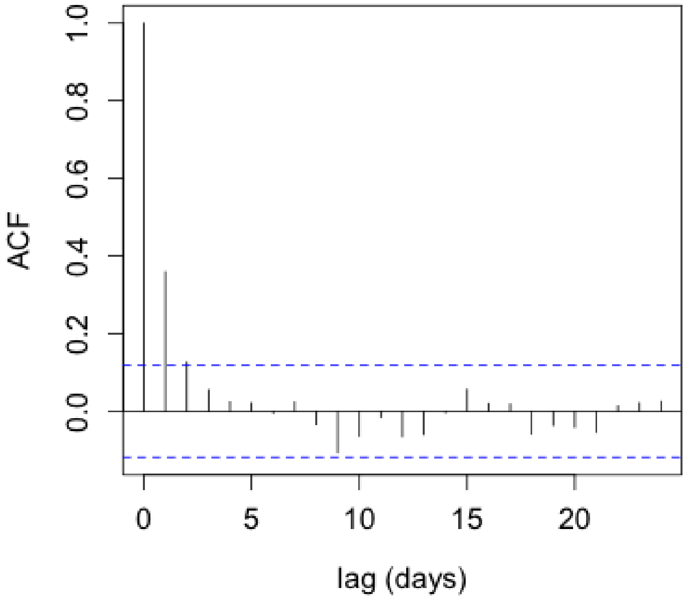


Figure 4.27: Corrleogram for autocorrelation coefficent of Pearson residuals from the negative binomial GAM of shark peak day counts from the SeaWatch SW survey, 2007 - 2010 (N = 271).

The model has good predictive power, accounting for the majority of the variability in the shark peak count data (63.5 % deviance explained). Plots comparing the model predicted daily peak count values against the observed data are given in figure 4.28, and show that the observed values generally fall within the confidence intervals of the model predictions, indicating a well fitting model. The model tends to perform better for the data from 2007 and 2008, and not so well for 2009 and 2010; when there were lower numbers of sharks recorded and more days when no sharks were seen (refer to figure 4.16).

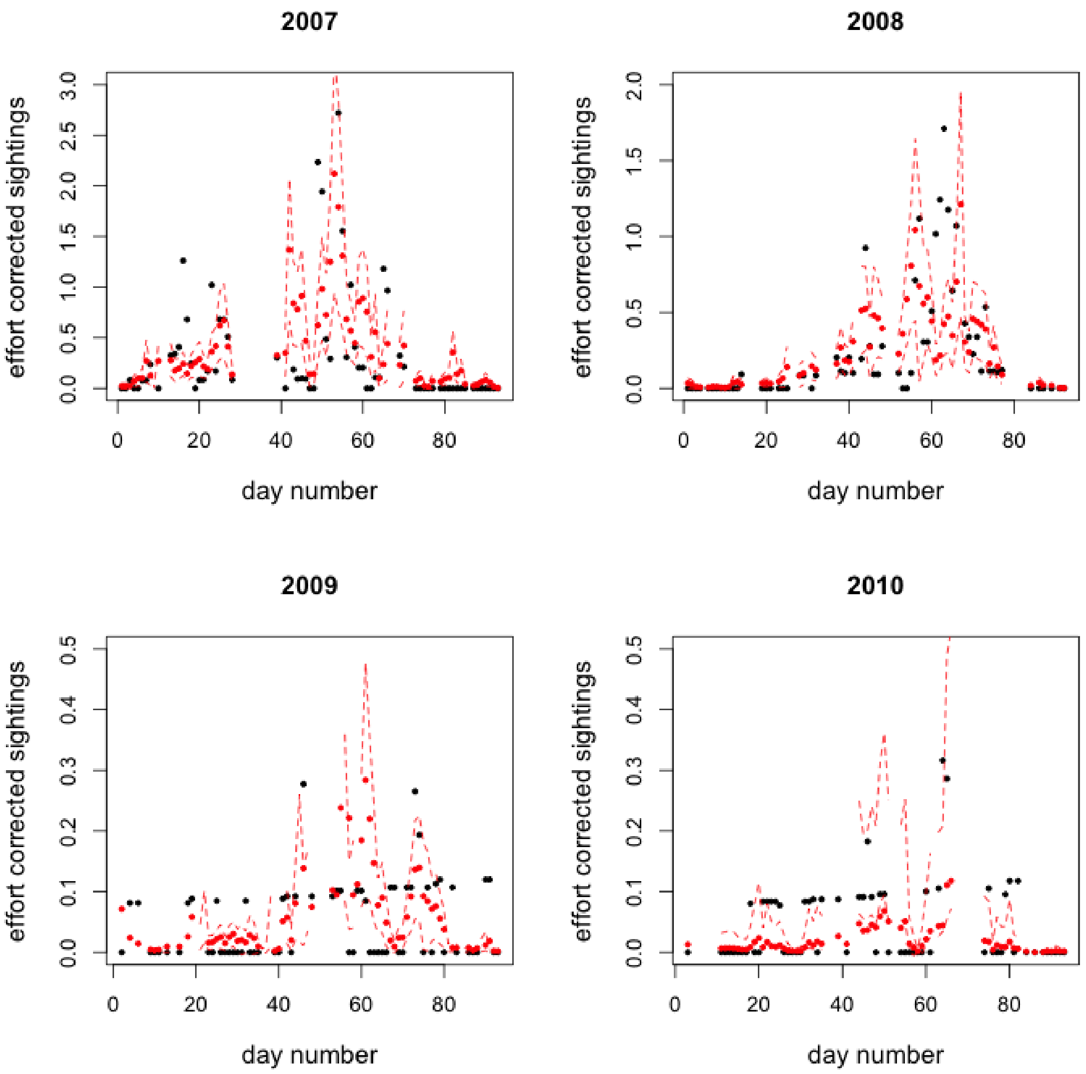


Figure 4.28: Negative binomial GAM model performance plots showing observed (black points) and model predicted data (red points) for effort corrected peak day counts of basking sharks for each year of the SeaWatch SW survey (2007 - 2010). Red dashed lines indicate 95 % CIs for model predictions.

4.4 Discussion

4.4.1 Temporal patterns in the basking shark sightings.

4.4.1.1 The effect of temperature on variability in shark sightings.

The basking shark sightings data show a high level of variability, both within and between the years of the survey. The most notable difference is the large decline in the number of sightings recorded in the constant-effort survey from 2007 – 2010 (figure 4.21-e). A similar pattern is evident in the public sightings data, which have decreased in both absolute and proportional terms in the southwest region over the period of the SeaWatch SW survey (Solandt and Ricks, 2009; Witt et al., 2012).

The SST anomaly data indicate that the 2007 SeaWatch SW survey period (July – October) coincided with higher-than-average temperatures in the southwest UK region (figure 4.19). 2007 was also the only year during the SWSW survey period when a positive mean winter NAO index was recorded the previous winter (i.e. in winter 2006/7) (Osborn, 2011). Due to the short temporal coverage of the SWSW survey (4 years), it is hard to draw conclusions regarding drivers behind the inter-annual variability, but results from previous studies have found similar links to NAO and average SST. Cotton *et al*. (2005) investigated patterns in the public sightings data collated by the MCS scheme from the southwest UK region. They found that higher relative abundance of basking sharks was linked to higher than average mean monthly SST (both real-time and lagged to a period of 1-month) and a preceding positive winter NAO index. In the same study, both the mean SST and the winter NAO index were found to be significant predictors of the regional monthly density of the calanoid copepod *Calanus helgolandicus,* a warm water species, previously identified as important prey for basking sharks in UK waters (Sims and Merrett, 1997). NAO has also been identified as a controlling factor for *Calanus sp*. abundance in the region by Fromentin and Planque (1996). Witt *et al* (2012) describe a significant positive relationship between the previous winter NAO index and the duration of the basking shark ‘season’ within the whole of the UK; defined as the period containing 90 % of the MCS public sighting records from each year, centred around the median date (1988 – 2008); with positive winter indexes generally being followed by sightings seasons of longer duration.

Although there were higher temperatures than the long-term mean during October in all four years of the SeaWatch SW survey (figure 4.19), it is unlikely that this would have a significant effect on the sharks as numbers in the southwest show a steep decline after the end of

September (figure 4.7), likely related to long-distance migratory patterns. Therefore the warmer conditions in October were probably too late in the season to effect a noticeable response in shark numbers.

The analyses presented in section 4.3.4 show that average SST from the 2-week period prior to each survey day was a significant predictor of basking shark peak day count from the SWSW survey, with a notable negative effect of mean SST below approximately 15 °C (figure 4.26-e); although this was one of the less important covariates in the model (explaining 5.5 % deviance). The environmental predictor variable that accounted for the highest amount of variance in the data was SST variability (represented by the standard deviation of the SST recorded over the 2-week period prior to each day of the survey), which explained 20.5 % of the variability in the peak day counts of sharks. There was a negative impact on shark peak counts when SST standard deviation increased to more than 0.25 °C during the preceding 2 weeks (figure 14.26-c).

The variability in SST may reflect changeable conditions resulting from unsettled and inconsistent weather, possibly related to increased westerly wind stress as a result of negative winter NAO index (Hurrell, 1995). Stronger westerly winds may act to break up the thermocline in the stratified waters offshore, affecting front development at the boundary between stratified and mixed waters. Increased wind and wave mixing is also likely to affect the distribution of productive patches of foraging habitat and may directly impact on fine- to meso-scale zooplankton dynamics (Irigoien et al., 2000), both of which will in turn affect the sharks. A similar impact has previously been identified in a study of the foraging success of little penguins around Australia (Ropert-Coudert et al., 2009). Inconsistent foraging opportunities, or dispersed prey as a result of wind and wave mixing (Lasker, 1978) is likely to cause individual sharks to move out of the survey area or southwest UK region in search of alternative prey resources (Humphries et al., 2010).

It is also possible that at a broader regional or national scale, basking sharks use absolute SST or SST variation may be used as a cue for long-distance movements. This may be associated with direct thermal preferences, or with indirect mechanisms such as the effect of absolute temperature or variability in temperature on zooplankton. Skomal *et al*. (2004) note that tagged basking sharks in the northwest Atlantic utilised a wide range of thermal habitat (5.8 – 17.5 °C), but seemed to show a preference for moderate temperatures, spending over 70 % of the time in waters between 15 – 17 °C. Tags from multiple sharks tracked around the coast of the UK recorded a temperature range of 8 – 16 °C, but there is little information regarding finer scale thermal habitat selection from these studies.

The seasonality of appearance of basking sharks in the coastal waters around the UK is well documented, with a defined 'season' extending from April to October (Bloomfield and Solandt, 2007; Witt et al., 2012). The long-term seasonal pattern in abundance of sightings in the southwest shows a strong peak in June-July, with a subsequent decrease through August and traditionally very few sightings in September (figure 4.7). This is contrary to the results of the effort based SWSW survey reported here, which found generally low numbers in July and early August, increasing to a peak in September. Although the absolute values of the peak counts varied by an order of magnitude between the years of the survey; the peak shark count in all four years of the survey was recorded during September (figure 4.16). There are also indications in the MCS public sightings data of a recent change in the timing of the basking shark season in the southwest region (since the mid 2000s), with a decrease in the predictability of the peak month for sightings in the southwest, associated with a change towards a later influx of shark sightings in the region (Bloomfield and Solandt, 2006; Parker and Solandt, 2007; Morgan and Solandt, 2008; Solandt and Ricks, 2009). It is likely that this altered phenology is related to environmental conditions and potentially a change in the horizontal or vertical distribution of prey, but it is unclear what the influencing factors may be.

Sims and Reid (2002) have previously linked declines in basking sharks off western Ireland between 1956 and 1975 with a shift in their distribution caused by an underlying change in the distribution of calanoid copepods in the area. It is possible that changing zooplankton dynamics have led to the recent change in the seasonal appearance of basking sharks around southwest UK. There was a notable increase in abundance of the warm water calanoid copepod *Calanus helgolandicus* in the northeast Atlantic over the last 20 years (Planque and Fromentin, 1996). This is particularly notable in the southern seas around the UK and Ireland where the previously dominant cold-temperate water species *Calanus finmarchicus* has decreased in abundance (Planque and Fromentin, 1996). These changes have been related to increasing SSTs as a result of climate change and associated northwards shifts in the distributions of the two species (Beaugrand et al., 2002). *C. helgolandicus* has two clear peaks in abundance though the year, one in spring and another generally larger peak around September, which is in contrast to the previously dominant *C finmarchicus* that has only one peak in the spring (Planque and Fromentin, 1996). The dependence of basking sharks on large calanoid copepod species (Sims, 1999), and the identification of *C. helgolandicus* as an important prey item during the UK sightings season (Sims et al., 1997) suggests that the altered zooplankton community dynamics described above may be exerting a 'bottom-up' control on basking shark seasonality around southern UK, evidenced by a later peak in the surface sightings when compared to the long-term pattern.

However, samples collected in the Continuous Plankton Recorder survey in spring 2009 show that for the first time in 20-years *C. finmarchicus* was again more numerous than *C. helgolandicus;* suggesting that the situation remains complex and variable (Edwards et al., 2011). Longer-term basking shark records (preferably effort based) and multi-season tracking data would be required to verify the impact of these *Calanus* species dynamics on the sharks' spatio-temporal distribution.

4.4.1.2 Daily and weekly variability in basking shark peak counts: is there evidence for a link with meso-scale tidal mixing fronts?

There is high variability in both the presence of sharks and the peak count values between subsequent days of the survey. In 2007, the maximum peak count recorded was 72 basking sharks (on the same day as 460 sharks were recorded off Land's End), which occurred one day after an average peak day count of 3 (figure 4.16). The intermittent, unusually high, peak counts recorded in the survey may be the result of large numbers of sharks moving into the survey area associated with transient patches of high zooplankton densities. This is supported by anecdotal reports from the survey area from ecotourism companies. Sharks have been shown to forage preferentially in areas with higher zooplankton densities (Sims and Merrett, 1997; Sims et al., 2006; Soldo et al., 2008) and to track productive patches of water over periods of days (Sims and Quayle, 1998) and distances of kilometres (Sims and Quayle, 1998; Priede and Miller, 2009).

It is possible that the, sometimes extreme, variability in the SWSW peak counts from one day to the next may be explained by large numbers of sharks associating with productive bodies of water that were moved into and out of the survey area by advection. The correlograms for 2007 and 2008 shown in figure 4.23 indicate a positive correlation between shark sightings at time-0 and fronts further offshore during previous weeks (i.e. high peak day counts of sharks were associated with major fronts at large distances offshore three or four weeks previously). This relationship switches to a negative correlation as real-time approaches (i.e. high peak day counts of sharks were associated with major fronts close to the box area at real-time and short time lags of 0 to 2 weeks). This pattern may be indicative of basking sharks following major fronts that were being advected closer to shore, possibly as a result of tidal or wind forcing.

The weekly cross-correlations (figures 4.22 and 4.23) suggest that there was some influence of the density of fronts recorded in the box area on the average weekly shark counts at lags of 1 to 2 weeks (2007 – 2009) and that major fronts closer to the box area were linked to higher shark counts in the subsequent 1 to 2 weeks in 2007 and 2009. These front metrics were not selected by the GAM as being significant predictors of the daily peak shark counts (table 4.3). These results may indicate that the impact of front density and distance from the study area is more significant at lagged periods than in real-time, possibly reflecting a bottom up influence of fronts which has a lagged impact on basking sharks through enhanced productivity and trophic transfer; as opposed to an immediate impact resulting from the direct provision of foraging habitat. Future work should investigate this by the inclusion of lagged front data in a model of daily shark counts. The results of the weekly analyses may also have been affected by the small sample size (14 data points per year) and may therefore not be as robust as the results from analyses using the daily data (N = 271).

Other than the points presented above, there is little evidence from the effort based survey data that thermal fronts have a significant real-time effect on the numbers of sharks recorded in the SWSW visual survey. None of the front metrics were found to be significant predictors of daily peak counts of sharks recorded in the survey. In fact the 2010 survey season coincided with the strongest front gradient strengths and the closest major fronts (figure 4.21-a, b and d), but had consistently low surface shark sightings (table 4.1, figure 4.21-e). This is a rather surprising result and is contrary to what is generally accepted regarding the relationship between basking sharks and fronts (Sims and Quayle, 1998; Sims et al., 2000; Sims, 2003; Sims et al., 2006; Sims, 2008; Priede and Miller, 2009). The result may represent a hierarchical effect of environmental variables on basking shark distribution indicating that, although they have previously been noted to make use of fronts, there were other environmental drivers (such as SST) that have a more significant effect on their distribution. There were also likely to be scale-effects at play, and it is possible that a mismatch between the spatial scale of the survey and the spatial and temporal scales of environmental variables that influence highly mobile species such as the basking shark, have affected the results of the study (further discussion of this in the limitations, section 4.4.1.5).

Previous studies have provided evidence for a link between the spatial and temporal distribution of seasonal tidal mixing fronts within the UK coastal seas and both basking shark surface sightings and locations from electronic tracking. Sims *et al*. (2000) describe the location of groups of sharks recorded in visual boat-based surveys between May and July 1996 – 1999 as being associated with tidal mixing fronts in SW UK. However, analyses of the data from 1996 and 1997 (when the largest amounts of survey effort were expended) appear to be based on linking the position of fronts identified in one SST image from a single day, with basking shark locations from surveys carried out over periods of 2-weeks to 2-months (Sims et al., 2000). Sims *et al* (2003b) also found that at least 2 out of 5 sharks that were elecronically tracked around the UK in early summer 2001 spent time in areas known for frontal actvity in the western Channel. One of these sharks was described as associating with the Ushant front, evidenced by temperature data collected by the electronic tag. Both of the sharks were found to spend time in recognised ‘frontal areas’ in the early summer (May – June), and this is discussed with reference to the high levels of phytoplankton and zooplankton abundance associated with the fronts. However, the empirical evidence from tidal mixing fronts on the UK shelf does not show a clear and robust link with increased zooplankton densities and the situation seems extremely complex, species specific and highly variable both spatially and temporally (Robinson et al., 1986; Beaugrand et al., 2000; Koski et al., 2011; Simpson and Sharples, 2012b).

Although there are instances of electronically tracked sharks associating with thermal boundaries at tidal mixing fronts (Sims and Quayle, 1998; Priede and Miller, 2009), these instances represent a small sample size and there is little description of the amount of time spent feeding at fronts relative to the amount of time spent feeding away from fronts, or of the overall frontal density in the area and thus an indication of the possibility that the animals may have foraged close to a front by chance. In addition, the ‘pop-up’ archival transmitting (PAT) tags that were used by Sims and Quayle (1998) rely on estimation of longitudinal position by light levels and latitudinal positions by calibration with SST, therefore the level of error on geo-locations is likely to be large enough to make it hard to state that the animals were definitely associating with frontal boundaries.

There are many studies that describe clear links between high densities of marine mega-vertebrates and large scale fronts and eddies in the open ocean and tropical seas (e.g. Podesta et al., 1993; Worm et al., 2005; Hyrenbach and Veit, 2006; O'Hara et al., 2006; Palacios et al., 2006; Kai et al., 2009). However, it should be acknowledged that the relationships in these marine systems are likely to be driven by processes operating at larger scales and the importance of these features may be very different in the context of the low productivity of the seas surrounding them (they have been likened to oases in the desert by Godø *et al*. (2012)). This is a different situation to that on the European continental shelf, where overall nutrient levels are higher than further offshore, and wind mixing and tidal forcing are very influential drivers of productivity (Simpson and Sharples, 2012a). These characteristics mean that that the shallower shelf seas are very dynamic areas, influenced by complex interactions between hydrodynamic features and marine productivity acting at a variety of scales.

Although this study has found only tentative evidence of a small-scale link between the presence or strength of fronts within the vicinity of the survey area and the number of shark sightings; the effect of frontal density and intensity may act on shark numbers at a broader scale or have a lagged effect. Future work should investigate the quantitative front metrics over larger areas (i.e. within each of the three broad hotspot areas) and look at whether the temporal patterns in front density/strength at these locations are related to shark counts from both public sightings and effort based monitoring surveys. It is well recognised that the areas of the UK continental shelf that basking sharks seasonally inhabit are known frontal regions (Pingree and Griffiths, 1978; Le Fevre, 1986; Sims, 2008), but because the shelf seas around the UK are generally extremely productive areas, it may be the overall productivity of the regions, rather than a direct fine-scale and real-time link with frontal boundaries, which is driving basking shark distribution and abundance. Evidence for alternative physical variables driving productivity at small-scales come from recent work by Scott *et al*. (2010), who describe patches of high productivity that are key foraging habitats for marine top predators, which are not associated with horizontal temperature gradients. Instead it seems that locally increased levels of vertical mixing drive the biophysical and trophic coupling observed in these locations.

4.4.1.3 Fine-scale patterns in the timing of peak day counts, the effect of time and tide.

The timing of the daily peak counts of sharks during the SWSW survey showed patterns associated with time of day, with peak counts tending to be recorded in the morning session of the survey followed by a notable drop off in the rate of peak counts recorded after 1500 hrs (figure 4.14). Similar results were reported in Sims *et al*. (2003a) who undertook a boat-based visual study of basking shark surfacing behaviour off Plymouth (southwest UK), and found that fewer sharks were sighted after 1200 h. Shepard *et al*. (2006) also documented strong circadian periodicity in the diving behaviour of five electronically tracked basking sharks off Plymouth and western Scotland (using 595 days of track data). All sharks showed a significant ~ 24 hr cycle in diving behaviour, but some sharks spent the day in the surface waters and the night at depth, and in others this pattern was reversed.

Diel patterns in the surface sightings of basking sharks in the SWSW survey and in the surfacing behaviour recorded in other studies around the UK are likely to be driven by the vertical distribution of their zooplankton prey (Sims, 2003), specifically the diel vertical migration (DVM) behaviour of the zooplankton. Vertical tracking of the most productive zooplankton patches will allow the sharks to increase their foraging success by orienting preferentially to depths where the highest zooplankton densities are located. Normal DVM is characterised by zooplankton spending more time in surface waters during the night and then occupying deeper waters during the day, whereas reverse DVM is the opposite pattern (Clarke, 1930). DVM in zooplankton is thought to be an evolved response for predator avoidance and the pattern can vary dependent on predation pressure, location, season, species and life-stage (Hays, 1996; Hays et al., 2001). Responses to the vertical distribution of planktonic prey have been documented for other large planktivores, such as the whale shark *Rhincodon typus* (Brunnschweiler et al., 2009), sei whale *Balaenoptera borealis* (Baumgartner and Fratantoni, 2008) and north Atlantic right whale *Eubalaena glacialis* (Baumgartner et al., 2003).

The diel pattern in the peak sightings of basking sharks from the SWSW survey suggests that zooplankton are likely to be more numerous in the surface waters of the survey area through the morning and early afternoon, a pattern which is most similar to reverse DVM (up at dawn and down and dusk). Sims *et al*. (2005b) found that electronically tagged sharks altered their diel diving behaviour in response to the changing DVM of their prey, which seemed to be somewhat dependent on habitat type. In deep water habitats 'normal' DVM was most common and zooplankton surveys showed the shark dive depths to be related to areas of highest densities of calanoid copepods and euphausiids. Reverse DVM was reported in the same study when sharks were in shallower, coastal seas (similar to the SWSW survey area), where calanoid copepods where shown to be most numerous in the top 10-m during the day. Reverse DVM in *Calanus* sp. was also documented by Irigoien *et al*. (2004) in a study of zooplankton in the Irish Sea, where the behaviour was proposed to be an avoidance response to high densities of predatory chaetognaths that were performing normal DVM. Hays *et al*. (1996) also report that the biomass of 'normally' migrating copepod zooplankton is less in the coastal seas around the UK than in other parts of the north Atlantic, a pattern which is likely to impact on the vertical distribution of planktivorous predators, such as the basking shark. In order to investigate the direct impacts of zooplankton DVM on the diel pattern in basking shark sightings from the SWSW survey, depth-resolved zooplankton surveys would need to be undertaken *in situ*.

The peak shark sightings recorded in the SWSW survey also show patterns associated with tidal period, at both daily and lunar cycles. At a fine scale, there were significantly higher numbers of peak counts made on the ebbing tide than would be expected (table 4.2), associated with strong easterly and westerly flows within the study area (figure 4.15). There were also significant effects of tidal range on the value of daily peak counts, with the lowest counts being made during the largest tidal ranges associated with spring tides (figure 4.26-d).

The fine scale effects of the semi-diurnal tidal cycle on peak shark sightings may be driven by a direct preference for specific flow speeds, possibly those associated with the strongest flow speeds occurring during neap tides. Theoretically, orienting into a stronger tidal flow should equate to an increase in the volume of water filtered through the gills and therefore a greater capacity for feeding (Sims, 2000). However this increase in the volume of filtered water would need to be offset against the energetic costs of swimming into the tidal current and the increase in drag associated with the basking sharks' open-mouthed feeding mechanism (Sims, 2000). This trade off will be specifically related to the density of zooplankton available, which would have to be above an optimum threshold, under which feeding in the strong current would no longer be beneficial and would cease (Sims and Merrett, 1997; Sims, 1999). Without information on either the exact tidal speeds or the plankton densities within the vicinity of each shark during the peak counts, it is impossible to comment further on this hypothesis.

An alternative driver of the fine scale tidal pattern in the timing of peak shark counts may be tidal forcing of prey aggregations, induced under specific flow dynamics associated with a particular period in the tidal cycle. There are a number of studies that report tidally influenced increases in surface zooplankton densities over abrupt topographies (Alldredge and Hamner, 1990; Zamon, 2003; Genin, 2004; Embling et al., 2012). Embling *et al*. (2012) present the first study to measure fine-scale physical parameters and concurrent biological data from multiple trophic levels in a coastal, tidal location. Their study specifically notes an increase of sandeels in the surface waters during ebbing tides, associated with high zooplankton densities during this tidal period.

Data from a single animal tracked by Shepard *et al*. (2006) identified a tidal periodicity in diving behaviour linked to the semi-diurnal tidal cycle. The shark was significantly shallower (and therefore more likely to be sighted at the surface) during the flood tide than during the ebb tide and it was suggested that this might be a response to localised, tidally induced prey aggregations within surface waters. It is possible that there is a similar effect of flow on zooplankton aggregation occurring within the Runnelstone Reef survey area, leading to tidal-topographically driven aggregations of zooplankton. It is likely, considering the spatial and temporal complexity of the fine-scale flow around the reef (discussed in chapter 3, see ADCP survey data in appendix 4) that any such effect would be spatially constrained and not uniform across the survey area, but unfortunately it has not been possible to analyse the fine scale spatial distribution of shark sightings.

From the overview map of all (unfiltered) shark sightings (figure 4.11), there does not appear to be any spatial clustering in the data. This is in contrast to the harbour porpoise data and is indicative of a different use of the survey area by these two species; observations suggest that the sharks are less depth constrained and making use of a wider range of the fine-scale habitat at the Runnelstone Reef, such as small inshore eddies and foam lines driven by Langmuir circulations, which may be aggregating buoyant particles at very local scales. Ongoing work, using a theodolite to track the basking sharks' movements within the survey area will be able to better constrain their movement patterns, periods of time spent at the surface, orientation with reference to direction of tidal flow and feeding behaviour. These additional data will enable assessment of foraging patterns against spatial distribution and tidal flow metrics. In addition it would be beneficial to collect further plankton net hauls, or to carry out a boat-based survey using an EK-60 to record zooplankton sound scattering layers across a full tidal cycle in an attempt to identify tidally induced aggregations. Zooplankton samples were collected over a period of 4-days within the survey area in 2010, however as a result of a general increase in the zooplankton biomass over the 4-day period of collection (associated with settled conditions and a secondary bloom); fine scale patterns in the distribution of zooplankton in relation to location within the study area, time of day and tidal period were difficult to tease out.

Over longer time scales (days to weeks), there is evidence from the model of daily peak counts (figure 4.26-d) and the cross-correlation analyses (figure 4.18) that basking sharks were sighted more frequently and in larger numbers on, or around, neap tide periods. It is possible that this is related to optimal foraging strategies and an avoidance of periods of strongest flows associated with spring tides, which may exceed the threshold limits beyond which the drag related to open-mouthed filtering overcomes the benefits associated with consuming prey (Sims, 1999), or act to disperse prey under more turbulent flows. Shepard *et al*. (2006) analysed dive data from multiple sharks using signal processing and found that spring tides were associated with more frequent dives to deeper depths, thought to be associated with flow-related prey resource distribution in deeper water. Should such an effect be occurring at the Runnelstone Reef, this diving behaviour would reduce the availability of basking sharks for inclusion in the visual survey.

4.4.1.4 Conservation and management implications.

Agreement between the broad temporal patterns in the distribution of surface sightings from the effort based SWSW survey and the public sightings data from the region is an important finding. There has previously been some concern over the use of the non-effort corrected MCS public sightings database, due to the possibility of bias introduced by increased observer ‘effort’ during periods of clement weather conditions. Here we describe concurrent trends in the effort-based survey data from SWSW and the MCS public sightings data, which provides support for the use of the long-term public sightings data as a spatio-temporal overview of the species’ distribution that may prove invaluable in the future to look at long-term patterns and variability in distribution. Further to this, the temporally and tidally linked patterns of surface sightings described in the SWSW data provide important information for future directed monitoring in terms of ensuring survey effort is spread evenly with respect to possible diel and tidal cycles, in order to prevent biasing survey results.

There is clearly a need to better constrain the nature of the relationship between basking sharks and tidal mixing fronts in the UK seas; an association that has been propagated in the literature, but which perhaps requires further empirical evidence. There is an increasing interest in the importance of frontal features for mobile marine species and proposals to use their locations as potential targets for UK marine protected areas. This is an exciting and important step forward for marine protected area policy, which has not previously been focussed on biophysical linkages. However, it is important that the evidence base for this policy focus is robust and that the mechanism(s) underlying the associations between the oceanographic features and the animals are understood. This will require a combination of fine to meso-scale effort-corrected monitoring data (which can provide a population scale view of the importance of fronts to distribution) and electronic tracking data (that can reveal the effect of fronts at the level of the foraging individual). In particular, it will be key to use tracking methods that can provide accurate, finely resolved spatial data to pin down the real-time importance of frontal boundaries as foraging habitat. Importantly, tracking data can provide a mechanism for understanding individual foraging decisions in the context of the environmental landscape at a variety of scales. It will be key to focus future tracking analyses not only on the oceanographic habitats that the sharks are using, but also on those that are locally available but are not being used.

The strong link between SST and the NAO on inter-annual variability in basking shark abundance and the effect of absolute water temperature and SST variability on sharks sightings at a finer temporal scale have clear implications in terms of climate change. The relationship with SST may be mediated through changes in specific thermal habitat for the sharks, or it may be a response to changing distributions of their zooplankton prey leading to altered foraging opportunites. It is clear however, that changes in temperature and temperature variation (possibly caused by the increasingly unsettled weather and high wind stress associated with predicted climate change) have the potential to impact the temporal and spatial distribution of available habitat for the species, but this effect will be both difficult to predict and difficult to counter.

4.4.2 Limitations

Some limitations have been addressed as part of the main discussion, but other noteworthy points are listed below.

When interpreting the results of visual surveys, there is always the caveat that they are only able to record the surface behaviour of the animals, therefore a reduction in sightings may not be indicative of a reduction of the number of sharks in a region, but may instead be indicative of changes in the surfacing behaviour of the sharks (possibly related to the depth distribution of prey), which would have affected the availability of the sharks for detection in the visual survey. A major drawback of the visual survey methods is therefore the inability to establish whether changes in sightings were as a result of changes in the distribution and/or abundance of animals, or changes in their surfacing behaviour. It is proposed here, that large inter-annual changes in the frequency of shark sightings and their relative abundance are representative of a change in their presence with the survey region, but this cannot be confirmed. At a finer temporal scale (hours to days), it is more plausible that the pattern in the sightings is a result of altered surfacing behaviour, related to both the horizontal and vertical distribution of the shark's zooplankton prey; but again this cannot be confirmed without identification of individual's movements. For this reason, the discussion has paid special attention to basking shark tracking studies, which report changes in diving behaviour in response to environmental variables. Additionally, the front data is based on AVHRR SST remote-sensed data, which only detects the temperature at the very surface of the sea, therefore cannot map frontal features that are not expressed by a thermal boundary at the surface.

There is a negative effect of sea state on the probability of sighting a basking shark in the SWSW visual survey and on the number of sharks recorded in daily peak counts (figures 4.12 and 4.13). These results show clearly the need to account for sea state and other survey variables that may affect detection availability in analyses. The shark sightings data were filtered to remove any sightings or effort carried out in sea states above 4, and sea state was also included as a covariate in the GAM of peak day counts of basking sharks. The model found that sea state was a significant linear predictor variable in the model, with a negative effect on peak counts and accounting for 13.6 % of the deviance (figure 4.26-a). It is possible that the effect of sea state is mediated, not only through a negative effect on detection of sharks, but also through altered behaviour, with less time spent at the surface in rougher conditions. This may be a direct reaction to the rougher conditions at the sea surface, or linked to the break down of discreet prey maxima under more turbulent conditions as proposed by Lasker (1978). This theory could be explored using tracking devices and data loggers such as accelerometers and time-depth recorders (TDRs), which can provide ultra-high resolution data on an individual's movement and depth profiles.

It is likely that the results of the exploratory data analyses from 2009 and 2010 (section 4.3.3.2) were affected by the overall low numbers of sightings and lower than average peak counts that were recorded in these years, which have led to increased zero counts and low power in the analyses. In addition, the results from the 2008 analyses should also be interpreted with caution, as sightings were not spread throughout the season, but instead were clustered into an approximately 2-week period in September (figure 4.16), which is likely to skew the analysis of the impact of envrionmental variables, such as temperature, by assuming a preference for conditions experienced during this short period (see figure 4.17-c). A similar effect of the strong temporal clustering of sightings in 2008 may have affected the analyses against tidal variables (figures 4.17-d and 4.18-d).

Year of the survey was included in the GAM of daily peak shark sightings and was found to be significant, accounting for 8.6 % of the deviance (figure 4.26-b). This was one of the less important direct predictor variables for the peak day count basking sharks (table 4.3). However, to ascertain whether the type or magnitude of other covariate effects was affected by year, interaction terms between each covariate and year should be introduced into the model. These interactions would indicate whether the relationship between the environmental covariates and shark peak counts has changed annually and/or become more or less significant over time (Panigada et al., 2008).

4.5 Conclusions

The results presented in this chapter describe the effect of environmental conditions on the temporal distribution of basking shark sightings in the SWSW effort-based survey. The results are in agreement with previous studies that have highlighted the importance of SST and NAO on inter-annual variability in surface observations of the species. In addition some novel aspects of the relationship between basking sharks and their environment were described at finer temporal scales, notably the effect of time of day and tidal cycle on the number of sharks recorded at the surface; which has implications for future directed monitoring efforts. An additional result that should be considered in respect of future monitoring is the extreme variability in sightings within this previously identified basking shark 'hotspot' area, and the impact that this variability may have on monitoring efforts that are less temporally intensive than the effort-based SeaWatch SW survey.

There was found to be a relationship between peak shark sightings and the timing of strongest flows within the semi-diurnal tidal period, as well as neap tides within the lunar tidal period. This temporal coupling with predictable tidal conditions provides evidence that tidal-topographic interactions may aggregate prey under specific flows at the survey site. A similar tidal control has previously been suggested from the interpretation of dive data from tracking studies.

A key result from the fine-scale temporal analysis of peak basking shark sightings is the lack of a definitive link with thermal front metrics, which have previously been suggested as a key driver for the spatio-temporal distribution of the species during its seasonal migration to the UK shelf seas. This is the first analysis of the effect of thermal fronts on basking sharks that uses effort-based monitoring data, along with quantitative front metrics at a scale relative to the size of the survey area; therefore the results are considered to be robust. The results suggest that further in-depth investigation of the relationship between basking sharks and fronts is required, particularly looking at their impact at a range of different scales and time lags. This is a key requirement for future work in light of recent interest from policy makers on the importance of fronts for this protected species.

Chapter 5 The spatial and temporal distribution of the Critically Endangered Balearic shearwater (*Puffinus mauretanicus*) in the UK and France.

This chapter is presented as a first authored paper that is currently in review with the international ornithological journal, *Ibis*.

The data presented in the paper describe the spatial and temporal patterns of the Critically Endangered Balearic shearwater *Puffinus mauretanicus* in the waters around northern France, the UK and Ireland, during the interbreeding period when the birds disperse away from the breeding colonies. The data used were a combination of effort-based monitoring data collected in various land and boat surveys and opportunistic data supplied to online databases by sea-watchers in the UK, Ireland and France.

An extended introduction to the paper, in the form of a short literature review for the species, is presented first; followed by the manuscript containing a summary, introduction, methods, results, discussion and conclusion sections. The electronic supplementary material is provided in appendix 6.

Note that a further co-authored paper on the post-breeding migration patterns of Balearic shearwaters using geo-locator tracking methods is given in appendix 7.

5.1 Introduction: Background information on the ecology, distribution and habitat use of the Balearic shearwater, *Puffinus mauretanicus*

5.1.1 Taxonomic classification and general biology.

The Balearic shearwater (*Puffinus mauretanicus*) is a member of the Procellariiformes, a diverse and globally distributed order of pelagic seabirds, which are often referred to collectively as the petrels (excepting Albatrosses). Balearic shearwaters are part of a smaller group (tribe) within the Procellariiformes, called the shearwaters, of which there are more than 30 species globally who share features such as medium size (usually between 400 – 800 g in weight) and long wings relative to body size. The majority of the shearwater species are contained in two of the 6 genuses; *Calonectris* and *Puffinus*.

Until the early 1990s the Balearic shearwater and the Yelkouan shearwater (P. *yelkouan*) were both considered as separate sub-species of the Manx shearwater (*P. puffinus*), and the Balearic shearwater was classified as *P. puffinus mauretanicus*. In 1991, Bourne *et al*. (1988) achieved re-classification of the Balearic and Yelkouan sub-species, which were then grouped together as one single species named *P. yelkouan mauretanicus*, or the Mediterranean shearwater. Subsequently morphological and genetic evidence were presented that distinguished Yelkouan and Balearic shearwaters and led to their separation into two distinct species (*P. yelkouan* and *P. mauretanicus* respectively) in 2001 (Sangster et al., 2002). However, there remains considerable taxonomic uncertainty regarding the species status of the Balearic shearwater, particularly in regard to its congener the Yelkouan shearwater, and direct evidence has been found for hybridisation in the parts of their ranges where breeding areas overlap (Genovart et al., 2005; Genovart et al., 2007). Below is the taxonomic hierarchy for the Balearic shearwater:

- **Kingdom**: Animalia
  - **Phylum**: Chordata (Subphylum: Vertebrata)
    - **Class**: Aves
      - **Order**: Procellariiformes
        - **Family**: Procellariidae
          - **Genus**: *Puffinus*
            - **Species**: *Puffinus mauretanicus* (Lowe, 1921)

Schreiber and Burger (2001) define seabirds as “those living in and making their living from the marine environment, which includes coastal areas, islands, estuaries, wetlands and oceanic islands”. Less than 3% of the World’s bird species live at sea as a result of the considerable adaptations required in order to survive in the open ocean, sometimes for years at a time, and to exploit marine resources (Croxall, 1987). Seabirds have considerably different life-histories to land birds including longevity (usually 20-60 years), late maturity and low fecundity (Schreiber and Burger, 2001). These differences are likely to result from adaptation to patchy prey distribution with associated energetic costs of rearing chicks and the reduced predation pressure for birds at sea (Weimerskirch, 2001).

The Balearic shearwater is a medium sized shearwater measuring 35 – 40 cm long with a wingspan of 85 – 90 cm and typically weighing around 500 g, although the species shows sexual dimorphism with males tending to be larger than females (Genovart et al., 2003). The plumage colour can be variable, but is generally a dark chocolate brown on the upperparts with a lighter underside characterised by dusky undertail covets and ‘armpits’ (Svensson and Grant, 2010) as illustrated in figure 5.1. The species is identifiable in the field from the closely related Manx shearwater due to the lack of strong black/white contrast between the upper and lower plumage, additionally the Balearic shearwater is slightly larger and more potbellied. Dark colour morphs of the species could be confused with the sooty shearwater (*Puffinus griseus*), but are slightly smaller, have shorter wings and always have some pale colouration on the underbelly.

Figure 5.1: Illustration of Balearic shearwater in flight showing chocolate brown upper parts and paler underside (RSPB, 2011)

The Balearic shearwater is endemic to the western Mediterranean and breeds only on the Balearic Islands, nesting in burrows, crevices or caves (Rodriguez and McMinn, 2002; Arcos, 2011). A single egg is laid and incubation lasts ~ 50 days with a further 65 – 70 day chick-rearing period (Oro et al., 2004). As with most seabirds, the Balearic shearwater is relatively long-lived; the maximum-recorded age at the main colony in Mallorca is 26 yrs (McMinn, pers comm.). The species also mature late; a ringing study by Oro *et al*. (2009) at two colonies in Mallorca, recorded a mean age at sexual maturity of 7.2 years. The species shows strong philopatry to breeding grounds, generally returning to the same breeding site each year and usually to the same nest location within that site (Oro et al., 2004). Additionally, pair bonds are strong and although there is evidence that they are not a strictly monogamous species, individuals may take a sabbatical from breeding if their partner does not return to the colony (McMinn, pers comm.).

There is still very little known about the feeding ecology of the Balearic shearwater and much has been assumed from the behaviour of their close relatives the Manx and Cory's shearwaters. It is known that the species often forages in flocks and primarily feeds by plunge and surface diving, sometimes associated with underwater pursuit diving (Aguilar et al., 2003). The species preys on small pelagic shoaling fish, particularly sardines and anchovies (Le Mao and Yésou, 1993; Navarro et al., 2009). Aguilar *et al*. (2003) provide some insight into the species' foraging behaviour in their study that collected flight and dive-depth data from three adult birds tagged with data-loggers at a colony on Mallorca. The study found that foraging was limited to daylight periods and there were no dives recorded before 05:00 or after 20:00. The birds flew an average of 6.8 hours a day, which would allow them to reach previously reported productive foraging areas along the coast of mainland Spain. The foraging dives averaged 10 m deep and 17.6 seconds long; but the deepest dive recorded was to 26 m and lasted 66 seconds (Aguilar et al., 2003).

The abundance and location of prey fish resources are variable in time and space and there has been a tendency for the Balearic shearwater to make use of fisheries discards, which are potentially easier to locate and less energetically demanding to catch (Arcos and Oro, 2002; Louzao et al., 2006b; Kakela et al., 2010; Louzao et al., 2011a). Using a bioenergetic model, Arcos & Oro (2002) estimated that fishery discards accounted for up to 41 % of the energetic requirements of Balearic shearwaters. More recently, the importance of discards as feeding resource to adults during the breeding season was investigated by Navarro *et al*. (2009) with blood stable isotope analysis. Using isotopic ratios it was possible to estimate the contributions that demersal and pelagic species made to the diet of the birds at different stages in the reproductive season. It was found that pelagic anchovies (*Engraulis encrasicolus*) and pilchards (*Sardina pilchardus*) were the most important food source during incubation and chick rearing, whereas prior to incubation, demersal species (presumably from fisheries discards) were the primary food source. The authors suggest that these results reflect seasonal variability in the nutritional demands on the birds, with higher value pelagic species being consumed during periods of increased energetic requirements (Navarro et al., 2009). These conclusions were supported by Käkelä *et al*. (2010) who investigated fatty acid signatures (FAS) in the blood of 20 adult Balearic shearwaters collected during chick-rearing at a colony in Mallorca. The results found that FAS composition in the blood during this reproductive stage was reflective of pelagic Mediterranean fish species, indicating a reliance on these prey resources over demersal fisheries discards; but they did find some evidence that demersal species were also utilised (Kakela et al., 2010).

Although more information is coming to light regarding the species prey requirements during the breeding season (e.g. Louzao et al., 2011a), there is still little known about the feeding habits and prey resources exploited by the species outside of the breeding season. Yesou (2003) identified a dependence on anchovies in the Bay of Biscay during the inter-breeding period throughout the 1980s and 1990s, but reductions in this prey resource since then are thought to have resulted in a re-distribution of the species during the post-breeding dispersal (Yésou, 2003; Wynn et al., 2007; Luczak et al., 2011). There is little information on the prey resources now being exploited by the species during the inter-breeding migration. It is key for the birds to be able to access reliable sources of prey during this period, as they are undertaking their post-breeding moult, which means their flight is compromised because of incomplete plumage. This necessitates residence in productive areas with consistent prey availability for the duration of moult.

5.1.2 Distribution and habitat associations.

5.1.2.1 Broad-scale distribution and habitat associations

The known range of the Balearic shearwater is shown in figure 5.2. Breeding occurs from March to May and the breeding areas (highlighted in red and yellow) are occupied by breeding and non-breeding birds from September to July (with the highest concentrations in the period March – May). During breeding, feeding areas along the east coast of the Iberian Peninsula, highlighted by boat-based surveys and EU-LIFE project telemetry data (Aguilar et al., 2003), were found to be positively associated with frontal features and elevated chlorophyll-a levels, indicating the birds associated with the most productive foraging habits (Louzao et al., 2006a).

From May, after breeding, productivity in the Mediterranean drops with the onset of stratification and birds migrate out to more productive areas (Mayol-Serra et al., 2000; Mourino et al., 2003).

Post breeding dispersal is typically northwards into coastal areas of the Atlantic, although a small population is thought to reside in the Mediterranean year-round and some birds disperse southwards along the Atlantic coast of Morocco (Mayol-Serra et al., 2000; Cuenca et al., 2006). Low numbers of birds, presumably non-breeders, are reported from the common non-breeding areas (dark blue on map in figure 5.2) throughout the year.

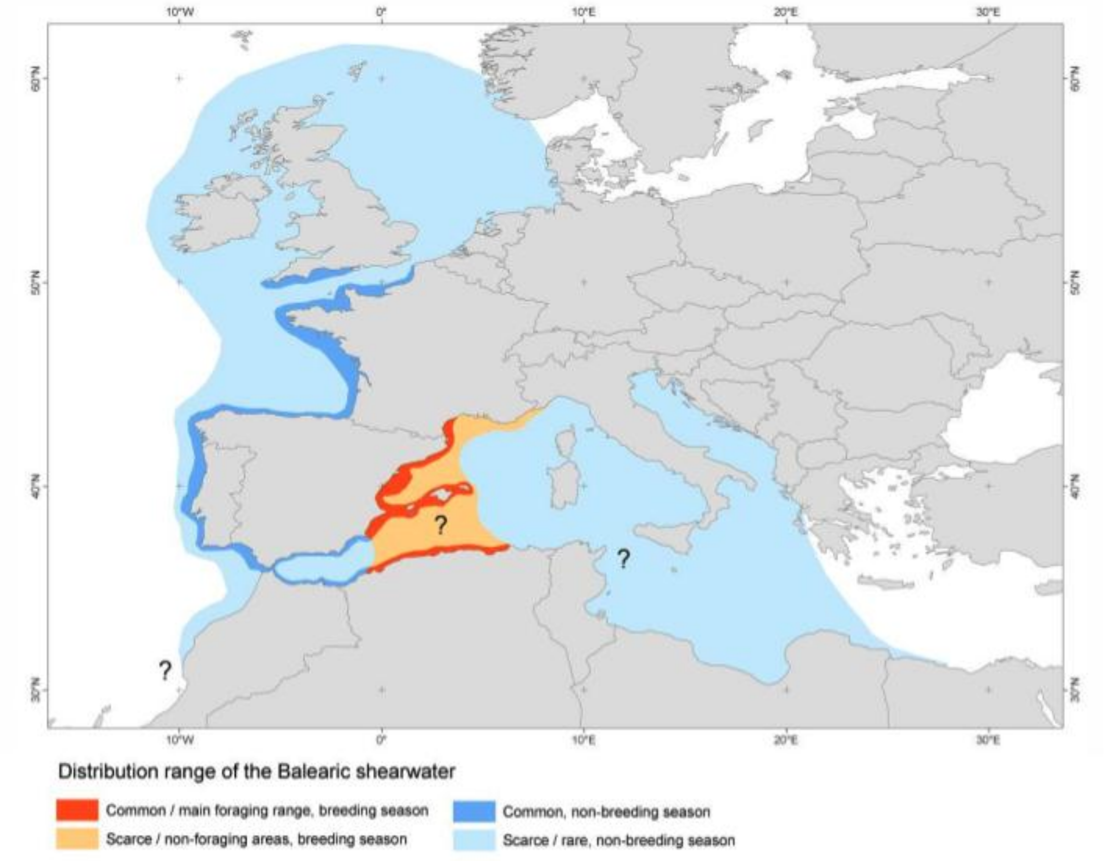


Figure 5.2: Known distribution of Balearic shearwaters throughout the year. Breeding areas have highest occupancy from March – July. From Arcos (2011).

The at-sea distribution of the species, outside of breeding periods, is typically coastal and within shelf seas where productivity is highest (Mourino et al., 2003) (dark blue areas on the map in figure 5.2). Typically the species was abundant during non-breeding periods along the northern coast of the Bay of Biscay, where they foraged on rich anchovy stocks (Mayol-Serra et al., 2000; Yésou, 2003). Since the mid 1990s there has been a significant increase in reports of Balearic shearwaters from along northwest European coasts during the post-breeding period (Wynn and Yésou, 2007). This northwards extension is coincident with declines in numbers in the Bay of Biscay (Yésou, 2003; Wynn and Yésou, 2007) indicating UK inshore waters and areas around the coast of northern Brittany are increasingly important for considerable numbers of Balearic

Shearwater (Wynn et al., 2007; Wynn and Yésou, 2007; Wynn and Brereton, 2009). The altered distribution may be associated with bottom-up controls related to increasing North Atlantic SST (Yésou, 2003; Wynn et al., 2007; Luczak et al., 2011) and related changes in prey fish availability in the Bay of Biscay (Yésou, 2003; Poulard and Blanchard, 2005; Irigoien et al., 2009). It is also hypothesised that increased SST along the southwest coast of Europe may have detrimental impacts on frontal features which historically provided important foraging habitat for the Balearic shearwater and other seabird species (Yésou, 2003).

It is widely acknowledged that seabird distribution is patchy in time and space in response to environmental controls and habitat selection (e.g. Amorim et al., 2009). Louzao *et al*. (2011) used evidence from stable isotopes to show that geographically distinct populations of breeding Balearic shearwaters exploit different prey resources. Stable isoptope values for the shearwaters varied with latitude relative to the location of an individual's breeding site, which indicates that the separate colonies were making use of distinct foraging areas and resources (Louzao et al., 2011b). Louzao's study is one of very few to present data on the controls associated with breeding Balearic shearwater foraging behaviour, and even less is known about the factors influencing the at-sea distribution of the species outside of the breeding season.

Manx shearwaters, a closely related species, have been tracked with geo-locators and shown to move in accordance with oceanic winds, weather patterns and the location of productive prey areas (Guilford et al., 2009). Similar controls were reported in a study on Cory's shearwaters, where satellite-tracking data were collected during chick rearing from a colony in the Canary Islands (Navarro and Gonzalez-Solis, 2009). The results showed oceanographic and wind factors influenced foraging behaviour and location (Navarro and Gonzalez-Solis, 2009). The distribution of tracked black petrels in New Zealand was found to be related to bathymetric features at the shelf edge where productivity is increased due to upwelling (Freeman et al., 2010). It is likely that similar environmental and oceanographic controls affect the spatio-temporal distribution of Balearic shearwaters throughout their life cycle, but further study is required in order to better understand the specific species-environment interactions.

5.1.2.2 UK distribution patterns: Spatial and Temporal.

Through the mid 1990's the numbers of Balearic shearwaters reported from around the coast of the UK and Ireland rose significantly from approximately 500 p.a. in previous years to a peak of 4824 p.a. in 2009 (Wynn and Yésou, 2007; Wynn et al., 2010a). This increase is thought to be associated with changing distributions of prey resources and thermal habitat (Wynn et al., 2007;

Luczak et al., 2011) (figure 5.3); although the changes in the taxonomic status of the species may have led to an increasing interest in its observation (Votier et al., 2008).

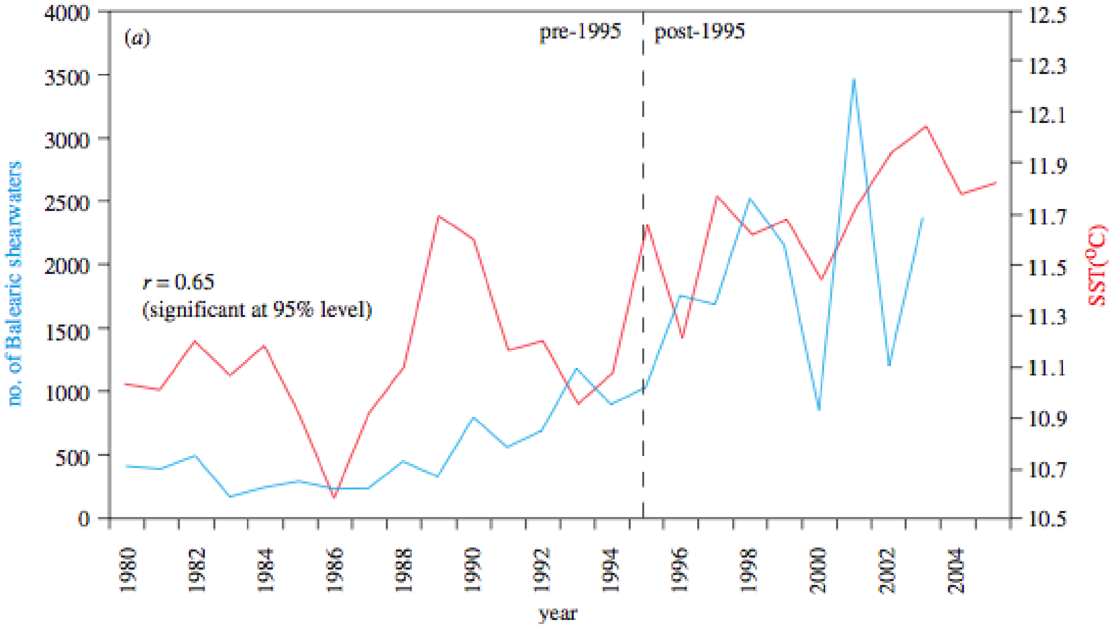
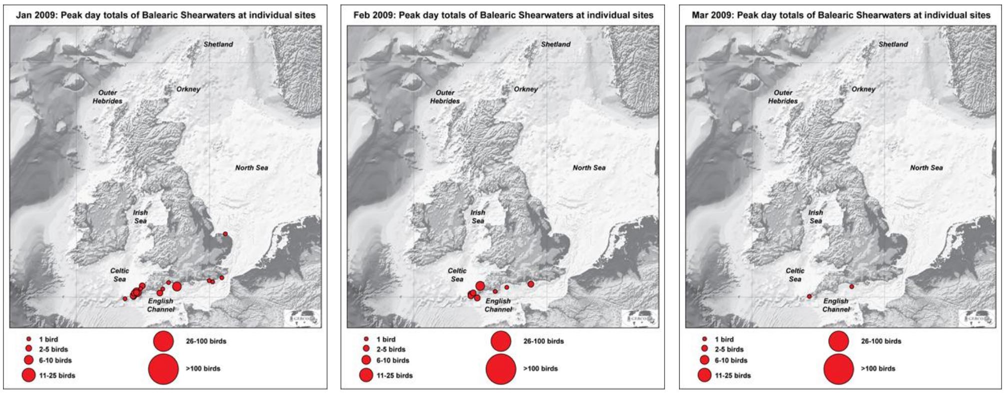
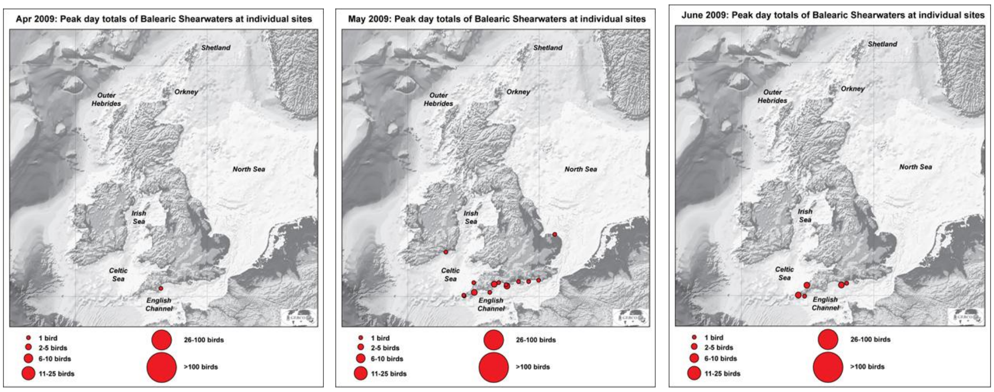


Figure 5.3: Time series of opportunistic Balearic shearwater sightings from the UK and Ireland (blue) and annually averaged SST in the same region (red). From Wynn *et al*. 2007.

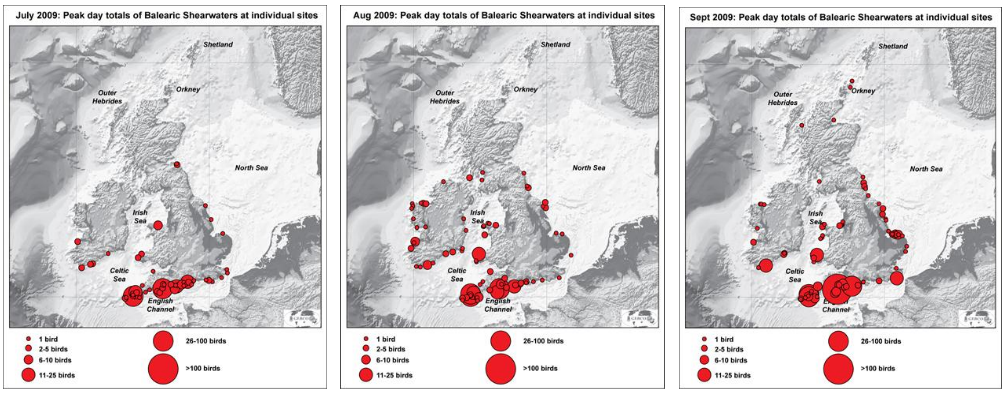
The annual numbers of sightings and birds recorded have remained consistently high throughout the 2000's, and their spatio-temporal distribution is surprisingly consistent (Wynn et al., 2010a). Opportunistic sightings, by month, for 2009 are shown in figure 5.4, and are also representative of the typical pattern of distribution through previous years (Wynn and Brereton, 2008, 2009). Most of the records from the UK are reported from southwest England between June – October, with highest concentrations in July, August and September. The birds are more scarcely reported from further north, but increasing numbers of records have been received from the Orkneys and parts of southern Scandinavia (Wynn and Yésou, 2007).



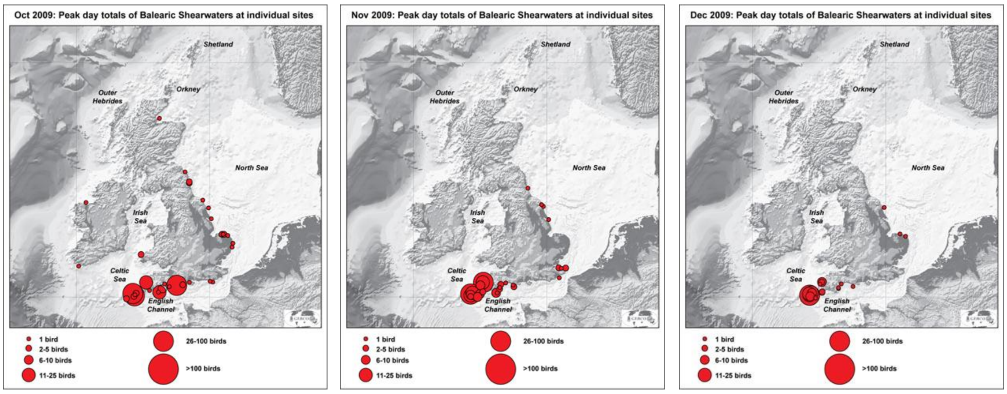
January 2009 **February 2009** **March 2009**



April 2009 **May 2009** **June 2009**



July 2009 **August 2009** **September 2009**



October 2009 **November 2009** **December 2009**

Figure 5.4: Monthly maps for Balearic shearwater sightings reported in the UK during 2009 (Wynn et al., 2010a).

5.1.3 Population structure and status, exploitation and threats.

Genovart *et al*. (2007) undertook an extensive genetic analysis of samples from throughout the species' breeding range and found no evidence for genetic structuring within the Balearic shearwater population, indicating a surprising level of gene-transfer between colonies for a bird considered to be strongly philopatric. The overall genetic variation within the population was considered high for such an endangered species, which may be evidence of a very recent decline that has yet to affect a change in genetic variability (Genovart et al., 2007). There remains some uncertainty about the relationship between the Yelkouan Balearic shearwater populations; with genetic studies indicating that hybridization between the two closely related species may have occurred in the past in Menorcan colonies, creating a genetically distinct 'Menorcan type' Balearic shearwater that may represent a distinct and genetically isolated sub-group, (Genovart et al., 2007).

Genetic evidence also suggests that the population of Balearic shearwaters has been dramatically reduced in the last few decades and that adult mortality is abnormally low (Genovart et al., 2007). This finding was supported by a demographic modelling study based on monitoring information from two Mallorcan colonies and a population size of 2,000 breeding pairs (Oro et al., 2004). The results of the model suggested that unless adult mortality rates are significantly reduced, the population might face extinction in as little as 2 generations (approximately 50 years) (Oro et al., 2004).

The breeding population of the Balearic shearwater was estimated as around 2,000 breeding pairs in a number of studies through the 1990s and 2000s, but this estimate was revised to over 3,000 in 2009 (Arcos, 2011). This increase is due to an rise in survey effort and the discovery of some new breeding areas, therefore does not represent a true increase in the species population; in fact evidence points to an overall drop in numbers of Balearic shearwaters in recent years (Oro et al., 2004). At-sea and migratory passage surveys through the Straits of Gibraltar suggest a population of up to 25,000 birds (Arroyo et al., 2008), which is considerably higher than extrapolation from numbers of breeding birds suggests. This indicates that either undiscovered breeding colonies or a 'floating' non-breeding population may exist, leaving some uncertainty as to species' demographics and census (OSPAR, 2008; Arcos, 2011). These factors are likely to boost the species resilience to extinction, but do not change the declining trend in the population of the species, evidenced from monitoring at a number of colonies on Mallorca, Menorca, Ibiza and Formentera (Oro et al., 2004; Arcos, 2011; Arcos et al., 2012).

Historically, the species' population decline is attributed to human consumption and habitat loss (Mayol, 1986; Alcover, 2000), but more recently the main threats to the species are egg, chick and adult mortality associated with predators on breeding grounds, and adult at-sea mortality associated with fishing (Mayol-Serra et al., 2000; Belda and Sanchez, 2001; Wynn et al., 2010b). In a recent study on the by-catch of Cory's shearwater in small-scale fisheries in the Mediterranean it was found that the birds are at much higher risk of long-line by-catch when trawling discards are unavailable (Laneri et al., 2010). The study also found that by-catch levels were higher during the egg formation and chick-rearing periods of the breeding season, which are associated with increased energetic requirements (Laneri et al., 2010). These findings are likely to be relevant to the Balearic shearwater as their breeding range overlaps with Cory's shearwater and adults of the species are documented as being at risk from by-catch in longline fisheries (Mayol-Serra et al., 2000).

Balearic shearwaters, in common with most seabirds, show strong philopatry to breeding sites and are reliant on local availability of prey items when nesting (Schreiber and Burger, 2001), therefore factors affecting prey fish abundance and distribution are likely to affect breeding success and at-sea adult mortality rates. There is concern that a reduction in the availability of natural prey due to overfishing, combined with a reduction in discard availability resulting from changes in fisheries policy, may affect both adult survival rates and breeding success (Arcos and Oro, 2002; Votier et al., 2004; Louzao et al., 2006b). Additionally, changes in the species' distribution and population decline have been linked with altered environmental conditions, which exert bottom up controls on marine food chains, although the direct effect of these remains unclear (e.g. Veit et al., 1996; Wynn et al., 2007; Luczak et al., 2011).

The Balearic shearwater is one of the rarest seabirds in the World (Oro et al., 2004) and as such is classified as Critically Endangered on the IUCN Red List of Threatened Species on the basis of its geographically limited breeding range and small, declining population (IUCN, 2011). Birdlife International (2011) also assign the species Critically Endangered status, which allows the designation of Important Bird Areas (IBAs) for the species within Europe. All IBAs for nesting Balearic shearwaters are also protected under regional laws by the Balearic Government. The species was recently listed (early 2012) on the Agreement of the Conservation of Albatrosses and Petrels (ACAP, 2009). It is the first northern hemisphere bird to be recognised by ACAP, highlighting the seriousness of the threats against the species. The species is also listed under a number of international conventions and lists including:

- Appendix II of the Bern Convention on the Conservation of European Wildlife and Natural Habitats.

- Appendix II of the Convention on Migratory Species.
- Annex I of the EC Birds Directive, which requires the designation of Special Protected Areas (SPA) for the species. Currently all breeding sites are protected as SPAs and form part of the Natura 2000 network.
- Annex II of the Mediterranean Special Protected Area/Birds Directive Protocol.
- OSPAR commission.

The main downfall in the safeguarding of the species lies in the lack of at-sea protection. BirdLife international has recommended a number of IBAs for the species, but notwithstanding the breeding colonies, only very few, small, coastal sites have been designated as SPAs by the Spanish and Portuguese governments (Arcos, 2011). With adult at-sea mortality viewed as the major threat to the species, identification and protection of key areas for the species outside of the breeding grounds is essential.

5.1.4 Research objectives

The following chapter describes the spatio-temporal patterns in sightings of Balearic shearwater recorded throughout northern France, Great Britain and Ireland in both opportunistic and targeted surveys. The aim of the work was to bring together the results of new and existing studies, providing an important synthesis of the available data on the inter-breeding distribution of this Critically Endangered seabird within NW Europe. It was hypothesised that recent records of the birds support a continued increase in numbers and altered temporal patterns in the appearance of the species within the study area, which represents the northernmost part of the species migratory range. It was identified that a study of this nature would have important applications in light of the conservation and management objectives for the species, which have been outlined above.

5.2 Submitted first authored paper: 'New insights into the at-sea distribution and behaviour of the Critically Endangered Balearic Shearwater, *Puffinus mauretanicus,* in UK, Irish and northern French waters'.

5.2.1 Overview and authorship information.

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Collected the data: RBW, AJ, PC, LS (UK and Ireland); TB, KL (Channel); LT, PY (France).

Analysed the data: AJ, PC, LS (effort-based and opportunistic data from land-based surveys in UK and France); TB, KL (boat-based data).

Wrote the paper: AJ, RBW and TB.

AJ was responsible for the data analysis and the bulk of writing of the paper, as well as collecting significant amounts of the effort-corrected data during the SWSW survey.

5.2.2 Summary

This study investigates the spatial and temporal distribution of the Critically Endangered Balearic Shearwater in UK, Irish and northern French waters, using a combination of land- and boat-based survey data collected in the period 2007-10. Peak counts were typically made along western Channel coasts of northwest France and southwest UK between July and October. Off northwest France, internationally important foraging aggregations were recorded in the large shallow embayments of northern Brittany, with a peak of 5780 birds in July 2010 (equivalent to ~20% of the estimated World population). Off southwest UK, most birds were recorded on passage, with a peak day count of 283 birds in Sept 2010 (~1% of the World population). The peak counts in 2010 are unprecedented, and support recent studies suggesting that the species is continuing to increase in abundance within the region. The temporal distribution within-year is also changing, with increased numbers of birds lingering into the mid-winter period. Boat-based observations reveal that relatively low numbers of Balearic Shearwaters occurred offshore beyond sight of land. Effort-corrected land-based monitoring from the southwest tip of the UK mainland, from 15 July to 15 Oct each year, provided additional insights into at-sea passage behaviour. Balearic Shearwaters were seen on 93.5% of survey dates, with 95% of birds passing west and birds per hour rates peaking in the morning between 0800-1100 hrs. A distance-from-shore analysis indicates that the species passes closer to shore than pelagic seabirds such as Sooty Shearwater. Overall, these results have important conservation implications, indicating that a significant proportion of the World population of this Critically Endangered species is now aggregating in spatially restricted areas of the western Channel during the inter-breeding period. These observations suggest the species could be vulnerable to impacts such as oil spills or disturbance from offshore construction projects.

5.2.3 Introduction

Effective protection of endangered seabirds is facilitated by a comprehensive understanding of the spatio-temporal patterns in the distribution of a species throughout its full range and for all age cohorts (Oppel et al., 2012). Improvements in tracking technologies have dramatically increased our ability to collect data on the movement and behaviour of individual birds, with high resolution and for prolonged time periods (e.g. Guilford et al., 2008; 2009). However, as a result of financial and logistical constraints, tracking studies are (1) typically focused on breeding birds, (2) are colony specific, and (3) can only include a small proportion of a species' population.

Therefore it is important to recognise the continued value of visual monitoring and the contribution that both opportunistic sighting records and systematic effort-based surveys can make to the understanding of seabird distributions, particularly when away from the breeding colonies. This is especially pertinent for rare or charismatic species with predominantly coastal distributions, which generate interest among seabird observers and as a result are often well recorded throughout their range. In this paper we use both opportunistic sightings and data from dedicated visual monitoring surveys to present an overview of the spatio-temporal distribution and behaviour of the Critically Endangered Balearic Shearwater *Puffinus mauretanicus* around the coasts of UK, Ireland and northwest France.

The Balearic Shearwater is endemic to the western Mediterranean, breeding only on the Balearic Islands (Arcos, 2011). Breeding areas are occupied by breeding and non-breeding birds from September to July and breeding occurs between March and May (Arcos, 2011; Guilford et al., 2012). After breeding, productivity in the Mediterranean Sea drops with the onset of stratification and birds migrate out to more productive waters, typically northwards into coastal areas of the northeast Atlantic, although some birds disperse southwards along the Atlantic coast of Morocco (Le Mao and Yésou, 1993; Mayol-Serra et al., 2000; Louzao et al., 2006a; Guilford et al., 2012).

In the past, the species was particularly abundant during non-breeding periods along the northern coast of the Bay of Biscay, where they foraged on rich anchovy stocks (Mayol-Serra et al., 2000; Yésou, 2003). Since the mid-1990s there has been a significant increase in reports of Balearic Shearwaters from along northwest European coasts during the post-breeding period (Wynn and Yésou 2007, Wynn 2009), particularly the Channel coasts of northern France and southern UK (Wynn and Yésou, 2007). This apparent northwards extension is coincident with a decline in numbers reported from the Bay of Biscay (Yésou, 2003) and indicates that inshore waters of more northerly regions are being utilised by increasing numbers of Balearic Shearwater (Wynn and Yésou, 2007; Wynn, 2009).

The recent changes in post-breeding distribution may be associated with bottom-up controls related to increases in North Atlantic sea surface temperature (SST) (Wynn et al., 2007; Luczak et al., 2011), and related changes in prey fish and discard availability in the Bay of Biscay (Yésou, 2003; Poulard and Blanchard, 2005; ICES, 2008a; Irigoien et al., 2009). It has also been suggested that the altered taxonomic status of the species in the early 1990s may have resulted in increased awareness and better recording, leading to the impression of increasing numbers further north (Votier et al., 2008). Nevertheless, the fact remains that internationally important numbers of Europe's only Critically Endangered seabird have been consistently recorded off northern French and southern UK and Irish coasts over the last 15 years (Wynn and Yésou, 2007; Wynn, 2009; Darlaston and Wynn, 2012).

The Balearic Shearwater is listed on the IUCN Red List as Critically Endangered as a result of its small breeding range and a dramatic population decline (BirdLife International 2011), with the most recent estimate of the breeding population at ~3200 pairs (Arcos, 2011). However, recent surveys of migratory passage through the Straits of Gibraltar, and wintering aggregations in the western Mediterranean, suggest a total population of up to 25,000 birds (Arroyo et al., 2008). This is considerably higher than extrapolation from estimates of the breeding population would suggest, although a recent tracking study by Guilford *et al*. (2012) shows that birds may move in and out of the Atlantic through the Straits of Gibraltar multiple times in a single season, and therefore may be contributing to duplication in the Gibraltar flyway point counts. Alternatively, there may be undiscovered breeding colonies or a large 'floating' non-breeding population, leaving some uncertainty as to the species' demographics and census (OSPAR, 2008; Arcos, 2011). However, these uncertainties do not change the overall declining trend in the population of the species, evidenced from monitoring at a number of colonies on Mallorca, Menorca, Ibiza and Formentera (Oro et al., 2004; Ruiz and Marti, 2004; Arcos, 2011).

The population decline is attributed to anthropogenic impacts leading to low adult survival rates of ~0.78 (Oro et al., 2004). The two main threats to the species are thought to be at-sea mortality as a result of bycatch in commercial fishing gear and predation of adult birds at the breeding colonies (Wynn et al., 2010b; Arcos, 2011). Breeding colonies in the Balearic Islands have therefore been designated as Important Bird Areas (IBAs) by BirdLife International and as Special Protection Areas (SPAs) under the EC Birds Directive (Annex I). However, the main downfall in the safeguarding of the species lies in the lack of at-sea protection (Arcos et al., 2012), therefore identification and protection of key areas for the species away from the breeding grounds is essential.

The primary aim of this study is to utilise an extensive land- and boat-based visual monitoring dataset, collected during 2007-10, to investigate the spatio-temporal distribution of the Balearic Shearwater off UK, Ireland and northwest France (figure 5.5); this will aid identification of seasonally important foraging/roosting sites and flyways that will help focus effective conservation efforts. Intensive effort-based surveys at a known flyway, Gwennap Head on the Land's End peninsula off southwest Cornwall, will provide additional insights into the species fine-scale migratory behaviour. Finally, the results will indicate whether recent inferred increases in the species abundance within the study area have been maintained.

5.2.4 Methods

5.2.4.1 Study area

A map indicating the extent of the study area is shown in figure 5.5. The area includes the full coastlines of the UK and Ireland, the Channel and the northern coast of France.

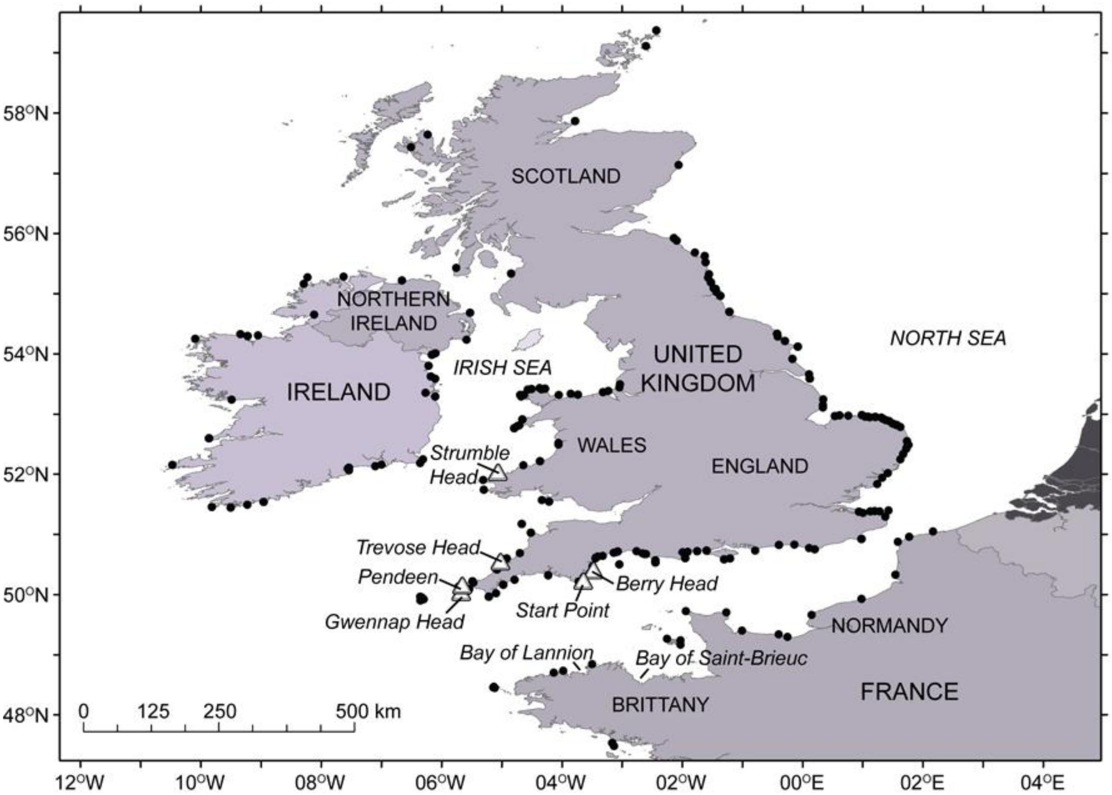


Figure 5.5: Study area map. Black filled circles represent locations of sites that submitted reports to *SeaWatch SW* Balearic Shearwater UK monitoring project or to *Trektellen* online database (French records), 2007-2010. Also marked are locations of the *SeaWatch SW* effort-based monitoring site at Gwennap Head (Cornwall, UK), the 'sister sites' off southwest UK, and the main embayment sites monitored in Brittany.

5.2.4.2 Opportunistic sightings from the UK, Ireland, and NW France (2007-2010).

Collation of UK and Irish data

The *SeaWatch SW* project (www.seawatch-sw.org) established a national monitoring programme for the Balearic Shearwater from 2007-2010; this programme involved collation of a sightings database of non-effort-based public sightings from the UK and Ireland. Only records with date, location, number of birds, and source were included in the final dataset, from which suspected duplicates were removed (for details see ESM 1 in appendix 6).

It should be noted that these data are not effort-based and, as with all opportunistic sightings, are subject to some significant limitations including: varying amounts of effort dependent on the site, observer, time of year and/or weather conditions; varying observer ability and optical equipment. There is also the possibility of duplication as a result of the same bird(s) passing a site(s) on the same or subsequent days. Additionally the reporting of sightings will have been affected by the level of awareness of individual observers about the *SeaWatch SW* Balearic Shearwater monitoring programme.

Collation of data from northwest France

Records of Balearic Shearwater sightings (2007-2010) were collated from the online database, *Trektellen* (Trektellen, 2012), which includes information on effort at each site (number of hours watched); this enables counts to be effort-corrected and presented as *birds per hour* (BPH). Additional data from targeted surveys and regional ornithological reports from Brittany and Normandy have also been included in the results. The same caveats as listed above apply to this opportunistic dataset.

Data analysis

The public sightings data cannot support statistical analyses due to their opportunistic nature. The UK, Irish and French records are therefore presented as uncorrected peak day-count maps, created in ArcGIS v.10, which show the highest cumulative day count per year and per season from each site (uncorrected for effort). The effort-corrected French data (BPH) are given in the ESM.

5.2.4.3 Marinelife boat-based visual monitoring surveys (2007-2010)

Marinelife (www.marine-life.org.uk) undertook a broad range of effort-related boat surveys within the Channel between 2007 and 2010. The primary objective of this work was to gain information on the spatio-temporal distribution of Balearic Shearwaters in a suspected key summering area, the western Channel, and to determine whether significant numbers of birds occurred in offshore waters, beyond the range of land-based observers. Surveys included (1) monthly surveys along three ferry routes, with occasional surveys on another five routes from 2007-2010; (2) volunteer surveys on dive, angling, eco-tourism and fishing boats from 2007-2010; (3) a systematic survey (stratified random design) of Lyme Bay (located off the Devon and Dorset coasts, marked in figure 5.6) in early winter 2009; (4) a systematic survey (stratified random design) of the entire western Channel in summer 2009; (5) targeted surveys in 10-km grid squares not previously surveyed by any of the above methods in 2010. In total, sailings were made from 26 English and seven French ports, using 45 different vessels, with 240 surveys completed, sampling 68,308 km of trackline. In addition, a citizen-science project was launched to encourage boat skippers and other members of the public to submit sightings (further details in ESM 2 in appendix 6).

For all *Marinelife* surveys, at-sea effort-related recording was undertaken. Data on survey effort were collected at 15-30 minute intervals (or whenever the course of the ship changed) and included direction of travel, speed and position of the ship, sea and weather conditions. On recreational dive and angling boat surveys, the time, location, and duration of stopping points (for dive or angling efforts) were also noted.

On all targeted surveys, ship speed and route location was organised by *Marinelife*, consequently it was possible to sample seabirds by best practice European Seabirds at Sea (ESAS) methods (for details see ESM 2 (in appendix 6) and http://www.jncc.gov.uk/page-4568, Tasker et al., 1984; Webb and Durinck, 1992). In total, 551 km^2 of sea area was sampled for seabirds by ESAS methods on 28 days (14 day surveys in 2009, 14 in 2010).

On all other (non-targeted) boat surveys, less rigorous methods were used, as survey methods were adapted to account for vessel type, ship speed and other limitations. During small boat surveys, seabirds were recorded within an assumed strip width of 500 m either side of ahead. Each seabird observed was counted once, with sightings grouped into one-minute periods. A separate recording form was completed for Balearic Shearwaters, which included additional information on behaviour at point of first observation (see ESM 2 in appendix 6 for details on methods). During ferry surveys, seabirds were recorded in two distance categories: a 300-m square box on the starboard side of the ship, and within an assumed strip width of 500 m either side of ahead.

Data analysis

Effort and Balearic Shearwater sightings data from all surveys (2007-2010) were combined into a single database, with each record representing information about a single survey leg, defined as the period between subsequent records of the ship’s position. These ship positions either represented points at which environmental data were recorded or a Balearic Shearwater sighting was made. Hence, each record contained information on the position of the ship and environmental conditions at the start of a survey leg, position at the end of a survey leg, the survey route, whether the starting position represented a Balearic Shearwater sighting (and if so, the number of birds) or an environmental record point, the time, day, month and year. A blank record was used to mark any breaks in survey effort during an individual survey. The data were subject to two validation stages to remove errors: (1) a first trawl using Memory Map O2004 software to rectify any obvious transcription errors relating to latitude and longitude positions, and (2) by running through the CREEM/JNCC Joint Cetacean Protocol validation tool (http://www.ruwpa.st-and.ac.uk/dpwebi/jcp/).

This database was then plotted in a geographic information system (GIS) created in ArcMap 9.3.1, and the path of each survey recreated from the positional information. The data were subsequently divided into a grid of 10 km X 10 km for the Channel. The amount of survey effort (km travelled) in each of the 616 grid cells sampled is shown in figure 5.6. A single measure of Balearic Shearwater abundance was derived for each grid cell using data pooled across all *Marinelife* effort-related surveys. Given that different recording methods were used (with density estimates not directly comparable for all surveys) data were amalgamated into a simple measure of relative abundance (number counted per km travelled). Sea state was not accounted for in the analysis as the majority of sightings were of birds in flight. Furthermore, almost all surveys were completed in calm to moderate seas, so relatively few birds near to the vessel were likely to have been missed.

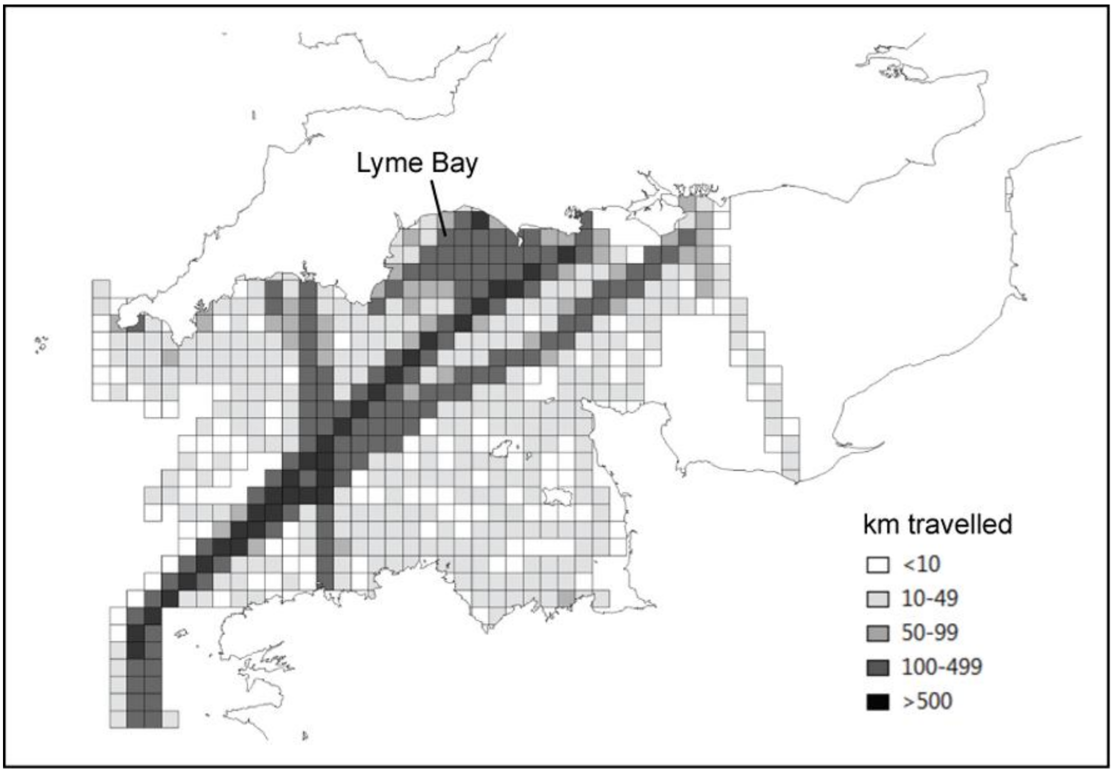


Figure 5.6: *Marinelife* boat-based visual survey effort in the western Channel (2007-2010), gridded at 10 x 10 km.

5.2.4.4 SeaWatch SW effort-based visual monitoring for Balearic shearwater (2007 – 2010).

Field data collection

Effort-based visual monitoring of Balearic Shearwaters was carried out during the annual *SeaWatch SW* survey from Gwennap Head, Cornwall; a south-facing headland located 30 m above sea level at the southwest tip of the UK mainland (figure 5.5, SeaWatch SW 2012). The site is recognised as an important flyway for Balearic Shearwaters and other seabirds passing between the western Channel and the Celtic Sea (Wynn and Yésou, 2007).

The *SeaWatch SW* survey ran for 93 days from 15 July to 15 October annually between 2007-2010. Survey dates were based on the peak period for Balearic Shearwaters off southwest UK (Wynn and Yésou, 2007). Observers employed continuous telescope, binocular and naked eye scanning to ensure even surveillance of near and far-fields. All observers (N = 29) were practised at seabird surveys and proven to have prior experience of Balearic Shearwater identification in the field (further details of survey methods in ESM 3 in appendix 6).

Although care was taken to reduce biases introduced by varied survey conditions and use of multiple observers, some important data limitations remain. Key limitations are: variation in observer ability, observer fatigue, variable quality of optical equipment and variable survey conditions, e.g. the impact of glare and visibility on detection of birds. It is also possible that there will be duplication due to birds repeatedly passing the watchpoint on the same or subsequent dates.

All records of Balearic Shearwater include date, time, number of birds, flight direction and estimated distance from watchpoint. Additionally, visibility (km), glare (% sea surface) and cloud cover (% visible sky) were recorded hourly. The number of hours observed in the four-year period totals almost 4000 (~1000 hours per year), but the dataset was filtered to remove effort and sightings collected in poor survey conditions. Periods with visibility <2 km and/or sightings that were estimated to be >2 km offshore have been excluded as a safeguard against introducing bias due to reduced detectability and identification ability. The final dataset contains 5394 sightings of Balearic Shearwater and 3324 full hours of survey effort (table S1, ESM 3 in appendix 6).

Data analysis

Sightings have been effort corrected by conversion into BPH. The significance of inter-year changes and diurnal patterns in BPH have been investigated using a generalised least squares (GLS) model, which contains parameters to account for the heterogeneity and correlation structure of the data. Analysis was carried out in the “R” software (R Development Core Team, 2011) using packages ‘nlme’ (Pinheiro et al., 2012) and ‘rms’ (Harrell, 2012). Hours of the daily cycle with a total effort of N <100 across all four years have been removed for this analysis; this affects only very early and very late time periods around dawn and dusk, which were rarely observed.

The *SeaWatch SW* survey protocol determines that records of Balearic Shearwater include an estimation of distance-from-shore. Distance is estimated by eye, with the aid of the Runnelstone Buoy as a marker, which is ~1.6 km south of the watchpoint. There is undoubtedly some error in the distance estimation, together with variability between observers; therefore distance-from-shore data have been grouped using 500-m intervals to allow for error. The empirical distribution of flight distance from shore for Balearic Shearwater is compared to the Sooty Shearwater (*Puffinus griseus)* using a two-sample Kolmogorov-Smirnoff test (‘ks.test’) in the base R ‘stats’ package (R Development Core Team, 2011).

5.2.4.5 SeaWatch SW sister site data (2007 – 2010).

There are a number of headland watchpoints around southwest UK where elevated levels of seabird visual observation have been carried out by experienced observers for many years. Four such sites are considered ‘sister sites’ to the main observation point at Gwennap Head (figure 5.5), and are extremely valuable for putting effort-based observations from there into a regional context. Survey effort is recorded at the ‘sister sites’, therefore data can be effort-corrected by conversion into BPH (details in ESM 4 in appendix 6). Results from monitoring at the sister sites are descriptive because the nature of the data does not support statistical analyses.

5.2.5 Results

5.2.5.1 Opportunistic sightings from the UK and Ireland.

Reports of Balearic Shearwater sightings were received from 339 different sites around the UK and Ireland for the period January 2007 to December 2010. The quality-controlled dataset contained a total of 3655 records (table 5.1). The annual number of reports (mean = 927, SD = 69.4, table 5.1) and their distribution show consistency between years (figure 5.7). More variability is present in the total number of birds reported each year (mean = 5697, SD = 1286) with a clear increase in 2010 when the total number of birds reported was over 2000 more than in any other year (table 5.1).

The spatial distribution of sightings throughout the study area is very consistent (figure 5.7), with the majority (~70%) of records each year coming from southwest UK (Dorset, Devon, Cornwall and Scilly), where records for day-counts of birds on passage were broken in 2009 and 2010 (table 5.1).

Table 5.1: Summary of UK and Irish Balearic Shearwater opportunistic sightings data (2007-2010), including the peak (cumulative) day count each year. Data were collated from a variety of sources including the *Birdguides* and *Trektellen* online databases and records submitted directly to the *SeaWatch SW* co-ordinator.

	2007	**2008**	**2009**	**2010**	**Total**
Numb. records in final dataset	819	988	937	911	**3655**
Total number of birds reported	5084	5373	4744	7587	▨
Number of sites with records	142	171	149	157	**339**
Peak day-count (birds)	117	115	145	268	▨
Date of peak day-count	8/7/07	6/10/08	2/9/09	18/9/10	▨
Location of peak day-count	Portland Bill	Porthgwarra	Berry Head	Porthgwarra	▨
Number of aggregations recorded	17	7	1	16	**41**

The largest numbers of sightings and birds occur in summer and autumn, between mid-July and early October, while few were seen in winter and spring (figure 5.8). Winter records were generally restricted to southwest England (figure 5.8); this region also holds all annual and seasonal maximum peak day counts of passing birds and most of the documented aggregations (defined as groups of ≥10 birds, typically foraging or roosting) (figure 5.9, table 5.1).

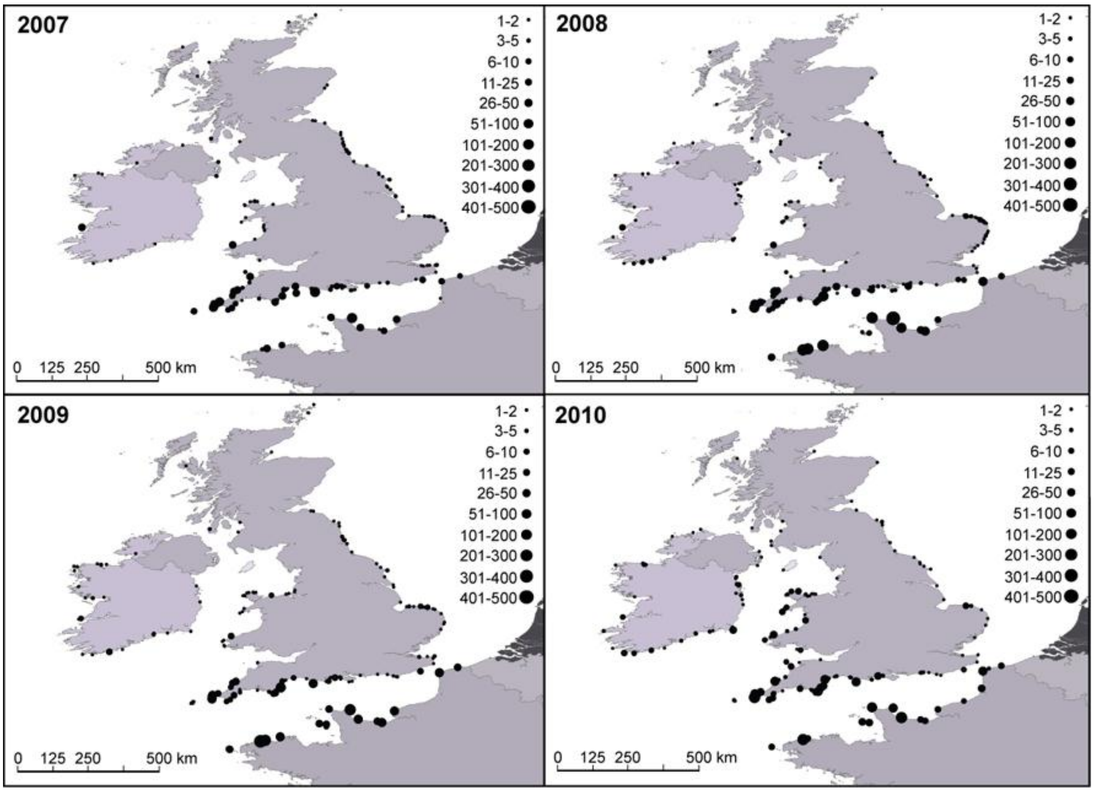


Figure 5.7: Annual peak day-counts of Balearic Shearwaters from opportunistic sightings at sites in UK, Ireland and northwest France (2007-2010). Scaled black circles indicate size of count. UK and Irish data are from the *SeaWatch SW* database and French records are from the *Trektellen* online database.

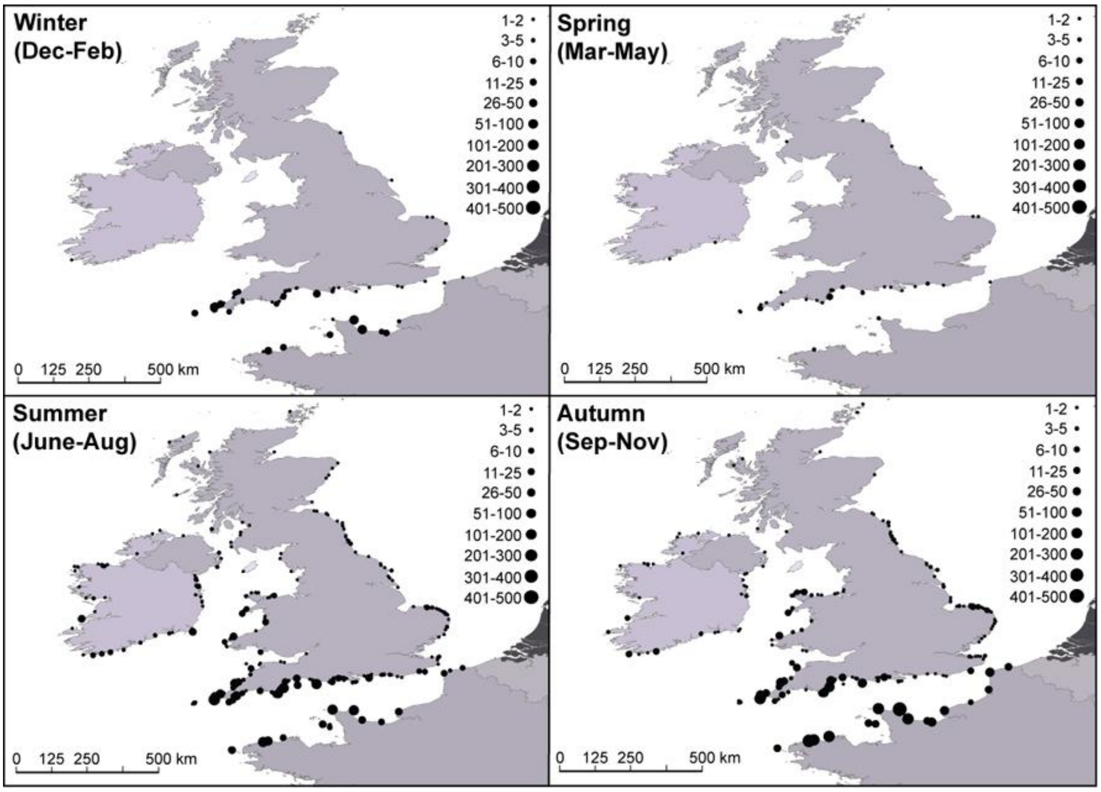


Figure 5.8: Seasonal peak day-counts of Balearic Shearwaters from opportunistic sightings at sites in UK, Ireland and northwest France (2007-2010). Scaled black circles indicate size of counts. Seasons defined as: Winter = Dec-Feb, Spring = Mar-May, Summer = Jun-Aug, Autumn = Sept-Nov.

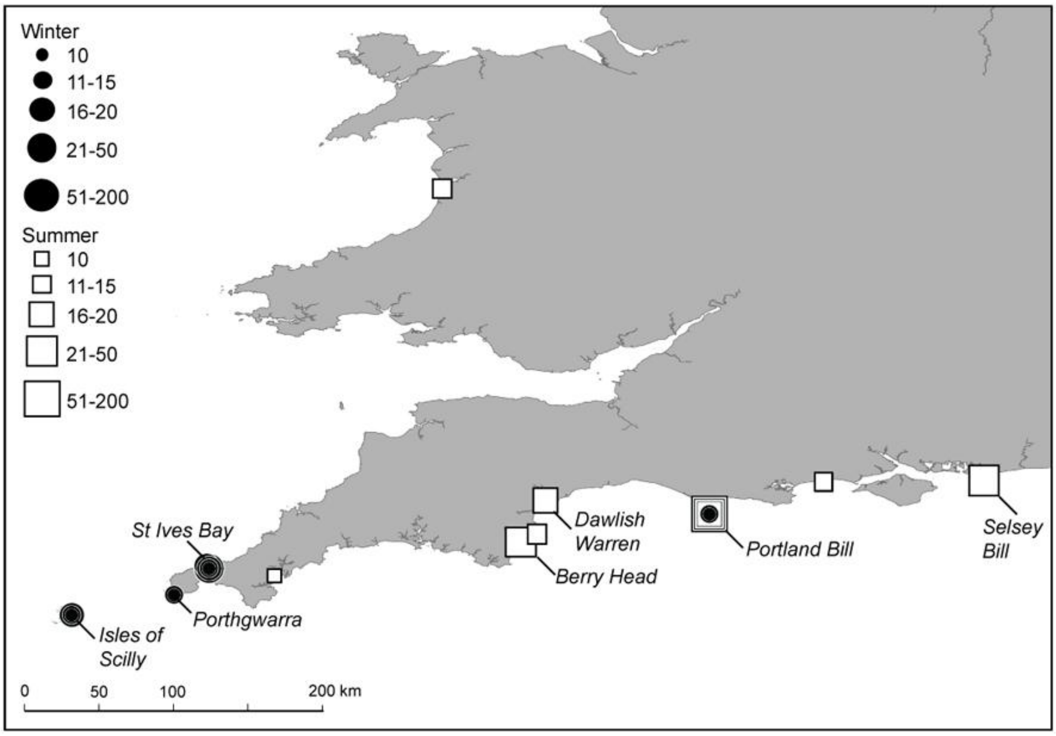


Figure 5.9: Map of reported aggregations of Balearic Shearwaters at sites in UK waters from opportunistic sightings (2007-2010). Aggregations are defined as groups of 10 or more birds. The position of both summer (white squares) and winter (black circles) aggregations are shown. Data are from the *SeaWatch SW* database.

5.2.5.2 Opportunistic sightings from NW France.

Reports of Balearic Shearwater sightings during 2007 to 2010 were submitted to *Trektellen* from 20 sites along the northwest French coast. The number of sites submitting records ranged from 12-16 per year (table 5.2). The pattern in the spatial distribution of sightings was similar in all four years, with a relatively even spread of sightings reported along the French Channel coast, from Brittany in the west to the French-Belgian border in the east (figure 5.7). The effort-corrected BPH data for the French sites follow a similar pattern to the day-count data and are presented for comparison in figures S1 and S2 in ESM 5 (appendix 6). After correction for effort, the annually averaged BPH value from the French sites was lowest in 2007 and highest in 2009 (table 5.2).

Table 5.2: Summary of Balearic Shearwater opportunistic sightings data from northwest France (2007-2010). Data were collated from the *Trektellen* online database.

	2007	**2008**	**2009**	**2010**
Number of sites with records	12	14	16	16
Average day-count of birds (SD)	28.1 (30.6)	141.5 (148.5)	89.8 (91.6)	62.9 (77.2)
Peak day-count (birds)	111	482	345	250
Average BPH (SD)	7.6 (6.8)	26.0 (28.6)	30.5 (42.7)	16.9 (16.5)
Peak BPH record	22	105	169	57
Location of peak BPH record	Roscoff	Gatteville	Roscoff	Pointe du Hoc

The temporal pattern in both the uncorrected sightings and BPH data from northwest France is comparable to that of the UK and Ireland (figure 5.8, S1 and S2 in ESM 5 in appendix 6), with highest numbers of birds reported during summer (peak day-count = 169, BPH = 88) and autumn (peak day-count = 482, BPH = 169). There is a paucity of sightings during the spring (breeding season) and reduced numbers in winter, which were restricted mainly to the western Channel, corresponding to the pattern seen off southern UK (figure 5.8).

In recent decades there have been records of internationally important foraging and roosting aggregations in summer/autumn off northwest Brittany, with maxima of 3200 in Sept 1983 and 2150-2250 in Sept 1996 and July 1997 (Liéron, 2000; Wynn and Yésou, 2007). However, this area was not well covered by the *Trektellen* database in 2007-10 (figure 5.5), so here we briefly summarise recent targeted monitoring data in this region (Thébault et al., 2010; Février et al., 2011; Yésou et al., 2011).

The largest concentrations of birds were seen in two broad embayments: Bay of Saint-Brieuc and Bay of Lannion (figure 5.5). In 2007 the peak count from this region was of 1500 birds in Bay of Saint-Brieuc on 19 October (Plestan et al., 2009). Many of these birds lingered into the winter, with at least 750 still present in January 2008 (associating with hundreds of Razorbills *Alca torda* and Kittiwakes *Rissa tridactyla*); this is an unprecedented winter concentration for northwest Brittany (Plestan et al., 2009). Numbers in 2008 and 2009 were unexceptional, with no recorded counts exceeding 550 birds (e.g. Yésou et al., 2011). However, a record influx was noted in summer 2010 with an estimated 5780 birds present in late July, including 4630 counted in Bay of Lannion and 1150 in Bay of Saint-Brieuc (Thébault et al., 2010; Février et al., 2011).

There were fewer data available for the eastern French Channel coast. Nevertheless, records from Groupe Ornithologique Normand (GONm) suggest a marked recent increase: the first record for Normandy east of Cotentin was from 1988 (there has been constant ornithological recording in Normandy since the late 1960s), and by 2000 the highest count had been seven in October 1997. The highest count increased to 31 at Antifer in 2001, and continued to increase during the 2007-2010 survey period, with 120 birds being counted on 20 September 2010 near Arromanches (for locations see figure 5.10), and 226 birds in three hours on 20 October 2010 off Saint-Pierre-de-Mont (Gérard Debout *in litt*.). At the extreme eastern end of the Channel, the situation at Cap Gris-Nez / Strait of Dover showed a similar increase: until 2007, no daily record exceeded 18 birds, then daily records were set at 84 on 7 September 2008, 100 on 5 September 2009 and 98 on 15 September 2010 (Dubois et al., 2012; Trektellen, 2012).

5.2.5.3 Boat based visual monitoring surveys from the Channel.

In total, there were 189 sightings relating to a cumulative total of 1397 Balearic Shearwaters observed in the Channel during 2007 to 2010. These included 33 sightings of a total of 72 birds during 114 ferry surveys, 156 sightings of a total of 1325 birds during 196 small boat surveys and 60 'casual' sightings of a total of 2058 birds, chiefly submitted by skippers of small boats (table S2, ESM 6 in appendix 6).

Distribution and abundance

On effort-related surveys, birds were patchily distributed in the Channel, being observed in only 14% of the sampled 10-km^2 grid cells (figure 5.10). 72% of sightings were of singletons, whilst 90% were of five or fewer birds. There were five records of groups totalling more than 100 birds, all of which were sighted in coastal areas of northern Brittany in late summer 2010. The largest rafts were of ~350 and ~100 birds in Bay of Lannion on 27 Aug 2010 (1100 were counted from land prior to sailing) and 260 and 150 in Bay of St Brieuc on 20 Sept 2010.

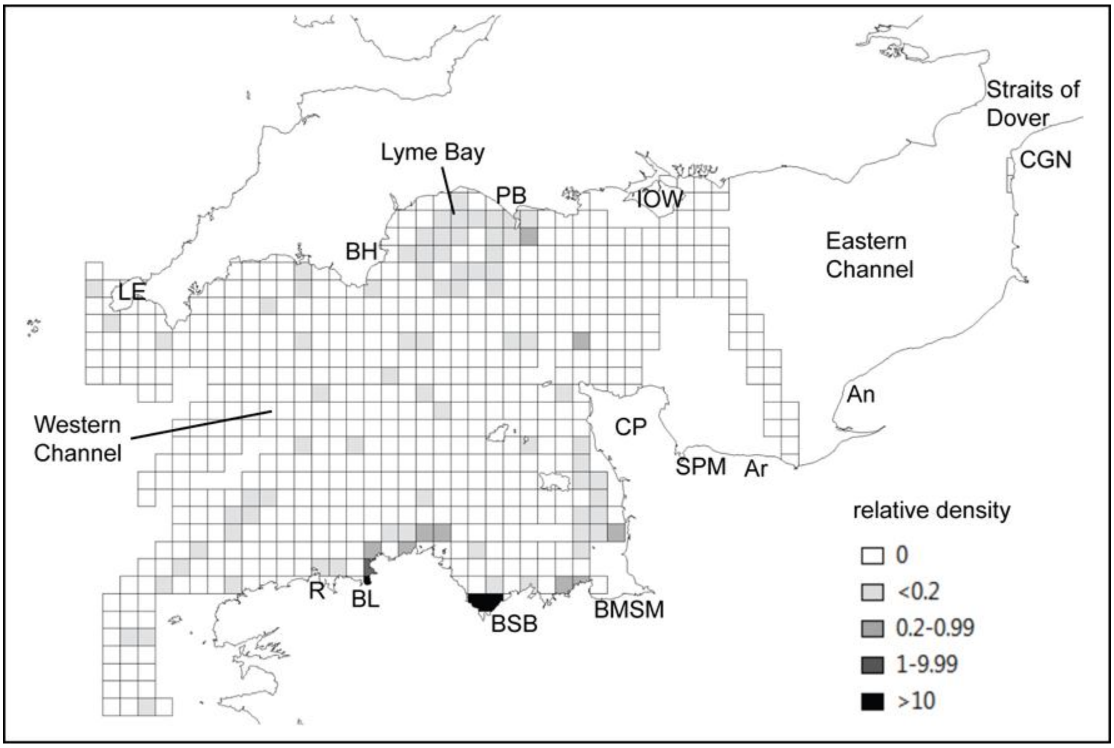


Figure 5.10: Relative density of Balearic Shearwaters (number counted per km travelled) in the western Channel from *Marinelife* effort-related boat surveys (2007-2010). All cells were surveyed; hollow cells show absence. LE = Land's End, BH = Berry Head, PB = Portland Bill, IOW = Isle of Wight, R = Roscoff, BL = Bay of Lannion, BSB = Bay of Saint-Brieuc, BMSM = Bay of Mont-Saint-Michel, CP = Cotentin Peninsula, SPM = Saint-Pierre-de-Mont, Ar = Arromanche, An = Antifer, CGN = Cap Gris-Nez.

On the English side of the Channel, the Portland Bill area had the highest relative density of birds (figure 5.10). The five 10-km^2 cells that were sampled adjacent to Portland Bill accounted for 72% of all birds counted in English waters of the Channel. Away from Portland, birds were only observed in very small numbers (1-3) in 32 of the 270 10-km^2 cells surveyed in English waters (figure 5.10).

During the western Channel summer survey (2009), where widespread spatial coverage was achieved over a short timescale, just nine singletons were seen (all in flight) giving an overall mean density (uncorrected) in the western Channel for that period of 0.016 birds per km^2. Casual sightings from boats reported to *Marinelife* (2007-2010), further confirm that Balearic Shearwaters were widely but sparsely distributed in small numbers (93% of casual sightings were of 1-4 birds) across the western English Channel during the summer months between 2007 and 2010. Further results and a plot of casual sightings are given in ESM 6 (figure S3 in appendix 6).

Behaviour

Behaviour was recorded for 83% of Balearic Shearwater sightings made during effort-related surveys. The most frequently recorded behaviour (72%) was of birds passing directly through the recording areas without stopping. Although moving birds made up the majority of sightings, the actual number of birds seen in flight was low, accounting for only a small proportion of the total birds seen. This is because a few sightings (24%) of larger aggregations of birds resting on the water accounted for the majority (64%) of the total number of birds counted.

Aggregations of resting/sleeping birds were only found in two areas – Portland Bill and the adjacent Shambles Bank immediately to the east, and along the north Brittany coast between Bay of Mont-Saint-Michel and Roscoff. Elsewhere, only very small numbers of birds were seen on the water (1-5 birds), either alone, or with Manx Shearwaters (*Puffinus puffinus)*.

Scavenging behaviour was observed in 15% of sightings where behaviour was recorded, although these observations only involved low numbers of birds (4 % of total birds counted). Eighteen of the 22 scavenging instances were around angling boats, likely representing greater sampling effort from/around this type of craft, with the maximum count during these encounters being six birds in August 2010. Self-foraging (feeding away from angling and fishing boats) was an infrequently recorded activity (observed in 8% of sightings where behaviour was recorded); however, these sightings related to more than 40% of the total number of birds counted. Further notes on behaviour have been included in ESM 6 (appendix 6).

Seasonality of occurrence

The highest percentage of offshore Balearic Shearwater sightings during 2007-2010 was recorded between July and September (figure 5.11), consistent with land-based data. In the Portland Bill area (where there is regular fishing effort from skippers who submit data to the project), the peak period for casual sightings of the species was also in July.

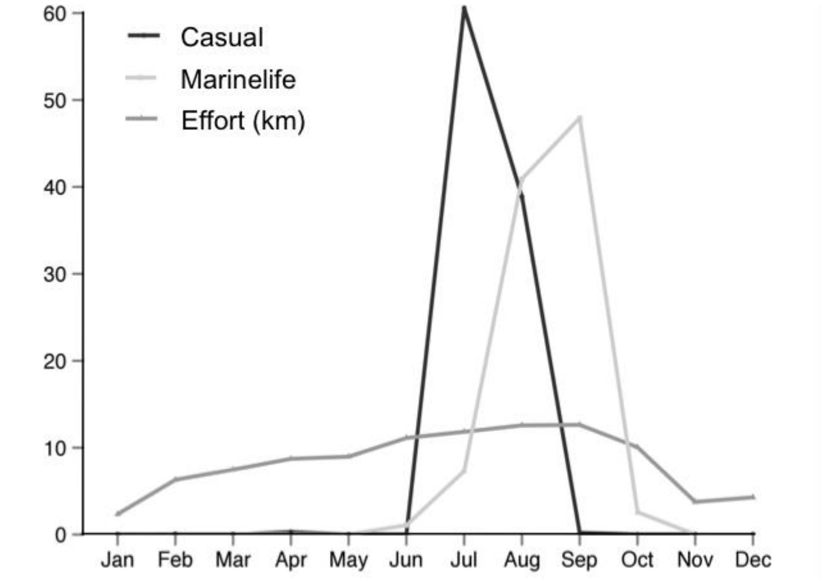


Figure 5.11: Offshore Balearic Shearwater sightings by month (% of total) from casual observations (N=84 sightings) and targeted *Marinelife* boat surveys (N=189 sightings), 2007-2010. Note that sightings rates per month have not been corrected for effort, but *Marinelife* survey effort (km) per month is plotted.

5.2.5.4 Effort-based monitoring from Gwennap Head and 'sister sites', 2007 – 2010.

Birds Per Hour (BPH) data analysis

The filtered hourly bird-count dataset from Gwennap Head contains 3324 hours of survey effort from 2007-2010, of which 55% of hours were positive for Balearic Shearwater sightings with an overall average BPH value of 1.62 (table 5.3). The probability of a sighting in any hour of the effort-based survey ranged between years from 0.48 to 0.67, with the highest likelihood in 2010 when there was also a large increase in the BPH compared to previous years (table 5.3).

Table 5.3: Summary of Balearic Shearwater sightings data from the effort-based *SeaWatch SW* survey at Gwennap Head (2007-2010). Data have been filtered to remove sightings and hours of effort with poor visibility. Sightings of birds passing >2 km from land are not included.

	2007	**2008**	**2009**	**2010**	**All years**
Hours of effort	829	824	821	850	**3324**
Total sightings (birds)	1163	837	1111	2315	**5394**
Positive hours	462	397	405	567	**1819**
Probability of sighting	0.56	0.48	0.49	0.67	**0.55**
Birds per hour (BPH)	1.40	1.02	1.35	2.72	**1.62**
Peak day count (birds)	67	71	79	127	▨
Sighting positive days	87 (92 %)	86 (92 %)	85 (91 %)	92 (99 %)	**350 (95.5 %)**

The BPH data, averaged by hour across all four years of the survey, show a diurnal pattern in sightings of Balearic Shearwaters, with higher BPH during the morning session of the survey (mean = 1.96, SD = 0.44) than in the afternoon session (average BPH = 1.12, SD = 0.26). Note that no data are available for the observer break-period between 1200-1400 hours.

A Durbin-Watson test showed that the hourly data were significantly temporally auto-correlated up to a lag of 14 hours (p = 0.012 at lag 14); approximately representing a daily survey period. This temporal dependence was accounted for in the analysis by including an AR1 correlation structure, based on the survey day ID, in a generalised least squares (GLS) model of the BPH data. Marginal ANOVA (F) tests on model results indicate that the factor variables of year of the survey ($F = 15.977_{DF = 3}$, p = < 0.001) and hour of the day ($F = 7.677_{DF = 12}$, p = <0.001) both had significant effects on the observed BPH. Post-hoc contrasts indicate that 2010 had significantly higher BPH values than all other years (all tests corrected p-values = <0.001) and 2008 had significantly lower hourly counts than other years (all tests corrected p-values = <0.05). The hourly-averaged BPH for 0800-1100 hrs were significantly higher than counts made at other times of the day (corrected p = <0.01 for all contrasts of 0800-1100 hrs against other hours of the day). All of the averaged BPH values from observed data fall within model estimate confidence intervals, indicating a well-fitting model and therefore high confidence in these results (figure 5.12).

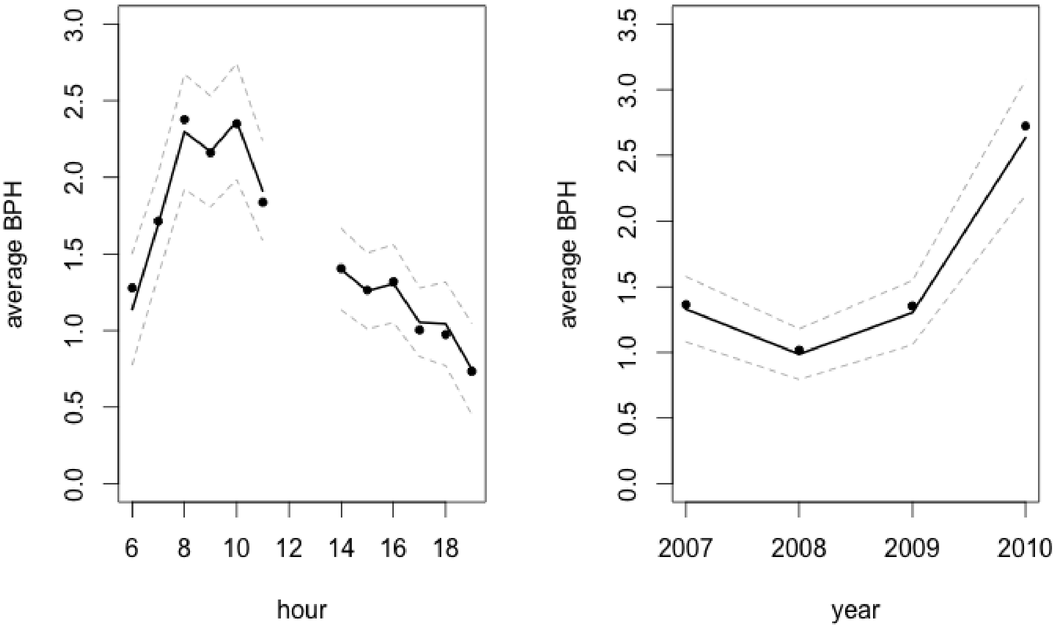


Figure 5.12: Hourly (left) and annually (right) averaged BPH values from the *SeaWatch SW* effort-based survey at Gwennap Head (2007-2010). Black line is model estimate; with 95% CIs indicated by dashed grey lines, black filled circles are the observed average BPH data (N = 3324 hrs). Model is GLS with unspecified variance structure and an AR1 autoregressive term to account for non-independence of observations.

Daily sightings data analysis

Balearic Shearwaters were recorded on 93.5% of days over the four-year survey period, with an inter-annual range of 91% (2007) to 99% (2010) (table 5.4). Day counts were generally less than 15, but there is a large amount of variability associated with this average (mean=14.62, SD=17.13). The percentage of days with counts over the 2007-2010 mean day count (14.62 birds) ranged from 17% (2008) to 54% (2010) (figure 5.13). Day counts of more than 50 were made occasionally throughout the four-year survey period (2007=2, 2008=1, 2009=3, 2010=12), but these rarely occurred on consecutive days (figure 5.13). Autocorrelation analysis on the daily bird-count data showed significant tmporal autocorrelation at a lag of one day in all years, and none at lags greater than one day.

The majority of birds seen from the survey watchpoint were flying west (95%) as opposed to flying east or foraging/loafing offshore (table 5.4). There was a high level of consistency in the pattern of movement of birds flying passed the watchpoint, even though absolute numbers varied between years (table 5.4).

Table 5.4: Summary of daily Balearic Shearwater sightings from the effort based *SeaWatch SW* survey at Gwennap Head, 2007-2010 (N = 5394). Data have been filtered to remove effort/sightings made in periods of poor visibility. Sightings of birds passing >2 km from land are also not included.

	2007	**2008**	**2009**	**2010**	**Total**
N (days)	90	93	93	93	363
Mean day count (birds)	12.9	9.0	11.9	24.9	14.62
SD of day count (birds)	11.4	9.9	14.2	24.4	17.13
Median day count (birds)	11	7	6	16	9
Max day count (birds)	67	71	79	127	127
Birds flying west (%)	94	95	95	96	95
Birds flying east (%)	3	4	4	3	3.5
Birds lingering offshore (%)	3	1	1	2	2

Distance from shore analysis

Data on the distance from shore that Balearic Shearwaters passed the survey watchpoint indicate that the majority of birds (69%) fly within 1 km of the shoreline. For comparison, distance data were also collected for the Sooty Shearwater, a species with a more pelagic ecology (Shaffer et al., 2006), which were found to fly further offshore (75% beyond 1 km from shore). The empirical distributions of the distance-from-shore for sightings of each species are significantly different (Two sample Kolmogorov-Smirnoff test, D = 0.47, $p = < 0.001$).

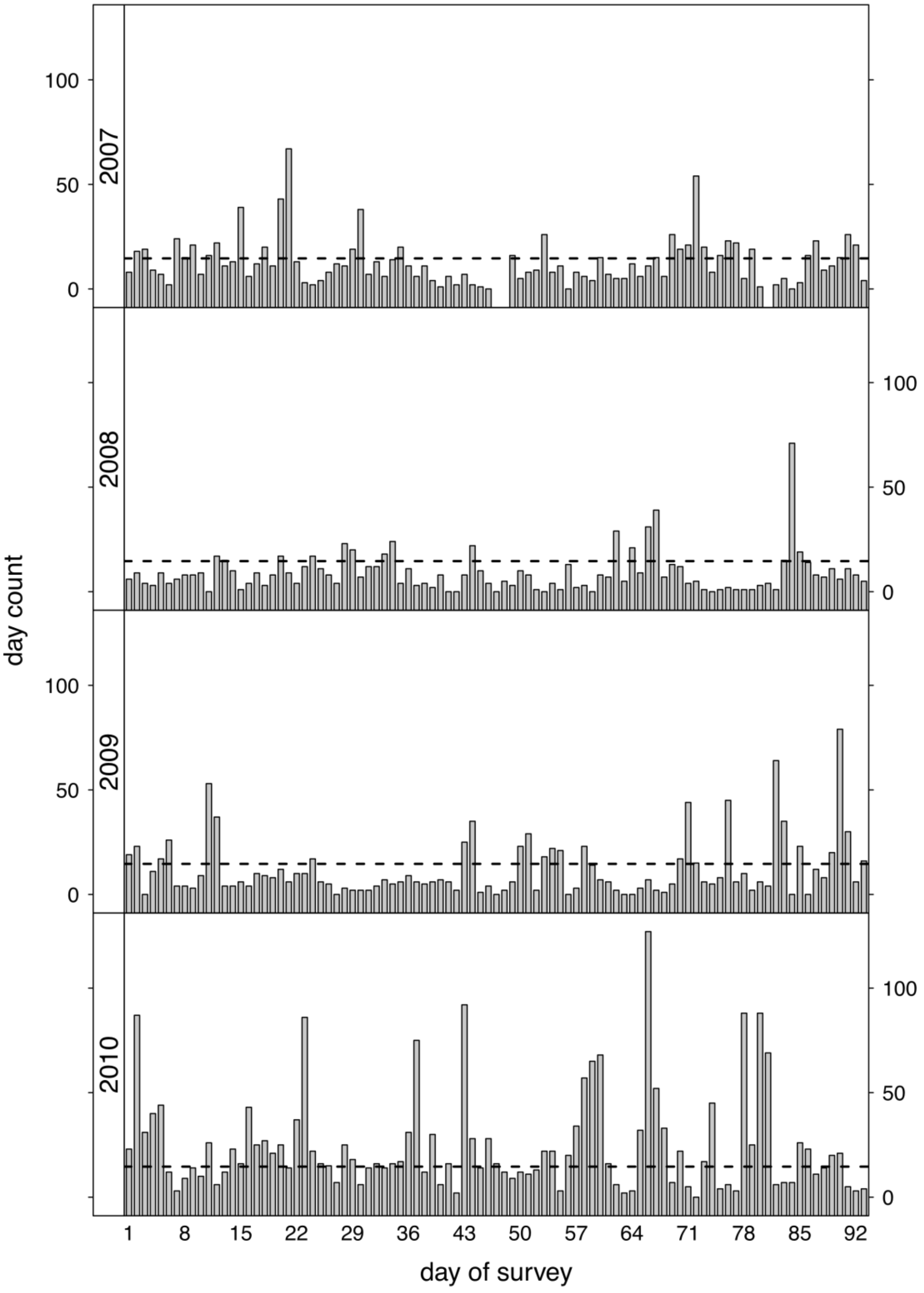


Figure 5.13: Cumulative day-counts of Balearic Shearwaters passing the *SeaWatch SW* survey watchpoint on Gwennap Head between 15 July and 15 October, 2007-2010 (N = 5394 sightings). Dashed lines show multi-year mean (14.6 birds per day).

Sister sites' data

Effort-corrected data (BPH) from the four *SeaWatch SW* sister sites in southwest UK were collected between 15 July and 15 Oct 2007-2010 (table 5.5). Highest average BPH values were recorded in 2010 at all sites. The data indicate that annually-averaged passage rates off southwest England (from Berry Head in Devon, Pendeen and Trevose Head in Cornwall) were in the range of 1.26-3.94 for the survey period, comparable to values of 1.02-2.72 from Gwennap Head (tables 5.5 and 5.3). Passage rates off Strumble Head in Pembrokeshire over the same period were markedly lower (0.26 – 0.7 BPH) (table 5.5).

Table 5.5: SWSW sister site sightings data for Balearic shearwater for the period 15th July - 15th October 2007 - 2010. These are not constant effort sites, but effort is recorded so BPH can be calculated. Location of sister sites is marked on the map in figure 5.5.

	2007	2008	2009	2010
Berry Head/Start Point				
No. of hours	71.25	190	135.5	103.6
No. of birds	128	496	379	307
Birds per hour	1.8	2.61	2.8	2.96
Peak BPH	2.5	10.9	11.8	9.3
Pendeen				
No. of hours	Not available	Not available	144	143.35
No. of birds	Not available	Not available	276	292
Birds per hour	Not available	Not available	1.92	2.04
Peak BPH	Not available	Not available	15.4	6.0
Trevose Head				
No. of hours	147	165	118	173
No. of birds	326	391	149	682
Birds per hour	2.22	2.37	1.26	3.94
Peak BPH	18	21	4.7	22
Strumble Head				
No. of hours	354.5	526.5	478	339
No. of birds	256	181	122	237
Birds per hour	0.7	0.34	0.26	0.7
Peak BPH	3.6	1.8	1.9	2.5

5.2.6 Discussion

The Balearic Shearwater datasets used in this study contain a large number of opportunistic and effort-based observations, and achieve good coverage of the survey area and period (figures. 5.7-5.9). The consistency in annual and seasonal patterns of data collected using both targeted and opportunistic methods gives high confidence in the results, and supports the use of opportunistic data for monitoring of this coastal species.

5.2.6.1 Spatial and temporal distribution

The spatial distribution of opportunistic sightings is consistent between years and reveals that the largest numbers of birds were concentrated along the western Channel coasts of northwest France and southwest England (figures 5.7 and 5.10). Numbers were generally lower in the eastern Channel and along Irish and North Sea coasts than in the western Channel (figure 5.7), consistent with previous studies (e.g. Wynn and Yésou, 2007). However, there are indications for increasing numbers reaching the eastern French Channel coast during the survey period (figure 5.7, Dubois et al., 2012).

Boat-based observations (opportunistic and targeted) suggest that Balearic Shearwaters were generally restricted to the coastal zone within the study area, with no high-density areas identified offshore in the Channel (figure 5.10). This is in agreement with previous surveys and habitat mapping studies from other parts of the species' range (Louzao et al., 2006a; Oppel et al., 2012). Results of boat-based surveys support targeted land-based observations; identifying the embayments of northwest Brittany (particularly Bay of Lannion and Bay of Saint-Brieuc) and the large embayment of Lyme Bay in southern England as 'hotspot' areas due to higher sighting densities (figure 5.10, Thébault et al., 2010).

The importance of targeted land-based surveys in northern Brittany is illustrated by the failure of the wider *Trektellen* dataset, which is mostly focussed on headland sites (figure 5.5), to capture the very large numbers of birds using the broad embayments in this region (compare patterns in figures. 5.7 and 5.10). *Trektellen* data for northwest France show a peak day count of 482 in the 2007-10 survey period (table 5.2), which is an order of magnitude lower than the peak counts made during targeted land-based surveys (Thébault et al., 2010). There is a higher density of observation sites spread evenly along the UK Channel coast, both on headlands and in bays (figure 5.5), therefore there is greater confidence that large aggregations were unlikely to have escaped detection in this part of the survey area.

Seasonal patterns in both land- and boat-based sightings were consistent through the four-year survey period, with highest numbers recorded through summer and autumn and lowest numbers during spring (figures 5.8 and 5.11). The spring withdrawal from northeast Atlantic waters corresponds to the breeding period, when most birds will be back at colonies in the Mediterranean (Le Mao and Yésou, 1993). The occurrence of significant numbers of birds lingering into the mid-winter period in southwest UK appears to be a relatively recent phenomenon (Wynn, 2009). There is also an indication of increasing winter numbers along the Brittany coast; an area where the species has been recognised to occur regularly during the winter in smaller numbers (~10) since the 1970s – 80s (Yésou, 1991). Unprecedented numbers were recorded in the Bay of Saint-Brieuc (Brittany) in winter 2007-2008 (Plestan et al., 2009) and, although such large aggregations have not been recorded since, targeted surveys have found higher than usual numbers in this region during the 2009-10 and 2010-11 winters.

Although records of foraging aggregations off southwest UK were relatively rare (possibly because most opportunistic sightings do not specify behaviour), analysis of the available data indicates that different sites were used in autumn and winter (figure 5.9). This may be a result of changing prey distributions between seasons. Summer aggregations were noted between Berry Head and Selsey Bill (figure 5.9), mostly in association with Manx Shearwaters. Anecdotal reports suggest that sandeel (*Ammodytes* sp*.)* and anchovy (*Engraulis encrasicolus)* may be important prey species at this season. Winter aggregations were centred on southwest Cornwall and the Isles of Scilly (figure 5.9), usually as part of much larger mixed-species aggregations numbering hundreds or thousands of birds and dominantly comprising Razorbills, Kittiwakes, Northern Gannets (*Morus bassanus)* and large gulls (*Larus sp*.). Similar mixed-species assemblages, including Balearic Shearwater, have recently been observed in mid-winter off northwest Brittany (Plestan et al., 2009), where anecdotal reports from commercial fishers indicate that small forage fish of the clupeid family, e.g. herring (*Clupea harengus*) and sprat (*Sprattus sprattus)*, are likely target species.

Recent studies have suggested that the Balearic Shearwater has increased in abundance within the study area since the mid-1990s (Yésou, 2003; Wynn et al., 2007; Luczak et al., 2011). Survey results from 2007-2010 reveal significantly higher abundance during 2010 (e.g. figure 5.12), with record numbers reported from northwest France and southwest UK. The peak count of 5780 from Bay of Lannion and Bay of Saint-Brieuc in late July 2010 equates to about 20% of the estimated World population of ~25,000 individuals (Arroyo et al., 2008; Arcos, 2011). Although large numbers have been recorded along this coastline in the past, e.g. 3200 at Cap Fréhel in Sept 1983 (Liéron, 2000), the numbers recorded in 2010 were unprecedented in this region (Thébault et al., 2010). Likewise, the peak count of 268 off Gwennap Head in Sept 2010 was a record day count for the county of Cornwall, where intensive seabird observations have been carried out for several decades. This record was broken again in Sept 2011, with a day count of 283 off Gwennap Head, likely related to the break-up of a foraging aggregation of up to 600 birds in Lyme Bay a few days earlier (Darlaston and Wynn, 2012). Combined with an increase in mid-winter records, these observations suggest that the species is continuing to increase in abundance in the northern part of its inter-breeding range, and the presence and abundance of the species is extending into the winter.

5.2.6.2 Evidence for age partitioning of the population during the inter-breeding period

The results of this and other studies are beginning to suggest that there may be age partitioning within the breeding and non-breeding distributions of the species. Breeding birds arrive back at the colonies on the Balearic Islands from September onwards. Guilford *et al*. (2012) tracked breeding adults from the largest known cave colony (at Sa Cella on Mallorca) with light-logging geolocators, and found that birds returned to the Mediterranean on a median date of 23 Sept 2010 (N = 26). The presence of many hundreds of Balearic Shearwaters in the western Channel in late autumn and winter (Oct - Jan; Plestan et al., 2009; Wynn, 2009) suggests that these lingering birds may therefore be non-breeders. Tentative evidence for age partitioning of the population throughout the inter-breeding period can also be found in the tracking data of Guilford *et al.* (2012), as none of the tracked breeding birds from Sa Cella dispersed further north than the Bay of Biscay in summer/autumn 2010, even though this period corresponded with the concentration of almost 6000 birds off northwest Brittany (Thébault et al., 2010).

5.2.6.3 Behavioural insights

A novel aspect of this study has been the application of effort-based monitoring from prominent headlands off southwest UK (figure 5.5), that are known to be sites that have recently hosted large numbers of passing shearwaters (Wynn et al., 2007; Wynn, 2009). Land-based monitoring is effective for this species because of its coastal affinity; this is supported by the lack of offshore observations during *Marinelife* boat-based surveys (figure 5.10), and also by the distance-from-shore data from Gwennap Head.

Effort-based surveys from the *SeaWatch SW* watchpoint at Gwennap Head during 2007-10 have revealed that Balearic Shearwaters pass offshore in small numbers (mean = 14.62) on an almost daily basis (93.5% of days) in the summer and autumn. There is a 55% chance of recording birds passing the watchpoint in any given hour, and there is a clear diurnal pattern to the rates of passing birds per hour, with significantly higher rates in the morning between 0800 and 1100 hrs (figure 5.12). The drivers behind this distribution are unclear, given that Balearic Shearwaters at this season are not 'central placed foragers' committed to regular feeding trips to provision young at the nest. Further effort-based observations from other headlands in the western Channel would be required to assess whether this pattern represents a local phenomenon or if it is representative at a broader scale.

Effort-corrected data from Gwennap Head and a series of four 'sister sites' off southwest England reveal annually-averaged BPH values of 1.02 to 3.96, with lower values of 0.26 to 0.7 off Strumble Head in southwest Wales (tables 5.3 and 5.5). The overall pattern of movement at sites in southwest England is westwards, on both south- and north-facing coasts. This is interpreted to represent birds moving between the western Channel and the Celtic/Irish Seas, and being deflected by the prominent peninsula of southwest England (figure 5.5). The numbers of birds using this 'flyway' in 2010-11 comprised 1-2% of the World population in a single day (Darlaston and Wynn, 2012), however, away from Lyme Bay, these birds did not linger and were rarely seen in large numbers on consecutive days (figure 5.13). In both 2010 and 2011 it is inferred that the record numbers of birds passing southwest UK originated from much larger aggregations across the Channel in northern Brittany; these sporadic influxes into UK coastal waters are therefore likely to have been foraging trips. This interpretation is supported by behavioural observations from *Marinelife* boat-based surveys, with only low densities of birds seen away from the 'hotspot' areas in large embayments (figure 5.10) and 72% of offshore sightings relating to birds in direct flight.

5.2.6.4 Conservation implications

Recent observations, indicating that up to 20% of the World population of this Critically Endangered species has aggregated in specific embayments off northwest France and southwest UK, highlights the potential risk from point-source pollution events such as oil spills (Arcos, 2011). The risk to the overall population from such events may also be accentuated by age partitioning of the population (Guilford et al., 2012). The sinking of the MV Erika off Brittany in Dec 1999 generated an oil spill that was considered to be one of the worst environmental disasters ever to affect France, with an estimated 100,000 seabirds being affected by the >10 million litres of oil released into the ocean (Cadiou et al., 2003; 2004). A similar disaster in summer off northern Brittany could have severe repercussions for the Balearic Shearwater, either through direct mortality or by forcing the birds to move away and search for other feeding sites.

Another potential threat comes from development of renewable energy infrastructure, e.g. offshore wind turbines. For example, in the identified Balearic Shearwater 'hotspot' area of Bay of Saint-Brieuc (figure 5.10) an offshore wind farm comprising 100 turbines and covering an area of 80 km^2 is planned (WindPower, 2012). Although shearwaters' moderate manoeuvrability and tendency to fly low to the water means that they are at low risk of actually striking wind turbines (Cook et al., 2011; Furness and Wade, 2012), there is potential for works associated with the construction and emplacement of turbines to lead to disturbance and displacement of foraging and/or roosting flocks.

Recent anecdotal reports from western Lyme Bay indicate that Balearic Shearwaters regularly follow commercial fishing boats in this area (Darlaston and Wynn 2012), suggesting that discards may be important to this species in certain locations and at certain times of year. Furthermore, on *Marinelife* surveys in English waters, scavenging around fishing and angling vessels was the most frequently encountered foraging behaviour. However, there is currently no evidence to suggest that fisheries bycatch has been a significant threat to the species within the study area in recent years, which contrasts with the situation in Portuguese and Mediterranean waters (ICES, 2008b; Laneri et al., 2010). Shearwaters are occasionally accidentally hooked by line fishers, but are usually released unharmed (Thébault, 2011). Further monitoring of interactions with commercial fishing boats will be required to assess whether bycatch is an issue on a larger scale. For example, there are currently plans to investigate the fine-scale spatial and temporal habitat use of Balearic Shearwaters (and other foraging seabirds) in St Ives Bay in northwest Cornwall in winter, as there have been recent incidents of seabird bycatch (up to 200 auks) in fixed nets in this area.

5.2.7 Conclusions.

This study has utilised an unusually extensive (land- and boat-based) sightings dataset to investigate the at-sea distribution and behaviour of the Critically Endangered Balearic Shearwater in northeast Atlantic waters. Results obtained from 2007 to 2010 indicate that a significant proportion (up to 20%) of the World population now visits the western Channel off northwest France and southwest UK during the inter-breeding period, although there is high inter-annual variability in the numbers of birds recorded and the sites used. Broad shallow embayments appear to be favoured habitats, and few birds were seen away from coastal areas. Recently reported increases in abundance in the study area appear to be continuing, with record counts at the main sites in 2010. The temporal distribution within-year is also changing, with more birds lingering beyond the traditional July-October period, and remaining into mid-winter.

We have combined effort-based and opportunistic data collected in land and boat sightings from both the UK and France for the first time, and as such offer a synopsis of the species distribution in an area that is clearly important for relatively large numbers of the species, but may not be highlighted through tracking studies of breeding birds. The next step will be to investigate the environmental drivers behind the distribution patterns we have described and potentially identify common habitat preferences highlighted in studies of the distribution and habitat associations of the species in its southerly range (Louzao et al., 2006a; Luczak et al., 2011; Louzao et al., 2012).

Our results highlight the importance of opportunistic public sightings data in supporting targeted effort-based survey data, and providing information that helps inform policy decisions, e.g. implementation of spatial protection measures. Extensive public sightings datasets have also proved useful in other recent studies investigating coarse-scale distributions of migratory marine megavertebrates, such as the Basking Shark *Cetorhinus maximus* (Witt et al., 2012), Manta Ray *Manta alfredi* (Jaine et al., 2012)and Leatherback Turtle *Dermochelys coriacea* (Houghton et al., 2006). We suggest that scarce or endangered species, with a high public profile and an inshore distribution for some or all of their annual cycle, are most suitable for co-ordinated 'citizen science' recording projects.

Although the designation of protective areas for Balearic shearwaters has been achieved at the breeding colonies and there are further measures proposed at identified hotspots within the Mediterranean (Arcos, 2011); there remains an urgent need to safeguard important sites for the species outside of the breeding areas. As highlighted in the recent paper by Louzao *et al* (2012), trans-boundary conservation measures are required in order to effectively protect this Critically Endangered species throughout its range. We have shown that significant numbers of the species continue to visit the coasts of the UK, Ireland and northern France, and the onus is on the Governments of these countries to monitor and safeguard the birds whilst in their waters, in line with their commitment to the European Birds Directive (2009/147/EC).

5.2.8 Acknowledgements

We would like to thank everyone who submitted reports of Balearic Shearwater to *SeaWatch SW*, *Birdguides* and *Trektellen*. Thanks to Gerard Troost of *Trektellen;* Gérard Debout and other members of Groupe Ornithologique Normand (GONm) for data from Normandy; members of Groupe Ornithologique Breton (GOB), Groupe d'Etudes Ornithologique des Côtes d'Armor

(GEOCA), the LPO réserve nationale des Sept-îles, Bretagne Vivante; the Parc National Marin d'Iroise (PNMI); the Association Naturaliste d'Ouessant (ANO); Jean Lawman for winter records from Cornwall. We would also like to acknowledge local co-ordinators at *SeaWatch SW* 'sister sites': Mark Darlaston, Stan Christophers, Ray Wilkinson, Graham Rees, Adrian Rogers, John Swann and John Foster. We are extremely grateful to all volunteer observers who participated in the *SeaWatch SW* and *Marinelife* surveys, in particular assistant *SeaWatch SW* co-ordinator John Swann. Thanks to Miguel McMinn and Ana Rodríguez for comments. We acknowledge financial support for *SeaWatch SW* and *Marinelife* from RSPB, BTO, Natural England, Naturetrek, Total Foundation for Biodiversity, SAHFOS, RNBWS, The Seabird Group and Birdguides. Much of the *Marinelife* survey effort was part funded by the EU (INTERREG IV A) under the Channel Intergrated Approach for Marine Resource Management

5.2.9 Supporting information.

Additional supporting information can be found in the Electronic Supplementary Material in appendix 6 (referred to as ESM in the main text) and described below:

ESM 1. Detailed methodology for collating the UK Balearic Shearwater opportunistic sightings database.

ESM 2. Overview of European Seabirds At Sea (ESAS) survey methods and variations on this employed during targeted *Marinelife* boat surveys.

ESM 3. Detailed methodology and survey effort information for the effort-based *SeaWatch SW* (land-based) Balearic Shearwater survey.

ESM 4. Details on data collection and processing methods for *SeaWatch SW* 'sister sites'.

ESM 5. Results of the effort- correct (BPH) Balearic Shearwater counts from French sites, using data from *Trektellen*. Maps of effort-corrected data are presented in **figure S1** (annual peak BPH) and **figure S2** (seasonal peak BPH).

ESM 6. Effort data and additional results from the *Marinelife* boat surveys in the western Channel (2007 – 2010) and some additional notes on behavioural observations of Balearic Shearwaters recorded in targeted boat surveys. **Figure S3** is a map of casual sightings reported through the *Marinelife* citizen-science project

Chapter 6 Conclusions and recommendations for future work.

The aims of this thesis were to describe and attempt to explain the spatio-temporal distribution, within the southwest UK study area, of three target species of conservation concern; harbour porpoise, basking shark and Balearic shearwater. Although the three target species are unrelated and the analyses were focused at different scales, the chapters are linked by the use of a central visual monitoring dataset collected through the SeaWatch SW survey. The effort-based nature of the SeaWatch SW dataset allows comparisons and analyses that could not be undertaken on non-effort-based (opportunistic) or presence-only survey data, where absence information is not available. The results presented represent an advance in our knowledge of the target species' distribution and the drivers behind it and are valuable for informing marine protected area policy and for ongoing monitoring of the target species, which is required of the UK Government due to their protected status.

The results from the harbour porpoise distribution study provide insights into the importance of fine scale tidal-topographic interactions that lead to ephemeral hydrodynamic features. There remain many unanswered questions, which a more intensive physical oceanographic survey would help to resolve. A combined array of moored, upward looking ADCPs and C-PODs, providing concurrent data, would greatly improve our understanding of the effect of fine scale hydrodynamics on the distribution of harbour porpoises. An associated EK-60 ('fish finder') survey would supply key information on the distribution of zooplankton and fish with reference to tidal period, filling in the 'missing link' in the present study and providing insights into trophic coupling at the study site.

The results of the basking shark study challenge the established hypothesis that there is a close temporal and spatial association between the location of meso-scale tidal mixing fronts and the seasonal appearance of basking sharks around the coast of Great Britain and Ireland. The analyses did not find evidence for a significant effect of front strength or density within the vicinity of the survey area on the peak day counts of sharks recorded in the effort-based survey. Larger scale analyses are now being undertaken in an attempt to understand whether the effect of thermal fronts is scale dependent. Additionally, longer term or multi season basking shark tracking studies would help to constrain this relationship. The improvements in both tracking/data logging technology and front mapping techniques since the bulk of the basking shark tracking data was published (late 1990s and early 2000s) should now allow an updated and finer scale investigation of track data relative to frontal locations, which could provide a quantitative assessment of the proportions of time spent in direct association with thermal fronts.

The Balearic shearwater chapter shows that there continue to be internationally important numbers of the species reported from within the coastal seas of the UK, Ireland and France, with evidence for increases in the numbers reported from this region through the study period. This is a key finding with respect to monitoring and protection of this endangered species. It is proposed that the majority of birds visiting the study area are non-breeders, which suggests that tracking studies based from the breeding colonies are unable to capture information on this important section of the population. Future will investigate the demographics and broader migratory distribution of the birds within the survey area by attaching long-deployment geo-locator devices to fledglings at the same colony where adult birds are also being tracked. This will be a speculative study, as the birds must eventually be recaptured to collect data from the geo-locators. Therefore the hope is that most of the tagged fledglings will return to their natal colonies once they are mature, in order to begin breeding. If successful, this tracking of fledglings will provide key information on the at sea behaviour of non-breeding birds; helping to constrain movement patterns and possibly identify key feeding areas and possible age partitioning in the migratory patterns of the species.

The information presented on the spatial and temporal patterns in the three species' distributions can be used to inform and improve future monitoring by refining survey methods and focusing future surveys at the most appropriate times and places. The data presented on all three species show high levels of temporal variability in the abundance of sightings. There are indications that time of day is a key predictor of sightings for all three species and that, particularly for Balearic shearwaters and basking sharks, there can be high variability in the number of sightings from day to day and month to month. These results indicate that short-term monitoring surveys (for example for Environmental Impact Assessment) must be undertaken for appropriate periods in order to capture the variability in the animals' abundance. If not, it is possible that short duration aggregations of these endangered animals, which are present seasonally or under specific environmental conditions, may be missed. In addition the difference between the patterns in detection of porpoises from the visual and acoustic surveys highlights the need to consider carefully what information a survey is attempting to gather about the species' distribution and whether it is appropriate to rely solely on data collected by single-method surveys.

The data collected through the SeaWatch SW survey have been used to address various research questions, hypotheses and analyses, posed at a variety of scales. The use of a single visual monitoring survey to investigate patterns in the spatial and temporal distribution of three species with very different ecologies can, in hindsight, be considered a type of 'methodological experiment'. The different ways in which the visual monitoring data have been used, allow a unique opportunity for an honest and open appraisal of the appropriateness of the survey methods and the robustness of the data in terms of quantitatively answering a range of scientific questions. In addition it is possible to outline some key criteria for future targeted surveys, in order to learn from the experiences gained through the 5-years of SeaWatch SW.

Of the three species studied, harbour porpoise appeared to be the most 'resident' within the survey area, regularly being recorded from identifiable sub-habitats within the larger reef area. Because of this residence and the presence of consistent numbers of sightings throughout all years of survey period, it was possible to focus spatio-temporal analyses of porpoises at a fine scale. This allowed a quantitative study of the animal's interaction with the very localised reef habitat, which provided new insights into potential mechanisms leading to biophysical coupling at the study site.

As discussed in chapter 2, there were issues with error on the visual estimation of porpoise positions, and these uncertainties created some significant problems with the data analyses. Assessment of the level of error on the visually estimated location of porpoises was undertaken through testing, which allowed an average error level to be calculated and subsequently propagated through the spatial analyses by gridding the data at an appropriate scale (600-m cell size). This gridding has, necessarily, reduced the resolution of the spatial analyses, which is a shame when the available supporting environmental data, such as bathymetry and acoustic Doppler current profiling, are of such high quality and resolution. However, without the error testing there would have been no way of quantifying the visual distance estimate errors and it would have been very difficult, and arguably meaningless, to undertake any kind of spatial analyses on the effort-based porpoise survey data. Future studies should ensure that adequate training of observers is carried out prior to surveying and that regular testing, by comparison against theodolite positions of animals, is undertaken on as large a number of observers as possible. The data collected during these error tests can also contribute to double observer trials, the results of which can be used to calculate a detection function for the survey data, as explained in chapter 2 (section 2.5).

Using a theodolite to accurately record the position of animals reduces location error on sightings by orders of magnitude. However, limiting visual surveys to only collecting data using a theodolite can significantly reduce the overall amount of survey effort because a higher level of training is required to use the instruments, which can also only be used in optimal conditions (they are not waterproof and can vibrate significantly in moderate winds, which affects the quality of the data). It is not felt essential to recommend that future surveys be limited to only using sightings data collected by a theodolite; although it is recognised that the choice of using one should be based on the accuracy required to answer the specific research question in each case (and the resolutions of supporting environmental data) and the exposure and climate at the survey site.

Another difficult and seemingly key methodological issue that was highlighted in the porpoise study was that of combining visual and acoustic methods of data collection. In terms of spatial distribution, both methods identified the same part of the study area (the reef margin) as having the highest relative densities of porpoises. However, when examining the temporal distribution in the data collected by the two methods, inconsistent relationships were identified with respect to variables such as month, time of day and tidal flow. It should be acknowledged that within the survey area, only three CPODs were deployed, which may not be considered optimum for the size of the area, as the instruments are limited to a range of approximately 200-300 m. It is likely that this, and the fact that the visual and acoustic surveys are essentially monitoring different things (i.e. one records the very localised, underwater echolocation behaviour and one records the surface behaviour within the entire survey area), may have led to the differences in the temporal patterns in the data collected. This should be borne in mind when planning future monitoring studies. Theodolite surveys are accurate enough to identify porpoise sightings from within the specific range of CPODs, which would enable direct comparison of the two methods.

The effort-based SeaWatch-SW survey covered only a small part of the range of the three target species. For porpoises, as discussed above, this was not an issue because analyses were focussed on the fine-scale distribution within a previously identified, locally important ‘hot-spot’ area. However, for the basking shark and Balearic shearwater studies, this mismatch of scales introduced some issues.

The basking shark study may be viewed as the least successful of the analyses in the thesis, and was certainly the most difficult in terms of the statistical modelling process. The results support previous studies, which highlighted the importance of sea surface temperature and the North Atlantic Oscillation on seasonal and inter-annual variability in the appearance of the species; but did not find evidence that thermal fronts are an important a driver of the species’ fine-scale temporal distribution, as has been previously proposed. This result may be a reflection of the scale of the analyses; therefore planned future work will use public sightings data from the three

UK ‘hot-spots’ to look at regional-scale patterns of shark abundance in response to thermal fronts. This investigation will provide an interesting comparison of the scales of effect of potential environmental drivers of shark distribution and will be the first research to use quantitative thermal front data in such a way. It is hoped that this will help to improve our understanding of the true importance of these features to the species and better understand the types of monitoring data required in order to answer important questions regarding the species spatio-temporal ecology.

Difficulties in the analyses of the basking shark data arose as a result of the large change in the number of sightings recorded through the monitoring period, and the associated issues of attempting to identify common drivers for basking shark temporal distribution in years with orders of magnitude difference in the amount of sightings recorded. In addition, the species is known to be migratory and its appearance (at least at the surface) within the coastal seas around the survey area is highly seasonal. This indicates that there are likely to be larger scale environmental variables at play, such as NAO and SST, which may affect the broad-scale distribution of the species, but there was not scope to account for these in the analyses. Mismatches in the scale of the environmental drivers (e.g. meso-scale front metrics) and the response (fine-scale shark distribution) of the generalised additive model may also have affected the outcome of the analyses presented in the basking shark study.

This is a difficult situation to address, as an effort-based dataset is preferable, possibly essential, in order to quantitatively assess links between basking shark sightings and environmental conditions. This is because of the potential biases and apparent resistance towards using public sightings data in published research. There are no larger scale effort-based shark sightings data available which have the uniquely extensive temporal coverage of the SeaWatch SW survey (i.e. dawn-to-dusk observations for a 93-day period each year). However, there are other, local scale, intensive effort surveys, such as the Manx Basking Shark Watch, which could provide some context for the analyses undertaken in this study, or a second survey site for comparative analysis. Additionally, there is recent evidence for an increase in published studies that use public sightings and ‘citizen science’ data, which can provide key information about long-term, broad scale trends in distribution of species that is extremely difficult (and expensive) to achieve with broad coverage, effort-based strategic monitoring surveys.

The Balearic shearwater study has made use of the small-scale intensive effort-survey data collected by SeaWatch-SW in a different way to the other chapters, in that the data are combined with a number of other broader-scale targeted and opportunistic data to provide a synthesis of the species distribution over a larger study area. In this respect the SeaWatch-SW data form only a small part of the overall data set, but along with the effort-corrected 'sister sites' data provide important calibration for the opportunistic data. The SeaWatch-SW data have also given insights into the species' diel passage behaviour, which could not have been identified using the offshore survey or opportunistic land-based sightings data. The Balearic shearwater chapter is considered a successful example of the type of applied study that can be achieved using all available data sets from within an area. The strength of the opportunistic data is its broad temporal and spatial coverage, which is complemented by effort-corrected targeted boat surveys. The SeaWatch-SW survey data provides key fine-scale information about passage behaviour, but alone would be very limited in what it could tell us about changes in the species' spatio-temporal distribution over time.

Having had the, fairly unique, experience of collecting and analysing a large volume of land-based effort-corrected visual monitoring data, it is possible to assess some of the successes and failures of the SeaWatch-SW dataset (described above), and to use the lessons learnt to outline some important considerations for the design of future studies:

- A standardised scanning methodology must be used; this is fully quantitative and ensures measured and even coverage of the survey area.
- Observer fatigue and ability should be considered. It should be ensured that all observers are able to identify relevant species and appropriate training should be undertaken. Multiple observers should always be present and regular breaks must be taken at designated intervals; even though this reduces overall effort, the data collected is likely to be of higher quality.
- Exploration of the detection and error limitations on sightings must be undertaken and where appropriate corrected for. It goes without saying that it will be harder to detect an animal (particularly in the water) at 1km than at 100m.
- Before deciding to undertake a land-based (or boat-based) monitoring survey, the availability of supporting environmental data should be explored. It is of limited use to spend time and effort collecting high-resolution constant-effort monitoring data if there are no environmental data available with which to compare species distribution. The resolution of environmental data for the area should also be taken into consideration. Key supporting environmental data sets include (but are not limited to): appropriately resolved bathymetry, wave buoy or light ship data (SST, wave height, wave direction), weather stations for meteorological data sets, tidal models or *in situ* current data and data on prey distribution (fisheries or scientific fish surveys, plankton samples, fluorescence data).

- Survey conditions must be accounted for in analyses of monitoring data, therefore a robust method of recording these must be in place. Periods when survey conditions are poor, or not recorded, cannot be included in analyses. Therefore the merits of constantly observing in all conditions should be considered, as it is likely that data collected in poor conditions may ultimately not be used. This is particularly the case for marine mammals, as indicated by the results of the porpoise study, which show that sighting rates are significantly negatively affected as sea state increases.

The key point at the basis of the successful use of single location land-based visual monitoring surveys is to understand and accept the limits of the data. It is not appropriate to extrapolate results to larger areas or longer time periods without significant support from alternative data sets. The clear benefit of intensive effort surveys, such as SeaWatch-SW, is the ability of the data to support quantitative statistical analyses, although this requires supporting environmental data, collected at an appropriate resolution. Additionally, the nature of constant-effort surveys may lead to zero-inflation of the data and the associated statistical difficulties.

Land-based visual monitoring surveys are ideal for studying fine scale distribution of species within identified coastal ‘hot-spots’. In addition, the methods are much less expensive than boat-based surveys and can achieve simultaneous and continuous coverage of a whole (small) survey area. It is hoped that this thesis, and in particular this overview of the successes and failures of the data set and analyses, will aid and encourage the use of land-based visual monitoring data in the future.

Chapter 7 Appendices

Appendix 1: SWSW recording forms.

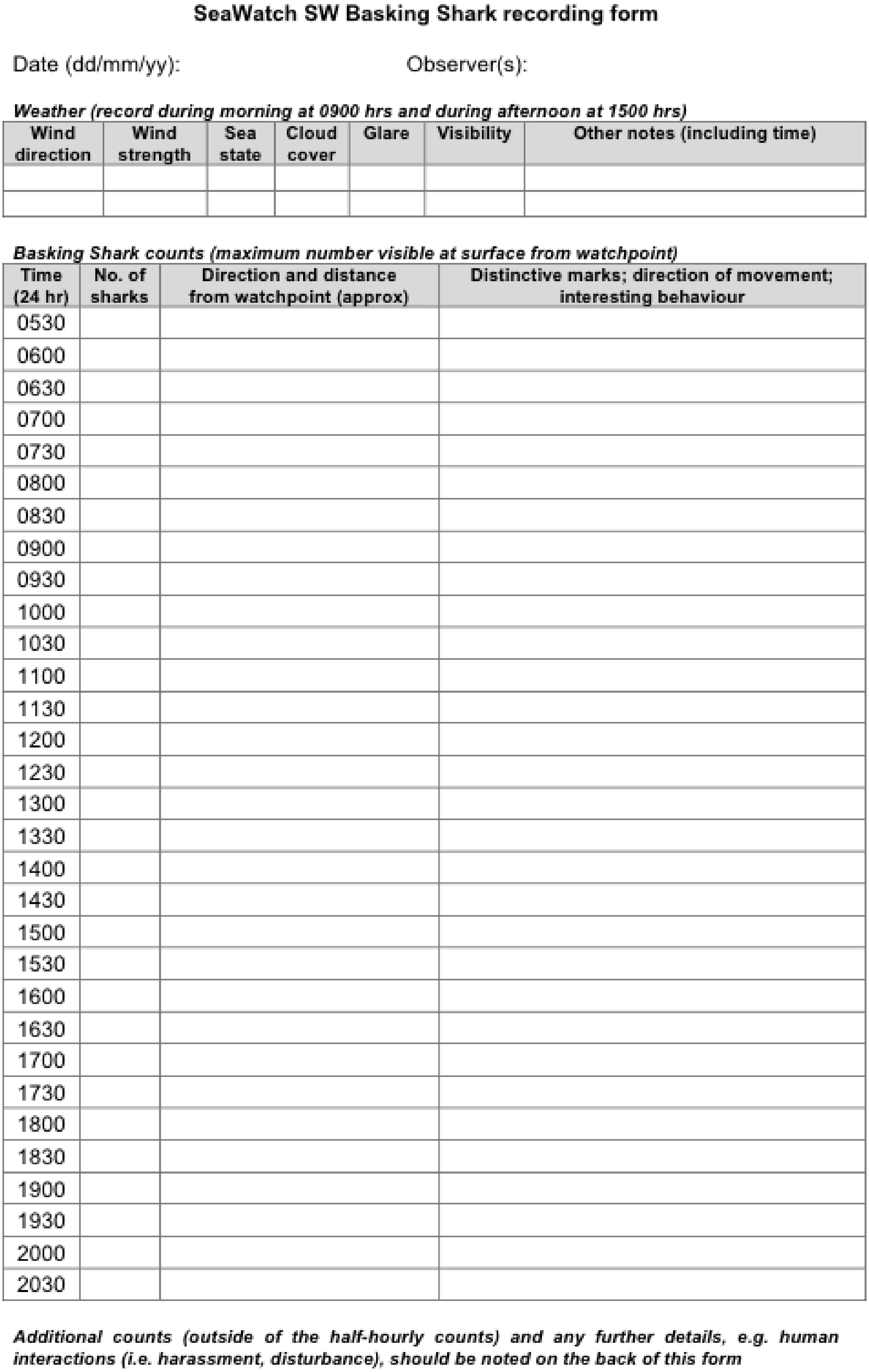
SeaWatch SW Balearic Shearwater recording form

Date (dd/mm/yy):

Observer:

Time (24 hr)	No.	Direction	Distance	Moult, plumage, behaviour, other species.

Day total:



SeaWatch SW Basking Shark recording form

Date (dd/mm/yy): Observer(s):

Weather (record during morning at 0900 hrs and during afternoon at 1500 hrs)

Wind direction	Wind strength	Sea state	Cloud cover	Glare	Visibility	Other notes (including time)

Basking Shark counts (maximum number visible at surface from watchpoint)

Time (24 hr)	No. of sharks	Direction and distance from watchpoint (approx)	Distinctive marks; direction of movement; interesting behaviour
0530			
0600			
0630			
0700			
0730			
0800			
0830			
0900			
0930			
1000			
1030			
1100			
1130			
1200			
1230			
1300			
1330			
1400			
1430			
1500			
1530			
1600			
1630			
1700			
1730			
1800			
1830			
1900			
1930			
2000			
2030			

Additional counts (outside of the half-hourly counts) and any further details, e.g. human interactions (i.e. harassment, disturbance), should be noted on the back of this form

SeaWatch SW general seabird recording form

(use new form at start of each hour)

Date (dd/mm/yy): Start/finish time (24 hour clock):

Observer:

Wind direction	Wind strength	Sea state	Cloud cover	Glare	Visibility	Other notes

Level 2 species (large shearwaters, Pomarine + Long-tailed Skuas, Leach's Storm-petrel, Sabine's Gull)

Species	No.	Time (24 hr)	Direction	Distance	Age/plumage/other notes

Level 3 species (all other seabirds not listed above, except Gannet, Fulmar and Shag)

Species	Direction	Number	Total

Other species (e.g. Basking Sharks, Ocean Sunfish, marine mammals, migrant birds/insects):

Remember – use a new form at the start of each hour, e.g. at start of watch at 0630 hrs and then at 0700 hrs, 0800 hrs etc.

SeaWatch SW Marine Wildlife recording form
(use as many forms as required each day)

Date (dd/mm/yy):　　　　Start/finish time (24 hour clock):

Observer(s):

Weather (record during morning at 0900 hrs and during afternoon at 1500 hrs)

Wind direction	Wind strength	Sea state	Cloud cover	Glare	Visibility	Other notes (including time)

Target species (Ocean Sunfish, whales, dolphins, seals, turtles, jellyfish, fish)

Species	No.	Time	Direction and distance	Size, direction of movement, behaviour

Additional notes, including human interactions (i.e. harassment, disturbance), should be noted below or on the back of this form

SeaWatch SW recording notes (for Gwennap Head)

The following list shows the target species for SeaWatch SW. Basically, if it moves, we record it! However, the level of detail we record (shown in brackets below) varies according to species. Level 1 species, e.g. Balearic Shearwater and Basking Shark, are recorded in the most detail, whereas only basic information is required for commoner species such as Kittiwake.

Level 1 (*time, number, direction, distance, age/plumage, behaviour*)
Balearic Shearwater *Puffinus mauretanicus*
*Basking Shark *Cetorhinus maximus*
*Ocean Sunfish *Mola mola*
*Any cetaceans (whales, dolphins) and turtles
Any rare seabirds considered by BBRC

Level 2 (*time, number, direction, age/plumage, other notes*)
Cory's Shearwater *Calonectris diomedea*
Great Shearwater *Puffinus gravis*
Sooty Shearwater *Puffinus griseus*
Leach's Storm-petrel *Oceanodroma leucorhoa*
Pomarine Skua *Stercorarius pomarinus*
Long-tailed Skua *Stercorarius longicaudus*
Sabine's Gull *Larus sabini*
Puffin *Fratercula arctica*

Level 3 (*day/half-day total, direction*)
Common Scoter *Melanitta nigra*
Manx Shearwater *Puffinus puffinus*
European Storm-petrel *Hydrobates pelagicus*
Cormorant *Phalacrocorax carbo*
Arctic Skua *Stercorarius parasiticus*
Great Skua *Stercorarius skua*
Mediterranean Gull *Larus melanocephalus*
Little Gull *Larus minutus*
Kittiwake *Rissa tridactyla*
Guillemot *Uria aalge*
Razorbill *Alca torda*
Any wildfowl (swans, geese, ducks), divers, grebes, waders, terns, auks not listed above
*Any seals
*Any jellyfish

*Recording of these species is primarily the responsibility of the Marine Wildlife Observer, but notes should also be made by the Seabird Observer whenever possible.
All observers are encouraged to record migratory land birds and insects, and any other interesting wildlife on, over or offshore of the watchpoint.

Seabird Recording

Note that Fulmar and Shag are local breeding species and are therefore not included in the survey, however, Seabird Observers are encouraged to make selected counts if time allows. Gannets are too numerous at this site to count thoroughly, and are therefore also not included in the survey.

On days of heavy seabird passage, focus on Level 1 species first, then Level 2 species, then Level 3 species. Some Level 3 species, e.g. Manx Shearwater, may be moving in such large numbers that counting individuals is impossible. In this case, take a 5 or 10 minute sample count every hour/half-hour until the passage eases.

Distant unidentifiable auks can be recorded as auk sp., however, all other species should only be recorded if the identification is 100% certain. See the SeaWatch SW website for some relevant ID info on Balearic Shearwater.

Marine Wildlife Recording

You should record everything that you see!

There are laminated examples of completed forms in the folder which you can use for guidance. Please try and write as clearly as possible and include as much info on each sighting as you can.

Basking shark sightings are recorded on the dedicated 'Basking Shark Recording Form'. Basking shark records should be made every 30 minutes by scanning the visible sea area offshore of the Gwennap Head watchpoint. Scanning should be undertaken with both binoculars and telescope to ensure coverage of the near- and far-fields. Please ensure you note down a 0 on the shark forms when you don't spot any sharks in your scan. If you see sharks outside of the 30 min scans please write the details of the sighting on the back on the shark form (remembering to include the time of the sighting).

All other marine wildlife (Harbour Porpoise, Bottlenose Dolphin, Common Dolphin, Risso's Dolphin, Minke Whale, Grey Seals and Sunfish are recorded on the 'Marine Wildlife Recording Form'.

Every record should include bearing, distance and direction of travel information. There are guidelines in the folder as to how to use a compass to get a bearing on a sighting.

Individual sightings of Basking Sharks, Ocean Sunfish, cetaceans and turtles are defined as those where individual animals are >100 m apart when first seen.

If you are SURE that the animals you are seeing are re-sightings (for example if you have followed the progress of a pod of cetaceans across the survey area and they were visible the whole time) – then note this on your form. Otherwise assume that sightings are separate and may be new animals.

On the rare occasions that you can follow an animal at the surface as it moves through the survey area, please try to give as much detail as possible on their movements; including bearing and distances at regular intervals (every few minutes if possible). Obviously if there are individual sharks at the surface for long periods (e.g. 30 mins or more) use your discretion as to how often you update their sightings record – in this instance every few minutes might be a bit excessive!

When assessing distance of animals, use the Runnelstone buoy as a marker. This is located about 1.5 km south of the watchpoint. Direction should be recorded using a compass (see guidelines).

Please also check the Grey Seal haulout at 30 minute intervals to count the number of seals hauled out on the rocks or in the surrounding water (this is located on the headland ~500 m NW of Gwennap Head and is visible from the watchpoint). Please note down 0 counts as well as positive counts – negative return data is just as important to us! This data goes on the marine wildlife recording forms.

Remember that we are specifically studying how marine animals interact with the Runnelstone reef and the associated tidal front, so add as much detail as you can about what you see in this area. There is a laminated bathymetry map in the folder, which shows that the reef extends NE-SW either side of the Runnelstone buoy, and the margin is often visible as a patch of disturbed water.

Additional observations, including human interactions, should be recorded on the reverse side of the record forms. Assuming the forms are in a weatherproof clipboard, fold them in half away from you and write on the reverse side (this avoids having to remove the forms from the clipboard).

Weather Recording

Wind direction

Provide a rough direction and compass bearing for the direction in which the wind is blowing from, e.g. SW 225°.

Wind strength

Use the Beaufort force values as follows (onshore indicators provided for guidance):

0 = Calm (smoke rises vertically)

1 = Very light breeze (wind motion visible in smoke)

2 = Light breeze (wind felt on exposed skin, leaves rustle)

3 = Gentle breeze (leaves and smaller twigs in constant motion)

4 = Moderate breeze (dust and loose paper raised, small branches begin to move)

5 = Fresh breeze (smaller trees sway)

6 = Strong breeze (large branches in motion, umbrella use difficult)

7 = Near gale (whole trees in motion, effort needed to walk into wind)

8 = Gale (twigs broken from trees, cars veer on road)

9 = Strong gale (light structural damage)

10 = Storm (trees uprooted, considerable structural damage)

Sea state (roughly equivalent to Beaufort scale):

0 = Flat sea, like a mirror

1 = Ripples without crests

2 = Small wavelets with glassy crests, not breaking

3 = Large wavelets, crests begin to break, scattered whitecaps

4 = Small waves becoming longer with frequent whitecaps

5 = Moderate height, longer waves with some foam and spray

6 = Large waves with foam crests and some spray

7 = Sea heaps up and foam begins to streak

8 = Moderately high waves with breaking crests forming spindrift, streaks of foam

9 = High waves with dense foam, wave crests start to roll over, considerable spray

10 = Very high waves, sea surface white with considerable tumbling, reduced visibility

Cloud cover

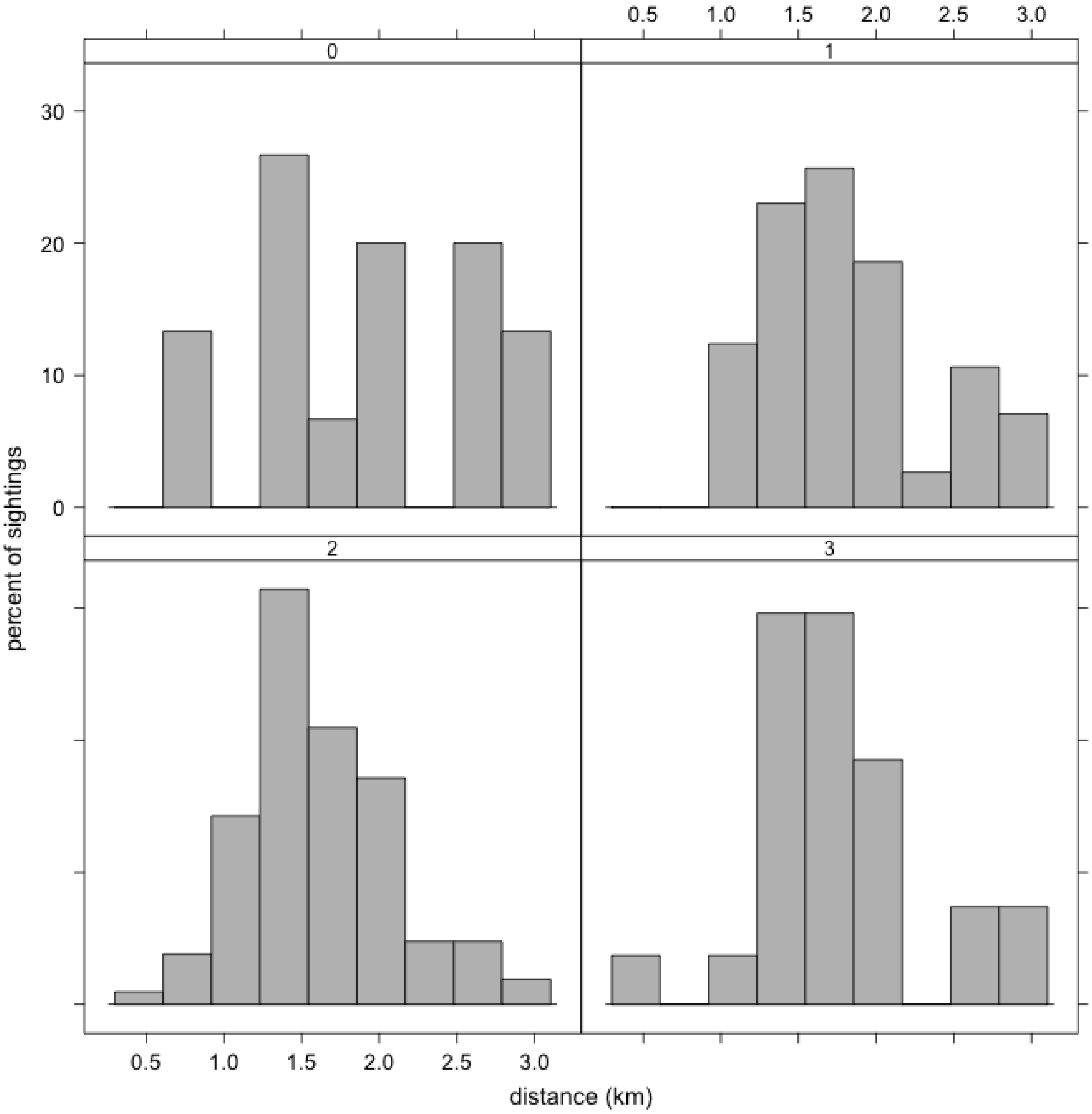
Give approximate percentage value to nearest 10%, i.e. clear sky = 0% and full cloud cover = 100%.

Glare (used to define how sea surface in front of observer is affected by reflected sunlight)

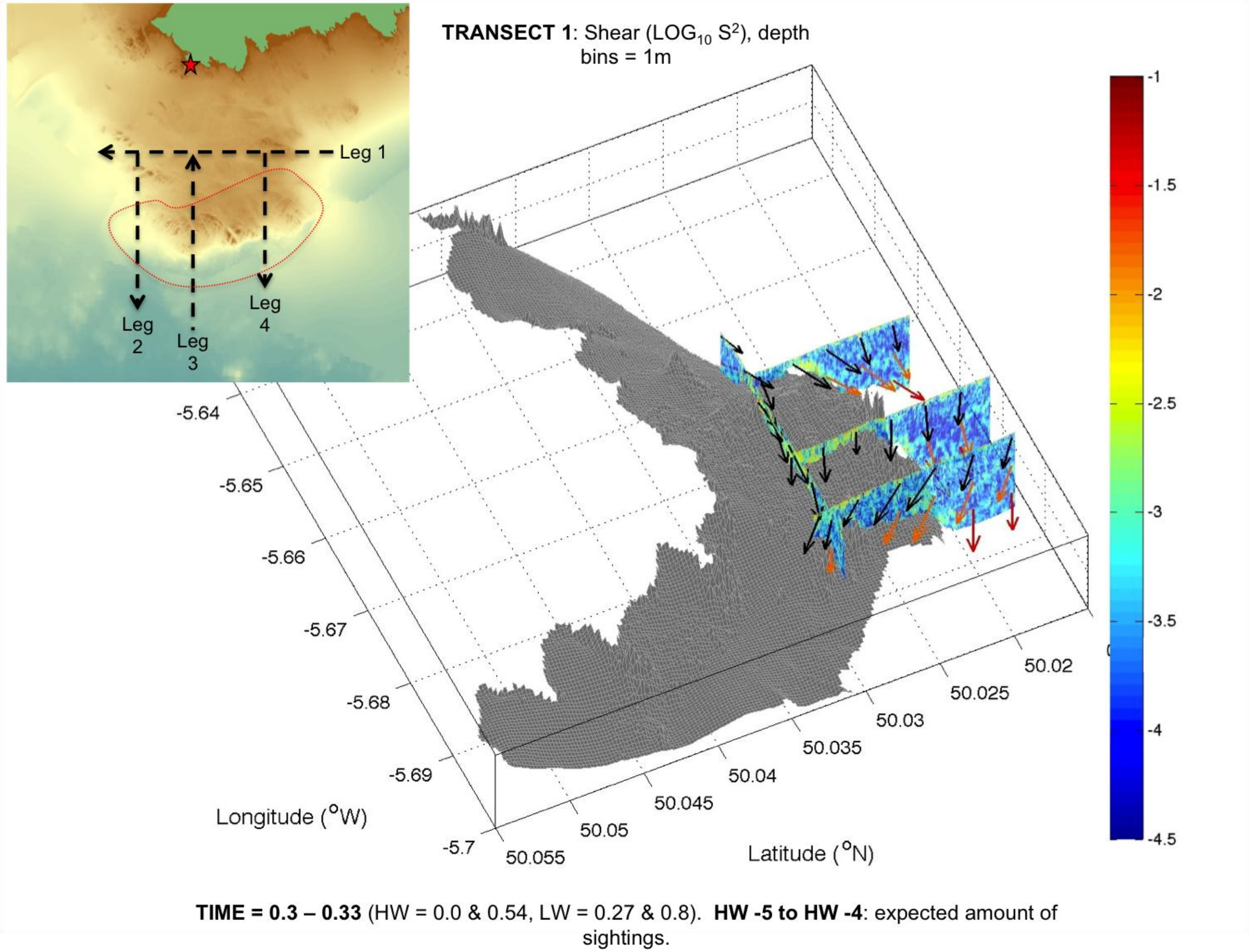
Give approximate percentage value to nearest 10%, i.e. no glare = 0% and full glare = 100%.

Visibility (furthest distance at which sea is visible, in km)

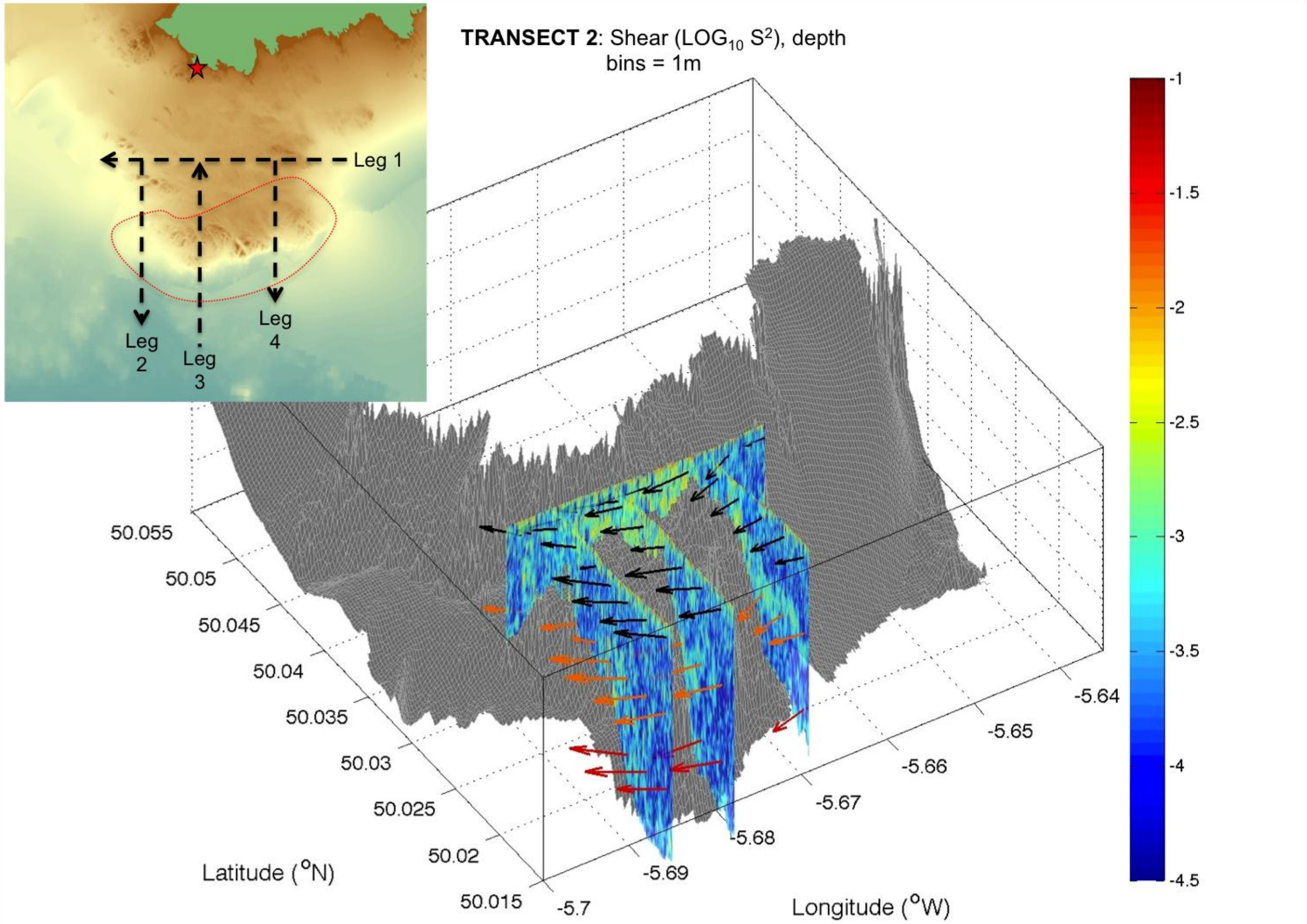
Use the Runnel Stone buoy as a marker, which is located about 1.5 km south of the watchpoint. If the Wolf Rock lighthouse is clearly visible then visibility is >15 km.



Appendix figure 1: Distribution of estimated distances to sightings of harbour porpoises under sea states 0 - 3. Data from the SWSW survey 2007 - 2010.



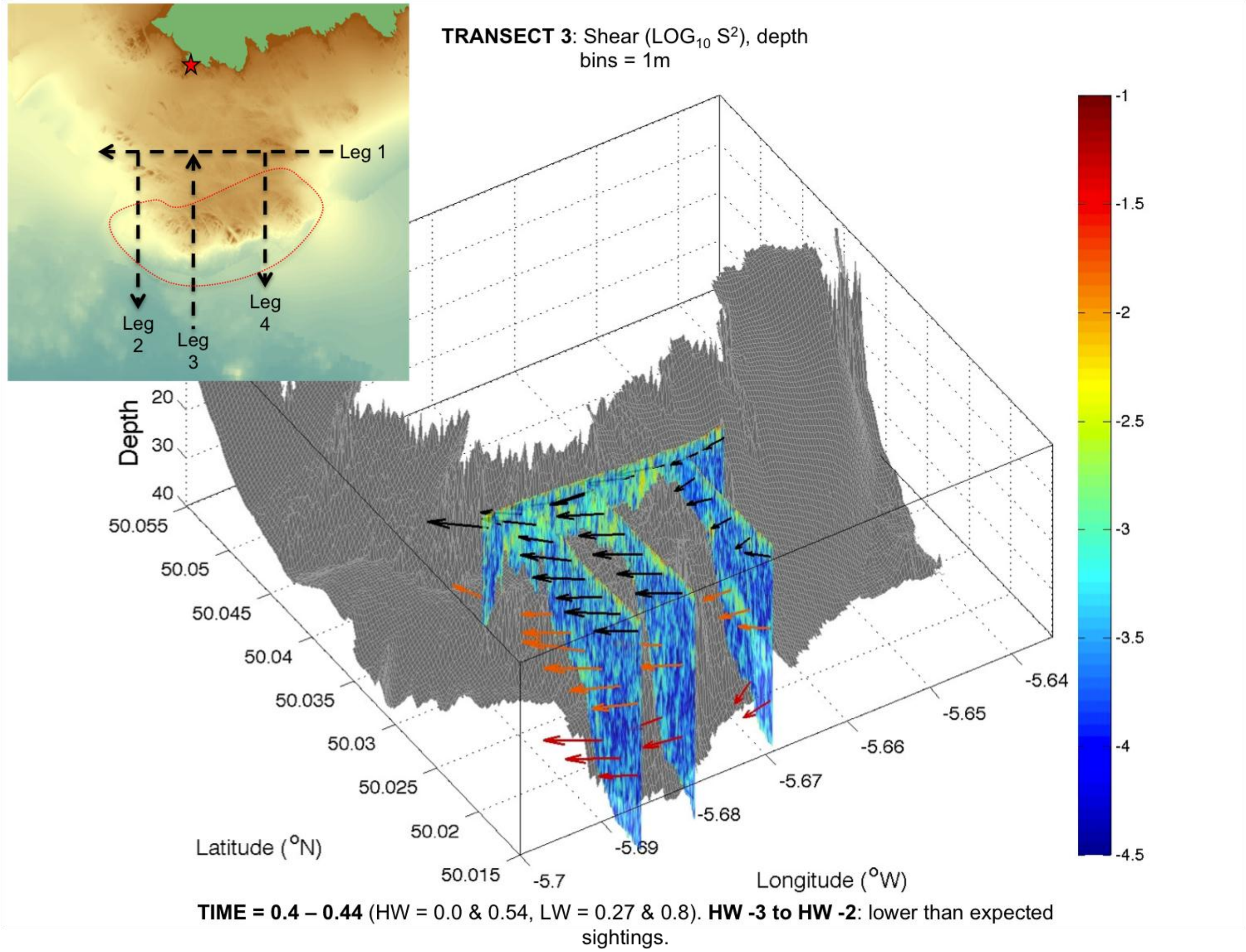
Appendix figure 2: Shear computed over 1-m vertical intervals for the first transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.



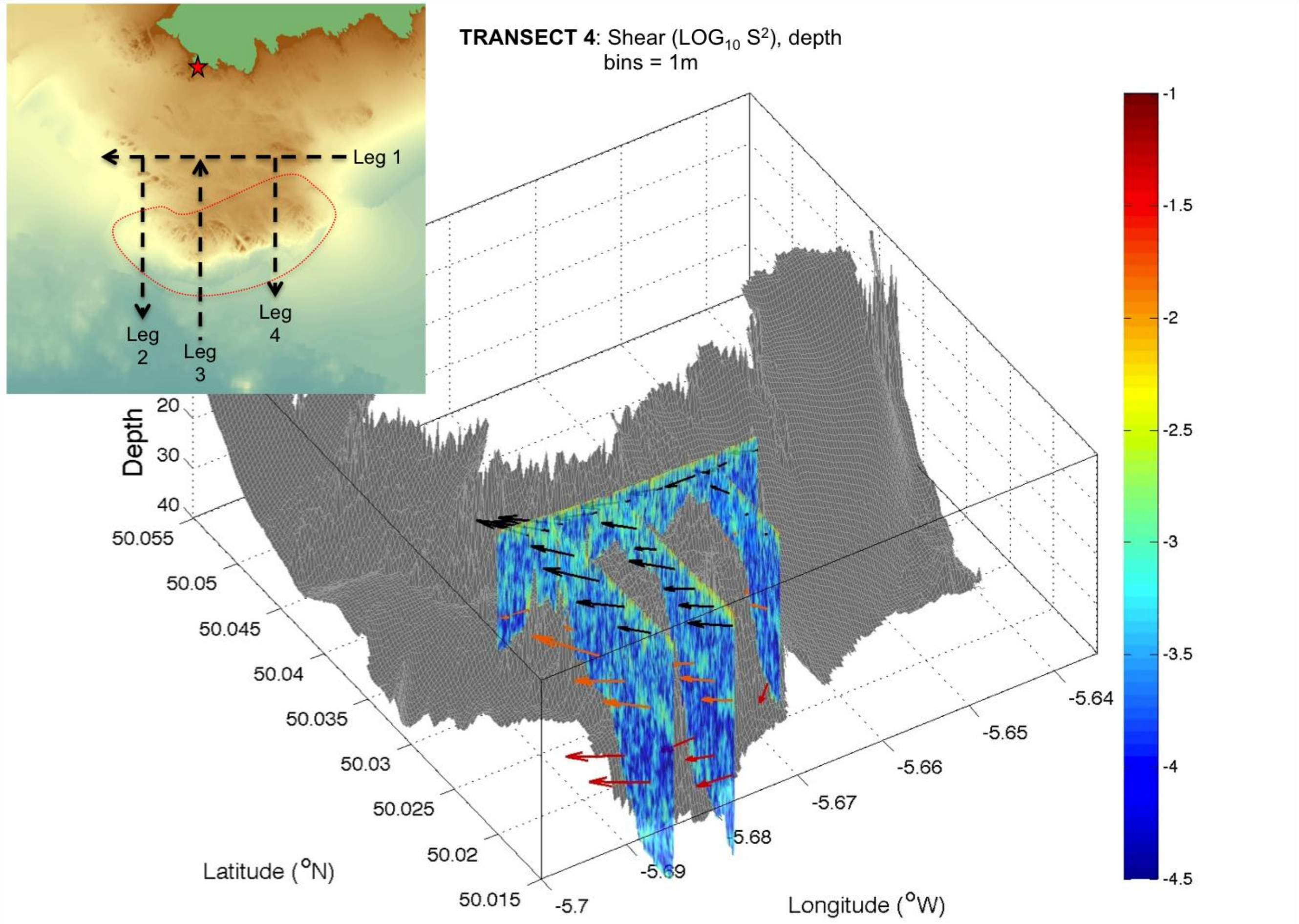
TRANSECT 2: Shear (LOG_{10} S^2), depth bins = 1m

TIME = 0.34 – 0.39 (HW = 0.0 & 0.54, LW = 0.27 & 0.8). **HW -4 to HW -3**: expected amount of sightings.

Appendix figure 3: Shear computed over 1-m vertical intervals for the second transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.

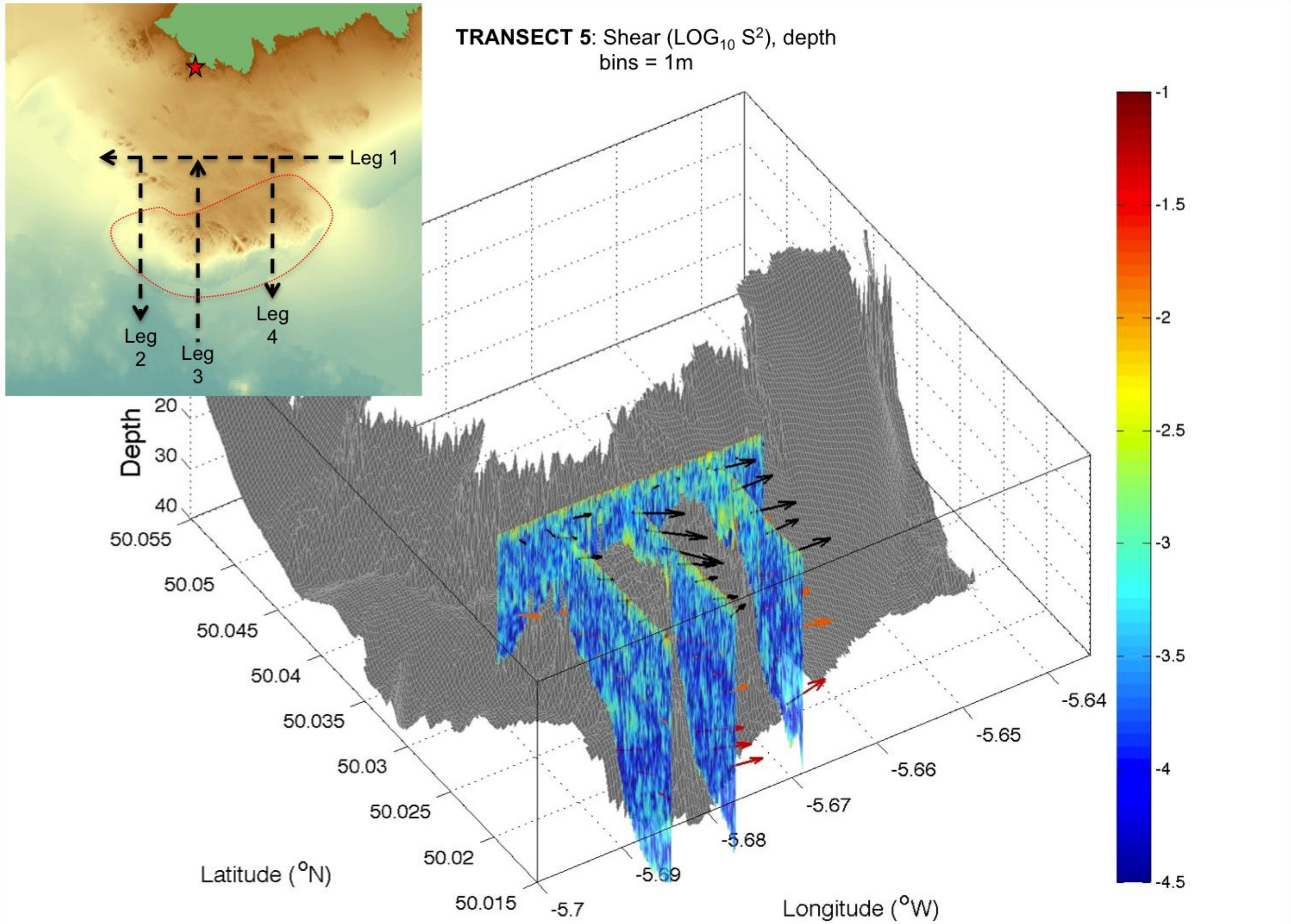


Appendix figure 4: Shear computed over 1-m intervals for the third transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.


TRANSECT 4: Shear (LOG_{10} S^2), depth bins = 1m

TIME = 0.45 – 0.5 (HW = 0.0 & 0.54, LW = 0.27 & 0.8). **HW -2 to HW -1**: lower than expected sightings.

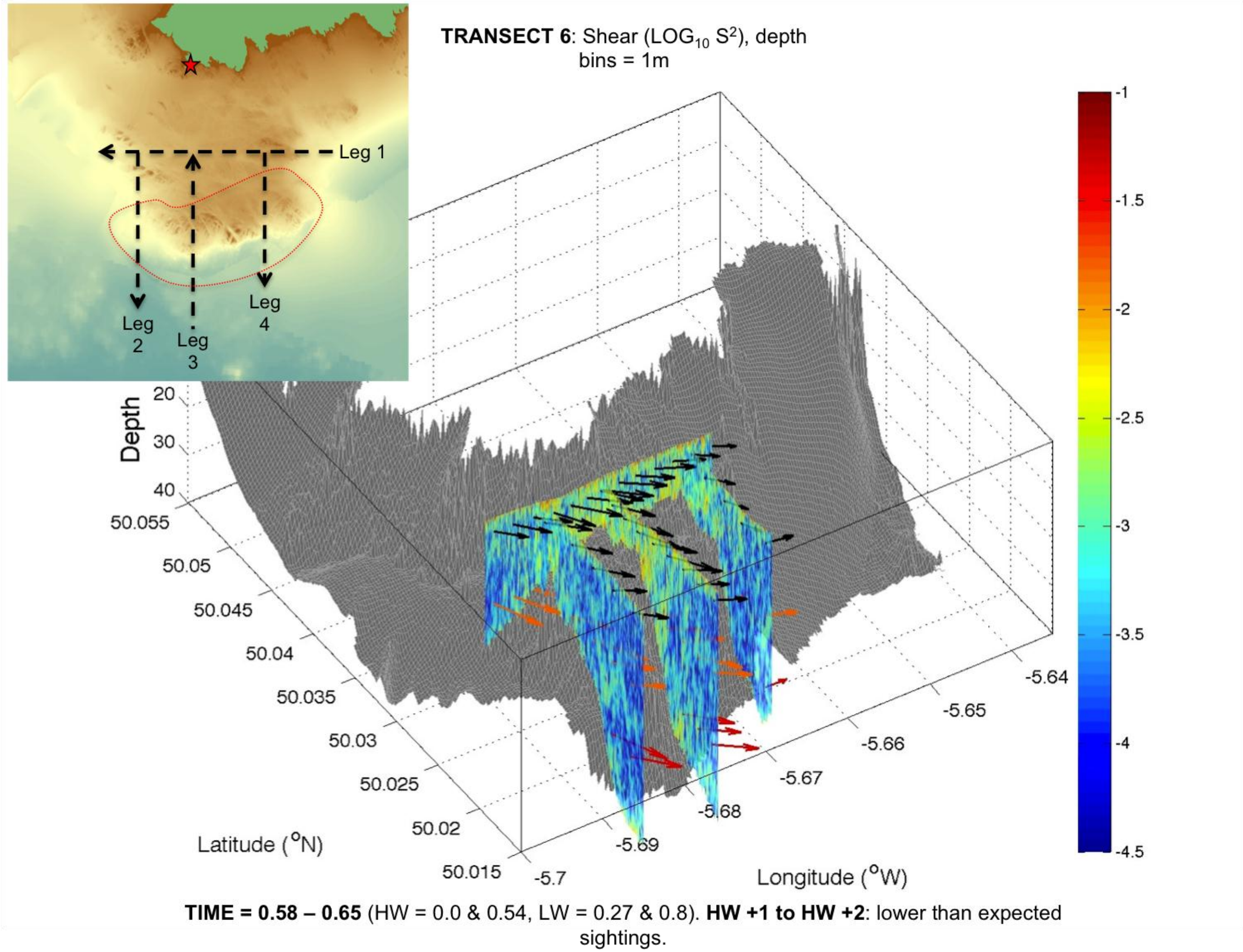
Appendix figure 5: Shear computed over 1-m vertical bins for the fourth transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.



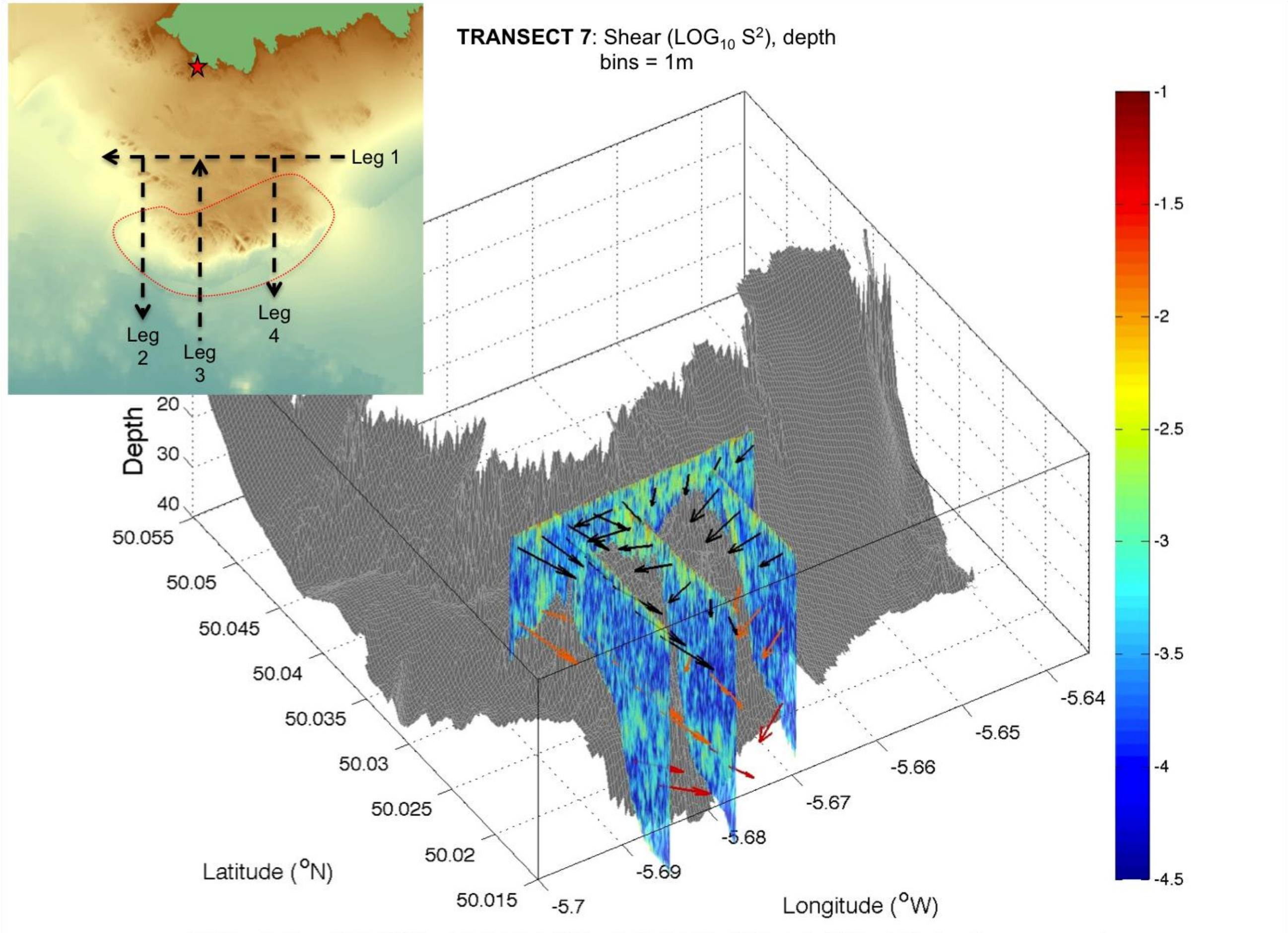
TRANSECT 5: Shear (LOG_{10} S^2), depth bins = 1m

TIME = 0.51 – 0.57 (HW = 0.0 & 0.54, LW = 0.27 & 0.8). **HW -1 to HW**: lower than expected sightings.

Appendix figure 6: Shear computed over 1-m depth intervals for the fifth transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.

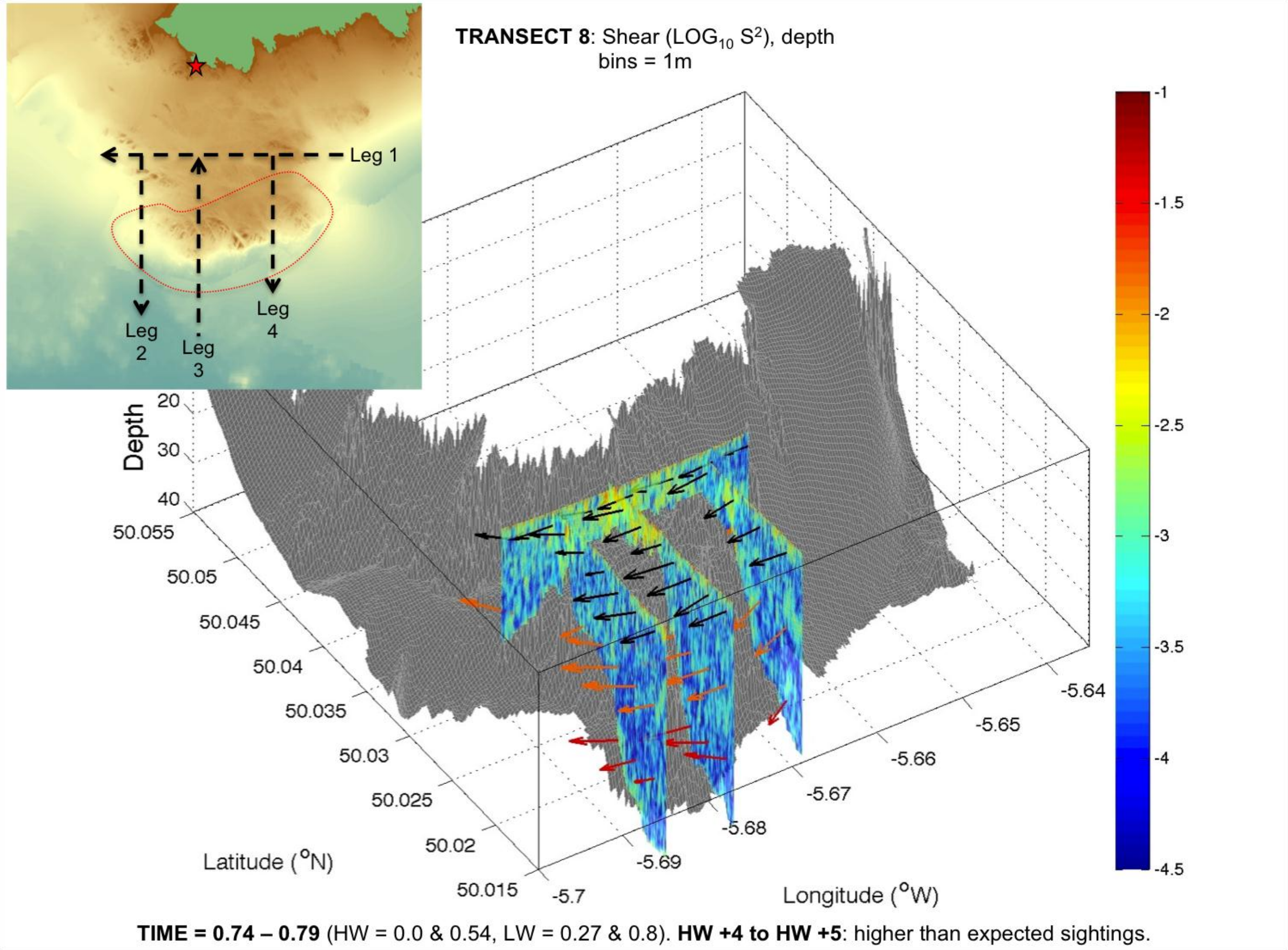


Appendix figure 7: Shear computed over 1-m vertical intervals for the sixth transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.

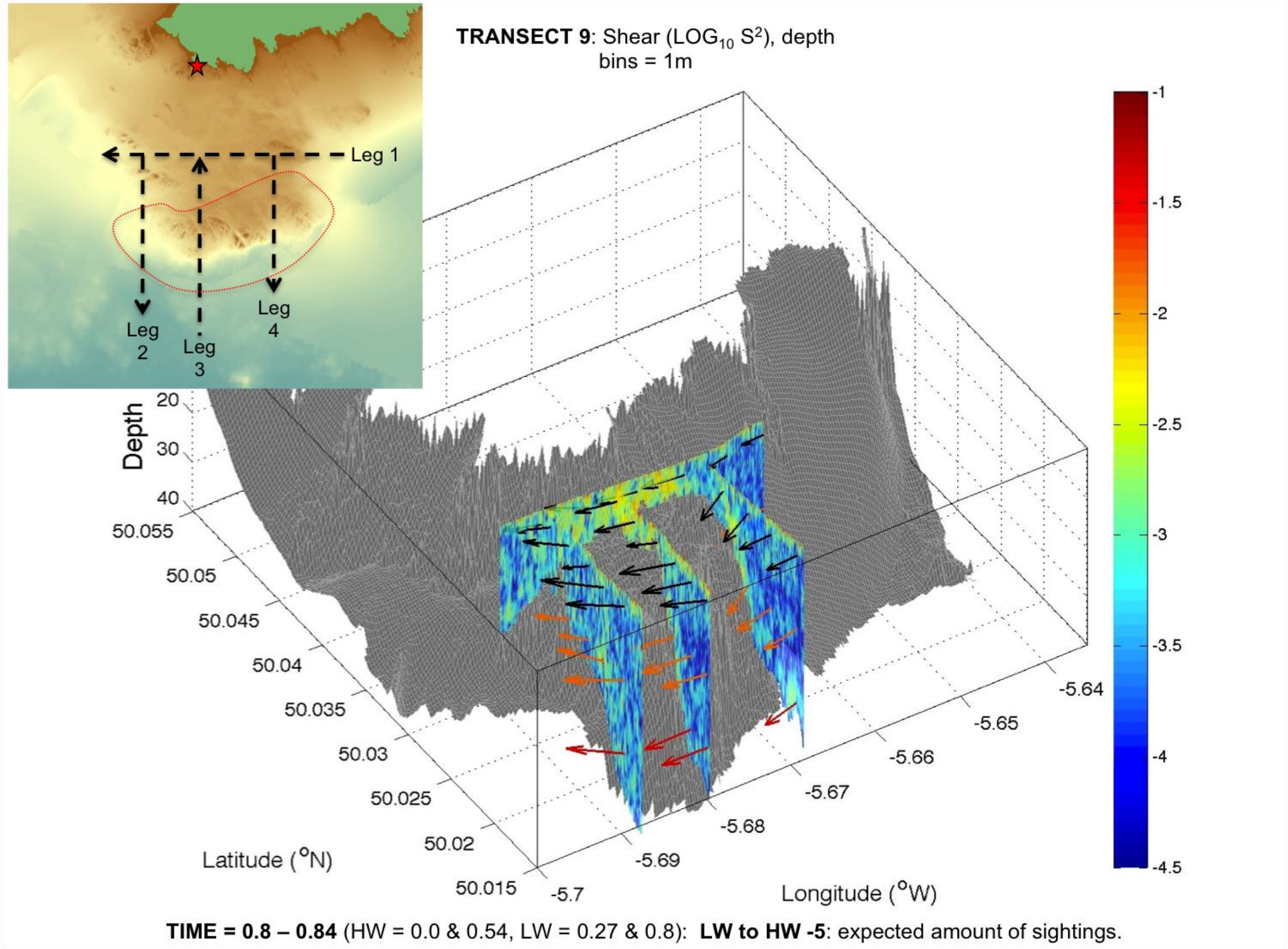

TRANSECT 7: Shear (LOG_{10} S^2), depth bins = 1m

TIME = 0.66 – 0.73 (HW = 0.0 & 0.54, LW = 0.27 & 0.8). **HW +3 to HW +4**: higher than expected sightings.

Appendix figure 8: Shear computed over 1-m vertical intervals for the seventh transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.



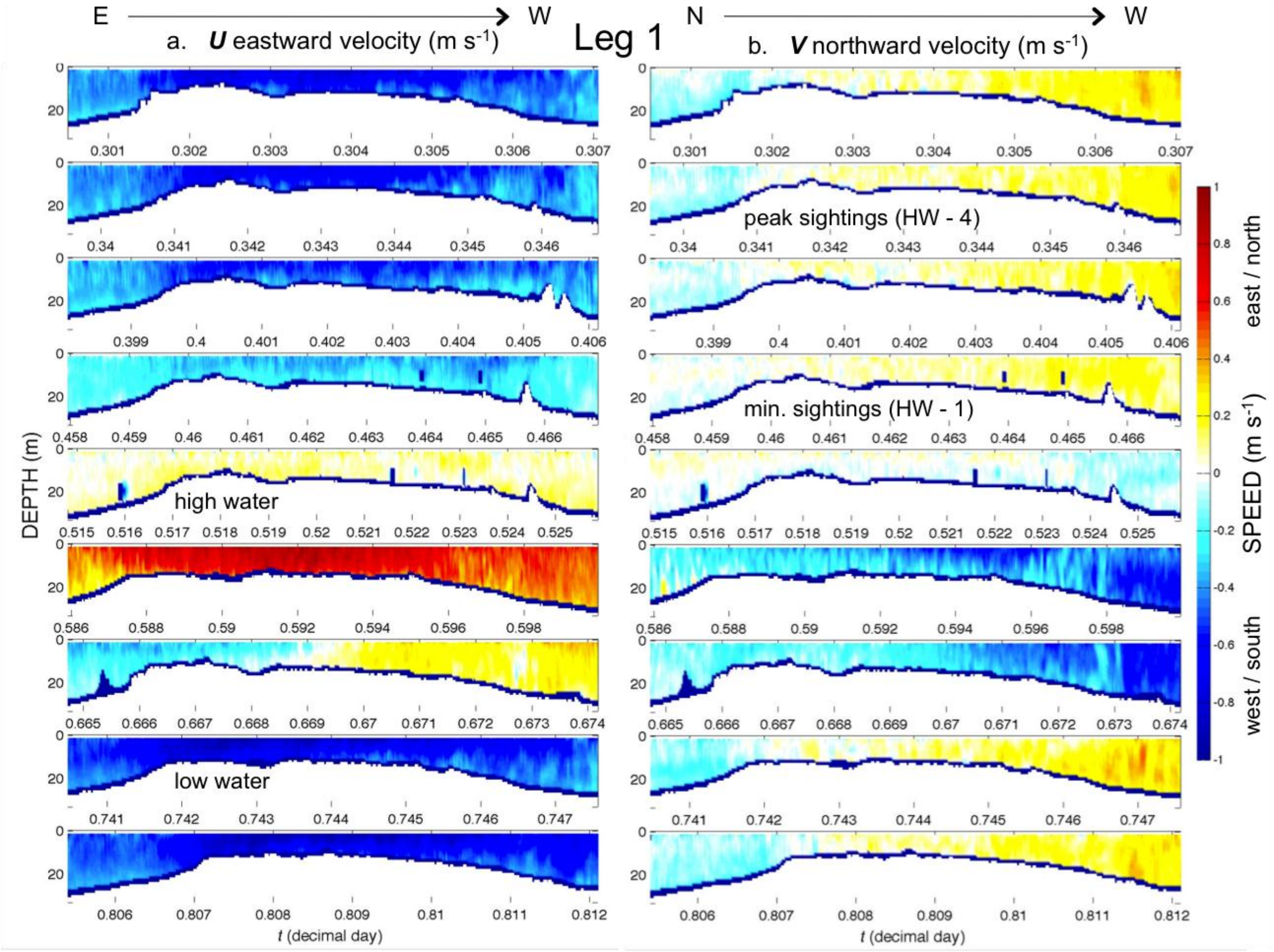
Appendix figure 9: Shear computed over 1-m vertical intervals for the eighth transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.



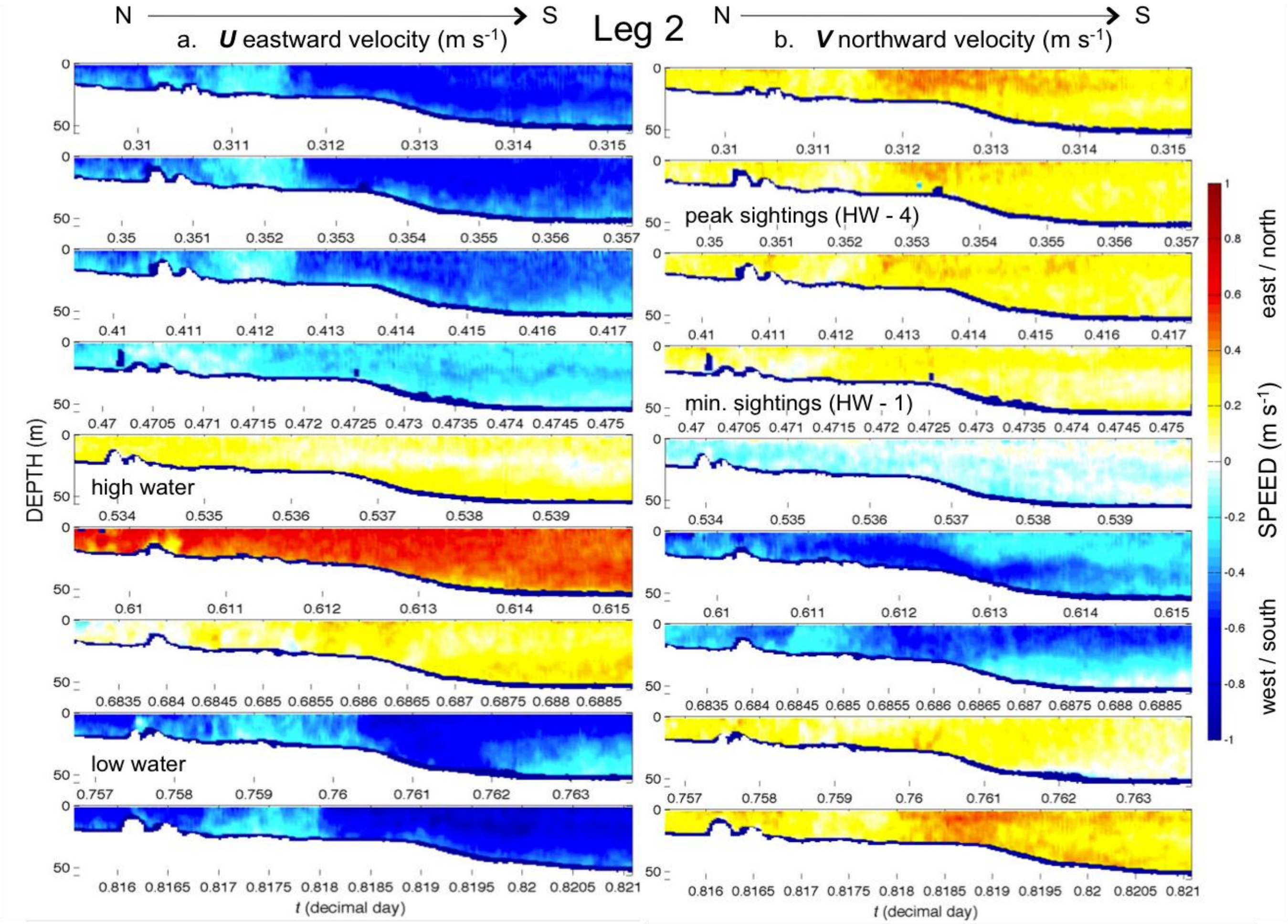
TRANSECT 9: Shear (LOG_{10} S^2), depth bins = 1m

TIME = 0.8 – 0.84 (HW = 0.0 & 0.54, LW = 0.27 & 0.8): **LW to HW -5**: expected amount of sightings.

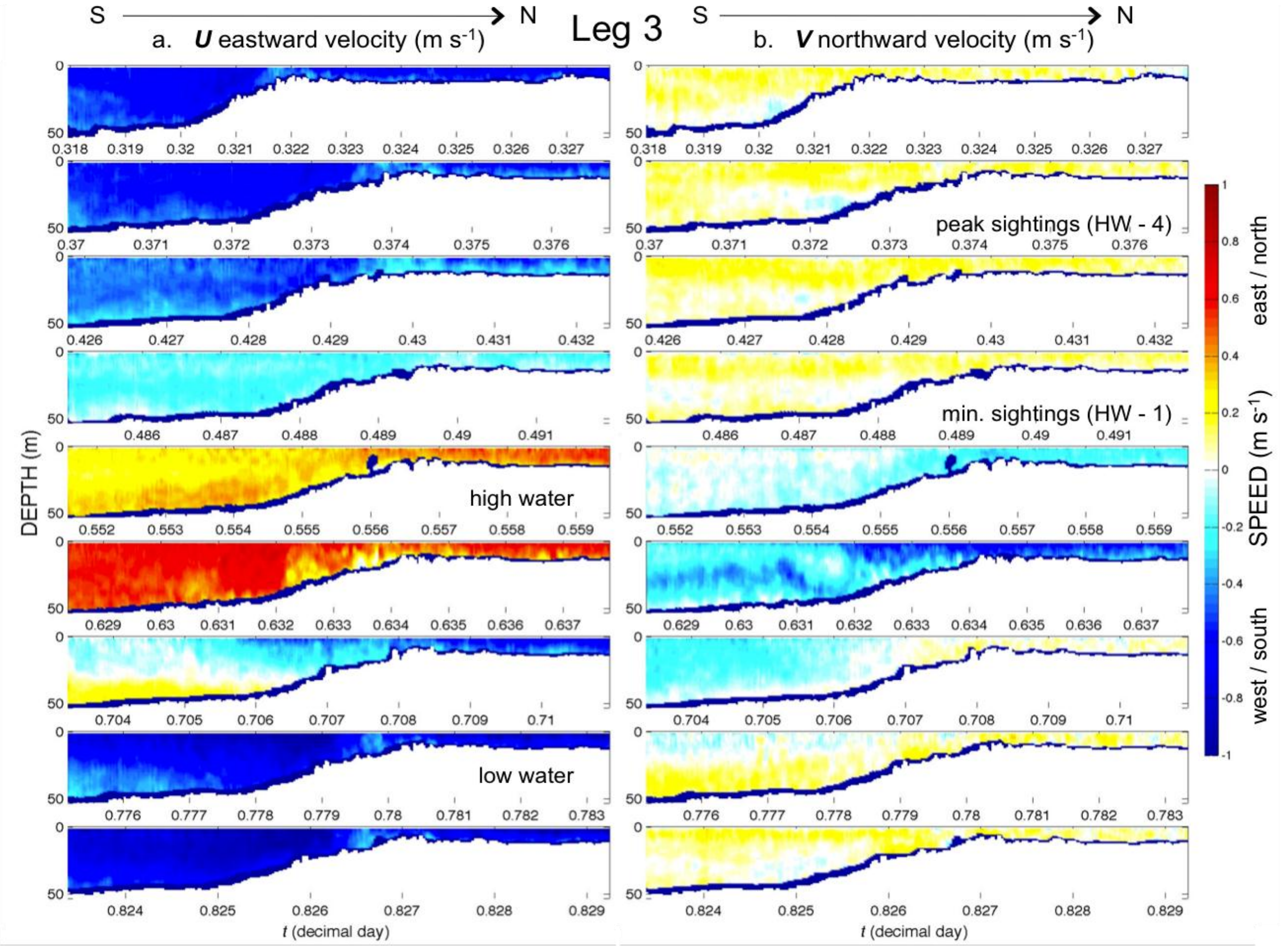
Appendix figure 10: Shear computed over 1-m vertical intervals for the ninth transect run. Units are $\log_{10} S^2$, velocity vectors (indicated by arrows) are plotted at 90-sec intervals along each leg at depths of 5 (yellow), 15 (orange) and 30 m (red). Current profile data were collected as 2-second ensembles in 1- m depth bins from a hull mounted ADCP on the RV Callista. Insert identifies transect line location with reference to the 50 % UD of the visual porpoise sightings. Data processed by Dr. P. Hosegood, Plymouth Uni.



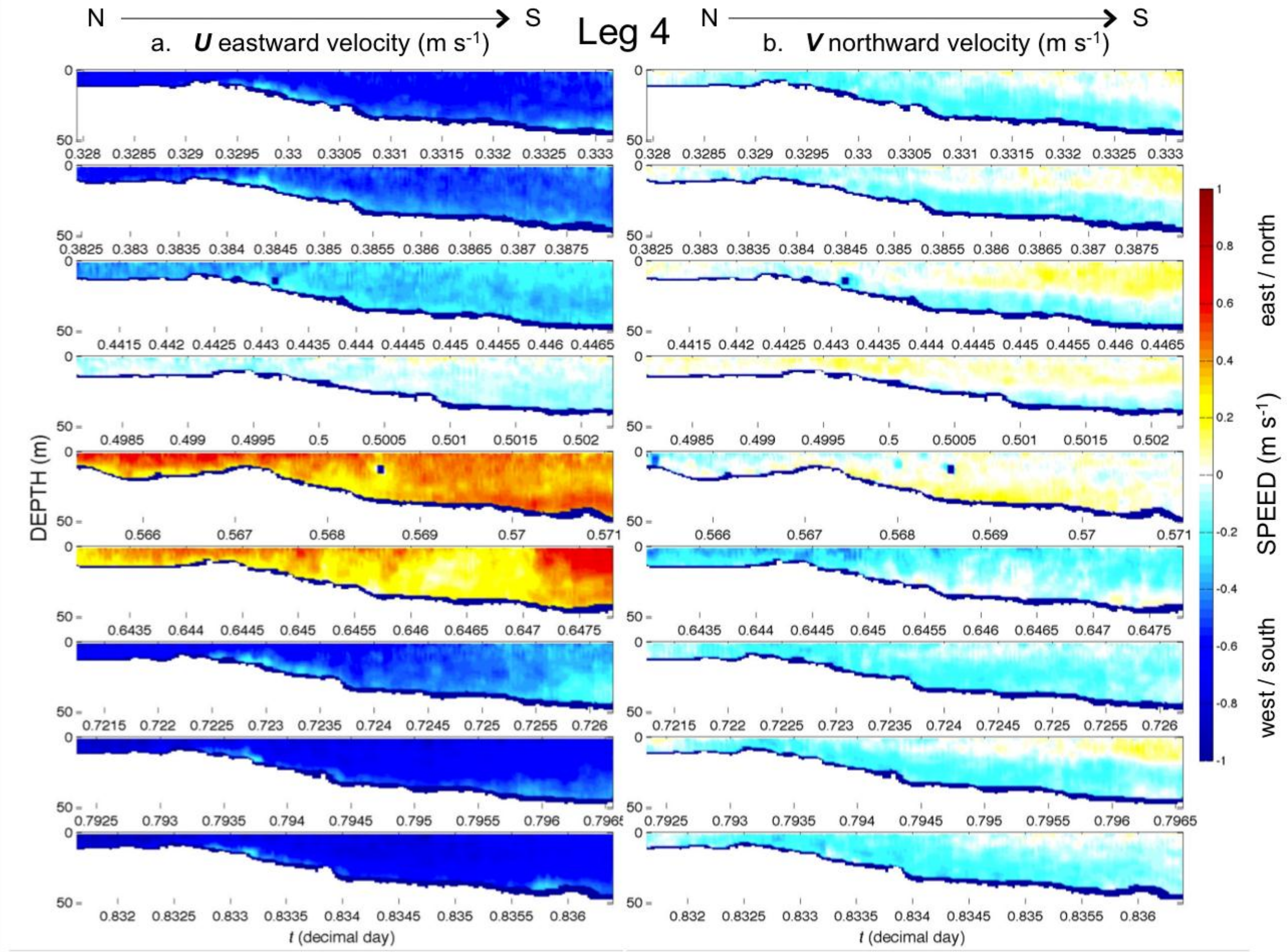
Appendix figure 11: Current velocity profiles from leg 1 (travelling east to west) of the ADCP survey of the SWSW survey area carried out 11th July from the RV Callista. Data are from a full tidal cycle. Decimal time relative to HW (0 and 0.5) is given along the x axes and water depth along the y axes. Current velocity is colour scaled with a) the eastward velocity component scaled from east in red to west in dark blue and b) the northward velocity component, colour scaled from north in red to south in dark blue. ADCP data processed by Dr. P. Hosegood, Plymouth University.



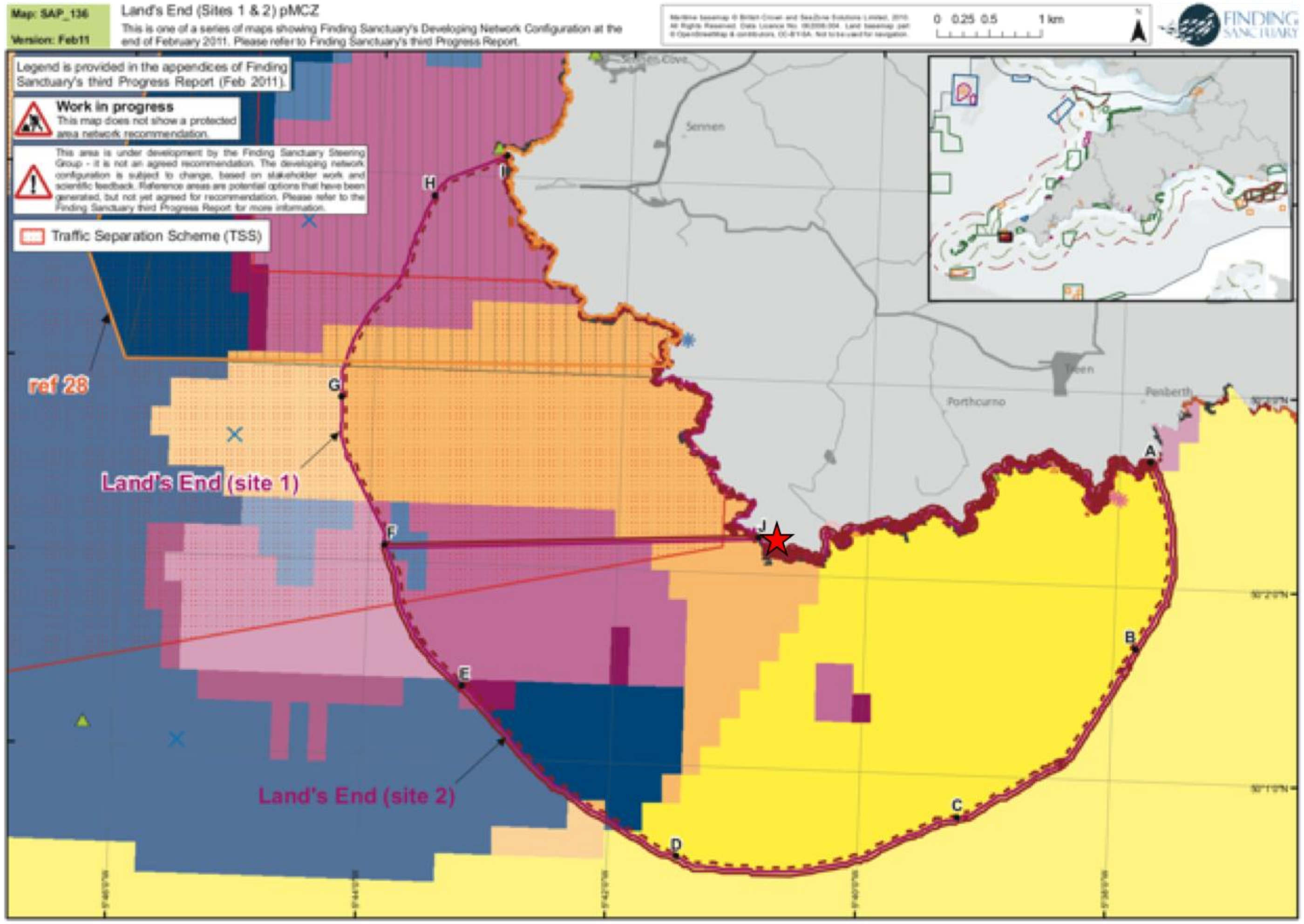
Appendix figure 12: Current velocity profiles from leg 2 (travelling north to south) of the ADCP survey of the SWSW survey area carried out 11th July from the RV Callista. Data are from a full tidal cycle. Decimal time relative to HW (0 and 0.5) is given along the x axes and water depth along the y axes. Current velocity is colour scaled with a) he eastward velocity component scaled from east in red to west in dark blue and b) the northward velocity component, colour scaled from north in red to south in dark blue. ADCP data processed by Dr. P. Hosegood, Plymouth University.



Appendix figure 13: Current velocity profiles from leg 3 (travelling south to north) of the ADCP survey of the SWSW survey area carried out 11th July from the RV Callista. Data are from a full tidal cycle. Decimal time relative to HW (0 and 0.5) is given along the x axes and water depth along the y axes. Current velocity is colour scaled with a) he eastward velocity component scaled from east in red to west in dark blue and b) the northward velocity component, colour scaled from north in red to south in dark blue. ADCP data processed by Dr. P. Hosegood, Plymouth University.



Appendix figure 14: Current velocity profiles from leg 4 (travelling north to south) of the ADCP survey of the SWSW survey area carried out 11th July from the RV Callista. Data are from a full tidal cycle. Decimal time relative to HW (0 and 0.5) is given along the x axes and water depth along the y axes. Current velocity is colour scaled with a) he eastward velocity component scaled from east in red to west in dark blue and b) the northward velocity component, colour scaled from north in red to south in dark blue. ADCP data processed by Dr. P. Hosegood, Plymouth University.



Appendix figure 15: Map of the proposed Land's End MPZ (Leiberknecht et al., 2011). There are two proposed areas, site 1 being larger than site 2 and extending around Land's End to Sennen in the northwest. The position of the SWSW watchpoint is marked by a red star.

ELECTRONIC SUPPLEMENTARY MATERIAL (ESM)

METHODS

ESM 1: Collation of opportunistic sightings reported from the UK and Ireland

From January 2007, regular appeals were made in the ornithological media for seabird observers to submit sightings of Balearic Shearwaters for addition to the UK and Irish national database, held by *SeaWatch SW*. Sightings were submitted (1) by email directly to the *SeaWatch SW* co-ordinator, (2) through the *SeaWatch SW* website (www.seawatch-sw.org), or (3) via *Birdguides* (www.birdguides.com) for inclusion in their Bird News Extra database. Additionally, efforts were made to seek out sightings from other sources such as *Trektellen*. Anomalous records were verified with the relevant county recorder or an experienced local observer; those that could not be verified were removed from the dataset. Records from each site were assigned geographical co-ordinates using the sites database on the *Birdguides* website (http://www.birdguides.com/sites/default.asp).

ESM 2: *Marinelife* boat-based visual monitoring surveys

European Seabirds At Sea (ESAS) survey methods

Birds on the sea were counted in different distance bands in a 300-m box located ahead and on one side of the vessel. Birds on the water were assigned to one of four transect bands (A= <50 m, B= 51-100m, C= 101-200 m, D= 201-300 m), according to their perpendicular distance from the ship's track. A snapshot technique was used to sample flying birds to minimise the biases of the movement of flying birds relative to the movement of the ship. Snapshot counts were made at ten-minute intervals in an arc scanning 180° ahead. Details on behaviour, age and moult of seabirds were recorded. Seabirds associating with fishing vessels were also counted, and noted as such.

During small boat surveys, behaviour at point of first observation was noted. Categories were as follows: (1) Flying - passing through, (2) Flying - responsive movement towards the boat, (3) Natural feeding - including seen in flight circling an area, (4) Scavenge feeding around fishing boats (including flying around the boat), and/or (5) Resting on the water. Subsequent behaviour (if different) for the duration of the sighting was also recorded, into one or more of the following categories: (6) Flying - passing through, (7) Flying - responsive movement towards the boat, (8) Natural feeding - including seen in flight circling an area, (9) Scavenge feeding around fishing boats (including flying around the boat), and/or (10) Resting on the water.

Marinelife citizen-science project

The casual sightings data recorded by *Marinelife* through the postcard and online reporting initiative were validated, in the majority of instances, by contacting recorders to ensure correct identification from non-specialist recorders, including from photographic evidence. Few misidentifications were apparent through this process. The results of this project are presented later in the supplementary material (ESM 6).

ESM 3: *SeaWatch SW* effort-based visual monitoring for Balearic Shearwater

Field data collection methods

Unless there were extreme weather conditions (e.g. winds >80 km/hr from a southerly aspect, which occurred very rarely over the four-year survey period), observations began no more than 40 minutes after sunrise and finished no more than 40 minutes before sunset, with a break between 1200 and 1400 hrs for logistical reasons (to prevent observer fatigue and to avoid the period of peak glare). There were 29 individual seabird observers involved in the project across the four-year period and many of these returned for multiple years of the survey. The number of observers per year was 14 in 2007, 11 in 2008, 13 in 2009 and 12 in 2010. Data were collected in the field on pre-printed forms and later transposed to a digital database.

Table S1: Summary of Balearic Shearwater sightings and hours of effort in the *SeaWatch SW* effort-based monitoring survey at Gwennap Head from 15 July to 15 Oct (2007-2010). Total sightings and effort are given before and after filtering (as described in the Methods).

	2007	2008	2009	2010	Total
Total number of sightings recorded	1267	932	1293	2831	6323
Number of sightings in final dataset after filtering	1163	837	1111	2315	5394
Number of hour/part hours observed	1028	992	985	1017	4022
Number of full hours in final dataset (after filtering)	829	824	821	850	3324
Full hours observed by time of day (after filtering)					
0600 - 0700	31	30	26	28	115
0700 - 0800	68	59	63	69	259
0800 - 0900	82	80	77	86	325
0900 - 1000	78	84	78	83	323
1000 - 1100	83	83	82	83	331
1100 - 1200	83	83	85	86	337
1400 - 1500	78	81	88	86	333
1500 - 1600	79	85	87	86	337
1600 - 1700	79	84	87	88	338
1700 - 1800	80	81	85	84	330
1800 - 1900	52	47	47	49	195
1900 - 2000	36	27	16	22	101

ESM 4: *SeaWatch SW* 'sister sites' data

All records of Balearic Shearwater from 'sister sites' include date, total number of birds seen per day, and amount of effort (hours) per day. Note that because 'sister sites' data are not collected in a systematic way, there may be biases introduced as a result of observers only attending the sites during conditions that are favourable for nearshore seabird passage, e.g. at certain times of day or in certain weather conditions. Consequently, BPH values from the 'sister sites' are likely to be elevated compared to those made during the continuous effort-based survey at Gwennap Head.

RESULTS

ESM 5: Effort corrected birds per hour (BPH) data for French sites

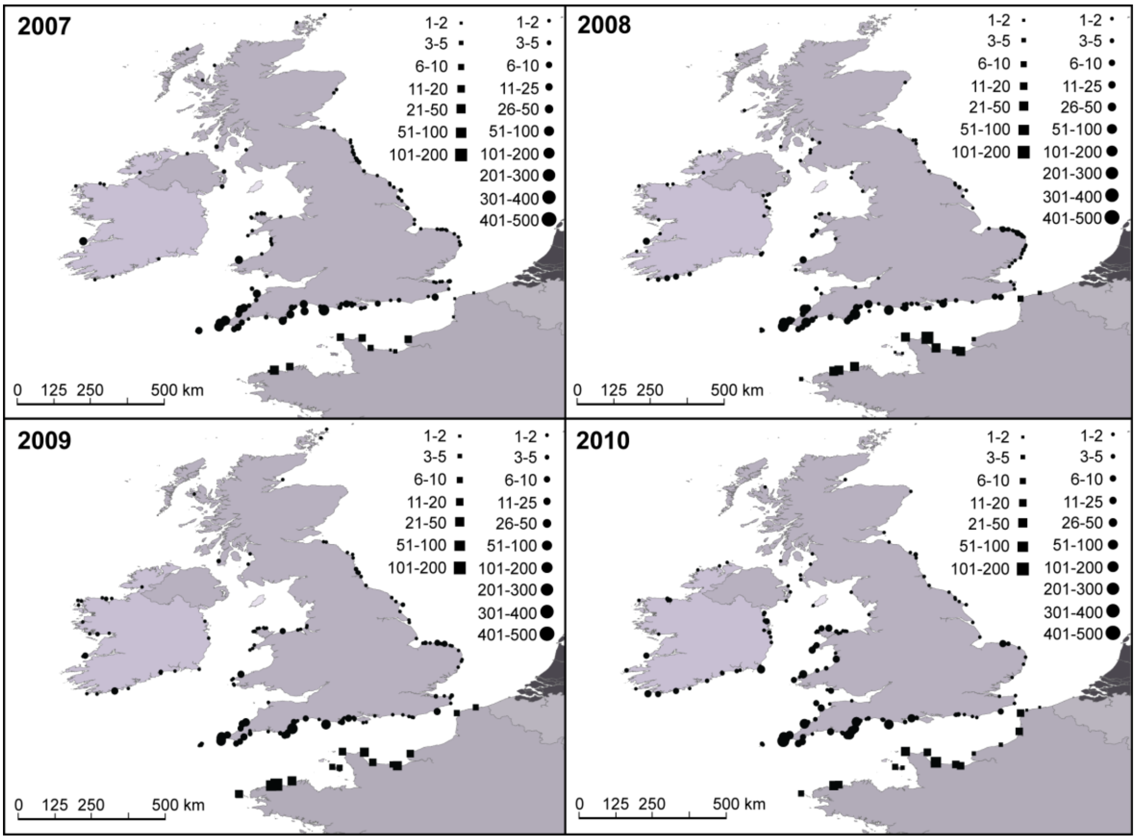


Figure S1: Annual peak day-counts of Balearic Shearwaters at individual sites in UK and Ireland, and effort-corrected birds per hour (BPH) data for northwest France (2007-2010). Data are from opportunistic sightings reported to the *SeaWatch SW* database (UK and Ireland) and *Trektellen* online database (France). Scaled black circles/squares indicate the size of count.

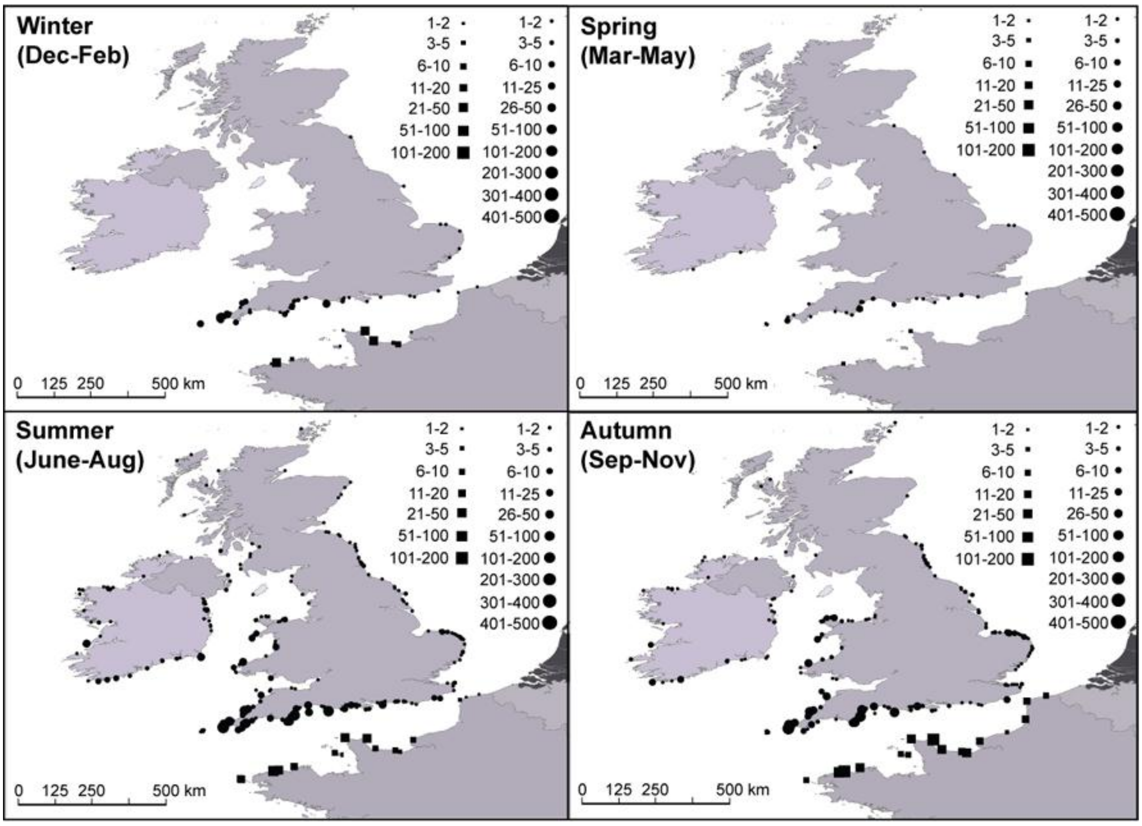


Figure S2: Seasonal peak day-counts of Balearic Shearwaters at individual sites in UK and Ireland, and effort-corrected birds per hour (BPH) data for northwest France (2007-2010). Data are from opportunistic sightings reported to the *SeaWatch SW* database (UK and Ireland) and *Trektellen* online database (France). Scaled black circles/squares indicate the size of count.

ESM 6: *Marinelife b*oat based visual monitoring surveys from the western Channel

Table S2: *Marinelife* at-sea records of Balearic Shearwater (2007-2010) by survey type. **Minimum estimate of days at sea by fishermen and skippers of dive, sea angling and pleasure boats (e.g. yachts) who supplied data to *Marinelife* and were thought to be regularly looking for birds on each trip.

Survey	Period	No. surveys	Km travelled	No. sightings	No. individuals
Effort-related ferry surveys					
Portsmouth - Bilbao	07 - 10	83	22190	9	12
Poole - Santander	08 - 10	66	21500	10	17
Plymouth - Roscoff	07 - 10	37	8201	14	43
Portsmouth - St Malo	2010	2	466	0	0
Poole - Cherbourg	07 - 10	4	NR	0	0
Portsmouth - Caen	07 - 10	3	417	0	0
Portsmouth - Le Havre	2010	1	NR	0	0
Dover - Boulogne	2010	1	3	0	0
Portsmouth - Fishbourne	2010	2	18	0	0
Weymouth - Guernsey	2010	2	102	0	0
Effort-related small boat surveys					
Volunteer surveys	07 - 10	97	9440	93	169
Lyme Bay winter survey	2009	10	1410	1	1
Western Channel summer survey	2009	18	3476	23	30
Targeted surveys	2010	14	2198	39	1125
Effort-related Totals	**07 - 10**	**240**	**68308**	**189**	**1397**
Casual (public) sightings	07 - 10	>500**		84	2085
Grand total	**07 - 10**			**351**	**3607**

Distribution and abundance from casual sightings

Casual boat-based sightings only included three double-figure observations, these being of 775 and 1120 birds in Bay of Lannion in August 2010, and 40 birds about 1.5 km off Dartmouth amongst a large (~400) raft of Manx Shearwaters (*Puffinus puffinus)* on 23 July 2010 (Fig. S3). There have been regular sightings of Balearic Shearwaters off Portland Bill in each year from 2007-2010 and this has proved the most reliable place to receive reports from skippers for this species off southwest England, especially during July on the Shambles Bank. 2007 appeared to be a good year off Portland, but fewer were seen from 2008-2010. In 2009 and 2010, anecdotal reports from local fishermen suggested that in the region of 10-25 birds were regularly present off Portland Bill over the summer period, chiefly scavenging around angling and fishing boats on the Shambles Bank and Portland Race or settled in small groups on the sea. Fewer birds (5-15) were thought to have been regularly present in the summers of 2008 and 2010.

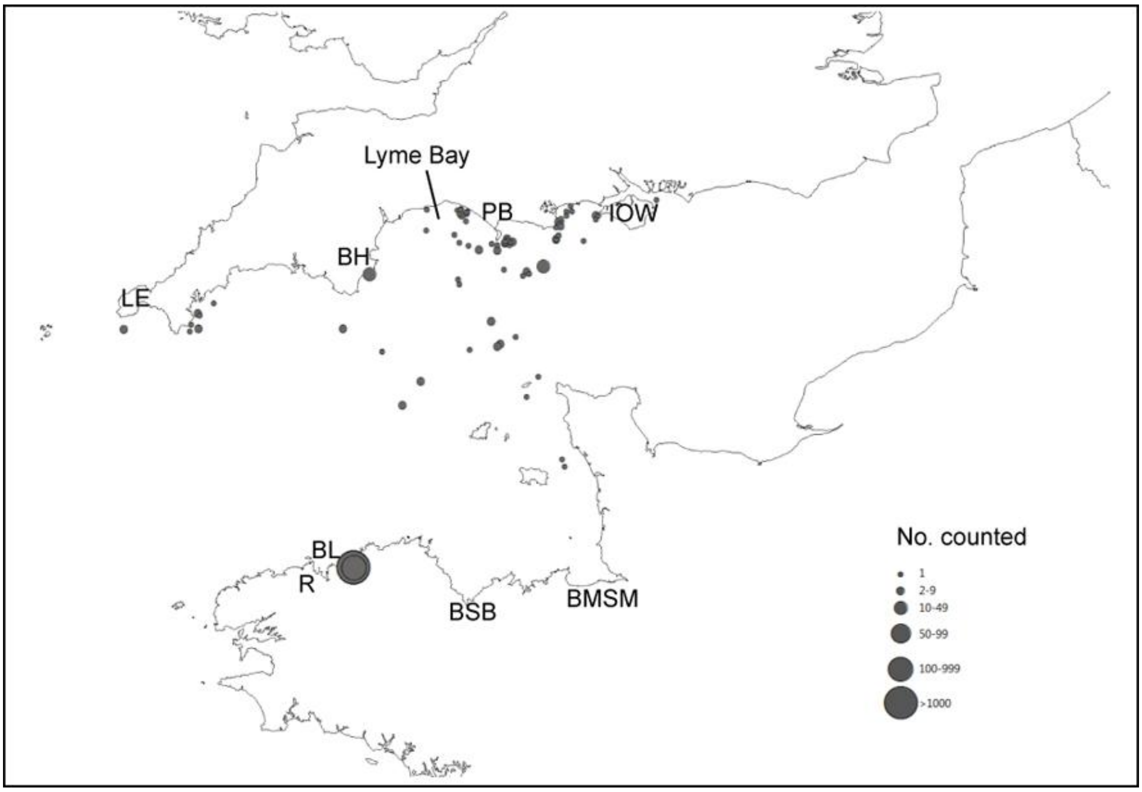


Figure S3: Distribution of all casual sightings (non effort-based) in the western Channel observed from vessels and reported to the *Marinelife* citizen-science project. The scale uses the following abundance categories (1 bird, 2-9, 110-49, 50-99, 100-999, >1000 birds).

The casual record of 40 birds off Dartmouth is of interest. From 2009-2010 a large and mobile feeding raft of Manx Shearwaters, which supported variable numbers of Balearic Shearwaters, was observed at times in the July/August period between Berry Head and Dartmouth. The potential local importance of this area is strengthened by anecdotal observations from Berry Head (Mark Darlaston, pers. comm.), with sporadic double-figure counts (maximum 12 on 2 July 2008) of Balearic Shearwaters following trawlers into Brixham suggesting local presence of feeding birds. Birds have also been seen here attending trawlers hauling their nets, with the maximum being eight on the 20th August 2008.

Additional notes on behaviour

Anecdotal records show that significant numbers of Balearic Shearwaters were recorded scavenging around commercial fishing boats (see above counts from Berry Head). Scavenging birds around angling and fishing boats were bold and tame at times and swam within a few metres of boats, highlighting their potential vulnerability to bycatch. Whilst scavenging, there was no evidence to indicate that Balearic Shearwaters were being unduly harassed by large gull species or other seabirds. In addition to scavenging behaviour, birds were also seen diving for fish around these boats, though encounters did not identify which prey species the birds were feeding on.

The most frequently recorded species seen in association with self-foraging Balearic Shearwaters include auks, terns, Manx Shearwater and Northern Gannet (*Morus bassanus)*. On the days when the highest numbers of self-foraging Balearic Shearwaters were observed at the Shambles Bank/Portland Bill and the Bay of Lannion, Brittany, there were anecdotal reports from local fishermen that large shoals of sandeels (*Ammodytes Sp.*) were present, indicating that this may be an important prey item in Channel waters. At Bay of Lannion on 28 August 2010, a feeding flock of 120 Balearic Shearwaters was observed close to the edge of the sandy beach on an ebbing tide in no more than 1.5 m of water. Several Sandwich Terns (*Sterna sandvicensis*) and Common Terns (*Sterna hirundo)* were present, which were also thought to be feeding on sandeels. At Shambles Bank/Portland Bill, anchovies (*Engraulis encrasicolus*) and sandeels have also been suggested (by local fishermen) as likely prey items. In western Lyme Bay, self-foraging birds have chiefly been seen in association with Manx Shearwaters, together with smaller numbers of Gannets, auks and Kittiwakes. Large rafts of Balearic Shearwaters in Bay of Lannion in August 2010 were seen to spend alternating periods of time self-foraging in flocks of up to 500 birds and resting on the sea, then dispersing in smaller flocks flying out to sea.

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PLoS one

Geolocators Reveal Migration and Pre-Breeding Behaviour of the Critically Endangered Balearic Shearwater *Puffinus mauretanicus*

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Abstract

Using combined miniature archival light and salt-water immersion loggers, we characterise the year-round individual at-sea movements of Europe's only critically endangered seabird, the Balearic shearwater *Puffinus mauretanicus*, for the first time. Focusing on the non-breeding period, we show that all of the 26 breeding birds tracked from their breeding site on Mallorca in the Mediterranean Sea successfully made a 2–4 month migration into the Atlantic Ocean, where they utilised well-defined core areas off Portuguese and French coasts. As well as identifying high-risk areas in the Atlantic, our results confirm that breeding birds spend most of the year concentrated around productive waters of the Iberian shelf in the western Mediterranean. Migration phenology appeared largely unrelated to the subsequent (distinctly synchronous) breeding attempt, suggesting that any carry-over effects were compensated for during a long pre-laying period spent over winter in the Mediterranean. Using the light and salt-water immersion data alone we were also able to characterise the pattern of pre-laying visits to the colony in considerable detail, demonstrating that breeding pairs appear to coordinate their over-day visits using a high frequency of night-time visits throughout the winter. Our study shows that geolocation technology is a valuable tool for assessing the spatial distribution of risks to this critically endangered species, and also provides a low-impact method for remotely observing the detailed behaviour of seabird species that may be sensitive to disturbance from traditional study methods.

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Introduction

Understanding the behaviour of migratory species that are endangered can be especially problematic because of their rarity and their sensitivity to disturbance, yet migration is a critical stage of their life history. A striking example is the Balearic shearwater *Puffinus mauretanicus*, a member of the highly pelagic Procellariiforms and currently Europe's only critically endangered seabird species [1]. The known breeding population comprises just ~3200 pairs [2], with models suggesting that adult survival at sea may be sufficiently low to precipitate extinction within a few generations [3]. Whilst recent studies have contributed valuable information on the species' life history and dietary requirements [4–7], remarkably little is known about its at-sea behaviour, especially the post-breeding migration from its breeding sites which are restricted to the Balearic islands in the western Mediterranean [2]. At-sea sightings suggest that birds migrate into the Atlantic in the late northern summer, occupying relatively shallow, coastal waters along northeast Atlantic coasts where they may both exploit, and become vulnerable to by-catch from, human fishing activity [8,9]. In addition to the inter-annual volatility of populations of prey fish, such as the small pelagic sardine [9], other factors such as longer-term climate change [10] and changes in discard availability [11] may influence the at-sea distribution of this species. In particular, there has been a large increase in numbers of birds recorded off northwest France and southwest UK since the mid-1990's [10,12–15], with recent aggregations off northwest Brittany holding as many as 6000 birds [16]. As with all such sightings, however, the provenance and age of birds forming these aggregations are unknown.

Here we report the first successful attempt, using miniature geolocation technology, to study directly the individual migratory movements of Balearic shearwaters of known provenance and breeding status across the entire annual cycle. We show that breeding birds from the species' largest known cave colony exhibit a consistent migration immediately post-breeding (no bird failed to migrate), concentrating in two areas off western Portugal and western France. None of the tracked breeding birds penetrated north of the Bay of Biscay in summer 2010, despite ~25% of the World population being concentrated off northwest France at this time. This implies colony- or age-specific migration strategies may be employed by this species. Furthermore, we demonstrate that data from geolocators can be used to characterise the migratory period rather precisely, and relate this to breeding phenology and success in a way that provides detailed behavioural information during breeding without disturbance to birds at the colony. In addition, by comparing this behaviour in the two birds within each nesting pair it is also possible to sex individuals uninvasively. We suggest that archival light-logging technology may offer a powerful tool for studying the behaviour of sensitive species with minimum disturbance.

Methods

Ethics Statement

All work was conducted in accordance with the appropriate Balearic Government (Servei de Protecció de Espècies) guidelines, and under permit numbers CAP31/2011 and CAP04/2010 from the Balearic Government (Servei de Protecció de Espècies).

The study was conducted at the largest extant breeding colony of Balearic shearwaters currently known, Sa Cella cave on the northwest coast of Mallorca, where a subset of nesting sites, usually scrapes on sediment surfaces or under protected shelves, have been numbered and monitored for some years [6,17] allowing us to utilise pairs of ringed birds of known established breeding success. To reduce impact, visits to nesting areas of the cave were minimized, and conducted using only dim red light or a night-vision scope. Birds were captured on the nest by hand and placed into cloth bags for weighing, carriage and handling. Instrument deployment and downloading or removal took place in dim light close to the cave entrance. BAS Mk15 geolocators weighing 2.4 g were attached to 17 breeding pairs (34 individuals) by two small cable ties to a hand-fashioned Darvik ring custom-sized to an incubating bird's leg during early April 2010. Correction fluid was used to mark temporarily the head and back after deployment to enable remote identification of changeovers at each nest. During late March 2011 visits were made to the cave to recover geolocator data, which were downloaded *in situ* whilst the logger remained on the leg to allow data-gathering in future years. At the same time, birds' legs were examined for signs of damage and faulty loggers or worn Darvik rings were replaced. Breeding success in the year of deployment was estimated during routine monitoring visits later in the season, as was that of 27 control nests interspersed amongst the experimental nests to provide an even match of conditions as far as possible.

Light-level data were analysed in BasTrak software to provide approximate positions twice daily throughout the year, based on day/night transitions estimated using a standard light threshold of 10, linear interpolation, and filtering of apparent light or dark period of less than 4 hours. For a sub-set of 10 birds, a sunset angle was chosen individually for each logger/bird combination which localized positions close to the colony on days either side of periods during which birds' positions could be surmised to be in the colony because of sustained logged daytime darkness (for example, during incubation). Most datasets were best ground truthed with an angle of -3.5, so this was then chosen for all remaining data sets. Resultant position estimates were then filtered by eye to remove locations requiring movement of more than 2 degrees, latitude or longitude, in 24 hours.

Because passage through the Straits of Gibraltar involves a purely longitudinal progression (passage is latitudinally constrained by Iberia to the north, and Africa to the south), it is possible to define individual Mediterranean exit and re-entry dates precisely using geolocator data despite inherent latitudinal inaccuracy, even around the equinox. Furthermore, the occurrence of complete daytime darkness in the logger trace allows identification of days spent in the colony, whilst sustained periods of night-time dryness in the salt-water immersion traces allows identification of visits to the cave during the night. We used these additional pieces of information from the loggers to pinpoint the phenology of annual events (migration, colony returns, egg laying) much more precisely than is possible using geolocation data alone.

Results

Impacts

Of the 34 deployments in 2010, 28 birds were recaptured breeding again at the colony in 2011, mostly in the same nests and with the same partners. All pairs hatched young successfully in 2011 post-deployment, but one chick failed to fledge. 6 birds were not re-encountered, giving a minimum annual survival of 82%. Although we did not measure over-winter return in the control nests, estimated adult survival between 1998–2002 was similar at 78% [3]. All but three experimental pairs bred successfully in the year of deployment, with two eggs failing to hatch and one chick failing to fledge. Hatching success was as good as that in controls nests (0.88 vs 0.82, Fisher's Exact test $p = 0.271$), as was fledging success (0.70 vs 0.63, Fisher's Exact test $p = 0.198$). One bird returned missing its geolocator, and one geolocator failed to yield data, leaving 26 complete data sets.

Sexing behaviourally

We were able to sex birds behaviourally. Petrels in general, and the closely related Manx shearwater (*Puffinus puffinus*) in particular [18], show a distinct pre-laying exodus in which the female is absent from the nest for 2–3 weeks whilst she builds her egg, yet the male continues to revisit the nest on most nights. We used the pattern of salt-water immersion data to identify night-time visits to the colony (see below). In the 10 pairs for which we have both birds tracked, one individual was always absent from the colony for an extended period prior to the start of incubation (the pre-laying exodus) whilst the other individual was apparently present on most nights. We used this distinction to assign sex, and durations of pre-laying absence from the colony were non-overlapping between putative males and females (male absence, median 1.5 days, range 0–4 days; female absence: median 13.5 days, range 5–22 days). We then cross-verified this categorization by identifying which bird provided the first incubation stint (which should be the male: 18). On 9 out of 10 occasions this cross-check was clear cut and correct, whilst on one occasion there was a slight ambiguity caused by a short (one day) first incubation stint. We then applied the pre-laying absence criterion to sex the remaining 6 birds.

At-sea movements

Figure 1 (inset) shows the 50% occupancy kernels for each individual's year-round daily locations, with each individual coloured separately. The data demonstrate clearly that birds divide their time principally between the breeding area centred north west of the colony on the Iberian shelf, where there is remarkable inter-individual consistency, and migration areas in the northeast Atlantic.

A clearer picture of the migration is obtained by filtering the data to exclude locations outside the migration period. Figure 1 (main figure) shows the 50% occupancy contours for all valid locations for each individual during migration alone, characterised as the period between first exit from and first re-entry to the Mediterranean. This demonstrates that all 26 tracked birds moved into the northeast Atlantic on post-breeding migration, returning to the colony in the autumn.

Migratory phenology

Figure 2 shows the individual timing of key events during the annual cycle determined using longitudinal progression or logged

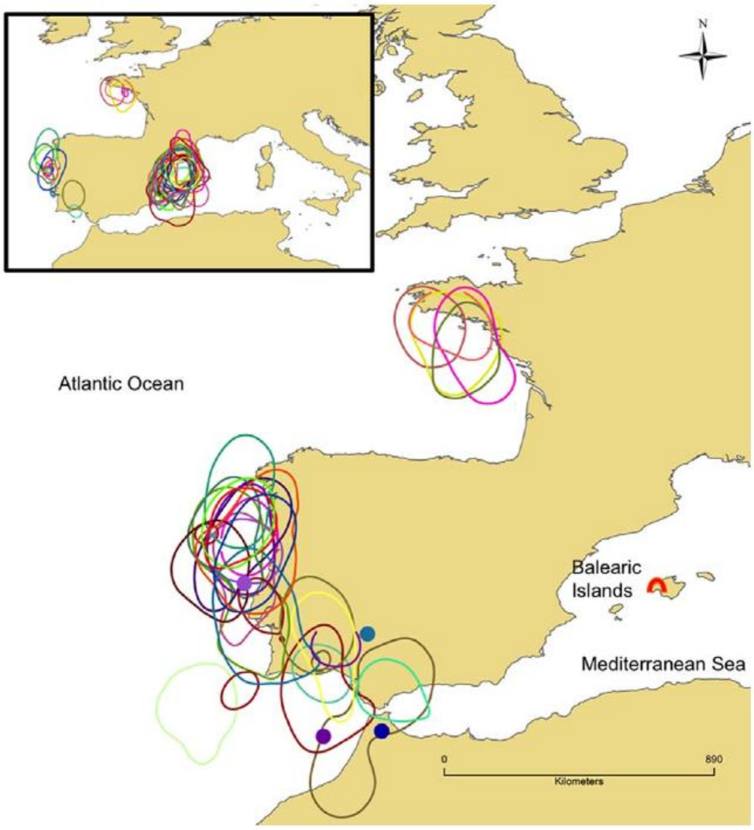

Figure 1. Balearic shearwater movements at sea. The inset shows the 50% occupancy kernels for all birds of all valid locations through the entire annual cycle, with each individual coloured separately. The main figure shows the 50% occupancy kernels for all birds of locations between leaving and returning to the Mediterranean on migration, in the same colours. The coloured circles are spatial median positions for four birds that made a second trip into the Atlantic post-migration (same individual colours). These latter estimated positions are very approximate, and should not be taken to signify that birds are inland. The red symbol is the position of the breeding colony at Sa Cella cave on Mallorca.
doi:10.1371/journal.pone.0033753.g001

day-time darkness. Where both birds of an original pair were successfully tracked, they are grouped together to enable visualization of synchrony between pair members.

The timing of the Atlantic migration, its duration, and the timing of return to the Mediterranean were rather variable. Median date of passage into the Atlantic was 27/06/2010 (range 31/05/2010-11-07/2010). We were able to relate migration to the previous (2010) breeding attempt by identifying the apparent end of incubation from the pattern of logged day-time darkness. Those individuals whose breeding failed, stopped incubation latest probably because they were unwittingly sitting on infertile or failed eggs, and then left earliest on migration (shown in Figure 3A). Otherwise, the timing of hatching was not significantly related to the timing of the parents' subsequent migration (Spearman's rho = 0.298 for males ($p = 0.347$) and 0.216 for females ($p = 0.549$), excluding failed breeders).

The Atlantic migration lasted about 3 months (median 88 days; range 66–137 days), with failed breeders tending to spend the longest away from the Mediterranean (median duration 120 days for failed breeders versus 86 days for successful breeders; Mann-Whitney U test $Z = 2.914$, $p = 0.004$). There was no obvious relationship between the migratory destination and breeding failure, with two failed breeders travelling to southwest Brittany (females), and two to Portugal (males). However, migratory destination was related to sex, with all five birds travelling the furthest, to southwest Brittany, being females (Fisher's Exact test $p = 0.012$). Females spent longer on migration than males (median duration 91 days for females and 83 days for males; Mann-Whitney U test $Z = 2.13$, $p = 0.033$), even if failed breeders are excluded (median duration 90 days for females and 80 days for males; Mann-Whitney U test, $Z = 2.605$, $p = 0.009$). In fact, the females that did not travel as far as southwest France still spent longer on migration than males (Mann-Whitney U test $Z = 1.986$, $p = 0.047$, excluding all failed breeders), so the more distant destination was apparently not the cause of longer migration (there is no difference in duration of migration with destination amongst all females: Mann-Whitney U test $Z = 1.467$, $p = 0.142$).

Return from migration was also rather variable (median date 23/09/2010; range 08/09/2010–03/11/2010). All birds then spent a long pre-laying period during autumn and winter in the Mediterranean (predominantly) after return from migration (median 157 days, range 117–176 days), and this was the same for males (median 157 days) and females (median 159 days). Lay dates were estimated by the onset of incubation discerned in the pattern of logged day-time darkness, and especially clear in the abrupt pattern of asynchronous presence in the cave visible within pairs in Figure 2. In contrast to the events of migration, laying was

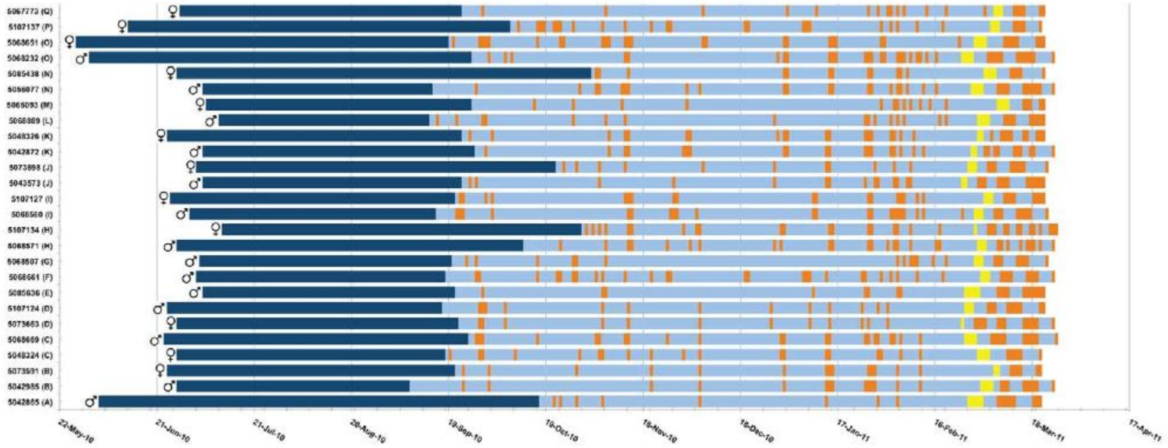

Figure 2. Individual pre-breeding phenologies. Individual phenology traces are represented for all 26 birds labeled by ring number, grouped by their original nest pairings (bracketed letters). Behaviourally determined sex is given for each bird. The first portion of each trace (dark blue) shows the timing and duration of migration, bounded by date first day in the Atlantic post-breeding and date of first return to the Mediterranean. Orange bars represent presumed over-day visits to the colony. The first incubation stint for each bird is shown in yellow, and the following asynchronous visits within pairs clearly show the pattern of coordinated incubation. Traces stop when devices were downloaded.
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remarkably synchronous, and was apparently unrelated to the length of migration (Figure 3B; Spearman's rho = 0.328 for males ($p = 0.253$) and 0.289 for females ($p = 0.362$)), or the date of first arrival back in the Mediterranean (Figure 3C; Spearman's rho = 0.323 for males ($p = 0.260$) and 0.005 for females ($p = 0.987$); see below) suggesting that there is no obvious carry-over effect from migration to the timing of breeding.

Pre-laying behaviour

We used prolonged periods (>2 hrs) of continuous dryness in the salt-water immersion data to identify periods on land at night, presumed to be visits to the colony, during the pre-laying period. Birds spent many nights, or part thereof, at the colony between migration and laying (females, median 42 nights, range 22–62 nights; males, median 61.5 nights, range 46–81 nights), with

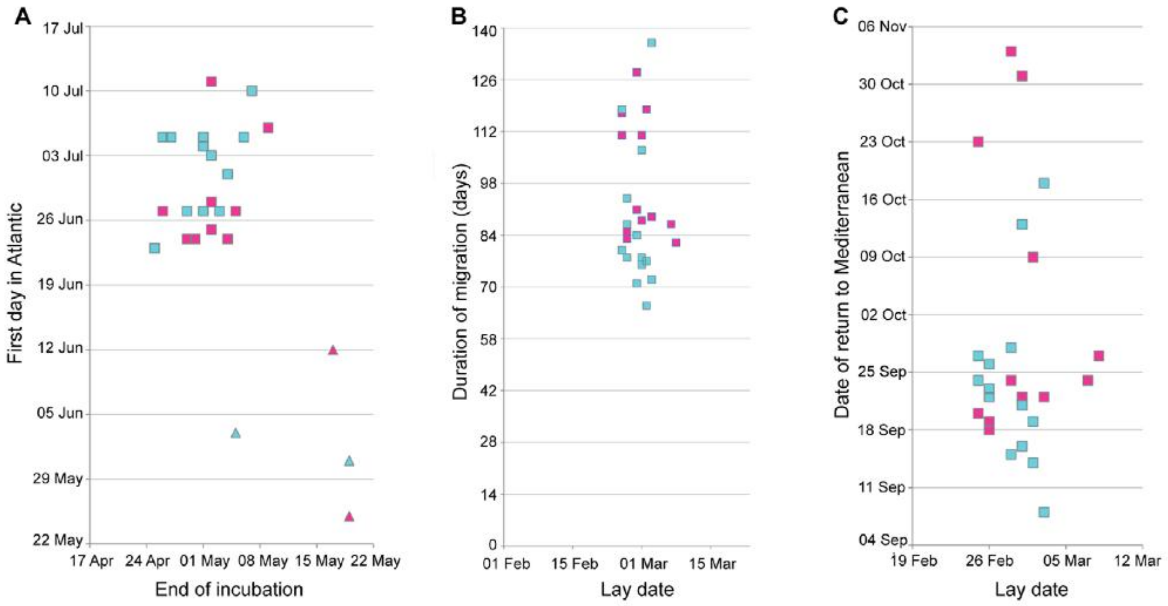

Figure 3. Relationships between timing of breeding and migration. A) Start of migration is not significantly related to last day of preceding incubation, except for failed breeders: males (blue); females (pink); successful breeders (squares); failed breeders (triangles). In neither males (blue) nor females (pink) does the duration of migration (**B**), or the date of return from migration (**C**), influence subsequent timing of breeding (plotted as lay date).
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males visiting the colony during this pre-laying period significantly more often than females (Two-sample t-test, $t = -4.37$, $N = 26$, $p < 0.001$). Birds first arrived back at the colony within one or two days of entering the Mediterranean (median delay 2 days; range 0–18 days), usually spending a day in the colony shortly, sometimes immediately, afterwards (median delay after migration 3 days; range 0–19 days), and continued to revisit the colony over-day at intervals throughout the winter until breeding in the spring (see Figure 2). Individuals within a pair are highly synchronous in their pattern of over-day visits to the colony, with between 28% and 92% (median 59%) of days spent together. The pair with the lowest degree of synchrony (28% & 31% of visits together; birds 5068532 & 5068651) had a failed egg in 2010, and were the earliest to lay in 2011, suggesting a possible relationship between pair synchronization and breeding performance. We also noticed that two birds (5068661 & 5107137) originally breeding in different pairs in 2010 showed synchronous visits during the winter return, and these two birds, one of whose partner failed to return, were subsequently found breeding successfully together in 2011. Synchronous day-time visits to the colony were usually preceded by a series of night-time visits by one or other bird which continued until the second bird made a night-time return, to be followed immediately by a day together in the cave. This suggests that synchrony emerges as a consequence of the pair meeting at the colony. Figure 4 shows an example of the pattern of night-time and day-time visits for a typical pair, both throughout the pre-laying period (Fig. 4A) and in the immediate run-up to laying when the female's pre-laying exodus clearly contrasts with male night-time visiting behaviour (Fig. 4B).

Over and above this within-pair synchrony, over-day visits to the colony were not randomly distributed, with visits, or periods of absence, clustered through the period (shown in figure 5). To eliminate the pseudo-replication effect caused by within-pair synchrony, we randomly excluded one bird from each pair for which we had both tracks, providing a sample of 10 to which we added the remaining 6 birds for whom we did not have the partner's track (Kolmogorov-Smirnov test: $N = 16$; ks2stat = 0.2105; $p < 0.011$). There is a gradual build up of day-time activity in the cave towards breeding, with incubation preceded by a short period in which most birds, and all females, are absent (the pre-laying exodus). We related over-day visits to the colony to moon phase. We plotted in figure 5 (inset) the remaining 89 over-day visits on a circular diagram against the daily phase of the moon between end of migration and start of incubation. A Rayleigh test shows that visits are significantly non-randomly distributed ($R = 10.576$, $p = 2.55 \times 10^{-5}$), whilst a V-test with new moon as the expected mean shows that visits are significantly clustered towards the new moon ($U = 4.324$, $p = 5.97 \times 10^{-6}$) which is within the 95% confidence limits of the distribution.

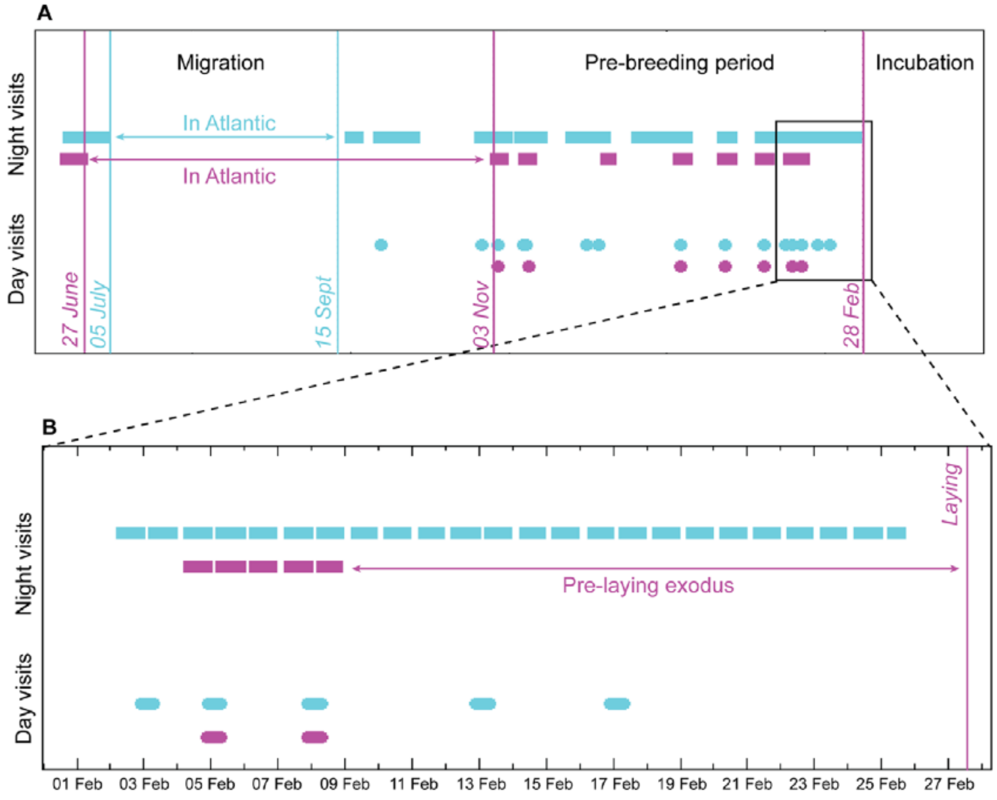

Figure 4. Pre-laying behaviour. Panel A shows the pattern of night-time visits (squares) and day-time visits (circles) for two birds in typical pair (N), the male in blue (556077) and the female in pink (5085438), over the entire post-migration, pre-laying period. Panel B shows a zoomed section covering the three week period before laying, which clearly shows the contrast between male visiting behaviour and female pre-laying exodus. Vertical lines show dates of exit into the Atlantic, entry into the Mediterranean, and laying, for both the male (blue) and the female (pink).
doi:10.1371/journal.pone.0033753.g004

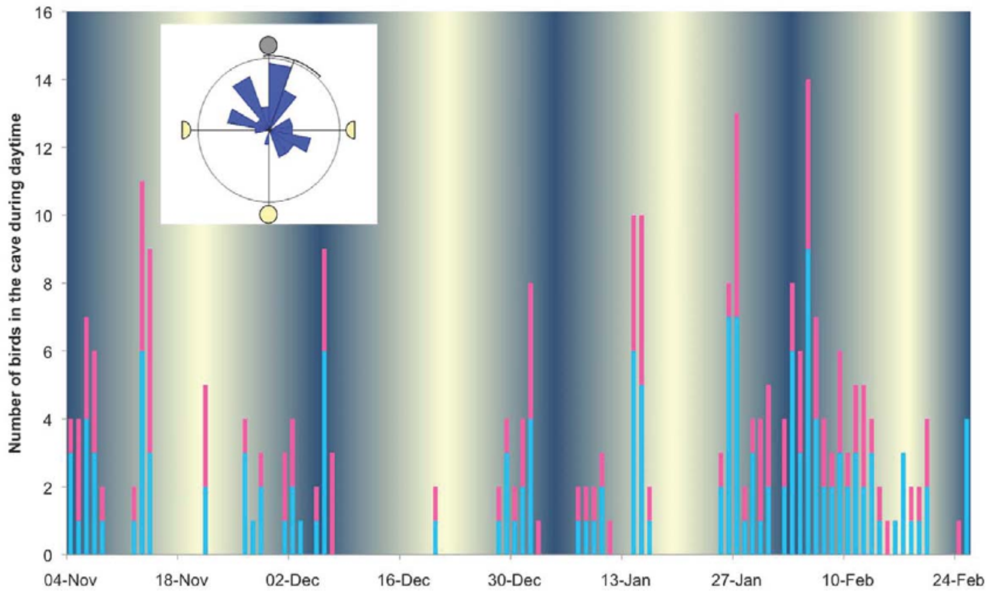

Figure 5. Distribution of day visits to colony in relation to lunar cycle. The main figure shows a histogram of over-day visits to the colony in relation to date and lunar cycle, for all 26 birds tracked and during the that portion of the pre-laying period in which all birds had returned from migration, but no bird had yet laid. Males are in blue, females are in pink. The Rose diagram (inset) shows the distribution of visits in relation to moon phase alone, with lunar progression clockwise, including one randomly selected bird from each of 10 pairs for which we have both partners' tracks, and 6 solo tracked birds ($N = 16$ birds, 89 day visits). Rayleigh test, $R = 10.576$, $p = 2.55\times10^{-5}$. V-test with new moon as expected mean, $U = 4.324$, $p = 5.97\times10^{-6}$. Circumferencial bar shows 95% confidence limits.
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Most birds spent the winter period between visits to the colony in the Mediterranean, but four birds showed an additional excursion into the Atlantic exiting the Mediterranean between 16th and 25th October for between 9 and 21 days. These excursions are plotted as spatial median positions in Figure 1, providing an approximate centre of location for the whole trip between entering and leaving the Atlantic. Because these involve rather few data, and probable rapid movement between different places which are spatially averaged, the positions are very approximate, especially in Latitude (for example, it is extremely unlikely that birds will actually be located over a landmass).

Discussion

Geolocation technology is increasingly used to study the migration patterns of ever smaller or more sensitive pelagic seabird species [19–22], and at ever increasing scales [23]. Here we demonstrate its successful, low impact use to study migratory and pre-breeding behaviour in, and determine the sexes of, a critically endangered seabird species.

At least in so far as our one-year sample from the world's largest known breeding colony is representative, the breeding Balearic shearwater's year at sea is divided predominantly between two distinct phases. During spring breeding, and in the autumn and winter months beforehand (about three quarters of the year), movements are predominantly concentrated in a remarkably restricted area around the Balearic Islands where they breed, extending to the Spanish mainland coast and encompassing the productive shallow waters of the Iberian continental shelf. This finding is consistent with previous work, largely based on at-sea sightings [5,24,25], and it is here around the Iberian shelf where breeding birds are likely to be most at risk at sea from fisheries by-catch, pollution, or, potentially, renewable energy developments. We also resolve occasional westerly movements during this period, in some cases as far as the Atlantic. Soon after breeding, birds migrate into the northeast Atlantic to coastal regions off Portugal and western France, where they spend about one quarter of the year.

We were able to characterize the timing of post-breeding migration quite precisely because it involves passage through the narrow straits of Gibraltar where movement is almost entirely longitudinal, circumventing the usual latitudinal inaccuracy of geolocation techniques around the equinoxes. It appears that all breeding individuals migrate into the Atlantic from the Mediterranean soon after they have finished breeding in mid-summer (median 27th June), presumably to exploit seasonally productive shelf waters around the Iberian and French Atlantic coasts, and to moult. Earlier attempts to track post-breeding dispersal, using satellite tracking [5], have suggested that at least some breeders may remain in the Mediterranean rather than migrate into the Atlantic, a result that contrasts with our own. This difference could be a genuine effect of differences between years, or perhaps an indication that the much heavier devices deployed in the earlier study disrupted normal behaviour. In our study, failed breeders make the Atlantic migration earliest, leaving before successful breeders have fledged their young, perhaps as soon as they perceive their own failure (as an egg that fails to hatch, for example). The Atlantic migration lasts around 3 months (median 88 days), but the longer migratory durations of failed breeders especially contribute to a rather variable length. Intriguingly, there is also a suggestion that females spend significantly more time in the Atlantic than males, but a larger sample will be needed to assess the generality of sex differences. Sightings of Balearic shearwaters apparently leaving the Mediterranean occur throughout the non-breeding period [5]. Our results show that an exodus of successful breeders is concentrated for a few weeks around the end of June, implying that the more broadly dispersed movements may be made up of young, immatures, and failed breeders. However, we also discovered that a small proportion of birds make (at least) an additional trip back into the Atlantic post-migration, a behaviour that presumably contributes to the sightings of outward movements throughout the non-breeding period.

Spatially, birds on migration appear largely to restrict their activity to one of two core areas off western Portugal or southwestern Brittany. Only one bird appeared to visit both areas. In our sample, only females travelled to southwestern Brittany raising the intriguing possibility that post-breeding migration strategies may differ, at least partially, between the sexes (echoing the differences in migratory duration discussed earlier). Previous observations have recorded concentrations of birds off these coasts before, and there may well be inter-annual shifts in distributions in relation, perhaps, to food availability [9,12,26]. Our results confirm that these areas, and the risks associated with them, are important for *breeding* individuals. However, and including the year that our study was conducted (2010), major concentrations of Balearic shearwater sightings have tended to be further north than these areas, off the coasts of northwest Brittany [16] and, increasingly frequently, off southwest UK [10,15]. We found no evidence of Mallorcan breeding birds utilizing these areas, suggesting either that such sightings comprise predominantly non-breeding birds, or that birds breeding at different colonies may show migratory segregation. Numbers of sightings further north start to build up in late May before our successful breeders are on migration, and can peak in late September after many breeders have returned to the Mediterranean [13,15], supporting the hypothesis that these are at least partially non-breeders. Intriguingly, an aggregation of approximately 6000 birds, representing as much as 25% of the estimated global population [2] was recorded off northwest Brittany in late July 2010 [16] at a time when all of our tracked Mallorcan breeders were further south. As well as age segregation, it is possible that migratory segregation between different colonies could also account for the lack of Mallorcan breeders in these concentrations. Migratory segregation between colonies could reduce the species' resistance to extinction, and determining the migratory patterns of birds breeding at other colonies in the Balearic Islands, such as Ibiza, is clearly important. In either case for approximately ¼ of the year, a large percentage of the world's population of breeding birds will be vulnerable to by-catch in these two core areas within the territorial waters of Portugal and France (a problem which could be worsened if the segregation we found between the sexes turns out to be robust in a larger sample).

Return from migration occurs predominantly during September (median 23/09/2010), and as early as 09/09/2010 in our study, but is quite variable. Using the presence of long dry periods in the salt-water immersion traces at night we were able to identify probable visits to the colony remotely from the geolocator logs alone. Strikingly, we found that most birds apparently visited the colony immediately (median 2 days) after returning to the Mediterranean, suggesting almost direct flight from the Atlantic. This calls into question earlier inferences from direct field observations that the presence of birds around colonies and on the nests in early September indicates that breeders may be present in the Mediterranean all year round [5]. Instead, it seems, breeding birds make a rapid return directly after migration in the Atlantic.

The period between migration and laying makes up close to half of the breeding shearwater's life-cycle (median 159 days for females, 157 days for males), when most of the time at sea is spent around the Iberian shelf. During this period, as previous observations have suspected [5], night-time visits to the colony are a frequent behaviour with males spending more than a third of nights apparently on land (median 39%), and females around a quarter (median 27%). Whilst nest defence may be one function of these night-time visits (particularly for males), the pattern strongly suggests a social function between pair members. Using the occurrence of logged day-time darkness we were also able to identify over-day visits to the colony, and relate these to the patterns of night-time visits. We found that birds appear to visit the colony on consecutive nights, returning to sea in the day, until their partner also visits at which point they are highly likely to spend the following day in the cave together. Such joint, over-day visits are generally followed by a more extended period at sea away from the colony. Synchronous over-day visits build up towards laying, culminating in a distinct pre-laying exodus period (a common feature of procellariiforms [18]) which allowed behavioural sexing remotely and uninvasively in this otherwise largely monotypic species. Over and above the within pair synchrony there is a significant relationship with the lunar cycle, visits significantly more likely to occur around the new moon. This might reflect a disadvantage to visiting the colony on bright nights (perhaps related to predation risk [18]), an advantage to foraging on bright nights, or an additional mechanism for synchronizing breeding across the whole colony. It is conceivable that weather effects are confounded with lunar phase in a single-year sample, and further data will be required to give more confidence in this result.

In contrast to the timing of events on migration, laying is highly synchronous, something which is strikingly found in some species of Procellariiform [27,28], but not others [18]. It appears to be unrelated to duration of migration, or return date, suggesting that lay date itself is not subject to obvious carry-over effects. Lay dates appear to vary between colonies and years [5], so it is possible that within-colony synchrony is itself a strategy for reducing the local risk of egg or chick predation, and that the synchronous colony visiting behaviour that we find during the pre-laying period may function to facilitate this.

Although further study of inter-annual and inter-colony variation, and of different life stages, will be of crucial importance for properly informing conservation priorities, our results help to crystalize the risk structure to breeding individuals of this critically endangered species outside of the breeding season itself. Individuals spend around a quarter of their year, the late summer, on migration at coastal sites relatively localized off northeast Atlantic coasts, especially Portugal and France, and then return directly to their breeding sites to spend around 5 months visiting the colony rather frequently even before egg laying. Although excursions westwards, even back into the Atlantic, occur on some occasions, it appears from the frequency of visits to the colony, and the general location of core positions, that birds are already dependent on Iberian shelf waters long prior to breeding. Furthermore, pre-breeding colony visits may be important for synchronizing breeding, and may have other as-yet unknown functions, emphasizing that disturbance to colonies could be detrimental to breeding over a large part of the year. Combined archival light and salt-water immersion logging devices (geolocators) have proved to be a powerful, lightweight, and minimally invasive tool in this study, and may have considerable scope for understanding the movements and behaviour of other sensitive species if appropriately used.

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Author Contributions

Conceived and designed the experiments: TG RW MM AR. Performed the experiments: TG RW MM AR LM AJ. Analyzed the data: TG AF RM. Contributed reagents/materials/analysis tools: AF. Wrote the paper: TG RW. Constructed figures: TG RW AF LM. Commented on manuscript: MM AR AJ LM AF RM.

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