PREDICTIVE MODELS OF CETACEAN DISTRIBUTIONS OFF THE WEST COAST OF SCOTLAND

Clare B. Embling

A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews

2007

Predictive models of cetacean distributions off the west coast of Scotland

Clare Beth Embling

A thesis submitted to the University of St Andrews for the degree of
Doctor of Philosophy

School of Biology
Sea Mammal Research Unit

September 2007

Author’s Declaration

I, Clare Beth Embling, herby certify that this thesis, which is approximately …..…….. words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted to any previous application for a higher degree.

Date:……………………………...

Signature of Candidate:………………………………………

I was admitted as a research student in October 2003 and as a candidate for the degree of PhD in the School of Biology in October 2004; the higher study for which this is a record was carried out in the University of St Andrews between 2003 and 2007.

Date:……………………………..

Signature of Candidate:……………………………………….

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date:……………………………..

Signature of Supervisor:………………………………………

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulation of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and abstract will be published, and that a copy of the work may be made and supplied in any bona fide library or research worker.

Date:………………………………

Signature of Candidate:………………………………………...

Table of contents

Abstract

The main purpose of this study was to produce and test the reliability of predictive models of cetacean distributions off the west coast of Scotland. Passive acoustic and visual surveys were carried out from platforms of opportunity between 2003 and 2005. Acoustic identifications were made primarily of harbour porpoises (*Phocoena phocoena*), delphinids, and sperm whales (*Physeter macrocephalus*). Generalised Additive Models (GAMs) were used to relate species' distributions to a range of environmental variables over a range of temporal and spatial scales.

Predictive models of delphinid distributions showed both inter-annual and inter-month variations. Combining data for all months and years resulted in a model that combined the environmental influences from each monthly and yearly model. Overall, delphinids were found to associate with the deep (> 400 m) warm water (10.5°C-12.5°C), and in areas of deep thermocline.

Relationships between sperm whales and environmental variables were consistent over changes in grain size (9 km or 18 km), but not between areas. Although sperm whales were distributed in deep water characterised by weak thermoclines and strong haloclines in the most northerly area (Faroe-Shetland Channel), they were found in deep productive areas with cold surface temperature in the more southerly waters (Rockall Trough).

Within the southern Inner Hebrides, high use areas for harbour porpoises were consistently predicted over time (in years) and with differing survey techniques (acoustic versus visual), but not over space (southern Inner Hebrides versus whole of the Inner Hebrides). Harbour porpoises were mainly distributed in areas with low tidal currents and with higher detection rates during spring tides.

The use of prey as a predictor variable within models of delphinid distribution shows some promise: there were correlations between delphinid and herring (*Clupea harengus*) in shelf-waters in 2005 but not in 2004. These models can be used in mitigating acoustic threats to cetaceans in predicted high use areas off the west coast of Scotland.

Acknowledgements

The PhD is a journey of self discovery, a roller-coaster ride that lasted 4 years for me. I've spent the PhD either laughing or crying, but it's an adventure I wouldn't have swapped for the world. To spend 4 years studying something that fascinates you is like living a dream, and makes the roller-coaster ride well worth the trip. I'd love to share the many ups and downs… the frustration of trying to solder a hydrophone plug with a gas soldering iron on the back deck of a boat in blowing wind and rain… the joys of seeing a humpback rise out of the water mouth first, fishy breath pervading, kittiwakes fleeing the sea surface and sprat spilling out of the huge mouth. But this would be a thesis in itself. The adventure that was this PhD would not have been possible without the support of a whole host of people, who I'd like to take the opportunity to thank…

Firstly, I'd like to thank my supervisors: Dr Jonathan Gordon and Professor Philip Hammond. Jonathan taught me everything I know about hydrophones: how to build one, how to gut one and how to blow one up (sorry Jonathan!!!). He was always at the end of a phone whenever I was having equipment problems and ready to send spares with lightening rapidity to the nearest port. And I always felt welcome in his home – so thanks must also go to Kate, Alex & Emma for letting me pop around & eat your food whenever I was on the prowl of equipment or help. Phil has been my little haven of calm in amongst the madness of fieldwork, so thank you for all the supporting words when I needed them. And thank you to both of you for all the support and feedback you've given me during the write-up phase, and all the interesting discussions about my analysis and results.

Huge thanks to my funders: NERC and DSTL, especially to Graham Jackson, Claire Burt, Matthew Summers, Ed Harland (Qinetiq) and Ben Maughan (UKHO) for organising my visit to pick their minds in the middle of my PhD.

All my fieldwork was carried out from platforms of opportunity, so this PhD would not be here today if it weren't for the generosity of the Fisheries Research Services (FRS), the Scottish Association for Marine Science (SAMs), the National Oceanographic Centre (NOC) and the Hebridean Whale and Dolphin Trust (HWDT). I'd like to thank each group in turn, but in no preferential order.

Firstly, the Faroe-Shetland Channel hydrographic surveys carried out by FRS allowed both Sónia Mendes and I to hitch aboard and tow our hydrophone – mainly thanks to Bill Turrell and George Slesser. At which point I also have to give a massive thank you and hug to Sónia Mendes for being the best co-worker I could have asked for, and for smiling despite the difficulty of overlapping interest in the sperm whale data. You've become a great friend, and I hope I get to hike the mountains and sail the seas with you in our Zissou red woolly hats for many years to come. The rest of the team on *FRV Scotia* were true stars: Malcolm & Dougal especially for keeping us both laughing all the time, but also all the scientists, cooks and crew of the *FRV Scotia*. I would just like to make a special mention of Richard 'Dick' Shelton, who taught me about the Atlantic adventures of salmon, entertained me in his book 'The Longshoreman' and has often popped in complete with hunting rifle to check up on me in St Andrews… thanks Dick!

The participation on the July 2003 and October 2005 Ellet Line surveys were thanks to the generosity of Toby Sherwin (SAMS) and John Allen (NOC). Sónia and I had a trip of a lifetime aboard the rusty but much loved *RSS Charles Darwin* travelling through Force 12 storms to Iceland and back. I don't think I can ever thank the other scientists and crew enough for making the trip so special and for making us feel so welcome. Special thanks have to go to Maria Nielsdóttir for giving us the worked up chlorophyll data (sorry for not using it!), to Peter Lamond for teaching us about acorn worms and other critters from the depths, for all the technicians, cooks for keeping us fat, and a great crew. The trip can be enjoyed for many years to come as 'CD176 – the movie'.

The generosity of Paul Fernandes & Dave Reid (FRS) allowed me to hitch aboard the herring abundance surveys on the west coast of Scotland for the first time, and trusted me enough to allow me to tow a hydrophone between fish trawls – thank you! These surveys would have been a real struggle without Eric Armstrong, who provided huge support especially on my first ever survey with a novel but very noisy and leaky hydrophone. I spent many hours of fishy fun with the other scientists: Emma Hatfield was a great cabin buddy, and she & Finlay Burns taught me all I know about fish id, determining the maturity state and sex of a herring, and many more weird and wonderful fishy facts. Thanks also to Isobel Rombouts for joining me on one of my surveys so that I didn't have to try and stay awake during all the 20 hours of each survey day! Thanks to each and every one of the science and boat crew of the *Enterprise* – I've never met such a great bunch of fishermen! An additional thank you goes to both Eric and Paul for processing the herring survey data for the west coast, and for all the discussions that formed my ideas for my dolphin-herring chapter. And a huge thank you to Doug Beare for: (a) being

a survey buddy who made me laugh; (b) joining in my brain storming session about my dolphin-herring analysis; (c) suggesting the Multinomial Logit Model to me; and (d) for letting me adapt his code.

How can I ever thank the Hebridean Whale and Dolphin Trust for letting me join the team, help on the trips, and for letting me use their data? The trips on the *Silurian* were pure indulgence: sailing around the stunning islands of the Inner Hebrides, mooring at a different port on a different island every night, and exploring the remotest parts of the west coast of Scotland. My love of the west coast is a result of these trips, and I came to think of Tobermory as my second home. So firstly massive thanks to Juliet Shrimpton, who ran all the surveys, kept the hydrophone working, and kept all the volunteers happy and on their toes for spotting critters during all 3 years of surveys. I miss our trips together, and I hope we'll get to do trips together again in the future. Thanks also have to go to each of the skippers who've managed to combine the odd requirements of surveying an area evenly to the whims of scientists **and** the weather **and** the location of ports, tides etc., and especially to Duncan Cameron who's kept the boat in tip-top condition (but stop with the anti-bac!). First mates Jamie Spears and Marcus Walters were great at juggling between keeping the boat sailing and helping out with the science… quite some task – so thank you! In 2005, Marjolaine Caillat was a massive support while on the boat during her masters, and helped me to stay laughing despite massive computer failure on the trip where we tried to run two hydrophones from one computer (don't try it!). Marjolaine & I with huge phone support from Guillaume managed to rebuild the computer and only lost out on a day's survey effort. Talking of equipment failures on the *Silurian*, I also have to thank Roy Wyatt (Seiche Electronics) for such good support for the porpoise boxes. Finally, back at base thanks go to Cally Fleming, Barbara Weir, and Fiona Quarmby who provided lots of support and smiles. But of course none of these surveys would have been possible at all if it weren't for the hard work from all of the HWDT and Earthwatch volunteers – I had so much fun working with you all, the trips would never have been so much fun if it weren't for your enthusiasm.

This project was also carried out in conjunction with Phil Gillibrand (SAMS), Steve Gontarek (SAMS) and Geert Arts (SMRU). Phil has been a great support in processing my environmental data for me, and being a great guide through the complexities of physical oceanography. Steve designed the **fabulous** tool for ArcGIS9 that loads all manner of weird and wonderful environmental data into a GIS database, and allows you to automatically pull out every environmental variable for each grid of locations you give

it. Thanks Steve for the great tool, and for being at the end of an email or phone whenever I needed help. Geert deserves huge thanks because I benefited from travelling in his wake – he did much of the work sourcing the environmental data, so that much of it was ready already when I needed to start my analysis. I have to tag on extra thanks to Clint Bight at this point for all the unpaid computer support he provides to the department, and for all the GIS problems he's helped me with despite being overrun with his own work.

Lots of SMRU & CREEM folks have given me a lot of help too: Rory Beaton, Colin Hunter, and Julian Dale gave me huge amounts of support in the early hydrophone building days. And of course thanks to Simon Moss for letting me take over the boat shed with my hydrophones and teaching me how to use a drill. Ana Katerina Alves and Anneli Englund were great helpers with the tedious task of processing some of my massive pile of acoustic data – thanks for doing a great job AND staying sane! Extra fieldwork assistance was provided by Tess Gridley, Cormac Booth, Caroline Weir and René Swift when either Sónia or I couldn't make the survey – thank you for doing a fantastic job! And Tess you were a great boat-buddy! Thanks for the sounding boards for ideas: Mike Lonergan, Doug Gillespie, Sinead Murphy, Simon Northridge, Charles Paxton, Monique Mackenzie, Vincent Janik and the bioacoustics group.

Thanks to all my proof readers! They are: Eric Armstrong, Peter Stevick, Phil Gillibrand, Paul Thompson, Kate Brookes, Simon Elwen and of course my long-suffering supervisors. Please don't blame them for my writing style – as Mrs Kubiak once wrote on my English homework 'too waffly'… I hope I've improved since then Mrs Kubiak!

Finally, huge thanks have to go to my 'keep Clare sane' team. Firstly, Gill Perris (née McLaughlin) thanks for inspiring me in February 2000 to change fields from engineering to biology – this thesis would never have been here if it hadn't been for your inspiration. Thank you too to my coffee buddy and old flat mate and token non-scientist pal Amanda Beattie – you've kept me smiling all through my PhD. Thanks too to my long-suffering office buddies and great friends: Sonja Heinrich, Louise Cunningham, Simon & Lisa Ruddell, and more recently Susan Gallon, Aline Ariola and Philippa Samarra. Thanks for getting my bod to the gym: Birgit Weinmann, and for keeping me smiling with you: Alice Mackey. Big thanks to Paul Thompson for letting me camp out in the lighthouse and eat cake & pizza. For friendship (in addition to those already mentioned!): Sophie Smout & family; Thomas Götz; Ricardo Antunes; Kelly, Al & Milly Macleod; the Gillespie clan; the Rendell clan; Ana Candido, Pedro & Lua; Andy Foote; Hera Sanger;

Ross Culloch; Barbara Cheney; Tim, Carrie, Sam & Megan (& Sorrel) Barton; Line Cordes; Theoni Photopolous; Gillian Riddoch; Paul, Helen & Emma Griffiths (& the gang!)… & many more…

At the heart of the 'keep Clare sane' team is my family, who've kept me grounded. My sisters: Kate & Rhoda you've been **the best sisters on the planet** and kept me grounded in the 'real world', taking me shopping, feeding me cocktails and generally spoiling me, but also always there to provide support no matter what. Mom & Pops – you've always believed in me even when I didn't believe in myself, and always been my haven of calm. Thank you.

Simon… words can't express my thanks but… it's over!!!!!! We can have a life!

I'd like to dedicate this PhD to the memory of my grandparents: John Francis Embling and Eileen Frost (née McGrath)… you were and still are my inspiration.

"Inside, I'm dancing" Eileen Frost, June 2000

Chapter 1

Introduction

Setting the scene

1.1 Predictive models in ecology

'A predictive model is one where confidence in the hypothesised relationships allows projections of observed patterns into independent situations' Araujo & Guisan (2006).

For a species to persist in a given environment it requires the resources and conditions to survive, grow and reproduce. This may be driven by physiological constraints, interspecific competition (Beare et al. 2003; Bearzi 2005; Parra 2006; Shane 1995; Sivertsen et al. 2006; Spitz et al. 2006), distribution of prey species (Benoit-Bird et a. 2003; Croll et al. 1998; Fiedler et al. 1998; Frederiksen et al. 2006; Gende & Sigler 2006; Schneider & Piatt 1986; Vlietstra 2005), and avoidance of predators (Hammerschlag et al. 2006; Wirsing et a. 2007). All of these factors can be linked back to the environmental conditions that persist in an area (Beaugrand & Reid 2003; Beaugrand et al. 2003; Croll et al. 2005; Friedlaender et al. 2006; Hunt 1997; Ichii et al. 2007; Soto et al. 2006; Zamon 2003). Modelling the distribution or abundance of a species allows us to quantify the needs of the animals in terms of the environmental variables in which they were observed.

Data on the distribution of the vast majority of species are sparse, resulting in information about species distributions that is inadequate for many applications (Elith et al. 2006). However, by modelling how a species distribution relates to its underlying environment, it is possible to provide more detailed predictions of distributions which are essential for conservation and population management (Anderson et al. 2003; Austin 2002; Elith et al. 2006; Guisan & Thuiller 2005; Pearce & Ferrier 2000). The use of such models allows us to efficiently monitor the distribution and abundance of a species over time and predict any future changes (Buckland & Elston 1993). By using a model to examine inter-annual changes in species distributions, it is possible to evaluate a species' persistence within a habitat and thus allow for identification of critical areas for conservation (Cañadas et al.

2005). Such models may also be used to predict a species' distribution into the future with habitat changes (e.g. climate change: Araujo et al. 2005; Bakkenes et al. 2002; Skov & Svenning 2004; Thomas et al. 2004). Also, although a species' habitat preferences may change between areas, predictive models allow the modeller to highlight areas that may be of importance to the species to allow for the direction of future survey effort (Cañadas et al. 2005).

The most recent developments in predictive modelling have taken place within climate change research, attempting to extrapolate the likely impacts of global climate change on species distributions (Araujo et al. 2005; Bakkenes et al. 2002; Skov & Svenning 2004; Thomas et al. 2004), or on the risk of extinction (Araujo et al. 2005; Thomas et al. 2004). Predictive modelling is also particularly important in conservation planning to ensure that any reserve network, or Marine Protected Area (MPA) is robust to the uncertainties resulting from incomplete or spatially biased survey data (Guisan & Thuiller 2005; Wilson et al. 2005), or from environmental fluctuations over time (Cañadas et al. 2005).

Predictive modelling has been used extensively in marine mammal conservation research (Aarts 2006; Cañadas et al. 2005; Ferguson et al. 2006; Jimenez 2005; Kaschner 2004; Moses & Finn 1997). For example, Cañadas et al. (2005) used Generalised Linear Models (GLMs) to generate predicted distribution and density maps for a number of cetacean species in Spanish waters, and these data were used to support proposals for a number of proposed Special Areas of Conservation (SACs). Their models were based on more than a decade of survey data, so these SACs are likely to be relatively robust over time within the area surveyed. There are also examples where extrapolation outwith the survey area has been used for conservation planning (Kaschner 2004; Macleod 2001; Moses & Finn 1997). For example, Moses & Finn (1997) used models based on known distribution of the endangered right whale (*Eubalaena glacialis*) to predict locations of currently unknown summering grounds. Such an exercise allows for better direction of research to investigate these unexplored areas, and the predictive models themselves were to be used within the recovery plan for the species.

In this thesis, predictive models of harbour porpoise (*Phocoena phocoena*), delphinid, and sperm whale (*Physeter macrocephalus*) occurrence off the west coast of Scotland are developed and explored. The main driver for this research was to provide models able to predict critical areas for cetacean species, such that the appropriate mitigation measures can be put into place in these areas to reduce risks to cetaceans from potentially harmful anthropogenic activities. This chapter provides further detail on predictive modelling techniques, some background information on the species studied and of the survey area, the main survey techniques used and some background on the effects of noise on cetaceans.

1.2 Aspects of predictive environmental modelling

Many aspects need to be considered when building environmental models of a species distribution, even more so when using these models to predict over space or time. These include: appropriate *direct* or *indirect* environmental predictors; the consideration of scale; the problem of autocorrelation; and model validation to ensure that models are the most robust to all of these aspects for predicting species distributions. Each of these aspects will be discussed in turn.

1.2.1 Direct or indirect predictor variables?

Factors that affect the distribution of a species can act either directly or indirectly (Austin 2002; Guisan & Thuiller 2005; Guisan & Zimmermann 2000). For example, the distribution of prey species is likely to have a *direct* effect on cetacean distribution: any animal will spend a lot of its time in locations where it can forage. However, other environmental features are likely to *indirectly* affect species distribution; examples include sediment type, tidal state, and tidal range, which affect a species’ distribution due to their spatial or time dependent correlation with prey distributions. Environmental features can vary in their effect on a species distribution due to their position in the chain of processes: from *proximal* (closest to being a causal effect) to *distal* (Austin 2002). For example, availability of sand/gravel habitat suitable for sandeel prey species (Wright et al. 2004) would have a more *proximal* influence on predators of sandeels than an environmental effect that in turn influences the recruitment success of sandeels, such as sea temperature (Arnott & Ruxton 2002). Clearly, for robust models applicable over large areas, the models should be based on direct and proximal variables (Guisan & Zimmermann 2000). However, as it is often difficult to measure direct variables such as prey distributions, so predictive models often have to resort to indirect measures (Austin, 2002). Prey availability is particularly difficult to measure for cetacean distributions because many are opportunistic foragers, feeding on a wide range of prey species. For their prey distributions, there are only detailed data for those species and areas that are important to commercial fisheries. Indirect variables are often easier to measure, with data on depth and sea surface temperature, for example, being readily available nearly anywhere in the world.

In this study, predictive models were based mainly on *indirect* environmental features that are likely to be readily available to managers for predicting cetacean distributions around the west coast of Scotland. The variables include readily available topographical and sediment gridded maps, satellite data for sea surface temperature (SST) and chlorophyll, and the outputs of tidal and oceanographic models available both for on-shelf and off-shelf waters off the west coast of Scotland. Chapter 5 investigates whether herring (*Clupea harengus*) distributions could be used as a *direct* predictor of delphinid distributions based on data collected simultaneously from the same platform in shelf waters to the west of Scotland.

1.2.2 Spatial scale in ecology

The concept of scale is important throughout studies of ecology (Wiens 1989), but particularly so in the development of environmental models of species distributions. Two types of scale can be defined: (i) *extent* – the overall area under study; and (ii) *grain* – the size of the units at which species-environment relationships are examined (Weins 1989). Increasing the *extent* while keeping the *grain* size constant would incorporate more heterogeneity so increasing between-*grain* variance. Whereas, increasing the *grain* size while keeping the *extent* constant results in more heterogeneity being contained within the *grain*, so reducing the between-*grain* variance, but reducing predictive accuracy.

This can translate into different relationships between a species distribution and the underlying environment dependent on the *extent* (Boyce et al. 2002; Fielding & Haworth 1995; Jimenez 2005; Moses & Finn 1997; Osborne & Suarez-Seoane 2002; Randin et al. 2006) and *grain* size selected (Bailey 2006; Fauchald et al. 2000; Guinet et al. 2001; Guisan & Thuiller 2005; Jaquet 1996; Jaquet & Whitehead 1996; Mehlum et al. 1999; Rose & Leggett 1990; Schneider & Piatt 1986). For example, if only a part of the range of an important environmental parameter is sampled within the *extent*, it can lead to incorrect interpretations of the ecological relationship of the species under study (Van Horn 2002).

The *extent* can be deliberately confined by partitioning the data into two or more separate areas or *extents* to investigate the *generality* (Fielding & Howarth 1995) or *transferability* (Randin et al. 2006) of species-environment relationships: that is, the ability of a model to predict species distributions in other areas. This is a form of cross-validation (Araujo & Guisan 2006) that is deemed essential if species distributions are to be predicted outwith the *extent* of the study (Boyce et al. 2002). This is of particular use for species for which there are very few data, where such techniques can be used to highlight high-use areas that have not yet been explored, or for identifying those areas that may have been important to the species in the past (Jimenez 2005; Moses & Finn 1997). Moses & Finn (1997) used spatial cross-validation to predict likely summering grounds for right whales where whaling had occurred historically, and used this to inform a recovery plan for the species. Using similar spatial cross-validation techniques, Jimenez (2005) discovered that lagoons were the key habitat for West Indian manatees (*Trichechus manatus*), highlighting the value of these areas for conservation and as potential re-introduction sites for the species.

The choice of *grain* size must be selected to match the scale at which the key environmental processes occur (Araujo & Guisan 2006; Guinet et al. 2001; Guisan & Thuiller 2005; Jaquet 1996; Jaquet & Whitehead 1996). It is also restricted to the resolution of the available environmental data, for example, in this study off-shelf data for many of the environmental variables were only available on a 9 km grid, so a smaller *grain* size could not be used in this area. *Grain* size is particularly important when considering predator-prey interactions (Fauchald et al. 2000; Guinet et al. 2001; Mehlum et al. 1999; Rose & Leggett 1990; Schneider & Piatt 1986), where relationships between predators and prey can only be identified at a *grain* size larger than the size of prey patches. This is illustrated very clearly in a study carried out by Guinet et al. (2001) which found a negative correlation between female Antarctic fur seals and prey density at a small *grain* size (0.1ºx0.1º or approx 10x10 km), but a positive correlation at a large *grain* sizes (> 0.2ºx0.2º or approx 20x20 km). Similar findings were reported by Jaquet & Whitehead (1996) in a study of sperm whale distributions in the Pacific Ocean in relation to secondary productivity.

The types of oceanographic processes within the *extent* of a study can be used to decide what *grain* size should be used (Jaquet 1996). Jaquet (1996) defined two main sets of processes which she suggested were relevant in predicting sperm whale distributions in the North Pacific, and should use different *grain* sizes. Very large *grain* sizes should be used for upwelling type environments, characterised by trophic lags of 4 months and several hundred kilometres between primary production peaks and peaks in sperm whale prey density. Smaller *grain* sizes should be used in areas with processes that tend to aggregate both primary production and prey within an area with no spatial lag.

In this thesis, Chapters two to four all investigate the effect of *extent* on resulting models, and Chapter three also examines the effect of *grain* size on predictive models of sperm whale distributions.

1.2.3 Autocorrelation in predictive modelling

Autocorrelation describes the synchronicity between adjacent points in time or space: ‘temporal’ or ‘spatial’ autocorrelation (Koenig & Knops 1998). Temporal and spatial autocorrelation (pseudoreplication) can occur during passive acoustic monitoring of cetacean distributions if the same animal or group of animals is heard over several sampling points (Gordon et al. 2000). Spatial autocorrelation can also occur when the species is associated with an environmental variable that exhibits some form of spatial pattern. For example, prey distributions are generally patchy, and exhibit considerable spatial autocorrelation at the scale of the patch size, so predators will tend to be aggregated at the same scale as the prey patches (Rose & Leggett 1990). Spatial and temporal autocorrelation can also occur if the species being studied occurs in large social groups that can be detected over several sampling points (Whitehead 2003).

The main problem with autocorrelation in environmental modelling is model ‘overfitting’. This is caused by underestimation of the standard errors resulting in variables being considered significant when in fact they are not (Borchers et al. 1997; Lennon 2000). Autocorrelation can be addressed in a number of ways in the modelling process. Firstly, each group of animals could be represented by a single presence per group positioned at the mid-point of the group. This method was applied to the modelling of sperm whale habitat use in the Mediterranean (Gannier et al. 2002; Gannier & Praça 2007; Gordon et al. 2000). However, this reduces the sample size significantly and ignores the fact that the animals are present over the whole habitat over which that group is spread, not just at the central position of the group.

Secondly, a *grain* size large enough to reduce the autocorrelation to a minimum could be applied to the data, allowing variables within each *grain* and group to be summarised. For example, if the data were autocorrelated to 60 km, then a >60 km *grain* size could be used for analysing the species-environment relationships. However this also reduces the number of samples significantly, and prevents fine scale evaluation of the importance of different environmental variables.

Thirdly, the data can be sub-sampled, for example, Paxton et al. (in review) found that humpback whales were still autocorrelated to 140 km even after modelling, so for variance bootstrapping they sampled every 20th data point (since the average segment length was 7.5 km). For building models, this method also reduces the sample size significantly, and would also result in a loss of data in the locations that were not sampled.

Fourthly, the autocorrelation can itself be modelled and included in the overall habitat models. These techniques are relatively new to the field of ecology, but so far include Generalised Linear Mixed Models (GLMMs - Stephenson et al. 2006), Generalised Additive Mixed Models (GAMMs – Mendes 2007), and Generalised Estimating Equations (GEEs) applied either to GLMs or GAMs (Bailey 2006; Scott-Hayward 2006). Although these methods show some promise, they are generally computer intensive, and methods such as GEEs fail to converge if the group or ‘cluster’ size is large relative to the number of ‘clusters’ (Bailey 2006). Mendes (2007) analysed the same sperm whale data as in this study using GAMMs and found that her models often failed to converge (Mendes pers. comm.) perhaps due to the large correlation but also due to small sample sizes of sperm whales encountered off the west coast of Scotland.

Finally, the method used in this thesis uses cross-validation methodology which provides a relatively simple way of accounting for the increased complexity (‘overfitting’) of models resulting from the autocorrelation of data. Cross-validation bases the model selection process on a ‘training’ set of data, and the model is tested against an independent ‘test’ data set, allowing for the removal of any ‘overfitted’ variables (Aarts 2006; Araujo & Guisan 2006; Boyce et al. 2002; Randin et al. 2006). Aarts (2006) used this same method for removing the additional ‘overfitted’ terms from spatially and temporally collected satellite tag data for grey seals (*Halichoerus grypus*) off the west coast of Scotland.

1.2.4 Model evaluation: cross-validation

Cross-validation methods detailed by Araujo & Guisan (2006) suggest building the model on a ‘training’ data set, and evaluating the model on a ‘test’ data set that can comprise either (i) sampled data to predict within the same region and time; (ii) the same region but at a different resolution; (iii) a different region; (iv) a different time period. Most studies tend to evaluate predictive models using only one of the four suggested evaluation techniques (Ferguson et al. 2006; Forney 2000; Gregr & Trites 2001; Hamazaki 2002; Hastie et al. 2005; Jimenez 2005; Moisen & Frescino 2002; Moses & Finn 1997). The favoured method for marine mammal predictive models tends to use data from a different year as a test data set (Ferguson et al. 2006; Forney 2000; Hamazaki 2004; Hastie et al. 2005), or a different area (Jimenez 2005; Moses & Finn 1997). Only one study has been found in the marine mammal literature in which random samples were taken from the original data set (for the same area and time) to evaluate the predictive models (Gregr & Trites 2001). However, this within-distribution data method appears to be used more extensively in other fields of ecology (Anderson et al. 2003; Moisen & Frescino 2002). Each evaluation technique evaluates a different aspect of the model robustness: testing on a sample from within the same dataset checks for model over-fit for that area and time and hence can identify and remove the effects of autocorrelation; testing on a different area evaluates the transferability of a model over space: i.e. the ability of a model to predict a species distribution into a different area; and testing on a different time period evaluates the transferability of a model over time: i.e. the ability of the model to predict a species distribution into the future. A search of the literature found no examples of models that have been evaluated in all three ways, yet to know whether a model is robust over time and space, it is essential to evaluate the model performance on these three criteria.

In this thesis, Chapter three and four evaluated model overfit within the same time and space by random allocation of the full *extent* of data into a test and training set using a sampling unit that minimised autocorrelation between the data sets. Chapter three evaluated the models ability to predict over the same *extent* but two *grain* sizes. By partitioning the data by area, chapters two, three and four evaluated the ability of the model to predict species distributions over space. Whereas by partitioning the data by month or year, chapters three and four evaluated the ability of the model to predict the species distribution over time.

1.3 Cetacean species off the west coast of Scotland

The west coast of Scotland is home to a wide range of cetaceans, from the small harbour porpoise (Evans et al. 2003; MacLeod et al. 2007; Macleod 2001; Mandleberg et al. in review; SCANS-II 2006; Skov et al. 1995; Weir et al. 2001) to large baleen whales, such as blue, fin and sei whales (Evans et al. 2003; Harwood & Wilson 2001; Macleod et al. 2003; Skov et al. 1995; Weir et al. 2001). Their habitat ranges from the shallow productive waters around the Hebrides to the deep productive waters of the Faroe-Shetland Channel. The most abundant small cetacean is the harbour porpoise in inshore waters (Evans et al. 2003; MacLeod et al. 2007; Weir et al. 2001), and the white-sided dolphin in offshore waters (Harwood & Wilson 2001; Macleod et al. 2003; Weir et al. 2001); however, larger odontocetes such as the long-finned pilot whale and the sperm whale are also found to be abundant in the deep offshore waters (Evans et al. 2003; Harwood & Wilson 2001; Macleod et al. 2003; MacLeod et al. 2007; Skov et al. 1995; Weir et al. 2001).

1.3.1 Harbour porpoise (Phocoena phocoena)

The harbour porpoise is the most common cetacean species in coastal areas off the west coast of Scotland (Weir et al. 2001). The few previous studies of cetacean distribution and abundance on the west coast of Scotland (Macleod 2001; MacLeod et al 2007; Mandleberg et al. in review) show that the main concentration of harbour porpoises lies within coastal shelf-waters, with only occasional sightings in off-shelf areas (Evans et al. 2003). During the SCANSII aerial surveys, it was found that the

Inner Hebrides had one of the highest densities of harbour porpoises in Europe (SCANS-II 2006).

The harbour porpoise is one of the smallest of cetaceans averaging 160 cm in females and 145 cm in males (Bjørge & Tolley 2002). The back is dark grey with a distinctive small triangular shaped dorsal fin and a white chin and underbelly (Bjørge & Tolley 2002). They are easily recognisable at sea from their characteristic swimming pattern of several short ‘rolling’ surfacings (Bjørge & Tolley 2002). Unlike the delphinids, harbour porpoises only produce echolocation click vocalisations between 110-150 kHz (Richardson et al. 1995): a much higher frequency than we are able to hear.

Due to the small size of harbour porpoises they have a relatively large surface area in relation to body mass. This means that they are more vulnerable to heat loss. Their small size also means that their energy stores are also quite low (Koopman 1998), so in order to obtain enough food to survive, harbour porpoises need to stay close to their food source and feed regularly (Kastelein et al. 1997). This will tend to influence the relationships between harbour porpoises and prey distribution which should lead to a closer link with oceanographic features likely to aggregate prey (Gregr & Trites 2001).

Habitat preference of harbour porpoises have been analysed in a number of studies (Bailey 2006; Calderan 2003; Carretta et al. 2001; Gridley 2005; Johnston et al. 2005; MacLeod et al. 2007; Mandleberg et al. in review; Palka 1995; Raum-Suryan & Harvey 1998; Smith & Gaskin 1983; Tynan et al. 2005; Watkins & Colley 2004; Watts & Gaskin 1985; Weir & O'Brien 2000). In the majority of the studies, depth was found to be an important habitat predictor of harbour porpoise distribution (Caretta et al. 2001; Gridley 2005; MacLeod et al. 2007; Mandleberg et al. in review; Read & Westgate 1997; Raum-Suryan & Harvey 1998; Watts & Gaskin 1985). These studies, which were mainly limited to inshore waters, found that harbour porpoises tended to prefer the deeper waters surveyed. Watts & Gaskin (1985) also found that harbour porpoises were found near ‘herring entry points’, defined as deep (> 80 m) shoreward penetrating channels that funnel tidal currents into shallower areas. Johnston et al. (2005) suggested that harbour porpoises may show a preference for a combination of depth, slope and distance to shore, but that their strongest preferences can be better described by examining the more dynamic variables such as currents, tides, and time of day. They found that tagged harbour porpoises core use areas were characterised by areas of island wakes, caused both by topography and tide, producing frontal zones that aggregated prey. Line transect surveys showed that harbour porpoises in these island wake frontal zones had densities five times higher during flood than to ebb tides. Calderan (2003) also found that harbour porpoises tended to occur at higher densities during flood tides within a tidal area off Anglesea in Wales. In Wales, Weir & O’Brien (2000) found that harbour porpoises occurred at higher densities on the mixed side of the Irish Sea front, an area shown to have increased prey densities (Fernandes 1993). Frontal zones were also shown to be important to harbour porpoises in the Pacific Ocean, with porpoises associating with upwelling fronts characterised by high sea surface salinity during the summer (Tynan et al. 2005).

There are a number of studies of porpoise diet from around the UK (Martin 1996; Rae 1973; Roberts 2005; Santos 1998; Santos & Pierce 2003; Roberts 2005), most of which are reviewed in Santos & Pierce (2003). Harbour porpoise diet in the North East Atlantic is predominated by whiting (*Merlangius merlangus*), herring (*Clupea harengus*), and sandeels (*Ammodytes* spp.), although the composition varied with area, season and year. Santos & Pierce (2003) did note that some benthic species such as Sepiloids & sandeels were present in the diet (the latter ‘hibernate’ in the sediment during the winter but still found in porpoise diet), leading them to suggest that porpoises may use echolocation to detect prey beneath the sea bed. Time-depth recorders placed on harbour porpoises showed that dives were mainly in flat-bottomed to a maximum recorded depth of 73 – 99 m (Otani et al. 1998; Westgate et al. 1995). There is some indication that click production and foraging may be diurnal with more clicks (Carlstrom 2005) and more foraging (Westgate et al. 1995) at night than during the day.

1.3.2 Delphinid species

The main delphinid species found off the west coast of Scotland are: long-finned pilot whales (*Globicephala melas*), Atlantic white-sided dolphins (*Lagenorhynchus acutus*), white-beaked dolphins (*Lagenorhynchus albirostris*), and common dolphins (*Delphinus delphis*).

1.3.2.1 Long-finned pilot whales (Globicephala melas)

Long-finned pilot whales are found in deep water off the west coast of Scotland (Cronin & Mackey 2002; Macleod 2001; Macleod et al. 2003; MacLeod et al. 2007; Moscrop 1997; O'Cadhla et al. 2004; Skov et al. 1995; Wall et al. 2006; Weir et al. 2001) with highest abundance in the waters to the south-west of the Faroe Islands (Buckland et al. 1993). They are often found in mixed-associations with white-sided dolphins (Cronin & Mackey 2002; O'Cadhla et al. 2004; Weir et al. 2001), bottlenose dolphins (Cañadas et al. 2002; O'Cadhla et al. 2004; Skov et al. 1995; Weir et al. 2001), common dolphins (Cañadas et al. 2002, O'Cadhla et al. 2004) or white-beaked dolphins (O'Cadhla et al. 2004).

They are one of the largest members of the Delphinidae family with the males in the Faroes averaging 570 cm and females 446 cm (Bloch et al. 1993). Their vocalisations include whistles with dominant frequencies between 1.6-6.7 kHz, and clicks between 1- 18 kHz (Richardson et al. 1995). Weilgart & Whitehead (1990) showed that the complexity of the whistles produced was associated with different behaviours, with simple whistles used more during resting and complex whistles and clicks produced more often during active behaviour such as foraging.

Long-finned pilot whales show a strong preference for water deeper than 600 m (Cañadas et al. 2002; Cañadas et al. 2005; Cronin & Mackey 2002; Hooker et al. 1999; Kiszka et al. 2007; Macleod 2001; Skov et al. 1995), and relatively high slopes (Hooker et al. 1999, Cañadas et al. 2002). They have generally been associated with the warmer water available within an area (Hooker et al. 1999), although Paxton et al. (in review) found an association with warmer water only in shallow areas. It was suggested by Hoydal & Lastein (1993) that movement into shelf waters with warmer SST is related to the movement of prey onto shelf waters. In US waters, pilot whales were found to move northwards and onto the shelf following the inshore movement of their squid prey (Payne & Heinemann 1993). Long-finned pilot whales' distributions have also been found to correlate with areas of higher primary productivity on the west coast of Scotland (MacLeod et al. 2007).

Prey taken by long-finned pilot whales sampled from the Faroes drive fishery predominantly comprised the squid species *Todarodes sagittatus* and *Gonatus* spp., though some pods were found to feed almost exclusively on fish species such as greater Argentine (*Argentina silus*) and blue whiting (*Micromesistius poutassou*) (Desportes & Mouritsen 1993). Off the west coast of Scotland these prey species are mainly found at the shelf-edge and deep waters between 100-500 m depth (Desportes & Mouritsen 1993), which corresponds to the depth at which pilot whales were shown to make foraging dives in the Mediterranean of 360-648 m (Baird et al. 2002).

1.3.2.2 Atlantic white-sided dolphin (Lagenorhynchus acutus)

Atlantic white-sided dolphins were found to be the most abundant cetacean species off the west coast of Scotland in a number of surveys (Compton et al. 2007; Macleod et al. 2003; Wall et al. 2006; Weir et al. 2001). They are allopatric to white-beaked dolphins, preferring deep waters in the north-east Atlantic whilst the white-beaked dolphins are predominantly a shelf species (Northridge et al. 1997), except in the North Sea (Hammond et al. 2002).

The Atlantic white-sided dolphin is smaller than the bottlenose dolphin (*Tursiops truncatus*) but larger and heavier than the common dolphin, reaching a maximum length of between 250-270cm (Cipriano 2002). Like most odontocetes, the white-sided dolphin produces both whistles and broadband clicks, with whistle dominant frequencies between 6-15 kHz (Richardson et al. 1995).

Habitat preferences of white-sided dolphins vary geographically, but in the north-east Atlantic they are found to prefer deep and shelf-edge waters (Macleod 2001; Macleod et al. 2003; MacLeod et al. 2007; O'Cadhla et al. 2004; Skov et al. 1995; Weir et al. 2001). However, they are also found to prefer areas of high seabed relief in the north-western Atlantic, and relatively cool sea surface temperatures compared to other species within the same area (Hooker et al. 1999; Selzer & Payne 1988).

The diet of the white-sided dolphin predominantly includes small pelagic schooling fish or squid such as the short-finned squid (*Illex illibrosis*), herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) (Couperus 1997; Palka et al. 1997).

1.3.2.3 White-beaked dolphin (Lagenorhynchus albirostris)

White-beaked dolphins off the west coast of Scotland are mainly concentrated on the northern Scottish shelf with concentrations around the northern Minch and northern Outer Hebrides especially in spring and summer (Northridge et al. 1995; Northridge et al. 1997; Macleod 2001; Skov et al. 1995; Weir et al. 2001). However, Bloor et al. (1996) also found that white-beaked dolphins were the most frequently recorded cetacean species in waters between the Shetland and the Faroe Islands.

The white-beaked dolphin is of a similar size and weight to the Atlantic white-sided dolphin, growing to 240-310 cm in length, with males generally larger than females (Kinze 2002). They produce both whistles and clicks, with whistle dominant frequencies between 8-12 kHz (Richardson et al. 1995), and broadband clicks extending as high as 120 kHz (Rasmussen et al. 2002).

Little is known about their habitat preferences, though they are predominantly a shallow coastal species (Evans 1990; Northridge et al. 1995; Northridge et al. 1997; MacLeod et al. 2007; Skov et al. 1995; Weir et al. 2001). MacLeod et al. (2007) found that white-beaked dolphins were allopatric to common dolphins in Scottish shelf waters, with white-beaked dolphins preferring cooler waters to those of common dolphins.

In Scottish waters, white-beaked dolphins have been found to eat mainly whiting (*Merlangius merlangus*), though stomach contents also included haddock, cod, hake, herring, mackerel, scad, sandeel and the octopus *Eledone cirrhosa* in the North Sea (Kinze et al. 1997; Santos et al. 1994).

1.3.2.4 Short-beaked common dolphin (Delphinus delphis)

The short-beaked common dolphin is found in both shelf and off-shelf waters off the west coast of Scotland (Macleod 2001; MacLeod et al. 2007; Moscrop 1997; O’Cadhla et al. 2004; Skov et al. 1995; Wall et al. 2006,), though the northern extent of the species is limited to < 56ºN (Skov et al. 1995), <59ºN (Macleod 2001) or <60ºN (Weir et al. 2001). There is some indication that the species is extending its range northwards as the sea warms (MacLeod et al. 2005).

The short-beaked common dolphin is the smallest of the delphinids found on the west coast of Scotland with males measured between 172-201 cm and females 164-193 cm in length (Perrin 2002). Their whistles are similar frequencies to both white-sided and white-beaked dolphins with dominant frequencies between 8-14 kHz (Richardson et al. 1995), and clicks with dominant frequencies between 23-67 kHz (Richardson et al. 1995).

Habitat preferences of common dolphins vary geographically, with the species being detected in depths from around 300 m off the west coast of Scotland (Macleod 2001) to deep water between 900-1100 m in the Bay of Biscay (Kizka et al. 2007) and in the NW Atlantic (Hooker et al. 1999). In some studies, common dolphin depth preferences were found to change between years (Cañadas et al. 2002; Forney 2000). However, they do appear to prefer areas with high sea floor relief (Hooker et al. 1999; Hui 1979; Kizka et al. 2007; Selzer & Payne 1988). They are generally a warm water species, being found to move inshore with increasing SST (Gaskin 1968; Goold 1998; Neumann 2001), presumed to be due to the changing distribution of their prey with SST. Temperature also divides the habitat preferences of common dolphins from that of white-sided dolphin (Selzer & Payne 1988) and the white-beaked dolphin (MacLeod et al. 2007), with common dolphins preferring warmer water than the other two species. Salinity was also found to divide the habitats of common dolphins from that of white-sided dolphins, with common dolphins preferring the warmer saltier water (Selzer & Payne 1988). In the eastern tropical Pacific, common dolphins associated with an upwelling habitat characterised by a shallow weak thermocline and high chlorophyll (Reilly & Fiedler 1994).

In Scotland, common dolphins have been found to feed mainly on whiting and sandeels (Santos et al. 1994), though elsewhere in the north Atlantic, stomach contents suggest a diet of anchovies *Engraulis encrasicolus*, sardines *Sardina pichardus*, *Trachurus* spp, and *Trisopterus* spp. (Silva 1999; Meynier 2004).

1.3.3 Sperm whales (Physeter macrocephalus)

The sperm whale is one of the most abundant of the large whales off the west coast of Scotland (O Cadhla et al. 2004; Weir et al. 2001), and is distributed throughout the deep waters of the Rockall Trough and Faroe-Shetland Channel (Hastie et al. 2003;

Macleod et al. 2003; Moscrop 1997; O'Cadhla et al. 2004; Skov et al. 1995; Weir et al. 2001). Around the British Isles, strandings of sperm whales have predominantly been of adult and sub-adult males (Berrow & Rogan 1997; Evans 1997; Santos et al. 1999). These animals are likely to have dispersed from their natal groups in lower latitudes to feed in the more productive higher latitudes, and may eventually return to lower latitudes seasonally to breed (Best 1979).

It is not known whether the deep waters off the west coast of Scotland form a migratory route or a more permanent feeding ground, although studies in similar temperate areas found that male sperm whales can remain within an area foraging for long periods of time (Whitehead et al. 1992). Evidence that this area may be used as a foraging ground comes from stable isotope analysis of stranded sperm whales from Scotland, suggesting that between the ages of 10 and 20 years sperm whales tend to remain in temperate waters to feed before travelling to higher latitudes shortly before breeding age (Mendes et al. 2007). It is therefore hypothesised that the deep waters of the west coast of Scotland form may form both a migratory route for large mature breeding males travelling to and from the breeding grounds and a foraging area for 'bachelor herds' of sperm whales.

Sperm whales are the largest of the odontocetes, with mature males reaching 16 m. Females are much smaller with an average length of 11m (Whitehead 2002). Their most distinctive feature is their large 'box-like' head which comprises around a third of the total body length, predominantly comprising the spermaceti organ (Whitehead 2002; Whitehead 2003). It is believed that this organ is primarily adapted for production of very powerful (223dB re 1μPa) directional clicks (Møhl et al. 2000) used for navigation (Johnson & Tyack 2003; Zimmer et al. 2003) and for foraging (Miller et al. 2004, Møhl et al. 2003). Sperm whale clicks have dominant frequencies between 2-4 kHz and 10-16 kHz (Richardson et al 1995), produced at very regular intervals of around a click every 0.5 seconds (Whitehead & Weilgart 1991). More rapid clicks occur in 'buzzes' or 'creaks' as the sperm whale closes down on a prey item (Miller et al. 2004). They are most easily detected acoustically rather than visually, since they spend around 80% of their time on foraging dives (Gordon & Steiner 1992), making it difficult to see them at the surface.

Sperm whales habitats are mainly characterised by deep water, especially with high gradients and at the shelf edge (Baumgartner et al. 2001; Davis et al. 1998; Davis et al. 2002; Gregr & Trites 2001; Hamazaki 2002; Kenney & Winn 1986; Macleod et al. 2003; O'Cadhla et al. 2004; Watwood et al. 2006; Weir et al. 2001; Whitehead et al. 1992). They are also often found in highly productive areas (Jaquet 1996; Jaquet & Whitehead 1996), including upwellings (Papastavrou et al. 1989; Smith & Whitehead 1993) and eddies produced on edges of warm and cold current confluences (Davis et al. 2002; Griffin 1999). However, they are also found in areas with very low productivity, where downwelling and aggregative processes take biological material into the deep sea ecosystem (Berzin 1971). All these preferences are hypothesised to be due to high densities of squid found in these areas (Davis et al. 1998; Papastavrou et al. 1989) though there is little independent information on the densities and distribution of squid.

Sperm whale distributions have been linked to features in sea surface temperature, which may be indicators of oceanographic processes acting to concentrate prey (Cañadas et al. 2005; Davies et al. 1998, Hamazaki 2002; Gannier & Praça 2007; Smith & Whitehead 1993). For example, Gannier & Praça (2007) found that sperm whales in the Mediterranean were found near fronts characterised by changes in SST. Whereas Smith & Whitehead (1993) found that sperm whales were associated with the cooler water brought to the surface by the upwelling around the Galapagos. Thermocline depth and strength have also been used as indirect indicators of the presence of eddies or warm-core rings to confirm that sperm whales were associating with these features (Baumgartner et al. 2000; Davis et al. 1998).

Sperm whale diet is dominated by cephalopods in most areas (Clarke 1996; Evans & Hindell 2004; Santos et al. 1999; Santos et al. 2002; Simon et al. 2003; Smith & Whitehead 2000), though some fish is also an important prey and can be the major component in some areas, for example in waters close to Iceland (Roe 1969; Martin & Clarke 1986). In Scottish waters, sperm whales diet was dominated by cephalopods, mainly *Gonatus fabricii* but also other oceanic cephalopods such as *Histioteuthis bonnelli*, *Teuthowenia megalops*, *Todarodes sagittatus* and the octopus *Haliphron atlanticus* (Santos et al. 1999; Santos et al. 2002).

1.4 Oceanography of the west coast of Scotland

The waters off the west coast of Scotland (Figure 1.1) can be divided into three main oceanographic areas: (i) shelf waters; (ii) off-shelf Rockall Trough waters including the isolated seamounts and offshore banks; and (iii) Faroe-Shetland Channel waters.

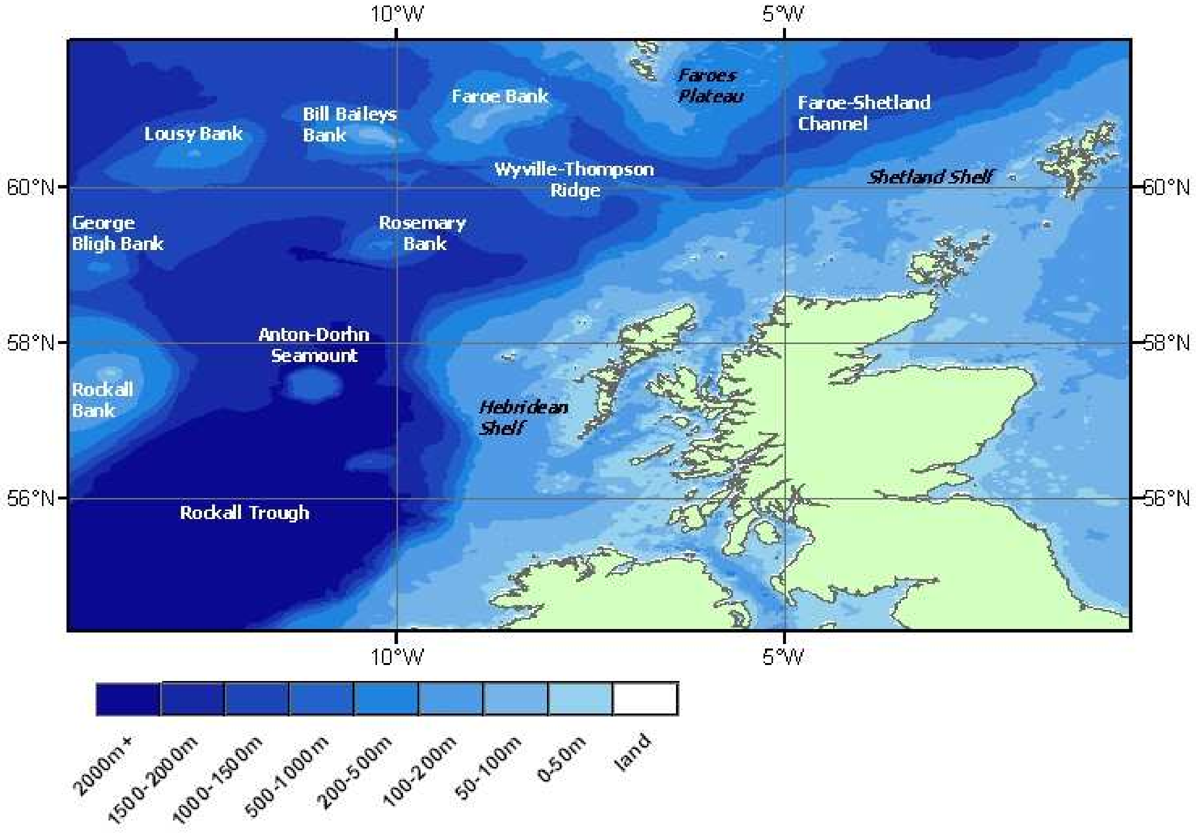


Figure 1.1 – West coast of Scotland survey area including GEBCO topography.

1.4.1 Shelf waters

The area around the Inner Hebrides covers all of the coastal islands and water between the Scottish mainland and the Outer Hebridean islands of Barra to the south and Lewis to the north (Figure 1.2). This is a tidally and topographically complex region, with three main water masses: (i) an inflow of Atlantic water travelling northwards from along the west coast of Ireland: the ‘Atlantic intrusion’; (ii) Irish sea inflow through the North Channel between the Mull of Kintyre and Ireland; (iii) coastal water with a lower salinity due to the high freshwater runoff from the mainland (Gillibrand et al. 2003).

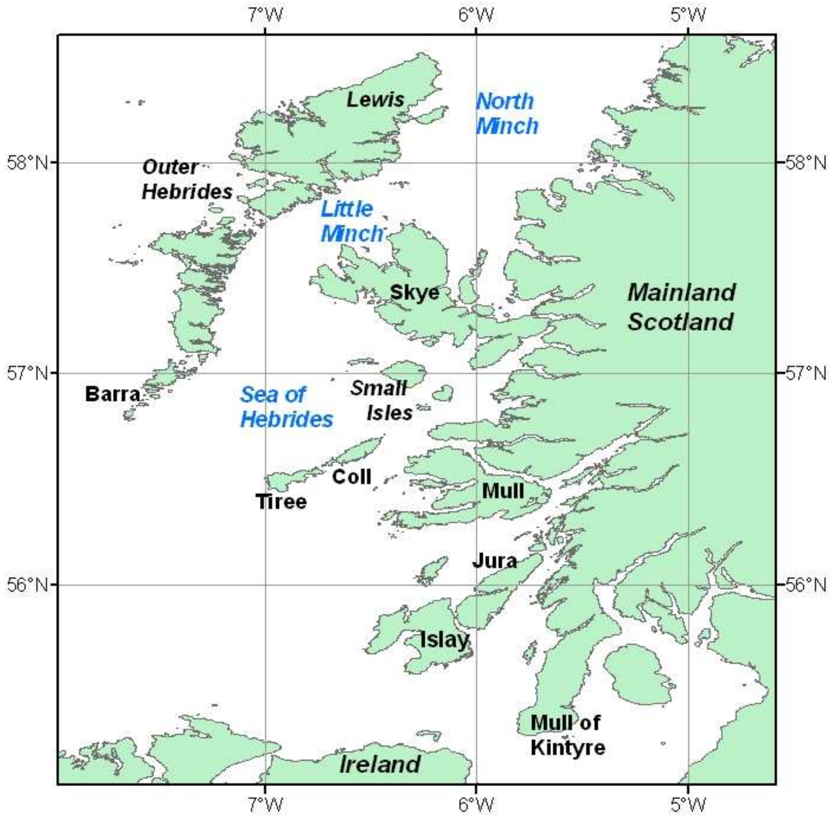


Figure 1.2 – Inshore waters off the west coast of Scotland

The Atlantic inflow brings high salinity, high nutrient warm water into the Sea of Hebrides causing cyclonic circulation within the Sea of Hebrides. The Islay Front is formed where the Atlantic water meets the Irish Sea water (Simpson et al. 1979). Because the tides from the Atlantic and Irish Sea are 180º out of phase with each other they cancel each other out and the tidal range is at a minimum where the two currents meet. Gillibrand et al. (2003) showed the existence of a strong southerly flow at depth through the Little Minch during spring, bringing with it high levels of nutrients. The combination of the Atlantic intrusion and the southerly flow through the Little Minch, makes the Sea of Hebrides a nutrient rich, and hence productive area. Moreover, Gillibrand et al. (2003) also showed high levels of productivity especially in autumn and spring around the coastline where there was high freshwater input from the land.

1.4.2 Rockall Trough

The waters of the Rockall Trough are composed of two main bodies: the surface North Eastern North Atlantic Water (NENAW), and the deep Labrador Sea Water

(LSW). The NENAW brings warm salty waters from the south (Ellett & Martin 1973; Holliday 2003) mainly along a 50km wide band along the Scottish shelf edge (Shelf Edge Current), over the Wyville Thompson Ridge, along the Shetland side of the Faroe-Shetland Channel and into the Norwegian Sea (New & Smythe-Wright 2001; Turrell et al. 1999). However, there is also a significant northward flow of warm salty NENAW in the upper layer on the west side of the Rockall Trough (Rockall Trough Current), which flows to the west of Anton Dohrn Seamount, and causes anticyclonic circulation around the seamount (New & Smythe-Wright 2001). The deep water (>1200 m) is characterised by the Labrador Sea Water, which is much fresher than the surface NENAW water, entering the Rockall Trough at its basin south-west of Ireland, but limited to the north of the Rockall Trough by shallowing topography (Ellet & Martin 1973; Holliday 2003). There is therefore a permanent deep thermocline within the Rockall Trough caused by this layering of water masses. At the upper end of the Rockall Trough the Labrador Sea Water forms a cyclonic gyre, mixing with the cold dense Norwegian Sea Deep Water (NSDW) that overflows from the Wyville-Thompson Ridge (New & Smythe-Wright 2001; Turrell et al. 1999).

1.4.3 Faroe-Shetland Channel

The waters of the Faroe-Shetland Channel (FSC) are the most complex, with five different water masses meeting in the deep channel, and resulting in a dynamic oceanic regime (Sherwin et al. 1999; Sherwin et al. 2006; Turrell et al. 1999). The surface water is characterised by the northward moving warm saline North Atlantic Water (NAW), which forms the Shelf Edge Current flowing along the Scottish shelf edge northwards. Adjacent to this water on the Faroes side of the FSC lies the Modified North Atlantic Water (MNAW) which is NAW water that has passed through Icelandic waters and therefore cooled and freshened before arriving from the north travelling south over the Faroes shelf forming the majority of the FSC surface waters. Where these two water masses meet a front is formed, which is advected into mesoscale meanders and cold core eddies by the large currents that move the NAW water northwards (Sherwin et al. 1999; Sherwin et al. 2006). Below this water on the Faroe Plateau side and at depths between 400-800 m is the Arctic Intermediate Water which is cooler and less saline than either the NAW or MNAW and mainly recirculates within the FSC (Turrell et al. 1999). Deeper still at between 600-800 m on the Faroe Plateau side of the FSC is the Norwegian Sea Intermediate Water (NSIW) which has the lowest salinity of all the bodies of water. On the Shetland shelf side of the channel this water body mixes with the AIW water due to the shallowness of both layers on that side of the channel. Finally, there is the deep layer below 800 m which forms the Faroe Shetland Channel Bottom Water (FSCBW), which has varying amounts of NSDW water (cooler but saltier than that NSIW layer) dependent on the varying supply of water from the Greenland Sea (Turrell et al. 1999).

1.4.4 Offshore biological oceanography

Biologically, the complex hydrography makes the west coast of Scotland a productive area, with high transport of many species of fish within the shelf current (Bartsch & Coombs 1997; Borja et al. 2002; Ibaibarriaga et al. 2007; Shelton et al. 1997). Fronts are formed at the shelf edge between the shelf water and warmer, saltier shelf edge current (Mann & Lazier 2006). Shelf-edge fronts are the most biologically active type of fronts in the ocean (Mann & Lazier 2006). The shelf edge therefore provides both food and transport for migrating species such as salmon and mackerel (Borja et al. 2002; Shelton et al. 1997), but alsoe attracts other non-migratory shelf-edge species such as blue whiting (Armstrong pers. comm.). The little data available for productivity within the Rockall Trough itself suggests that the Rockall Trough Gyre also aggregates both zooplankton (*Calanus*: Planque & Fromentin 1996), and fish (blue whiting larvae: Barsch & Coombs 1997).

1.5 Monitoring species distributions using passive acoustics

Recently, passive acoustic methods have become established as an effective method of surveying some cetacean species (Clark & Fristrup 1997; Gillespie 1997; Goold 1998; Gordon et al. 2000; Hastie et al. 2003 & 2005; Leaper et al. 1992). They are especially useful for studying the distribution of those species that are difficult to see, such as harbour porpoises (Bailey 2006; Gillespie & Chappell 2002; Gillespie et al. 2005, Gridley 2005), or those that spend long periods underwater, such as sperm whales (Bailey 2006; Clark & Fristrup 1997; Fristrup & Clark 1997; Gannier & Praca 2007; Gillespie 1997; Gillespie & Chappell 2002; Gordon et al. 2000; Gridley 2005; Hastie et al. 2003; Hastie et al. 2005; Leaper et al. 1992; Leaper et al. 2000; Lewis et al. 2007). The merits of passive acoustic methods for understanding species distributions can be quite compelling, with detection rates for harbour porpoises over

8 times higher that for visual methods due to the ability to survey even in poor sea states (Gillespie et al. 2005). Not only does passive acoustics allow for detection of cetaceans in most sea states, during the night and in poor weather conditions, but since it can be highly automated it also requires fewer people than visual surveying methods. This is particularly useful in platforms of opportunity studies where there is often space for only a few researchers and this is one of the main reasons that we have used these methods so widely in this study.

1.5.1 Passive acoustics for harbour porpoises

Since harbour porpoises show little of themselves at the sea surface and move slowly through the water leaving little spray or wake, they are very difficult to observe visually except in very calm seas. Sightings rates for porpoises decrease by 75% from Beaufort sea state 0 to Beaufort sea state 2 or 3 (Palka 1996). Passive acoustic systems that can detect the echolocation sounds of harbour porpoises allow for detection of porpoises even when they cannot be seen. Passive acoustic systems have therefore come into importance recently for studying the distribution of harbour porpoises (Bailey 2006; Gillespie et al. 2005; Gridley 2005; SCANS-II 2006).

Harbour porpoises echolocation clicks have been measured in captivity and in the wild to between 110-150 kHz peak frequency (Goodson & Sturtivant 1996; Hatakeyama & Soeda 1990; Richardson et al. 1995). Due to the high frequency nature of harbour porpoise vocalisations, special equipment is required to automatically detect their clicks. The most-widely used system for automatic detection of harbour porpoise clicks was developed by the International Fund for Animal Welfare (IFAW: Chappell et al. 1996; Gillespie & Chappell 2002; Leaper et al. 1992). This system is able to detect the high frequency vocalisations of the harbour porpoises converting it to an audible click that can be heard by an acoustic ‘observer’. The software is able to detect a wide range of pulsed high frequency sounds within the 115 – 145 kHz band, which in addition to the porpoise clicks include clicks from other sources such as snapping shrimp, white-beaked dolphins, pilot whales, and vessel-sourced noise (Gillespie & Chappell 2002). By also measuring the energy in two ‘noise’ bands at 50 and 75 kHz, the system is able to classify clicks by their frequency characteristics: porpoise clicks by their high frequency component but lack of low frequency components; snapping shrimp, white-beaked dolphins and pilot whales by their broadband components over all three frequencies; and noise which is generally confined to lower frequencies (Gillespie & Chappell 2002). Since the hydrophone includes two elements spaced a known distance apart, it is also possible to estimate the bearing to the clicks (with no left or right discrimination) based on the difference in the arrival time of each click at each hydrophone. High frequency sounds are attenuated over relatively small distances in the ocean (Urick 1983), so the range to which harbour porpoises can be detected is equally small, with highest detection at around 100 m, and dropping rapidly such that clicks are rarely detected > 300 m (Gillespie & Chappell 2002).

At the time of the fieldwork carried out during this thesis, the porpoise detection software was only able to classify clicks that had clearly higher amplitude within the high frequency band (Embling 2003). Since porpoises tend to scan the area around them by moving their head or body from side to side (Goodson & Sturtivant 1996), most click trains tend to be made up of a combination of on-axis clicks and lower amplitude off-axis clicks on the same bearing. These off-axis clicks have a much lower source level and possibly different spectral characteristics because the echolocation clicks of harbour porpoises are highly directional (Au et al. 1999). They are thus not generally identified by the software as porpoise clicks. Identification of porpoise clicks not automatically recognised by the software was then only possible through a time-consuming visual inspection of the click data, post survey. However, some attempts have been made to automate this process (Caillat 2005; Embling 2003) with some success, and the new generation of porpoise detector that was used during SCANS-II harbour porpoise abundance surveys throughout European waters have had these improvements incorporated.

1.5.2 Passive acoustics for sperm whales

Sperm whales produce distinctive loud (up to 236 dB re 1μPa) directional clicks (Møhl et al. 2003) between 0.1-30 kHz with dominant frequencies between 2-4 kHz and 10-16 kHz (Richardson et al. 1995). They spend around 80% of their time underwater on foraging dives (Gordon & Steiner 1992, Papastavrou et al. 1989, Watwood et al. 2006), during which they click nearly continuously (Douglas et al. 2005; Watwood et al. 2006). These characteristics mean that passive acoustic techniques are ideal for locating sperm whales in studies of their behaviour (Mullins et al. 1988; Papastavrou et al. 1989; Smith & Whitehead 1992; Watkins & Schevill 1977; Whitehead & Weilgart 1991), ecology and distribution (Gannier et al. 2002; Gannier & Praça 2007; Gillespie 1997; Gordon et al. 2000; Leaper et al. 1992; Jaquet & Gendron 2002; Jaquet & Whitehead 1996, Rendell et al. 2004; Whitehead et al. 1992), and for estimating abundance (Barlow & Taylor 2005; Gillespie 1997; Hastie et al. 2003; Leaper et al. 1992). Similar to that for harbour porpoises, the use of a two-element towed hydrophone array for detecting sperm whales makes is possible to measure bearings to vocalising animals (Gillespie 1997; Leaper et al. 1992). This allows for individual sperm whales to be tracked and the distance to each whale to be estimated using target motion analysis (Gillespie 1997; Hastie et al. 2003; Leaper et al. 1992). Previous studies estimated effective strip width distances from 5.5 km (Hastie et al. 2003) to 8.0 km (Leaper et al. 2001). Although Barlow & Taylor (2005) found that the effective strip width (esw) changed depending on whether slow clicks were detected (esw = 19.6 km), or whether faster clicks were detected (esw = 4.5 km). This effective strip width distance is much greater than that achieved for visual methods (Barlow & Taylor 2005), and so allows for larger area coverage during surveys.

Although the automatic identification of sperm whales is automated to a much greater degree to that for harbour porpoises, identification of individual tracks of whales still requires a time-consuming visual inspection of the click data, post survey. Methods of automatic tracking of individual whales from their clicks are currently being investigated for sperm whales (Gillespie pers. comm.), however were not available at the time of this thesis

1.5.3 Passive acoustics for delphinids

The use of passive acoustics for delphinids has the main benefit of requiring fewer people than the equivalent visual survey methods, so it is ideal for platforms of opportunity where space is often limited with only enough space for one or two researchers. Detection can be made relatively automated, with the automatic detection of whistles (Lewis et al. 2000) and automatic acoustic recordings made at regular intervals that can be listened to post-survey. However, passive acoustics for delphinids is limited by the difficulty of species identification using acoustic cues. Previous studies have suggested that some species can be reliably distinguished on the basis of their whistles (Oswald et al. 2003; Rendell et al. 1999; Steiner 1981), but these involved making time consuming measurements by hand and only recently have near real-time species identification tools been developed for Pacific Ocean species (Oswald et al. 2007). Therefore, currently passive acoustics only allows for the study of 'whistling odontocete' distribution rather than individual delphinid distributions.

There is some evidence to suggest that delphinids can be detected acoustically to at least the same range as visual techniques (Gordon et al. 2000). Delphinid active space (the distance at which another delphinid can perceive the whistle of a conspecific) was estimated to have a radius of 14-25 km for bottlenose dolphins (*Tursiops truncatus*) and 10-15 km for killer whales (*Orcinus orca*) (Janik 2000; Miller 2006). This suggests that it may be possible to detect delphinids to a much greater range to that of visual methods. However, little is known about the behavioural changes in vocalisation rates of delphinids. There is some evidence that delphinids change vocalisation rates and patterns with different behaviours (Cook et al. 2004; Janik 2000; Jones & Sayigh 2002). Janik (2000) found that a specific type of whistle was produced just before bottlenose dolphin fed on salmon; however Jones & Sayigh (2002) found that vocalisation rates in bottlenose dolphins were generally less for feeding than for travelling and socialising. There is therefore the chance that a group of delphinids may be missed if they are not vocalising during the time at which a survey vessel passes within acoustic range, or that detections may be biased towards certain behaviours. Despite these limitations, passive acoustic monitoring for 'whistling odontocetes' still remains the most cost effective and efficient technique for platforms of opportunity.

1.5.4 Passive acoustics in this study

In this thesis, passive acoustic methods were used alongside visual survey methodology to survey for harbour porpoises in the coastal waters of the west coast of Scotland (Chapter 4). Passive acoustic methods were used on their own from platforms of opportunity to monitor off-shore distributions of both sperm whales (Chapter 3) and delphinids (Chapters 2 & 5).

1.6 Cetaceans and noise

The west coast of Scotland and the ‘Atlantic Frontier’ that it adjoins both an important area for cetaceans (Buckland et al. 1993; Cronin & Mackey 2002; Evans 1990; Macleod 2001; Macleod et al. 2003; MacLeod et al. 2007; Moscrop 1997; O’Cadhla et al. 2004; Skov et al. 2001; Wall et al. 2006; Weir et al. 2001; Zachariassen 1993), and also for offshore industrial development (Harwood & Wilson 2001) and military exercises (MacLeod et al. 2007). Developments include seismic surveys for oil and gas, construction of oil and gas production platforms and associated structures, potential offshore windfarms, and associated boat traffic, all of which create acoustic noise pollution (Harwood & Wilson 2001; Richardson et al. 1995). It is this noise pollution which is the main concern for cetacean distributions off the west coast of Scotland, the effects of which are reviewed briefly below.

Boat traffic produces relatively low frequency noise < 500 Hz (Richardson et al. 1995). Behavioural response from cetaceans to vessel noise often varies depending on the behaviour or species. For example, Würsig (cited in Richardson et al. 1995) found that resting dolphins tended to avoid the vessel, foraging dolphins would ignore the vessel, and socialising animals would be attracted to the vessel. Other species, such as killer whales, have been shown to increase the length of their vocalisations in response to increased boat traffic; perhaps to compensate for the ‘masking’ of sounds by this increased ambient noise level (Foote et al. 2004). Similar findings were found for other animals in noisy environments: for example nightingales were found to sing louder in noisier environments (Brumm 2004). On the whole, for any species that uses sound as a form of communication or for foraging, high levels of ambient noise will mask their signals and thus impair the exchange of vital information (Brumm 2006). Other than changes in vocalisation loudness (Brumm 2004), complexity (Slabbekoorn & den Boer-Visser 2006), or length (Foote et al. 2004), physical displacement from the preferred habitat may occur (Caron & Sergeant 1988).

The recent development of offshore windfarms has resulted in a number of studies of the effects of the noise created during the construction phase (Carstensen et al. 2006; David 2006; Tougaard et al. 2003; Tougaard et al. 2005). Carstensen et al. (2006) showed that harbour porpoises frequented the area around a wind farm less during the pile driving phase of construction than previous to pile driving, increasing the time between encounters from 6 hours to 3 days. This reaction was mirrored in studies carried out at other windfarm construction sites (Tougaard et al. 2003; Tougaard et al. 2005) with significant effects up to 15 km from the construction site during pile driving (Tougaard et al. 2003). David (2006) suggested that the sound from pile driving could be detectable to bottlenose dolphin to up to 40 km, and might mask vocalisations at 9 kHz as far as 10-15 km. This is likely to reduce the distance over which dolphins will be able to communicate with each other and the ability to detect other sounds. However, little is known of the importance of such long-range communication or the effect that masking is likely to have on the population.

Seismic surveys use arrays of airguns which are amongst the most powerful underwater sound sources and this has given rise to concerns about their effects on marine mammals (Gordon et al. 2004). Airguns release high pressure air into the water every few seconds producing a pulsed sound as the air pulse expands and contracts through the water (Richardson et al. 1995). This produces a very loud (248-255 dB re 1μPa rms) broadband sound pulse which travels both horizontally and vertically through the water column (Richardson et al. 1995). The sounds are so loud that they have been picked up by an array of hydrophone moored near the mid-Atlantic Ridge over 3000 km from the seismic airguns (Nieukirk et al. 2004). Cetacean reactions to such sounds vary from changes in migration paths (Malme et al. 1984), to behaviour that results in serious harm or death (Cox et al. 2006). Malme et al. (1984) showed that gray whales (*Eschrichtius robustus*) migrating along the California coast reacted to airgun pulses by turning away from the noise source and increasing respiration rates, causing temporary disturbance to migration patterns. Goold (1996) and Goold & Fish (1998) showed that common dolphins (*Delphinus delphis*) reduced vocalising during seismic activity in the Irish Sea, with only 4% of acoustic cues heard during periods when airguns were firing in comparison to 96% when the airguns weren’t in use. The most extreme reaction to airguns used during seismic surveys was death: beaked whales found stranded in the Gulf of California in September 2002 were linked to seismic activity that had been conducted within the vicinity and time that the strandings occurred (Cox et al. 2006).

However, it is military sonar that has received the most attention (Barlow & Gisiner 2006; Cox et al. 2006; Dalton 2006; Frantzis 1998; Jasney et al. 2005; Jepson et al.

2003; Miller et al. 2000; Rendell & Gordon 1999; Rommel et al. 2006). Strandings of mainly beaked whales have been linked to the use of low or mid-range sonar < 10 kHz (Barlow & Gisiner 2006; Cox et al. 2006; Dalton 2006; Frantzis 1998; Jepson et al. 2003). Beaked whale strandings linked with military sonar have taken place in: Greece in May 1996 (Frantzis 1998); the Bahamas in March 2000 (Barlow & Guisiner 2006); Madiera in May 2000 (Cox et al. 2006); the Canary Islands in September 2002 (Jepson et al. 2003), and more recently Spain in January 2006 (Dalton 2006). In several cases it was found that the whales had gas-bubble lesions with strong evidence that they had been formed *in vivo* (Dalton 2006; Jepson et al. 2003). Such evidence from the pathological studies suggests that these bubbles were formed through a decompression-type mechanism probably related to changes in behaviour in response to anthropogenic noise sources such as sonar (Jepson et al. 2003; Jepson et al. 2006). However, other behavioural changes have been observed, including increasing the length of male humpback song (Miller et al. 2000) and changes in long-finned pilot whale whistle behaviour (Rendell & Gordon 1999), the consequences of which are less clear.

Military exercises are conducted regularly off the west coast of Scotland (Parsons et al. 2000; DSTL pers. comm.), and often involve the testing of the low to mid-frequency sonar systems used to detect submarines (MacLeod et al. 2007). Harwood (2002) suggested that one of the ways of reducing the exposure of sensitive species to any impact is to reduce the use of these noise sources in areas of critical habitat. Therefore one of the mitigation measures being put into place by NATO and the Royal Navy involves the development of predictive tools for the distribution of cetaceans, and an acoustic risk mitigation tool (Carron 2004). Knowledge of marine mammals offshore, and the development of predictive tools for the distribution of marine mammals can help with mitigation by allowing threats and sensitive animals to be separated in time and/or space.

1.7 Thesis structure

This thesis forms the first predictive modelling study of cetaceans off the west coast of Scotland. It is based on those species that can be detected using passive acoustics, namely: harbour porpoises (Chapter 4); dolphins (Chapter 2 & 5) and sperm whales

(Chapter 3). State of the art predictive modelling techniques were used to investigate model robustness over both time and space.

Chapters 2 and 3 analyse data collected from platforms of opportunity during hydrographic surveys carried out by the Fisheries Research Services (FRS), Scottish Association for Marine Science (SAMS) and the National Oceanography Centre (NOC) in offshore waters to the west of Scotland. Chapter 2 presents the results of the predictive models of delphinid distributions. Chapter 3 is based on the sperm whale passive acoustic detections, and examines the effect of spatial scale both by *extent* and *grain* size on model selection and environmental smooths.

Chapter 4, which deals with harbour porpoises, is based on data collected in conjunction with the Hebridean Whale and Dolphin Trust (HWDT) within the Inner Hebrides, and was also the only data set to combine both visual and passive acoustic survey data. In this chapter I was therefore able to compare predictive models based on the different survey methodologies, in addition to examining the effect of both time (in years) and space on the predictive models and species-environment relationships.

Chapter 5 uses data collected from a platform of opportunity during the FRS herring stock assessment surveys, which were carried out in shelf waters to the west of the Hebrides. The primary purpose of this survey was to provide an assessment of the distribution and density of herring using active acoustic techniques (ICES 2005, 2006). Thus in this chapter I have been able to examine the correlation between delphinid and herring distributions to evaluate whether herring could be used as an appropriate *direct* predictor of delphinid distributions. It also investigates a new methodology for investigating species co-occurrences, based on a technique used within fisheries research.

Chapter 6 (final discussion) provides a final synthesis of the thesis results, and places them into context within the overall framework of mitigating acoustic threats to cetaceans populations.

1.8 References

Aarts, G. 2006. Modelling space-use and habitat preference from wildlife telemetry data. PhD Thesis. School of Biology. University of St Andrews.

Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162:211-232.

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

Araujo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14:529-538.

Arnott, S. A., and G. D. Ruxton. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Marine Ecology Progress Series 238:199-210.

Au, W. W. L., R. A. Kastelein, T. Rippe, and N. M. Schooneman. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). J. Acoust. Soc. Am. 106:3699-3705.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157:101.

Bailey, H. 2006. Distribution and habitat use of bottlenose dolphins (*Tursiops truncatus*) at varying temporal and spatial scales. PhD Thesis. Department of Zoology. University of Aberdeen.

Baird, R. W., J. F. Borsani, M. B. Hanson, and P. L. Tyack. 2002. Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. Marine Ecology Progress Series 237:301-305.

Bakkenes, M., R. M. Alkemade, F. Ihle, R. Leemans, and J. B. Latour. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology 8:390-407.

Barlow, J., and R. Gisiner. 2006. Mitigating, monitoring and assessing the effects of anthropogenic sound on beaked whales. J. Cetacean Res. Manage. 7:239-249.

Barlow, J., and B. L. Taylor. 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. Marine Mammal Science 21:429-445.

Bartsch, J., and S. Coombs. 1997. A numerical model of the dispersion of blue whiting larvae, *Micromesistius poutassou* (Risso), in the eastern North Atlantic. Fisheries Oceanography 6:141-154.

Baumgartner, M. F., K. Mullin, L. N. May, and T. D. Leming. 2001. Cetacean habitats in the northern Gulf of Mexico. Fishery Bulletin 99:219-239.

Beare, D. J., D. G. Reid, and E. McKenzie. 2003. Fish schooling behaviour in the northwest North Sea: interspecific associations measured by acoustic survey. Aquatic Living Resources 16: 307-312

Bearzi, M. 2005. Habitat partitioning by three species of dolphins in Santa Monica Bay, California. Bull. Southern California Acad. Sci. 104(3): 113-124.

Beaugrand, G., K. M. Brander, J. A. Lindley, S. Soussi, and P. C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. Nature 426: 661-664.

Beaugrand, G., and P. C. Reid. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology 9: 801-817.

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

Berrow, S. D., and E. Rogan. 1997. Review of cetaceans stranded on the Irish coast, 1901-95. Mammal Review 27:51-76.

Berzin, A. A. 1971. The sperm whale. Yablokov, A. V. (ed), Pischevaya Promyshlenmost; translation by Israel Program for Scientific Translations, Moscow. As cited in Jaquet (1996).

Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn, and B. L. Olla, editors. Behaviour of marine mammals. Plenum Press, New York.

Bjørge, A., and K. A. Tolley. 2002. Harbour porpoise *Phocoena phocoena*. Pages 549-551 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press.

Bloch, D., C. Lockyer, and M. Zachariassen. 1993. Age and growth parameters of long-finned pilot whale off the Faroe Islands. Report of the International Whaling Commission Special Issue 14:163-207.

Bloor, P., J. Reid, A. Webb, G. Begg, and M. L. Tasker. 1996. The distribution of seabirds and cetaceans between the Shetland and Faroe Islands. JNCC Report 226.

Borchers, D. L., S. T. Buckland, I. G. Priede, and S. Ahmadi. 1997. Improving the precision of the daily egg production method using generalised additive models. Can. J. Fish. Aquat. Sci. 54:2727-2742.

Borja, A., A. Uriarte, and J. Egana. 2002. Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north-east Atlantic coasts of Europe. Fisheries oceanography 11:116-127.

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

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73: 434-440.

Brumm, H. 2006. Animal communication: city birds have changed their tune. Current Biology 16(23): R1003-R1004

Buckland, S. T., D. Bloch, K. L. Cattanach, T. Gunnlaugsson, K. Hoydal, S. Lens, and J. Sigurjonsson. 1993. Distribution and abundance of long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. Report of the International Whaling Commission Special Issue 14:33-49.

Buckland, S. T., and D. A. Elston. 1993. Empirical models for the spatial distribution of wildlife. Journal of Applied Ecology 30(3): 478-495.

Caillat, M. 2005. Harbour porpoise (*Phocoena phocoena*) Acoustics: Investigating species discrimination and acoustic behaviour using output from a new detector. MRes Thesis. School of Biology. University of St Andrews.

Calderan, S. V. 2003. Fine-scale temporal distribution by harbour porpoise (*Phocoena phocoena*) in North Wales: acoustic and visual survey techniques. MSc Thesis. School of Biological Sciences. University of Wales, Bangor.

Cañadas, A., R. Sagarminaga, R. De Stephanis, E. Urquiola, and P. S. Hammond. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conserv: Mar. Freshw. Ecosyst. 15:495-521.

Cañadas, A., R. Sagarminaga, and S. Garcia-Tiscar. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters of southern Spain. Deep-Sea Research I 49:2053-2073.

Carlstrøm, J. 2005. Diel variation in echolocation behavior of wild harbor porpoises. Marine Mammal Science 21:1-12.

Caron, L. M. J., and D. E. Sergeant. 1988. Yearly variation in the frequency of passage of beluga whales (*Delphinapterus leucas*) at the mouth of the Sagueney River, Quebec, over the past decade. Naturaliste Canadienne 155:111-116. As cited in Richardson et al. (1995).

Carretta, J. V., B. L. Taylor, and S. J. Chivers. 2001. Abundance and depth distribution of harbor porpoise (*Phocoena phocoena*) in northern California determined from a 1995 ship survey. Fishery Bulletin 99:29-39.

Carron, M. 2004. NATO SACLANTCEN marine mammal risk mitigation program (sound, ocean, and living marine resources) in P. G. H. Evans, and L. A. Miller, editors. Workshop on active sonar & cetaceans, European Cetacean Society, Canary Isles.

Carstensen, J., O. D. Henriksen, and J. Teilmann. 2006. Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). Marine Ecology Progress Series 321:295-308.

Chappell, O., R. Leaper, and J. Gordon. 1996. Development and performance of an automated harbour porpoise click detector. Report of the International Whaling Commission 46:587-594.

Cipriano, F. 2002. Atlantic white-sided dolphin *Lagenorhynchus acutus*. Pages 49-51 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press.

Clark, C. W., and K. M. Fristrup. 1997. Whales '95: A combined visual and acoustic survey of blue and fin whales off Southern California. Report of the International Whaling Commission:583-600.

Clarke, M. R. 1996. Cephalopods as prey. III. Cetaceans. Philosophical Transactions of the Royal Society London B 351:1053-1065.

Compton, R., A. Banks, L. Goodwin, and S. K. Hooker. 2007. Pilot cetacean survey of the sub-Arctic North Atlantic utilising a cruise-ship platform. Journal of the Marine Biological Association of the United Kingdom 87:321-325.

Couperus, A. S. 1997. Interactions between dutch midwater trawl and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) southwest of Ireland. Journal of Northwest Atlantic Fishery Science 22:209-218.

Cox, T. M., T. J. Ragen, A. J. Read, E. Vos, R. W. Baird, K. Balcomb, J. Barlow, J. Caldwell, T. Cranford, L. Crum, A. D'Amico, G. D'Spain, A. Fernandez, J. Finneran, R. Gentry, W. Gerth, F. Gulland, J. Hildebrand, D. Houser, T. Hullar, P. D. Jepson, D. Ketten, C. D. MacLeod, P. Miller, S. Moore, D. C. Mountain, D. Palka, P. Ponganis, S. Rommel, T. Rowles, B. Taylor, P. Tyack, D. Wartzok, R. Gisiner, J. Mead, and L. Benner. 2006. Understanding the impacts of anthropogenic sound on beaked whales. J. Cetacean Res. Manage. 7:177-187.

Croll, D. A., R. Termillo, and B. R. Tershy. 2005. From wind to whales: trophic links in a coastal upwelling system. Marine Ecology Progress Series 289: 117-130.

Croll, D. A., B. R. Tershy, R. P. Hewitt, D. A. Demer, P. C. Fiedler, S. E. Smith, W. Armstrong, J. M. Popp, T. Kiekhefer, V. R. Lopez, J. Urban, D. Gendron. 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea Research II 45: 1353-1371.

Cronin, M., and M. Mackey. 2002. Cetaceans and seabirds in waters over the Hatton-Rockall region. Unpublished Cruise Report. Coastal and Marine Resources Centre, University College Cork.

Dalton, R. 2006. More whale strandings are linked to sonar. Nature 440:593.

David, J. A. 2006. Likely sensitivity of bottlenose dolphins to pile-driving noise. Water and Environment Journal 20:48-54.

Davis, R. W., G. S. Fargion, L. N. May, T. D. Leming, M. F. Baumgartner, W. E. Evans, L. J. Hansen, and K. Mullin. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. Marine Mammal Science 14:490-507.

Davis, R. W., J. G. Ortega-Ortiz, C. A. Ribic, W. E. Evans, D. C. Biggs, P. H. Ressler, R. B. Cady, R. R. Leben, K. D. Mullin, and B. Würsig. 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. Deep-Sea Research I 49:121-142.

Desportes, G., and R. Mouritsen. 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Report of the International Whaling Commission Special Issue 14:305-324.

Douglas, L. A., S. M. Dawson, and N. Jaquet. 2005. Click rates and silences of sperm whales at Kaikoura, New Zealand. J. Acoust. Soc. Am. 118:523-529.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijimans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann.

2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

Ellett, D. J., and J. H. A. Martin. 1973. The physical and chemical oceanography of the Rockall Channel. Deep-Sea Research 20:585-625.

Embling, C. 2003. Harbour porpoise (*Phocoena phocoena*) detection and track recognition from acoustic survey data. MRes Thesis. School of Biology. University of St Andrews & University of Dundee.

Evans, K., and M. A. Hindell. 2004. The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters. ICES Journal of Marine Science 61:1313-1329.

Evans, P. G. H. 1990. European cetaceans and seabirds in an oceanographic context. Lutra 33:95-125.

Evans, P. G. H. 1997. Ecology of sperm whales (*Physeter macrocephalus*) in the Eastern North Atlantic, with special reference to sightings & strandings records from the British Isles. Bulletin de l'Institut Royal des Sciences Naturelle de Belgique: Biologie 67-Suppl.:37-46.

Evans, P. G. H., P. Anderwald, and M. E. Baines. 2003. UK Cetacean status review. Sea Watch Foundation. Report to English Nature & Countryside Council for Wales.

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

Ferguson, M. C., J. Barlow, P. Fiedler, S. B. Reilly, and T. Gerrodette. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling 193:645-662.

Fernandes, P. G. 1993. An investigation into the ecology of the Irish Sea front. PhD Thesis. University of Liverpool.

Fiedler, P. C., S. B. Reilley, R. P. Hewitt, D. Demer, V. A. Philbrick, S. Smith, W. Armstrong, D. A. Croll, B. R. Tershy, and B. R. Mate. 1998. Blue whale habitat and prey in the California Channel Islands. Deep-Sea Research II 45: 1781-1801.

Fielding, A. H., and P. F. Haworth. 1995. Testing the generality of bird-habitat models. Conservation Biology 9:1466-1481.

Forney, K. A. 2000. Environmental Models of Cetacean Abundance: Reducing Uncertainty in Population Trends. Conservation Biology 14:1271-1286.

Frantzis, A. 1998. Does acoustic testing strand whales? Nature 392:29.

Frederiksen, M., M. Edwards, A. J. Richardson, N. C. Halliday, and S. Wanless. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. Journal of Animal Ecology 75: 1259-1268.

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

Fristrup, K. M., and C. W. Clark. 1997. Combining visual and acoustic survey data to enhance density estimation. Reports of the International Whaling Commission 47:933-936.

Gannier, A., V. Drouot, and J. C. Goold. 2002. Distribution and relative abundance of sperm whales in the Mediterranean Sea. Marine Ecology Progress Series 243:281-293.

Gannier, A., and E. Praca. 2007. SST fronts and the summer sperm whale distribution in the north-west Mediterranean Sea. Journal of the Marine Biological Association of the UK 87:187.

Gaskin, D. E. 1968. Distribution of Delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. New Zealand Journal of Marine & Freshwater Research 2:527-534.

Gende, S. M, and M. F. Sigler. 2006. Persistence of forage fish 'hot spots' and its association with Stellar sea lions (*Eumetopias jubatus*) in southeast Alaska. Deep-Sea Research II 53: 432-441.

Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the RSV Aurora Australis. Report of the International Whaling Commission 47:897-907.

Gillespie, D., P. Berggren, S. Brown, I. Kuklik, C. Lacey, T. Lewis, J. Matthews, R. McLanaghan, A. Moscrop, and N. Tregenza. 2005. Relative abundance of harbour porpoises (*Phocoena phocoena*) from acoustic and visual surveys of the Baltic Sea and adjacent waters during 2001 and 2002. J. Cetacean Res. Manage. 7:51-57.

Gillespie, D., and O. Chappell. 2002. An automatic system for detecting and classifying the vocalisations of harbour porpoises. Bioacoustics 13:37-61.

Gillibrand, P. A., P. J. Sammes, G. Slesser, and R. D. Adams. 2003. Seasonal water column characteristics in the Little and North Minches and the Sea of the Hebrides. I. Physical and chemical parameters. Fisheries Research Services Internal Report No 08/03.

Gómez de Segura, A., P. S. Hammond, A. Cañadas, and J. A. Raga. 2007. Comparing cetacean abundance estimates derived from spatial models and design-based line transect methods. Marine Ecology Progress Series 329: 289-299.

Goodson, A. D., and C. R. Sturtivant. 1996. Sonar characteristics of the harbour porpoise (Phocoena phocoena): source levels and spectrum. ICES Journal of Marine Science 53:465-472.

Goold, J. C. 1996. Acoustic assessment of populations of common dolphin *Delphinus delphis* in conjunction with seismic surveying. Journal of the Marine Biological Association of the United Kingdom 76:811-820.

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

Goold, J. C., and P. J. Fish. 1998. Broadband spectra of seismic survey air-gun emissions, with reference to dolphin auditory thresholds. Journal of the Acoustical Society of America 103:2177-2184.

Gordon, J. C., D. Gillespie, J. R. Potter, A. Frantzis, M. P. Simmonds, R. Swift, and D. Thompson. 2004. A review of the effects of seismic surveys on marine mammals. Marine Technological Society Journal 37:16-34.

Gordon, J. C. D., J. N. Matthews, S. Panigada, A. Gannier, J. F. Borsani, and G. Notarbartolo Di Sciara. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. Journal of Cetacean Research and Management 2:27-36.

Gordon, J. C. D., and L. Steiner. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. Report of the International Whaling Commission 42:561-565.

Gregr, E. J., and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Colombia. Canadian Journal of Fisheries and Aquatic Sciences 58:1265-1285.

Gridley, T. 2005. Combining acoustic and visual survey techniques to determine the factors affecting marine mammal distribution in the outer Moray Firth (NE Scotland). MRes Thesis. Department of Zoology. University of Aberdeen.

Griffin, R. B. 1999. Sperm whale distributions and community ecology associated with a warm-core ring off Georges Bank. Marine Mammal Science 15:33-51.

Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J.-P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographical information systems. Marine Ecology Progress Series 219:251-264.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993-1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147-186.

Hamazaki, T. 2002. Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). Marine Mammal Science 18:920-939.

Hamazaki, T. 2004. Modeling species-habitat relationship in the marine environment - a response to Gregr (2004). Marine Mammal Science 20:356-358.

Hammerschlag, N., R. A. Martin, and C. Fallows. 2006. Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillis pusillis*) at Seal Island, South Africa. Environ. Biol. Fish. 76: 341-350.

Hammond, P. S., P. Berggren, H. Benke, D. L. Borchers, A. Collet, M. P. Heide-Jorgensen, S. Heimlich, A. R. Hiby, M. F. Leopold, and N. Øien. 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. Journal of Applied Ecology 39:361-376.

Harwood, J. 2002. Mitigating the effects of acoustic disturbance in the oceans. Aquatic Conservation: Marine & Freshwater Ecoystems 12:485-488.

Harwood, J., and B. Wilson. 2001. The implications of developments on the Atlantic Frontier for marine mammals. Continental Shelf Research 21:1073-1093.

Hastie, G. D., R. J. Swift, J. C. D. Gordon, G. Slesser, and W. R. Turrell. 2003. Sperm whale distribution and seasonal density in the Faroe Shetland Channel. Journal of Cetacean Research and Managment 5:247-252.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson, and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. ICES Journal of Marine Science 62:760-770.

Hatakeyama, Y., and H. Soeda. 1990. Studies on echolocation of porpoises taken in salmon gillnet fisheries. Pages 269-281 in J. A. Thomas, and R. A. Kastelein, editors. Sensory abilities of cetaceans/ Laboratory and field evidence. Plenum.

Hedley, S. L., S. T. Buckland, and D. L. Borchers. 1999. Spatial modelling from line transect data. Journal of Cetacean Research and Management 1(3): 255-264.

Holliday, N. P. 2003. Extremes of temperature and salinity during the 1990s in the northern Rockall Trough: results from the "Ellet line". ICES Marine Science Symposia 219:95-101.

Hooker, S. K., H. Whitehead, and S. Gowans. 1999. Marine Protected Area Design and the Spatial and Temporal Distribution of Cetaceans in a Submarine Canyon. Conservation Biology 13:592-602.

Hoydal, K., and L. Lastein. 1993. Analysis of Faeroese catches of pilot whales (1709-1992) in relation to environmental variations. Report of the International Whaling Commission Special Issue 14:89-106.

Hunt, L. G. 1997. Physics, zooplankton, and the distribution of least auklets in the Bering Sea - a review. ICES Journal of Marine Science 54: 600-607.

Hui, C. A. 1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the Southern California Bight. Journal of Mammalogy 60:521-527.

Ibaibarriaga, L., X. Irigoien, M. Santos, L. Motos, J. M. Fives, C. Franco, A. Lago de Lanzos, S. Acevedo, M. Bernal, N. Bez, G. Eltink, A. Farinha, C. Hammer, S. A. Iverson, S. P. Milligan, and D. G. Reid. 2007. Egg and larval distributions of seven fish species in north-east Atlantic waters. Fisheries Oceanography 16:284-293.

Ichii, T., J. L. Bengston, P. L. Boveng, Y. Takao, J. K. Jansen, L. M. Hiruki-Raring, M. F. Cameron, H. Okamura, I. Hayashi, and M. Naganobu. 2007. Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. Marine Ecology Progress Series 344: 277-297.

Janik, V. M. 2000. Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. Journal of Comparative Physiology A 186:673-680.

Jaquet, N. 1996. How spatial and temporal scales influence understanding of Sperm Whale distribution: a review. Mammal Review 26:51-65.

Jaquet, N., and D. Gendron. 2002. Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. Marine Biology 141:591-601.

Jaquet, N., and H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135:1-9.

Jasney, M., J. Reynolds, C. Horowitz, and A. Wetzler. 2005. Sounding the depths II: The rising toll of sonar, shipping and industrial ocean noise on marine life. Natural Resources Defense Council.

Jepson, P. D., M. Arbelo, R. Deaville, I. A. P. Patterson, P. Castro, J. R. Baker, E. Degollada, H. M. Ross, P. Herraez, A. M. Pocknell, F. Rodriguez, F. E. Howie, A. Espinosa, R. J. Reid, J. R. Jaber, V. Martin, A. A. Cunningham, and A. Fernandez. 2003. Gas-bubble lesions in stranded cetaceans. Nature 425:575-576.

Jepson, P. D., R. Deaville, J. A. P. Patterson, A. M. Pocknell, H. M. Ross, J. R. Baker, F. E. Howie, R. J. Reid, A. Colloff, and A. A. Cunningham. 2005. Acute and cronic gas bubble lesions in cetaceans stranded in the United Kingdom. Vet Pathol 42: 291-305.

Jimenez, I. 2005. Development of predictive models to explain the distribution of the West Indian manatee *Trichechus manatus* in tropical watercourses. Biological Conservation 125:491-503.

Johnson, M., and P. L. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE Journal of Oceanic Engineering 28:3-12.

Johnston, D. W., A. J. Westgate, and A. J. Read. 2005. Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. Marine Ecology Progress Series 295:279-293.

Kaschner, K. 2004. Modelling and mapping resource overlap between marine mammals and fisheries on a global scale. PhD Thesis. Department of Zoology. The University of British Columbia.

Kastelein, R. A., J. Hardeman, and H. Boer. 1997. Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). Pages 217-233 in A. J. Read, P. R. Wiepkema, and P. E. Nachtigall, editors. The biology of the harbour porpoise. De Spil Publishers, Woerden, The Netherlands.

Kenney, R. D., and H. E. Winn. 1986. Cetacean high-use habitats of the NE US continental shelf. Fishery Bulletin 84:345-357.

Kinze, C. C. 2002. White-beaked dolphin *Lagenorhynchus albirostris*. Pages 1332-1334 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press.

Kinze, C. C., M. J. Addink, C. Smeenk, M. G. Hartmann, H. W. Richards, R. Sonntag, and H. Benke. 1997. The white-beaked dolphin (Lagenorhynchus albirostris) and the white-sided dolphin (Lagenorhynchus acutus) in the North and Baltic Seas: review of available information. Report of the International Whaling Commission 47:675-681.

Kiszka, J., K. Macleod, O. V. Canneyt, D. Walker, and V. Ridoux. 2007. Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay. ICES Journal of Marine Science 64:1033-1043.

Koenig, W. D., and J. M. H. Knops. 1998. Testing for spatial autocorrelation in ecological studies. Ecography 21:423-429.

Koopman, H. N. 1998. Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). Journal of Mammalogy 79:260-270.

Leaper, R., O. Chappell, and J. Gordon. 1992. The development of practical techniques for surveying sperm whale populations acoustically. Report of the International Whaling Commission 42:549-560.

Leaper, R., D. Gillespie, and V. Papastavrou. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. J. Cetacean Res. Manage. 2:187-196.

Lennon, J. 2000. Red-shifts and red herrings in geographical ecology. Ecography 23:101-113.

Lewis, T., D. Gillespie, J. Gordon, and O. Chappell. 2000. Acoustic cetacean monitoring 1996 to 1999: Towards the development of an automated system. Summary Report. A report to Shell UK Ltd. Contract C10563. Birmingham Research & Development Ltd.

Lewis, T., D. Gillespie, C. Lacey, J. Matthews, M. Danbolt, R. Leaper, R. McLanaghan, and A. Moscrop. 2007. Sperm whale abundance estimates from acoustic surveys of the Ionian Sea and Straits of Sicily in 2003. Journal of the Marine Biological Association of the UK 87:353.

MacLeod, C. D., C. R. Weir, C. Pierpoint, and E. J. Harland. 2007. The habitat preferences of marine mammals west of Scotland (UK). Journal of the Marine Biological Association of the UK 87:157-164.

Macleod, K. 2001. The spatial and temporal distribution of cetaceans off the west coast of Scotland in relation to environmental factors: the implications for marine management. PhD Thesis. University of Greenwich.

Macleod, K., M. P. Simmonds, and E. Murray. 2003. Summer distribution and relative abundance of cetacean populations off north-west Scotland. Journal of the Marine Biological Association of the United Kingdom 83:1187-1192.

Malme, C. I., P. R. Miles, P. Tyack, C. W. Clark, and J. E. Bird. 1984. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whales behavior/Phase II: January 1984 migration. BBN Rep. 5851; OCS Study MMS 85-0019. Rep. from BBN Labs Inc., Cambridge, MA, for U.S. Minerals Managm. Serv., Anchorage, AK. NTIS PB86-218385. As cited in Richardson et al. (1995).

Mandleberg, L., C. D. MacLeod, C. Schweder, S. M. Bannon, and G. J. Pierce. in review. A comparison of the predictive abilities of four approaches for modelling the distribution of cetaceans. Biological Conservation.

Mann, K. H., and J. R. N. Lazier 2006. Dynamics of marine ecosystems (3rd Edition). Blackwell Scientific Publications, Cambridge.

Martin, A. R. 1996. The diet of harbour porpoises (*Phocoena phocoena*) in British waters. International Whaling Commission, SC/47/SM48.

Martin, A. R., and M. R. Clarke. 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. Journal of the Marine Biological Association of the United Kingdom 66:779-790.

Mehlum, F., G. L. H. Jr, Z. Klusek, and M. B. Decker. 1999. Scale-dependent correlations between the abundance of Brunnich's guillemots and their prey. Journal of Animal Ecology 68:60-72.

Mendes, S. 2007. Male sperm whales (*Physeter macrocephalus*) in the Northeast Atlantic: Insights into movements, distribution and foraging ecology. PhD Thesis. Department of Zoology. University of Aberdeen.

Mendes, S., J. Newton, R. J. Reid, A. F. Zuur, and G. J. Pierce. 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. Oecologia 151:605-615.

Meynier, L. 2004. Food and feeding ecology of the common dolphin, *Delphinus delphis,* in the Bay of Biscay: intraspecific dietary variation and food transfer modelling. MSc Thesis. Department of Zoology. University of Aberdeen.

Miller, P. J., N. Biassoni, A. Samuels, and P. L. Tyack. 2000. Whale songs lengthen in response to sonar. Nature 405:903.

Miller, P. J. O. 2006. Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. Journal of Comparative Physiology A 192:449-459.

Miller, P. J. O., M. P. Johnson, and P. L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. Proceedings of the Royal Society B 271:2239-2247.

Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt, and A. Lund. 2003. The monopulsed nature of sperm whale clicks. Journal of the Acoustical Society of America 114:1143-1154.

Moisen, G. G., and T. S. Frescino. 2002. Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling 157:209.

Moscrop, A. 1997. Cetaceans of the North-East Atlantic Fringe. Page 46. Greenpeace UK.

Moses, E., and J. T. Finn. 1997. Using Geographical Information Systems to Predict North Atlantic Right Whale (*Eubalaena glacialis*) Habitat. J. Northw. Atl. Fish. Sci. 22:37-46.

Mullins, J. H., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. Canadian Journal of Fisheries & Aquatic Sciences 45:1736-1743.

Neumann, D. R. 2001. Seasonal movements of short-beaked common dolphins (*Delphinus delphis*) in the north-western Bay of Plenty, New Zealand: influence of sea surface temperature and El Nino/La Nina. New Zealand Journal of Marine & Freshwater Research 35:371-374.

New, A. L., and D. Smythe-Wright. 2001. Aspects of the circulation in the Rockall Trough. Continental Shelf Research 21:777-810.

Nieukirk, S. L., K. M. Stafford, D. K. Mellinger, R. P. Dziak, and C. G. Fox. 2004. Low-frequency whale and seismic airgun sounds recorded in the mid-Atlantic Ocean. Journal of the Acoustical Society of America 115:1832-1846.

Northridge, S. P., M. L. Tasker, A. Webb, K. Camphuysen, and M. F. Leopold. 1997. White-beaked Lagenorhynchus albirostris and Atlantic white-sided dolphin L. acutus distributions in northwest European and US Atlantic waters. Report of the International Whaling Commission 47:797-805.

Northridge, S. P., M. L. Tasker, A. Webb, and J. M. Williams. 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirostris* Gray), and minke whales (*Balaenoptera acutorostrata* Lacepede) around the British Isles. ICES Journal of Marine Science 52:55-66.

O'Cadhla, O., M. Mackey, N. Aguilar de Soto, E. Rogan, and N. Connolly. 2004. Cetaceans and Seabirds of Ireland's Atlatnic Margin. Volume II - Cetacean distribution & abundance. Page 82. Report on research carried out under the Irish Infrastructure Prograp (PIP): Rockall Studies Group (RSG) projects 98/6 and 00/13, Porcupine Studies Group project P00/15 and Offshore Support Group (OSG) project 99/38.

Osborne, P. E., and S. Suarez-Seoane. 2002. Should data be partitioned spatially before building large-scale distribution models? Ecological Modelling 157:249-259.

Oswald, J. N., J. Barlow, and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. Marine Mammal Science 19:20-37.

Oswald, J. N., S. Rankin, J. Barlow, and M. O. Lammers. 2007. A tool for real-time acoustic species identification of delphinid whistles. Journal of the Acoustical Society of America 122:587-595.

Otani, S., Y. Naito, A. Kawamura, M. Kawasaki, S. Nishiwaki, and A. Kato. 1998. Diving behavior and performance of harbor porpoises, *Phocoena phocoena*, in Funka Bay, Hokkaido, Japan. Marine Mammal Science 14:209-220.

Palka, D. 1995. Influences on spatial patterns of Gulf of Maine harbour porpoises. Pages 69-75 in A. S. Blix, L. Walloe, and O. Ulltang, editors. Whales, Seals, Fish and Man. Elsevier Science, Amsterdam.

Palka, D. 1996. Effects of Beaufort sea state on the sightability of harbour porpoises in the Gulf of Maine. Report of the International Whaling Commission 46.

Palka, D., A. Read, and C. Potter. 1997. Summary of knowledge of white-sided dolphins (*Lagenorhynchus acutus*) from US and Canadian Atlantic waters. Report of the International Whaling Commission 47:729-734.

Papastavrou, V., S. C. Smith, and H. Whitehead. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. Canadian Journal of Zoology 67:839-846.

Parra, G. J. 2006. Resource partitioning in sympatric delphinids: space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. Journal of Animal Ecology 75: 862-874.

Parsons, E. C. M., I. Birks, P. G. H. Evans, J. C. D. Gordon, J. H. Shrimpton, and S. Pooley. 2000. The possible impacts of military activity on cetaceans in west Scotland. 14:185-190.

Paxton, C. G. M., M. L. Burt, G. A. Vikingsson, T. Gunnlaugsson, G. Desportes, N. Øien, and J. Harwood. in review. Density surface fitting to estimate the abundance of humpback, sperm, northern bottlenose and long-finned pilot whales based on the combined NASS aerial and shopboard and Norwegian surveys in the North Atlantic and Barents Sea in 2001.

Payne, P. M., and D. W. Heinemann. 1993. The distribution of pilot whales (*Globicephala* spp.) in shelf/shelf-edge and slope waters of the Northeastern United States, 1978-1988. Report of the International Whaling Commission Special Issue 14:51-68.

Pearce, J., and S. Ferrier. 2000. An evaluation of alternative algorithms for fitting species distribution models using logistic regression. Ecological Modelling 128:127-147.

Perrin, W. F. 2002. Common dolphins: *Delphinus delphis, D. capensis,* and *D. tropicalis*. Pages 245-248 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press.

Planque, B., and J.-M. Fromentin. 1996. *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal pattersn of *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series 134:101-109.

Rae, B. B. 1973. Additional notes on the diet of the common porpoise (Phocoena phocoena). Journal of Zoology, London 169:127-131.

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

Rasmussen, M. H., L. A. Miller, and W. W. L. Au. 2002. Source level of clicks from free-ranging white-beaked dolphins (*Lagenorhynchus albirostris* Gray 1846) recorded in Icelandic waters. Journal of the Acoustical Society of America 111:1122-1125.

Raum-Suryan, K. L., and J. T. Harvey. 1998. Distribution and abundance of and habitat use by harbour porpoise, *Phocoena phocoena*, off the northern San Juan Islands, Washington. Fishery Bulletin 96:808-822.

Reilly, S. B., and P. C. Fiedler. 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986-1990. Fishery Bulletin 92:434-450.

Rendell, L., H. Whitehead, and R. Escribano. 2004. Sperm whale habitat use and foraging success off northern Chile: evidence of ecological links between coastal and pelagic systems. Marine Ecology Progress Series 275:289-295.

Rendell, L. E., and J. C. D. Gordon. 1999. Vocal response of long-finned pilot whales (*Globicephala melas*) to military sonar in the Ligurian Sea. Marine Mammal Science 15:198-204.

Rendell, L. E., J. N. Matthews, A. Gill, J. C. D. Gordon, and D. W. Macdonald. 1999. Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. Journal of the Zoological Society of London 249:403-410.

Richardson, W. J., C. R. Green Jr., C. I. Malme, and D. H. Thomson 1995. Marine Mammals and Noise. Academic Press, Inc., San Diego, CA.

Roberts, C. 2005. Trends in the diet of the harbour porpoise in British waters. BSc Thesis. Department of Biology. University of St Andrews.

Roe, H. S. J. 1969. The Food and Feeding Habits of the Sperm Whales (*Physeter catodon* L.) Taken off the West Coast of Iceland. ICES J. Mar. Sci. 33:93-102.

Rommel, S. A., A. M. Costidis, A. Fernandez, P. D. Jepson, D. A. Pabst, W. A. McLellan, D. S. Houser, T. W. Cranford, A. L. Van Helden, D. M. Allen, and N. B. Barros. 2006. Elements of beaked whale anatomy and diving physiology and some hypothetical causes of sonar-related stranding. Journal of Cetacean Research and Management 7:189-209.

Rose, G. A., and W. C. Leggett. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. Ecology 71:33-43.

Santos, M. B. 1998. Feeding ecology of harbour porpoises, common and bottlenose dolphins and sperm whales in the Northeast Atlantic. PhD Thesis. University of Aberdeen.

Santos, M. B., and G. J. Pierce. 2003. The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Oceanography and Marine Biology: an Annual Review 41:355-390.

Santos, M. B., G. J. Pierce, P. R. Boyle, R. J. Reid, H. M. Ross, I. A. Patterson, C. C. Kinze, S. Tougard, R. Lick, U. Piatkowski, and V. Hernandez-Garcia. 1999. Stomach contents of sperm whales Physeter macrocephalus stranded in the North Sea 1990-1996. Marine Ecology Progress Series 183:281-194.

Santos, M. B., G. J. Pierce, M. G. Hartmann, C. Smeenk, M. J. Addink, T. Kuiken, R. J. Reid, I. A. P. Patterson, C. Lordan, E. Rogan, and E. Mente. 2002. Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom 82:501-507.

Santos, M. B., G. J. Pierce, H. M. Ross, D. G. Reid, and B. Wilson. 1994. Diets of small cetaceans from the Scottish coast. International Council for the Exploration of the Sea, Marine Mammal Committee. ICES CM 1994/N:11.

SCANS-II. 2006. The quarterly newsletter for project SCANS-II: Small Cetaceans in the European Atlantic and North Sea. Issue 7: June 2006.

Schneider, D. C., and J. F. Piatt. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Marine Ecology Progress Series 32:237-246.

Scott-Hayward, L. A. S. 2006. Modelling the spatial distribution of sperm whales, *Physeter macrocephalus*, in the Gulf of Mexico. MRes Thesis. Department of Biology. University of St Andrews.

Selzer, L. A., and P. M. Payne. 1988. The distribution of white-sided (Lagenorhynchus acutus) and common dolphins (Delphinus delphis) vs.

environmental features of the continental shelf of the northeastern United States. Marine Mammal Science 4:141-153.

Shane, S. 1995. Relationship between pilot whales and Risso's dolphin at Santa Catalina Island, California, USA. Marine Ecology Progress Series 123: 5-11.

Shelton, R. G. J., W. R. Turrell, A. Macdonald, I. S. McLaren, and N. T. Nicoll. 1997. Records of post-smoult Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. Fisheries Research 31:159-162.

Sherwin, T. J., W. R. Turrell, D. R. G. Jeans, and S. Dye. 1999. Eddies and a mesoscale deflection of the slope current in the Faroe-Shetland Channel. Deep-Sea Research I 46:415-438.

Sherwin, T. J., M. O. Williams, W. R. Turrell, S. L. Hughes, and P. I. Miller. 2006. A description and analysis of mesoscale variability in the Faroe-Shetland Channel. Journal of Geophysical Research 111:1-17.

Silva, M. A. 1999. Diet of common dolphins, *Delphinus delphis*, off the Portuguese continental coast. Journal of the Marine Biological Association of the United Kingdom 79:531-540.

Simon, M. J., T. K. Kristensen, O. S. Tendal, C. C. Kinze, and S. Tougaard. 2003. *Gonatus fabricii* (Mollusca, Theuthida) as an important food source for sperm whales *(Physeter macrocephalus)* in the Northeast Atlantic. Sarsia 88:244 - 246.

Simpson, J. H., D. J. Edelsten, A. Edwards, N. C. G. Morris, and P. B. Tett. 1979. The Islay front: physical structure and phytoplankton distribution. Estuarine and Coastal Marine Science 9:713-726.

Sivertsen, S. P., P. Torstein, U. Lindstrøm, and T. Haug. 2006. Prey partitioning between cod (*Gadus morhua*) and minke whale (*Balaenoptera acutorostrata*) in the Berents Sea. Marine Biology Research 2: 89-99.

Skov, F., and J.-C. Svenning. 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. Ecography 27:366-380.

Skov, H., J. Durinck, F. Danielsen, and D. Bloch. 1995. Co-occurrence of cetaceans and seabirds in the Northeast Atlantic. Journal of Biogeography 22:71-88.

Slabbekoorn, H., and A. den Boer-Visser. 2006. Cities change the song of birds. Current Biology 16:2326-2331.

Smith, G. J. D., and D. E. Gaskin. 1983. An environmental index for habitat utilization by female harbour porpoises with calves near Deer Island, Bay of Fundy. Ophelia 22:1-13.

Smith, S. C., and H. Whitehead. 1993. Variations in the feeding success and behaviour of Galapagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. Canadian Journal of Zoology 71:1991-1996.

Smith, S. C., and H. Whitehead. 2000. The diet of Galapagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. Marine Mammal Science 16:315-325.

Soto, K. H., A. W. Trites, and M. Arias-Schreiber. 2006. Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. Marine Ecology Progress Series 312: 277-290.

Spitz, J., Y. Rousseau, and V. Ridoux. 2006. Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? Estuarine, Coastal and Shelf Science 70: 259-270.

Steiner, W. W. 1981. Species-specific differences in pure tonal whistle vocalizations of five western North Atlantic dolphin species. Behavioural Ecology and Sociobiology 9:241-246.

Stephenson, C. M., M. L. MacKenzie, C. Edwards, and J. M. J. Travis. 2006. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. Ecological Modelling 193:747-758.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. J. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427:145-148.

Tougaard, J., J. Carstensen, O. D. Henriksen, H. Skov, and J. Teilmann. 2003. Short-term effects of the construction of wind turbines on harbour porpoises at Horn Reef. Hedeselskabat, Roskilde, Technical report to TechWise A/S. HME/362-02662, Hedeselskabat, Roskilde.

Tougaard, J., J. Carstensen, J. Teilmann, and N. I. Bech. 2005. Effects of the Nysted Offshore wind farm on harbour porpoises. Technical report to Energi E2 A/S. NERI, Roskilde.

Turrell, W. R., G. Slesser, R. D. Adams, R. Payne, and P. A. Gillibrand. 1999. Decadal variability in the composition of Faroe Shetland Channel bottom water. Deep-Sea Research I 46:1-25.

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

Urick, R. J. 1983. Principles of underwater sound. Peninsula Publishing, Los Altos, CA.

Van Horn, B. 2002. Approaches to habitat modelling: the tensions between pattern and process and between specificity and generality. Pages 63-72 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, CA.

Vlietstra, L. S. 2005. Spatial associations between seabirds and prey: effects of large-scale prey abundance on small-scale seabird distribution. Marine Ecology Progress Series 291: 275-287.

Wall, D., J. O'Brien, J. Meade, and B. M. Allen. 2006. Summer distribution and relative abundance of cetaceans off the west coast of Ireland. Proceedings of the Royal Irish Academy 106B:135-142.

Watkins, H., and R. Colley. 2004. Harbour porpoise *Phocoena phocoena* occurrence Camarthen Bay - Gower Penninsula - Swansea Bay. December 2002 - February 2004. Gower Marine Mammals Project. August 2004.

Watkins, W. A., and W. E. Schevill. 1977. Spatial distribution of *Physeter catodon* (sperm whales) underwater. Deep-Sea Research 24:693-699.

Watts, P., and D. E. Gaskin. 1985. Habitat Index Analysis of the Harbor Porpoise (*Phocoena phocoena*) in the Southern Coastal Bay of Fundy, Canada. Journal of Mammalogy 66:733-744.

Watwood, S. L., P. J. O. Miller, M. Johnson, P. T. Madsen, and P. L. Tyack. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). Journal of Animal Ecology 75:814-825.

Weilgart, L. S., and H. Whitehead. 1990. Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. Behavioral Ecology and Sociobiology 26:399-402.

Weir, C. R., and S. H. O'Brien. 2000. Association of the harbour porpoise (*Phocoena phocoena*) with the western Irish sea front. Pages 61-65 in P. G. H. Evans, editor. European Research on Cetaceans - 14. Proceedings of the Fourteenth Annual Conference of the European Society, Cork, Ireland, 2-5 April 2000.

Weir, C. R., C. Pollock, C. Cronin, and S. Taylor. 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. Continental Shelf Research 21:1047-1071.

Westgate, A. J., A. J. Read, P. Berggren, H. N. Koopman, and D. E. Gaskin. 1995. Diving behaviour of harbour porpoises, *Phocoena phocoena*. Can. J. Fish. Aquat. Sci. 52:1064-1073.

Whitehead, H. 2002. Sperm whale *Physeter macrocephalus*. Pages 1165-1172 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press.

Whitehead, H. 2003. Sperm whales: Social evolution in the ocean. University of Chicago Press.

Whitehead, H., S. Brennan, and D. Grover. 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology 70:912-918.

Whitehead, H., and L. Weilgart. 1991. Patterns of visually observable behaviour and vocalisations in groups of female sperm whales. Behaviour 118:275-296.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Williams, R. 2003. Cetacean studies using platforms of opportunity. PhD thesis, University of St Andrews.

Wilson, K. A., M. I. Westphal, H. P. Possingham, and J. Elith. 2005. Sensitivity of conservation planning to different approaches to using predicted species distribution data. Biological Conservation 122:99-112.

Wirsing, A. J., M. R. Heithaus, and L. M. Dill. 2007. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. Animal Behaviour 74: 93-101.

Wright, P. J., H. Jenson, and I. Tuck. 2004. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. Journal of Sea Research 44:243-256.

Zachariassen, P. 1993. Pilot whale catches in the Faroe Islands, 1709-1992. Report of the International Whaling Commission Special Issue 14:68-88.

Zamon, J. E. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago dependent on flooding tidal currents. Marine Ecology Progress Series 261: 243-255.

Zimmer, W. M. X., M. P. Johnson, A. D'Amico, and P. L. Tyack. 2003. Combining the data from a multisensor tag and passive sonar to determine the diving behaviour of a sperm whale (*Physeter macrocephalus*). IEEE Journal of Oceanic Engineering 28:13-28.

Chapter 2

Predictive models of delphinid distributions off the west coast of Scotland

Evaluation of autocorrelation & temporal scale

Abstract

Passive acoustic techniques were used to monitor delphinid distributions from platforms of opportunity off the west coast of Scotland between July 2003 and October 2005. The use of acoustics as a survey tool allowed delphinid distributions to be monitored by a single field worker, in poor weather conditions as well as during the night, although it could not differentiate between species. Dolphin schools could be heard to a greater range than the spacing between track segments and to avoid pseudo-replication, objective rules were developed to allow a particular delphinid group to be allocated reliably to a track segment. These data were used to model delphinid group occurrence (presence/absence) to a range of survey variables using Generalised Additive Models (GAMs) over monthly and yearly scales. At a monthly scale, delphinids were detected to a greater degree in more northerly areas (Faroe-Shetland Channel) during October than during May. In October, SST was the most significant predictor of delphinid occurrence and appeared to explain their more northerly distribution during that month. At a yearly scale, SST was also a significant predictor in explaining the occurrence of delphinids in 2003-2004 but not in 2005. This is likely to be explained by the lower SST signal resulting from the high cloud cover and high winds that occurred in the survey area during 2005. Where SST was not significant in explaining delphinid occurrence (May and 2005), thermocline depth was a significant predictor. Overall, delphinids were found to associate with the deep (> 400 m) warm water (10.5°C-12.5°C) within the survey area, and in areas of deep thermocline (the maximum surveyed was 800 m depth). Although delphinids were found to be relatively evenly distributed throughout the waters off the west coast of Scotland, the models were able to highlight areas of high-use within the deep areas especially close to the productive shelf edge. These models can be used in mitigating acoustic threats to cetaceans in predicted high use areas off the west coast of Scotland.

2.1 Introduction

The ability of a model to predict a species distribution through time and space is an important measure of the robustness of a model (Boyce et al. 2002). However, predictive models have to contend with seasonal, yearly or spatial changes of habitat preference, due to fluctuations in resources and the availability of prey or habitat within an area (Boyce et al. 2002).

Many species of cetacean have been shown to change their distribution seasonally (Ballance et al. 2006; Croll et al. 2005; Hamazaki 2002; Hastie et al. 2005; Kenney & Winn 1986; Moore et al. 2000; Northridge et al. 1997; Northridge et al. 1995; Payne & Heinemann 1993; Smith & Whitehead 1993; Tynan et al. 2005). For example, blue whales (*Balaenoptera musculus*) return to Monterey Bay, California every summer to make use of seasonally high production supported by the seasonal coastal upwelling (Croll et al. 2005). In the North West Atlantic long-finned pilot whales (*Globicephala melas*) exhibit seasonal shifts in distribution, with an onshore movement during the summer closely coinciding with the abundance of prey species (Payne & Heinemann 1993). These seasonal movements can also result in changes in behaviour and vocalisation rates (Jacobs et al. 1993). For example, Jacobs et al. (1993) associated the doubling of bottlenose dolphin (*Tursiops truncatus*) vocalisation rates from summer to autumn with a behavioural change from socialising during the summer to foraging during the autumn in preparation for migration.

Changes in distribution and behaviour also occur between years due to fluctuating oceanography and hence resources. For example, Galapagos sperm whales (*Physeter macrocephalus*) had lower foraging success in years during which El Niño suppressed upwelling than in other years (Smith & Whitehead 1993). Similarly, Reilley & Fiedler (1994) found common dolphins (*Delphinus delphis*) exhibited inter-annual changes in distribution that could be explained by changes in the oceanographic conditions driven by El Niño and La Niña. In this latter study, the inter-annual variation in common dolphin distributions was fully explained by environmental variables that were associated with its habitat preferences.

Little is known about temporal variation in habitat preferences of delphinids off the west coast of Scotland (Hastie et al. 2005; Northridge et al. 1995; Northridge et al. 1997). The main species of delphinid seen off the west coast of Scotland are long-finned pilot whales (*Globicephala melas*), Atlantic white-sided dolphins (*Lagenorhynchus acutus*), white-beaked dolphins (*Lagenorhynchus albirostris*), and common dolphins (*Delphinus delphis*) (Harwood & Wilson 2001; MacLeod et al. 2007; Macleod 2001; Macleod et al. 2003; Northridge et al. 1997; Northridge et al. 1995; Skov et al. 1995; Wall et al. 2006; Weir et al. 2001). However, there is evidence to suggest that white-sided dolphins show seasonal movement onshore during the summer months (Northridge et al. 1997). Similarly, long-finned pilot whale exhibit some seasonal movement into inshore areas around the Faroe Islands in years with higher SST, which is assumed to be linked to the onshore movement of the squid species *Todarodes sagittatus* (Zachariassen 1993). Delphinids surveyed acoustically in the Faroe-Shetland Channel also showed some seasonality, with changes in distribution and abundance being mainly influenced by changes in SST between months (Hastie et al. 2005).

Conventionally, delphinids have been surveyed using visual methods to detect species at the surface. However, the ability to detect delphinids visually is strongly affected by weather conditions; reducing with increasing sea state, swell height, and fog (Barlow et al. 2001). Passive acoustic techniques allow for the detection of vocalising delphinids in most weather conditions as well as during the night, and since it can be highly automated it also requires fewer people than visual surveying methods. This is particularly useful for studies using platforms of opportunity where there is often space for only a few researchers. Passive acoustic techniques have been useful in identifying the habitat preferences of delphinids (Gordon et al. 2000; Hastie et al. 2005) however, one drawback of passive acoustics for delphinids is the difficulty of species identification from whistles. Previous studies have suggested that some species can be reliably distinguished on the basis of their whistles (Oswald et al. 2003; Rendell et al. 1999; Steiner 1981), but these involved making time consuming measurements by hand and only recently have near real-time species identification tools been developed for Pacific Ocean species (Oswald et al. 2007), no such data exist for North Atlantic species. Therefore, using passive acoustics to study the distribution of dolphins, it is only possible to determine overall delphinid distribution rather than distributions of individual species.

A further consideration for passive acoustic methods is that delphinid vocalisations can be heard at much larger distances than they can be seen (Janik 2000; Miller 2006). However, this also means that delphinid groups may be heard over long portions of the survey track as the vessel approaches and passes the group. This will result in autocorrelation between sampling units if they are spaced closer together than the distance over which the dolphins can be heard. Autocorrelation in environmental modelling results in model ‘overfitting’ caused by underestimation of the standard errors resulting in variables being considered significant when in fact they are not (Borchers et al. 1997; Lennon 2000).

In this study I used passive acoustic techniques from platforms of opportunity to investigate delphinid distribution off the west coast of Scotland with the following aims: (i) to investigate the influence of autocorrelation; and (ii) to investigate the influence of temporal scale on predictive models of delphinid distributions off the west coast of Scotland; and (iii) to explore the delphinid-environment relationships in this area of the North Atlantic.

2.2 Methods

2.2.1 Data collection

Surveys were carried out opportunistically on a number of oceanographic survey vessels between July 2003 and October 2005 in shelf, shelf-edge and deep waters off the west coast of Scotland (55°30’-62°00’N, 0°01’-14°10’E) (Table 2.1, Figure 2.1). The main purpose of the surveys was to carry out hydrographic sampling along set lines across the Faroe-Shetland Channel and along the Ellet Line (Figure 2.1). Additional sampling was carried out in other areas of oceanographic interest such as the Wyville-Thompson Ridge. A hydrophone array was towed 400 m behind the vessel whilst steaming, and retrieved at stations where the vessel was stationary. The hydrophone was only deployed between stations that were likely to have at least half an hour monitoring time between them (generally when stations were > 7 nm).

The hydrophone was built to the same IFAW (International Fund for Animal Welfare) design as used in other similar studies (Gillespie 1997; Gordon et al. 2000; Hastie et al. 2003; Hastie et al. 2005; Leaper et al. 2000). The hydrophone array was towed on 400m of Kevlar-reinforced cable, and comprised two Benthos AQ4 elements positioned 3 m apart within a 10 m long, 25 mm diameter, oil-filled polyurethane tube.

Table 2.1 – Survey times, platforms, collaborators, and spatial extent of the opportunistic surveys for dolphins carried out off the west coast of Scotland. Collaborators were those organisations running the hydrographic surveys: NOC = National Oceanographic Centre, Southampton; SAMS = Scottish Association for Marine Science, Dunstaffnage; FRS = Fisheries Research Services, Aberdeen.

Survey dates	Vessel	Collaborators	Latitude range	Longitude range
19-25 July 2003	*R/V Poseidon*	NOC, SAMS	55°31’ - 57°35’N	6°30’ - 13°32’E
16-28 September 2003	*FRV Scotia*	FRS	59°22’ - 61°59’N	1°06’ - 8°06’E
13-29 May 2004	*FRV Scotia*	FRS	58°19’ - 61°57’N	1°08’ - 10°16’E
5-17 October 2004	*FRV Scotia*	FRS	56°45’ - 62°00’N	0°59’ - 9°31’E
8-26 May 2005	*FRV Scotia*	FRS	57°08’ - 62°00’N	0°01’W - 9°13’E
27 Sept – 8 Oct 2005	*FRV Scotia*	FRS	57°45’ - 61°58’N	1°09’ - 6°40’E
7-25 October 2005	*RSS Charles Darwin*	SAMS, NOC	55°30’ - 61°30’N	6°01’ - 14°10’E

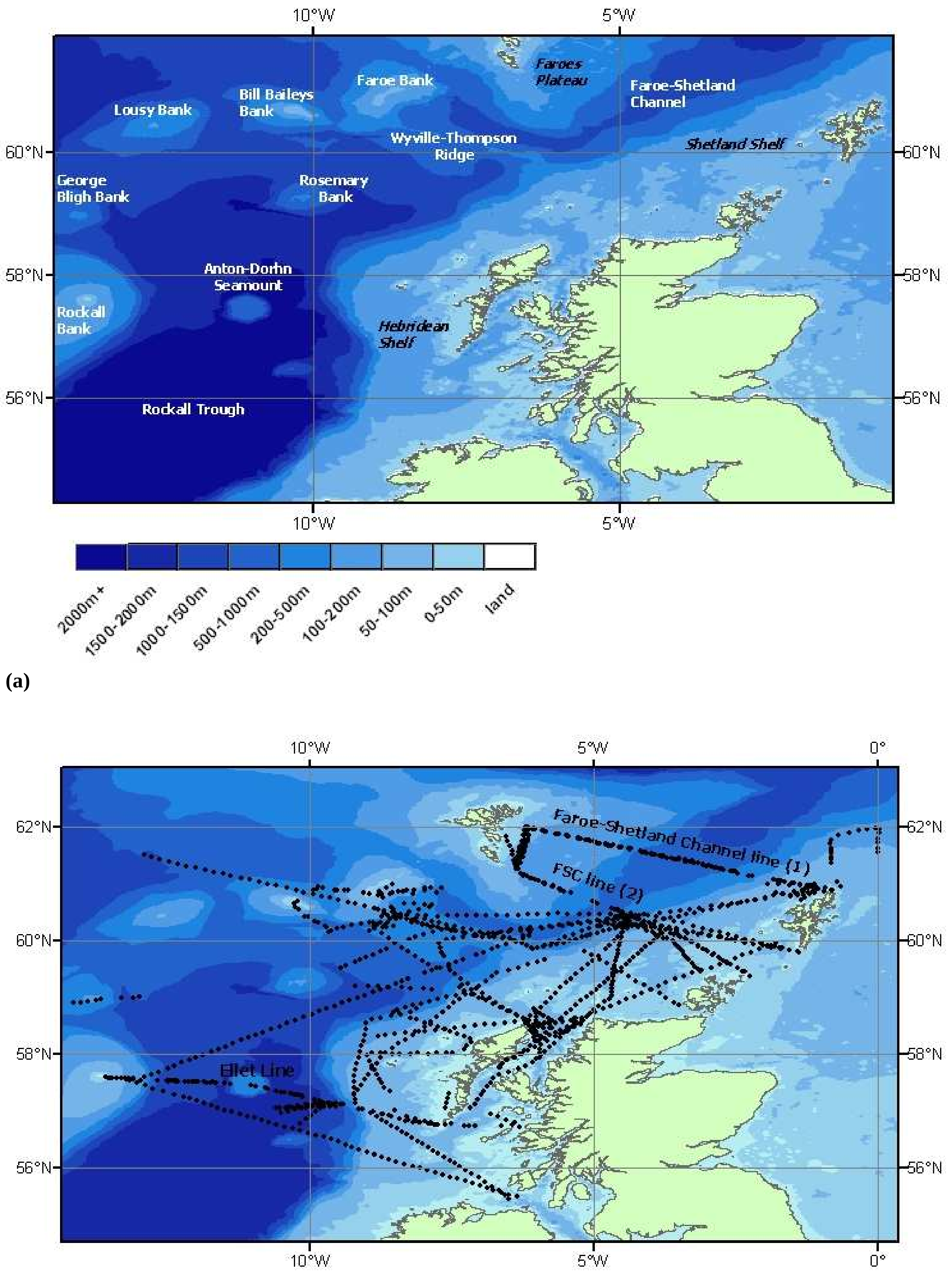


Figure 2.1 – (a) GEBCO bathymetric map of the survey area off the west coast of Scotland, and (b) with 9km surveyed segments overlaid (each black dot is a 9km segment) for surveys carried out opportunistically between July 2003 and October 2005

The use of two hydrophone elements allowed for the calculation of bearings to animals, which provided some ability to locate them. Each AQ-4 element was mounted close to a HP/02 (Magrec, Devon, UK) low noise preamplifier providing a gain of 30 dB to allow for loss of signal in the 400 m of cable and improve signal to noise ratio. The response of the hydrophone/preamplifier unit was flat within 3 dB between 100 Hz and 35 kHz.

The hydrophone was connected to an audio amplifier, sound card and computer via a 20 m deck cable. The hydrophone signal is first passed through an HP27ST amplifier/conditioner unit (Magrec, Devon, UK) where it could be amplified (10-40 dB) and filtered by applying high pass filters at between 100-3600 Hz to filter out low frequency noise before passing to a USB Quattro soundcard (M-Audio) sampling at 48 k Hz in 2003-2004 (i.e. giving a maximum frequency of 24 kHz), and at 96 kHz in 2005 (i.e. giving a maximum frequency of 48 kHz). Detection and recording programs ran in real time on a laptop running the IFAW logging software package *Logger 2000* (Gillespie 1997), 30-second recordings of the hydrophone were made to hard disk every 2 minutes. All events including recordings were linked to GPS location within an Access database. Real-time monitoring of whistles was carried out using the IFAW software packages *Whistle*. This program was specially designed to detect and measure bearings to dolphin whistles (*Whistle*), and was run continuously whenever the hydrophone was deployed. In addition, acoustic listening stations of 1 minute were carried out by acoustic monitors every 15 minutes scoring for survey vessel noise, water noise, remote vessel noise, and dolphin whistles on a subjective scale of 0 (inaudible) to 5 (loud). Two acoustic monitors rotated the listening shifts, and throughout the surveys at least one of the same three experienced acoustic monitors was present to maintain consistency in sound level measurement. Environmental conditions were recorded every hour, with boat speed & direction, wind speed & direction, sea state and swell (the latter two were only possible during daylight hours) entered directly into *Logger 2000*.

2.2.2 Environmental data

A range of environmental variables were available for inclusion in analysis from a range of sources, as listed in table 2.2.

The temporal variable *TimeDayNight* was calculated to compensate for variation in the number of hours of daylight throughout the survey season. *TimeDayNight* was calculated as a ratio between the amount of time elapsed since sunrise to the amount of time between sunrise and sunset (for daylight hours), or as the amount of time elapsed since sunset to the amount of time between sunset and sunrise (for night hours) + 1. This resulted in a continuous variable that ranged from 0-2, with 0-1 representing position within daylight, and 1-2 representing position within the night.

Environmental data covering the entire survey area were available for topographical, oceanographic and current variables. Depth was available at a 1 minute resolution GEBCO grid (IOC et al. 2003). Satellite images were obtained from the Remote Sensing Data Advisory Service (RSDAS) at Plymouth Marine Laboratory. For all years, SST was sourced from the AVHRR satellite, whereas chlorophyll was sourced from the SeaWifs satellites for images from 2003-2004, and from the MODIS satellite in 2005. Due to the high level of cloud cover, the images were supplied both as weekly and monthly composites. The ascii satellite images were converted into imagine grid files and a raster catalogue generated from these images using the *STJG tools* extension version 1.0.1 (Gontarek 2005) in ArcGIS 9.1 (ESRI Inc).

Oceanographic and current data were sourced from the FOAM (Forecasting Ocean Assimilation Model; Bell et al. 2000) modelled data supplied at a 9 km resolution by the UK Met Office. These data were supplied at a 12-level depth breakdown and were processed into the summary variables shown in Table 2.2 by Phil Gillibrand at the Scottish Association for Marine Science (SAMS). To check for consistency between the modelled FOAM data and satellite data, SST values were compared using a Spearman's rank correlation test along the survey trackline in groups of two listening stations (around 9 km segments at an average vessel speed of 10 knots). FOAM and satellite SST were significantly strongly correlated ($r = 0.879$, $p < 0.001$, $n = 478$). For modelling, SST was sourced from the most accurate data available in the following order of preference: weekly satellite, monthly satellite or FOAM SST.

Table 2.2 – Spatial, temporal, environmental, and modelled environmental variables sourced for modelling the offshore survey data to the west of Scotland. BODC = British Oceanographic Data Centre, PML = Plymouth Marine Laboratory, RSDAS = Remote Sensing Data Advisory Service, HaloDepth = halocline depth, SBSalinity = halocline strength, SSS = Sea Surface Salinity, ThermoDepth = thermocline depth, SBT = thermocline strength, SurfCurSpeed = surface current speed, BotCurSpeed = bottom current speed.

Variable	Description	Source	Resolution	Unit
Vessel speed	*In situ* measurement	Garmin GPS	Every 10 secs (approx 50 m)	knots
Wind speed	*In situ* measurement	Vessel anemometer	Every hour (approx 18 km)	knots
Survey vessel noise	Discrete (0 no noise – 5 very loud) survey vessel noise	Acoustic monitor	Every 15 mins (approx 5 km)	-
Water noise	Discrete (0 no noise – 5 very loud) water noise (water flow, rain, turbulence)	Acoustic monitor	Every 15 mins (approx 5 km)	-
Remote vessel noise	Discrete (0 no noise – 5 very loud) remote vessel noise	Acoustic monitor	Every 15 mins (approx 5 km)	-
TimeDayNight	Ratio: (time since sunrise/sunset) / (time between sunrise-sunset or sunset-sunrise) + 1 if after sunset. Results scale 0-2 where 0-1 is daylight, and 1-2 is night.	Time based on Garmin GPS time, sunrise/set times POLTIPS	Every segment (5 km)	-
Depth	Seabed depth	GEBCO (BODC)	1 min lon/lat (1-1.9km)	m
SST	Chosen in order of availability : (1) weekly composite satellite SST, (2) monthly satellite SST, (3) FOAM modelled SST	satellite = PML (RSDAS), FOAM = Met Office	1km (AVHRR) and 9km (FOAM)	°C
Chlorophyll	Chosen in order of availability: (1) weekly composite, or (2) monthly composite satellite chlorophyll	PML (RSDAS)	1km (pre-2005 SeaWifs, 2005 MODIS)	mg/m^3
HaloDepth	Predicted depth of the halocline	UK Met Office (FOAM)	9km	m
SBSalinity	Predicted surface to bottom salinity difference (halocline strength)	UK Met Office (FOAM)	9km	psu
SSS	Predicted surface salinity	UK Met Office (FOAM)	9km	psu
ThermoDepth	Predicted depth of the thermocline	UK Met Office (FOAM)	9km	m
SBT	Predicted surface to bottom temperature difference (thermocline strength)	UK Met Office (FOAM)	9km	°C
SurfCurSpeed	Predicted mean daily surface current	UK Met Office (FOAM)	9km	m/s
BotCurSpeed	Predicted mean daily bottom current	UK Met Office (FOAM)	9km	m/s

Surface chlorophyll values were sourced from weekly satellite images in preference to monthly composites where available. Data were extracted for any data point with a given latitude, longitude and date/time using the *STJG tool* (Gontarek 2005) in ArcGIS 9.1.

2.2.3 Acoustic data analysis

Dolphins can be heard over large distances, resulting in the same group of vocalising animals being heard over several listening stations, causing serial autocorrelation (or pseudoreplication) and lack of independence between sampling units. This autocorrelation can be removed completely if the group is only recorded as present at the time at which it passed abeam of the vessel.

Tracks of dolphin groups relative to the survey vessel can be identified using the bearings estimated to whistles by the *Whistle* software. However the accuracy of the estimated bearing is relatively poor in comparison to sperm whale or harbour porpoise clicks due to the complex nature of whistles and because many animals within a dolphin group vocalise simultaneously. Nevertheless, tracks of whistles allow for the number of groups to be estimated, and a rough calculation of the time the group comes abeam of the vessel and the distance to the trackline (i.e. how far the group was when it passed abeam of the vessel). Estimation of distance to the trackline is particularly difficult for dolphins because their rate of movement in relation to the vessel is relatively high and changes in bearing are caused both by the vessel moving in relation to the dolphin group and due to the dolphin group moving in relation to the vessel. However, it does allow for the measurement of an approximate time at which the dolphins passed abeam of the vessel. If this were done for every group of dolphins heard, it would be possible to associate each dolphin group with the closest listening station, and so only recording a single presence for the dolphin group.

Due to the time consuming nature of this process, a small sample of 21 dolphin group tracks was analysed and a rule for deriving appropriate sampling units from a series of listening stations was developed. These tracks took around two weeks to process and analyse, yet only formed a small proportion of two surveys. This rule was based on minimising the number of stations over which an individual dolphin group could be heard, resulting in listening stations which were independent with respect to individual dolphin groups.

To determine a rule to make listening stations independent, the acoustically scored levels of dolphin whistles (0-5) were compared with the bearings obtained from the same period of time for whistles detected by the *Whistle* software. This was done for a sample of the data over a range of different habitat types (on shelf or off shelf). The bearings were plotted against time, and the time and distance at which each group passed abeam of the boat was estimated by eye from the bearing-time graph based on a vessel speed of 10 knots (Figures 2.2 & 2.3). This is a similar technique to that used for determining distance to individual sperm whale clicks in other studies (Hastie et al. 2003; Leaper et al. 2000).

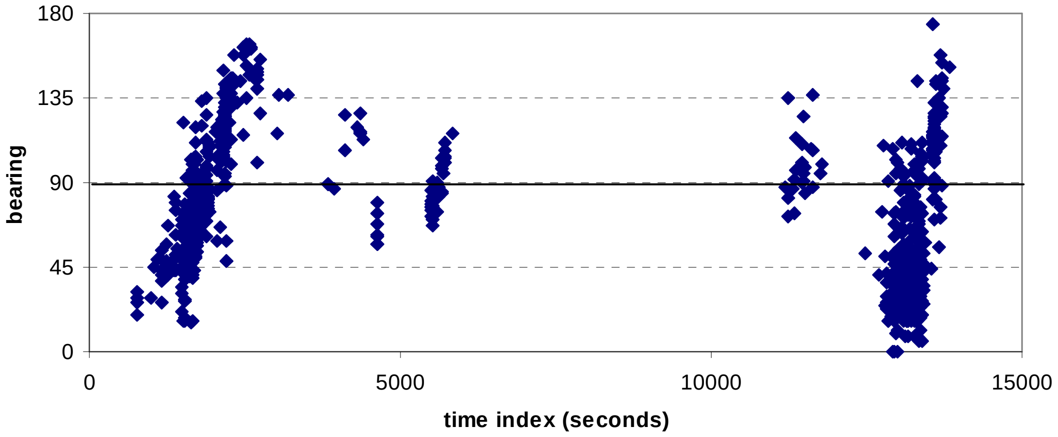


Figure 2.2 – An example of bearings to whistles during 4 hours (equivalent of 75 km) of real-time automatic whistle detection by the IFAW software *Whistle*. Note how detections are typically ahead of the vessel (bearing < 90°) then move astern (bearing > 90°) as the vessel passes a vocalising group. Each group of clicks crossing the 90° bearing represents a group of dolphins passing abeam of the vessel.

Based on crossing bearing of continuous tracks of dolphin group whistles identified using the *Whistle* software, measured distances from the trackline to the dolphin group as they passed abeam of the vessel ranged from 0 m to 3.8 km from the vessel at a median of 500 m (Inter-quartile range (IQR) = 80 m – 1.7 km, n = 17). Four out of the 21 dolphin tracks were not clear enough to estimate the distance to the trackline.

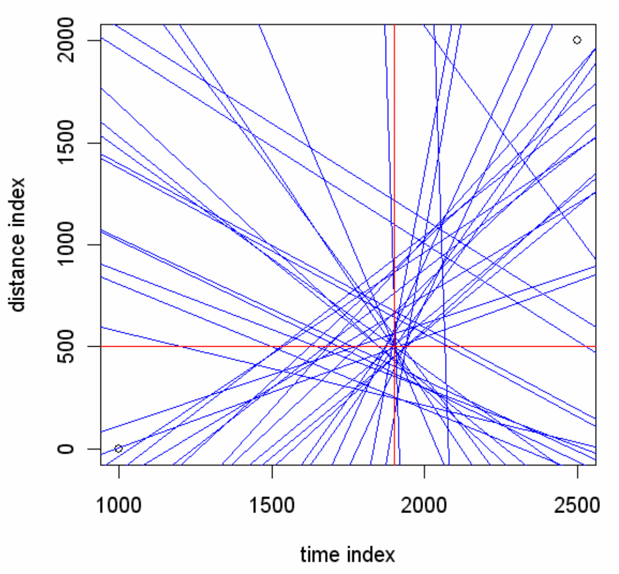


Figure 2.3 – Plot of bearing lines used to locate a dolphin group during an encounter (the first of the whistle groups shown in figure 2.2). The vessel's movement over time (in seconds) is represented by the x-axis, with each blue line indicating the estimated bearing to a group of whistles. The point at which the line intersect shows the time at which the group passed abeam, and the distance of the group to the trackline. This intersection of bearings changes over time due to dolphin movement. The estimated distance of the group at the time at which it passes abeam is indicated in red (in this case the group passed abearm at a range of approx 1 km from the vessel (index x 1.84 = distance in meters).

Where there was a single group not accompanied by any other groups, the distance over which the same group of dolphins could be heard was estimated. The maximum distance over which dolphin groups were found to be autocorrelated was 30 km, suggesting that under certain oceanographic conditions a group of dolphins could be heard to 15 km.

Based on the sample of data including 21 dolphin whistle tracks, a 'true distribution' of dolphin groups was generated, i.e. presence of a dolphin group at the point at which it passed abeam of the vessel, but absence elsewhere. If a dolphin group passed abeam of the vessel during the 15 minute period centred at the time of the listening station (i.e. within 7.5 minutes before or after the start of the 1 minute listening station), then the dolphin group was associated with that listening station. This 'true distribution' was compared to the acoustically scored levels of dolphin whistles (0-5).

Different rules were applied to the acoustically scored levels of dolphin whistles to classify the different levels as a presence/absence of dolphin groups:

i) Considering whistles >0 loudness, consecutive detections were considered one group encounter until no dolphins (0 loudness) had been detected for 30 minutes (9 km), with one presence at the mid point of the group;

ii) Considering whistles >0 loudness, consecutive detections were considered one group encounter until no dolphins (0 loudness) had been detected for 45 minutes (15 km) (Gordon et al. 2000), with one presence at the mid point of the group;

iii) Considering whistles >1 loudness, consecutive detections were considered one group encounter until no dolphins (≤ 1 loudness) had been detected for 45 minutes (15 km), with one presence at the mid point of the group;

iv) Considering whistles >2 loudness, consecutive detections were considered one group encounter until no dolphins (≤ 2 loudness) had been detected for 45 minutes (15 km), with one presence at the mid point of the group.

By comparing the distributions resulting from application of these rules with the ‘true distribution’ it was possible to calculate the percentage correctly classified. Each of the rules performed well, but rule (iii) performed best with 88% correctly classified at mimicking the ‘true’ distribution to within one listening station, and with a false positive detection rate of less than 3%. Therefore, this latter rule was used to generate the data on which subsequent analyses were based. This method would remove much of the autocorrelation in the data caused by hearing the same group of animals over several listening stations, and avoided counting the same group more than once.

2.2.4 Statistical analysis

2.2.4.1 Pre-modelling analysis

Since the coarsest scale for the environmental data was 9 km (for the FOAM oceanographic and current data), survey segments were defined as the trackline between two consecutive listening stations per segment (at 10 knots this is the equivalent of 9 km segments). Where the environmental variables were stored within the survey Access database files (such as noise levels, vessel speed, etc.), the environmental variables were either averaged over each segment (e.g. vessel speed), or the most recent value for that variable (e.g. last recorded wind speed) were determined using macros written in Access. For all other variables (topography, satellite and FOAM variables), values were determined for the mid-point of each segment using the STJG GIS extraction tool version 1.0.1 (Gontarek 2005) in ArcGIS 9.0 (ESRI Inc).

Prior to modelling, a Spearman’s Rank Correlation test was carried out using Minitab v12.23 (Minitab Inc. 1999) to test for correlations between environmental variables. If there was a strong correlation ($r > 0.8$) between variables, the first of the variables selected by the step-wise model selection (detailed in the next section) was retained and any variables with which it was correlated were discarded.

2.2.4.2 Modelling dolphin occurrence – model selection

Generalised Additive Models (GAMs) were used to relate dolphin presence/absence per 9 km segment to the survey (vessel speed, survey vessel noise, remote vessel noise & water noise), temporal, and environmental variables listed in Table 2.2. Generalised additive modelling is a method of analysing data responses that may be non-normal with non-linear smooths of predictor variables, with the general form (Hastie & Tibshirani 1990):

$$E[y] = g^{-1}\left(\beta_0 + \sum_k S_k(x_k)\right)$$

Where $E[y]$ is the expected value of the response variable y (dolphin group presence per 9km segment), $g()$ is the function linking the response to the non-linear smooths S of the k predictor variables x_k and the intercept term β_0. A binomial distribution was assumed for the response variable with the logit link function (Chambers & Hastie 1991):

$$g(p) = \log\left(\frac{p}{1-p}\right)$$

Where p is the probability of dolphin presence. The GAMs were fitted in R version 2.3.0 (The R Foundation for Statistical Computing 2006) using the MGCV (Multiple

Generalised Cross Validation) library (Wood 2006b). Unlike the standard GAM library in R/S+, the degree of smoothness (or degrees of freedom) of the smooths of the predictor variables is determined as part of the model fitting process (Wood 2006a). The default smoothing spline used in the MGCV smooth *s()* is a Thin Plate Regression Spline (TPRS), which allows a smooth to be estimated with multiple predictor variables in noisy data, without knowledge of the knot locations (where the different splines join) being required (Wood 2006a). This method removes the subjectivity that is introduced by estimating knot locations, that is required for other smoothing methods. TPRS are good for smooth interactions of parameters that are in the same units (such as latitude & longitude). In this spline smoother, the default *dimension* (k = equivalent to setting the maximum number of degrees of freedom for each smooth) is 10 for 1-way smooths, 30 for 2-way smooths, and 90 for 3-way smooths. To reduce potential overfitting of smooths to the data, two approaches were used. Firstly, a α=1.4 was used in the model fitting as suggested by Kim & Gu (2004), which forces the estimated degrees of freedom in a smooth to count for 1.4 degrees of freedom in the UBRE score (Wood 2006a), so penalising the GAM function for using too many degrees of freedom. Secondly, the smooths for each of the variables, excluding latitude and longitude, were limited to 4 or less estimated degrees of freedom.

Stepwise addition of environmental variables to the null model (no predictor variables) was carried out (forward step-wise selection), and models compared based on minimising the UBRE (UnBiased Risk Estimator) score. The UBRE score is the Poisson GAM equivalent of the AIC value (in effect, just a linear transformation of AIC), and scores on both fit and the number of parameters used to describe the model (Wood 2006a). In selecting the best model, predictor variables were only added if :

i) they reduced the AIC equivalent of the UBRE score (multiplying UBRE by n) by 2 or more, as recommended by Burnham & Anderson (2002).

ii) the variables were significant at $p < 0.05$

Firstly, survey variables (water noise, survey vessel noise & type, remote vessel noise, wind speed, and vessel speed) were added to the model to compensate for survey effects, since variables such as wind speed are known to affect noise conditions in the ocean and hence the ability to hear dolphin vocalisations (Urick 1983). Also different survey vessels produce different amounts of noise that can strongly influence the detectability of animals (Swift pers. comm.). So vessel type was coded: 1 for *FRV Scotia*, 2 for *RV Poseidon*, and 3 for *RSS Charles Darwin*, and included as a factor variable in the models.

Time was then allowed to be added to the model, since dolphin vocalisations have been shown to vary diurnally in other studies (Goold 2000; Hastie et al. 2005). After compensating for survey and diurnal effects on the detection rate of dolphin whistles, the topographical, oceanographic and current variables were added.

Variables included in the model selection included: depth, SST, SSS, chlorophyll, halocline depth & strength, thermocline depth & strength, surface & bottom current speed. As a first step, a check was carried out to see whether month (as a factor variable: 1 = May, 2 = July, 3 = September/October) or year (as a factor variable: 1 = 2003, 2 = 2004, 3 = 2005) were significant in the models before adding the environmental variables, and then subsequently to see whether there was any remaining unmodelled variance that could be explained by month or year. Models were also built separately for the May and September/October survey data to examine the variables influencing the distribution of delphinids in either month.

2.2.4.3 Modelling dolphin occurrence - model evaluation

A model should be able to fully describe the species distribution without any remaining temporal or spatial autocorrelation. Remaining autocorrelation in the residuals would imply that either the data being modelled is too highly autocorrelated for the environmental variables to explain the autocorrelation, or that an important variable, that was itself autocorrelated on the temporal and spatial scale sampled, has not been included in the model. In this study, the Wald-Wolfowitz run test was used to test for any remaining nonrandomness in the model residuals (Hardin & Hilbe 2003). The test looks for patterns within the residuals by coding the residuals as to whether they are positive (1) or negative (-1) and looking for continuous runs of positive or negative residuals.

The number of runs in the sequence allows an evaluation of the nonrandomness in the residuals to be made according to the following equations (Hardin & Hilbe 2003):

$$E(T) = \frac{2n_p n_n}{n_p + n_n} + 1$$

$$V(T) = \frac{2n_p n_n (2n_p n_n - n_p - n_n)}{(n_p + n_n)^2 (n_p + n_n - 1)}$$

Where *E(T)* is the expected value of the number of runs in the sequence of residuals *T*, and *V(T)* is the expected variance of *T*; n_p is the total number of positive residuals; n_n is the number of negative residuals in the sequence. The test statistic is thus:

$$W_Z = \frac{T - E(T)}{\sqrt{V(T)}}$$

Where W_Z has approximately a normal distribution such that extreme values (>|1.96| for $p<0.05$) indicate that there is remaining non-randomness in the residuals, and that the model therefore does not adequately account for the underlying distribution of the data. This could indicate that a variable was missing from the model, or that the delphinid groups were clumped in some way behaviourally.

The final models were predicted over 18x18 km grid cells, set to twice the size of the segment size as recommended by Hedley (2000). This allowed for visual evaluation of the models against the actual detections, and of predicted distributions between different models. Predictions were based on environmental variables available from 14 October 2004 for comparing the majority of models, 14 October 2005 for the 2005 model, and 21 May 2004 for the May model. These dates were selected for several reasons: they were based days that were actually surveyed, formed the mid points of the survey data, and for the full model October was the only month during which both areas around the Faroe-Shetland Channel and the Ellet Line were surveyed.

2.2.4.4 Models constructed

To meet the objectives of this chapter, the analysis was divided into a number of sections and models. Firstly, the effect of autocorrelation within the data caused by hearing the same group of dolphins over several listening stations (‘acoustic autocorrelation') was investigated. The original data were modelled and compared with the models obtained with the acoustic autocorrelation removed according to the rule described in §2.2.3. Secondly, to examine the effect of time on the models, 2003-2004 data were modelled separately to the 2005 data, and these were compared with each other and with models of all data together. 2003-2004 were chosen to be clumped separately to 2005, due to anomalously poor weather conditions in 2005 as well as unusual changes in the Hebridean ecosystem observed that year (Stevick et al. 2007). Thirdly, to examine the effect of changes in spatial *extent* on the models, the models for the full dataset were compared with those based on the Faroe-Shetland Channel surveys (excluding the Ellet Line and Rockall Trough surveys). Finally, to examine the ability of the models to account for seasonal changes in distribution, the May Faroe-Shetland Channel surveys were modelled separately to the October Faroe-Shetland Channel surveys and the models compared with the predictions from the full model based on both seasons for the same area.

2.3 Results

A total of 11 475 km were surveyed off the west coast of Scotland between July 2003 and October 2005, as detailed by survey in Tables 2.1 & 2.3. Overall there were 1247 9 km segments with 624 hours of listening effort for which all environmental variables were available. Of these, 420 segments (33.7%) had whistle detections ≥ 1 loudness and 139 segments (11.1%) had dolphin group presence (using the rule detailed in §2.2.3). Dolphins were detected fairly evenly over the survey area, but with fewer detections over shallower shelf waters (Figure 2.4). Overall there was relatively even survey coverage of both shelf (<200m) and off-shelf waters (>200m) with 41.5% of effort concentrated in shelf habitats. Despite this, only 28.3% of all dolphin whistle groups were detected in the shelf (<200m) habitat.

Table 2.3 – Acoustic effort (in numbers of segments and km) and the autocorrelated and grouped whistle detection rates (based on the rule explained in §2.2.3) by number of segments with presence, and by % of segments for the oceanographic surveys carried out off the west coast of Scotland.

Survey Date	Number of segments (overall distance in km)	Number of segments with any whistles (% of segments)	Number of segments with whistle groups (% of segments)
19-25 July 2003	114 (1050 km)	55 (48.2%)	15 (13.2%)
16-28 September 2003	137 (1260 km)	36 (26.3%)	15 (10.9%)
13-29 May 2004	244 (2245 km)	62 (25.4%)	22 (9.0%)
5-17 October 2004	189 (1740 km)	75 (39.7%)	26 (13.8%)
8-26 May 2005	226 (2080 km)	51 (22.6%)	19 (8.4%)
27 Sept – 8 Oct 2005	130 (1195 km)	31 (23.8%)	7 (5.4%)
7-25 October 2005	207 (1905 km)	110 (53.1%)	35 (16.9%)
TOTAL	**1247 (11 475 km)**	**420 (33.7%)**	**139 (11.1%)**

2.3.1 Environmental variables

A summary of the environmental variables is given in Table 2.4. Coverage of variables differed between surveys and years depending both on the type of survey (Faroe-Shetland Channel or Ellet Line hydrographic lines) and the additional aims of the survey (e.g. during the May 2005 survey, the second half of the survey involved surveying for salmon smoult along the shelf edge).

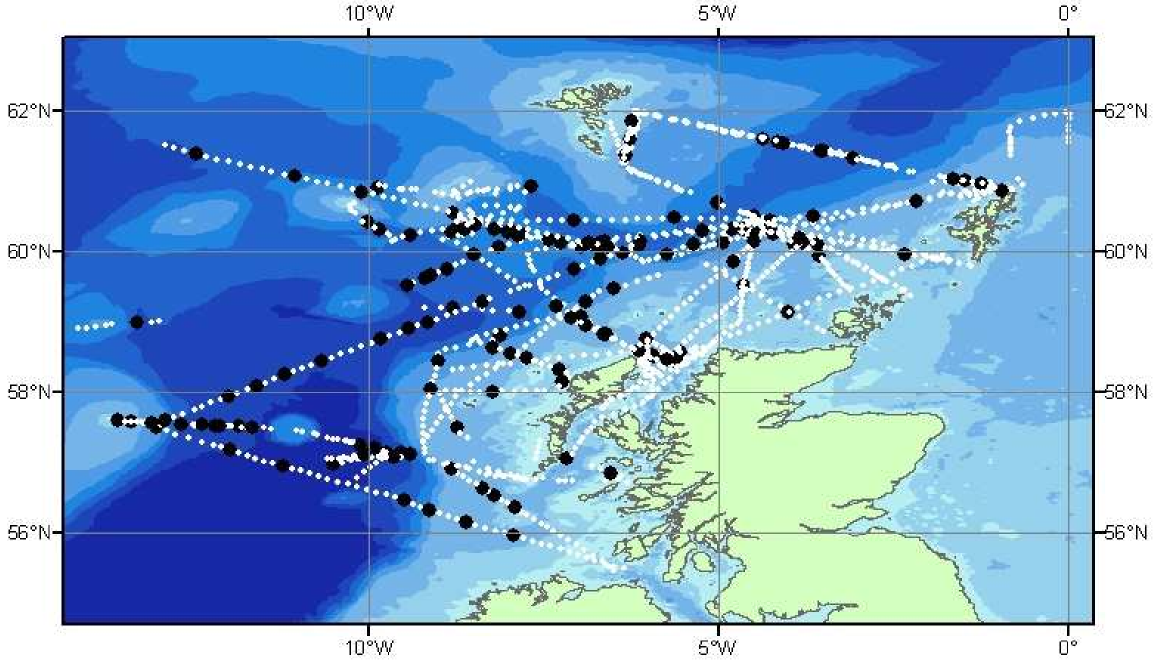


Figure 2.4 – Survey effort (9 km segments, *n* = 1247) and delphinid group detections (*n* = 139) for the west coast of Scotland surveys carried out between July 2003 and October 2005. Segments in which delphinid groups were detected are presented as black dots and white dots where dolphin groups are absent. Data are overlaid on bathymetry (GEBCO 2003).

The Spearman's rank correlation test (Appendix Table A1.2) showed no significant correlations with r > 0.8 between any of the variables included in the model selection. There were 'relatively strong' correlations (r > 0.5) between month and SST, with warmer sea surface temperatures as the seasons progressed from spring (May) to autumn (October). Year was negatively correlated with SST and surface chlorophyll, but positively correlated with thermocline depth (r > 0.5). Chlorophyll was also negatively correlated with thermocline depth (r > 0.5), with higher levels of surface chlorophyll in areas of shallower thermoclines. Finally, water depth was correlated with both halocline depth & strength and thermocline strength (r > 0.5) but in opposite directions: halocline depth & strength increased with increasing depth, whereas thermocline strength decreased with increasing water depth.

The survey area combines shelf waters (50-200m), shelf edge (200-500m), and deep waters dropping off to deeper than 2000m (Figure 2.1a). The area is topographically complex with many sea-mounts, banks, ridges (Wyville-Thompson Ridge) in addition to the Faroese and Scottish shelf edges.

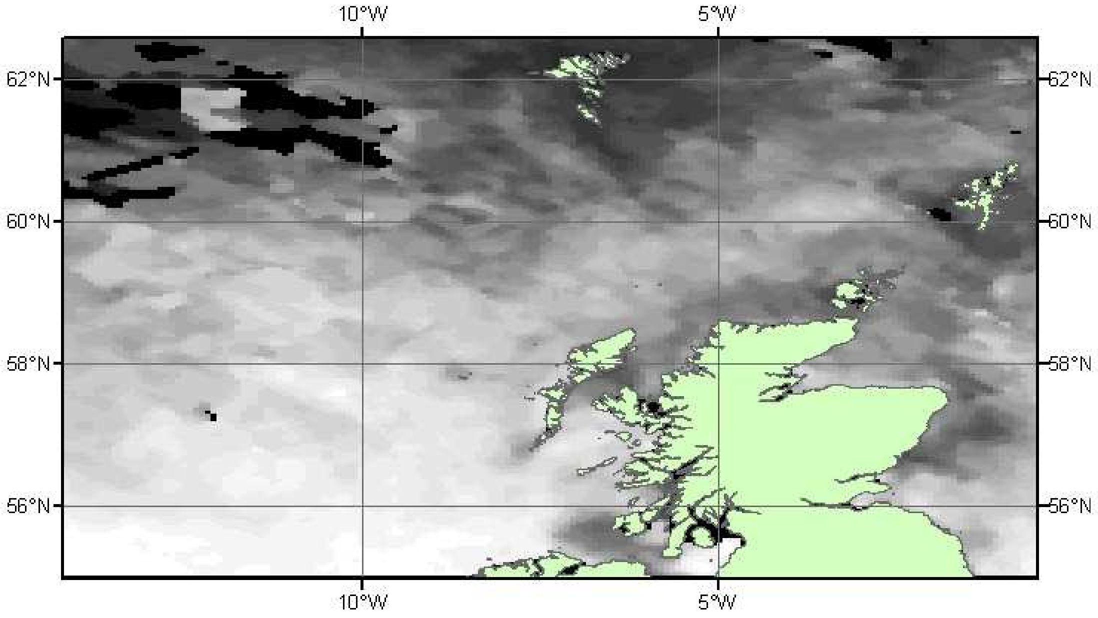
Table 2.4 – Summary statistics for the environmental variables for the oceanographic survey years grouped by 2003-2004 surveys, and 2005 surveys off the west coast of Scotland. Results of a Mann-Whitney test compare the two data sets are shown, where * $p<0.05$; **$p<0.01$; and ***$p<0.001$.

Parameter		2003-2004	2005
Survey effort with environmental data available			
Distance surveyed (km)		6840	5580
Number of stations/segments		684	558
Segments with dolphin whistles or clicks		106 (15.5%)	77 (13.8%)
Survey variables			
Vessel speed	range (knots)	3.3-12.8	3.4-13.7
	mean (standard deviation)	9.7 (1.9)	9.8 (1.7)
WaterNoise	range	0-5	0-4***
	median (IQR)	2 (1-3)	1.5 (1-2)
SurveyVesselNoise	range	0-4	0-4***
	median (IQR)	3 (2-3)	2 (1.5-3)
Temporal variables			
TimeDayNight	range	0-2	0-2***
	mean (standard deviation)	0.95 (0.55)	1.08 (0.54)
Topographical variables			
Depth	range (m)	15-2374	28-2300***
	median (IQR)	419 (133-958)	202 (110-806)
Satellite data			
SST	range (°C)	5.7-15.3	6.8-14.5***
	mean (standard deviation)	11.6 (1.9)	10.8 (1.5)
Chl	range (mg/m^3)	0.06-22.1	0.03-2.99***
	median (IQR)	0.75 (0.43-1.45)	0.28 (0.19-0.43)
FOAM variables			
HaloDepth	range (m)	30-1335	30-920***
	median (IQR)	120 (50-255)	100 (50-145)
SBS	range (psu)	-0.38-0.2	-0.44-0.15
	median (IQR)	0.0 (-0.13-0.04)	0.0 (-0.03-0.02)
SSS	range (psu)	35.0-35.4	35.0-35.4
	median (IQR)	35.25 (35.2-35.3)	35.27 (35.2-35.3)
ThermDepth	range (m)	20-470	55-774***
	median (IQR)	78 (40-470)	113 (79-159)
SBT	range (ºC)	-12.5-0.11	-9.5-0.02***
	median (IQR)	-2.2 (-4.8--1.0)	-0.88 (-3.33--0.05)
SurfCurSpd	range (m/s)	0-0.58	0.01-0.53**
	median (IQR)	0.134 (0.06-0.19)	0.125 (0.07-0.21)
BotCurSped	range (m/s)	0-0.46	0-0.39
	median (IQR)	0.07 (0.03-0.13)	0.07 (0.04-0.09)

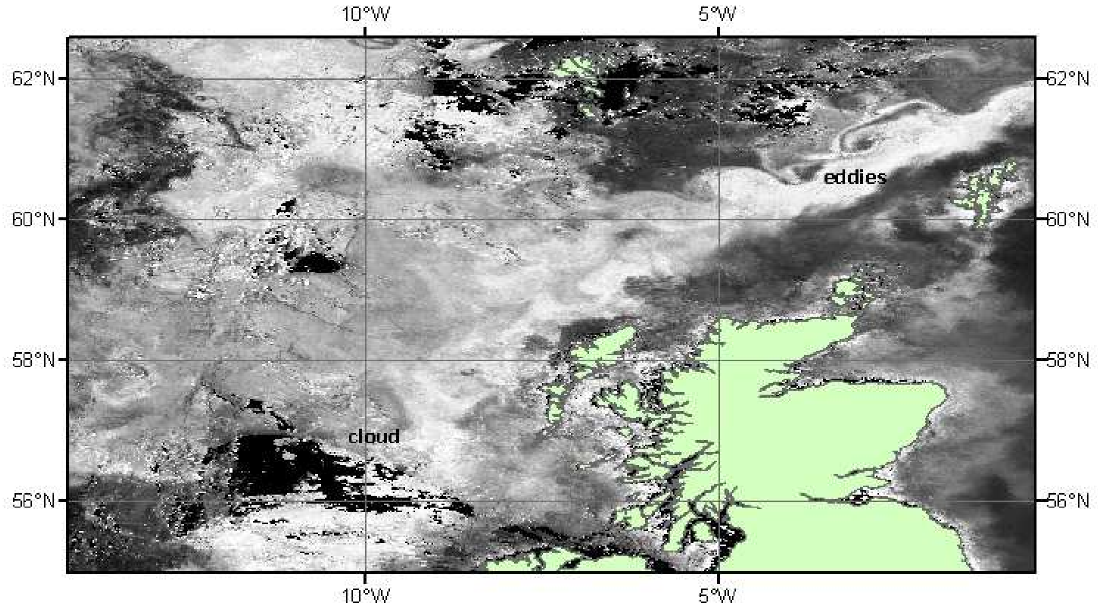
Sea surface temperature was generally warmer in the southern part of the survey area decreasing with increasing latitude; however a tongue of warm water travelled up through the Faroe-Shetland Channel with the North Atlantic Water (NAW) flow (Gulf Stream) (Figure 2.5a). This same area had high levels of primary productivity with surface chlorophyll concentrated within eddies as indicated on the satellite images (Figure 2.5b), and as identified by Sherwin et al. (1999, 2006). The distribution and levels of surface chlorophyll varied significantly over time, in no clearly predictable way. However, as an example, a satellite image taken from July 2003 (Figure 2.5b) showed high surface levels of chlorophyll concentrated along the shelf edge and in mixed coastal waters, but low levels in shelf waters of the Faroe Plateau and Shetland shelf (Figure 2.5b).

The FOAM oceanographic variables (halocline strength and surface current speed) strongly reflected the effect of the topography and different bodies of water on the resulting oceanography. As an example, the figure of halocline strength (Figure 2.6a) clearly shows the presence of the fresh deep Norwegian Sea Deep Water (NSDW) sitting below the warmer more saline surface North Atlantic Water (NAW) in the Faroe-Shetland Channel, resulting in a strong negative halocline. The shelf edge waters have a strong positive halocline with the surface waters being less saline than the deeper water.

The complex topography through the Faroe-Shetland Channel, and around the Wyville-Thompson Ridge results in a complex pattern of current speeds (although this is also wind-moderated at the surface). Figure 2.6b shows the strong surface currents in the Faroe-Shetland Channel, travelling along the Shetland shelf side of the channel and along the Wyville-Thompson Ridge. There are also big swirls of high surface current speed in the deep offshore water to the south of the Faroes that appear to vary on a daily basis. In summary, the survey area in this part of the North Atlantic, is subject to wide variations in the oceanographic conditions that were used to determine dolphin distributions.

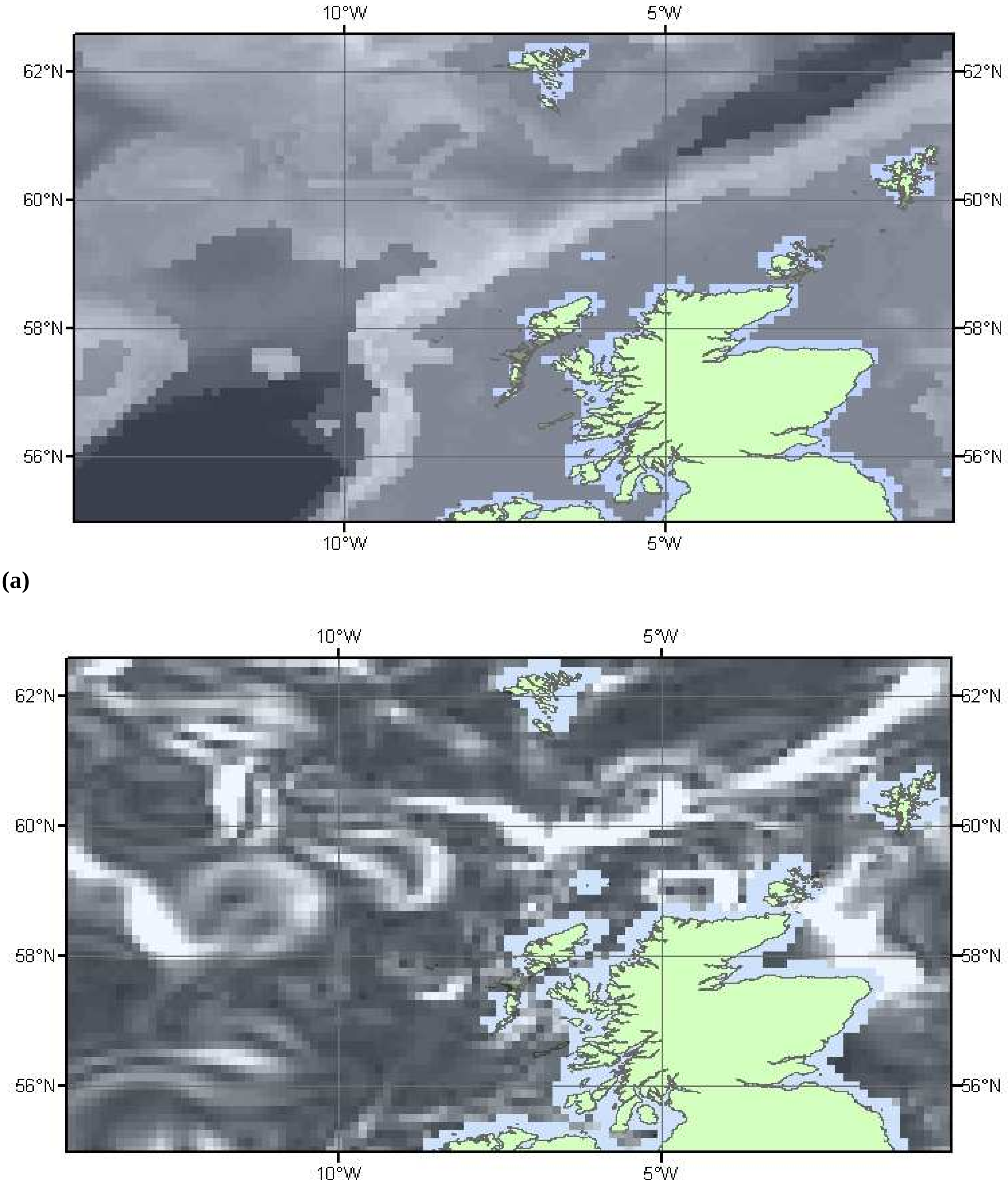


(a)



(b)

Figure 2.5 (a) Weekly composite satellite image of sea surface temperature for the week beginning 23 May 2004 where black = 0°C (or cloud) – white = 12.6°C; and (b) weekly composite satellite image of surface chlorophyll concentrations for the week beginning 13 July 2003 where black = 0 chlorophyll (or cloud) – white = 65 mg/m^3 density of chlorophyll. Note the clouds obscuring observations in both images (black patches), and the swirling eddies of high chlorophyll concentrations in the Faroe-Shetland Channel.



(a)

(b)

Figure 2.6 – (a) FOAM modelled halocline strength (surface to bottom salinity) for 27 September 2003 with dark grey representing a strong negative halocline strength (i.e. bottom water fresher than surface water), and white a strong positive halocline strength (i.e. bottom water more saline than surface water); (b) FOAM modelled surface current speed (m/s) for 27 September 2003 with dark grey representing low current speeds, and white high current speeds.

2.3.2 Effect of 'acoustic autocorrelation' on model selection

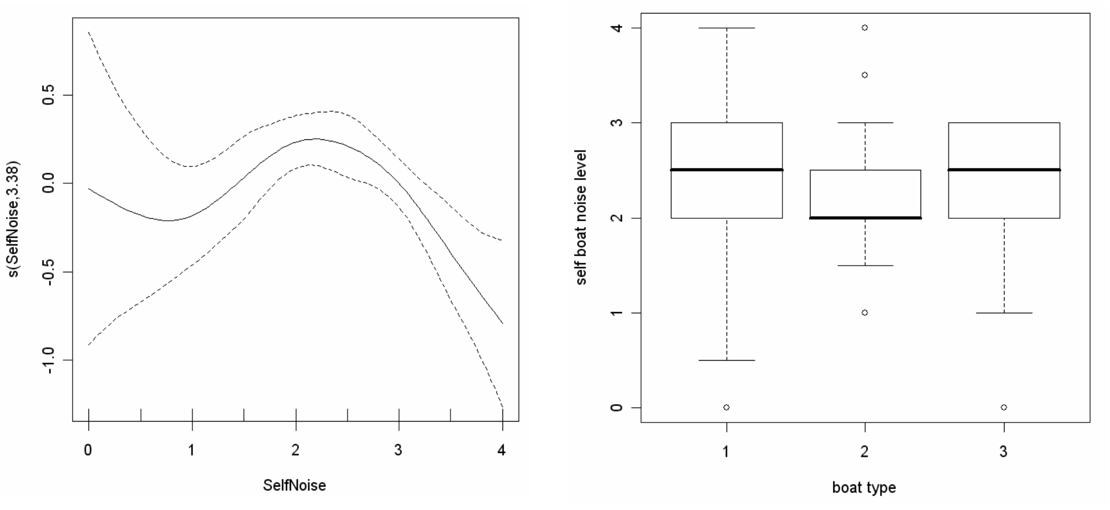
The best model for the ungrouped delphinid whistle occurrence data (the original data before the rule detailed in §2.2.3 was applied) included five terms (in order of selection): a two way smooth of survey vessel noise with vessel type, depth, SST, thermocline depth and halocline strength, explaining 15.3% of the deviance (Table 2.5). The grouped delphinid occurrence model (after application of the rule detailed in §2.2.3) included three of the same variables but excluded interaction term of survey vessel noise with vessel type, and halocline strength, explaining 5.3% of the deviance (Table 2.5).

Survey effects were only significant in explaining the detection of the ungrouped delphinid whistles and explained 5.7% of the deviance. The interaction between survey vessel noise and vessel type showed whistle detection dropping rapidly above survey vessel noise levels of ≥ 4 in loudness (Figure 2.7). Also, *R/V Poseidon* had lower reported levels of self boat noise than either the *FRV Scotia* or the *RSS Charles Darwin* (Figure 2.7). This was no longer significant when the whistles were grouped into single delphinid encounters.

Table 2.5 – Summary of delphinid occurrence GAM models for the west coast of Scotland. Linear fits are represented by "L1", whereas smoothing terms are represented by "S#", where # is the number of degrees of freedom, number in superscript denotes order of importance within the model. Acronym definitions: FSC = Faroe-Shetland Channel; VN:V = two-way smooth of vessel noise with vessel type; HaloD = halocline depth; ThD = thermocline depth. Table design based on Ferguson et al (2006).

Model	Predictor variables										
	Speed	VN:V	Time	Depth	SST	Chl	HaloD	SBS	SSS	ThD	SBT
Ungrouped		S6.6^{1}		S3.6^{2}	S2.1^{3}			S2.5^{5}		L1^{4}	
Grouped				S1.9^{1}	S3.2^{2}					L1^{3}	
2003-2004				S2.1^{1}	S2.8^{2}						
2005				L1^{1}						L1^{2}	
FSC					S2.6^{1}			S2.7^{3}		L1^{2}	
FSC May							S1.5^{1}			L1^{2}	
FSC October					S2.8^{1}						

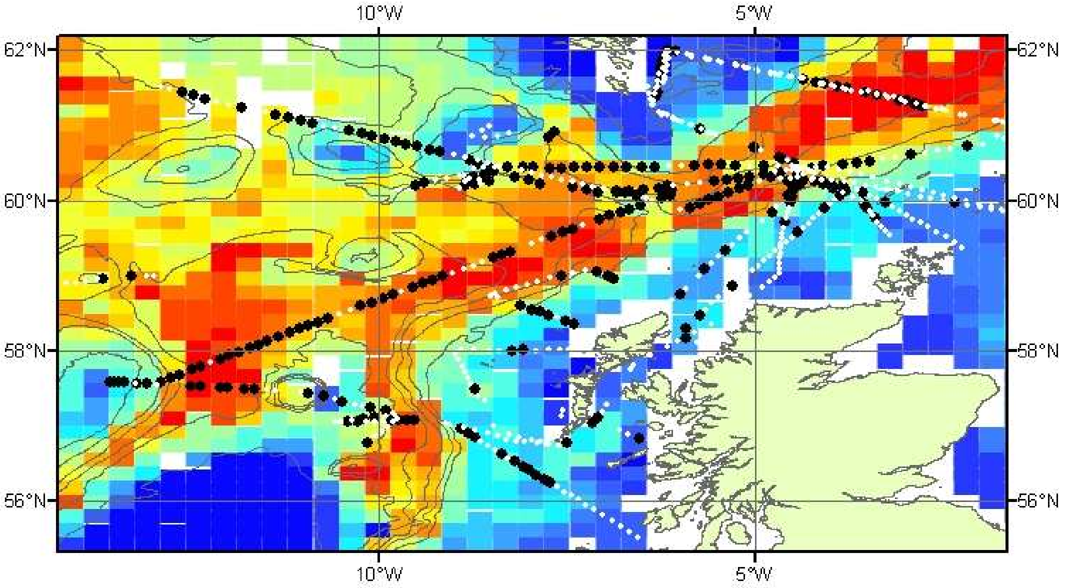
Delphinid whistles or groups of whistles were most likely to be heard in water deeper than 400 m (Figure 2.9c), in water warmer than 10.5°C (smooth similar to that shown in Figure 2.12a), and in areas of deeper thermoclines.



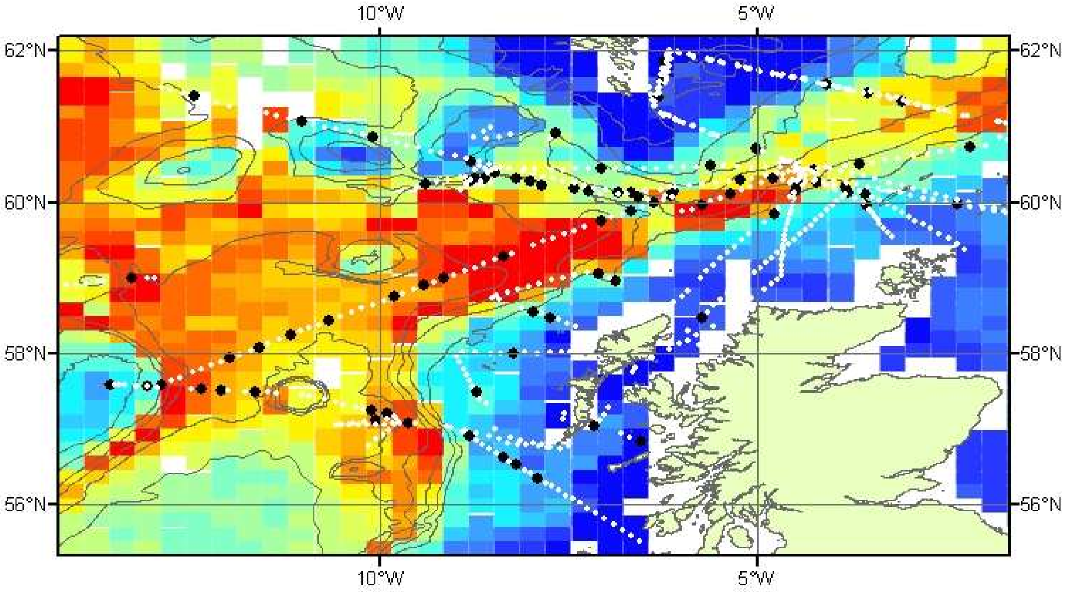
(a) (b)

Figure 2.7 – (a) Delphinid whistle occurrence per 9km segment (*n* = 1247) modelled as a GAM smooth function of perceived survey vessel noise level (d.f. = 3.4) for all survey data collected off the west coast of Scotland between July 2003 and October 2005. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show 95% confidence intervals; (b) Perceived survey vessel noise levels by survey vessel type (1 = *FRV Scotia*, 2 = *R/V Poseidon*, and 3 = *RSS Charles Darwin*): median noise levels = thick black bars, inter-quartile range = box, range = extent of dotted line, outliers = open circles.

Overall, environmental variables were able to explain 9.6% of the deviance in the original ungrouped delphinid whistle model, and 5.3% of the deviance for the grouped whistle model. However, the ungrouped model failed to fully model the autocorrelation in the data since the residuals were significantly non-randomly distributed (W_z = -18.1, $p < 0.001$). There was no autocorrelation within the residuals of the grouped whistle model (W_z = 0.82, $p = 0.793$). Comparison of predictions based on each model show some differences (Figure 2.8). The ungrouped delphinid model predicts higher probability of delphinid occurrence in the Faroe-Shetland Channel and on the Wyville-Thompson Ridge than the grouped delphinid model. However, both models predict high probability of delphinid occurrence along the Scottish shelf edge from around the Wyville-Thompson Ridge southwards and alongside the steep side of Rockall Bank.



(a)



(b)

Figure 2.8 - Spatial prediction based on environmental variables available for 14 October 2004 of the probability of detecting delphinid whistles per 20km grid for (a) the best model based on all (ungrouped) delphinid whistles, and (b) the best model based on grouped delphinid whistles, for all survey data from July 2003 – October 2005. 9km segments (*n* = 1247) are presented as black dots where delphinid whistles (a) or groups of whistles (b) are present and white dots where absent. Data are overlaid on bathymetry (solid lines) (GEBCO, BODC 2003). Grid colours represent the probability of delphinid whistle presence from low (blue) to high (red), ranging from 0-0.8 for the ungrouped model (a) and 0-0.4 for the grouped whistle model (b), colour gradation based on 20 levels using quantile classification.

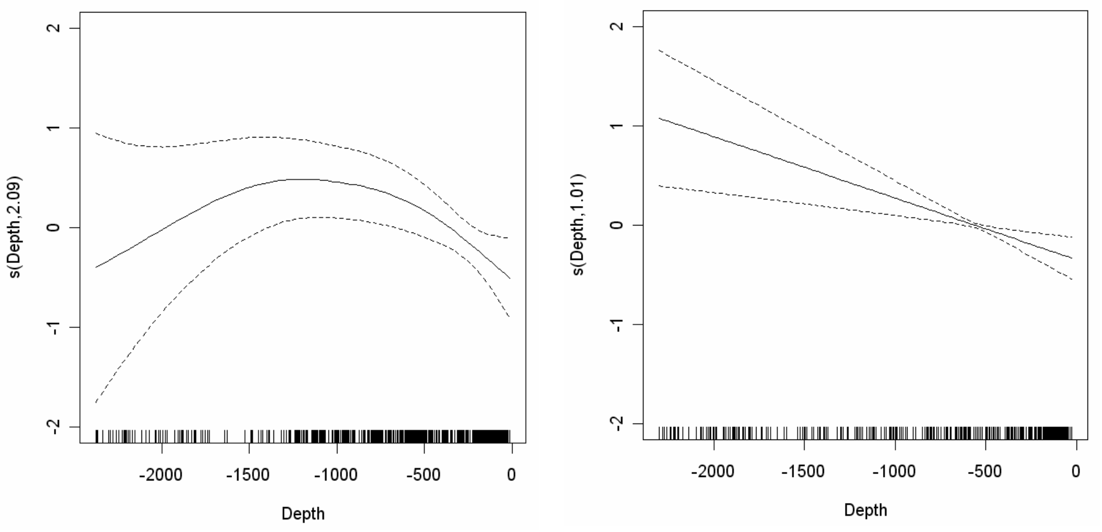
2.3.3 Effect of year on model selection

The best delphinid group occurrence model for the 2003-2004 data included two terms (in order of selection): depth and SST, explaining 4.1% of the deviance (Table 2.5). The best model for the 2005 data also included depth but the second variable changed from SST to thermocline depth, with both terms explaining an overall 4.9% of the deviance (Table 2.5).

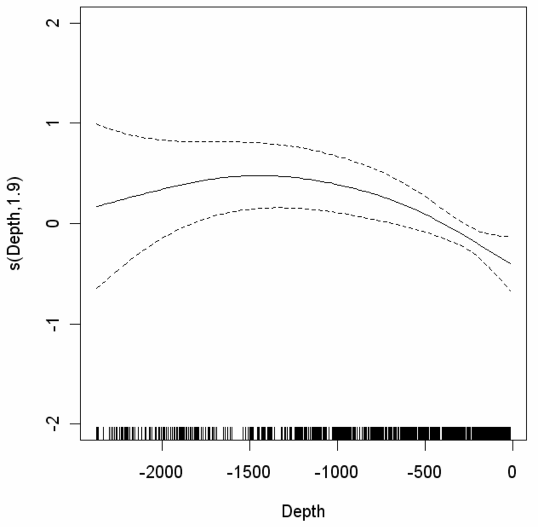
Depth was the only variable to be significant in explaining the distribution of delphinids in all three combinations of years: 2005, 2003-2004 and 2003-2005 (Table 2.3), however the relationship varied between years. In 2003-2004, delphinid groups were most likely to be heard in waters deeper than 400 m, with a peak between 1000-1500 m, however the confidence limits above 1500 m were too large to determine preference above this depth (Figure 2.10a). This relationship was nearly identical to that for the 2003-2005, although the preference was not as strong (Figure 2.10c). In 2005, the preference for depth changed from a non-linear to a linear relationship with delphinid occurrence increasing with depth, animals preferring waters deeper than 600m (Figure 2.10b).

Although the remaining environmental predictor was different between 2003-2004 and 2005 models, both SST (for 2003-2004) and thermocline depth (for 2005) had identical relationships with delphinid distributions to those predicted by the full three year model.

Comparing predicted distributions of delphinids based on the two models, both models predicted low probability of occurrence in the shallower on-shelf waters, and high probability of occurrence in a small patch just south of the Wyville-Thompson Ridge towards Rosemary Bank (Figure 2.11). Otherwise, the models predicted different areas of high probability of occurrence, with the 2003-2004 model hotspots found in the Faroe-Shetland Channel, along the steeper shelf edges, and in a band west of the patch south of the Wyville-Thompson. Of the areas surveyed, the 2005 model predicted high probability of delphinid presence to the east of the Anton Dorhn seamount and to the east of Rosemary Bank.

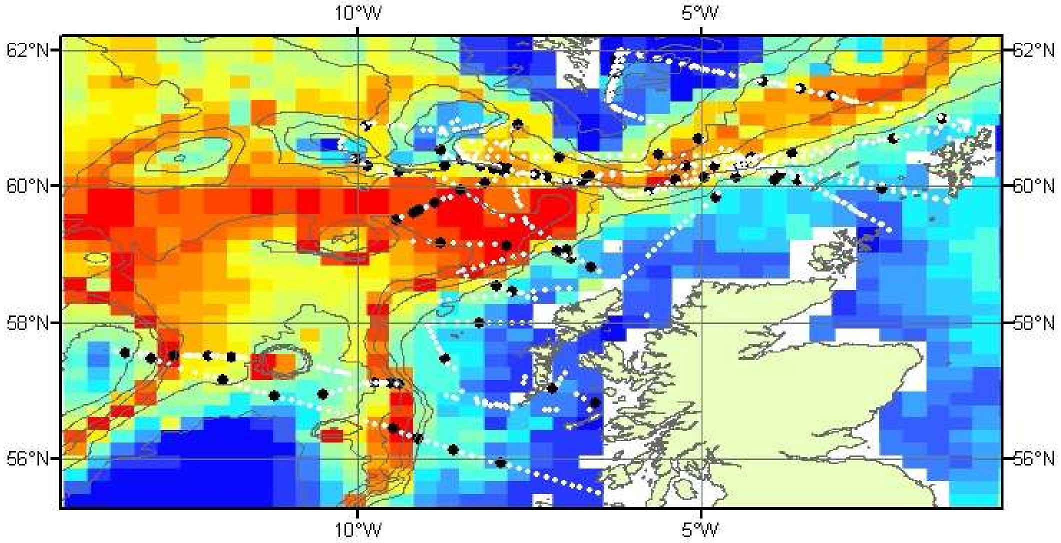


(a) **(b)**

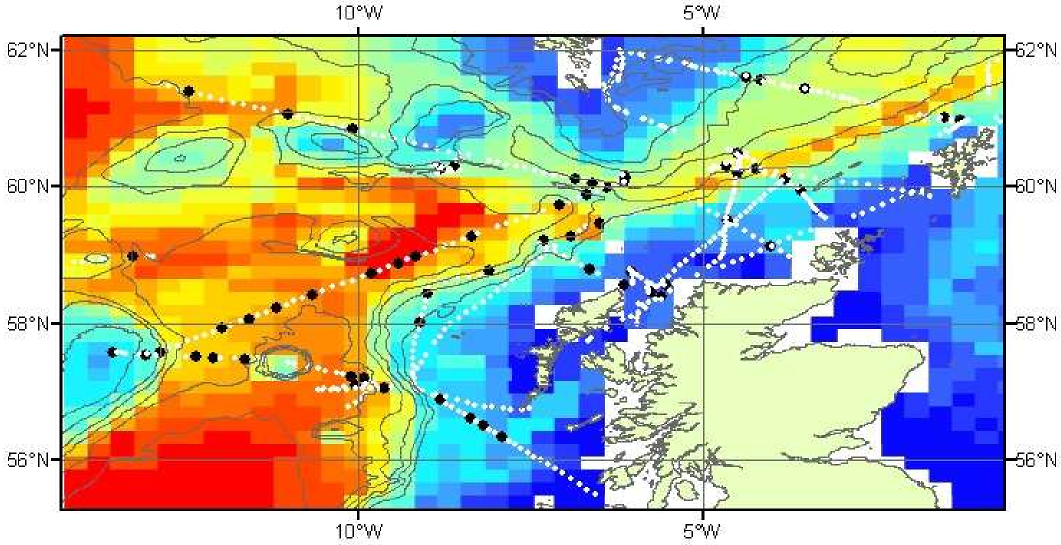


(c)

Figure 2.9 Delphinid group whistle occurrence per 9km segment modelled as a GAM smooth function of depth for (a) 2003-2004 (d.f. = 2.1, *n* = 684), (b) 2005 (d.f. = 1, *n* = 558), (c) 2003-2005 (d.f. = 1.9, *n* = 1247) survey data collected off the west coast of Scotland. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show approximate 95% confidence intervals



(a)



(b)

Figure 2.10 - Spatial prediction based on the best model for the occurrence of delphinid groups in a 20km grid cell for (a) for the 2003-2004 data based on 14 October 2004; and (b) for the 2005 data based on 14 October 2005. Overlaid on the maps are the effort segments (white dots) and the dolphin whistle group detections (black dots) for each data set. Also overlaid are GEBCO depth contours (dark grey lines). Colours represent probability of delphinid group presence from low (blue) to high (red), ranging from 0-0.2 for the (a) 2003-2004 model and 0-0.3 for the (b) 2005 model, colour gradation based on 20 levels using quantile classification.

2.3.4 Effect of change in spatial extent on model selection

The best delphinid group occurrence model for the Faroe-Shetland Channel survey data included three terms (in order of selection): SST, thermocline depth and halocline strength, explaining 7.2% of the deviance (Table 2.5).

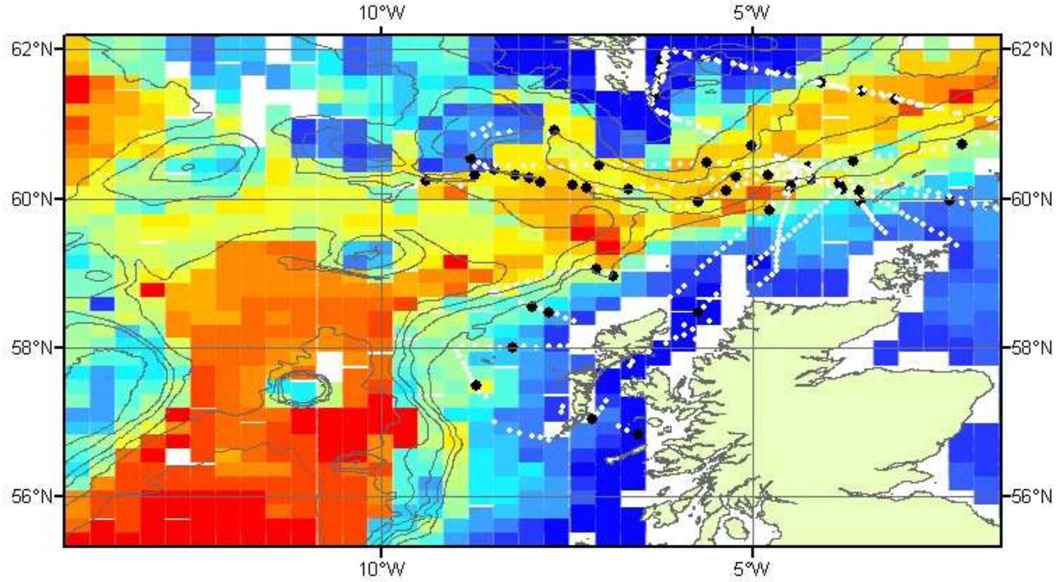
When compared with the model for the full survey area, both SST and thermocline depth were significant predictors with similar predicted relationships (Table 2.5). The key difference between the models was the lack of significance of depth in predicting delphinids within the Faroe-Shetland Channel surveys (Table 2.5).

If the Faroe-Shetland Channel model was used to predict outwith the survey extent on which it was based, and compared with the model based on the whole survey area, the models predict quite different areas of high probability of occurrence (Figure 2.12). The Faroe-Shetland Channel model predicted highest probability of delphinid occurrence throughout the Rockall Trough waters south of Rosemary bank (in water >1500 m), and in small patches just south of the Wyville-Thompson Ridge and the southerly reaches of the Faroe-Shetland Channel. The main similarity between the model predictions was found in on-shelf and shallow off-shelf waters where there was a low predicted probability of delphinid occurrence. They both also predicted high probability of occurrence in the southern end of the Faroe-Shetland Channel, just south of the Wyville-Thompson Ridge, and along the shelf edge. However, the model based on all survey data predicted high probability of delphinid occurrence in a large patch between the shelf edge and Rosemary Bank, which was not predicted by the FSC model (Figure 2.12).

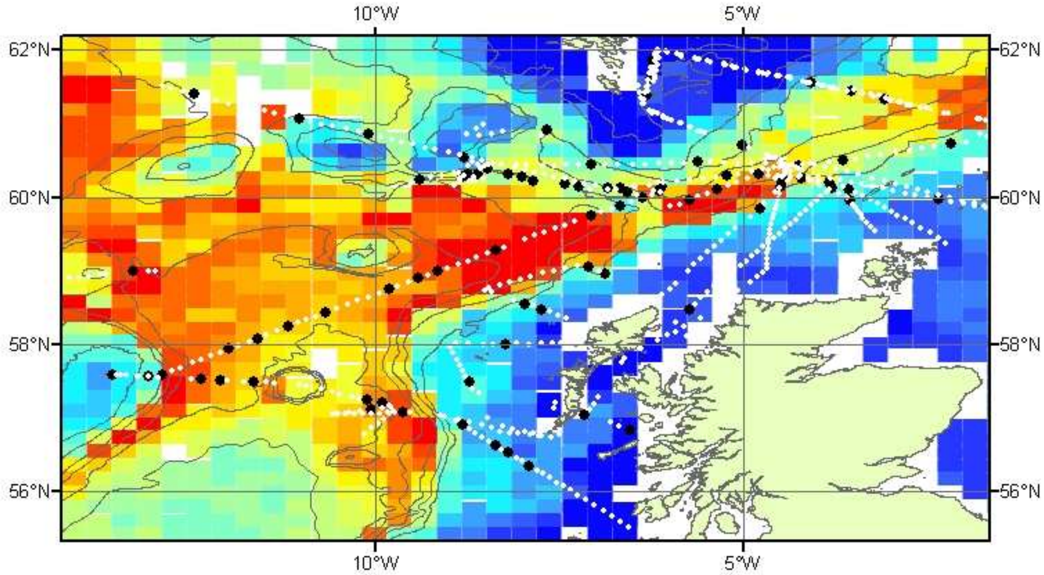
2.3.5 Effect of month on model selection

The best delphinid group occurrence model for the May Faroe-Shetland Channel survey data included two terms (in order of selection): halocline depth and thermocline depth, explaining 6.8% of the deviance (Table 2.5). The best model for the October Faroe-Shetland Channel only included SST which explained 6.1% of the deviance (Table 2.5).

The full model for the Faroe-Shetland Channel data was detailed in §2.3.4, and has one variable in common with each of the two seasonal models: thermocline depth in the May model, and SST in the October model. The relationship between delphinid group occurrence and thermocline depth was identical between the two models (full model and the May model for Faroe-Shetland Channel survey data). However the prediction for SST is slightly different between the full monthly model and the October model (Figure 2.13).

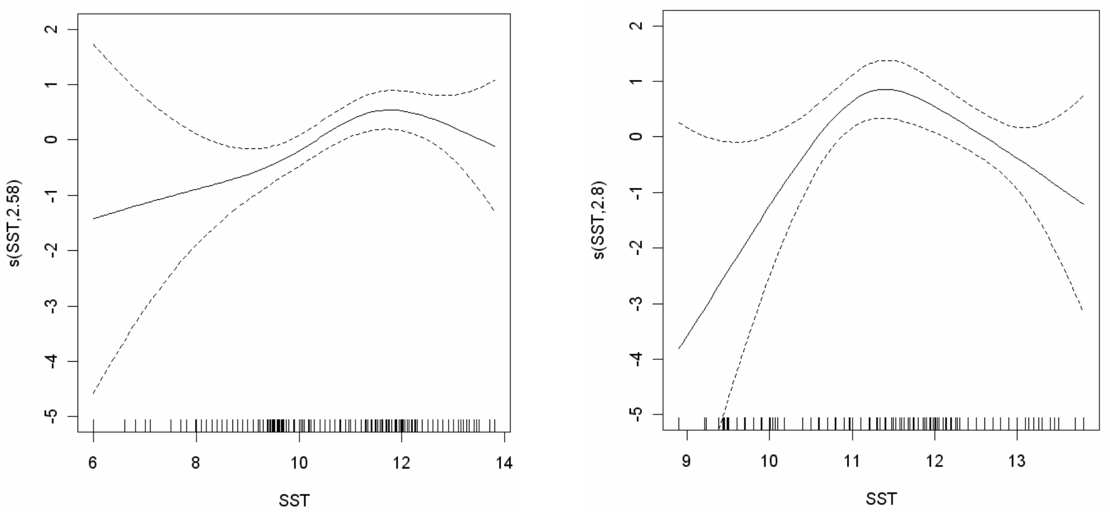


(a)



(b)

Figure 2.11 - Spatial prediction based on the best model for the probability of detecting delphinid group occurrence in a 20km grid cell for the (a) Faroe-Shetland Channel survey data (*n* = 918), and (b) all survey data (*n* = 1247) collected between July 2003 and October 2005 based environmental variables from 14 October 2004. Overlaid on the maps are the effort segments (white dots) and the delphinid whistle group detections (black dots) for the October survey for each data set. Also overlaid are GEBCO depth contours (dark grey lines). Colours represent probability of whistle presence from low (blue) to high (red), ranging from 0-0.4, colour gradation based on 20 levels using quantile classification.



(a) **(b)**

Figure 2.12 Delphinid group whistle occurrence per 9km segment modelled as a GAM smooth function of SST for (a) all Faroe-Shetland Channel survey data (d.f. = 2.6, *n* = 918), (b) Faroe-Shetland Channel October survey data (d.f. = 2.8, *n* = 456) collected off the west coast of Scotland. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show 95% confidence intervals.

The October model predicts a slightly tighter preference for SST (10.5-12.5°C) than the model including both months (10.5-13.5°C), and a slightly lower peak in preference (11.4°C versus 12°C).

Visually comparing predictive maps for the full model predicted for May and October, with the models based only on the May or October data (predictions for 21 May or 14 October 2004), the predictions were very similar (Figure 2.14). May had consistently high predicted probability of delphinid occurrence to the west of the shelf edge, with relatively low predicted probability of occurrence in the Faroe Shetland Channel and Wyville-Thompson Ridge. By contrast, October had consistently high predicted probability of occurrence throughout the Faroe-Shetland Channel, across the Wyville-Thompson Ridge and in the off-shelf waters to the west.

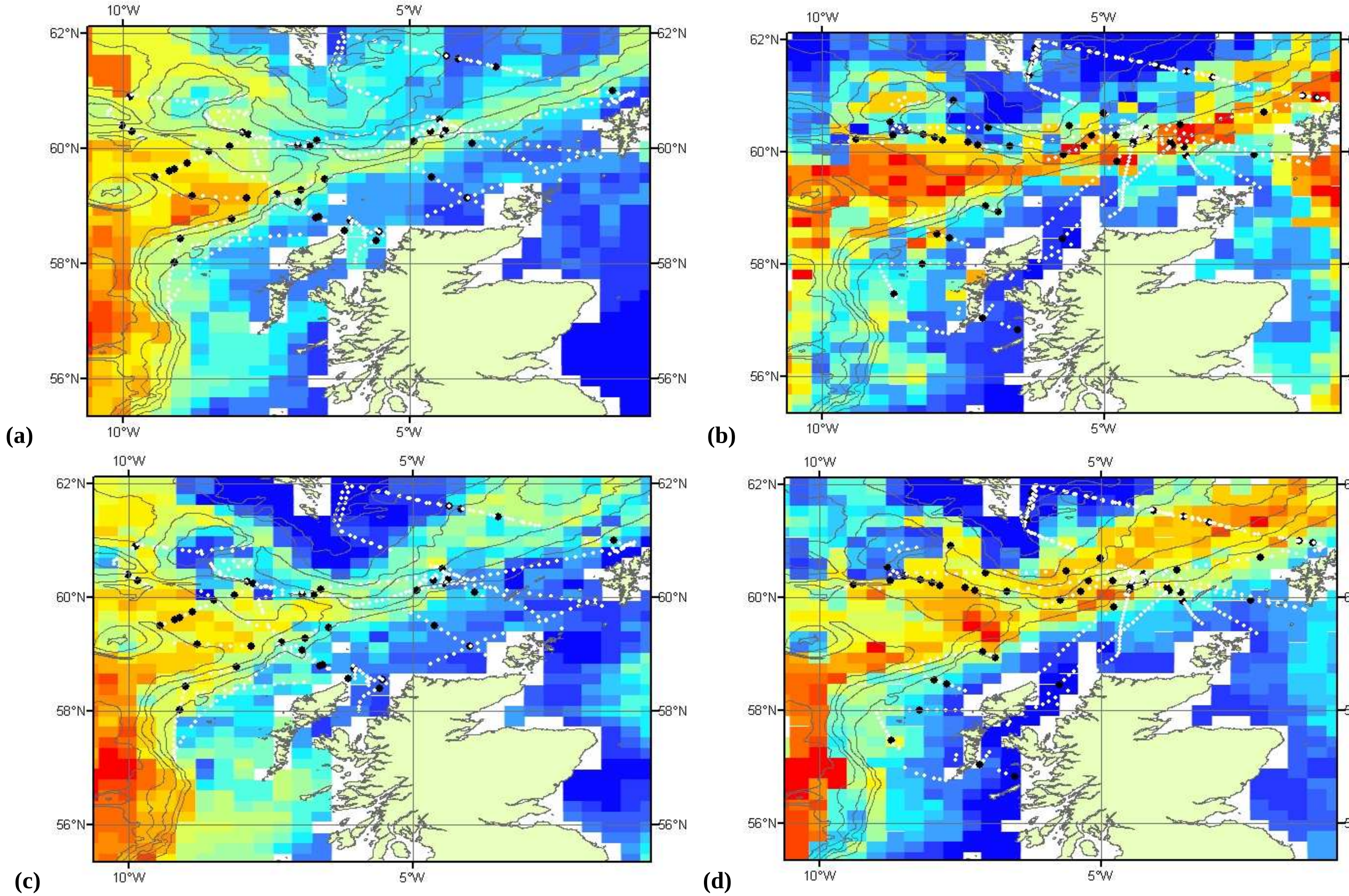


Figure 2.13 - Spatial prediction based on the best model for the probability of detecting delphinid whistle groups in the area around the Faroe-Shetland Channel on a 20km grid for (a & b) the best individual models based only on (a) May & (b) October data; (c & d) the best model for all data as predicted for (c) May & (d) October. Environmental variables were taken from 21 May 2004 or 14 October 2004. Overlaid on the maps are the effort segments (white dots) and the whistle group detections (black dots) for the relevant seasons survey for each data set. Also overlaid are GEBCO depth contours (dark grey lines). Colours represent probability of whistle presence from low (blue) to high (red), ranging from (a & c) 0-1 for the May predictions; and (b & d) 0-0.4 for the October predictions, colour gradation based on 20 levels using quantile classification.

2.4 Discussion

In this study, I have investigated the effect of autocorrelation and temporal scale on predicting delphinid distributions off the west coast of Scotland at both yearly and monthly temporal scales. The study also included a preliminary investigation of the effect of constraining the *extent* of the study on model selection. This has provided insight both into the temporal robustness of the predictive models and into the habitat preferences of delphinids in this part of the North Atlantic.

2.4.1 Passive acoustics & problems of autocorrelation

Modelling the acoustic detections of delphinids with environmental variables is complicated by the fact that the data would have been severely autocorrelated. This autocorrelation was mainly due to acoustically detecting the same group of delphinids over large distances (‘acoustic autocorrelation’). For example, based on a small sample of tracks, I estimated that delphinids in this study could be heard from over 15km under certain oceanographic conditions. This is similar to the active space measurements for bottlenose dolphin (Janik 2000) and killer whales (Miller 2006), where active space is the distance at which another dolphin/killer whale can perceive the whistle of a conspecific (Janik 2000). Bottlenose dolphin whistles between 3.5-10 kHz were predicted to have an active space radius of 14-22 km in shallow water at sea state four, and as much as 20-25 km in sea state zero (Janik 2000). Similarly the higher frequency components of killer whale vocalisations (1-12 kHz) had a mean active space distance of 10-15 km in sea state zero (Miller 2006). In a line transect survey, this long range of whistle propagation means that a vocalising delphinid group can be heard over a large distance (up to 30 km in the data presented here), resulting in highly autocorrelated survey data.

It was possible to remove the autocorrelation in the data by using the properties of the whistle data to group the detections into individual encounters (§2.2.3). The effect of retaining this autocorrelation in the model could thus be evaluated. Two variables were retained in the ungrouped model that were not significant in the grouped model: a survey effect (an interaction between survey vessel noise and survey vessel) describing some of the variation in autocorrelation, and one retained environmental variable (halocline strength).

Vessel noise masks the ability of an acoustic monitor on a survey vessel to detect delphinid whistles (Richardson et al. 1995). Thus as vessel noise increases, the range at which dolphins can be heard above vessel noise will reduce (Richardson et al. 1995). This results in a reduction in whistle detection, and a reduction in autocorrelation due to the distant whistles of the delphinids being masked, with only those whistles close range of the vessel being heard. Vessel noise was shown to influence the level of autocorrelation (i.e. the distance and time over which a group is heard) rather than ability to detect a dolphin group – which will be heard provided it comes closer to the vessel than the masking distance (Richardson et al. 1995).

As expected, the autocorrelation within the ungrouped whistle data resulted in an additional environmental variable being retained in the model. This is an effect of an inflation of the number of degrees of freedom (Koenig 1999), and underestimation of the standard errors resulting in variables being considered significant when in fact they are not (Lennon 2000; Borchers et al 1997). Also, by applying the Wald-Wolfowitz test for non-randomness in the residuals (Hardin and Hilbe 2003) it was found that even with the additional environmental variable, the model was unable to fully compensate for the autocorrelation, resulting in non-random serial distribution of residuals. The predictions themselves (Figure 2.9) showed little difference between the models, the main difference being that the ungrouped autocorrelated data over-emphasised the importance of the Faroe-Shetland Channel for delphinids. Whereas, the grouped delphinid whistle occurrence model suggested a preference for the southern end of the Faroe-Shetland Channel (FSC) and for the Wyville Thompson Ridge (WTR). This preference for the southern part of the FSC and WTR has been found in previous surveys off the west coast of Scotland for long-finned pilot whales and white-sided dolphins (Macleod 2001).

2.4.2 Model robustness over time & space

Boyce et al. (2002) highlighted three of the main issues in attempting to build robust predictive models of species distributions: (i) yearly changes in habitat selection due to fluctuation of resources; (ii) seasonal changes in habitat preferences due to changes in resources; and (iii) spatial variation in habitat selection depending on the spectrum of habitats available within an area. All three aspects were evaluated to the extent possible within the data set for delphinids off the west coast of Scotland.

Firstly, at the yearly scale there was significant variation between variables selected within the models and their relationships with delphinid occurrence. Depth was the only predictor to be selected consistently in all years, finding that delphinids were found preferentially in water off the shelf edge (> 400 m). However, the deep water preferences differed between the 2003-2004 model and the 2005 model, with delphinids showing a linear increase in preference as depth increased in 2003-2004, but a peak in preference for depth between 1000 m and 1500 m in the 2005 model. Some of this change may be partly due to differences in the surveyed *extent* between years. A significantly higher proportion of shallow water was surveyed in 2005, which is likely to be mainly due to the second half of the May survey having been devoted to monitoring post-smoult salmon along the shelf edge. However, the Faroe-Shetland Channel and Ellet Line hydrographic lines were consistently surveyed in both the 2003-2004 survey period and in 2005, providing some ability to elucidate changes due to year rather than area.

The key differences between years over the full survey *extent* were the preferences for SST in 2003-2004 and thermocline depth in 2005. This preference for SST in some years and not others was also found by Hastie et al. (2005) in their study of delphinid distributions from the same platform of opportunity (*FRV Scotia*) and same area as this study but between 2001 and 2002. Similarly, Forney (2000) found SST to vary in importance between years in predicting Dall’s porpoises (*Phocoenoides dalli*) and short-beaked common dolphins (*Delphinus delphis*) off California. So it would appear that SST, though an important predictor of delphinid distributions overall, is not a temporally robust measure.

To try to understand why SST may be a generally good predictor of delphinid distributions, but poor in some years, it is necessary to have a grasp of oceanography. SST is dependent on several factors, including: heating by the sun, and the amount of wind-induced mixing at the surface (Mann & Lazier 2006). Increased cloud cover decreases the amount of solar warming in the surface layer of the ocean (Mann & Lazier 2006). Higher winds result in a deeper mixed layer than in low winds, resulting in any surface heating being spread over a greater depth so resulting in a smaller temperature rise from the surface heating during the day (Mann & Lazier 2006). During this study, 2005 had significantly higher cloud cover than 2003-2004 with 41.6% and 0% of the monthly and weekly satellite images obscured respectively. The weather conditions were also significantly worse in 2005 with higher winds recorded during the surveys ($t = -4.48$, $p < 0.001$, d.f. = 595) than during 2003-2004. It was evident from the FOAM model that this stormy weather created a lot of wind-induced surface mixing of the sea (Gillibrand pers. comm.), mixing the warm surface layer with cooler deeper water and reducing the surface SST signal. Therefore, it is possible that SST is a good predictor of dolphin distributions when there is not too much wind-induced mixing, but a poor predictor in years with poor SST signal, i.e. in those years with poor weather conditions.

Secondly, seasonal changes in model selection were evaluated by building separate models for May and October. The analysis was restricted to the Faroe-Shetland Channel surveys since these had similar distribution of effort per season and per survey, however there were some differences in coverage with a slightly lower range of depths being surveyed in October than in May. No variables were significant at predicting occurrence of delphinids in both months. This suggests that models based on a single month or season should not be used for predicting distributions of species into other seasons or months. When considering the large differences in predictions that occurred from both monthly and yearly scale analysis, it is evident that within such dynamic systems as the marine environment, models based on data from the present and past are no guarantee of future predictive performance (Oreskes et al. 1994). Only those studies carried out over a long enough time span to capture the variations between years and seasons are likely to have enough predictive power to predict distributions into the future (e.g. the 10+ year study of cetaceans in the Mediterranean by Cañadas et al. 2005).

One of the reasons for modelling May separately to October was to determine whether the model including both seasons was able to fully account for this change in distribution with season. Initially, a check was carried out in the full models to find out whether month was significant in the models before adding the environmental variables, and then after to see whether there was any remaining un-modelled variance that could be explained by month. In all cases month was a significant variable prior to environmental variables being added, but not after, suggesting that the models were fully able to account for the seasonal trends.

By modelling May separately from October it was also possible to determine which oceanographic variables influenced delphinid distributions in the two months. In May, predictors of delphinid distribution included halocline and thermocline depth, whereas in October only SST was the only important predictor. The changes in preference between months probably reflect the change in oceanography and hence prey distributions as the year progresses. Many of the surveyed ranges of oceanographic variables were significantly different between survey months: depth, SST, chlorophyll, halocline depth & strength, thermocline depth, and current speeds (Appendix Table A1.4). As expected, SST was significantly higher in October after the summer heating, than in May. It is likely that this explains why SST was significant at predicting delphinids in October rather than May, since they consistently showed a preference for warmer waters: in this case, warmer than 10.5°C and peaking at 11.4°C. The predicted probability of delphinid occurrence within the Faroe-Shetland Channel is therefore much higher in October than in May (Figure 2.13). This result is nearly identical to that found for delphinids carried out from the same platform of opportunity (*FRV Scotia*) in the same area and time as this study but between 2001 and 2002 (Hastie et al. 2005). Although Hastie et al. (2005) did not analyse the survey data by month, they did find that the preference of delphinids for water warmer than 10°C partly explained their significantly higher abundance in October than in May. Combining the two datasets into one, results in a model that included both SST to explain October distribution and thermocline depth to explain May distribution, with nearly identical relationships to that exhibited for the individual months. This showed how the full model is fully able to model the changes between months using oceanographic variables, and has some degree of robustness.

Finally, to evaluate spatial robustness, a model based on the Faroe-Shetland Channel surveyed *extent* was compared with the model based on the full survey *extent* (§2.3.4). The two *extent* had two environmental variables in common with similar relationships: SST and thermocline depth. So these variables were spatially robust between the constrained *extent* and the full *extent*, having the ability to predict delphinid distributions in both areas. However, although depth was the most significant variable for the full *extent* it was not significant in explaining delphinid distributions in the Faroe-Shetland Channel *extent.* A narrower and shallower range of depths was surveyed in the Faroe-Shetland Channel in comparison to the overall area which included deep areas such as Rockall Trough. This is mainly due to the relatively low availability of deep water within the Faroe-Shetland Channel rather than a survey bias. This absence of preference for depth in the Faroe-Shetland Channel is the opposite of that found in the study carried out by Hastie et al. (2005) in the same area during 2001-2002, who found that delphinid occurrence peaked between 750-1100m. However, their study also did not compensate for the autocorrelation caused by hearing the same group of delphinids over several listening stations, so depth may be an overfitted term in their study. In fact, in a side-analysis carried out as part of this study modelling the *ungrouped* data for the FSC extent, it was found that depth was the most important predictor of delphinids rather than SST for the Faroe-Shetland Channel *ungrouped* delphinid occurrence (Appendix Table A1.1).

Incomplete sampling of a species environment parameter space has been highlighted as one of the main issues in trying to model species distributions (Guisan & Thuiller 2005; Peterson & Cohoon 1999). Also Van Horn (2002) cautions against overly constrained *extent* since it can lead to incorrect interpretation if only part of an environmental range is sampled. In the case of depth, the Faroe-Shetland Channel has a much lower availability of deep water than in the Rockall Trough. However, since the relationship with depth varies even between years for the full *extent*, overall depth does not appear to be a robust predictor of delphinid distribution off the west coast of Scotland despite being one of the most significant predictors in the full area.

2.4.3 Habitat preferences of delphinids off the west coast of Scotland

The most significant predictor of delphinid distributions over the full surveyed *extent* off the west coast of Scotland was depth. The delphinids showed a greater use of the deep water off the shelf edge with some indication of a peak in preference between 1000-1500m in 2003-2004, but a linear increase with depth in 2005 (Figure 2.9). This variation in preference with depth is likely to be due to the differences between the species included in the “whistling odontocetes” group. Of the whistling odontocete species represented off the west coast of Scotland, the long-finned pilot whale and the Atlantic white-sided dolphin have the deepest depth preferences (Buckland et al. 1993; Cañadas et al. 2005; Cañadas et al. 2002; Hamazaki 2002; Kaschner 2004; MacLeod et al. 2007; Macleod et al. 2003; O'Cadhla et al. 2004; Wall et al. 2006;

Weir et al. 2001). Although the two species have been seen to occur in mixed groups (Cronin & Mackey 2002; O Cadhla et al. 2004; Weir et al. 2001; pers. obs.), long-finned pilot whales have been shown to prefer deeper water (1400-2000 m, MacLeod et al. 2007) than white-sided dolphins (mean depth of 996 m, Macleod et al. 2003; MacLeod et al. 2007). It is therefore likely that these are the two main species represented within this dataset. The absence in this model of any obvious preference for the shelf waters, and the lower occurrence of dolphins on shelf (28.3% of all dolphin groups detected) suggests few on-shelf species of dolphin were detected during the surveys (such as white-beaked dolphins).

Sea surface temperature (SST) was the second most important variable in many of the models with delphinids showing a strong preference for water warmer than 10.5°C, and in the Faroe-Shetland Channel *extent* confined to less than 12.6°C (Figure 2.12). Of the four main delphinid species likely to be represented in this study, short-beaked common dolphins (*Delphinus delphis*) are known to have the warmest water preference (Kaschner 2004), occurring at the upper end of their range off the west coast of Scotland (Macleod 2001; Skov et al. 1995; Weir et al. 2001). Long-finned pilot whales and Atlantic white-sided dolphins appear to have similar temperature preferences to each other in water > 10.9°C with a mean of 12.2°C (Macleod 2001), which is very similar to the results of this study. White-sided dolphins have also been shown to be allopatric to common dolphins (Selzer & Payne 1988), replacing common dolphins in areas of cooler water. The coldest water species of the “whistling odontocetes” likely to be represented off the west coast of Scotland is the white-beaked dolphin (Northridge et al. 1995; Northridge et al. 1997; Macleod 2001; MacLeod et al. 2007; Skov et al. 1995; Weir et al. 2001). They have been shown to prefer water <11.5°C in shelf waters towards the northern part of the Scottish continental shelf (MacLeod et al. 2007). The SST preference of the delphinids in this study covers all these species’ ranges in SST preference, though the upper range of 12.5°C for the model concentrating on the northern surveys in the Faroe-Shetland Channel would tend to suggest that the species detected in this northern area are likely to mainly be the colder water species. Certainly, previous studies have rarely detected common dolphins further north than 60°N (Macleod 2001; Skov et al. 1995; Weir et al. 2001).

The third of the main predictors of dolphin distribution was thermocline depth, with dolphins showing a preference for deeper thermoclines. This is the first time that this or any of the other oceanographic variables have been used to predict cetacean distributions off the west coast of Scotland. The majority of studies that have examined the oceanographic associations of dolphins have been conducted in the eastern Pacific (Ballance et al. 2006; Ferguson et al. 2006; Reilly & Fiedler 1994; Tynan et al. 2005). Generally it was found that dolphins tended to be associated with particular water masses, for example Reilley and Fiedler (1994) found that although common dolphins (*Delphinus delphis*) tended to associate with upwelling habitat characterised by shallow thermoclines and cool SST, whitebelly spinner dolphins (*Stenella longirostris*) associated to a greater extent with deeper thermocline offshore waters. In addition, Baumgartner et al. (2001) used thermocline depth (characterised by the 15°C isotherm depth) to indicate the presence of mesoscale warm-core eddies, with a deeper thermocline indicative of the presence of a warm-core feature. Off the west coast of Scotland, the deepest thermocline appears to be associated with the shelf edge current from around the Wyville-Thompson Ridge, which continues up through the Faroe Shetland Channel (Appendix Figure A1.1). This area has been shown to be both productive and highly dynamic, with the shelf-edge current bringing warm saline water from the south along with many migratory species of fish (Bartsch & Coombs 1997; Borja et al. 2002; Shelton et al. 1997). The warm saline water also forms a front with the cooler Modified North Atlantic Water flowing over the Faroe Bank, causing mesoscale eddies (Sherwin et al. 1999; Sherwin et al. 2006), and higher chlorophyll is evident on the satellite images within these frontal regions and meanders (Figure 2.5b). This combination of features in this area, may at least in part explain the preference of these areas to delphinids.

Overall, the environmental variables explain only a small proportion of the deviance, with each variable explaining on average 2.7% of the deviance, with the highest amount of explained deviance for any single variable being 6.1% for SST in the October model. The distribution of delphinids was very widespread, with no clear hotspots (Figure 2.4). Combining “whistling odontocetes” into a single group may account for much of this since the habitat preferences of each species are likely to be different. Ferguson et al. (2006) also found that by grouping delphinids from data collected in the Eastern Tropical Pacific it was only possible to explain a small amount of the deviance (12.1% for delphinid encounter rate). Further, if delphinids are detected when travelling between foraging locations, links with oceanographic variables may not reflect habitat preferences, reducing the ability to explain model deviance (Ballance et al. 2006).

Overall, the preferences of delphinids off the west coast of Scotland suggest that the main “whistling odontocetes” encountered were long-finned pilot whales and Atlantic white-sided dolphins. Their preference for depth, SST and thermocline depth are likely to be related to their prey preferences, and the location of prey within this habitat. The core high-use area was predicted to be along steep slopes of the shelf-edge, and in a large patch just south of the Wyville-Thompson Ridge between the shelf edge and Rosemary Bank.

2.4.4 Conclusions & further work

By comparing model selection between years and months, no variables were shown to be robust at predicting delphinid distribution over time. However, the full models with all years and months incorporated the same habitat preferences shown by the individual yearly and monthly models, so capturing the preferences over time within a single model.

Constricting the *extent* of the model resulted in two variables that showed some degree of spatial robustness: SST and thermocline depth. However, although depth had been the most significant predictor of delphinid distributions in the full *extent*, it was not significant at predicting delphinid distribution over a constrained *extent*. Overall, these results suggest that depth is a poor predictor of delphinid distributions off the west coast of Scotland. However, this result is likely to be influenced by the difficulty in separating out the depth preferences of different delphinid species.

Overall, delphinids were found to be distributed fairly evenly over the deep waters of the west coast of Scotland, with lower rates of detection in shelf waters. They were found to associate with the deep (> 400 m) warm water (10.5°C-12.5°C) of the area, and in areas of deep thermocline. These results suggested that the most abundant species detected during the surveys were likely to be long-finned pilot whales and Atlantic white-sided dolphins, and that may be using the deep thermocline of the Shelf-Edge Current as a foraging ground. The areas highlighted to be of importance to delphinids off the west coast of Scotland included the area south of the Wyville-Thompson Ridge, lying between the Scottish shelf edge and Rosemary Bank, and the shelf-edge itself. However, the models were able to explain only a small proportion of the deviance. Models that explain a higher amount of deviance may be obtained if future methods allow for the automatic identification of species from their whistles.

2.5 References

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

Barlow, J., T. Gerrodette, and J. Forcada. 2001. Factors affecting perpendicular sightings distances on shipboard line-transect surveys for cetaceans. J. Cetacean Res. Manage. **3**:201-212.

Bartsch, J., and S. Coombs. 1997. A numerical model of the dispersion of blue whiting larvae, *Micromesistius poutassou* (Risso), in the eastern North Atlantic. Fisheries Oceanography **6**:141-154.

Baumgartner, M. F., K. Mullin, L. N. May, and T. D. Leming. 2001. Cetacean habitats in the northern Gulf of Mexico. Fishery Bulletin **99**:219-239.

Bell, M., J., R. M. Forbes, and A. Hines. 2000. Assessment of the FOAM global assimilation system for real-time operational ocean forecasting. Journal of Marine Systems **25**:1-22.

Borchers, D. L., S. T. Buckland, I. G. Priede, and S. Ahmadi. 1997. Improving the precision of the daily egg production method using generalised additive models. Can. J. Fish. Aquat. Sci. **54**:2727-2742.

Børja, A., A. Uriarte, and J. Egana. 2002. Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north-east Atlantic coasts of Europe. Fisheries oceanography **11**:116-127.

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

Buckland, S. T., D. Bloch, K. L. Cattanach, T. Gunnlaugsson, K. Hoydal, S. Lens, and J. Sigurjonsson. 1993. Distribution and abundance of long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. Report of the International Whaling Commission **Special Issue 14**:33-49.

Burnham, K. P., and D. R. Anderson 2002. Model selection and multimodel inference. A practical information-theoretic approach. Springer-Verlag, New York.

Cañadas, A., R. Sagarminaga, R. De Stephanis, E. Urquiola, and P. S. Hammond. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conserv: Mar. Freshw. Ecosyst. **15**:495-521.

Cañadas, A., R. Sagarminaga, and S. Garcia-Tiscar. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters of southern Spain. Deep-Sea Research I **49**:2053-2073.

Chambers, J. M., and T. J. Hastie 1991. Statistical Models. Chapman & Hall/CRC Press, Boca Raton.

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

Cronin, M., and M. Mackey. 2002. Cetaceans and seabirds in waters over the Hatton-Rockall region. Unpublished Cruise Report. Coastal and Marine Resources Centre, University College Cork.

Ferguson, M. C., J. Barlow, P. Fiedler, S. B. Reilly, and T. Gerrodette. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling **193**:645-662.

Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the RSV Aurora Australis. Report of the International Whaling Commission **47**:897-907.

Gontarek, S. 2005. STJG Tools for ArcGIS v9 - GIS Extract, SAMS, Dunstaffnage, Oban.

Goold, J. C. 2000. A diel pattern in vocal activity of short-beaked common dolphins, Delphinus delphis. Marine Mammal Science **16**:240-244.

Gordon, J. C. D., J. N. Matthews, S. Panigada, A. Gannier, J. F. Borsani, and G. Notarbartolo Di Sciara. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. Journal of Cetacean Research and Management **2**:27-36.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Hamazaki, T. 2002. Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). Marine Mammal Science **18**:920-939.

Hardin, J. W., and J. M. Hilbe 2003. Generalized Estimating Equations. Chapman & Hall/CRC.

Harwood, J., and B. Wilson. 2001. The implications of developments on the Atlantic Frontier for marine mammals. Continental Shelf Research **21**:1073-1093.

Hastie, G. D., R. J. Swift, J. C. D. Gordon, G. Slesser, and W. R. Turrell. 2003. Sperm whale distribution and seasonal density in the Faroe Shetland Channel. Journal of Cetacean Research and Managment **5**:247-252.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson, and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. ICES Journal of Marine Science **62**:760-770.

Hastie, T. J., and R. J. Tibshirani 1990. Generalised Additive Models. Chapman & Hall, London.

Hedley, S. 2000. Modelling heterogeneity in cetacean surveys. PhD Thesis. Department of Statistics. University of St Andrews.

IOC, IHO, and BODC. 2003. Centenery Edition of the GEBCO Digital Atlas, published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission & the International Hydrographic Organisation as part of the General Bathymetric Chart of the Oceans. British Oceanographic Data Centre, Liverpool, UK.

Jacobs, M., D. P. Nowacek, D. J. Gerhart, G. Cannon, S. Nowicki, and J. R. B. Forward. 1993. Seasonal changes in vocalisations during behaviour of the Atlantic bottlenose dolphin. Estuaries **16**:241-246.

Janik, V. M. 2000. Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. Journal of Comparative Physiology A **186**:673-680.

Kaschner, K. 2004. Modelling and mapping resource overlap between marine mammals and fisheries on a global scale. PhD Thesis. Department of Zoology. The University of British Columbia.

Kenney, R. D., and H. E. Winn. 1986. Cetacean high-use habitats of the NE US continental shelf. Fishery Bulletin **84**:345-357.

Kim, Y. J., and C. Gu. 2004. Smoothing spline gaussian regression: more scaleable computation via efficient approximation. Journal of the Royal Statistical Society, Series B **66**:337-356.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. TREE **14**:22-26.

Leaper, R., D. Gillespie, and V. Papastavrou. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. J. Cetacean Res. Manage. **2**:187-196.

Lennon, J. 2000. Red-shifts and red herrings in geographical ecology. Ecography **23**:101-113.

Lewis, T., D. Gillespie, J. Gordon, and O. Chappell. 2000. Acoustic cetacean monitoring 1996 to 1999: Towards the development of an automated system. Summary Report. A report to Shell UK Ltd. Contract C10563. Birmingham Research & Development Ltd.

MacLeod, C. D., C. R. Weir, C. Pierpoint, and E. J. Harland. 2007. The habitat preferences of marine mammals west of Scotland (UK). Journal of the Marine Biological Association of the UK **87**:157-164.

Macleod, K. 2001. The spatial and temporal distribution of cetaceans off the west coast of Scotland in relation to environmental factors: the implications for marine management. PhD Thesis. University of Greenwich.

Macleod, K., M. P. Simmonds, and E. Murray. 2003. Summer distribution and relative abundance of cetacean populations off north-west Scotland. Journal of the Marine Biological Association of the United Kingdom **83**:1187-1192.

Mann, K. H., and J. R. N. Lazier 2006. Dynamics of marine ecosystems (3rd Edition). Blackwell Scientific Publications, Cambridge.

Miller, P. J. O. 2006. Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. Journal of Comparative Physiology A **192**:449-459.

Moore, S. E., D. P. DeMaster, and P. K. Dayton. 2000. Cetacean habitat selection in the Alaskan Arctic during summer and autumn. Arctic **53**:432-447.

Northridge, S. P., M. L. Tasker, A. Webb, K. Camphuysen, and M. F. Leopold. 1997. White-beaked Lagenorhynchus albirostris and Atlantic white-sided dolphin L.

acutus distributions in northwest European and US Atlantic waters. Report of the International Whaling Commission **47**:797-805.

Northridge, S. P., M. L. Tasker, A. Webb, and J. M. Williams. 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirostris* Gray), and minke whales (*Balaenoptera acutorostrata* Lacepede) around the British Isles. ICES Journal of Marine Science **52**:55-66.

O'Cadhla, O., M. Mackey, N. Aguilar de Soto, E. Rogan, and N. Connolly. 2004. Cetaceans and Seabirds of Ireland's Atlatnic Margin. Volume II - Cetacean distribution & abundance. Page 82. Report on research carried out under the Irish Infrastructure Prograp (PIP): Rockall Studies Group (RSG) projects 98/6 and 00/13, Porcupine Studies Group project P00/15 and Offshore Support Group (OSG) project 99/38.

Oreskes, N., K. Shader-Frechette, and K. Belitz. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. Science **263**:641-646.

Oswald, J. N., J. Barlow, and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. Marine Mammal Science **19**:20-37.

Oswald, J. N., S. Rankin, J. Barlow, and M. O. Lammers. 2007. A tool for real-time acoustic species identification of delphinid whistles. Journal of the Acoustical Society of America **122**:587-595.

Payne, P. M., and D. W. Heinemann. 1993. The distribution of pilot whales (*Globicephala* spp.) in shelf/shelf-edge and slope waters of the Northeastern United States, 1978-1988. Report of the International Whaling Commission **Special Issue 14**:51-68.

Peterson, A. T., and K. P. Cohoon. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. Ecological Modelling **117**:159-164.

Reilly, S. B., and P. C. Fiedler. 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986-1990. Fishery Bulletin **92**:434-450.

Rendell, L. E., J. N. Matthews, A. Gill, J. C. D. Gordon, and D. W. Macdonald. 1999. Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. Journal of the Zoological Society of London **249**:403-410.

Richardson, W. J., C. R. Green Jr., C. I. Malme, and D. H. Thomson 1995. Marine Mammals and Noise. Academic Press, Inc., San Diego, CA.

Selzer, L. A., and P. M. Payne. 1988. The distribution of white-sided (Lagenorhynchus acutus) and common dolphins (Delphinus delphis) vs. environmental features of the continental shelf of the northeastern United States. Marine Mammal Science **4**:141-153.

Shelton, R. G. J., W. R. Turrell, A. Macdonald, I. S. McLaren, and N. T. Nicoll. 1997. Records of post-smoult Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. Fisheries Research **31**:159-162.

Sherwin, T. J., W. R. Turrell, D. R. G. Jeans, and S. Dye. 1999. Eddies and a mesoscale deflection of the slope current in the Faroe-Shetland Channel. Deep-Sea Research I **46**:415-438.

Sherwin, T. J., M. O. Williams, W. R. Turrell, S. L. Hughes, and P. I. Miller. 2006. A description and analysis of mesoscale variability in the Faroe-Shetland Channel. Journal of Geophysical Research **111**:1-17.

Skov, H., J. Durinck, F. Danielsen, and D. Bloch. 1995. Co-occurrence of cetaceans and seabirds in the Northeast Atlantic. Journal of Biogeography **22**:71-88.

Smith, S. C., and H. Whitehead. 1993. Variations in the feeding success and behaviour of Galapagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. Canadian Journal of Zoology **71**:1991-1996.

Steiner, W. W. 1981. Species-specific differences in pure tonal whistle vocalizations of five western North Atlantic dolphin species. Behavioural Ecology and Sociobiology **9**:241-246.

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

Urick, R. J. 1983. Principles of underwater sound. Peninsula Publishing, Los Altos, CA.

Van Horn, B. 2002. Approaches to habitat modelling: the tensions between pattern and process and between specificity and generality. Pages 63-72 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, CA.

Wall, D., J. O'Brien, J. Meade, and B. M. Allen. 2006. Summer distribution and relative abundance of cetaceans off the west coast of Ireland. Proceedings of the Royal Irish Academy **106B**:135-142.

Weir, C. R., C. Pollock, C. Cronin, and S. Taylor. 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. Continental Shelf Research **21**:1047-1071.

Wood, S. N. 2006a. Generalised Additive Models - An Introduction with R. Chapman and Hall/CRS, Boca raton, Florida.

Wood, S. N. 2006b. The mgcv package. R statistical group.

Zachariassen, P. 1993. Pilot whale catches in the Faroe Islands, 1709-1992. Report of the International Whaling Commission **Special Issue 14**:68-88.

Chapter 3

Predictive models of sperm whale *Physeter macrocephalus* distributions off the west coast of Scotland

Evaluation of spatial scale

Abstract

The aim of this study was to investigate the effect of spatial scale on predictive models of sperm whale *Physeter macrocephalus* distribution off the west coast of Scotland. The data were collected using passive acoustic monitoring techniques from platforms of opportunity during hydrographic surveys off the west coast of Scotland between July 2003 and October 2005. Generalised Additive Models (GAMs) were used to relate sperm whale occurrence to survey variables (vessel speed, survey vessel noise, remote vessel noise, and water noise), temporal variables (time of day, month and year), and environmental variables (depth, SST, surface chlorophyll, surface salinity, thermocline depth & strength, halocline depth and strength, and bottom & surface current speeds). Models were fitted to sperm whale data over two different survey extents (Faroe-Shetland Channel & Rockall Trough) and two different scales or ‘grain sizes’ (9 km & 18 km). Cross validation was carried out by dividing the data into test and training sets: the models were built on the training data and tested on their ability to predict the test data. Detections of sperm whales were aggregated over large distances, with the largest aggregation dispersed over 60 km. Over the whole survey area sperm whales were generally distributed in deep water areas characterised by weak thermoclines and strong haloclines. Increasing grain size from 9 km to 18 km resulted in the same relationships but the last variable (halocline strength) was no longer significant. However, sperm whale habitat preference did change with extent. In the Faroe-Shetland Channel sperm whales were distributed over medium depth waters (500-1100 m) with strong deep haloclines, weak thermoclines and a bimodal preference for either fresh or salty surface water. In the Rockall Trough sperm whales were distributed in deep (> 600 m), cold (< 12.7ºC) waters with high surface salinity (>35.22 psu). In combination with evidence from other studies of sperm whale

ecology in the Northeast Atlantic, these variables suggest that sperm whales may be using the west coast of Scotland as a foraging ground.

3.1 Introduction

The concept of scale is important throughout studies of ecology (Wiens 1989), but particularly so in the development of environmental models of species distributions. Two types of scale can be defined: (i) *extent* – the overall area under study; and (ii) *grain* – the size of the units at which species-environment relationships are examined (Wiens 1989). Different relationships between a species distribution and the underlying environment can result by changing either the *extent* (Boyce et al. 2002; Fielding & Haworth 1995; Jimenez 2005; Moses & Finn 1997; Osborne & Suarez-Seoane 2002; Randin et al. 2006) or *grain* size selected (Bailey 2006; Fauchald et al. 2000; Guinet et al. 2001; Guisan & Thuiller 2005; Jaquet 1996; Jaquet & Whitehead 1996; Mehlum et al. 1999; Rose & Leggett 1990; Schneider & Piatt 1986).

Spatial scale has been highlighted as being one of the key considerations in the modelling of sperm whale distributions with oceanographic features (Jaquet 1996; Jaquet & Whitehead 1996). The types of oceanographic processes within the *extent* of a study can be used to decide what *grain* size should be used (Jaquet 1996). Jaquet (1996) defined two main sets of processes which she suggested were relevant in predicting sperm whale distributions in the North Pacific, and should use different *grain* sizes. Very large *grain* sizes should be used for upwelling type environments, characterised by trophic lags of 4 months and several hundred kilometres between primary production peaks and peaks in sperm whale prey density. Smaller *grain* sizes (of the order of tens of kilometres – Jaquet & Whitehead 1996) should be used in areas with processes that tend to aggregate both primary production and prey within an area with no spatial lag.

In the deep waters off the west coast of Scotland, the study area for the work presented here, aggregative processes dominate. Here, warm saline water from the ‘Gulf Stream’ (or North Atlantic Water, NAW) travels along the western side of the Faroe-Shetland Channel abutting the cooler fresher modified NAW water travelling along the eastern side of the channel and over the Faroe Plateau (Turrell et al. 1999). Where this convergence occurs, meanders and cold core eddies are produced (Sherwin et al. 1999; Sherwin et al. 2006). Both of these processes will tend to act to aggregate prey within the convergence and eddies (Mann & Lazier 2006). The entire area off the west coast of Scotland is also characterised by complex topography with many seamounts, steep sided banks, and ridges (Figure 1.1) that will tend to cause vertical mixing of the water column and enhance productivity and prey aggregation (Jaquet 1996; Mann & Lazier 2006). Thus, since aggregative rather than upwelling processes dominate off the west coast of Scotland, there should be no spatial or temporal lag between oceanographic conditions and the distribution of prey (squid or fish) and sperm whales. According to Jaquet (1996), these processes lend themselves towards a relatively small *grain* size in analysing sperm whale distributions with oceanographic processes (due to the lack of spatial or temporal lag between oceanographic processes and prey distributions.

Sperm whales, the focal species in this study, are among the most abundant of the large whales on the west coast of Scotland (O'Cadhla et al. 2004; Weir et al. 2001), and are found distributed throughout the deep waters of the Rockall Trough and Faroe-Shetland Channel (Hastie et al. 2003; Macleod et al. 2003; Moscrop 1997; O'Cadhla et al. 2004; Skov et al. 1995; Weir et al. 2001). Around the British Isles, strandings of sperm whales have been predominantly adult and sub-adult males (Berrow & Rogan 1997; Evans 1997; Santos et al. 1999). These animals are likely to have dispersed from their natal groups in lower latitudes to feed in the more productive higher latitudes, and may eventually return to lower latitudes seasonally to breed (Best 1979). It is therefore not known whether the deep waters off west coast of Scotland form a migratory route or a more permanent feeding ground. If the area were used as a migratory route, it is expected that the species would show little relationship to the environmental features than if the area was being used for foraging.

Sperm whales spend around 80% of their time underwater on foraging dives (Gordon & Steiner 1992; Papastavrou et al. 1989; Watwood et al. 2006), during which they click nearly continuously (Douglas et al. 2005; Watwood et al. 2006). These characteristics mean that passive acoustic techniques are ideal for locating sperm whales in studies of their ecology and distribution (Gannier et al. 2002; Gannier & Praça 2007; Gillespie 1997; Gordon et al. 2000; Jaquet & Gendron 2002; Jaquet & Whitehead 1996; Leaper et al. 1992; Rendell et al. 2004; Whitehead et al. 1992).

Therefore this study used passive acoustic techniques from platforms of opportunity to survey the distribution of sperm whales in deep waters off the west coast of Scotland with the following aims: (i) to investigate the influence of scale, both in terms of *extent* and *grain* size on predictive models of sperm whale distributions off the west coast of Scotland; and (ii) to explore the sperm whale-environment relationships in this area of the North Atlantic to investigate whether it is being used as a foraging ground for male sperm whales.

3.2 Methods

3.2.1 Data collection

Sperm whale data were collected simultaneously to the dolphin distribution data as detailed in §2.2.1. Real-time detection and tracking of sperm whale clicks detected by the hydrophone array was carried out using the IFAW software packages *Rainbow Click* (Gillespie 1997; Leaper et al. 2000). This software detects and measures bearings to transients such as sperm whale clicks and was run continuously whenever the hydrophone was deployed. In addition, every 15 minutes an experienced monitor actively listened to the hydrophone for 1 minute (a listening station), scoring for boat noise from the survey vessel, water noise, remote vessel noise, and sperm whale clicks on a subjective scale of 0 (inaudible) to 5 (loud). Since sperm whales click at a regular interval usually from different directions, it was usually possible to distinguish the number of sperm whales vocalising, which was also noted during the listening station. If there were too many whales present to determine the number vocalising, the number of individual tracks identified by *Rainbow Click* were counted and noted instead. Two acoustic monitors rotated the listening shifts within survey trips (usually alternating every 6 hours over a 24 hour period), and on all surveys at least one of three specialised acoustic monitors was present to maintain consistency in sound level measurement.

3.2.2 Environmental data

The environmental variables used were the same as those described in §2.2.2, and included survey variables, temporal variables, topographic variables, satellite surface environmental variables, and Forecasting Ocean Assimilation Model (FOAM – Bell et al. 2000) oceanographic variables. Survey variables included vessel speed, survey vessel noise, remote vessel noise, and water noise (Table 2.2). Temporal variables included time of day (calculation given in §2.2.2), and month where 1 = May, 2 = July, and 3 = September & October. Topographic variables only included depth. Satellite variables included Sea Surface Temperature (SST), and surface chlorophyll (Table 2.2). FOAM oceanographic variables included SST, thermocline depth & strength (where thermocline strength is calculated as the difference in temperature between surface and bottom waters), halocline depth & strength (where halocline strength is calculated as the difference in salinity between surface and bottom waters), surface and bottom current speeds (Table 2.2).

3.2.3 Acoustic data analysis

Sperm whales can be heard over large distances, resulting in the same whale being heard over several listening stations, causing serial autocorrelation (or pseudoreplication) and lack of independence between sampling units. Ideally, the tracks of all sperm whales would have been analysed and the distance to the track line estimated for every animal: only those animals within a certain range of the hydrophone would be included in the analysis. Due to the time consuming nature of this process, a small sample of 30 sperm whale tracks was analysed and a rule for deriving appropriate sampling units from series of listening stations was developed. This rule was based on minimising the number of stations over which an individual sperm whale could be heard, resulting in sampling units which were independent with respect to individual sperm whales.

To give an indication of the time involved in processing just this small sample, 30 tracks took around two weeks to manually select the clicks for each of the individual sperm whale tracks, export to R and run the script to estimate the time at which the animal passed abeam, and to estimate the distance of the animal to the trackline. This sample formed less than half of one survey, so each survey would take at least a month to process dependent on the number of sperm whales heard.

To determine a rule to make listening stations independent, the acoustically scored levels of sperm whale clicks (0-5) and the number of individuals heard were compared with the bearings obtained from the same period of time for clicks detected by the *Rainbow Click* software, and the number of individual tracks. This was carried out for data collected over a range of different habitat types (Faroe-Shetland Channel and Rockall Trough). The whale's location was assessed by eye based on the crossed bearings and the range of this from the trackline was measured (in a similar manner §2.2.3). From this it was also possible to estimate the time at which the animal passed abeam, and hence which listening station it corresponded to. This technique has been used to estimate whale locations in other studies using similar towed hydrophones e.g. Leaper et al. (2000) and Hastie et al. (2003). Sperm whale clicks could usually be resolved as trains from individual whales rather than groups, so the number of individual tracks at different bearings represented the number of individuals vocalising within range of the hydrophone (Figure 3.1).

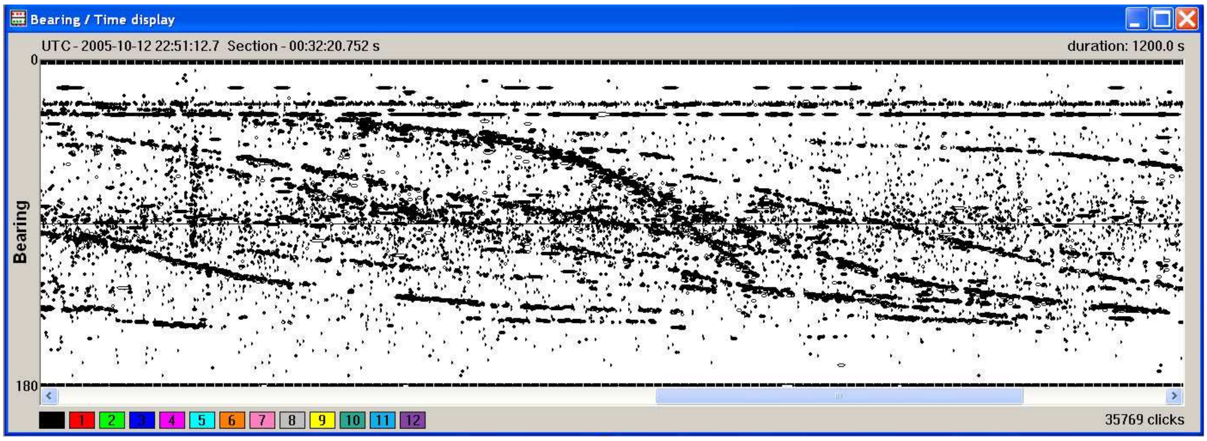


Figure 3.1 – Rainbow Click bearing-time plot of clicks recorded from the *RSS Darwin* on 12th October 2005. Time is shown along the x-axis (total length of 20 minutes displayed), and bearing in degrees along the y-axis from 0º (ahead of the vessel) to 180º (behind the vessel). The black line through the middle of the display represents the 90º line, indicating any clicks heard abeam of the vessel. The two parallel tracks at the top of the display remaining at the same bearing for the duration of the time sample are noise clicks originating from the survey vessel. All other tracks of black dots are the clicks of individual whales of which there are over 15 animals within the time sample shown here. Tracks with steeper slopes crossing the 90º abeam line are closer to the vessel than those with shallower slopes.

Based on crossing bearing of clear continuous tracks of sperm whale clicks identified using the *Rainbow Click* software, distances from the trackline ranged from 700 m to 12 km from the vessel at an average of 4.7 km (sd = 2.6 km), though sporadic clicks were occasionally measured at ranges of up to 23 km. Most acoustic detections of sperm whales were made in groups spread over a large area (average 32 km assuming an average vessel speed of 10 knots). The largest group was spread out over 60 km in the Rockall Trough and comprised a large number (estimated to be > 30) of individual sperm whales. This results in severe serial autocorrelation in the data, not only due to the large distance over which detections could be made, but also due to the large group sizes or ‘super aggregations’ (Jaquet & Gendron 2002).

Based on the sample of data including 30 sperm whale tracks, a ‘true distribution’ of sperm whales was generated. If a sperm whale passed abeam of the vessel during the 15 minute period centred at the time of the listening station (i.e. within 7.5 minutes before or after the start of the 1 minute listening station), then the sperm whale was associated with that listening station. This ‘true distribution’ was compared to the acoustically scored levels of sperm whale clicks (0-5).

Different rules were applied to the acoustically scored levels of sperm whale clicks to classify the levels as a presence/absence of sperm whales:

i) Presence when acoustically scored level of sperm whale clicks >0, absence when = 0

ii) Presence when acoustically scored level of sperm whale clicks >1, absence when ≤ 1

By comparing the distributions resulting from application of these rules with the ‘true distribution’ it was possible to calculate the percentage correctly classified. Using all sperm whale vocalisations (i.e. ≥ 1) resulted in only a 45% correct classification rate. Whereas, excluding the quiet sperm whale vocalisations (≤ 1) predicted the ‘true distribution’ of sperm whales correctly 65% of the time. Therefore, this latter rule (rule i) was used to generate the data on which subsequent analyses were based. This method removed much of the autocorrelation in the data caused by hearing the same animal over several listening stations, but will not have removed the autocorrelation due to large group sizes.

Previous studies of sperm whale distributions (Gannier et al. 2002; Gannier & Praça 2007; Gordon et al. 2000) have eliminated autocorrelation by considering each series of consecutive positive segments as a single group presence, centred in the middle of the group. This method is useful for creating independent samples, but raises questions about handling environmental data recorded in areas where the whales were actually present, but not considered the centre of the group. For this analysis it was therefore decided to allow serial autocorrelation due to large group sizes (which would tend to produce overfitted models), and remove the resultant overfitting of the model selection process by carrying out cross-correlation on an independent data set (detailed in §3.2.4.1). Aarts (2006) used a similar method to remove overfitting of models resulting from serial autocorrelation in individually tracked grey seal (*Halichoerus grypus*) locations to predict their habitat preferences.

3.2.4 Statistical analysis

3.2.4.1 Pre-modelling analysis

Since the coarsest scale for the environmental data was 9 km (for the FOAM oceanographic and current data), either consecutive pairs of listening stations were grouped into segments (at 10 knots this is the equivalent of 9 km segments), or four consecutive stations were grouped to make a segment (equivalent of 18 km segments). Environmental variables collected in the field were averaged over each segment. All other variables (topography, satellite and FOAM variables), values were determined for the mid-point of each segment using the STJG GIS extraction tool version 1.0.1 (Gontarek 2005) in ArcGIS 9.0 (ESRI Inc). For the 18 km segments, values were averaged over every two 9 km segments.

Prior to modelling, a Spearman's Rank Correlation test was carried out using Minitab v12.23 (Minitab Inc. 1999) to test for correlations between environmental variables. If there was a strong correlation ($r > 0.8$) between variables, the first of the variables selected by the step-wise model selection was retained and any variables with which it was correlated were discarded.

The dataset was divided into a 'training' and 'test' dataset. One method of testing for overfitting within the full dataset was to randomly divide the data such that 75% of the segments were included in the 'training' dataset and used as the basis of the model selection, and the remaining 25% of the segments were used as the 'test' dataset, on which the predictive performance of the models were evaluated (Araujo & Guisan 2006). To ensure as much independence between re-sampling units as possible while retaining as much of the original spatial coverage surveyed as possible, the data were randomly sampled by groups of 5 segments. Groups of 5 segments (around 23 km) were unlikely to be autocorrelated according to the detected range of the sperm whales (upper 95% confidence limit of 9.7 km). Test and training datasets were also created based on only Faroe-Shetland Channel (FSC) surveys, and Ellet Line (EL) surveys (both formed a training and test set for each other). This latter analysis allowed for testing the spatial robustness of the models.

3.2.4.2 Modelling sperm whale occurrence – model selection

Generalised Additive Models (GAMs) were used to relate sperm whale presence/absence to the survey, temporal, topographical, oceanographic and current variables. The GAMs were fitted in R version 2.3.0 (The R Foundation for Statistical Computing 2006), using the MGCV library (Wood 2006). Forward step-wise model selection of variables to the null model (of no predictor variables) was carried out. Firstly, survey variables which were likely to affect detection probability (water noise, survey vessel noise, remote vessel noise, and vessel speed) were added to the model to compensate for survey effects. Time was also added to the model to investigate whether there were diurnal changes in vocalisations. Once compensated for survey and diurnal effects on the detection rate of sperm whale clicks, the topographical, oceanographic and current variables were selected using forward step-wise model selection.

Any of the predictor variables (survey, temporal or environmental) were only added if:

i) they reduced the AIC equivalent of the UBRE score (multiplying UBRE by n the sample size) by 2 or more, as recommended by (Burnham & Anderson 2002).

ii) the variables were significant at $p < 0.05$

Variables included in the model selection included: depth, SST, SSS, chlorophyll, halocline depth & strength, thermocline depth & strength, surface & bottom current speed. Month and year were added to the model after the survey and temporal effects but before the environmental variables to determine whether there was a significant difference between seasons, or years, prior to modelling. They were not included in the models at this stage. After adding environmental variables, they were tested to see if there was any deviance remaining that could be explained by month or year (to check that the environmental variables were able to model season and yearly differences).

3.2.4.3 Modelling sperm whale occurrence - model evaluation

Ideally, any model developed should be able to fully model the species distribution without any remaining temporal or spatial autocorrelation. Remaining autocorrelation in the residuals could imply that important variables have not been included in the model. The Wald-Wolfowitz run test was used to test for any remaining non-randomness in the model residuals (Hardin & Hilbe 2003; §2.2.4.3).

Having assessed whether the model has adequately modelled the autocorrelation (if it exists), models were evaluated using the Receiver Operator Characteristic (ROC) curves and Area Under the Curve (AUC) (Pearce & Ferrier 2000). For binomial data, predictive models are best evaluated using the ROC since they are not sensitive to the threshold used to decide whether a predictive score is a presence or absence (Boyce et al. 2002). The measure is used extensively to evaluate the predictive ability of binomial models within ecology (Boyce et al. 2002; Cumming 2000; Fielding & Bell 1997; Osborne & Suarez-Seoane 2002; Pearce & Ferrier 2000; Thuiller et al. 2004). A ROC curve plots the sensitivity and the specificity of the model predictions over a range of threshold values (Pearce & Ferrier 2000). The sensitivity of a model is a measure of the model to predict presence of a species where it is actually present, whereas the specificity is a measure of the ability of a model to predict absence where the species was actually absent (Boyce et al. 2002). The ROC curve is essentially 1-specificity plotted against the sensitivity for a range of cut-off thresholds, and the AUC value is the area under this ROC curve. For the model to have predictive power, it should have an AUC of > 0.5 (i.e. the area under a 45° line), for perfect model prediction the AUC would equal 1. Pearce and Ferrier (2000) consider AUC values < 0.7 to have poor predictive power, values between 0.7-0.9 to have reasonable predictive power, and values >0.9 to have excellent predictive power.

The ROC AUC values were evaluated for each model based on the original data for a measure of model performance, and against other data sets to gain a measure of the predictive performance of a model. By using both ROC AUC values and dividing data into test and training data sets from (i) within the same datasets; (ii) by area (*extent*); and (iii) by scale (*grain* size), it was possible to evaluate the most robust model in space and remove overfitted terms due to the autocorrelation inherent in the data.

The final models were predicted over a 18x18 km grid, set to twice the size of the segment size as recommended by Hedley (2000). This allowed for visual evaluation of the model against the actual detections, and between different models. Predictions were based on environmental variables available from 14 October 2004. This date was selected for several reasons: it was based on a day that was actually surveyed, forms the mid point of all the survey data, and October was the only month during which both areas around the Faroe-Shetland Channel and the Ellet Line were surveyed.

3.2.4.4 Models constructed

Environmental models of sperm whale occurrence (based on listening stations with loudness >1) were constructed in several stages. Firstly, to evaluate overfitting within the full 9 km segment dataset due to autocorrelation of sperm whale detections, the dataset was randomly divided into a 75% training and 25% test dataset. Models were developed based on the ‘training’ data and evaluated on the ‘test’ data. Secondly, to examine spatial robustness over different areas, models based on the 9 km segments were developed separately for the Faroe-Shetland Channel surveys and for the Ellet Line surveys, and evaluated on the other dataset. Finally, models were developed for the full data set at the 18 km scale, and compared to those at the 9 km scale to determine whether models were consistent over these two spatial scales. The overall aim of the analysis was to obtain the most spatially robust model for sperm whale distributions off the west coast of Scotland, to explore the reliability of extrapolation between areas, and to understand some of the spatial variability in habitat preferences.

3.3 Results

A total of 11 426 km of surveys were carried out off the west coast of Scotland between July 2003 and October 2005, as detailed in Table 3.1. Overall there were 1242 9 km segments, with 622 hours of listening effort for which all environmental variables were available. Of these, 203 (16.3%) had any sperm whale click detections (i.e. 1-5 loudness) and 100 (8.1%) had the presence of sperm whale clicks greater than level 1 loudness. Sperm whales were detected mainly in the deep off-shelf waters of the Faroe-Shetland Channel (FSC), Wyville-Thompson Ridge (WTR) and throughout the Rockall Trough south of the WTR (Figure 3.2). There were also a few on-shelf detections of sperm whales on the Faroe Plateau.

Table 3.1 – Acoustic effort (in numbers of segments and km), the number of segments with any sperm whale clicks (1-5 loudness), and the number of segments with sperm whale clicks >1 loudness for the oceanographic surveys carried out off the west coast of Scotland.

Survey Date	Number of segments (distance in km)	Number of segments with any clicks (% of segments)	Number of segments with distant clicks removed (% of segments)
19-25 July 2003	114 (1050 km)	18 (15.8%)	12 (10.5%)
16-28 September 2003	137 (1260 km)	8 (5.8%)	3 (2.2%)
13-29 May 2004	244 (2245 km)	78 (32.0%)	39 (16.0%)
5-17 October 2004	189 (1740 km)	13 (6.9%)	6 (3.2%)
8-26 May 2005	221 (2033 km)	14 (6.3%)	4 (1.8%)
27 Sept – 8 Oct 2005	130 (1195 km)	8 (6.2%)	1 (0.8%)
7-25 October 2005	207 (1905 km)	64 (30.9%)	35 (16.9%)
TOTAL	**1242 (11,426 km)**	**203 (16.3%)**	**100 (8.1%)**

3.3.1 Environmental variables

A summary of the environmental variables is detailed in Table 3.2. There were significant increases in depth, Sea Surface Temperature (SST), and thermocline depth, and significant decreases in vessel speed, surface chlorophyll, and bottom current surveyed during the Ellet Line (EL) surveys in comparison to the Faroe-Shetland Channel (FSC) surveys (Table 3.2). For more detail, refer to §2.3.1.

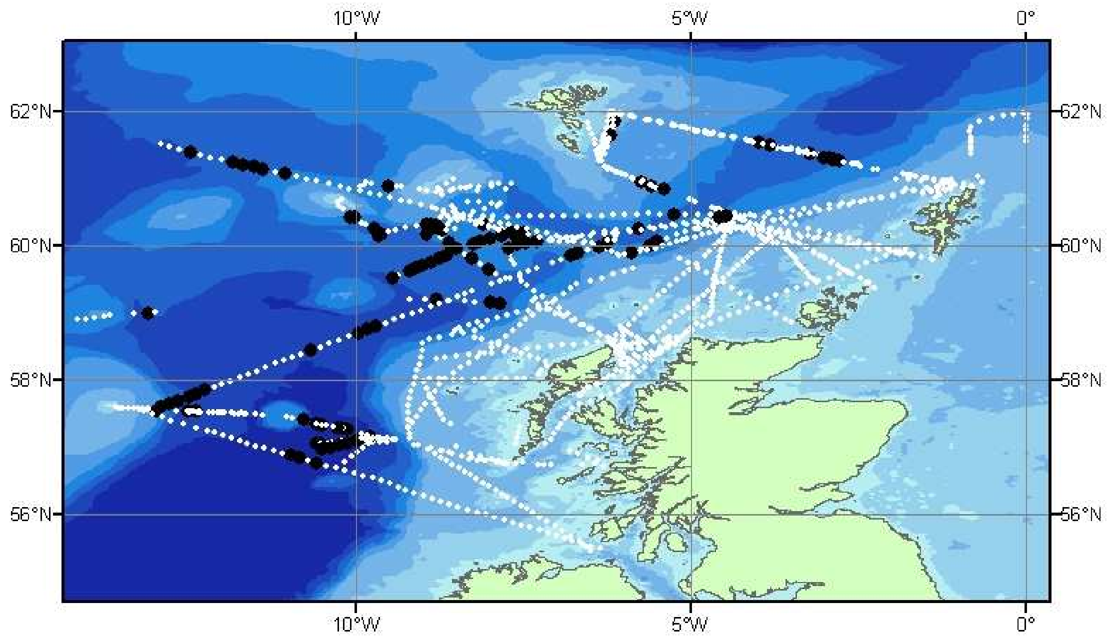


Figure 3.2 – Survey effort and sperm whale detections for the west coast of Scotland surveys carried out between July 2003 and October 2003. 9km segments (n = 1242) are presented as black dots where sperm whales are present (>1 loudness) and white dots where sperm whales are absent (≤1 loudness). Data are overlaid on bathymetry (GEBCO).

3.3.2 Model selection: full dataset

Of the 930 segments in the 75% training data set, there were 75 segments with sperm whale detections with greater than 1 loudness level (8.1%). Of the survey variables, only vessel speed was a significant predictor; there were fewer sperm whale detections as boat speed increased (Figure 3.3).

Once survey effects had been incorporated into the model, environmental variables were added to the model by forward step-wise selection (Figure 3.4). The best model is shown in Figure 3.4 and included, in order of importance: depth, thermocline strength, and halocline strength (Figure 3.5). Sperm whale clicks were most likely to be heard in waters deeper than 350 m; in areas with relatively weak thermoclines (between -1 to -5°C difference between the surface and the bottom temperature); and in areas with a strong negative halocline (i.e. where the deep water is fresher than the surface water).

Table 3.1 – Summary statistics for the environmental variables for the oceanographic survey data for July 2003-October 2005 grouped by Faroe-Shetland Channel surveys, and Ellet Line surveys carried out off the west coast of Scotland. Results of a Mann-Whitney test to test between the two data sets environmental variable distributions are shown if significant, where * $p<0.05$; **$p<0.01$; and ***$p<0.001$.

Parameter		*Scotia*	Non-*Scotia*
Survey effort with environmental data available			
Distance surveyed (km)		8262	2889
Number of stations/segments		918	321
Segments with sperm whale clicks (>1 loud)		53 (5.8%)	47 (14.6%)
Survey variables			
Boat speed	range (knots)	3.3-13.7	4.9-12.9***
	mean (standard deviation)	9.9 (1.9)	9.1 (1.5)
WaterNoise	range	0-5	0-5
	median (IQR)	2 (1-2.5)	2 (1-3)
SelfNoise	range	0-4	0-4
	median (IQR)	2.5 (2-3)	2 (2-3)
Temporal variables			
TimeDayNight	range	0-2	0-2
	mean (standard deviation)	1.02 (0.53)	0.97 (0.60)
Topographical variables			
Depth	range (m)	15-1641	21-2374***
	median (IQR)	202 (116-626)	1130 (223-1883)
Satellite data			
SST	range (°C)	6-13.8	9.7-15.3***
	mean (standard deviation)	10.8 (1.4)	12.8 (1.8)
Chl	range (mg/m^3)	0.03-22	0.03-10***
	median (IQR)	0.53 (0.29-0.99)	0.32 (0.20-1.26)
FOAM variables			
HaloDepth	range (m)	30-815	30-1335
	median (IQR)	100 (50-200)	105 (60-145)
SBS	range (psu)	-0.38-0.15	-0.44-0.20*
	median (IQR)	0.0 (-0.06-0.02)	0.0 (-0.25-0.06)
SSS	range (psu)	35.0-35.4	35.0-35.4
	median (IQR)	35.26 (35.2-35.3)	35.26 (35.2-35.3)
ThermDepth	range (m)	29-774	20-359*
	median (IQR)	85 (67-132)	113 (30-135)
SBT	range (ºC)	-12.6-0.11	-10.0-0.02***
	median (IQR)	-1.13 (-2.79- -0.10)	-3.70 (-8.12- -2.26)
SurfCurSpd	range (m/s)	0.01-0.58	0.00-0.49
	median (IQR)	0.120 (0.07-0.20)	0.12 (0.06-0.19)
BotCurSped	range (m/s)	0.00-0.46	0.00-0.39***
	median (IQR)	0.08 (0.04-0.14)	0.05 (0.02-0.09)

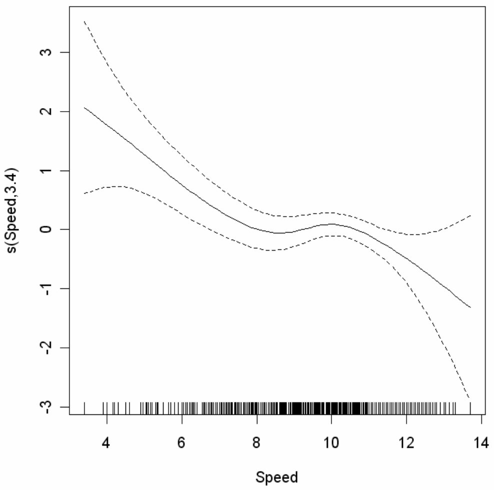


Figure 3.3 – Sperm whale occurrence per 9km segment (*n* = 930) modelled as a GAM smooth function of vessel speed (d.f. = 3.4) for all survey data collected off the west coast of Scotland between July 2003 and October 2005. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show 95% confidence intervals.

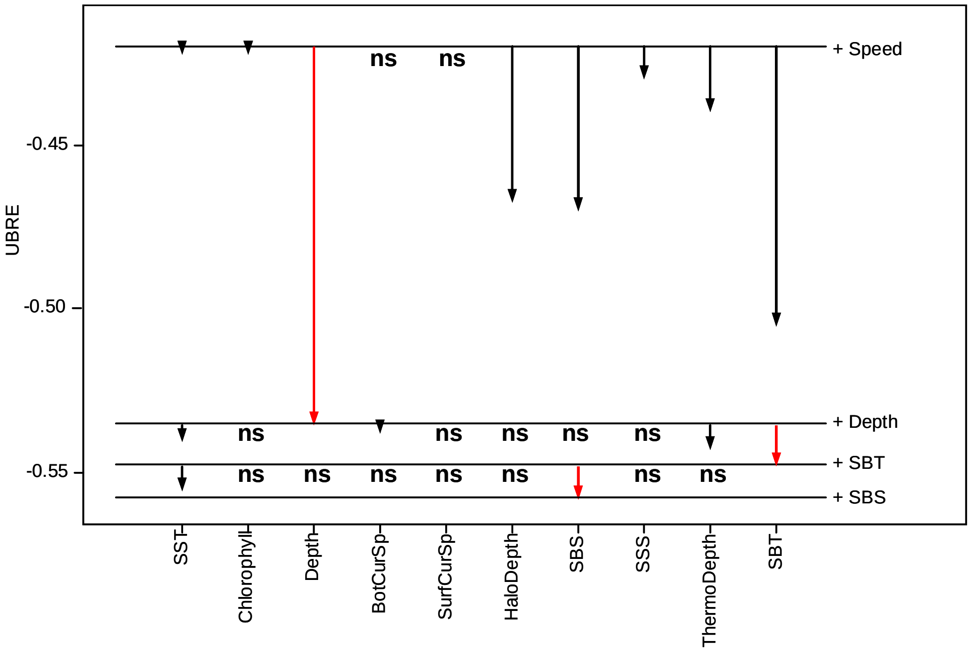
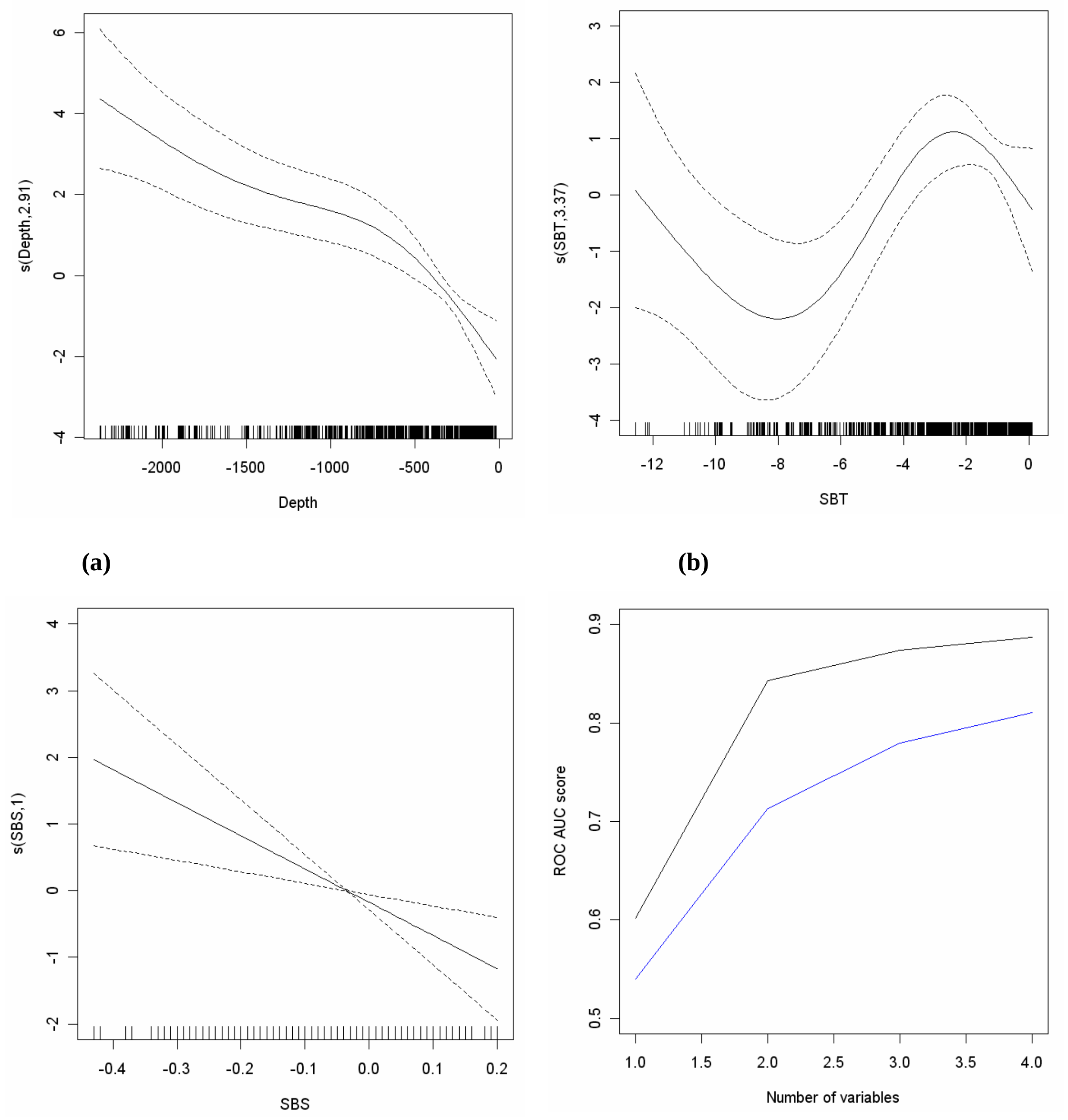


Figure 3.4 - Forward model selection for the model of the occurrence of sperm whale clicks (>1 loudness) detected per 9km segment for all survey data from July 2003-October 2005 on the environmental variables: sea surface temperature (SST), chlorolphyll, depth, bottom current speed (BotCurSp), surface current speed (SurfCurSp), halocline depth (HaloDepth), halocline strength (SBS), sea surface salinity (SSS), thermocline depth (ThermDepth) and thermocline strength (SBT). The arrows indicate the change in UBRE score between models (horizontal lines) as a result of adding an environmental variable. Red arrows indicate those variables that decrease the UBRE score by the largest amount and so included in the model. 'ns' indicates that the variable is not significant to p < 0.05. Based on visualisation of GAMs model selection by Aarts (2006).



(a) (b)

(c) (d)

Figure 3.5 – Sperm whale occurrence per 9km segment (*n* = 930) modelled as GAM smooth functions of (a) depth (d.f. = 2.9), (b) thermocline strength SBT (d.f. = 3.4), (c) halocline strength SBS (d.f. = 1) for all survey data collected off the west coast of Scotland between July 2003 and October 2005. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show 95% confidence intervals. (d) The performance of the 75% full data model at predicting the (black) 75% training data and (blue) 25% test data set as each of the variables are added to the model: 1 = s(Speed); 2 = s(Depth); 3 = s(Thermocline Strength); 4 = s(Halocline strength).

The overall model was able to explain 30.8% of the deviance of which 27.8 % was explained by environmental variables (Table B1, in Appendix B):

$$SpWhOcc \sim s(Speed) + s(Depth) + s(ThermStrength) + s(HaloStrength)$$

The Wald-Wolfowitz test statistic $W_z = -14.5$, indicating that the residuals were not randomly distributed ($p < 0.001$), and that there was un-modelled autocorrelation remaining within the data.

This model of sperm whale occurrence performed well on predicting the 75% data set (ROC AUC = 0.887). The biggest improvement occurred when depth was added to the model (Figure 3.5d). Testing the model on the 25% training set as each variable was added resulted in the ROC AUC changes in scores shown in Figure 3.5d. The best model performance when predicting the 25% test data set was achieved for the full model (ROC AUC = 0.811). This suggests that there are no unnecessary overfitted variables in the model.

Using this best model, a predictive map was generated over a 20km grid covering the whole survey area where the environmental variables were available based on data from 14 October 2004 (Figure 3.6).

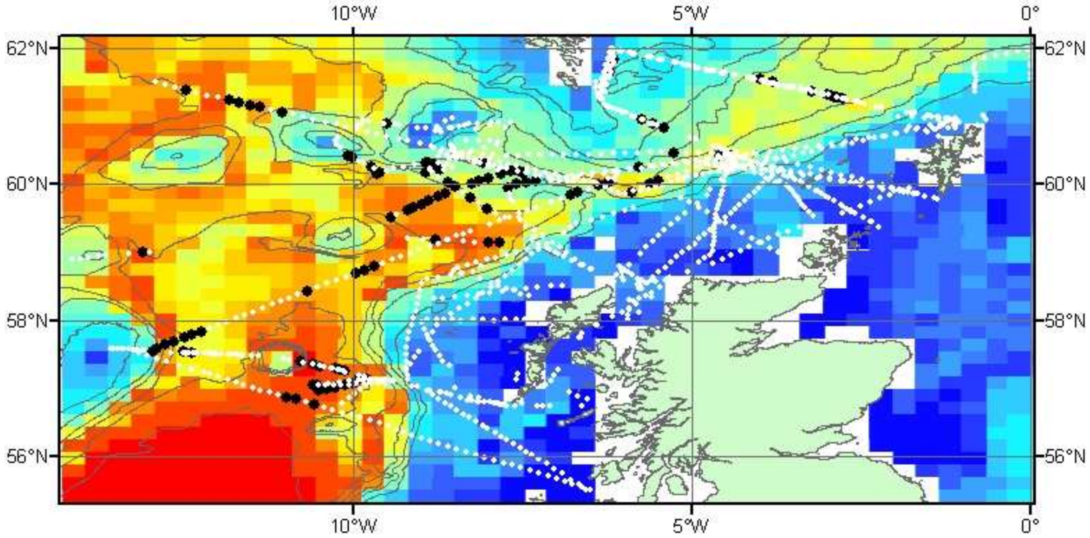


Figure 3.6 - Spatial prediction based on environmental variables available for 14 October 2004 of the probability of sperm whale occurrence per 20km grid for the best model for all survey data from 2003-2005. Overlaid on the maps are the effort segments (white dots) and the sperm whale detections (black dots) for all sperm whale detections of loudness >1 for all survey data. Also overlaid are GEBCO depth contours (dark grey lines). Colours represent probability of sperm whale click detection from low (blue) to high (red), ranging from 0 - 0.9, colour gradation based on 20 levels using quantile classification.

The highest probability of the occurrence of sperm whales was predicted in the entire upper Rockall Trough, being greatest in the deepest water but still moderately high up to the Wyville-Thompson Ridge. A relatively low probability of occurrence was predicted in the Faroe-Shetland Channel. Very low probability of occurrence of sperm whales is predicted for all on-shelf areas and water shallower than around 300m.

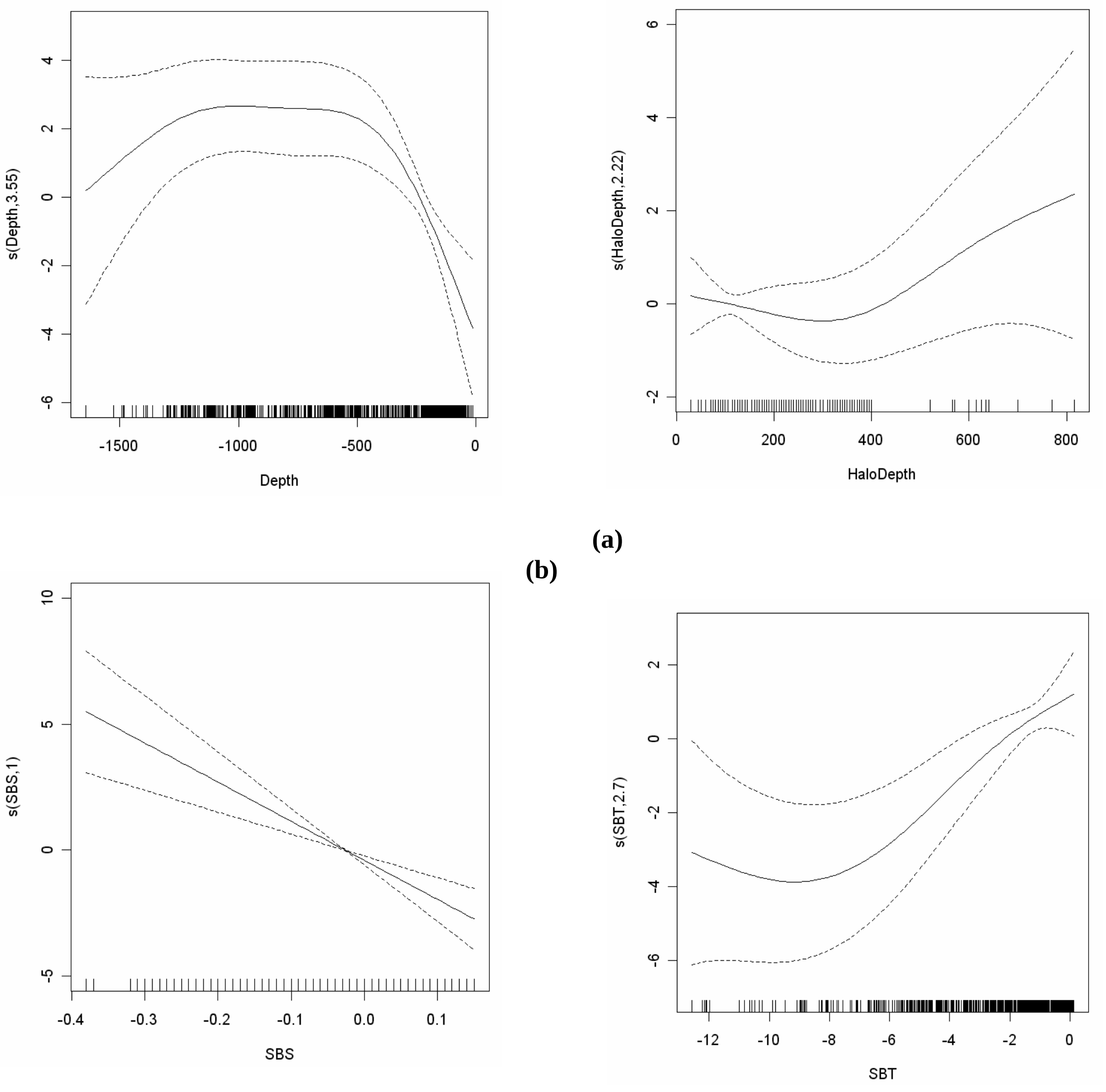
3.3.3 Model selection: spatial robustness between areas

To explore spatial robustness between areas, the models were developed on one geographical area (training data) and tested on their ability to predict distributions in the other geographical area (the test data).

3.3.3.1 Faroe-Shetland Channel survey data

The Faroe-Shetland Channel surveys were mainly confined to the hydrographic lines crossing the northern and southern parts of this area, but also included areas surrounding the Wyville-Thompson Ridge and some shelf waters. A narrower range of depths and halocline strengths, a lower range of SST values, and a wider range of thermocline depths & strengths, and current speeds were recorded in these areas (Table 3.2).

Of the survey variables added to the model, only vessel speed showed the same relationship in both models (Figure 3.3), with reduced detections of sperm whales at higher vessel speeds. Forward step-wise selection of environmental variables resulted in a model that included (in order of importance): depth, thermocline strength, halocline depth, halocline depth and sea surface salinity. Sperm whale clicks were most likely to be heard in off-shelf waters deeper than 350 m, peaking between 500-1100 m, and decreasing in preference above 1100 m; shallow (< 100 m) or deep (> 450 m) halocline depth; stronger negative haloclines (fresher deep than surface water); weak thermoclines (> -2°C difference between surface and bottom water temperature); and either fresh (< 35.17 psu) or salty (>35.36) surface salinity. It should be noted that there is considerable uncertainty around some of the predicted relationships. In particular, the smooth of sperm whale occurrence with halocline depth shows very wide confidence intervals around the predicted relationship with the zero preference line being included within the confidence intervals over the whole range of the predictor variable.

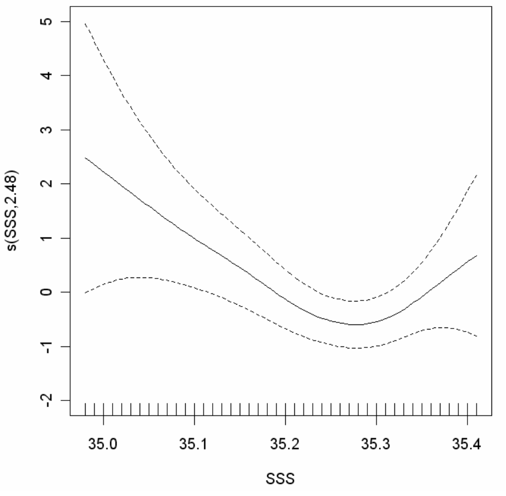


(a)

(b)

(c)

(d)



(e)

Figure 3.7 – Sperm whale occurrence per 9km segment (*n* = 918) modelled as a GAM smooth function of (a) depth (d.f. = 3.6), (b) halocline depth (d.f. = 2.2), (c) halocline strength (d.f. = 1), (d) thermocline strength (d.f. = 2.7), and (e) Sea Surface Salinity SSS (d.f. = 2.5) for Faroe-Shetland Channel survey data collected off the west coast of Scotland between September 2003 and October 2005. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show 95% confidence intervals.

The overall model was able to explain 36.6% of the deviance of which 33.9% was explained by environmental variables (Table B2, Appendix B):

$$SpWhOcc_{FSC} \sim s(Speed) + s(Depth) + s(HaloDepth) + s(HaloStrength) + s(ThermoStrength) + s(SurfaceSalinity)$$

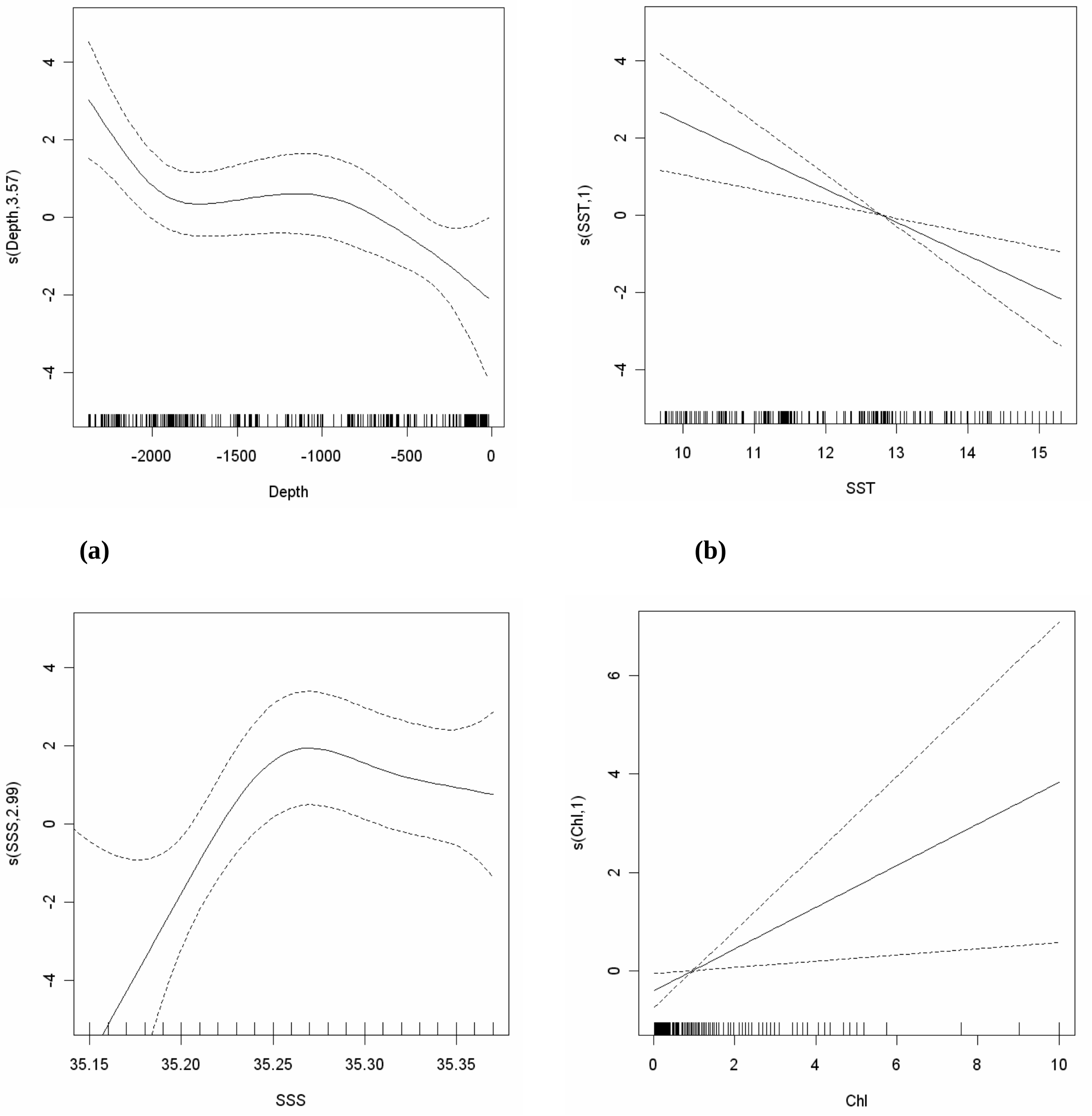
The Wald-Wolfowitz test statistic $W_z = -14.3$, indicating that the residuals were not randomly distributed ($p < 0.001$), and that there is un-modelled autocorrelation remaining within the data. However, the model performed well on predicting the occurrence of sperm whales in the data set with a very high ROC AUC score of 0.914.

The model predicts sperm whale occurrence throughout the deep water areas surveyed (Figure 3.9). There is high predicted probability of occurrence in the deepest parts of the Faroe-Shetland Channel, and in a band just south of the Wyville-Thompson Ridge between the shelf-edge and Rosemary Bank. Low probability of occurrence of sperm whales is predicted for any on-shelf or shallow waters such as the Wyville-Thompson Ridge and the Faroe Bank.

3.3.3.2 Ellet-Line survey data

The Ellet Line surveys were based on hydrographic surveys of the Ellet Line; a straight line that travels out from shallow waters near to Oban, across and off the shelf edge, crossing the Rockall Trough over the Anton Dorhn seamount and onto the Rockall Bank (Figure 2.1). However, the surveys also included some tracks within adjacent areas within the Rockall Trough to the north up to the Wyville-Thompson Ridge, and further west beyond Bill Bailey's Bank. The surveys therefore included a much wider range of depths than the Faroe-Shetland Channel surveys, as well as including warmer SST (probably due to the Gulf Stream), a wider range of halocline strengths, and a smaller range of thermocline depths & strengths, and current speeds.

None of the survey effect variables were significant in modelling the occurrence of sperm whales in this data set. The environmental variables selected by forward model-selection included (in order of importance): depth, SST, sea surface salinity, and chlorophyll concentration (Figure 3.8). Sperm whale clicks were most likely to be heard in off-shelf waters deeper than 600 m; water cooler than 12.7°C; in water saltier than 35.22 psu; and areas of high primary productivity.



(a) (b)

(c) (d)

Figure 3.8 – Sperm whale occurrence per 9km segment (*n* = 321) modelled as a GAM smooth function of (a) depth (d.f. = 3.6), (b) SST (d.f. = 1), (c) Sea Surface Salinity SSS (d.f. = 3.0), and (d) surface chlorophyll (d.f. = 1) for Ellet Line survey data collected off the west coast of Scotland between July 2003 and October 2005. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show 95% confidence intervals.

However, the confidence intervals around the linear relationship between sperm whale occurrence and chlorophyll are very wide, with the lower CI only just above the zero preference line, suggesting a relatively weak positive relationship between the two.

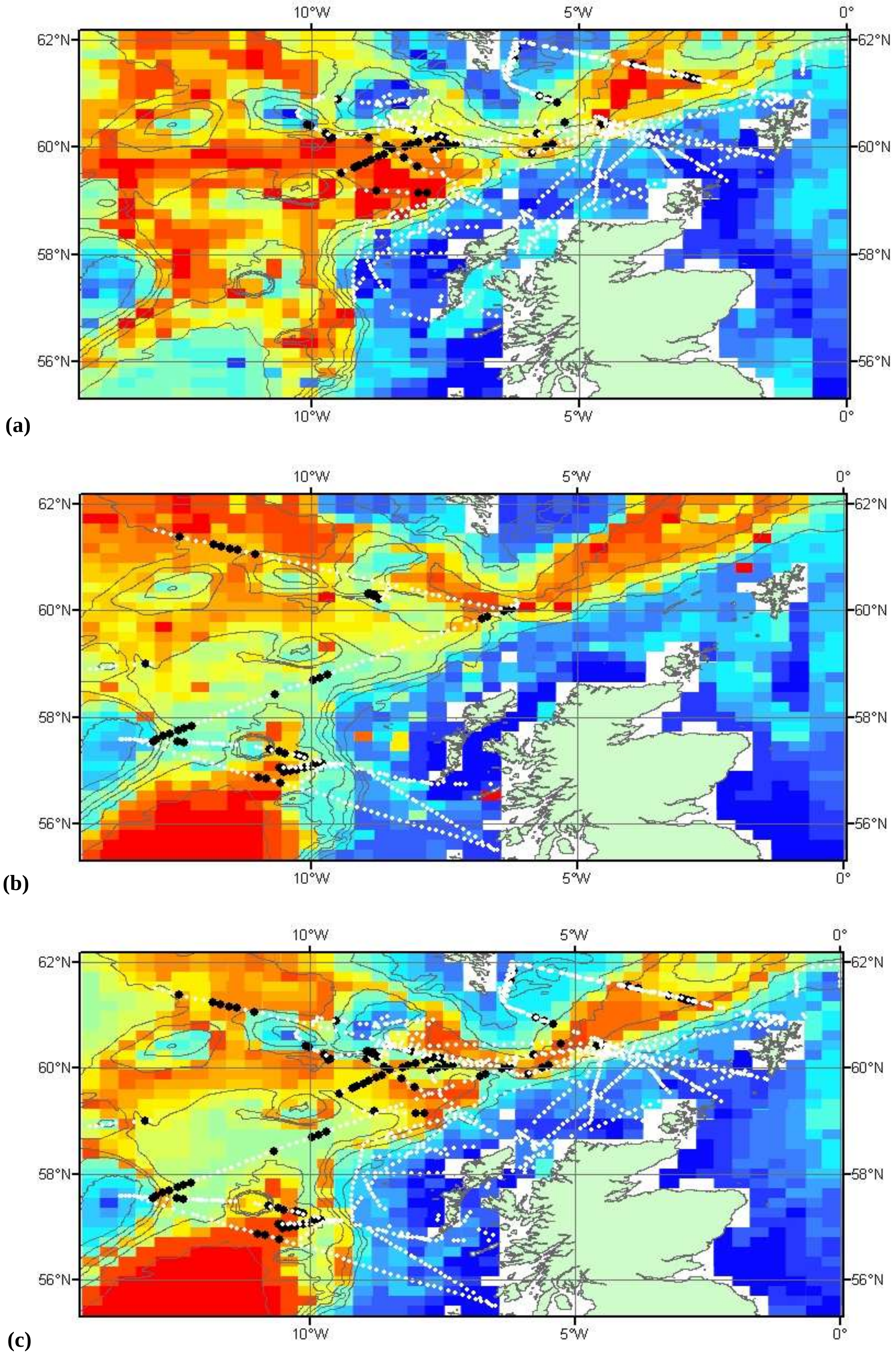

10°W
5°W
0°
62°N
60°N
58°N
56°N
(a)
10°W
5°W
0°
62°N
60°N
58°N
56°N
(b)
10°W
5°W
0°
62°N
60°N
58°N
56°N
(c)

Figure 3.9 (previous page) - Spatial prediction of sperm whale occurrence per 20 km grid cell using environmental data from 14 October 2004 for (a) the best Faroe-Shetland Channel (FSC) model, (b) the best Ellet Line (EL) model, and (c) the most spatially robust model based on the variables selected by the FSC and EL models. Based on data collected between July 2003 – October 2005 off the west coast of Scotland. Overlaid on the maps are the effort segments (white dots) and the sperm whale detections (black dots) for each model. Also overlaid are GEBCO depth contours (dark grey lines). Colours represent probability of sperm whale click detection from low (blue) to high (red), ranging from 0-1, colour gradation based on 20 levels using quantile classification.

Overall, 25.6% of the deviance was explained by the resultant model, of which 25.6% was explained by environmental variables (Table B3, Appendix B):

$$SpWhOcc_{EL} \sim s(Depth) + s(SST) + s(Surface\ Salinity) + s(Chlorophyll)$$

Less non-randomness was observed in the residuals ($W_z = -8.4$) than in the previous model and it performed well, with a high ROC AUC score of 0.848. However, the Wald-Wolfowitz test statistic was still significant ($W_z = -8.4$, $p < 0.001$), indicating that the model was unable to fully model the autocorrelation.

The model predicted highest probability of occurrence of sperm whales in either the northern part of the Rockall Trough, around the Wyville-Thompson Ridge and west of Bill Bailey's Bank, or in the deep southern Rockall Trough to the east of Anton Dorhn seamount. There was relatively low predicted probability of occurrence in the mid-depth Rockall Trough (between the 1500 m and 2000 m isobaths).

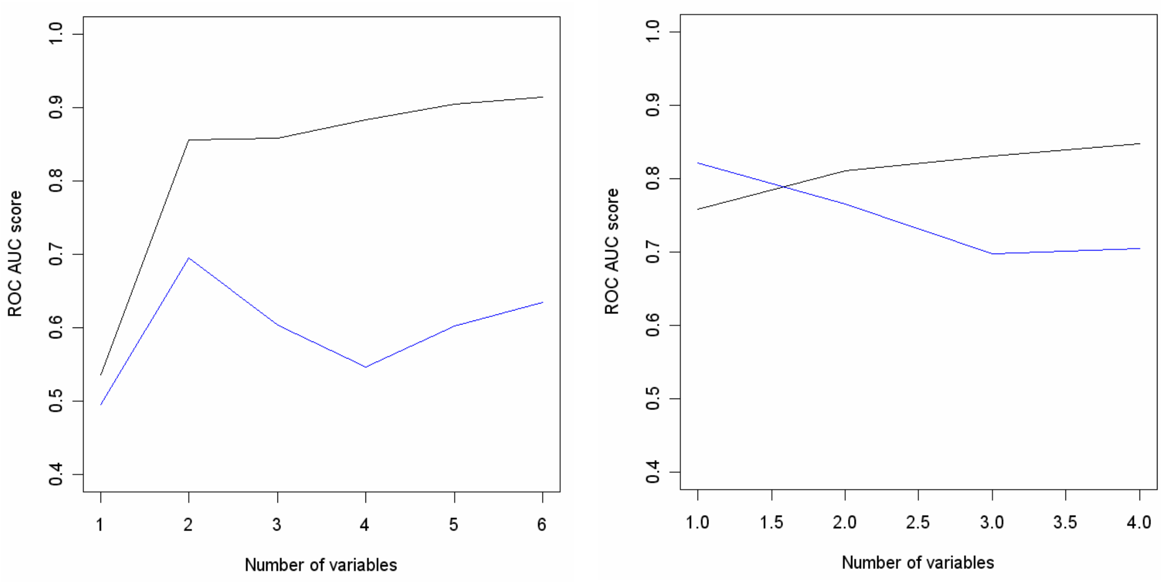
3.3.3.3 Comparison of Faroe-Shetland Channel & Ellet Line models

Testing each model against its ability to predict the other data set, the Faroe-Shetland Channel model performed the worst, with a maximum ROC AUC score of only 0.695 when depth was the only variable in the model (Figure 3.10). The Ellet Line model performed better, though again with best performance when depth was the only variable in the model, performing better on predicting the *Scotia* data (ROC AUC 0.822) than the non-*Scotia* data (ROC AUC 0.759).

These results suggest that the most robust model for predicting distribution over space, based on the two different geographical areas only includes depth, with the smooth based on the Ellet Line survey data:

$SpWhOcc_{SpatialRobust} \sim s(Depth)_{EL}$

This spatially robust model predicts highest probability of sperm whale occurrence in the southern parts of the Rockall Trough to the east of Anton Dohrn seamount, with high probability of occurrence also predicted along the shelf edges, deep Faroe-Shetland Channel on both deep sides of the Wyville-Thompson Ridge, and to the west of Bill Bailey's Bank.



(a) **(b)**

Figure 3.10 - the performance (ROC AUC) of the sperm whale occurrence model based on (a) Faroe-Shetland Channel survey data and (b) Ellet line survey data as applied to the original data (black line) and the opposite data set (blue line) as each of the variables are added to the model: (a) 1 = s(Speed); 2 = s(Depth); 3 = s(HaloDepth); 4 = s(HaloStrength); 5 = s(ThermoStrength); 6 = s(SurfaceSalinity), (right) 1 = s(Depth); 2 = s(SST); 3 = s(SurfaceSalinity); 4 = s(Chlorophyll).

3.3.4 Model selection: spatial robustness with scale

3.3.4.1 18km scale model

The data were divided into groups of four listening stations, the equivalent of an 18 km scale when the vessel travels at an average of 10 knots. Using data from all surveys from July 2003 - October 2005, there were 615 18km segments 69 of which had sperm whale detections of >1 loudness (11.2%). When sperm whale occurrence was modelled with environmental variables using the same methodology as in previous sections, the model and the smooths were identical to that for the 9 km model (Figure 3.5), except that no variables were significant after thermocline strength was added to the model. Overall the model was able to explain 28.1% of the deviance, of which 24.2% was explained by environmental variables (Table B4, Appendix B):

$SpWhOcc_{18km} \sim s(Speed) + s(Depth) + s(ThermoStrength)$

Non-randomness in the residuals was lower than previous models, but the Wald-Wolfowitz test statistic remained significant ($W_z = -6.0$, $p < 0.001$), indicating that un-modelled autocorrelation in the residuals were still present. The model performed well, with an ROC AUC score of 0.855.

3.4 Discussion

In this study, I have investigated the effect of spatial scale on predicting sperm whale distributions off the west coast of Scotland by varying both *extent* and *grain* sizes. This has provided insight both into the spatial robustness of the predictive models and into the habitat preferences of sperm whales in this part of the North Atlantic.

3.4.1 Influence of autocorrelation & scale on model robustness

Modelling acoustic detections of sperm whales with environmental variables at such a small *grain* size was complicated by the fact that the data were severely autocorrelated. This autocorrelation was partly due to detecting individuals acoustically over large distances (‘acoustic autocorrelation’), and partly due to the large size of groups/aggregations of sperm whales. For example, based on a small sample of tracks, I estimated that sperm whales could be detected at a maximum of 23 km. This range is close to the maximum detected by Leaper et al. (1992) of 28 km using similar methods to estimate the distance to sperm whales. The advantage of estimating the distance of each sperm whale to the trackline is that any sperm whales further than half the segment length (and therefore out of range of the environmental variables) could be excluded. However, the extraction of all sperm whale tracks, and the subsequent estimation of the distance of sperm whales to the track line is a time consuming task (around a month per survey of track data) and was not possible in this study. Instead, an alternative objective ‘rule’ that removed some of the ‘acoustic autocorrelation’ was applied. Although this reduced the amount of autocorrelation resulting from hearing the same animal over several segments, it was unlikely to have removed it completely.

Sperm whale distributions remained autocorrelated despite removal of much of the ‘acoustic autocorrelation’. This is because the sperm whales were aggregated into large groups, which were sometimes dispersed over 60 km within the Rockall Trough. This is comparable to the size of ‘super-aggregations’ of sperm whales detected within the Gulf of California with sizes of 55-75 km (Jaquet & Gendron 2002). They found that sperm whales formed these ‘super-aggregations’ at times of high squid abundance, so hypothesised that they may be aggregating on prey. These aggregations may therefore be a simple aggregation of sperm whales in areas of high squid abundance, and may explain the ‘batchelor herds’ of pre-breeding males observed by Best (1979).

Applying the first of the cross-validation methods recommended by Araujo & Guisan (2006), there was no apparent overfitting of the model to the survey data, since the model performed well on both the training and test set at predicting sperm whale occurrence over the whole surveyed *extent* (Figure 3.5d). However, when model selection and cross-validation was carried out on the two different *extents* only depth remained significant at explaining sperm whale occurrence in both areas. In addition, the estimated smooths for the two different *extent* were different, with a drop off in depth preference above 1200 m in the Faroe-Shetland Channel, but a continuing increasing preference for waters >1200 m (to the maximum depth surveyed 2374 m) in the Rockall Trough (Figures 3.7 & 3.8). A narrower and lower range of depths was surveyed in the FSC in comparison to the RT. This is mainly due to the relatively low availability of deep water within the FSC rather than a survey bias.

Incomplete sampling of a species environment parameter space has been highlighted as one of the main issues in trying to model species distributions (Guisan & Thuiller 2005; Peterson & Cohoon 1999). For example, Randin et al. (2006) found that only 68% of the models they fitted to Alpine and sub-Alpine plant species in Switzerland could not explain their distribution within Austria. This was hypothesised to be partly due to different ranges of environmental variables available to the species in either area. Nevertheless, developing models for different areas or *extents* does allow for those variables that are key to the distribution of a species to be highlighted. For example, Jimenez (2005) modelled the habitat preferences of West Indian manatees (*Trichechus manatus*) in two different areas: Costa Rica and Nicaragua, finding that although the species had different habitat preferences in each area, they consistently preferred lagoons regardless of area.

In this study, depth was highlighted as the main predictor of sperm whales off the west coast of Scotland, and therefore has the best promise of predicting sperm whale occurrence outwith the surveyed *extent*. However, the fact that the smooth is different between different *extents* cautions against any attempts to try and apply the model elsewhere. Of the two relationships between sperm whale occurrence and depth, the smooth based on the Ellet Line data performs well on predicting both survey areas (Faroe-Shetland Channel & Ellet Line). It is therefore likely to be the more accurate of the two smooths at predicting the sperm whale's relationship with depth. Other than depth, the majority of the ranges of the remaining variables included in the model selection for either area were also significantly different (Table 3.2). It is likely that the different oceanographic regimes within the two areas result in a different distribution of squid prey. In addition, the Wyville-Thompson Ridge forms a clear barrier between the deep water fauna of the Faroe-Shetland Channel and the Rockall Trough (Bett 2001), which is likely to result in different species of deep water squid being available in either area. Both these factors may explain the selection of different environmental variables in explaining sperm whale occurrence in the two areas.

Finally, examining a different *grain* size (or what is commonly thought of as 'scale') does not appear to have a major effect on the model selection over the *grain* sizes analysed in this study. At both the 9 km and 18 km *grain* sizes, the first two variables selected (depth and thermocline strength) and their smooths were very similar. Fewer variables were selected at the larger *grain* size, but it is not known whether this is due to the smaller sample size, or due to sperm whales reacting only to relatively fine scale changes in thermocline strength. That the same variables were selected at both *grain* sizes is perhaps not surprising given that the large scale at which some oceanographic processes have been shown to influence sperm whales is of the order of hundreds of kilometres (Jaquet & Whitehead 1996). Jaquet & Whitehead (1996) found that sperm whales related to steep topography and secondary productivity at *grain* sizes of 320-640 nm (equivalent of 600-1200 km), but they analysed sperm whales over the whole Pacific Ocean. In this study, since aggregations could be of the order of 60 km, it is likely that a change in preference would be highlighted at a scale larger than the size of an aggregation, say 100 km. However, the *extent* of the study was not sufficiently large to permit this analysis.

One consequence of increasing the *grain* size was that the autocorrelation remaining in the residuals was reduced by around half that in the original *grain* size. However, none of the models were able to fully model the autocorrelation within the data, since the residuals of all the models were significantly non-random. This would suggest that there is either an environmental variable missing from the model on which the sperm whales are aggregating (e.g. prey distribution), or another variable to explain the aggregation of whales (e.g. social cohesion). Methods such as Generalised Estimating Equations (GEEs – Hardin & Hilbe 2003) allow for any autocorrelation remaining in the residuals to be modelled, and may be worth further investigation in the future.

3.4.2 Habitat preferences of sperm whales off the west coast of Scotland

All models found depth to be the most important predictor of sperm whale occurrence, with more sperm whales detected in deep water off the shelf edge (Figure 3.5), than in shallow waters. Sperm whales are usually found in deep water off the west coast of Scotland (Evans 1997; Macleod et al. 2003; Mendes 2007; Skov et al. 1995; Weir et al. 2001), and elsewhere in the world (Baumgartner et al. 2001; Cañadas et al. 2005; Davis et al. 1998; Davis et al. 2002; Gregr & Trites 2001; Hamazaki 2002; Kaschner 2004; Kenney & Winn 1986; Whitehead et al. 1992). This preference is strongly influenced by the location of sperm whale prey, predominantly comprising mesopelagic and bathypelagic cephalopods (Evans & Hindell 2004; Martin & Clarke 1986; Santos et al. 1999; Santos et al. 2002; Simon et al. 2003; Smith & Whitehead 2000). Little is known about the ecology of deep water species of cephalopod off the west coast of Scotland, but there is evidence that a wide range of deep water species occur in this area (Collins et al. 2001).

Thermocline strength was the second most important predictor of sperm whale occurrence off the west coast of Scotland, with sperm whales associating with weak thermoclines (Figures 3.5 & 3.7). Thermocline depth and strength have been used in other studies of sperm whales as an indicator of the presence of eddies or ‘cyclones’ to confirm that sperm whales were associating with these features (Baumgartner et al. 2000; Davis et al. 1998). However, off the west coast of Scotland the weakest thermoclines were found along the shelf, shelf edges, upper Rockall Trough, and around the Wyville-Thompson Ridge (Appendix Figure A1.1). This is likely to be indicative of mixing that occurs around the steeper slopes of the shelf edges, and around some of the complex topography that dominates the region (Mann & Lazier 2006). Similarly Burrows & Thorpe (1999) found that dispersal of surface NAW water into deeper waters occurs at topographical irregularities such as the Anton Dohrn seamount. This is considered a downwelling area, and hypothesised to be the ideal conditions for the development of deep water fauna due to the increased supply of macrozooplankton and dissolved oxygen supplied from the surface (Berzin 1971).

To my knowledge, this is the first study of sperm whales to investigate the effect of halocline depth and strength on sperm whale distribution, but it has been used in the study of other species distributions (Mehlum et al. 1998; Tynan et al. 2005). For example, in a study of thick-billed murres (*Uria lomvia*) in the Berents Sea, the largest aggregations of birds were found over strong shallow haloclines associated with frontal zones (Mehlum et al. 1998). In my study, both halocline depth and strength were significant in explaining the occurrence of sperm whales in the Faroe-Shetland Channel survey data, but not for sperm whales in the Rockall Trough. Sperm whales were found in areas with strong deep negative haloclines (surface water saltier than the bottom water). This deep strong halocline is characteristic of the deep waters of the Faroe-Shetland Channel, where the salty Gulf Stream NAW water at the surface flows north over the south flowing deep fresh Norwegian Sea Deep Water (NSDW: Turrell et al. 1999). Little is known about the ecology of deep living squid in this area, though it does form the southern part of the range of one of the key sperm whale prey species, *Gonatus fabricii* (Bjorke 2001; Pierce et al. 2004; Santos et al. 1999).

Surface oceanographic features have been used to identify biological hotspots (Issue 53 Deep Sea Research II 2006; Ballance et al. 2006) and foraging areas of marine mammals (Polovina et al. 2001; Worm et al. 2005). In other studies, sea surface temperature was correlated with sperm whale occurrence (Cañadas et al. 2005; Davis et al. 1998; Hamazaki 2002; Mendes 2007; Smith & Whitehead 1993; Whitehead et al. 1989). In my study, SST was also significant in explaining the occurrence of sperm whales in the Rockall Trough and, in common with the other studies, sperm whales preferred cooler waters (Figure 3.8). In waters around the Galapagos Islands a preference for colder surface waters was believed to be linked with upwelling events (Smith & Whitehead 1992). However, off the west coast of Scotland there is no known upwelling, the coolest surface waters being associated with the Modified North Atlantic Water (MNAW) on the Faroe Plateau side of the Faroe-Shetland Channel, and in the waters around the Wyville-Thompson Ridge, Faroe Bank and Bill-Baileys Bank. Based on examination of chlorophyll satellite images, this area's complex topography appears to promote productivity.

Chlorophyll was also a significant predictor of sperm whales in the Rockall Trough being found in areas of high chlorophyll (Figure 3.8). Since primary productivity indicators such as chlorophyll are indirect indicators of productivity up the trophic chain, correlations are often only found at a large scale or *grain* size (Guinet et al. 2001). This is due to the time lag between a peak in primary productivity and a peak in squid prey of around 4 months and several hundred kilometres (Vinogradov 1955). In areas where oceanography does not aggregate this productivity, areas of high prey concentrations for whales can be displaced by several hundred kilometres (Jaquet 1996). However, in this study a positive relationship between sperm whale occurrence and chlorophyll was found at a relatively small scale, suggesting that oceanographic processes do aggregate this productivity within defined locations at which squid also aggregate in the Rockall Trough.

The final significant variable at explaining distributions of sperm whales in both the Faroe-Shetland Channel and the Rockall Trough was sea surface salinity (SSS). The relationships with SSS were different within the Rockall Trough and the Faroe-Shetland Channel. There was a clear preference for areas with mainly high salinity in the Rockall Trough, but a bimodal preference for both low and high salinity in the Faroe-Shetland Channel (Figures 3.7 & 3.8). This preference can be explained by the different water masses found in the surface waters off the west coast of Scotland. The Rockall Trough surface water is dominated by the warm salty Gulf Stream (North

Atlantic Water NAW) water, whereas the Faroe-Shetland Channel has both the warm salty NAW water mainly on the eastern side of the channel, and the cooler fresher Modified NAW (MNAW) water on the Faroese side of the channel (Turrell et al. 1999). The bimodal preference shows a main preference for fresher waters and a smaller preference for salty waters, perhaps reflecting preference mainly for the fresher MNAW side of the Faroe-Shetland Channel, and to a lesser extent the saltier Gulf Stream NAW side of the channel.

Overall, the environmental variable were able to explain up to 36.6% of the deviance, which is a high proportion in comparison to other studies of cetacean species (Ferguson et al. 2006a; Ferguson et al. 2006b), and similar to other habitat models of sperm whales (Gregr and Trites 2001; Mendes 2007). This was mainly due to their clear preference for deep water, with depth explaining around 22% of the deviance, and the other environmental variables only explaining 2% - 6% individually (Appendix Table A2.1-2). This is may be due to the fact that within their deep water habitat, sperm whales are relatively evenly distributed throughout the surveyed area. This is partly due to detecting sperm whales both during travel and foraging activity, the latter more likely to be associated with prey habitat. Identification of foraging habitat through analysis of feeding buzzes or ‘creaks’ (Miller et al. 2004) may allow for increased explained deviance, however in this study too few ‘creaks’ were obtained to allow such an analysis (Mendes 2007).

Overall, these results suggest that sperm whales are using the west coast of Scotland as a foraging ground, rather than solely as a migration route between high latitude feeding and low latitude breeding grounds. There is also some evidence for this hypothesis from the acoustic data itself, because feeding buzzes or ‘creaks’ were detected on several occasions (Mendes 2007), which have been associated with foraging behaviour (Miller et al. 2004). Further evidence from the analysis of sperm whale teeth from around Scotland, suggests that young pre-breeding males tend to stay within more temperate zones to feed before moving to the higher latitude productive feeding grounds shortly before approaching breeding age (Mendes et al. 2007).

3.4.3 Conclusions

This study has investigated the effects of both *extent* and *grain* size on the modelling of sperm whale occurrence off the west coast of Scotland. It found that depth was the most important predictor of sperm whale occurrence, with sperm whales found preferentially in off-shelf deep water. This preference for depth and the preference for weak thermoclines were consistent over different *grain* sizes, and can be considered ‘robust’ over *grain* sizes analysed within the *extents* analysed. No variables were spatially robust, so the models should not be used to extrapolate predictions into other areas. Finally, halocline strength was only important at explaining sperm whale occurrence within the *extent* and 9 km *grain* size, with a preference for strong negative haloclines. These environmental variables and the aggregations of whales support the hypothesis that the west coast of Scotland forms a foraging ground for pre-breeding male sperm whales.

3.4.4 Further work

The main challenge with passive survey data collected on the distribution of sperm whales is the problem of autocorrelation. Both sources of autocorrelation – ‘acoustic’ and ‘aggregative’ – would benefit from further analysis. Firstly, ‘acoustic autocorrelation’ could be removed completely if the distance to the track line was estimated for every sperm whale, or if alternative objective ‘rules’ were developed to further reduce the effect of hearing the same whale over several segments. Such rules save analysis time in comparison to analysing every single track and estimating the time abeam and distance to the trackline, at least until more automated methods have been developed.

Secondly, although a wide range of oceanographic variables were included in this model; there was still remaining autocorrelation in the model residuals. Generalised Estimating Equations (GEEs – Hardin & Hilbe 2003) show some promise as a method of modelling the autocorrelation after the environmental variables have been fitted. This allows the environmental variables to explain as much of the autocorrelation as they are able, while ensuring that all residual autocorrelation is also modelled.

3.5 References

Aarts, G. 2006. Modelling space-use and habitat preference from wildlife telemetry data. PhD Thesis. School of Biology. University of St Andrews.

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

Bailey, H. 2006. Distribution and habitat use of bottlenose dolphins (*Tursiops truncatus*) at varying temporal and spatial scales. PhD Thesis. Department of Zoology. University of Aberdeen.

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

Baumgartner, M. F., K. Mullin, L. N. May, and T. D. Leming. 2001. Cetacean habitats in the northern Gulf of Mexico. Fishery Bulletin **99**:219-239.

Bell, M., J., R. M. Forbes, and A. Hines. 2000. Assessment of the FOAM global assimilation system for real-time operational ocean forecasting. Journal of Marine Systems **25**:1-22.

Berrow, S. D., and E. Rogan. 1997. Review of cetaceans stranded on the Irish coast, 1901-95. Mammal Review **27**:51-76.

Berzin, A. A. 1971. The sperm whale. Yablokov, A. V. (ed), Pischevaya Promyshlenmost; translation by Israel Program for Scientific Translations, Moscow. As cited in Jaquet (1996).

Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn, and B. L. Olla, editors. Behaviour of marine mammals. Plenum Press, New York.

Bett, B. J. 2001. UK Atlantic Margin Environmental Survey: Introduction and overview of bathyl benthic ecology. Continental Shelf Research **21**:917-956.

Bjorke, H. 2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. Fisheries Research **52**:113-120.

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

Burnham, K. P., and D. R. Anderson 2002. Model selection and multimodel inference. A practical information-theoretic approach. Springer-Verlag, New York.

Burrows, M., and S. A. Thorpe. 1999. Drifter observations of the Hebrides slope current and nearby circulation patterns. Annales Geophysicae **17**:280-302.

Cañadas, A., R. Sagarminaga, R. De Stephanis, E. Urquiola, and P. S. Hammond. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conserv: Mar. Freshw. Ecosyst. **15**:495-521.

Collins, M. A., C. Yau, L. Allcock, and M. Thurston. 2001. Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom **81**:105-117.

Cumming, G. S. 2000. Using between-model comparisons to fine-tune linear models of species ranges. Journal of Biogeography **27**:441-455.

Davis, R. W., G. S. Fargion, L. N. May, T. D. Leming, M. F. Baumgartner, W. E. Evans, L. J. Hansen, and K. Mullin. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. Marine Mammal Science **14**:490-507.

Davis, R. W., J. G. Ortega-Ortiz, C. A. Ribic, W. E. Evans, D. C. Biggs, P. H. Ressler, R. B. Cady, R. R. Leben, K. D. Mullin, and B. Wursig. 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. Deep-Sea Research I **49**:121-142.

Douglas, L. A., S. M. Dawson, and N. Jaquet. 2005. Click rates and silences of sperm whales at Kaikoura, New Zealand. J. Acoust. Soc. Am. **118**:523-529.

Evans, K., and M. A. Hindell. 2004. The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters. ICES Journal of Marine Science **61**:1313-1329.

Evans, P. G. H. 1997. Ecology of sperm whales (*Physeter macrocephalus*) in the Eastern North Atlantic, with special reference to sightings & strandings records from the British Isles. Bulletin de l'Institut Royal des Sciences Naturelle de Belgique: Biologie **67-Suppl.**:37-46.

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

Ferguson, M. C., J. Barlow, P. Fiedler, S. B. Reilly, and T. Gerrodette. 2006. Spatial models of delphnid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling **193**: 645-662.

Ferguson, M. C., J. Barlow, S. B. Reilly, and T. Gerrodette. 2006. Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean. Journal of Cetacean Research and Management **7**(3): 287-299.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Fielding, A. H., and P. F. Haworth. 1995. Testing the generality of bird-habitat models. Conservation Biology **9**:1466-1481.

Gannier, A., V. Drouot, and J. C. Goold. 2002. Distribution and relative abundance of sperm whales in the Mediterranean Sea. Marine Ecology Progress Series **243**:281-293.

Gannier, A., and E. Praca. 2007. SST fronts and the summer sperm whale distribution in the north-west Mediterranean Sea. Journal of the Marine Biological Association of the UK **87**:187.

Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the RSV Aurora Australis. Report of the International Whaling Commission **47**:897-907.

Gontarek, S. 2005. STJG Tools for ArcGIS v9 - GIS Extract, SAMS, Dunstaffnage, Oban.

Gordon, J. C. D., J. N. Matthews, S. Panigada, A. Gannier, J. F. Borsani, and G. Notarbartolo Di Sciara. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. Journal of Cetacean Research and Management **2**:27-36.

Gordon, J. C. D., and L. Steiner. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. Report of the International Whaling Commission **42**:561-565.

Gregr, E. J., and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Colombia. Canadian Journal of Fisheries and Aquatic Sciences **58**:1265-1285.

Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J.-P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographical information systems. Marine Ecology Progress Series **219**:251-264.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Hamazaki, T. 2002. Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). Marine Mammal Science **18**:920-939.

Hardin, J. W., and J. M. Hilbe 2003. Generalized Estimating Equations. Chapman & Hall/CRC.

Hastie, G. D., R. J. Swift, J. C. D. Gordon, G. Slesser, and W. R. Turrell. 2003. Sperm whale distribution and seasonal density in the Faroe Shetland Channel. Journal of Cetacean Research and Managment **5**:247-252.

Hedley, S. 2000. Modelling heterogeneity in cetacean surveys. PhD Thesis. Department of Statistics. University of St Andrews.

Jaquet, N. 1996. How spatial and temporal scales influence understanding of Sperm Whale distribution: a review. Mammal Review **26**:51-65.

Jaquet, N., and D. Gendron. 2002. Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. Marine Biology **141**:591-601.

Jaquet, N., and H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series **135**:1-9.

Jimenez, I. 2005. Development of predictive models to explain the distribution of the West Indian manatee *Trichechus manatus* in tropical watercourses. Biological Conservation **125**:491-503.

Kaschner, K. 2004. Modelling and mapping resource overlap between marine mammals and fisheries on a global scale. PhD Thesis. Department of Zoology. The University of British Columbia.

Kenney, R. D., and H. E. Winn. 1986. Cetacean high-use habitats of the NE US continental shelf. Fishery Bulletin **84**:345-357.

Leaper, R., O. Chappell, and J. Gordon. 1992. The development of practical techniques for surveying sperm whale populations acoustically. Report of the International Whaling Commission **42**:549-560.

Leaper, R., D. Gillespie, and V. Papastavrou. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. J. Cetacean Res. Manage. **2**:187-196.

Macleod, K., M. P. Simmonds, and E. Murray. 2003. Summer distribution and relative abundance of cetacean populations off north-west Scotland. Journal of the Marine Biological Association of the United Kingdom **83**:1187-1192.

Mann, K. H., and J. R. N. Lazier 2006. Dynamics of marine ecosystems (3rd Edition). Blackwell Scientific Publications, Cambridge.

Martin, A. R., and M. R. Clarke. 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. Journal of the Marine Biological Association of the United Kingdom **66**:779-790.

Mehlum, F., G. L. J. Hunt, M. B. Decker, and N. Nordlund. 1998. Hydrographic features, cetaceans and foraging of thick-billed murres and other marine birds in the Northwestern Barents Sea. Arctic **51**:243-252.

Mehlum, F., G. L. H. Jr, Z. Klusek, and M. B. Decker. 1999. Scale-dependent correlations between the abundance of Brunnich's guillemots and their prey. Journal of Animal Ecology **68**:60-72.

Mendes, S. 2007. Male sperm whales (*Physeter macrocephalus*) in the Northeast Atlantic: Insights into movements, distribution and foraging ecology. PhD Thesis. Department of Zoology. University of Aberdeen.

Mendes, S., J. Newton, R. J. Reid, A. F. Zuur, and G. J. Pierce. 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. Oecologia **151**:605-615.

Miller, P. J. O., M. P. Johnson, and P. L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. Proceedings of the Royal Society of London B **271**: 2239-2247

Moscrop, A. 1997. Cetaceans of the North-East Atlantic Fringe. Page 46. Greenpeace UK.

Moses, E., and J. T. Finn. 1997. Using Geographical Information Systems to Predict North Atlantic Right Whale (*Eubalaena glacialis*) Habitat. J. Northw. Atl. Fish. Sci. **22**:37-46.

O'Cadhla, O., M. Mackey, N. Aguilar de Soto, E. Rogan, and N. Connolly. 2004. Cetaceans and Seabirds of Ireland's Atlatnic Margin. Volume II - Cetacean distribution & abundance. Page 82. Report on research carried out under the Irish Infrastructure Prograp (PIP): Rockall Studies Group (RSG) projects 98/6 and 00/13, Porcupine Studies Group project P00/15 and Offshore Support Group (OSG) project 99/38.

Osborne, P. E., and S. Suarez-Seoane. 2002. Should data be partitioned spatially before building large-scale distribution models? Ecological Modelling **157**:249-259.

Papastavrou, V., S. C. Smith, and H. Whitehead. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. Canadian Journal of Zoology **67**:839-846.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling **133**:225-245.

Peterson, A. T., and K. P. Cohoon. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. Ecological Modelling **117**:159-164.

Pierce, G. J., M. B. Santos, E. Mente, J. Wang, G. Stowasser, and P. R. Boyle. 2004. An overview of cephalopods relevant to the SEA4 area. Strategic Environmental Assessment - SEA4. Department of Trade & Industry.

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

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

Rendell, L., H. Whitehead, and R. Escribano. 2004. Sperm whale habitat use and foraging success off northern Chile: evidence of ecological links between coastal and pelagic systems. Marine Ecology Progress Series **275**:289-295.

Rose, G. A., and W. C. Leggett. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. Ecology **71**:33-43.

Santos, M. B., G. J. Pierce, P. R. Boyle, R. J. Reid, H. M. Ross, I. A. Patterson, C. C. Kinze, S. Tougard, R. Lick, U. Piatkowski, and V. Hernandez-Garcia. 1999. Stomach contents of sperm whales Physeter macrocephalus stranded in the North Sea 1990-1996. Marine Ecology Progress Series **183**:281-194.

Santos, M. B., G. J. Pierce, M. G. Hartmann, C. Smeenk, M. J. Addink, T. Kuiken, R. J. Reid, I. A. P. Patterson, C. Lordan, E. Rogan, and E. Mente. 2002. Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom **82**:501-507.

Schneider, D. C., and J. F. Piatt. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Marine Ecology Progress Series **32**:237-246.

Sherwin, T. J., W. R. Turrell, D. R. G. Jeans, and S. Dye. 1999. Eddies and a mesoscale deflection of the slope current in the Faroe-Shetland Channel. Deep-Sea Research I **46**:415-438.

Sherwin, T. J., M. O. Williams, W. R. Turrell, S. L. Hughes, and P. I. Miller. 2006. A description and analysis of mesoscale variability in the Faroe-Shetland Channel. Journal of Geophysical Research **111**:1-17.

Simon, M. J., T. K. Kristensen, O. S. Tendal, C. C. Kinze, and S. Tougaard. 2003. *Gonatus fabricii* (Mollusca, Theuthida) as an important food source for sperm whales *(Physeter macrocephalus)* in the Northeast Atlantic. Sarsia **88**:244 - 246.

Skov, H., J. Durinck, F. Danielsen, and D. Bloch. 1995. Co-occurrence of cetaceans and seabirds in the Northeast Atlantic. Journal of Biogeography **22**:71-88.

Smith, S. C., and H. Whitehead. 1993. Variations in the feeding success and behaviour of Galapagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. Canadian Journal of Zoology **71**:1991-1996.

Smith, S. C., and H. Whitehead. 2000. The diet of Galapagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. Marine Mammal Science **16**:315-325.

Thuiller, W., L. Brotons, M. B. Araujo, and S. Lavorel. 2004. Effects of restricting environmental range of data to project current and future species distributions. Ecography **27**:165-172.

Turrell, W. R., G. Slesser, R. D. Adams, R. Payne, and P. A. Gillibrand. 1999. Decadal variability in the composition of Faroe Shetland Channel bottom water. Deep-Sea Research I **46**:1-25.

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

Vinogradov, M. E. 1955. Vertical migrations of zooplankton and their role in feeding of the deepwater pelagic fauna. Trudy IO AN SSSR, Vol. 13. As cited in Jaquet (1996).

Watwood, S. L., P. J. O. Miller, M. Johnson, P. T. Madsen, and P. L. Tyack. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). Journal of Animal Ecology **75**:814-825.

Weir, C. R., C. Pollock, C. Cronin, and S. Taylor. 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. Continental Shelf Research **21**:1047-1071.

Whitehead, H., S. Brennan, and D. Grover. 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology **70**:912-918.

Whitehead, H., V. Papastavrou, and S. C. Smith. 1989. Feeding success of sperm whales and sea-surface temperatures off the Galapagos Islands. Marine Ecology Progress Series **53**:201-203.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

Wood, S. N. 2006. The mgcv package. R statistical group.

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

Chapter 4

Predictive models of harbour porpoise *Phocoena phocoena* distribution in the Inner Hebrides, Scotland

Evaluating the effect of survey technique, time and space on model robustness

Abstract

The aim of this study was to investigate the effect of survey technique, time and space on predictive models of harbour porpoise (*Phocoena phocoena*) distribution in the Inner Hebrides, off the west coast of Scotland. Monthly visual (2003-2005) and passive acoustic (2004-2005) surveys were conducted from the Hebridean Whale and Dolphin Trust motor-sailor, *Silurian*, in the Inner Hebrides, Scotland. Generalised Additive Models were used to relate the relative density of harbour porpoises to temporal, tidal and topographical covariates. GAMs were built separately for: (i) the visual and acoustic survey data, (ii) each year and combinations of years (2003-2005) with visual survey data, and (iii) two areas with visual survey effort in 2005: the southern Inner Hebrides, and the whole of the Inner Hebrides. Predictions were made over the survey area and compared visually for similarities. Visual detection rates were most influenced by sea state, with detections decreasing above sea state 1. Acoustic detection rates were most influenced by high frequency ambient noise levels, with detection rates decreasing with increasing noise levels. After compensating for these survey effects, different environmental variables were selected for each data set. Although the best visual and acoustic models used different environmental variables, the predicted distribution maps were very similar with overlapping ‘hotspot’ areas (this is partly because the environmental variables selected were strongly correlated). Comparing models of visual detection rates over years, the same key variables were selected consistently: namely maximum tidal current, and position in the spring-neaps cycle. Harbour porpoises were detected to a greater extent in areas of low tidal currents at spring tides. This indicates models were robust between years. However, when models of visual detection rates were compared between areas, different variables were selected with the most important predictor changing from maximum tidal current to spring tidal range. Harbour

porpoises were detected more in areas of high tidal range when areas north of Skye were included in the models. In conclusion, high use areas were predicted consistently over time within the southern Inner Hebrides regardless of survey technique. However, caution should be exercised when trying to extrapolate beyond the surveyed *extent*. It is hoped that this model could be used to mitigate noise threats to harbour porpoises in the Inner Hebrides.

4.1 Introduction

Predictive models of cetacean distribution are usually based on data obtained using visual survey techniques such as those recommended by Buckland et al. (2001). However, increasingly passive acoustic survey techniques have been used to gain a better understanding of a species distribution, especially for those species that are difficult to see, such as harbour porpoises (Bailey 2006; Gillespie et al. 2005; Gridley 2005). The merits of passive acoustic methods for understanding species distributions can be quite compelling, with detection rates for harbour porpoises over 8 times higher that for visual methods due to the ability to survey even in poor sea states (Gillespie et al. 2005). The use of acoustic data within predictive or habitat models is increasing, though still relatively limited (Bailey 2006; Gannier & Praca 2007; Gridley 2005; Hastie et al. 2005). For harbour porpoises, habitat modelling based on acoustic survey data is limited to only a handful of studies (Bailey 2006; Gridley 2005). Both these studies combined visual with acoustic detections of porpoises and modelled all detections together without first compensating for the different survey effects likely to influence detection rates. Although survey influences have been investigated for visual survey methods especially in relation to harbour porpoises (Barlow et al. 2001; Palka 1996; Palka & Hammond 2001), there have been few studies that examined the survey effects inherent in acoustic survey techniques (Gordon et al. 2000; Hastie et al. 2005), and none for harbour porpoises. However, with visual and acoustic survey techniques using very different detection modalities and methodologies the survey effects are likely to be quite different. It would seem imprudent to combine data subject to different influences (whether due to the environment or due to animal behaviour) without some understanding of the influences involved.

There are methods to ensure predictive model robustness both over time and space (Araujo & Guisan 2006). Methods detailed by Araujo & Guisan (2006) suggest building the model on a ‘training’ data set, and evaluating the model on a ‘test’ data set that can comprise either (i) sampled data to predict within the same region and time; (ii) a different region; (iii) a different time period. Most studies evaluate predictive models using only one of the three suggested evaluation techniques (Ferguson et al. 2006; Forney 2000; Gregr & Trites 2001; Hamazaki 2002; Hastie et al. 2005; Jimenez 2005; Moisen & Frescino 2002; Moses & Finn 1997). The favoured method for marine mammal predictive models tends to use data from a different year as a test data set (Ferguson et al. 2006; Forney 2000; Hamazaki 2004; Hastie et al. 2005), or a different area (Jimenez 2005; Moses & Finn 1997). Only one study has been found in the marine mammal literature in which random samples were taken from the original data set (for the same area and time) to evaluate the predictive models (Gregr & Trites 2001).

Each evaluation technique evaluates a different aspect of the model robustness: testing on a sample from within the same dataset checks for model over-fit for that area and time; testing on a different area evaluates the ability of a model to predict species distributions into other areas; and testing on a different time period evaluates the ability of a model to predict species distributions through time. A search of the literature found no examples of models that have been evaluated on all these three scales, yet for a model to be robust over time and space, it is essential to evaluate the model performance on these three criteria.

The focal species of this study is the harbour porpoise, which is the most common cetacean species in coastal areas off the west coast of Scotland (MacLeod et al. 2007; Macleod 2001; Weir et al. 2001). The Inner Hebrides is also home to one of the highest densities of harbour porpoise in Europe (SCANS-II 2006). However, there are a number of threats to harbour porpoises in the area, the most important of which is noise pollution (Parsons et al. 2000b). The main sources of noise pollution to harbour porpoises on the west coast of Scotland are: (i) boat traffic; (ii) acoustic deterrent devices used on fish farms to scare seals; and (iii) military activities (Parsons et al. 2000b).

Acoustic deterrent devices (ADDs) are used extensively on salmon farms throughout the west coast of Scotland to deter seals (Gordon & Northridge 2002; Quick et al. 2002). They transmit pulses of loud (191-200 dB re 1μPa @ 1m) sounds at frequencies between 2.5-100 kHz, though more typically between 8-15 kHz (Gordon & Northridge 2002). These sounds are within harbour porpoise hearing range (Richardson et al. 1995), and have been shown to deter harbour porpoises from their habitat (Johnston 2002; Olesiuk et al. 2002). For example, harbour porpoise abundance decreased significantly at ranges over 3.5 km from an active ADD in Retreat Passage, British Columbia (Olesiuk et al. 2002). Within the Sound of Mull, part of the focal area studied in this chapter, several different types of ADDs have been deployed (Götz pers. comm.), which could be heard on the hydrophone for several kilometres (pers. obs.). The Sound of Mull is used extensively by harbour porpoises (Mandleberg et al. in review), although it is not known to what extent harbour porpoises are affected by ADDs within this area.

With respect to the last of the noise threats on the west coast of Scotland, much of the entire west coast of Scotland, both coastal and offshore, is an important training ground for the military. Every year since 1946, NATO has conducted Joint Maritime Course (JMC) training exercises three times a year in March, July and November (Parsons et al. 2000a). These activities increase underwater noise levels due to increased boat traffic, submarine activity, military jets, and sonar activity. Parsons et al. (2000a) suggested that a decrease in sightings of harbour porpoises and minke whales (*Balaenoptera acutorostrata*) observed around Gairloch and the Small Isles during the JMC training exercises may be attributed to these increased noise levels.

Predictive distribution maps of harbour porpoise distribution can be used to determine the relative risk of noise threats such as ADDs and military activities in different areas, locating lower density areas where risks can be minimised. One purpose of this analysis was therefore to produce and test the reliability of predictive maps for harbour porpoise distributions in the coastal waters off the west coast of Scotland. The task was divided into the following aims: (i) to investigate the differences between models obtained using visual versus acoustic survey data collected for harbour porpoises in the Inner Hebrides; (ii) to investigate the temporal robustness; and (iii) to investigate the spatial robustness of predictive models of harbour porpoise distribution in the Inner Hebrides.

4.2 Methods

4.2.1 Data collection

Systematic visual cetacean surveys were carried out on a monthly basis from the Hebridean Whale and Dolphin Trust (HWDT) motor-sailor research vessel, *Silurian*, in the Inner Hebrides, Scotland (55°14’-58°25’N, 5°26’-7°43’W) over 3 consecutive summers from 2003-2005. Passive acoustic surveys were carried out simultaneously with the visual surveys during the later two summers from 2004-2005. At least once a month the core study area around the Argyll Islands (55°18-56°51N, 5°26’-7°25’W) was surveyed in a zag-zag type survey design with the aim of covering the area fairly evenly over a period of ten days given the constraints of weather conditions and location of ports. Additional surveys were occasionally conducted outwith the Argyll Islands, covering the Small Isles in 2003 & 2004 (up to 57°8’N), and the entire Inner Hebrides in several surveys in 2005 (up to 58°25’N and out to 7°43’W) (Figure 4.1).

The surveys were carried out at an average speed of 6 knots, under motor when winds were low, and under sail when winds were sufficiently high enough. Visual observations were carried out from the front deck (2m above sea level) in Beaufort sea state ≤ 3, by teams of trained volunteers. Two observers were positioned on the front deck searching the water from -5° to 90° of the transect line on either side of the vessel by eye and with 7 x 50 binoculars (Marine Opticron). If any cetaceans were spotted, the distance, bearing (using an angle board), heading of the group/individual, species, group size and behaviour was recorded directly into a computer running the International Fund for Animal Welfare (IFAW) software Logger 2000. Visual observers switched sides after 30 minutes, and the watch was changed every hour to avoid observer fatigue. Occasionally, deviations were made from the trackline in order to take photo-id pictures, during which time the effort was recorded as ‘with whales’ and excluded from analysis. Subsequently, the vessel would return to the trackline and effort changed back to ‘on-effort’. All effort was recorded directly to an Access database via Logger 2000.

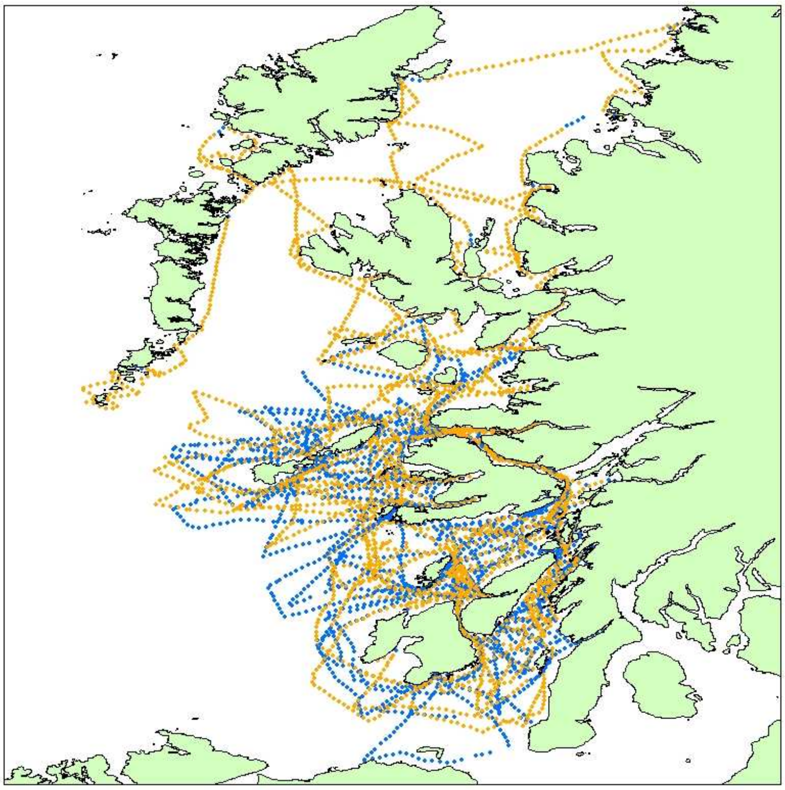


Figure 4.1 – Survey effort showing the mid-points of all 2 km segments with visual survey effort (blue dots) and all 2 km segments with visual and acoustic survey effort (orange dots) in the Inner Hebrides, off the west coast of Scotland during 2003-2005.

Passive acoustic monitoring was carried out in all sea states in sea depths of > 10 m using an automatic porpoise detection system (Gillespie & Chappell 2002), designed to detect the high frequency echolocation clicks of harbour porpoises. The hydrophone system is based on systems described by Leaper et al. (1992) and Chappell et al. (1996). Gillespie & Chappell (2002) later adapted the Chappell system to allow two hydrophone elements to be used, so that click bearing and range can be estimated. The array comprised two high frequency hydrophone elements (HS150 ball hydrophones, Sonar Products Ltd.) with highest sensitivity at 150 kHz. The hydrophone elements were positioned very close to custom-built pre-amplifiers (for circuit diagram and description see IFAW 2003). Pre-amplifiers were potted within a copper tube to provide an electrical screen (i.e. protect the amplifier circuit from electromagnetic noise). The pre-amplifiers were set up to provide a gain of around 40 dB. The hydrophones were placed 3 m apart and sealed within a 35 mm diameter oil-filled polyeurythane tube, and were towed 100 m behind the vessel on a Kevlar-strengthened towing cable.

The signal from each hydrophone element was brought back into a ‘porpoise detection box’ (Seiche Electronics), and split into three separate frequency bands. These frequency bands covered the porpoise band 115-145 kHz, and two control noise bands centred at 50 and 75 kHz. Within each band the signal envelope was traced, digitised and passed to the ‘Porpoise Detector’ software for automatic click detection (Gillespie & Chappell 2002). The Porpoise Detector software detects a ‘click’ whenever the envelope traced level on any one of the three frequency bands rises above a threshold amplitude value. For each click the envelope traces for all four channels (the 125 kHz band from both elements, and the 75 & 50 kHz bands from just one element) are saved, along with the click start time in a binary data file that can be exported to an external database (Gillespie & Chappell 2002). The software is also able to calculate the bearing (with no left or right discrimination) to clicks based on the difference in the arrival time of each click at each hydrophone element. The bearing estimate is subject to some error, being more accurate for sounds perpendicular to the hydrophone array, and decreasing as the sound moves away from the hydrophone (Gillespie & Chappell 2002). The Porpoise Detector software automatically classifies clicks as ‘Porpoise’, ‘Broadband’ or ‘Unknown’ based on the energy within each of the frequency bands. The classification was based on a study carried out by Gillespie and Chappell (2002), according to measurements carried out on a variety of different click types.

All survey data was recorded via Logger 2000 to an Access database, automatically recording GPS location every 10 seconds along with depth, wind speed & direction and boat speed from the NMEA ship computer. Environmental conditions (sea state, swell, visibility, sun glare, and weather conditions) were recorded every 15 minutes or whenever they changed significantly, directly to the Logger 2000 database. Survey effort and engine on/off was noted whenever it changed, and all boat traffic was logged whenever it approached within 2 nm of the vessel.

4.2.2 Environmental data

A range of environmental variables were available for inclusion in analysis from a range of sources, as listed in Table 4.1.

Table 4.1 – Spatial, temporal, environmental, and modelled environmental variables sourced for the surveys carried out in the Inner Hebrides, on the west coast of Scotland. Acronyms: BGS = British Geological Survey; UKHO = UK Hydrographic Office; POLCOMS = Proudman Oceanographic Laboratory Coastal Oceanography Modelling System; UKMO = UK Met Office.

Variable	Description	Source	Resolution	Unit
Boat speed	*In situ* measurement of boat speed	Garmin GPS	Every 10 s (≈ 50m)	knots
Sea state	Sea state (0-6 in half sea states)	Field observation	Every 15 min (≈ 5km)	-
TimeSunrise	Ratio: (time in minutes from sunrise) / (total number of minutes between sunrise and sunset)	Time based on Garmin GPS time	Every 2 km	-
ClosetoSW	Ratio: (tidal range for the given day and location of a segment) / (Spring tidal range for the same area) based on closest tidal port	Time based on Garmin GPS, tide based on POLTIPS	Every 2 km	-
TimeFrLW	Ratio: (time since low water in minutes) / (time in minutes between adjacent low waters) based on the closest tidal port	Time based on Garmin GPS, tide based on POLTIPS	Every 2 km	-
Depth	Seabed depth	Digibath 250 BGS	1 km	m
Slope	Seabed slope	Digibath 250 BGS	1 km	º
Sediment	RSDB code indicating sediment type	UKHO	Variable	-
MixedDepth	Predicted depth of the mixed layer	POLCOMS UKMO	1.8 km	m
SBDensity	Predicted surface to bottom density difference (pycnocline strength)	POLCOMS UKMO	1.8 km	σ_t
SurfDens	Predicted surface density	POLCOMS UKMO	1.8 km	σ_t
HaloDepth	Predicted depth of the halocline	POLCOMS UKMO	1.8 km	m
SBSalinity	Predicted surface to bottom salinity difference (halocline strength)	POLCOMS UKMO	1.8 km	psu
SSS	Predicted surface salinity	POLCOMS UKMO	1.8 km	psu
ThermDepth	Predicted depth of the thermocline	POLCOMS UKMO	1.8 km	m
SBS	Predicted surface to bottom temperature difference (thermocline strength)	POLCOMS UKMO	1.8 km	°C
SST	Predicted sea surface temperature	POLCOMS UKMO	1.8 km	°C
SurCurDay	Predicted mean daily surface current	POLCOMS UKMO	1.8 km	m/s
MidCurDay	Predicted mean daily mid-depth current	POLCOMS UKMO	1.8 km	m/s
BotCurDay	Predicted mean daily bottom current	POLCOMS UKMO	1.8 km	m/s
SurCurHr	Predicted mean hourly surface current	POLCOMS UKMO	1.8 km	m/s
MidCurHr	Predicted mean hourly mid-depth current	POLCOMS UKMO	1.8 km	m/s
BotCurHr	Predicted mean hourly bottom current	POLCOMS UKMO	1.8 km	m/s
MaxTideCr	Maximum tidal current	POL	1.8 km	m/s
STideRange	Spring water tidal range	POL	1.8 km	m

Standardised temporal variables were calculated after the surveys. Time of day (*TimeSunrise*) was determined as a ratio between time elapsed since sunrise to the time between sunrise and sunset. Sunrise and sunset times were based on Tobermory (the starting point of all surveys: 56°37’N, 6°4’W) sourced from POLTIPS (Version 3.2.4, Proudman Oceanographic Laboratory). This method of calculation compensated for the varying length of day throughout the survey season.

For the tidal variables, it was first necessary to determine the closest port to each data point on which to base the tidal data (calculating using ESRI ArcGIS 9.0, based on tidal ports from POLTIPS). To calculate the position of each data point within the spring-neaps tidal cycle (ClosetoSW) a ratio was calculated between the actual tidal range (based on the date and tidal range for the closest port) and the spring water tidal range in metres (for the same port). Tidal state was converted into a continuous index from 0 to 1, calculated as a ratio between the time elapsed since the last low water to the total time between two low tides. To translate this index into tidal states: 0-0.1 was the first low water slack tide; 0.1-0.3 was flood tide; 0.3-0.6 was high water slack tide; 0.6-0.9 is ebb tide; and 0.9 to 1.0 was the second low water slack tide.

Depth and slope were sourced from the Digibath 250 bathymetry (Version 1.0, BGS), extracted from TINS using the ArcGIS 9.0 data extraction tool (Gontarek 2005) for each data point. Sediment type was available as categorical data (RSDB codes) describing the different sediments types, so the classes were transformed to values for the percentages of mud, gravel and sand in the sediment using the Folk-classification (Folk 1980).

Oceanographic and current variables were based on predicted values from the Proudman Oceanographic Laboratory Coastal Oceanography Modelling System (POLCOMS) (Holt et al. 2005; Holt & James 2006; Met Office 2006). The model outcomes were processed by Phil Gillibrand (SAMS) using the following methodology. Data were provided in Gridded Binary (GRIB) format with output fields including: (i) daily values of temperature, salinity, north and east components of current speeds; and (ii) hourly rates of north and east components of current speed. This data was provided over the shelf waters off the west coast of Scotland at 18 different depths through the water column (spaced evenly through the water column). The data were processed into the summary variables detailed in Table 2.1, and saved in ERDAS Imagine format for easy access for ArcGIS 9.0. Tidal range (SWTideRange) and maximum tidal current (MaxTideCur) were sourced from the Proudman Oceanographic Laboratory high resolution CS20 model.

4.2.3 Acoustic data analysis

Although the Porpoise Detection software was able to automatically classify porpoise clicks (Gillespie & Chappell 2002), it was necessary to process the files manually to scan for trains of porpoise-type clicks. The porpoise detection software was set up to classify clicks as ‘porpoise clicks’ if they had a minimum amplitude of 105dB re 1μPa in the ‘porpoise’ band (115-145 kHz), and a difference of over 30dB above the mean amplitude of the two ‘noise’ bands (50 & 75 kHz). These settings were based on those used in the study by Gillespie et al. (2005) in order to reduce the number of false-positives.

For this analysis, both porpoise classified clicks and ‘unclassified’ clicks (lower amplitude clicks and clicks that cannot be clearly identified as porpoise clicks from their amplitudes in the different bands) were used to define porpoise trains (Figure 4.2). It is believed that these ‘unclassified’ clicks, when on the same bearing as the ‘porpoise’ clicks may be off-axis clicks, hence their lower amplitude (Gillespie et al. 2005). Off-axis clicks have a much lower source level and possibly different spectral characteristics because the echolocation clicks of harbour porpoises are highly directional (Au et al. 1999). Maximum energy would only be received at the hydrophone when the porpoise is echolocating towards it. Since porpoises tend to scan the area around them by moving their head or body from side to side (Goodson & Sturtivant 1996), most clicks trains tend to be made up of a combination of high amplitude ‘porpoise’ clicks, and the lower amplitude ‘unclassified’ clicks on the same bearing (Figure 4.2).

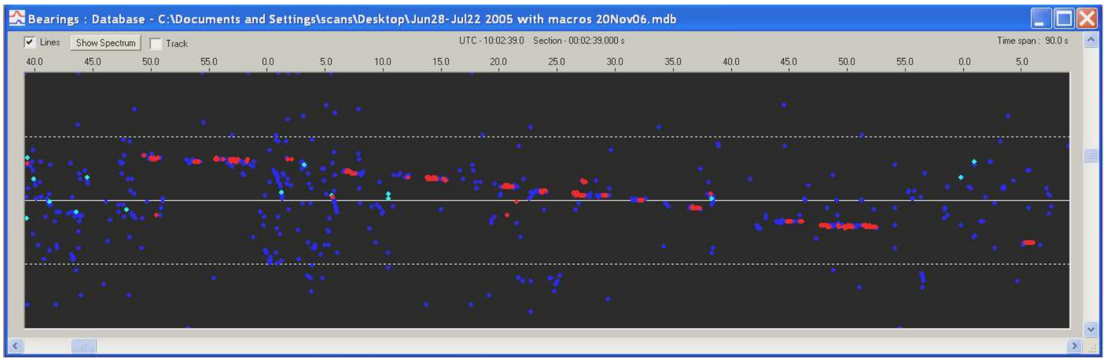


Figure 4.2 – Track of a single harbour porpoise as it travels past the survey vessel and random noise clicks as output from the Porpoise Detector software. Time in seconds shown on the x-axis and bearing on the y-axis from 0° (ahead of the hydrophone) at the top of the plot to 180° (behind the hydrophone) at the bottom of the plot. Automatically classified porpoise clicks are shown in red, clicks classified as broadband are shown in light blue, and quiet or 'unknown' porpoise clicks are shown in dark blue.

Porpoise trains were firstly classified subjectively as 'excellent', 'good', 'probable' or 'unlikely' according to the following criteria: 'excellent' click trains comprised of at least 10 'porpoise' classified clicks in a clear track with click amplitudes recorded at > 130 dB re 1μPa; 'good' click trains had at least 5 'porpoise' classified clicks in a clear train, with click amplitudes well above the background noise levels; 'probable' click trains comprised at least 3 'porpoise' classified click of high enough amplitude to be visible above background noise levels, and accompanied by a rapid train of at least 5 'unclassified' clicks on the same bearing; 'unlikely' click trains included any 'porpoise' classified clicks that were not accompanied by other 'classified' or 'unclassified' clicks on a similar bearing. To keep the probability of false detections low, all click trains classed as 'unlikely' were discarded.

In the second stage of analysis, the porpoise tracks were classified into 'groups' of trains thought likely to be from a single pod. A 'group' was defined as any series of tracks not separated by a period of at least two minutes. This time period was based on the amount of time it would take to pass a stationary porpoise at a boat speed of 6 knots based on an acoustic detection range of 400m travelling at an average speed of around 1.25 knots, plus some contingency to compensate for porpoises swimming in the same direction as the vessel. A table was created in the Access database with one record entry per porpoise group, and automatically linked to the GPS location for the mid point of the encounter using a pre-written macro (Gillespie pers. comm.).

4.2.4 Statistical analysis

4.2.4.1 Pre-modelling analysis

Since the coarsest scale for the environmental data was 1.8 km (for the POLCOMS oceanographic data), all on-effort tracks from surveys carried out between May-September 2003-2004 were divided into 2 km segments. Where data were stored within the survey Access database, the environmental variables were determined for the mid-point of each segment, or the most recent value for that variable (e.g. last recorded sea state) using macros written in Access. For all other variables (topography, sediment & POLCOMS oceanographic variables), values were determined for the mid point of each segment using the STJG GIS extraction tool version 1.0.1 (Gontarek 2005) in ArcGIS 9.0 (ESRI Inc).

Prior to modelling, a Spearman's Rank Correlation test was carried out using Minitab v12.23 (Minitab Inc. 1999) to test for correlations between environmental variables. If there was a moderate to strong correlation ($r > 0.3$) between variables, the first of the variables selected by the step-wise model selection was retained and any variables with which it was correlated were discarded.

The dataset was divided into a 'training' and 'test' dataset. This was done in a number of ways, firstly, any dataset under analysis was randomly divided such that 75% of the segments were included in the 'training' dataset and used as the basis of the model selection, and the remaining 25% of the segments were used as the 'test' dataset, on which the predictive performance of the models were evaluated. To ensure as much independence between re-sampling units as possible while retaining as much of the original spatial coverage surveyed as possible, the data were randomly sampled by groups of 4 segments. Groups of 4 segments (around 8 km) were unlikely to be autocorrelated.

4.2.4.2 Modelling porpoise density – model selection

Generalised Additive Models (GAMs) were used to relate the number of groups of porpoises per 2 km segment to the spatial, environmental and temporal variables (§2.2.4.2). Since the response data was Poisson (count) data, a Poisson distribution was assumed with the log link function (Wood 2006a).

The GAMs were fitted in R version 2.3.0 (The R Foundation for Statistical Computing 2006) using the MGCV library (Wood 2006b). To reduce potential overfitting of smooths to the data, two approaches were used. Firstly, a $\alpha=1.4$ was used in the model fitting as suggested by Kim & Gu (2004), which forces the estimated degrees of freedom in a smooth to count for 1.4 degrees of freedom in the UBRE score (Wood 2006a), so penalising the GAM function for using too many degrees of freedom. Secondly, the smooths for each of the variables, excluding latitude and longitude, were limited to ≤ 4 estimated degrees of freedom.

Stepwise addition of environmental variables to the null model (no predictor variables) was carried out (forward step-wise selection), and models compared based on minimising the UBRE (UnBiased Risk Estimator) score. The UBRE score is the Poisson GAM equivalent of the AIC value (in effect, just a linear transformation of AIC), and scores on both fit and the number of parameters used to describe the model (Wood 2006a). In selecting the best model, predictor variables were only added if they reduced the AIC equivalent of the UBRE score (multiplying UBRE by n the sample size) by 2 or more, as recommended by Burnham & Anderson (2002). Survey variables (sea state, boat speed, engine on/off and noise levels) were added to the model first, to compensate for the change in sighting ability and acoustic detectability, before adding environmental variables. Latitude and longitude were only included in the model selection if none of the remaining environmental variables were neither significant nor reduced the UBRE score. The other environmental variables were considered more biologically meaningful to porpoises than a simple combination of space (latitude and longitude), and would allow for prediction of distributions outwith the surveyed area.

4.2.4.3 Modelling porpoise density - model evaluation

Models were subsequently evaluated using a cross-validation technique developed by Heinrich (2006) for evaluating habitat models for Chilean dolphins. This technique compares the predictive performance of the model under analysis with the predictive performance of 10,000 random simulations of data taken from a random (intercept-only) model. The simulated number of porpoise groups per segment was randomly generated for every segment i according to a Poisson distribution with the actual mean number of groups of porpoises per segment for the dataset under analysis.

The predictive performance was calculated as:

$$\overline{q} = 1 - \frac{\sum_{i=1}^{n} \left| (y_i - \hat{p}_i) \right|}{n}$$

Where:

$\overline{q}$ is the mean proportion of all correct predictions

y_i is the number of porpoise groups in segment *i*

$\hat{p}_i$ is the estimated number of porpoise groups in segment *i*

n is the total number of segments

The predictive performance of each of the 10,000 simulated datasets results in a distribution that forms the test statistic against which the predictive performance $\overline{q}$ of the model under analysis was compared. Thus, the proportion of the simulations that the model performs worse than the random simulated data, gives the test statistic (a good model having $p < 0.05$).

The same methodology can be used to compare complex models with simpler models, either evaluating a model for one year against the model for another year on a dataset, or for evaluating potential overfit. In this case, the predictions from the simpler model were used to generate the simulated dataset (i.e. using the predicted number of groups for a segment as the mean when sampling from a Poisson distribution for that segment).

The final models were predicted over a 4x4 km grid, set to twice the size of the segment size as recommended by Hedley (2000) for visual comparison between models for different years and survey data.

4.2.4.4 Modelling acoustic noise

Generalised Additive Models (GAMs) were used to relate the acoustic noise levels per 2 km segment to the environmental temporal variables. Noise levels are normally distributed, so the GAM was modelled using a Gaussian distribution with an identity link function. The environmental variables included in the model selection were: sea state, boat speed, engine on/off (as a factor variable), tidal state (TimeFrLW), depth, slope, sediment type (% sand, mud or gravel), maximum tidal current, and spring tidal range. No oceanographic variables were included since they were not available for the 2005 acoustic survey data.

As with the porpoise modelling, GAMs were run using the MGCV library (Wood 2006a) in R version 2.3.0 (The R Foundation for Statistical Computing 2006). To reduce potential overfitting of the smooths to the data, $\alpha = 1.4$ was used in the model fitting to penalise for using too many degrees of freedom (Kim & Gu 2004), and the smooths were limited to ≤ 4 estimated degrees of freedom.

Stepwise addition of environmental variables to the null model (no predictor variables) was carried out (forward step-wise selection), and models compared based on minimising the GCV (Generalised Cross Validation) score. The GCV score is the Gaussian GAM equivalent of the AIC and scores on both fit and the number of parameters used to describe the model (Wood, 2006a). In selecting the best model, predictor variables were only added if they increased the amount of deviance explained by 1% or more.

The best environmental model for noise levels was then used to make a prediction over a 4x4 km grid, to compare against the detections of harbour porpoises visually, acoustically or by both methods to examine whether (i) there were visual detections not accompanied by acoustic detections in areas of high predicted noise; (ii) there were acoustic detections not accompanied by visual detections in areas of low predicted noise. The main aim of this exercise was to investigate whether noise affected acoustic detections in different habitats.

4.2.4.5 Models constructed

The acoustic and visual data were modelled separately to allow for the difference in collection methods to be modelled within the structure of the GAM. In order to directly compare visual and acoustic models, only those segments containing both visual and acoustic survey effort (at sea state ≤ 3) were included in the analysis for 2004 & 2005. In 2005, a larger area was surveyed, so the data was stratified such that analysis was initially carried out for the same core area surveyed as in 2003-2004, but models compared with those for the larger area in 2005 to examine any potential geographical variation in habitat preference. Also, in 2005, there was no available

POLCOMS oceanographic data, so the environmental variables had to be limited to topographical, sediment, temporal and tidal variables.

Two stages of analysis and models were carried out: (i) comparison of predictive models of harbour porpoise distribution based on visual and on acoustic data for 2004-2005; (ii) construction of best temporal visual predictive model for harbour porpoises by examining the effect of year on predictions, initially modelling 1 year of data (2003, 2004, and 2005 separately), then modelling 2 years of data (2003& 2004, 2004&2005) and finally constructing a model based on all 3 years of data; (iii) examining the effect of geographical area on the model for 2005.

4.3 Results

A total of 14 700 km were surveyed in the Inner Hebrides off the west coast of Scotland during the summers between 2003 to 2005, of which 11 300 km had visual survey effort, and 6 700 km had acoustic survey effort (Figure 4.1 & 4.3). Overall, during 2003-2005, in good sightings conditions (sea state ≤ 3) there were 437 groups of a total of 787 harbour porpoises detected visually (0.091 porpoises per km). During the 2004-2005 analysed acoustic effort, there were 986 groups of a total of 1539 harbour porpoises detected acoustically (0.231 porpoises per km). Where there was simultaneous visual and acoustic effort, 55% of visual sightings were accompanied by acoustic detections, but only 18% of acoustic detections were accompanied by visual detections. Acoustic detections made up 72% of the overall detections of harbour porpoises. Harbour porpoise detections were scattered fairly evenly over the survey area, though they appeared to be concentrated more within coastal areas, with fewer detections in the more offshore areas to the west of Islay, Mull and Coll & Tiree (Figure 4.3).

4.3.1 Environmental variables

Only a sub-sample of this data was used in the analysis due to the lack of availability of environmental data for the highly coastal areas such as the Sound of Mull, the upper Firth of Lorne and the upper Sound of Jura. A summary of the environmental variables is given in Table 2.2 for 2003-2005 where all variables were available, and for 2003-2004 for POLCOMS oceanographic data (since this was not available for 2005). The general trend shows a gradual increase of the range of each survey variable covered as the survey area increased year on year from 2003-2005.

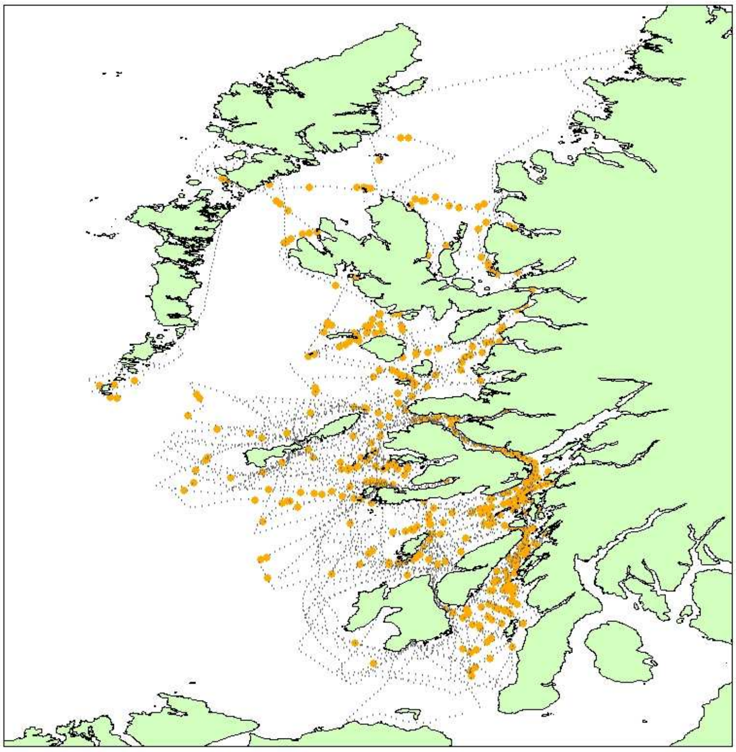
Spearman’s rank correlation tests on environmental variables (Appendix Table A3.2) showed moderate-strong correlation ($r > 0.3$) between all the oceanographic variables, all the current speed variables, between % mud and % gravel, and between latitude and the oceanographic variables, and longitude and the tidal current speed variables. Correlations suggest the proportion of mud in the sediment increases in deeper water and slower current speeds, but that the proportion of gravel does the opposite with more gravel in shallower high current areas. The proportion of mud in the sediment also correlates with salinity, with lower surface salinity and stronger haloclines in areas with high mud content, and a correlation with longitude suggesting these low salinity, high mud areas were found close to the mainland. The oceanographic variables change with current speeds, with deeper halo & thermoclines, weaker stratification, and higher surface temperature & salinity in areas of higher current speeds. In addition, some of the oceanographic variables correlate with position in the tidal cycle (ClosetoSW), with a shallower thermocline around spring tide, and therefore shallower mixed depth. Of the survey variables, the engine tended to be on more in lower sea states, and correlated with higher boat speeds. Noise levels were correlated positively with boat speed and % gravel, and negatively with sea state, depth and % mud in the sediment. Plots of a sample of the environmental variables are shown in Figures 4.4-4.6.

The survey area is mainly < 100 m depth with few areas deeper than 200 m (Figure 4.4a). Sediment type is dominated by sand (Figure 4.5a); with small areas of mud in areas such as the Sea of Hebrides and around the Small Isles (Figure 4.5b), and gravel in high current speed areas such as west of Islay (Figure 4.4b). Unfortunately the sediment type data was missing for some parts of the survey area, in the coastal areas of the Sound of Mull, upper Firth of Lorne, and upper Sound of Jura. It is also evident that the sediment data has variable resolution, with very fine detail in some areas (such as the Sea of Hebrides & Minch area), but with very coarse detail in others (such as the Sound of Jura).

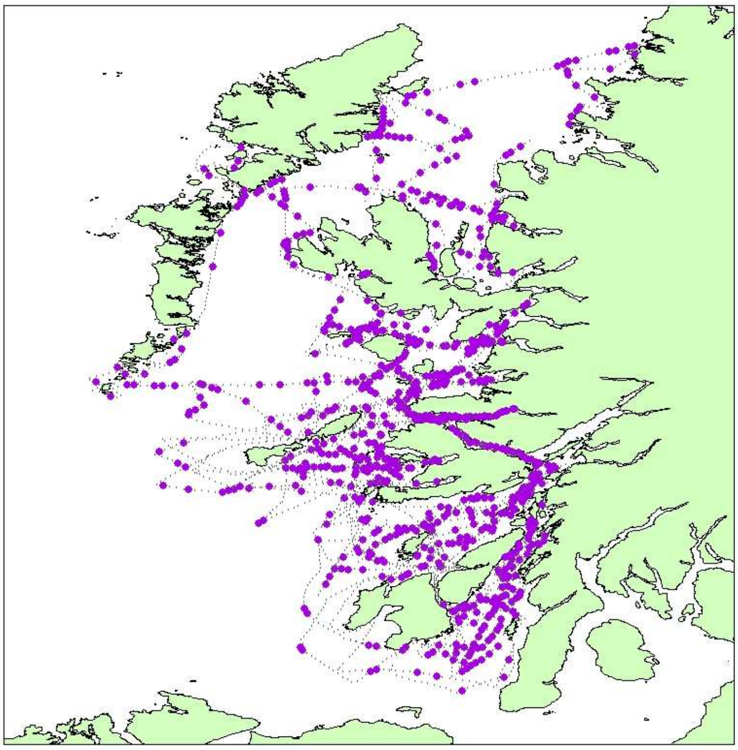
The tidal data shows a large area of high maximum tidal currents, and very low spring tide range in the area where the Irish Sea current meets the North Atlantic current passing around the west of Ireland (Figure 4.6). Tidal currents are also high in other narrow channels bounded by islands, such as the Little Minch, Tiree Passage, Sound of Islay and Firth of Lorne (Figure 4.6a). Spring tide range increases from virtually zero at Islay, to a maximum around Skye (Figure 4.6b).

Table 4.2 – Summary statistics for the environmental variables for the three survey years, results of a Mann-Whitney test to test between 2003 & 2004 and 2004 & 2005 environmental variable distributions are shown if significant, where * p<0.05; **p<0.01; and ***p<0.001.

Parameter		2003	2004	2005
Survey effort with environmental data available				
Distance surveyed (km)		1638	1214	2104
Number of stations/segments		819	607	1052
Segments with visual porpoise groups		54 (6.6%)	46 (7.6%)	109 (10.4%)
Segments with acoustic porpoise groups		-	121 (19.9%)	255 (24.2%)
Survey variables				
Boat speed	range (knots)	2.1-10.3	1.2-10.0	0.8-10.3
	mean (standard deviation)	5.9 (1.1)	6.0 (1.2)*	6.5 (1.0)***
Sea state	range	0-3	0-3	0-3
	median (IQR)	2 (1-3)	2 (1.5-3)	2.5 (1.5-3)***
Engine on/off	mean	not recorded	0.88	0.85
DC noise	range (dB)	-	258-610	48-551
	mean (standard deviation)	-	338 (40)	331 (40)**
Temporal variables				
TimeSunrise	range	0.06-0.95	0.10-0.92	0.12-0.81
	mean (standard deviation)	0.48 (0.19)	0.50 (0.17)**	0.48 (0.15)*
ClosetoSW	range	0-2.26	0-1.24	0.29-1.44
	mean (standard deviation)	0.83 (0.36)	0.56 (0.24)***	0.73 (0.23)***
TimeFrLW	range	0-1	0-1	0-1
	median (IQR)	0.54 (0.3-0.8)	0.46 (0.3-0.7)	0.3 (0.3-0.8)**
Topographical variables				
Depth	range (m)	8-208	7-215	10-212
	mean (standard deviation)	63 (35)	60 (33)	70 (39)***
Slope	range (?)	0-14	0-22	0-19
	median (IQR)	0.3 (0-0.8)	0.3 (0-1.0)	0.5 (0-1.4)***
PctSand	range (%)	0-94	0-94	0-94
	median (IQR)	56 (43-76)	69 (43-94)***	43 (30-76)***
PctMud	range (%)	0-100	0-100	0-100
	median (IQR)	5 (2-30)	5 (4-30)***	5 (4-69)***
PctGravel	range (%)	0-100	0-100	0-100
	median (IQR)	1 (1-55)	1 (1-20)***	1 (1-20)
Tidal variables				
SWTideRange	range (m)	0.4-2.4	0.6-2.4	0.5-2.6
	median (IQR)	1.9 (1.9-2.0)	2.0 (1.9-2.1)***	2.1 (1.9-2.3)***
MaxTideCur	range (m/s)	0-3.1	0-2.6	0-3.1
	median (IQR)	0.5 (0.3-0.7)	0.5 (0.2-0.6)	0.4 (0.2-0.6)
Selected oceanographic				
SurfCurDay	range (m/s)	0-0.49	0-0.26	not available
	median (IQR)	0.07 (.04-.12)	0.07 (.05-.10)	
BotCurHour	range (m/s)	0-0.93	0-0.78	not available
	median (IQR)	0.11 (.06-.23)	0.09 (.04-.16)***	



(a)



(b)

Figure 4.3 – (a) Visual survey effort and visual detections of harbour porpoises showing all 2 km segments (black dots) and those segments with harbour porpoise sightings (orange dots) for surveys carried out between 2003-2005; (b) Acoustic survey effort and acoustic detections of harbour porpoises showing all 2 km segments for which there is both visual and acoustic survey effort (black dots) and those segments with harbour porpoise acoustic detections (purple dots) for surveys carried out between 2004-2005 in the Inner Hebrides, off the west coast of Scotland.

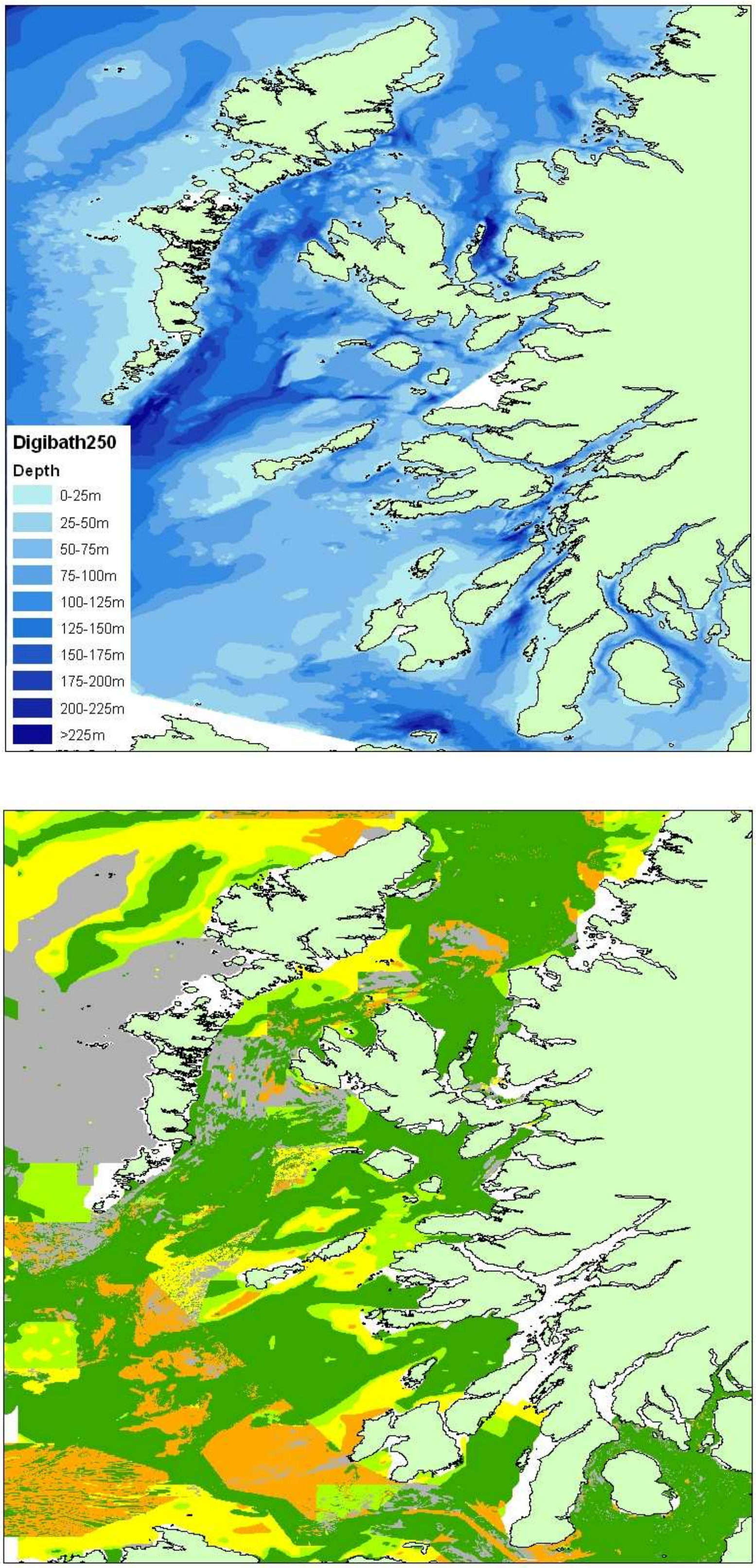
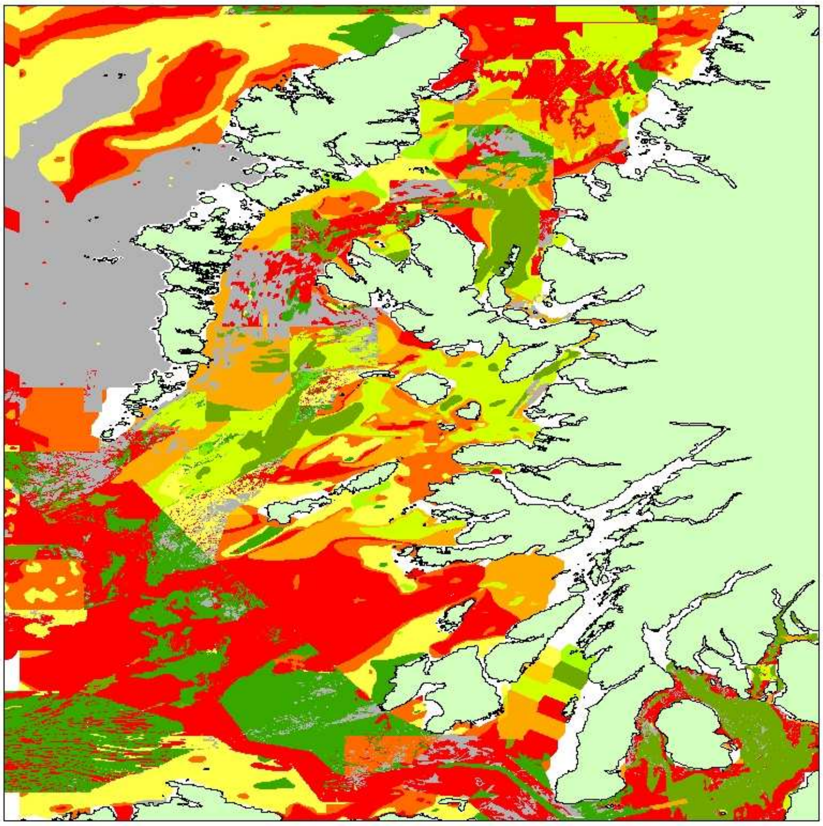
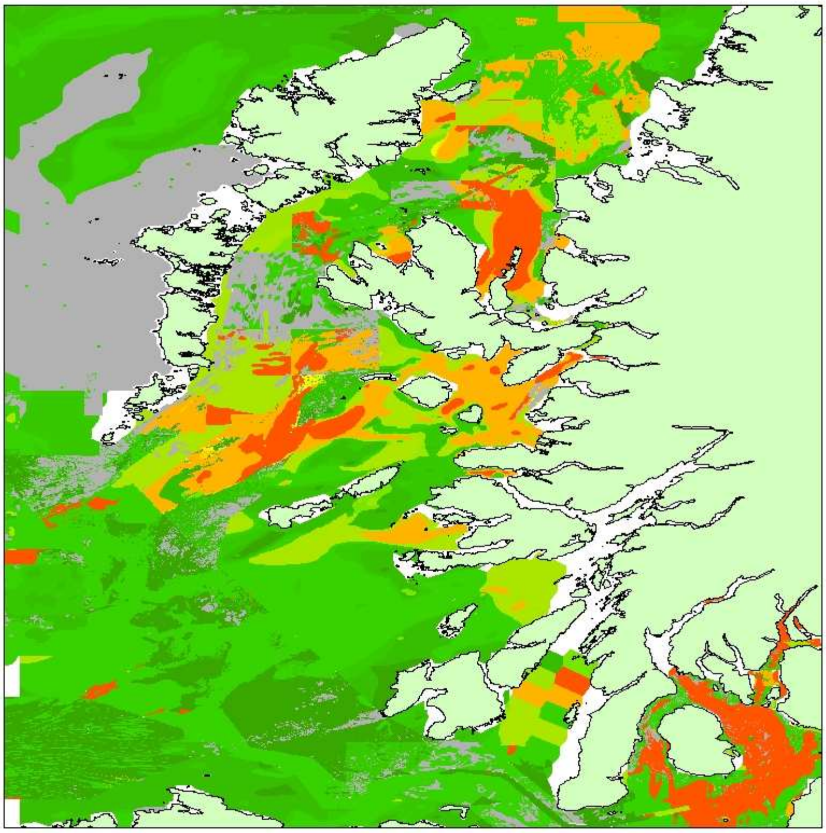


Figure 4.4 – (a) DIGIBATH 250 depth data, and (b) % gravel based on translation of UKHO RSDB sediment code using the Folk triangle conversion (Folk 1980) for the Inner Hebrides. % gravel colours: grey = rock; dark green = 0-5% gravel; light green = 5-30% gravel; yellow = 30-80% gravel; and orange = 80-100% gravel.



(a)



(b)

Figure 4.5 – Sediment type based on conversion of UKHO sediment type RSDB code into (top) % sand, and (bottom) % mud based on the Folk triangle conversion (Folk 1980). Colours: dark green = 0% → yellow = 50% → red = 100%.

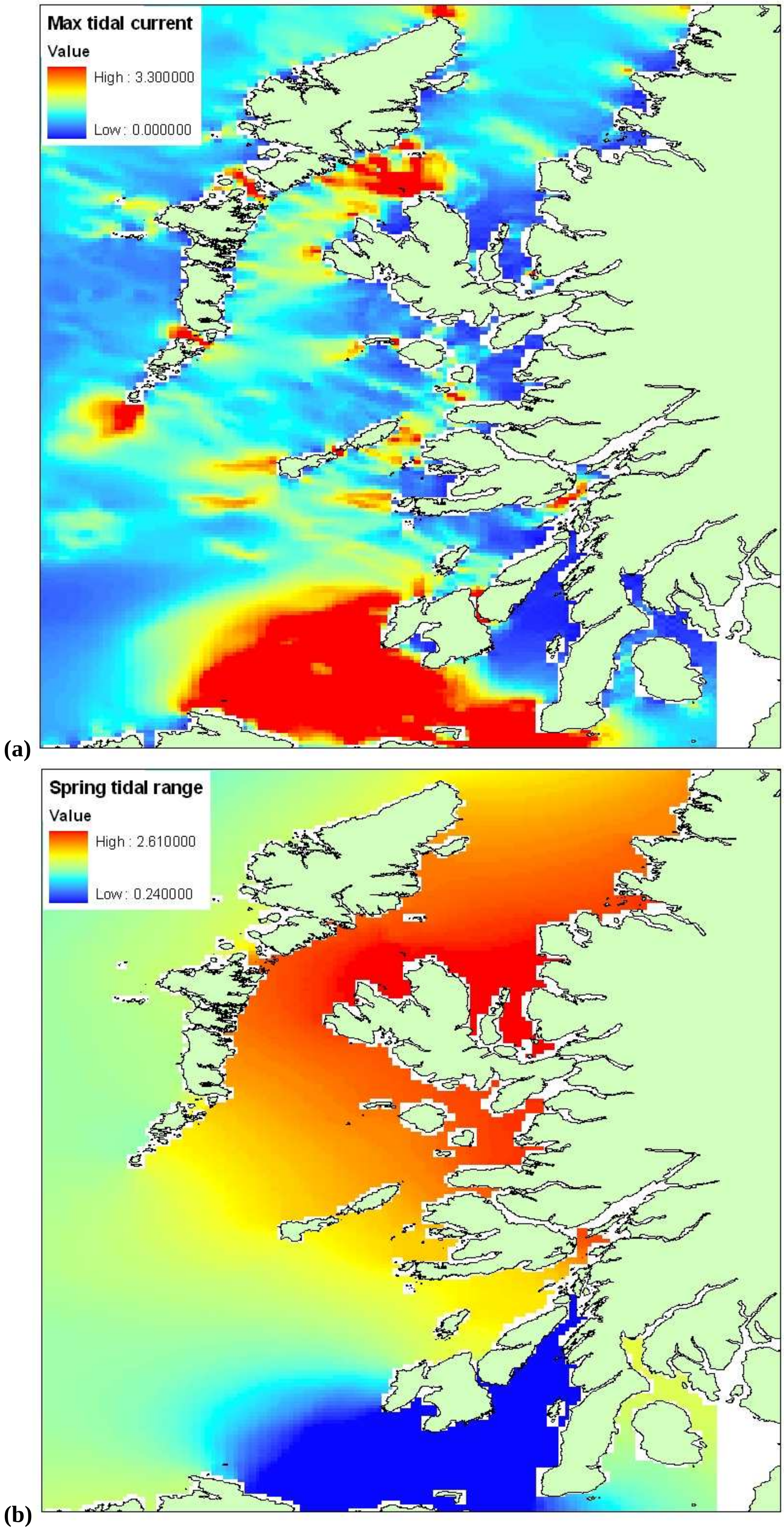


Figure 4.6 – Proudman Oceanographic Laboratory (POL) tidal data with (a) maximum tidal speed in m/s, and (b) spring tidal range in metres for the Hebrides.

4.3.2 Model selection: visual vs acoustic

4.3.2.1 Visual models

Of the survey variables, only sea state and engine on/off were significant in explaining the distribution of harbour porpoises in the core survey area during 2004-2005. Sea state explained over 10% of the deviance, with highest detections at sea state 1, dropping off rapidly with a negative effect on sightings above sea state 2 (Figure 4.8). Engine on/off only explained 2% of the deviance, with higher detections when the engine was on than off.

The best model for the visual detections of harbour porpoises during 2004-2005 explained 21.3% of the deviance of which 9.7% was explained by environmental variables (Appendix Table A3.3). The model included the environmental variables (in order of importance): maximum tidal current, position in the tidal cycle, and slope (Figure 4.7). Harbour porpoises were more likely to be seen in areas with low tidal current and high slopes and during spring tides (Figure 4.8). Despite the higher detection rates in areas of steep topography, the confidence intervals are very wide (Figure 4.8 d) suggesting there is a high degree of uncertainty in preference above 2°.

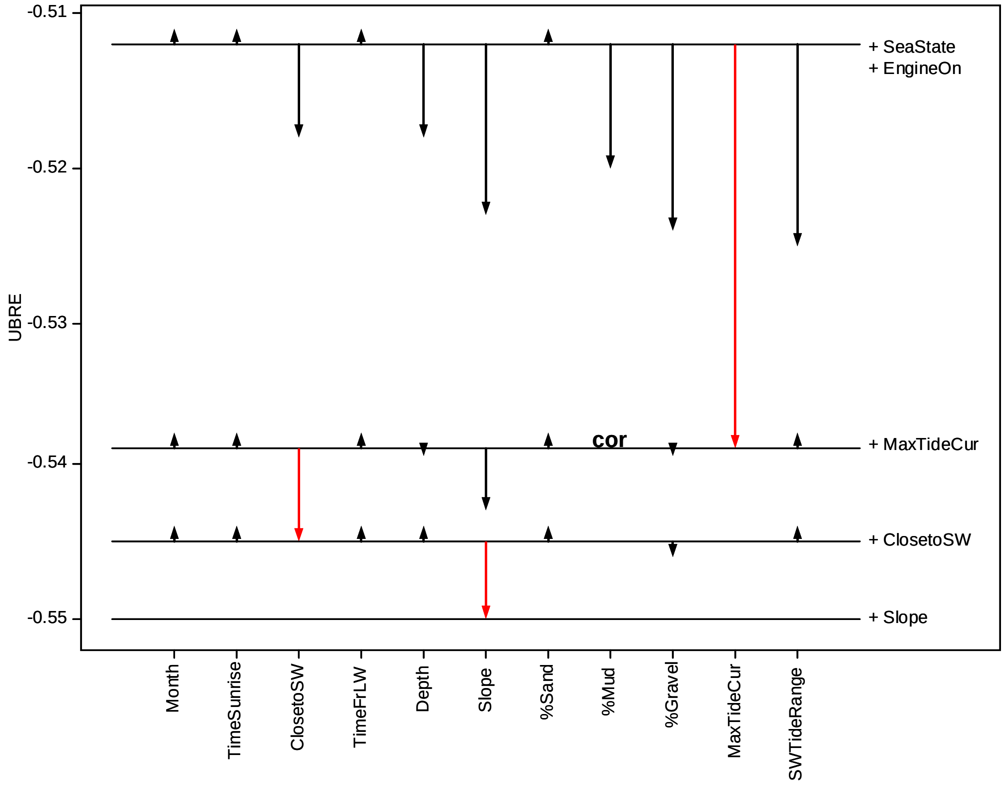
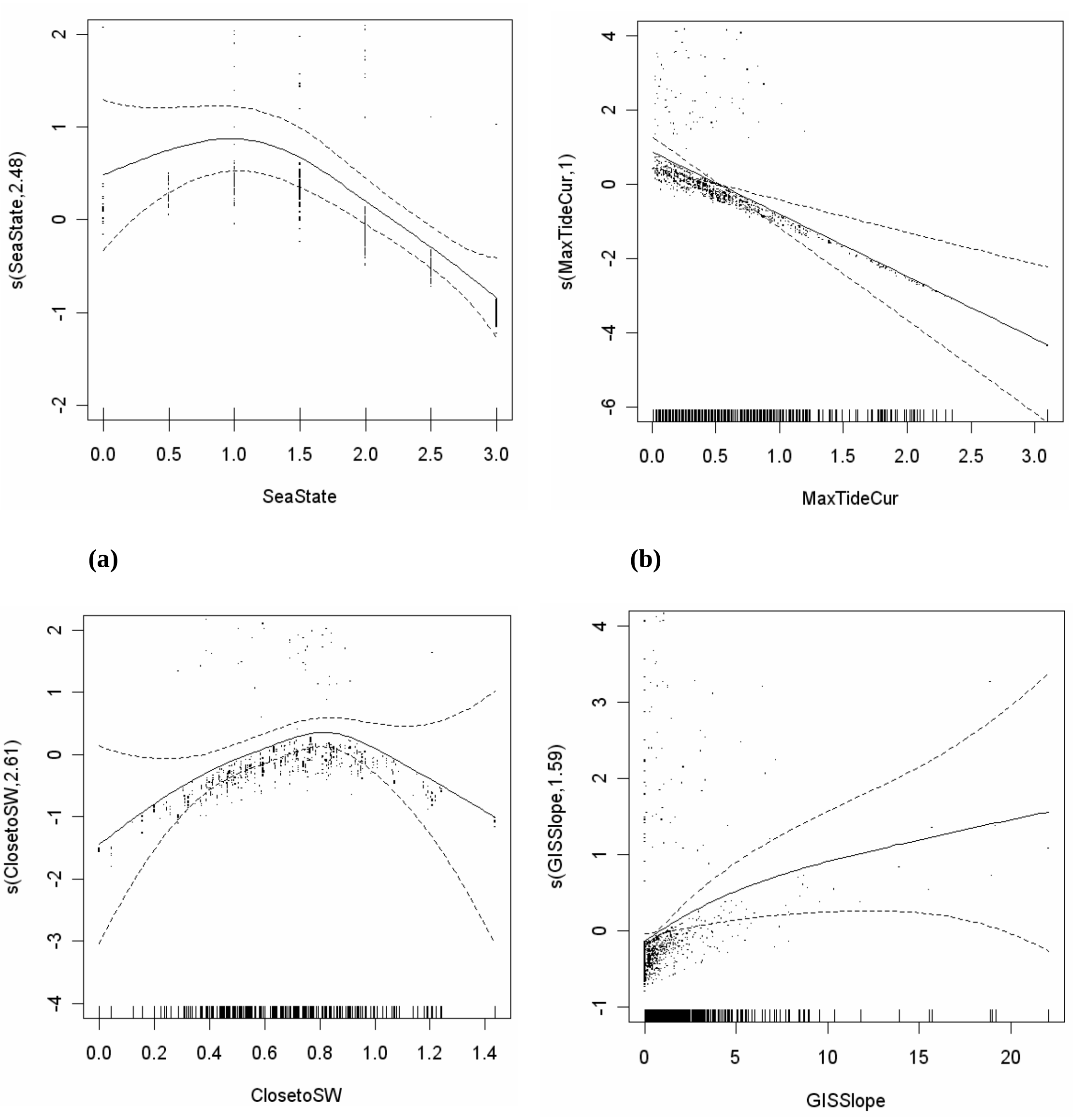


Figure 4.7 – Forward model selection for the number of harbour porpoise groups visually detected per 2km segment in 2004-2005 on the environmental variables: month, time of day (TimeSunrise), position in the tidal cycle (ClosetoSW), tidal state (TimeFrLW), depth, slope, % sand, % mud & % gravel in the sediment, maximum tidal current (MaxTideCur), and spring tidal range (SWTideRange). The arrows indicate the change in UBRE score between models (horizontal lines) as a result of adding an environmental variable. Red arrows indicate those variables that decrease the UBRE score by the largest amount and so included in the model. 'cor' indicates that the variable is strongly correlated with the last added variable and is so excluded from model selection. Based on visualisation of GAMs model selection by Aarts (2006).

Testing the full model with those excluding the last 1, 2, 3, or 4 variables, suggests that all variables should be retained in the overall model (no model overfit). The overall model was significant to $p < 0.05$, although the model performed equally well if slope was excluded from the model. High density areas were predicted for the coastal areas around the Argyll Islands (Sound of Jura, Firth of Lorne, to the west of Mull around the Treshnish Islands, and some indication of the mouth of the Sound of Mull), and around the Small Isles (Figure 4.11). This appears to correspond well with the actual sightings of harbour porpoises, except to the west of Mull (beyond the Treshnish Islands) and around Colonsay: where low density is predicted but where there were a few sightings.



(a) (b)

(c) (d)

Figure 4.8 – Relationship between visual detections of harbour porpoises and (a) sea state (d.f. = 2.5), (b) maximum tidal current in m/s (d.f. = 1), (c) position in the spring-neaps cycle (d.f. = 2.6), and (d) seabed slope in ° (d.f. = 1.6) for all 2 km segments (n = 972) surveyed within the core area around the southern Inner Hebrides between 2004 to 2005. The 95% confidence intervals are shown by the dotted lines, and black dots show the residuals around the smooths.

4.3.2.2 Acoustic models

Of the survey variables, only boat speed and noise levels were significant predictors of the acoustic detection of harbour porpoises in the core survey area during 2004-2004. Noise levels explained 5.9% and boat speed explained 2.5% of the deviance, in both cases with detections decreasing linearly with increasing noise or boat speed (Figure 4.10).

The best model for the acoustic detections of harbour porpoises during 2004-2005 explained 14.0% of the deviance of which 5.6% was explained by environmental variables (Appendix Table A3.4). The model included the environmental variables (in order of importance): percentage mud in the sediment, and spring tidal range (Figure 4.9).

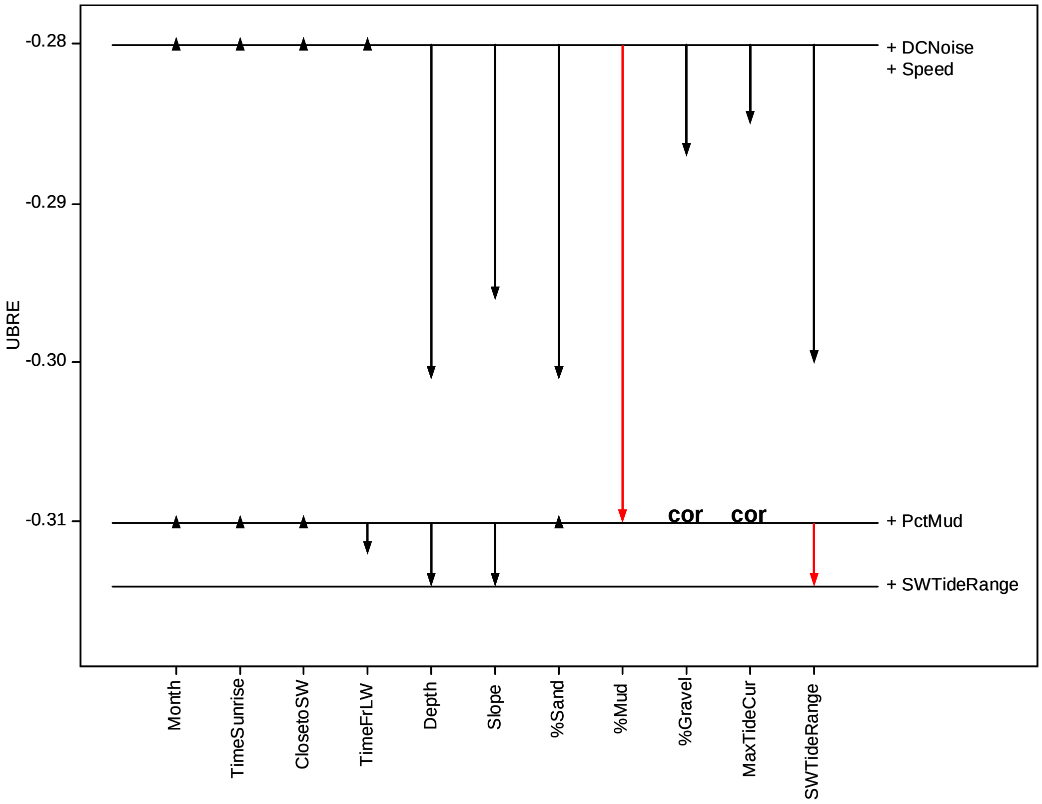
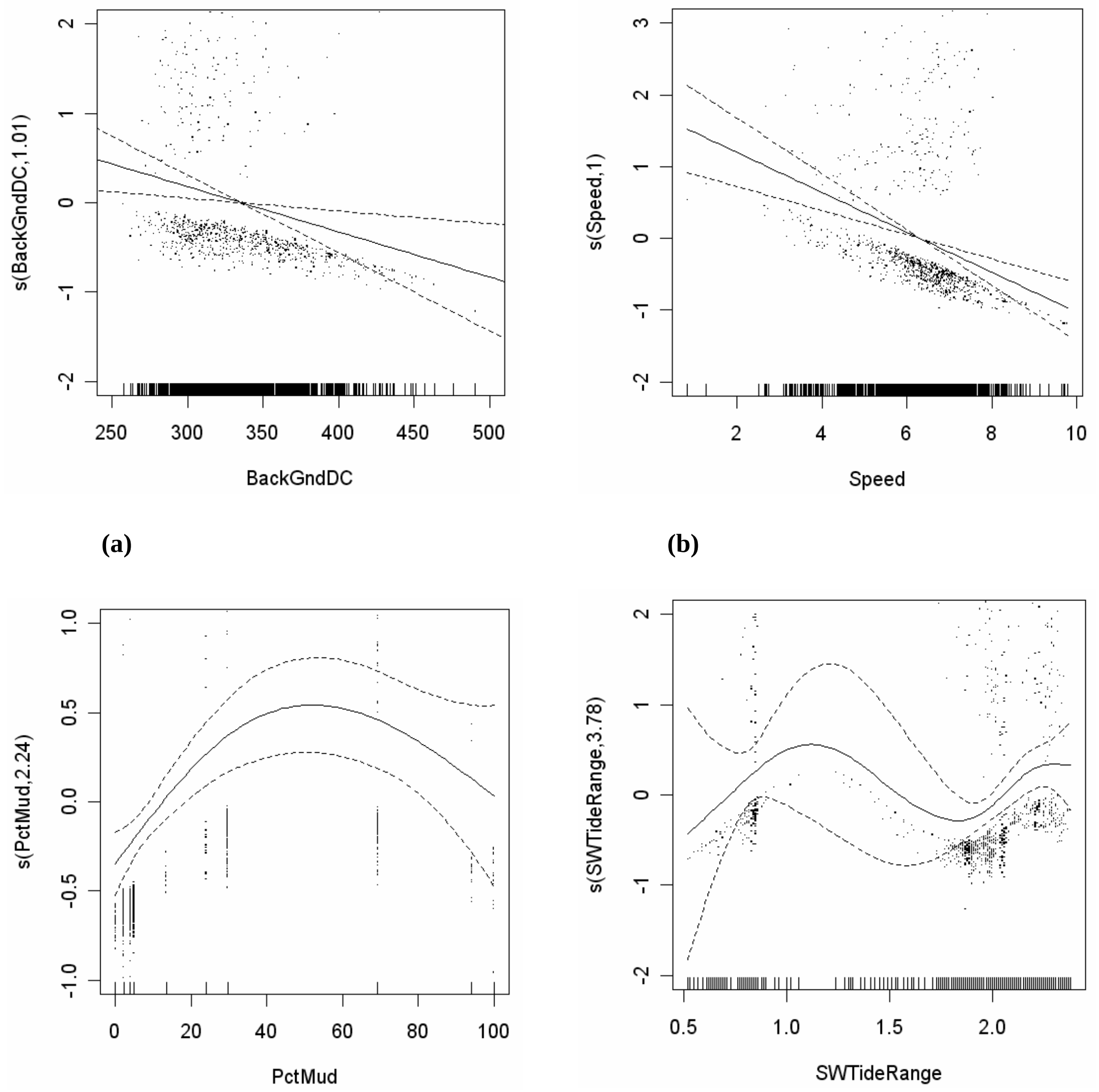


Figure 4.9 – Forward model selection for the number of harbour porpoise groups detected acoustically per 2 km segment during 2004-2005 with the environmental variables: month, time of day (TimeSunrise), position in the tidal cycle (ClosetoSW), tidal state (TimeFrLW), depth, slope, % sand in the sediment, % mud in the sediment, % gravel in the sediment, maximum tidal current (MaxTideCur), and spring tidal range (SWTideRange). The arrows indicate the change in UBRE score between models (horizontal lines) as a result of adding an environmental variable. Red arrows indicate those variables that decrease the UBRE score by the largest amount and so included in the model. 'cor' indicates that the variable is strongly correlated with the last added variable and is so excluded from model selection. Based on visualisation of GAMs model selection by Aarts (2006)



(a) (b)

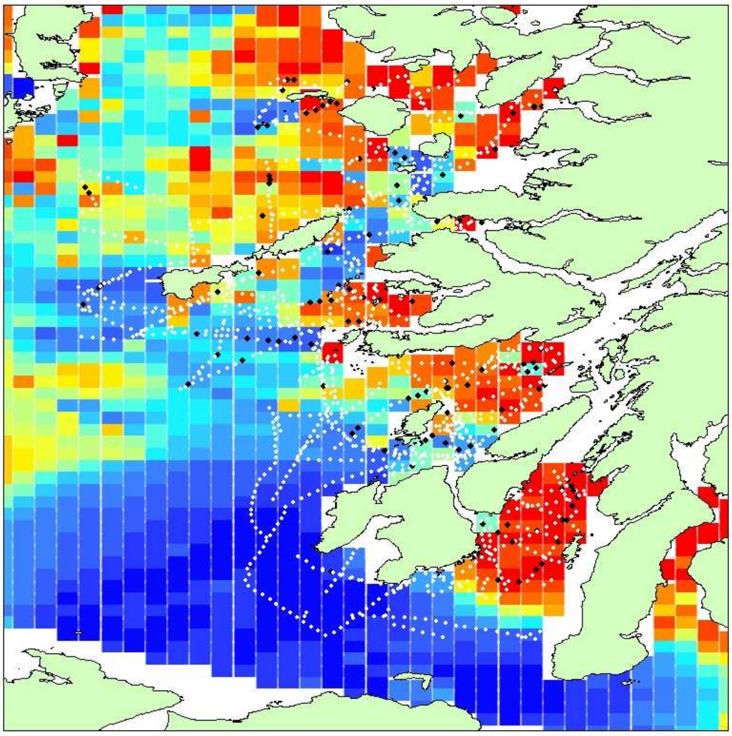
(c) (d)

Figure 4.10 – Relationship between acoustic detections of harbour porpoises and (a) noise levels (d.f. = 1), (b) boat speed in knots (d.f. = 1), (c) % mud in the sediment (d.f. = 2.2), and (d) spring tidal range in metres (d.f. = 3.8) for all 2 km segments (n = 972) surveyed within the core area around the southern Inner Hebrides between 2004 to 2005. The 95% confidence intervals are shown by the dotted lines, and black dots show the residuals around the smooths.

Harbour porpoises were more likely to be heard in areas with > 15% mud in the sediment (peaking at 50% mud) and in areas of either medium or high tidal range (Figure 4.10). The confidence intervals around the smooth for spring tidal range are very wide for very low and medium tidal ranges (Figure 4.10d). Therefore, only the preference for increasing tidal range above around 2 m has any certainty, below around 1.8 m there is no clear preference.

Testing the full model with those excluding the last 1, 2, or 3 variables, suggests that all variables should be retained in the overall model (no model overfit). The overall model was significant to $p < 0.01$ when compared to the test dataset. High density areas of harbour porpoises were predicted within the more coastal areas of the Argyll Islands (Sound of Jura, upper Firth of Lorne, west of Islay, west of Mull, and mouth of the Sound of Mull), and for the area around the Small Isles (Figure 4.11). This prediction appears to match the acoustic detections of porpoises reasonably well, except in two areas: (i) underestimating density of harbour porpoises around Colonsay (as did the visual model), and (ii) overestimating the density of harbour porpoises to the west of Islay.

(a)



(b)

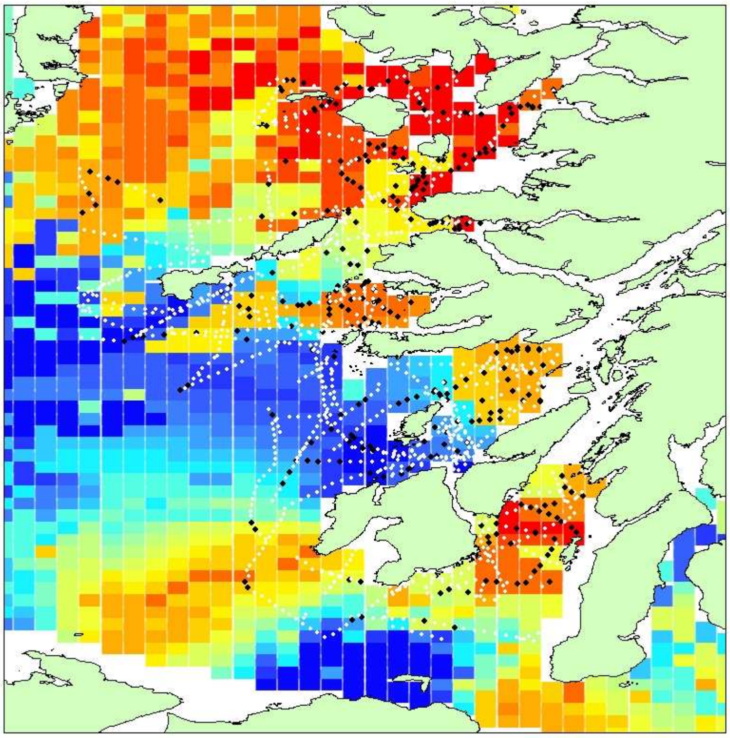
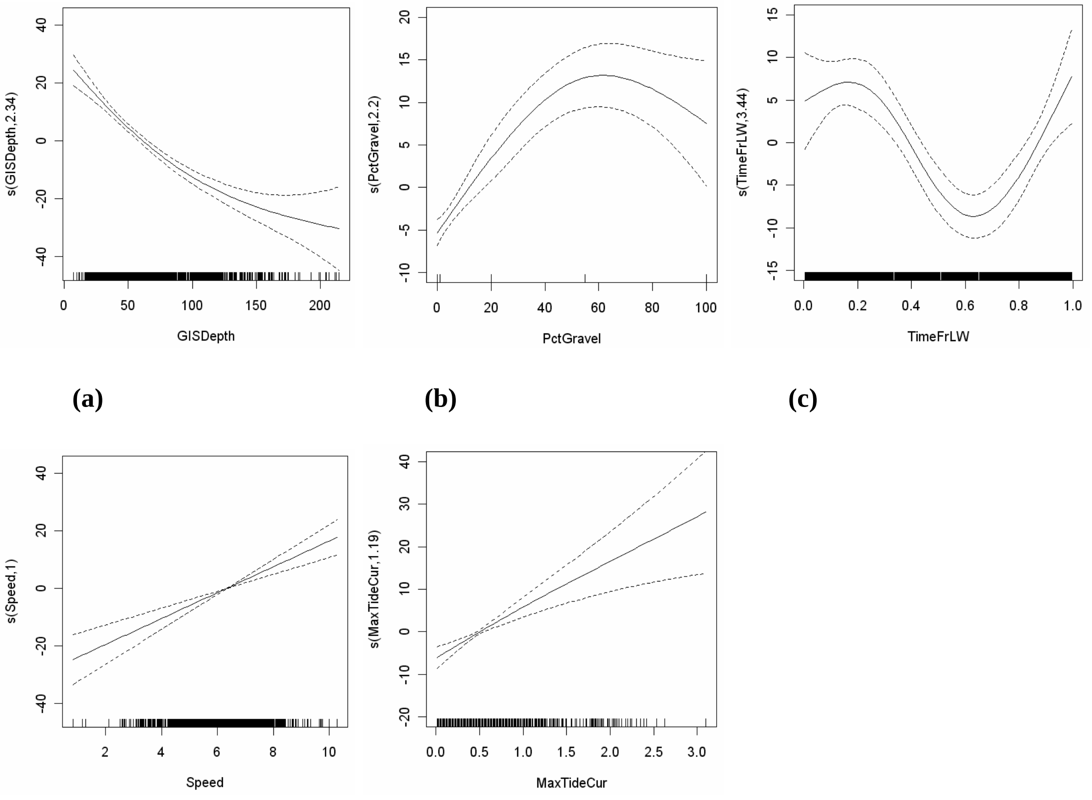


Figure 4.11 – Spatial prediction of harbour porpoise density (groups/2km) for (a) the best model based on visual detections, and (b) the best model based on acoustic detections for 2004-2005. Segments in which harbour porpoises were detected (a) visually or (b) acoustically are presented as black dots and white dots are where harbour porpoises are absent. Colours represent predicted porpoise density from low (blue) to high (red), ranging from (a) 0-0.1 for the visual model, and (b) 0-0.6 for the acoustic model, colour gradation based on 20 levels using quantile classification.

4.3.2.3 Noise model

The best model for noise levels based on all acoustic survey data collected between 2004-2005 explained 30.0% of the deviance, and included (in order of importance): depth, % gravel in the sediment, engine on/off, tidal state, boat speed, and maximum tidal current (Appendix Table A3.1). Noise levels were highest in areas that had shallow water, gravel sediments and high tidal currents, they were also higher at flood than ebb tide, and at higher boat speeds with the engine on (Figure 4.12).



(a) **(b)** **(c)**

(d) **(e)**

Figure 4.12 – Relationship between noise levels and (a) depth in metres (d.f. = 2.3), (b) % gravel in the sediment (d.f. = 2.2), (c) tidal state (d.f. = 3.4), (d) boat speed in knots (d.f. = 1) and (e) maximum tidal current in m/s (d.f. = 1.1) for all 2 km segments (n = 1554) surveyed throughout the Inner Hebrides between 2004 to 2005. The 95% confidence intervals are shown by the dotted lines.

Noise levels were predicted to be highest in a band encompassing Jura, Islay, Colonsay and to the south-west, off the Ross of Mull, all around Coll, Tiree, Eigg & Muck, and in a small patch just south-west of Canna (Figure 4.13). Locations at which there were visual detections of porpoises but no acoustic detections appear to be concentrated in areas predicted to have high noise levels (Figure 4.13). Analytically, visual detections were recorded to a greater extent in higher *predicted* noise areas than acoustic detections ($p < 0.05$, W = 96739, $n_{VisPres} = 155$, $n_{AcPre\ s}=376$). However, there was no significant difference in the visual and acoustic detection of porpoises based on the true *measured* noise levels ($p > 0.05$, W = 97177, $n_{VisPres}=155$, $n_{AcPres}=376$).

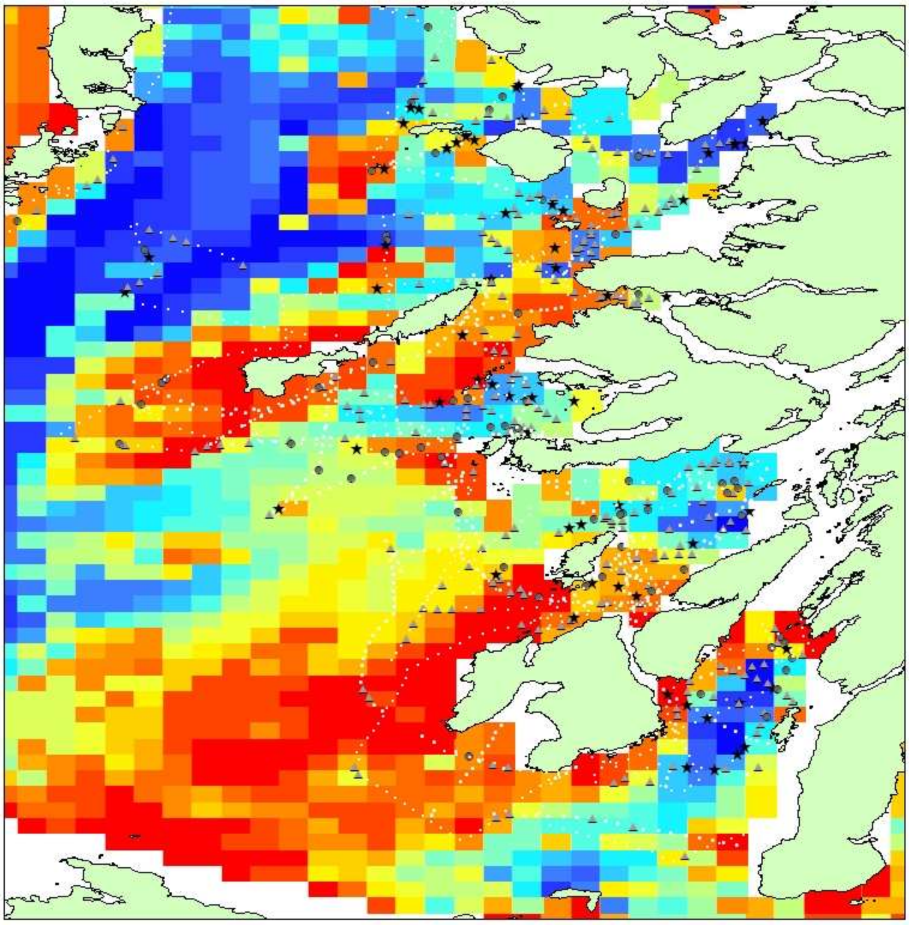


Figure 4.13 - Spatial prediction of acoustic noise levels for the best model based on all acoustic survey data collected between 2004-2005. Overlaid on the maps are the effort segments (white dots) and the segments with visual but no acoustic detections (dark grey circles), segments with acoustic but no visual detections (grey triangles), and segments with both visual and acoustic detections of harbour porpoises (black stars). Colours represent noise levels from low (blue) to high (red), ranging from 270-360 dB, colour gradation based on 20 levels using quantile classification.

4.3.3 Model selection: temporal robustness with year

Of the survey variables, sea state was the most important predictor of the number of groups of porpoises detected visually in all models, explaining between 3.2% (2003) to 18.2% (2005) of the deviance (Appendix Table A3.3, A3.4 & A3.6). As before, detections decreased significantly above sea state 1. Boat speed generally had no effect on sightings rate, except in 2003 when it was the most important survey variable, but only explained 3.7% of the deviance. In this one case, porpoise sightings decreased linearly with increasing boat speed. Engine on/off as a factor variable was also only significant at explaining the detection of harbour porpoises in one model: that for 2004-2005, and showed higher detections when the engine was on, explaining only 1.4% of the deviance.

The best models for each year individually, and grouped by two or three years is shown in Figure 4.14 and in Appendix Table A3.3, A3.4 & A3.6. Maximum tidal speed was the most significant predictor of harbour porpoise visual detections in all models, explaining between 2.7% (2005) to 9.0% (2003) of the deviance. Harbour porpoises visual detections were shown to decrease relatively linearly with increasing tidal speed (Figure 4.8 & 4.14). Position in the spring-neaps cycle was a significant predictor of harbour porpoises in all but one model (2005), explaining between 1.3% (2003-2005) to 6.3% (2003) of the deviance. As shown previously, harbour porpoises were seen more during spring than during neap tides (Figure 4.8 & 4.14).

Of the remaining environmental variables, longitude was significant in explaining harbour porpoise detection rates in 2003 and in the two year 2003-2004 model, explaining between 1.0 to 1.3% of the deviance respectively. Harbour porpoises were found preferentially towards the east (towards the mainland) of the survey area, than to the west. Also in 2003, harbour porpoises were detected to a greater degree during slack tides than during flood or ebb (Figure 4.14), with position in the tidal cycle explaining 8.9% of the deviance (Appendix Table A3.6). In two-year model for 2003-2004, depth and the amount of sand in the sediment were the final two significant predictors of harbour porpoises. Depth explained 1.5%, and the proportion of sand in the sediment explained 3.2% of the deviance (Appendix Table A3.5), with porpoises detected to a greater degree in deeper water and in areas with between 20-70% sand in the sediment.

In the final full three-year model of the number of harbour porpoise groups detected per 2 km segment, time of day was also a significant predictor variable explaining 1.9% of the deviance and showing a maximum detection rate during the middle of the day (Figure 4.14, Appendix Table A3.6).

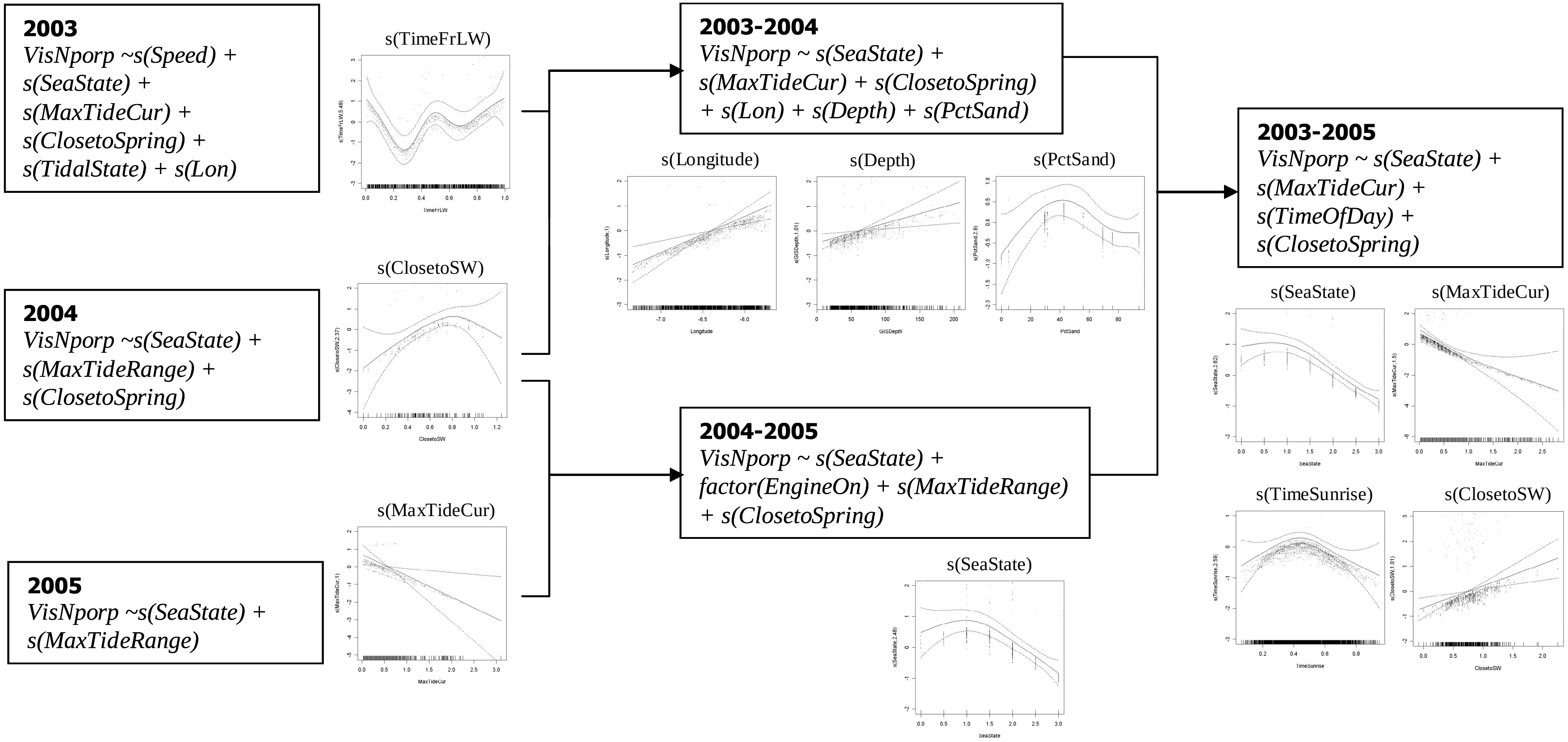


Figure 4.14 – Schematic of the best GAM models for the core survey area for all years 2003-2005 individually, and grouped by 2 or 3 years. Selected smooths are shown to illustrate the relationships between the numbers of harbour porpoise groups seen per 2 km and the environmental variables. Smooths are only shown where they were different, any smooths not shown can be assumed to be the same as for the full three year model.

Overall, the best model for the full three years (2003-2005) for the core survey area explained 15.9% of the deviance, of which 8.2% was explained by environmental variables:

VisNporp ~ s(SeaState) + s(MaxTideCur) + s(Time) + s(CloseToSpring)

Each of the variables in each of the best models was tested to determine whether overfitting was occurring by comparing the full model with those excluding the last 1, 2, 3, 4 or 5 variables by calculating its performance on the test dataset. This suggested that the majority of models were not overfitted except for the 2003 model, which suggested that neither tidal state nor longitude were required in the model.

The model for 2003-2004 performed the best with $p < 0.05$ based on the training dataset, and $p < 0.01$ for the test dataset (Table 4.3). All the models with two-three years data modelled together resulted in a model that was significantly ($p < 0.05$) better than a random intercept-only model based on the training 75% dataset on which the models were built.

Table 4.3 – Significance of each of the models on the training 75% randomly sampled segments, and on the test 25% remaining segments for each of the models.

Dataset	Model	Training 75%	Test 25%
2003	VisNporp ~ s(Speed) + s(SeaState) + s(MaxTideCur) + s(ClosetoSpring)	0.0843 (n=714)	0.564 (n=238)
2004	VisNporp ~ s(SeaState) + factor(EngineOn) + s(MaxTideCur) + s(ClosetoSpring)	0.0682 (n=455)	0.9547 (n=152)
2005	VisNporp ~ s(SeaState) + s(MaxTideCur)	0.0809 (n=516)	**< 0.01** (n=172)
2003-2004	VisNporp ~ s(SeaState) + s(MaxTideCur) + s(ClosetoSpring) + s(Lon) + s(Depth) + s(%Sand)	**< 0.05** (n=996)	**< 0.01** (n=332)
2004-2005	VisNporp ~ s(SeaState) + factor(EngineOn) + s(MaxTideCur) + s(ClosetoSpring)	**< 0.05** (n=972)	0.1125 (n=324)
2003-2005	VisNporp ~ s(SeaState) + s(MaxTideCur) + s(TimeOfDay)+ s(ClosetoSpring)	**< 0.05** (n=1712)	0.1138 (n=570)

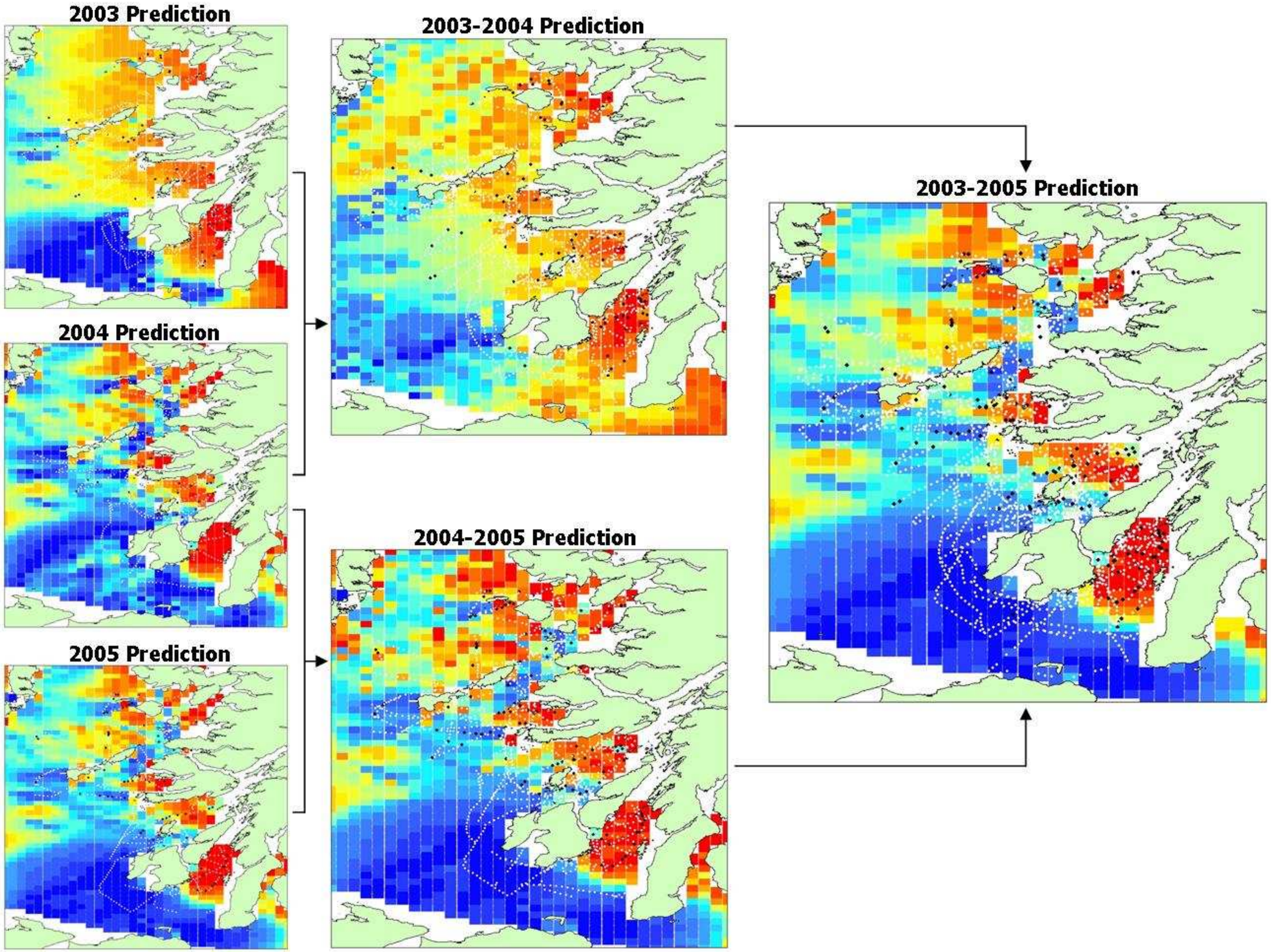

2003 Prediction
2003-2004 Prediction
2003-2005 Prediction
2004 Prediction
2004-2005 Prediction
2005 Prediction

Figure 4.15 (previous page) – Predictive plots based on the best GAM models by forward model selection for 2003, 2004, 2005, two-year models 2003-2004 and 2004-2005, and the full three year model for 2003-2005 modelling the number of harbour porpoise groups per 2 km segment based on surveys carried out in the core area around the Argyll and Small Isles. Overlaid on the maps are the effort segments (white dots) and the visual detections (black dots). Colours represent density from low (blue) to high (red), ranging from 0 to 2.3, colour gradation based on 20 levels using quantile classification (ArcGIS 9.0).

The predictive plots for 2004, 2005, 2004-2005, and 2003-2005 are very similar but also have very similar models (Figure 4.15). There is also very little difference between the predictive plots for 2004-2005, and 2003-2005, despite the latter including three additional variables (longitude, depth and proportion of sand in the sediment). However, this model prediction suggested that some of the more westerly areas such as north of Coll & Tiree were predicted to have high densities of porpoises despite there being very few observed porpoises in this area. As in the previous section (§ 4.3.1), the model predicts low porpoise densities around Colonsay, to the west of the Ross of Mull (Iona), and around Eigg & Muck, where there were quite a high density of sightings.

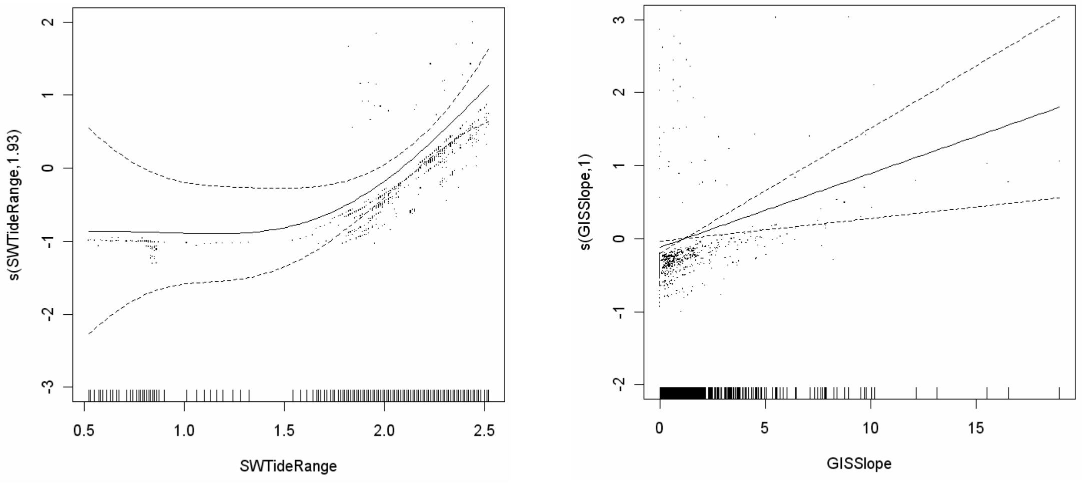
The remaining two models (2003 and 2003-2004) predicted that harbour porpoises were spread over a wider proportion of the survey area than the other models, with higher densities predicted over the whole survey area. However, all models predicted highest porpoise densities towards the coastal areas, i.e. in the Sound of Jura, Firth of Lorne, west of Mull (around the Treshnish Isles) and around the Small Isles.

4.3.4 Model selection: Effect of expanding survey extent

In 2005, the surveys extended to the whole of the Inner Hebrides, surveying areas throughout the Minch and in the coastal areas around the Outer Hebrides (Figure 4.1). Models were therefore constructed separately for 2005 with the expanded survey area to determine the effect on the overall model selected.

The most important environmental predictor for the expanded survey area changed from maximum tidal current to spring tidal range explaining 7.6% of the deviance (Appendix Table A3.6). Harbour porpoise sightings were higher in areas with high spring tidal range (Figure 4.16). The best model for the expanded survey area for 2005 also included a smooth of slope, with a suggested preference of harbour porpoises for areas of higher slope (Figure 4.16), though it only explained 1.1% of the deviance (Appendix Table A3.6). The overall model explained 23.7% of the deviance, of which 9.8% of the deviance was explained by environmental variables (Appendix Table A3.6).

There were no significantly over-fitted terms within the full model, and the model was significant to $p < 0.01$ when compared to a random intercept-only model based on the training data. Although the model was not significant ($p = 0.131$) when compared to a random intercept-only model based on the test data, it still performed better than the random model ($p < 0.5$).



(a) **(b)**

Figure 4.16 – Relationship between visual detections of harbour porpoises and (a) spring tidal range in metres (d.f. = 1.9), and (b) slope in ° (d.f. = 1) for all 2 km segments (n = 788) surveyed over the whole surveyed area around Inner Hebrides in 2005. The 95% confidence intervals are shown by the dotted lines, and black dots show the residuals around the smooths.

This model suggested that the highest density of harbour porpoises is predicted around Skye, in common with the areas with highest tidal range (Figure 4.17). Moderately high densities are predicted throughout the Inner Hebrides, with very low densities predicted in the Sound of Jura, and in a rough line running from the west of Islay to the tip of Barra.

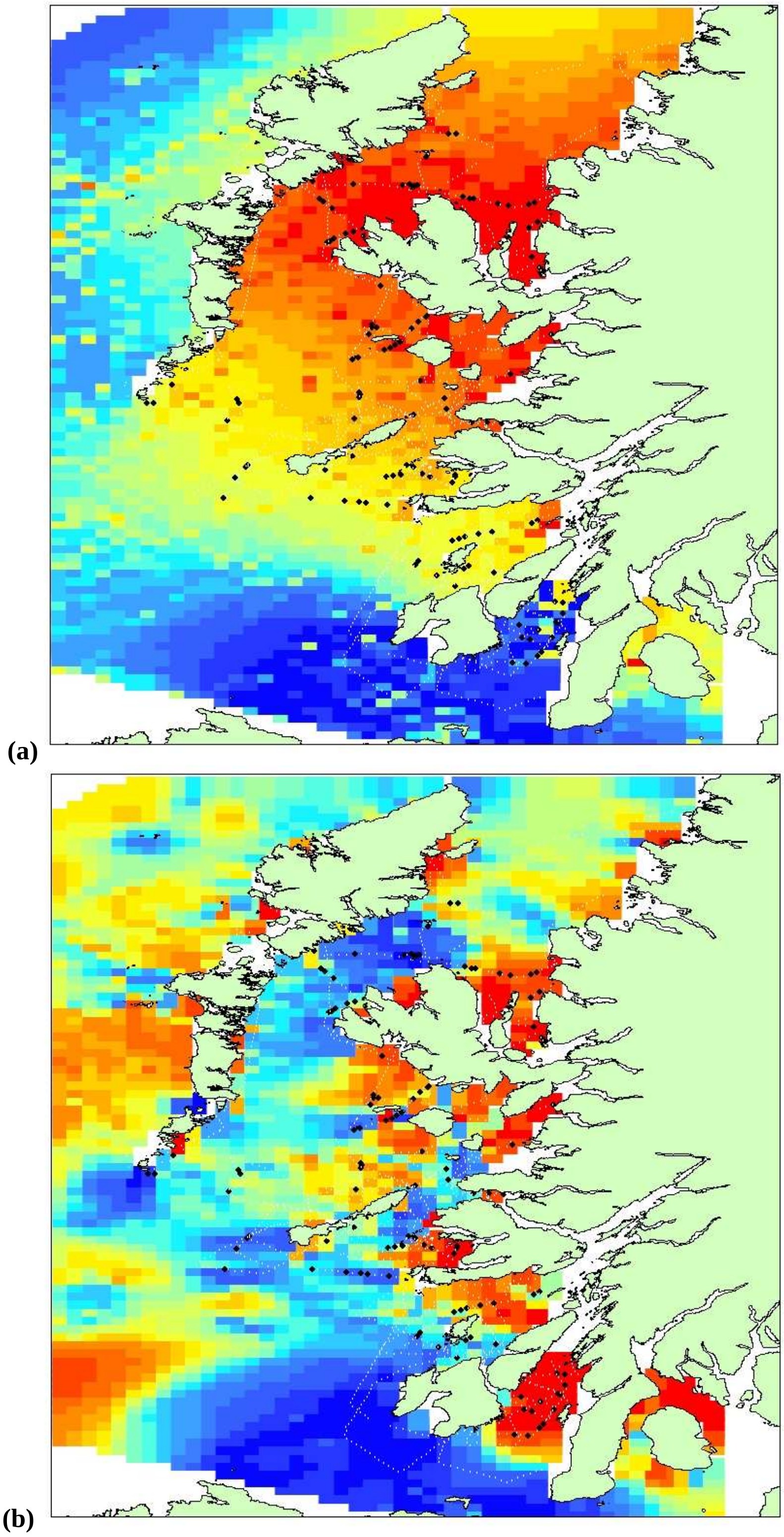


Figure 4.17 – Spatial prediction of harbour porpoise density (groups/2km) for the best model based on visual detections for surveys carried out (a) throughout the Hebrides, and (b) confined to the southern Inner Hebrides during 2005. Segments in which harbour porpoises were detected visually are presented as black dots and white dots are where harbour porpoises were absent. Colours represent predicted porpoise density from low (blue) to high (red), ranging from 0-3.6 for the visual model, colour gradation based on 20 levels using quantile classification.

4.4 Discussion

4.4.1 Comparing visual and acoustic predictive models

The rates of acoustic and visual detections were significantly different. Over twice the number of harbour porpoise pods were detected acoustically than visually in those segments which had both visual and acoustic effort with sea state ≤ 3. When data from higher sea states were included, the ratio of acoustic to visual harbour porpoise detections increased significantly, by 8 times or more. This is consistent with other studies on similar platforms, for example, 8 times as many harbour porpoise pods were detected acoustically than visually in surveys carried out in the Baltic Sea from the IFAW research motor-sailor *Song of the Whale* (Gillespie et al. 2005). In my analysis, the reduced visual sightings rate was mainly explained by the effect of sea state on porpoise sightings. In some years, sea state explained as much as 18.2% of the deviance (even when restricted just to sea state ≤ 3), and similar to other studies (Palka 1996), this was mainly due to the rapid drop in sightings rates above sea state 1, with few sightings in sea states > 2.

Although to a much lesser degree (maximum explained deviance of 5.9%), high frequency noise levels significantly affected the acoustic detection rates of harbour porpoises. Detection rates of harbour porpoises decreased with increasing noise levels. This reduction in acoustic detection rate with ambient noise levels is similar to that found for other studies of different cetacean species (Gordon et al. 2000). In my study area, the main factors influencing high frequency ambient noise levels included depth, sediment type, tidal state and current speeds, the engine being on or off, and boat speed. Ambient noise levels were shown to increase when the engine was on and with increasing speed, similar to that found by Erbe (2002). The increase in noise levels in shallower water and gravel substrate are likely to result from the reflective properties in these habitats (Urick 1983). Sound, such as that produced by the survey vessel, will be absorbed differently by different substrate types: mud absorbs sound energy so reflects less sound than sand or gravel substrate (Urick 1983). Sound also reverberates in shallow water, but distributed and absorbed over a wider volume in deeper water (Urick 1983). So any noise produced by the vessel either from the engine or flow noise through the water, is likely to be reflected and amplified within shallow, gravelly habitats.

Similarly, noise generated by the environment will also be a source of ambient noise (Urick 1983). The amount of gravel in the sediment was correlated with tidal current: areas with high tidal currents had more gravel in the substrate. Tidal state and speed may therefore have the effect of moving substrate, or creating more wave action, creating a different source of noise in the water column. Certainly Urick (1983) suggests that noise levels are generally higher in areas of tidal currents. Biological sources of high frequency noise include snapping shrimp, which was suggested by Johnson et al. (1947) to be the main source of high frequency ambient noise in shelf waters. Snapping shrimp are crustaceans that create a very loud broad band click (2-200 kHz) when they snap their claws in order to scare off predators or stun their prey (Au & Banks 1998). They are bottom living species that tend to prefer gravely substrates (Nadia et al. 2005), or habitats with crevices or holes in which the shrimp can burrow. There is some suggestion that they also prefer areas of low current and shallower water (< 60 m), even if their preferred bottom habitat is available in deeper water (Johnson et al. 1947). Since very loud broadband clicks thought to originate from snapping shrimp were heard and detected frequently throughout the survey area, it is possible that the varying levels of high frequency ambient noise in differing habitats may also reflect the habitat preferences of snapping shrimp.

Modelled noise levels showed that the locations at which there were high predicted noise levels often had visual detections not accompanied by acoustic detections. Higher ambient noise levels are likely to mask quieter or more distant harbour porpoise vocalisations, thus reducing the detection range of the hydrophone (Richardson et al. 1995). Also, if the habitat is acting to amplify vessel noise (e.g. in shallow areas with gravel substrate) then porpoises may respond to the vessel by moving away (Palka & Hammond 2001). Since visual detections of porpoises are made ahead of the vessel but acoustic detections behind the vessel, any movement away from the vessel would result in porpoises that are detected visually not being detected acoustically. The combination of both reduced detection range, and movement of porpoises away from the vessel in environments that amplify vessel noise may explain this higher detection visually than acoustically in noisy habitats.

The inclusion of sea state and noise levels within the models should compensate for the variation in detection rates due to each variable. However, despite compensating for all measured survey effects, different environmental variables described harbour porpoise distribution when based on visual survey data than when based on acoustic survey data. For example, position in the spring-neaps tidal cycle was an important predictor of visually detected harbour porpoise distributions, but excluded from the acoustic models. In this case, porpoises were visually detected at a higher rate during higher tides (i.e. closer to spring tide). This suggests that porpoises may be more visible at this time, perhaps due to more vigorous foraging activity creating stronger visual cues. Certainly, evidence suggests that prey tend to be more aggregated during spring tides and more dispersed during neaps tides (Irons 1998). This possible change in behaviour of porpoises over the tidal cycle appears to be more evident visually than acoustically, though it would be interesting to analyse foraging sounds (rapid clicks or ‘buzzes’) to see if these are recorded more often in certain areas or certain tidal states.

However, the most significant variables in both models (maximum tidal current and percentage mud in the sediment) were correlated, with higher mud in the sediment of areas with low tidal currents. Also examining the predictions based on the visual and acoustic models, they were very similar for the core high predicted density areas despite the models being very different. The high density areas were predicted in both models to be the more coastal areas of the Sound of Jura, Firth of Lorne, around the Treshnish Isles and the Small Isles.

Despite the differences in data collection methodologies, and in detection rates, the models were able to reliably predict high-use areas for harbour porpoises in the southern Inner Hebrides. However, the results of the modelling suggest exercising caution when combining data sets, especially without first compensating for survey effects in the visual survey data and the acoustic survey data separately before combining data sets (unlike Bailey 2006 & Gridley 2005).

4.4.2 Model robustness over time

One of the key requirements for a robust predictive model, is that it is able to reliably predict distributions through time (Araujo & Guisan 2006; Boyce et al. 2002). This is essential if areas are to be used for conservation purposes, whether for understanding which areas are critical to the species in order to avoid activities likely to harm the species (Harwood 2002), or for the designation of Marine Protected Areas (Cañadas et al. 2005).

In this analysis, the same one or two environmental variables were found to be significant in explaining the distribution of harbour porpoises detected visually over time: maximum tidal current and position in the spring-neaps cycle. The relationship between harbour porpoises and these environmental variables did not change over time: with higher detection rates in areas of low tidal current, and at spring tides. The models therefore predict the same core areas of high density year on year from 2003-2005. Core high density areas were predicted in the Sound of Jura, Firth of Lorne, west of Mull around the Treshnish Isles, and in patches around the Small Isles.

There were some inter-annual differences between the models and the model predictions. This appeared to be partly, if not entirely, driven by the change in detection rates with sea state. In 2003, weather conditions were excellent, and sea state only explained 3.2% of the deviance. In this year it was possible to explain the maximum amount of explained deviance with environmental variables of all the models (25.2%): tidal state was able to explain a large portion of the deviance in addition to maximum tidal speed and position in the spring-neaps cycle. In contrast, 2005 had the worst weather conditions and the worst sea state, with sea state explaining 18.2% of the deviance. This meant that maximum tidal state was the only environmental variable included in the model and explained only 2.7% of the deviance. Forney (2000) showed a similar result when modelling the species-environment relationship for Dall's porpoises (*Phocoenoides dalli*) off the Californian coast. She found that sea state was much worse in 1996 than in the previous two years of her study, such that the model was unable to fully capture the species-environment relationship for the species during that year.

4.4.3 Model robustness over space

The final check for a robust predictive model, is that a model is transferable in space, i.e. it can be applied to other areas (Araujo & Guisan 2006; Boyce et al. 2002; Fielding & Bell 1997; Fielding & Haworth 1995; Randin et al. 2006). For harbour porpoises, little was known about their distribution outwith the core area surveyed by the Hebridean Whale and Dolphin Trust (i.e. outwith the coastal areas around the southern Inner Hebrides). However, during 2005, the first surveys were carried out in the northern Hebrides. This made it possible to investigate whether the model based on the core survey area was able to predict distributions throughout the Hebrides, but also whether a model based on the full area would result in a different environmental model and predictions.

The environmental variables explaining the distribution of harbour porpoises in the core area were different from those for the full area surveyed in 2005. The most important variable changed from maximum tidal current to spring tidal range, with higher detection of harbour porpoises in areas of higher tidal range, such as areas around the Isle of Skye in the full survey *extent*. In addition, there were significant differences between the predicted harbour porpoise density maps. For the model based on the full survey extent, harbour porpoise density was predicted to be highest around the Isle of Skye. However, for areas such as the Sound of Jura a low density of harbour porpoises was predicted based on the full area model, but high with the core area model. The change in variables selected between *extents* suggests that the model from the core survey area does not apply well to other areas. Guisan & Thuiller (2005) suggested that incorrect models can be arrived at if only part of an important environmental gradient is sampled. For example, in 2005 the survey covered a significantly wider range of spring tidal ranges than in previous years, with more survey effort carried out around Skye (where tidal ranges are highest). It is possible that tidal range is a more significant predictor of harbour porpoise distributions over the whole of the Inner Hebrides than tidal current, but that the limited coverage of spring tidal range in the core area was not sufficient to model it. Other studies also failed to find good transferability of models between areas (Fielding & Bell 1997; Randin et al. 2006), though these studies found that the ability for a model to predict distributions reliably into other areas depended both on the species, and the differences in the availability of habitat between areas.

The extent to which the species-environment relationships could be modelled in 2005 was limited due to the poor sea state in that year. In addition, during 2005 there was also a significant change in the ecosystem on the west coast of Scotland, for example: minke whales that had been abundant in the region during the summer virtually disappeared from the area, basking sharks significantly increased in abundance, and some seabird populations, such as kittiwakes, guillemots and puffins, failed to fledge chicks (Stevick et al. 2007).

In general, the results of this analysis suggest caution when trying to apply a model outside the area surveyed. Due to the worse weather conditions, and the ecosystem changes that took place in 2005, it is recommended that further years data from the entire Inner Hebrides are obtained and analysed. This may allow evaluation of (a) potential changes in distribution and habitat preferences due to the ecological changes that have taken place, and (b) whether predictive models and habitat preferences are different for the entire Inner Hebrides.

4.4.4 Harbour porpoise habitat preferences

Harbour porpoises were predominantly influenced by tidal variables in the coastal waters of the west coast of Scotland. The most important of the tidal variables in explaining harbour porpoise distribution *visually* was maximum tidal current, with sightings rates higher in areas of low tidal current. This is counter what would be expected from the literature: studies suggest harbour porpoises are found in areas of high tidal currents (Calderan 2003; Johnston et al. 2005). However, the majority of studies examining cetaceans with tidal currents and tidal state were single location studies carried out at sites known to have strong tidal activity (Calderan 2003; Johnston et al. 2005; Mendes et al. 2002; Philpott et al. 2007). Thus these studies examined harbour porpoise relative abundance at a single spatial location at a very fine temporal scale, whereas this study examined porpoise relative abundance at a large area and relatively large spatial scale over a large temporal scale. This suggests that although cetaceans such as harbour porpoises may associate with areas of high tidal current at a small temporal and spatial scale (small *extent*), they may not associate with areas of high tidal current at a large temporal and spatial scale (large *extent*).

Off the west coast of Scotland, the areas of highest tidal current were found in areas where sea water has to pass through narrow channels between land masses. The largest area of very high tidal currents lies between the Mull of Kintyre off Scotland and Ireland (North Channel), where the Irish Sea current meets the Atlantic water travelling around the west of Ireland. The two currents have tides that are 180° out of phase resulting in a difference in sea height where the two meet. Water travels down this sea height gradient causing the high tidal currents which are found to the west of Islay and through the North Channel (Gillibrand pers. comm.). This area was not often surveyed due to the frequent poor sea states, due in part perhaps to the large tidal currents in the area. There were therefore very few sightings of porpoises in this area: even on good weather days there was usually a large swell (pers. obs.), making sightings of porpoises very challenging. The importance of maximum tidal current in explaining visual detections of harbour porpoises could therefore be due to a combination of factors: firstly, sightings are poor in large areas of high tidal currents due to the worse sea state in the areas; and secondly, porpoises may only prefer areas of high tidal current when at a spatial scale that is lower than the predictions were made here, or that the analysis was done (Johnston et al. 2005; Watts & Gaskin 1985).

The overall second best predictor of visually detected harbour porpoises was the position in the spring-neaps tidal cycle, with higher sightings of harbour porpoises towards spring tides rather than neap tides. Spring tidal currents are higher than neap tidal currents, and so are usually strong enough to break up any stratification in the water column causing tidal mixing (Mann & Lazier 2006). Areas in which tidal mixing occurs are generally quite productive due to nutrients being brought from the bottom to the surface encouraging primary production (Mann & Lazier 2006). There is some evidence that behaviour is different during different tidal speeds for fish species (Nichol & Somerton 2002), and top predators such as sea birds (Irons 1998). In a study of kittiwakes (*Rissa tridactyla*), Irons (1998) found that the birds took longer foraging trips during neap than spring tides, with some individuals changing their foraging locations between spring and neaps tides. He suggested that this change in behaviour and foraging time was due to the reduced tidal currents during neap tides not concentrating prey as well as the powerful spring tidal currents, thus making prey less available to foragers. If prey is more aggregated during spring tides than during neap tides, harbour porpoises may be foraging more vigorously during this time creating stronger visual cues.

To a similar extent, harbour porpoises were visually detected to a greater amount in ebb rather than slack or flood tides in 2003. This preference for ebb tides, is actually the opposite than that found in other studies of harbour porpoises, where they showed a strong increase in detection rates during flood tides (Calderan 2003; Johnston et al. 2005). However, the literature does suggest that this is a site-specific phenomena since aggregation of prey tends to occur either at flood (Alldredge & Hamner 1980; Cotte & Simard 2005; Zamon 2002, 2003) or ebb (Coyle et al. 1992; St John et al. 1992). Some marine animals, such as black-legged kittiwakes, have been found to associate with either the ebb or flood tides in different foraging locations (Irons 1998). Similar to the findings for higher sightings rates of porpoises at spring tides, the higher sightings rates at ebb tides may reflect the aggregation of prey at this time, resulting in more vigorous foraging by harbour porpoises and thus stronger visual cues.

Of the last of the tidal variables, spring water tidal range was the most significant environmental predictor variable for the models based on the full surveyed *extent* and a significant predictor for the core surveyed *extent* in the acoustic model for 2004-2005. Harbour porpoise detection rates were higher in areas with high tidal range. This association with high tidal range may seem contradictory to the association with low maximum tidal current, however tidal range and tidal current were found to be negatively correlated ($r = -0.325$, $p < 0.001$). This appears counter-intuitive, however, if the maps of spring tidal range and maximum tidal current are compared (Figure 4.6), it can be seen that the area of very high tidal currents between Scotland (Mull of Kintyre & Islay) has a very low tidal range. This lack of tidal range in the area is due to the Atlantic water propagating northward along the west coast of Ireland meeting the Irish Sea water passing northwards through the North Channel (Simpson et al. 1979). Since the two currents are 180° out of phase, the tides cancel out resulting in little or no tidal range to the south west of Islay (Gillibrand pers. comm.). This phenomenon is only evident in the area surrounding the North Channel, although it dominates a large proportion of the south-west part of the survey area. This area obviously covers a larger proportion of the core survey extent than in the full survey extent, so is therefore likely to bias variable selection to a greater degree in the core area than the full area. Outside of the area surrounding the North Channel, high tidal range provides an indication that an area is likely to be subject to tidal activity, even if the current is only strong when it is combined with topography (narrow channels amplifying the effect of tide). This general association between harbour porpoise detection rates and high tidal ranges, may therefore be due to the higher productivity (higher prey) associated with these tidally mixed areas.

The relationship between time of day and harbour porpoise sightings rates suggested that more porpoises were detected visually in the middle of the day, with lowest detections around sunrise and sunset. There is some indication of diurnal variation in surfacing behaviour of cetaceans (Benoit-Bird & Au 2003; Otani et al. 1998; Westgate et al. 1995), however these studies mostly showed day-night changes in behaviour. Benoit-Bird & Au (2003) also showed a diurnal change in water depth usage, with dolphins following the vertical migration of their prey. Diurnal changes in prey distribution are well documented, for example, Atka mackerel (*Pleurogrammus monopterygius*) in the Aleutian Islands were show to increase vertical migration with changes in light levels, with maximum movement towards the surface in the middle of the day, and minimum at sunrise and sunset (Nichol & Somerton 2002). Sandeels (*Ammodytes* spp.) are also known to emerge from the sediment in daylight hours to feed (Winslade 1974). Though whether this makes them more or less vulnerable to harbour porpoise predators is not known. If harbour porpoise prey is more available with increasing light levels, the increase in sightings rates at this time may reflect increased visibility during foraging activity, though this requires further investigation.

Sediment type was the most significant predictor of the acoustic detection of harbour porpoises within the southern Inner Hebrides, with porpoises detected to a greater degree in areas with high mud content. There was also some indication of increased visual detection rates in sandy substrates (2003-2004). Other studies have linked a preference for certain substrate types to the habitats suitable for prey species (Aarts 2006; Macleod et al. 2004). For example, in the study carried out by Macleod et al. (2004), minke whale (*Balaenoptera acutorostrata*) distribution in the same area as this study (Isle of Mull) was compared to predicted sandeel (*Ammodytes marinus*) and pre-spawning herring (*Clupea harengus*) habitat based on the reported sediment preferences for these species. They showed that minke whales aggregated in areas of sandeel habitat (sand/gravel) during the spring, but shifted distribution towards predicted pre-spawning herring habitat (gravel) as the summer progressed. Aarts (2006) modelled grey seal (*Halichoerus grypus*) distribution off the west coast of

Scotland (mainly from the outer Hebrides out towards the shelf edge) and found that grey seals preferred areas of high gravel and sand content, which he linked with sandeel habitat. Similarly, harbour porpoises around the British Isles have been found to forage both on sandeels and herring, though more predominantly whiting (*Merlangius merlangus*) (Martin 1996; Rae 1973; Roberts 2005; Santos 1998; Santos & Pierce 2003). Whilst pre-spawning herring associate with gravel substrates (Maravelias et al. 2000), sandeels prefer areas of sand in which they burrow during the night and over the winter, both as an anti-predator behaviour and to conserve energy (Wright et al. 2004). In 2003-2004, the increased detection rates of harbour porpoises in areas with higher amounts of sand in the sediment may reflect foraging behaviour on sandeels.

Little is known about the sediment preferences of whiting, which comprises a very large proportion of harbour porpoise diet in British waters (Roberts 2005). Therefore, based on prey species it is difficult to determine why the acoustic detection rates of harbour porpoises were so high within areas with high mud. There is a possibility that whiting are found over this type of substrate, but there is not enough information on whiting distribution to be certain. Species that are known to prefer muddy sediment include flatfish such as some sole species, flounder, and young halibut (Cabral 2000; Howell et al. 1999; Stoner & Abookire 2002). It is more likely that the increased detection rate in muddy areas is related to the strong correlation between maximum tidal current and the percentage mud in the sediment ($r = -0.541$, $p < 0.001$). Areas that had low tidal current also had a higher proportion of mud in the sediment. So the increased acoustic detection rates within muddy substrates may be another reflection of a preference for low tidal current areas.

4.4.5 Conclusions

Visual and acoustic data were best fitted by predictive models with different parameters, the cause of which is difficult to prove without further investigation. However, despite the difference in overall models, the two main predictor variables (maximum tidal current and percentage mud in the sediment) were strongly correlated, and the same areas of high density were predicted.

The model explaining the distribution of harbour porpoises detected visually within the southern Inner Hebrides was consistent over time, with the same two predictor variables selected every year. The most important predictive variables for explaining harbour porpoise distribution consistently over time included maximum tidal current, and position in the tidal cycle, with preferences for areas of low mean tidal currents, and for spring tides. It is evident that this only applies at this scale of analysis and over the study area. At a smaller scale harbour porpoise distribution is likely to be more closely tied to small scale combination of tidal currents, topography (proximity to narrow channels) and oceanographic variables that influence both productivity and aggregation of prey (Johnston et al. 2005).

Different variables explained the distribution of visually detected harbour porpoises over the whole of the Inner Hebrides, than in the southern Inner Hebrides. In general, the results of this analysis suggest caution when trying to apply a model outside the area surveyed.

4.5 References

Aarts, G. 2006. Modelling space-use and habitat preference from wildlife telemetry data. PhD Thesis. School of Biology. University of St Andrews.

Alldredge, A. L., and W. M. Hamner. 1980. Recurring aggregation of zooplankton by a tidal current. Estuarine and Coastal Marine Science **10**:31-37.

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

Au, W. W. L., and K. Banks. 1998. The acoustics of the snapping shrimp *Synalpheus parneomeris* in Kaneohe Bay. J. Acoust. Soc. Am. **103**:41-47.

Au, W. W. L., R. A. Kastelein, T. Rippe, and N. M. Schooneman. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). J. Acoust. Soc. Am. **106**:3699-3705.

Bailey, H. 2006. Distribution and habitat use of bottlenose dolphins (*Tursiops truncatus*) at varying temporal and spatial scales. PhD Thesis. Department of Zoology. University of Aberdeen.

Barlow, J., T. Gerrodette, and J. Forcada. 2001. Factors affecting perpendicular sightings distances on shipboard line-transect surveys for cetaceans. J. Cetacean Res. Manage. **3**:201-212.

Benoit-Bird, K. J., and W. W. L. Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behav Ecol Sociobiol **53**:364-373.

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

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas 2001. Introduction to Distance Sampling - Estimating abundance of biological populations. Oxford University Press, Oxford.

Burnham, K. P., and D. R. Anderson 2002. Model selection and multimodel inference. A practical information-theoretic approach. Springer-Verlag, New York.

Cabral, H. N. 2000. Distribution and abundance patterns of flatfishes in the Sado Estuary, Portugal. Estuaries **23**:351-358.

Calderan, S. V. 2003. Fine-scale temporal distribution by harbour porpoise (*Phocoena phocoena*) in North Wales: acoustic and visual survey techniques. MSc Thesis. School of Biological Sciences. University of Wales, Bangor.

Cañadas, A., R. Sagarminaga, R. De Stephanis, E. Urquiola, and P. S. Hammond. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conserv: Mar. Freshw. Ecosyst. **15**:495-521.

Chappell, O., R. Leaper, and J. Gordon. 1996. Development and performance of an automated harbour porpoise click detector. Report of the International Whaling Commission **46**:587-594.

Cotte, C., and Y. Simard. 2005. Formation of dense krill patches under tidal forcing at whale feeding hotspots in the St. Lawrence Estuary. Marine Ecology Progress Series **288**.

Coyle, K. O., G. L. J. Hunt, M. B. Decker, and T. J. Weingartner. 1992. Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. Marine Ecology Progress Series **83**:1-14.

Erbe, C. 2002. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. Marine Mammal Science **18**:394-418.

Ferguson, M. C., J. Barlow, P. Fiedler, S. B. Reilly, and T. Gerrodette. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling **193**:645-662.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Fielding, A. H., and P. F. Haworth. 1995. Testing the generality of bird-habitat models. Conservation Biology **9**:1466-1481.

Folk, R. L. 1980. Petrology of sedimentary rocks, Hemphill, Austin.

Forney, K. A. 2000. Environmental Models of Cetacean Abundance: Reducing Uncertainty in Population Trends. Conservation Biology **14**:1271-1286.

Gannier, A., and E. Praca. 2007. SST fronts and the summer sperm whale distribution in the north-west Mediterranean Sea. Journal of the Marine Biological Association of the UK **87**:187.

Gillespie, D., P. Berggren, S. Brown, I. Kuklik, C. Lacey, T. Lewis, J. Matthews, R. McLanaghan, A. Moscrop, and N. Tregenza. 2005. Relative abundance of harbour porpoises (*Phocoena phocoena*) from acoustic and visual surveys of the Baltic Sea and adjacent waters during 2001 and 2002. J. Cetacean Res. Manage. **7**:51-57.

Gillespie, D., and O. Chappell. 2002. An automatic system for detecting and classifying the vocalisations of harbour porpoises. Bioacoustics **13**:37-61.

Gontarek, S. 2005. STJG Tools for ArcGIS v9 - GIS Extract, SAMS, Dunstaffnage, Oban.

Goodson, A. D., and C. R. Sturtivant. 1996. Sonar characteristics of the harbour porpoise (Phocoena phocoena): source levels and spectrum. ICES Journal of Marine Science **53**:465-472.

Gordon, J., and S. Northridge. 2002. Potential impacts of Acoustic Deterrent Devices on Scottish marine wildlife. Scottish Natural Heritage Commissioned Report F01AA404.

Gordon, J. C. D., J. N. Matthews, S. Panigada, A. Gannier, J. F. Borsani, and G. Notarbartolo Di Sciara. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. Journal of Cetacean Research and Management **2**:27-36.

Gregr, E. J., and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Colombia. Canadian Journal of Fisheries and Aquatic Sciences **58**:1265-1285.

Gridley, T. 2005. Combining acoustic and visual survey techniques to determine the factors affecting marine mammal distribution in the outer Moray Firth (NE Scotland). MRes Thesis. Department of Zoology. University of Aberdeen.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Hamazaki, T. 2002. Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). Marine Mammal Science **18**:920-939.

Hamazaki, T. 2004. Modeling species-habitat relationship in the marine environment - a response to Gregr (2004). Marine Mammal Science **20**:356-358.

Harwood, J. 2002. Mitigating the effects of acoustic disturbance in the oceans. Aquatic Conservation: Marine & Freshwater Ecoystems **12**:485-488.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson, and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. ICES Journal of Marine Science **62**:760-770.

Hedley, S. 2000. Modelling heterogeneity in cetacean surveys. PhD Thesis. Department of Statistics. University of St Andrews.

Heinrich, S. 2006. Ecology of Chilean dolphins and Peale's dolphins at Isla Chiloe, southern Chile. PhD Thesis. Department of Biology. University of St Andrews.

Holt, J. T., J. I. Allen, R. Proctor, and F. Gilbert. 2005. Error quantification of a high-resolution coupled hydrodynamic-ecosystem coaastal-ocean model: Part 1 model overview and assessment of the hydrodynamics. Journal of Marine Systems **57**:167-188.

Holt, J. T., and I. D. James. 2006. An assessment of the fine-scale eddies in a high-resolution model of the shelf seas west of Great Britain. Ocean Modelling **13**:271-291.

Howell, P. T., D. R. Molnar, and R. B. Harris. 1999. Juvenile winter flounder distribution by habitat type. Estuaries **22**:1090-1095.

IFAW. 2003. How to build and test IFAW's porpoise hardware, International Fund for Animal Welfare.

Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology **79**:647-655.

Jimenez, I. 2005. Development of predictive models to explain the distribution of the West Indian manatee *Trichechus manatus* in tropical watercourses. Biological Conservation **125**:491-503.

Johnson, M. W., F. A. Everest, and R. W. Young. 1947. The role of snapping shrimp (Crangon and Synalpheus) in the production of underwater noise in the sea. Biological Bulletin **93**:122-138.

Johnston, D. W. 2002. The effect of acoustic harassment devices on harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada. Biological Conservation **108**:113-118.

Johnston, D. W., A. J. Westgate, and A. J. Read. 2005. Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises

Phocoena phocoena in the Bay of Fundy. Marine Ecology Progress Series **295**:279-293.

Kim, Y. J., and C. Gu. 2004. Smoothing spline gaussian regression: more scaleable computation via efficient approximation. Journal of the Royal Statistical Society, Series B **66**:337-356.

Leaper, R., O. Chappell, and J. Gordon. 1992. The development of practical techniques for surveying sperm whale populations acoustically. Report of the International Whaling Commission **42**:549-560.

MacLeod, C. D., C. R. Weir, C. Pierpoint, and E. J. Harland. 2007. The habitat preferences of marine mammals west of Scotland (UK). Journal of the Marine Biological Association of the UK **87**:157-164.

Macleod, K. 2001. The spatial and temporal distribution of cetaceans off the west coast of Scotland in relation to environmental factors: the implications for marine management. PhD Thesis. University of Greenwich.

Macleod, K., R. Fairbairns, A. Gill, B. Fairbairns, J. Gordon, C. Blair-Myers, and E. C. M. Parsons. 2004. Seasonal distribution of minke whales Balaenoptera acutorostrata in relation to physiography and prey off the Isle of Mull, Scotland. Marine Ecology Progress Series **277**:263-274.

Mandleberg, L., C. D. MacLeod, C. Schweder, S. M. Bannon, and G. J. Pierce. in review. A comparison of the predictive abilities of four approaches for modelling the distribution of cetaceans. Biological Conservation.

Mann, K. H., and J. R. N. Lazier 2006. Dynamics of marine ecosystems (3rd Edition). Blackwell Scientific Publications, Cambridge.

Maravelias, C. D., D. G. Reid, and G. Swartzman. 2000. Seabed substrate, water depth and zooplankton as determinants of the prespawning spatial aggregation of North Atlantic herring. Marine Ecology Progress Series **195**.

Martin, A. R. 1996. The diet of harbour porpoises (*Phocoena phocoena*) in British waters. International Whaling Commission, SC/47/SM48.

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

Moisen, G. G., and T. S. Frescino. 2002. Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling **157**:209.

Moses, E., and J. T. Finn. 1997. Using Geographical Information Systems to Predict North Atlantic Right Whale (*Eubalaena glacialis*) Habitat. J. Northw. Atl. Fish. Sci. **22**:37-46.

Nadia, E. P., J.-M. Marie Antoinette, and K. Ilan. 2005. Behavior of the burrowing shrimp Alpheus macellarius in varying gravel substrate conditions. Journal of Ethology **V23**:173.

Nichol, D. G., and D. A. Somerton. 2002. Diurnal vertical migration of the Atka mackerel *Pleurogrammus monopterygius* as shown by archival tags. Marine Ecology Progress Series **239**:193-207.

Olesiuk, P. F., L. M. Nichol, M. J. Sowden, and J. K. B. Ford. 2002. Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbour porpoises (*Phocoena phocoena*) in Retreat Passage, British Columbia. Marine Mammal Science **18**:843-862.

Otani, S., Y. Naito, A. Kawamura, M. Kawasaki, S. Nishiwaki, and A. Kato. 1998. Diving behavior and performance of harbor porpoises, *Phocoena phocoena*, in Funka Bay, Hokkaido, Japan. Marine Mammal Science **14**:209-220.

Palka, D. 1996. Effects of Beaufort sea state on the sightability of harbour porpoises in the Gulf of Maine. Report of the International Whaling Commission **46**.

Palka, D. L., and P. S. Hammond. 2001. Accounting for responsive movement in line transect estimates of abundance. Canadian Journal of Fisheries and Aquatic Sciences **58**:777-787.

Parsons, E. C. M., I. Birks, P. G. H. Evans, J. C. D. Gordon, J. H. Shrimpton, and S. Pooley. 2000a. The possible impacts of military activity on cetaceans in west Scotland. **14**:185-190.

Parsons, E. C. M., J. Shrimpton, and P. G. H. Evans. 2000b. Cetacean conservation in northwest Scotland: perceived threats to cetaceans. European Research on Cetaceans **13**:128-133.

Philpott, E., A. Englund, S. Ingram, and E. Rogan. 2007. Using T-PODs to investigate the echolocation of coastal bottlenose dolphins. J. Mar. Biol. Ass. UK **87**:11-17.

Quick, N. J., S. J. Middlemas, and J. D. Armstrong. 2002. The use of anti-predator controls at Scottish salmon farms. Fisheris Services Report No 03/02. FRS Freshwater Laboratory, Pitlochry.

Rae, B. B. 1973. Additional notes on the diet of the common porpoise (Phocoena phocoena). Journal of Zoology, London **169**:127-131.

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

Richardson, W. J., C. R. Green Jr., C. I. Malme, and D. H. Thomson 1995. Marine Mammals and Noise. Academic Press, Inc., San Diego, CA.

Roberts, C. 2005. Trends in the diet of the harbour porpoise in British waters. BSc Thesis. Department of Biology. University of St Andrews.

Santos, M. B. 1998. Feeding ecology of harbour porpoises, common and bottlenose dolphins and sperm whales in the Northeast Atlantic. PhD Thesis. University of Aberdeen.

Santos, M. B., and G. J. Pierce. 2003. The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Oceanography and Marine Biology: an Annual Review **41**:355-390.

SCANS-II. 2006. The quarterly newsletter for project SCANS-II: Small Cetaceans in the European Atlantic and North Sea. Issue 7: June 2006.

Simpson, J. H., D. J. Edelsten, A. Edwards, N. C. G. Morris, and P. B. Tett. 1979. The Islay front: physical structure and phytoplankton distribution. Estuarine and Coastal Marine Science **9**:713-726.

St John, M. A., J. Stevenson MacDonald, P. J. Harrison, R. J. Beamish, and E. Choromanski. 1992. The Fraser River plume: Some preliminary observations on the distribution of juvenile salmon, herring and their prey. Fisheries oceanography **1**:153-162.

Stevick, P. T., S. V. Calderan, C. Speedie, J. Shrimpton, and C. B. Embling. 2007. A trophic shift off west Scotland: minke whales and basking sharks in P. G. H. Evans, editor. 21st Annual Conference of the European Cetacean Society, San Sebastian, Spain.

Stoner, A. W., and A. A. Abookire. 2002. Sediment preferences and size-specific distribution of young-of-the-year Pacific halibut in an Alaska nursery. Journal of Fish Biology **61**:540-559.

Urick, R. J. 1983. Principles of underwater sound. Peninsula Publishing, Los Altos, CA.

Watts, P., and D. E. Gaskin. 1985. Habitat Index Analysis of the Harbor Porpoise (*Phocoena phocoena*) in the Southern Coastal Bay of Fundy, Canada. Journal of Mammalogy **66**:733-744.

Weir, C. R., C. Pollock, C. Cronin, and S. Taylor. 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. Continental Shelf Research **21**:1047-1071.

Westgate, A. J., A. J. Read, P. Berggren, H. N. Koopman, and D. E. Gaskin. 1995. Diving behaviour of harbour porpoises, *Phocoena phocoena*. Can. J. Fish. Aquat. Sci. **52**:1064-1073.

Winslade, P. 1974. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) II. The effect of light intensity on activity. Journal of Fish Biology **6**:577-586.

Wood, S. N. 2006a. Generalised Additive Models - An Introduction with R. Chapman and Hall/CRS, Boca raton, Florida.

Wood, S. N. 2006b. The mgcv package. R statistical group.

Wright, P. J., H. Jenson, and I. Tuck. 2004. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. Journal of Sea Research **44**:243-256.

Zamon, J. E. 2002. Tidal changes in copepod abundance and maintenance of a summer *Coscinodiscus* bloom in the southern San Juan Channel, San Juan Islands, USA. Marine Ecology Progress Series **226**:193-210.

Zamon, J. E. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelgo depend on flooding tidal currents. Marine Ecology Progress Series **261**:243-255.

Chapter 5

The relationship between delphinid and herring *Clupea harengus* distributions

Evaluation of a direct predictor variable

Abstract

Direct predictors are rarely included in environmental models of cetacean distributions due to the difficulty of obtaining prey distribution data at the same temporal and spatial scale as the cetacean distribution data. This study made use of fisheries stock assessment surveys as platforms of opportunity to simultaneously measure and investigate the correlation between delphinids and herring (*Clupea harengus*) distributions. The main aim of the study was to investigate the spatial and temporal correlation between the species and to determine whether herring distributions could be used as direct predictors in environmental models of delphinid distributions. A two-element audio (100 Hz – 24 kHz) hydrophone was towed 400m behind a chartered pelagic fishing vessel, *Enterprise,* during one of the Fisheries Research Services (FRS) annual active acoustic surveys for herring in July 2004 and July 2005. The survey covered the continental shelf waters (out to the 250 m depth contour) to the west of Scotland from 56°N to 60°N. 30-second listening stations were carried out every 15 minutes, and dolphin whistle and click sound levels were assessed and noted to provide data on dolphin distribution. A Simrad EK500 echosounder operating at 38, 120 and 200 kHz was used, in conjunction with pelagic trawling, to collect data on the distribution and abundance of herring. The relationship between dolphin and pelagic fish distributions was examined within a Multinomial Logit Model (MLM) framework using an average segment length of 5 km. There was a significant correlation ($p < 0.01$) between delphinids and herring in 2005 but not in 2004, with positive correlation occurring along the shelf edge, and in a small patch in the Minch. This suggests that herring may be a direct predictor of some shelf-edge species such as Atlantic white-sided dolphins (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*). However, additional data on the distribution of other key prey species such as mackerel (*Scomber scombrus*), whiting (*Merlangius*

merlangus), and sandeels (*Ammodytes* spp.) that were not surveyed here may also affect delphinid distributions.

5.1 Introduction

In modelling species distributions, explanatory variables can have direct or indirect influences over a species distribution (Austin 2002; Guisan & Thuiller 2005; Guisan & Zimmermann 2000). For example, the distribution of prey species is likely to have a *direct* effect on cetacean distribution: any animal will spend a lot of its time in locations where it can forage. However, other environmental variables are likely to *indirectly* affect a species distribution; examples include sediment type, tidal state, and tidal range. These indirect variables can affect a species' distribution due to their spatial or time dependent correlation with direct variables such as prey distribution. Clearly, robust models applicable over large areas should be based on *direct* variables (Guisan & Zimmermann 2000). However, as it is often difficult to measure the direct variables such as prey distributions, so predictive models often have to resort to *indirect* measures (Austin 2002).

There are very few studies that incorporate *direct* variables into habitat models of species distributions (Guinet et al. 2001; Hooker 1999; Tynan et al. 2005). Tynan et al. (2005) used a wide range of *indirect* oceanographic variables and *direct* prey variables in models of cetaceans in the Californian Current System. With this combination of both direct and indirect variables, they were able to explain up to 94.4% of the variation in humpback whale (*Megaptera novaeangliae*) distribution in spring. However, the Tynan et al. (2005) study used overall acoustic backscatter at different frequencies rather than actual species of prey. In contrast, Guinet et al. (2001) conducted trawls around the foraging grounds of Antarctic fur seals (*Arctocephalus gazella*) which, combined with satellite telemetry and time-depth recorders, was able to show that fur seals were associating with their myctophid prey at scales larger than 0.2ºx0.2º (around 36x36 km) but not at smaller scales. The paucity of research conducted in this area of ecology is in part due to the difficulty in conducting simultaneous measurement of predators and their prey, in addition to the large amount of resources required to conduct such surveys.

Simultaneous surveys for predator and prey species in the marine environment are relatively rare (Benoit-Bird & Au 2003; Benoit-Bird et al. 2004; Croll et al. 2005;

Fiedler et al. 1998; Smout & Lindstrom 2007; Tynan et al. 2005). Of these studies, only the work carried out by Fiedler et al. (1998), Benoit-Bird et al. (2003, 2004), and Tynan et al. (2005) collected data on the distribution of delphinids and prey species simultaneously. In the unique study carried out by Benoit-Bird and colleagues (2003, 2004) using active acoustics to detect both delphinids and prey synoptically, not only did they find delphinids associating with high prey densities, but also co-operatively corralling prey into smaller patches for feeding. Fiedler et al. (1998) conducted one of the few concurrent hydroacoustic and delphinid visual surveys, relating dolphin distribution to acoustic backscatter (as an indicator of prey density). Their study found an overall correlation of dolphins with backscatter strength, but neither study carried out spatial analysis of correlation between the two variables. Although not simultaneous, Smout & Lindstrøm (2007) carried out acoustic surveys and trawls to identify minke whale (*Balaenoptera acutorostrata*) prey distribution and abundance only 2 days after whale capture in order to parameterise the whales' functional response curve. By using a combination of both active acoustic surveys for prey, and trawls, it was possible to determine distribution and abundance of the individual prey species. This same methodology was used in my study to carry out the first simultaneous study of delphinids and herring distributions in the North Atlantic.

The distribution and abundance of pelagic schooling fish, especially herring, are regularly assessed using active “fisheries” acoustic techniques (Simmonds & MacLennan 2005). In summer, herring form large schools in mid-water that can be detected effectively by echosounders, providing information that is vital to herring stock assessments (Simmonds 2003). As a means to estimate abundance, acoustic surveys are an efficient tool as they offer almost continuous detection of objects (echotraces) in the whole water column, at a very high resolution (typically 20 cm in the vertical), over large distances. The ICES International North Sea Herring Acoustic Survey (INSHAS) is one such example of a multi-vessel acoustic survey with a time series of over 20 years: see Bailey et al. (1998) for a review. The survey takes place each year with the participation of the United Kingdom (Scotland), the Netherlands, Norway, Germany, and Denmark, covering the whole of the North Sea and the west coast of Scotland (ICES 2004). On some surveys, additional environmental sampling is also carried out using RoxAnn sediment type profilers, and continuous temperature and salinity recorders.

These acoustic surveys for assessing fish stocks provide an ideal platform of opportunity from which to conduct surveys for top predators such as cetaceans and seabirds. However, space is often limited such that the cetacean acoustic researcher(s) have to share duties with the fisheries researchers monitoring the fisheries acoustics echotraces for fish school echo-returns. Passive acoustic methods for the detection of cetaceans is relatively automated, requiring fewer people than the equivalent visual survey methods, so is ideal from this type of platform. This also allows for simultaneous monitoring of both ‘vocalising odontocetes’ using earphones, and monitoring of the echotraces for fish schools visually. However, passive acoustic monitoring for delphinids is limited by the difficulty of species identification using acoustic cues. Previous studies have suggested that some species can be reliably distinguished on the basis of their whistles (Oswald et al. 2003; Rendell et al. 1999; Steiner 1981), but these involved making time consuming measurements by hand and only recently have near real-time species identification tools been developed for Pacific Ocean species (Oswald et al. 2007). Therefore, using passive acoustics to study the distribution of dolphins, it is only possible to determine overall delphinid distribution rather than distributions of individual species.

In the shelf waters off the west coast of Scotland, the focal area of this study, the three main delphinid species are known to be common dolphins (*Delphinus delphis*), Atlantic white-sided dolphins (*Lagenorhynchus acutus*), and white-beaked dolphins (*Lagenorhynchus albirostris*) (MacLeod et al. 2007; Macleod 2001; Northridge et al. 1997; Northridge et al. 1995; Weir et al. 2001). These species have been shown to be opportunistic foragers, feeding mainly on shoaling fish (Brophy 2003; Couperus 1997; Overholtz & Waring 1991; Reeves et al. 1999; Santos 1998; Santos et al. 1994). For example dolphins bycaught in the mackerel fishery in south-western Irish waters were found with fresh mackerel (*Scomber scombrus*) in their stomachs, but also otoliths from shoaling mesopelagic fish from deeper waters, suggesting a spatial and temporal change in foraging behaviour (Brophy 2003). Unfortunately, there are very few diet studies of delphinids from the west coast of Scotland to confirm foraging preferences of delphinids, mainly because there are very few strandings and little bycatch in this area. The most recent diet study in Scottish waters (Murphy pers. comm.) analysed 9 common dolphins stomachs from Scottish waters and found that the most common prey consumed were mackerel, whiting and herring (25.6%, 18.5%

and 13.4% of the estimated prey weight respectively). But very few of the other diet studies either for delphinids within Scottish waters (Santos 1998; Santos et al. 1994) or for other delphinids from North Atlantic waters (Brophy 2003; Couperus 1997; Overholtz & Waring 1999; Reeves et al. 1999) suggest that common, white-sided or white-beaked dolphins eat substantial amounts of herring. However, during July the main mid-water shelf species of fish off the west coast of Scotland are the large pre-spawning aggregations of herring (pers. obs.). In addition, given the high energy content of herring (Anthony et al. 2000; Lawson et al. 1998), it would be surprising if delphinids did not take advantage of this available nutritious food source. It is likely, therefore, that although herring may not be the preferred prey of delphinids off the west coast of Scotland, that they may forage on schools opportunistically.

Herring (*Clupea harengus*) are found distributed throughout the shelf waters all around the coast of Scotland (ICES 2004, 2005, 2006; Maravelias 1999, 2001; Maravelias & Reid 1997; Maravelias et al. 2000a, 2000b). The species forages in spring time on species such as *Calanus finmarchicus*, and around July time start to aggregate into large pre-spawning schools to migrate towards the spawning grounds in the waters around the Shetland, Orkney Isles and the Hebrides (Maravelias 1999). They have been shown, in a number of studies carried out by Maravelias et al. (1997, 1999, 2000, 2001) to migrate towards shallower water with sand/gravel type substrate with high zooplankton abundance. Maravelias et al. (2000b) showed that during the summer, herring were closely associated with well-mixed waters and frontal zones, staying below the thermocline, thus following the summer vertical migration of their main *Calanus* prey. The stock size of autumn spawning herring on the west coast of Scotland has been shown to lie around 200,000-400,000 tonnes, and showed a slight increase in stock over the 7 years up to 2004 (ICES 2005, 2006). This represents around 10% of the total West Coast-North Sea-Western Baltic autumn spawning herring stock (ICES Divisions IIIa, IVa, IVc and IVa (North)).

The main aim of this study was to investigate the relationship between distributions of delphinids and herring (*Clupea harengus*), and to explore a new method of evaluating this relationship on a spatial and temporal scale. This was carried out in order to explore the use of herring distributions as a *direct* predictor of delphinid distributions.

5.2 Methods

5.2.1 Data collection

The surveys were carried out on the chartered Motorised Fishing Vessel (MFV) *Enterprise* in July 2004 and July 2005. The area covered was north and west of Scotland from longitude 3°W to the shelf edge (250 m) from 56° N to 60° N (Figure 5.1). The survey design (Figure 5.1) was stratified according to the expected herring distribution based on results from the survey time series. Regular parallel transects were used along lines of latitude. In 2004, the transect spacing was set to 15, 7.5 or 3.75 nm, giving 2, 4 or 8 transects per ICES statistical rectangle respectively. In 2005, due to time constraints, the transect spacing was set to 15 or 7.5 nm. giving 2 or 4 transects per ICES statistical rectangle respectively. The sea area between the Hebrides and the mainland (the Minch) is difficult to survey with the above design, so a zig-zag design with 15 nm spacing was adopted. The total effective cruise track length (i.e. the times at which both active acoustic fish data and passive acoustic delphinid data were collected simultaneously) was 3 241 km in 2004, and 2 530 km in 2005 (Table 5.1 & Figure 5.1).

5.2.1.1 Delphinid data collection

The same hydrophone as described in §2.2.1 was used in these surveys, and was towed 400 m behind the vessel between trawling for herring. Detection and recording programs ran in real time on a laptop running the IFAW logging software package *Logger 2000* (Gillespie 1997), 30-second recordings of the hydrophone were made to hard disk every 2 minutes. All events including recordings were linked to DGPS location within an Access database. In addition, acoustic listening stations of 1 minute were carried out by acoustic monitors every 15 minutes scoring for self survey vessel noise, water noise, remote vessel noise, and delphinid whistles and clicks on an subjective scale of 0 (inaudible) to 5 (loud). Environmental conditions were recorded every hour, with boat speed & direction, wind speed & direction, sea state and swell (the latter two were only possible during daylight hours) entered directly into *Logger*. In 2005, two acoustic monitors rotated the listening shifts. However, in 2004 there had only been space for one person to carry out the cetacean acoustic monitoring, so it was not possible to listen continuously for the 20-hour survey periods, hence continuous listening with listening stations every 15 minutes was only carried out for half the time. Subsequent to this survey, acoustic listening stations of 30 seconds every 15 minutes (or the closest recording to this time) were analysed scoring sounds using the same scale as that used during the survey.

5.2.1.2 Herring data collection

The methods used to carry out the acoustic survey were common to those employed throughout the INSHAS: these are detailed in the Manual for Herring Acoustic Surveys in ICES Divisions III, IV and VIa (ICES 2004) and follow the general principles described in Simmonds et al. (1992) and Simmonds & MacLennan (2005). Acoustic data were collected using a Simrad EK500 scientific echosounder (Bodholt et al. 1989), with three transducers at frequencies of 38, 120 and 200 kHz. The transducers were mounted in a streamlined body towed at a depth of approximately 3-5 m and deployed from the ship's crane approximately 3 m off the starboard side amidships. The echosounder was configured to ping at each frequency simultaneously, every 1 second, with pulse lengths of 1.0 ms. The performance of the echosounder was monitored using standard target calibration techniques (Fernandes & Simmonds 1996). Two calibrations were carried out at the beginning and in the middle of both surveys. The acoustic data were only collected from 03:00 to 23:00 hrs: outwith this collection period (at night) the herring disperse and rise to the surface making them unavailable to the acoustic apparatus.

Major echotrace concentrations were sampled with a pelagic trawl with a net of 20 mm mesh in the codend. When trawling at a speed of approximately four knots the trawl's vertical opening was 12 metres and the horizontal opening was 20 m. A total of 42 trawl catches in 2004, and 34 trawl catches in 2005 provided samples to identify the echotraces and determine the size and age structure of the herring represented in the trawl.

Data were logged from the echosounder to a personal computer with SonarData's Echolog software (SonarData Pty Ltd., GPO Box 1387 Hobart, Tasmania, Australia). The raw data were collected as echogram (Q) telegrams consisting of time stamped digitised volume backscattering strengths (VBS), each pixel on the echogram corresponding to a VBS (unit: dB re $1m^{-1}$). Other telegrams collected included detected seabed depth and geographic location (latitude and longitude). Data were integrated over 2.5 nm (15 minutes at 10 knots) equivalent distance sampling units (EDSU) to determine the Nautical Area Scattering Coefficient (NASC) for herring. The NASC is proportional to herring abundance (MacLennan et al. 2002) and is ultimately used in conjunction with the information from the trawl to determine the abundance of herring at age. For the purposes of the current exercise, the NASC value was summarised into a simple measure of presence/absence within an EDSU. The analysis of the echotraces and translation into herring abundance (NASC) and herring presence/absence was carried out by Eric Armstrong at the Fisheries Research Services (FRS).

5.2.1.3 Environmental data collection

Continuous monitoring of the seabed was carried out in 2005 using the substrate classification system RoxAnn (Marine Microsystems, Aberdeen). It was connected to one of the quadrants of the SIMRAD EK500 38kHz echosounder in operation during the survey. RoxAnn provides two measures of sediment type; E1 representing bottom roughness, and E2 representing bottom hardness (Chivers et al. 1990). According to Maravelias (1999), based on grab sampling and ground truthing carried out by Fisheries Research Services (FRS, Aberdeen), the E2 (roughness) values can be translated into seabed type. Values of E2 less than 0.6V represented soft sediment types such as sand and silt, 0.6-1.2V is characterised by sand/gravel substrate, 1.2-1.5V is typical of a stony-type substrate, and any values above 1.5V are typically rocky substrates. It was also possible to extract seabed depth from the echosounder for both 2004 and 2005. Depth, E1 and E2 were recorded with time and GPS location every 10 seconds. The mean value per 15 minute segment for each environmental variable was calculated for inclusion in the analysis.

5.2.2 Analysis

5.2.2.1 Correlation between delphinids & herring

The relationship between herring and delphinids was examined within a Multinomial Logit Model (MLM) framework, which has previously been used to investigate the interspecific associations between fish species (Beare et al. 2003). This model is able to examine the relationship between patchy distributions where there are a high number of zeros in both data sets. If delphinids are taken to be species A, and herring species B, four categories can be defined (with the probability of each category shown in brackets):

1. Absence of both species A and species B (P_{00})
2. Presence of species A and absence of species B (P_{A0})
3. Absence of species A and presence of species B (P_{B0})
4. Presence of both species A and species B (P_{AB})

These probabilities were taken from the multinomial distribution for the four probabilities:

$$P_{00}^{n_0} P_{A0}^{n_1} P_{B0}^{n_2} P_{AB}^{n_3}$$

where n_i is the number of samples in each category *i*. Beare et al. (2003) model the multinomial distribution by rewriting the equation in terms of nested conditional events:

$$\prod_{i=0}^{3} p_i^{n_i} (1 - p_i)^{n_0 + \ldots + n_{i-1}}$$

with:

$$p_1 = \frac{P_{A0}}{(1 - P_{AB} - P_{B0})}$$ i.e. the probability of there being delphinids without herring given the probability of there being no herring

$$p_2 = \frac{P_{B0}}{(1 - P_{AB})}$$ i.e. the probability of there being herring without delphinids

given the probability of herring & delphinids not being found together

$$p_3 = P_{AB}$$ i.e. the probability of herring & delphinids being found together

These probabilities were then modelled using Generalised Additive Models (GAMs) with the environmental variables shown in Table 5.2, using forward step-wise selection (§5.2.2.2). E1 and E2 were left out of the modelling process for two main reasons; (i) they were only available for 2005, so comparison between years would not be possible, and (ii) it was not possible to match RoxAnn sediment data to an available grid of sediment data for predicting over the whole spatial extent.

In order to produce predictive grids for each of the models for p_i, it was necessary to generate a grid of latitude, longitude and depth. Grid cells based on approximately the same size as the trackline segment size were used for prediction (5 km x 5 km). Latitude and longitude were determined for the middle of each grid cell, and the depth value for this point was queried using the *STJG Tools* (Gontarek 2005) function in ArcGIS 9.0 (ESRI Inc.) from the GEBCO (BODC 2003) bathymetry chart. The best GAM models were used to generate a grid of predicted probability values for p_i, and used to calculate the correlation coefficient between delphinids and herring according to the expression (Beare et al. 2003):

$$r = \frac{P_{AB} - P_A P_B}{\sqrt{P_A(1-P_A)P_B(1-P_B)}}$$

where P_A is the probability of detecting delphinids and P_B is the probability of detecting herring in a grid cell. P_A and P_B can then be calculated as:

$$\begin{aligned} P_A &= p_1(1-p_2)(1-p_3)+p_3 \\ P_B &= p_2(1-p_3)+p_3 \\ P_{AB} &= p_3 \end{aligned}$$

This method captures the information from the joint distribution (P_{00}, P_{A0}, P_{B0}, P_{AB}), which modelling P_A and P_B directly would miss. The correlation coefficient gives a positive high value (maximum 1) if the species are positively associated with one another (i.e. herring and delphinids present at the same time). A high negative correlation coefficient (minimum –1) suggests that the species are negatively associated with each other (i.e. one species found in a segment when the other is not). This model allows a spatial analysis of association between delphinids and herring.

5.2.2.2 *Generalised Additive Models of p_1, p_2 and p_3*

Generalised Additive Models (GAMs) were used to relate p_1, p_2, and p_3 to the geographic, environmental and temporal variables independently (§2.2.4.2).

A binomial distribution was assumed for the response variables with the logit link function (Chambers & Hastie 1991):

$$g(p) = \log\left(\frac{p}{1-p}\right)$$

Where p is the probability of getting the response. The GAMs were carried out in R (Version 2.3.0, R Foundation for Statistical Computing 2006) using Simon Wood's MGCV (Multiple Generalised Cross Validation) library (Wood 2006b). The default smoothing spline used in the MGCV smooth *s()* is a Thin Plate Regression Spline (TPRS), and is good for smooth interactions of parameters that are in the same units (such as latitude & longitude, or E1 & E2). For smooth interactions of parameters in different units (such as depth & longitude), Wood (2006a) recommends the use of the tensor product smoother *t()* which allows non-equal smooths in 2 dimensions. In both these spline smoothers, the default *dimension* (*k* = equivalent to setting the maximum number of degrees of freedom for each smooth) is 10 for 1-way smooths, 30 for 2-way smooths, and 90 for 3-way smooths. During analysis, if any model failed to converge, *k* was increased or decreased in order to enable model fitting.

Stepwise addition of environmental variables to the null model (no predictor variables) was carried out (forward step-wise selection), and models compared based on minimising the UBRE (Un-Biased Risk Estimator) score. The UBRE score is the binomial GAM equivalent of the AIC value (in effect, just a linear transformation of AIC), and scores on both fit and the number of parameters used to describe the model (Wood, 2006a). In selecting the best model, predictor variables were only added if they reduced the UBRE score by more than 0.01.

Only variables that were collected simultaneously to the delphinid and herring data were used in the analysis to provide as accurate a measure as possible at exactly the same scale as the delphinid and herring data. Also, unlike previous models, latitude and longitude were allowed in the model selection to provide a better representation of the overall distribution of species, and to mop up more of the deviance. The parameters used in the modelling were therefore latitude, longitude, depth, E1 (seabed roughness), E2 (seabed hardness), day and time category (sunrise 03:00-08:00, morning 08:00-13:00, afternoon 13:00-18:00 and sunset 18:00-23:00). Interactions

(2-way smooths) were determined by looking at the correlation between parameters, and resulted in the terms listed in Table 5.1.

GAMs were also used to test whether delphinid presence/absence could be significantly explained by either herring abundance or herring presence/absence in 2004 and 2005 by direct inclusion in the model of delphinid occurrence. Herring abundance (NASC) was included as a smooth of the log, since there were several orders of magnitude difference between the low abundance and high abundance values. Alternatively herring was also tested by inclusion as a binary presence/absence factor variable. This basic GAM model was carried out prior to the MLM GAM modelling to determine whether there was likely to be an overall relationship between delphinid and herring distributions. The MLM GAM modelling allows for a more spatial analysis of the relationship between the two species.

Table 5.1 – Linear and non-linear terms used in the GAM forward step-wise selection for delphinid presence/absence, herring presence/absence, p_1, p_2, and p_3. * indicates inclusion in the 2005 models only, ** indicates inclusion in the delphinid presence/absence models only, and § indicates the terms that are included in the GAM models of p_1, p_2, and p_3.

1-way smooths	2-way smooths	3-way smooths	Linear terms
s(Lon)§, s(Lat)§	s(Lon,Lat) §, s(E1,E2)*	s(Lon,Lat,Time) §	factor(Day) §
s(Depth) §, s(E1)*, s(E2)*	te(Depth,Lon) §		factor(Time) §
s(log(NASC+1))**	te(Depth,E1)*		HerringPresence**
	te(Depth,E2)*		WaterNoise, BoatNoise

5.2.2.3 Autocorrelation

Autocorrelation can exist in a dataset both spatially and temporally, but is difficult to evaluate for binary data since all the statistical methods that I am aware of are based around continuous data. However, it is possible to evaluate the amount of residual autocorrelation left after the modelling process by analysing the partial residuals from the models in the autocorrelation functions. Ideally, the models will have no residual autocorrelation, since it should have been explained within the smoothing terms themselves. In this study spatial correlation was examined using the variogram – a standard geostatistics tool used in evaluating the spatial structure of fish schools (Rivoirard et al. 2000) and other ecological variables (Bellehumeur et al. 1997). The variogram examines the correlation over distance, so is often used for species that move little in time and space relative to the sampling frequency in this case related to ship speed (such as herring – Hafsteinsson & Misund 1994).

It measures, on average, the half variability between two points, as a function of their distance (Matheron 1971, Rivoirard et al. 2000):

$$\gamma^*(h) = 0.5\frac{1}{N(h)}\sum[I(x_i) - I(x_i + h)]^2$$

where $\gamma^*(h)$ is the experimental variogram, $N(h)$ is the number of pairs of points separated by the distance h, and $z(x)$ is the value of the variable at location x such that:

$$I(x_i) = \begin{cases} 1, z(x) > 0 \\ 0, z(x) = 0 \end{cases} \qquad I(x_i + h) = \begin{cases} 1, z(x+h) > 0 \\ 0, z(x+h) = 0 \end{cases}$$

For patchy data the variogram levels off at the ‘sill’, this occurs at a distance called the ‘range’ (Bellehumeur et al. 1997; Rivoirard et al. 2000), which is equivalent to the patch diameter of the variable.

For species that are more mobile than herring, such as delphinids, the variogram is likely to have less meaning. The survey vessel travels along lines of latitude, so if a delphinid group is detected that is travelling north, then by the time the vessel has reached the end of the transect, travelled north to the next transect, and travelled along the next line of latitude, the delphinids may have been resampled. In this case measuring temporal correlation is probably more meaningful. The autocorrelation function in R (Gilbert & Plumber) was used to calculate the temporal correlation between samples.

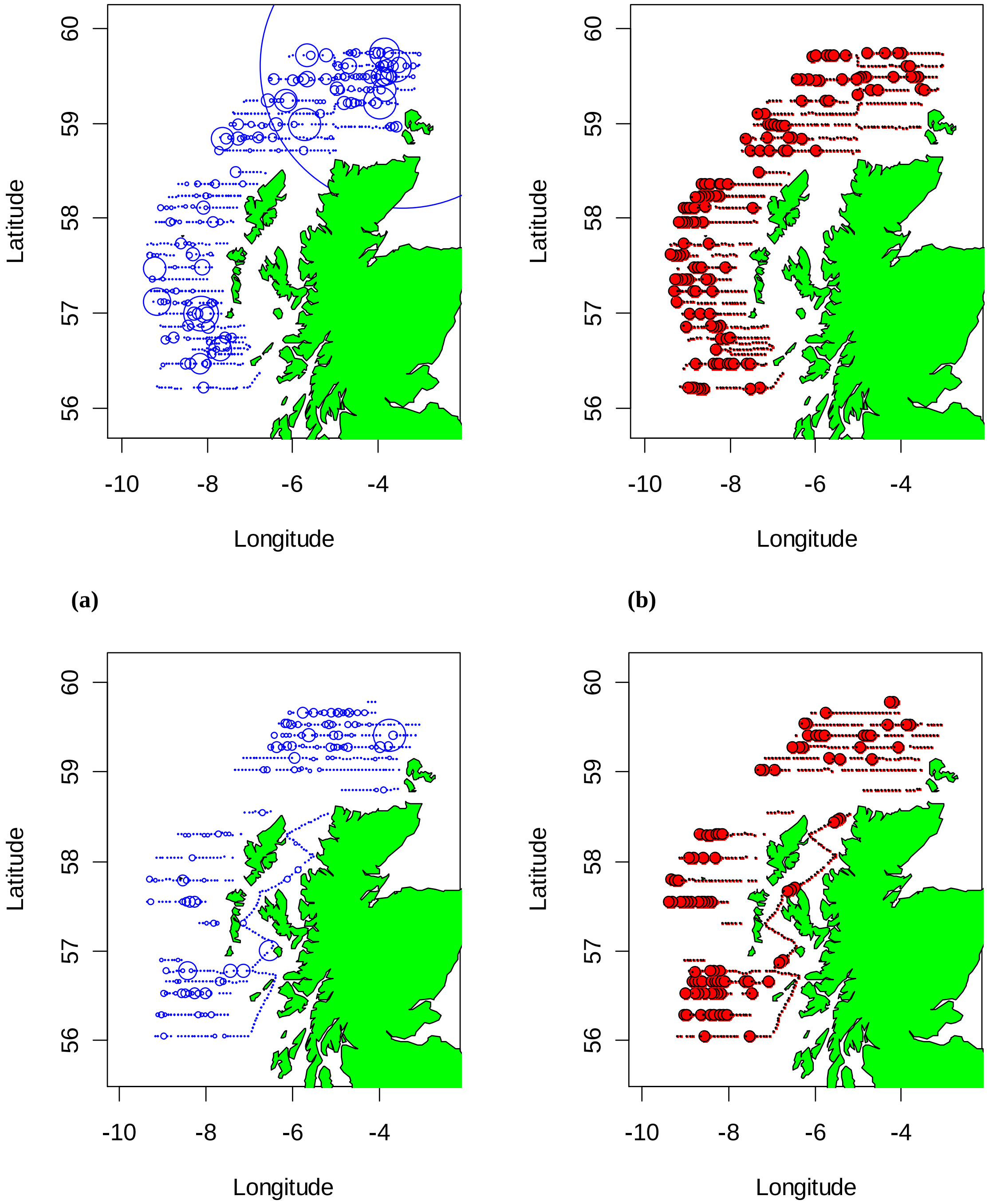
5.3 Results

5.3.1 Survey data

Delphinids were detected acoustically at 18.9% of listening stations in 2004 and 17.0% in 2005, whereas herring were detected in 38.9% of the EDSU segments in 2004 and 40.2% in 2005 (Table 5.2). There were opportunistic sightings of delphinids: mainly white-beaked dolphins (*Lagenorhynchus albirostris*), common dolphins (*Delphinus delphis*) and Atlantic white-sided dolphins (*Lagenorhynchus acutus*). Common and Atlantic white-sided dolphins were found throughout the survey area, whereas white-beaked dolphins were only sighted north of the Outer Hebrides (>59ºN). Herring distribution was similar in both years but the abundance was 40% lower in 2005 than in 2004 (ICES 2005, 2006).

Table 5.2 - Summary of the survey effort and parameters included in later analyses. This includes distance surveyed; the number of listening stations and proportion of which had delphinids/ herring; and the range and mean/median values for the herring NASC, water depth, E1 (seabed roughness) and E2 (seabed hardness).

Parameter	2004	2005
Survey effort		
Distance surveyed (km)	3241	2530
Number of stations/segments	700	547
Number of stations with delphinids	132 (18.9%)	93 (17.0%)
Number of stations with herring	272 (38.9%)	220 (40.2%)
Herring (NASC)		
Range	0-182913	0-2603
Median (of non-zero values)	78	40
Inter-quartile range	28-213	14-102
Water depth (m)		
Range	29-490	30-239
Mean (standard deviation)	124 (51)	112 (38)
95% confidence intervals	40-209	50-174
E1 (seabed roughness)		
Range	NA	0.14-1.92
Median	NA	0.41
Inter-quartile range	NA	0.25-0.59
E2 (seabed hardness)		
Range	NA	0.24-1.99
Median	NA	1.21
Inter-quartile range	NA	0.93-1.39



(a) (b)

(c) (d)

Figure 5.1 – Distributions of herring and delphinids off the west coast of Scotland during acoustic surveys carried out in (a) & (b) 2004 and (c) & (d) 2005. Listening stations/EDSUs were approximately every 2.5 n.mi. and are presented in small blue dots showing herring absence, large blue circles showing the relative abundance of herring presence (size of circle related to the square root of the NASC), small red dots showing delphinid absence, and large red dots showing delphinid presence. There was one very large school of herring in the north-east of the survey area in 2004 (NASC = 182913) which is represented by the large blue circle on the map.

5.3.2 Correlation between delphinid & herring distributions

5.3.2.1 Direct inclusion in GAM

The direct inclusion of either herring presence/absence (as a factor variable) or the log of herring abundance (log(NASC+1)) in a GAM model of delphinid occurrence resulted in neither variable being significant in explaining the distribution of delphinids in 2004. However, in 2005 both herring occurrence and abundance were significant in explaining the distribution of delphinids, explaining 2.0-2.3% of the deviance ($p < 0.01$). Neither variable was significant in explaining delphinid occurrence after the addition of environmental variables (Appendix §A4).

5.3.2.2 Multinomial Logit Model

The best models for p_1, p_2, and p_3 for 2004 and 2005, with respect to latitude, longitude, depth and time of day, are shown in Tables 5.3 & 5.4 respectively. Latitude, longitude and depth were important parameters in all of the models, whereas time was only important in explaining p_2. In 2004 herring detections were significantly different throughout the day, with more herring detections in the middle of the day ($p < 0.001$ for the morning category 08:00-13:00, and $p < 0.01$ for the afternoon category 13:00-18:00). However, in 2005 only the sunrise category had significantly fewer detections of herring ($p < 0.001$ for sunrise category 03:00-08:00). The variations in delphinid detections over time were not significantly different between the different time categories.

In three out of four of the models for p_1 and p_3, the most important predictors included a two-way smooth of depth with longitude and a smooth of latitude. These two-way smoothes mainly showed a preference for deep (> 100 m) westerly (> 7ºW) parts of the survey area. Even without the additional environmental variables of E1 (roughness) and E2 (smoothness), the models for 2005 explain more of the deviance than that for 2004. In both years, p_2 had the lowest % explained deviance, the modelling of this response also resulted in potentially over-fitted models (a three-way smooth of longitude, latitude and time with 76 degrees of freedom for 2004, and the smooth of depth reducing the UBRE score by a little less than 0.01 in 2005). To examine the effect of such over-fitting on the resulting examination of correlation between the species, two models were included into the correlation analysis for p_2:

(i) the potentially over-fitted model and (ii) the next best model excluding the over-fitted smooth (Table 5.3).

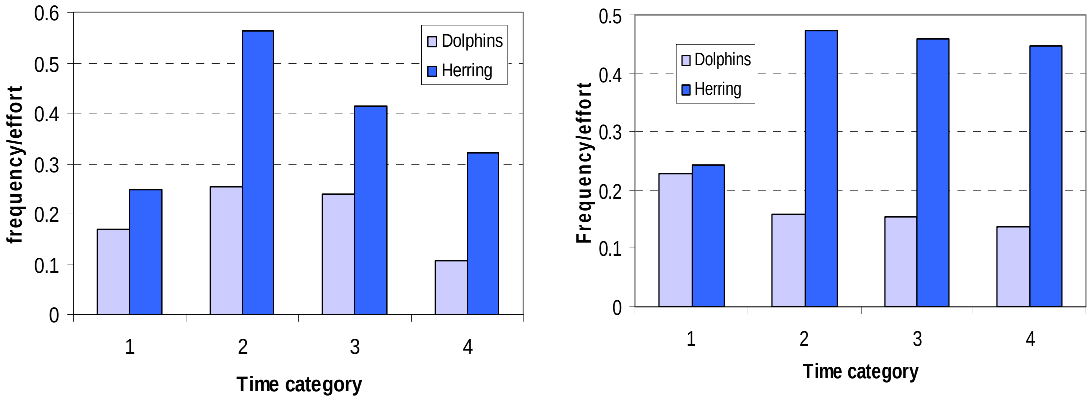


Figure 5.2 – Effort related detections of delphinids (light blue) and herring (dark blue) per time category for (a) 2004 and (b) 2005. the time categories are 1 = sunrise (03:00-08:00), 2 = morning (08:00-13:00), 3 = afternoon (13:00-18:00), and 4 = sunset (18:00-23:00).

There was very little residual autocorrelation either temporally or spatially, although half the models suggest slight autocorrelation to one segment (15 minutes), and there was some spatial autocorrelation evident for p_3 in 2004 (to around 20 km: Figure 5.3).

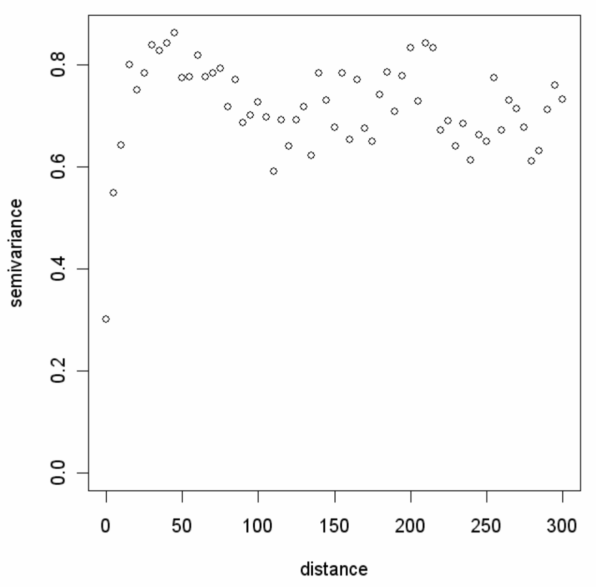


Figure 5.3 – Remaining spatial autocorrelation based on Pearson residuals from the best GAM models for 2004 *p3*. Variograms were based on the partial residuals from the model with distance measured in km.

Table 5.3 – Best GAM models for p_1, p_2, and p_3 in 2004 based on model selection by lowest UBRE score, with the parameters; latitude, longitude, depth & time of day. The parameter smooths (spline s or tensor te) and the linear parameters (of day or time of day as factors) are shown in the order they were selected by forward stepwise model selection. Degrees of freedom for each smooth or linear predictor are given in the parentheses, %dev = the percentage explained deviance by adding the term to the model, and UBRE score for the addition of each parameter. The total % explained deviance is given at the bottom for each of the four models. * indicates that the % explained deviance is reduced by adding the smooth of depth, because it reduces the estimated degrees of freedom for s(Lon,Lat) from 27 to 4 degrees of freedom. Two models are given for p_2, since the first model has a very high estimated degrees of freedom & may over-fit the data.

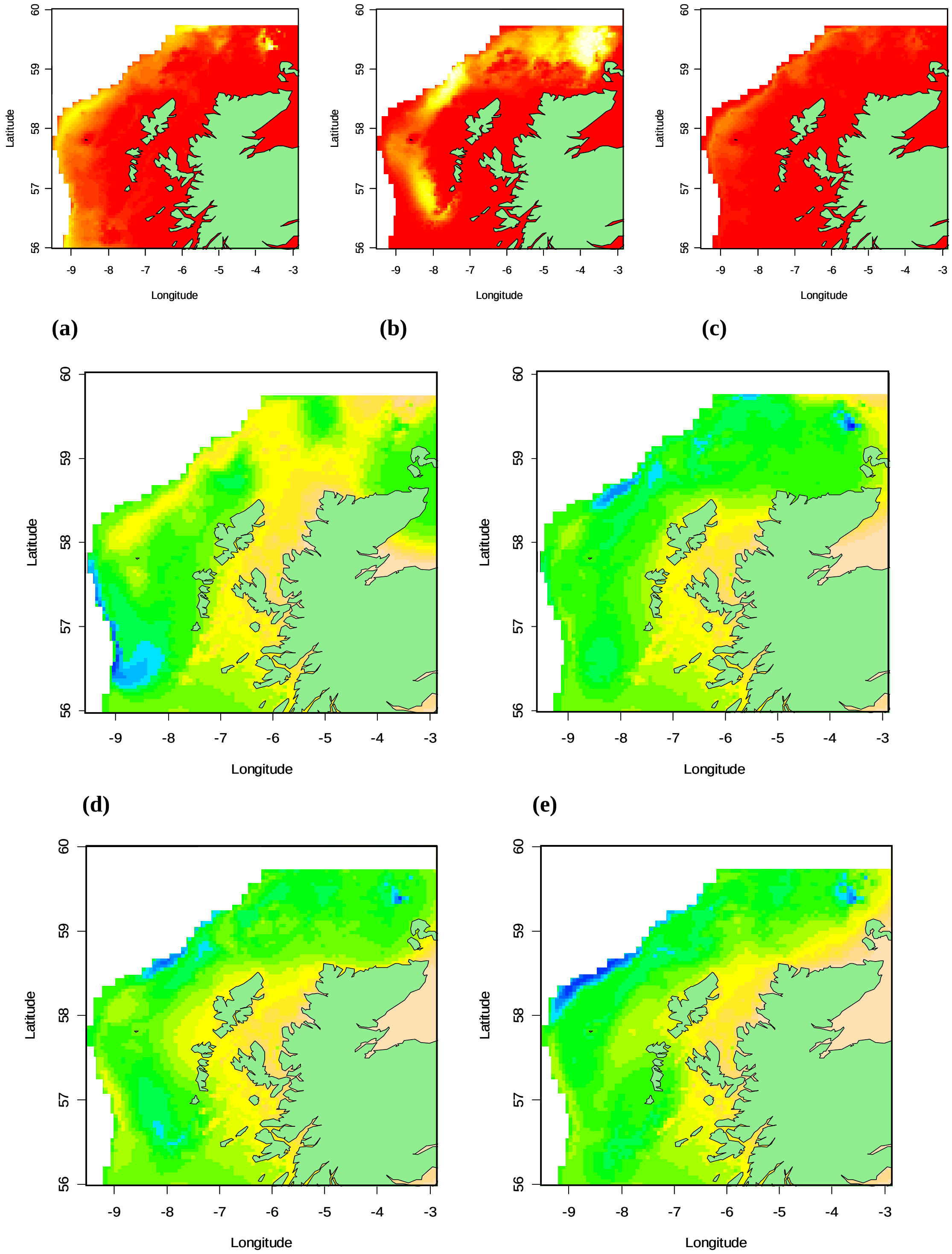
Parameter order	p_1			p_2			p_3		
	Term	% dev	UBRE	Term	% dev	UBRE	Term	% dev	UBRE
1	te(Depth,Lon,8)	25.6%	-0.283	s(Lon,Lat,Time,76)	34.5%	0.060	s(Lon,Lat,4)	25.8%	-0.482
2	s(Lat,3)	+2.9%	-0.301	s(Depth,5)	+4.5%	0.029	s(Depth,3)	-4.6%*	-0.512
Dev expl.		28.5%			39.0%			21.2%	
1				s(Lon,Lat,18)	16.7%	0.132			
2				s(Depth,5)	+3.3%	0.075			
					21.0%				

Table 5.4 – Best GAM models for p_1, p_2, and p_3 in 2005 based on model selection by lowest UBRE score, with the parameters; latitude, longitude, depth & time of day. The parameter smooths (spline s or tensor te) and the linear parameters (of day or time of day as factors) are shown in the order they were selected by forward stepwise model selection. Degrees of freedom for each smooth or linear predictor are given in the parentheses, %dev = the percentage explained deviance by adding the term to the model, and UBRE score for the addition of each parameter. The total % explained deviance is given at the bottom for each of the four models. * indicates that the reduction in UBRE score is >0.01 so this term is removed from the model to reduce over-fitting the data in version 2 of the analysis.

Parameter order	p_1			p_2			p_3		
	Term	% dev	UBRE	Term	% dev	UBRE	Term	% dev	UBRE
1	te(Depth,Lon,12)	18.1%	-0.283	s(Lon,Lat,27)	24.3%	0.088	te(Depth,Lon,7)	26.8%	-0.523
2	s(Lat,8)	+13.8%	-0.351	factor(Time,30)	+3.6%	0.055	s(Lat,8)	+9.8%	-0.546
3	-			s(Depth,5)	+2.0%	0.047*	-		
Dev expl.		31.9%			29.9%			36.6%	

The model predictions for p_1, p_2 and p_3 for 2004 and 2005 are shown in the upper plots of Figures 5.4 & 5.5 respectively with the correlation plot outcomes of the Multinomial Logit Model (MLM). When examining all predictive and correlation plots, it is important to bear in mind that the predictions are only applicable to where there are data, i.e. only in the Minch in 2005. In 2004, p_1 (delphinids) were predicted to have highest probability of occurrence along the shelf edge but low occurrence in-shore of the shelf-edge (Figure 5.4a). Similarly, p_2 (herring) were found to have a high probability of occurrence along the shelf edge around 59ºN, but also mid-shelf south of 58.5ºN, and throughout the shelf waters to the west of Orkney (Figure 5.4b). p_3 (herring & dolphin presence) had a similar predicted distribution of slightly higher occurrence along the shelf as to p_1 (Figure 5.4c). In 2004, the main positive correlation between herring and delphinids was found on the shelf edge to the south of the survey area (< 58°N) with negative correlation on the shelf edge to the north of the survey area (> 58°N) (Figure 5.4d-g). There were some differences in correlation throughout the day, with negative correlation on the shelf edge south of 58ºN and positive along the north of the shelf edge and to the north of the Outer Hebrides at sunrise (Figure 5.4d).

In 2005, p_1 (delphinids) were also predicted to have high predicted probability of occurrence concentrated mainly along the shelf edge, although stretching further inland in patches just south of Barra, and just south of St. Kilda (Figure 5.5a). High probability of occurrence was also predicted west of the Shetlands, and to a lesser extent in a patch to the north of Lewis at the top of the Outer Hebrides. p_2 (herring) were predicted to have high occurrence over a larger area than in 2004, with herring predicted to occur in most inshore waters, though not to the west of St. Kilda, nor significantly in the Minch or in the waters bounding the southern Outer Hebrides (Figure 5.5b). p_3 (herring & delphinids) were predicted to have a higher probability along the whole of the shelf edge than in 2004, and to a greater degree towards the south of the surveyed area (Figure 5.5c). In 2005, the correlation between delphinids and herring was consistent over time, with positive correlation in the southwest along the shelf edge south of 58ºN (similar to 2004) and in a patch along the shelf edge further north between 59-59.5ºN (Figures 5.5d-g). There was also a very small patch of positive correlation in the Minch between Skye and Uist. Negative correlation occurred to the north of the Outer Hebrides (>58.5ºN) in a large patch.

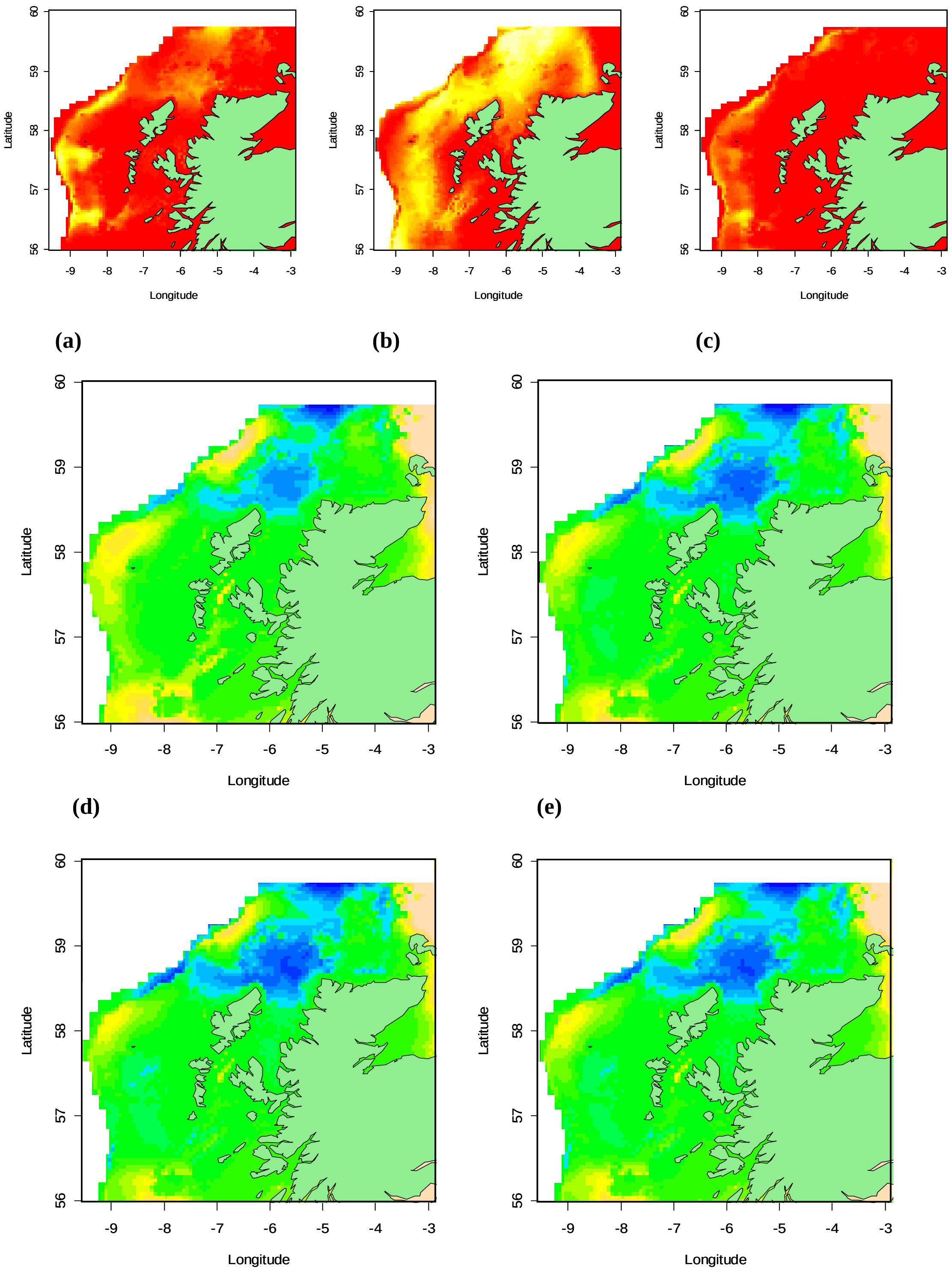


(a) **(b)** **(c)**

(d) **(e)**

(f) **(g)**

Figure 5.4 – Predictive plots of the best models for 2004 (a) p_1, (b) p_2, and (c) p_3, with a colour scale from red (*low* probability) to white (*high* probability). For p_2 the model for time category 3 (afternoon) is shown. (d) to (g) show the Multinomial Logit Model plots of correlation between delphinids and herring for 2004 with a colour scale from blue (negative correlation) to green (no correlation) to yellow/white (positive correlation). The plots are shown for (d) time category 1 sunrise, (e) time category 2 morning, (f) time category 3 afternoon, and (g) time category 4 sunset.



(a) (b) (c)

(d) (e)

(f) (g)

Figure 5.5 – Predictive plots of the best models for 2005 (a) p_1, (b) p_2, and (c) p_3, with a colour scale from red (*low* probability) to white (*high* probability). For p_2 the model for time category 3 (afternoon) is shown. (d) to (g) show the Multinomial Logit Model plots of correlation between delphinids and herring for 2004 with a colour scale from blue (negative correlation) to green (no correlation) to yellow/white (positive correlation). The plots are shown for (d) time category 1 sunrise, (e) time category 2 morning, (f) time category 3 afternoon, and (g) time category 4 sunset.

When model inputs were changed to reduce over-fitting, there was virtually no change between the predicted correlation between delphinids and herring (Figure 5.6 & 5.7). In the 2004 data set, the model for p_2 was reduced from a potentially over-fitted model $p_2 \sim s(Lon,Lat,Time) + s(Depth)$ with a total estimated degrees of freedom of 82, to $p_2 \sim s(Lon, Lat) + s(Depth)$ with only 24 estimated degrees of freedom. There was little change in the predicted correlation, although the change in model resulted in virtually no predicted correlation between delphinids and herring in 2004.

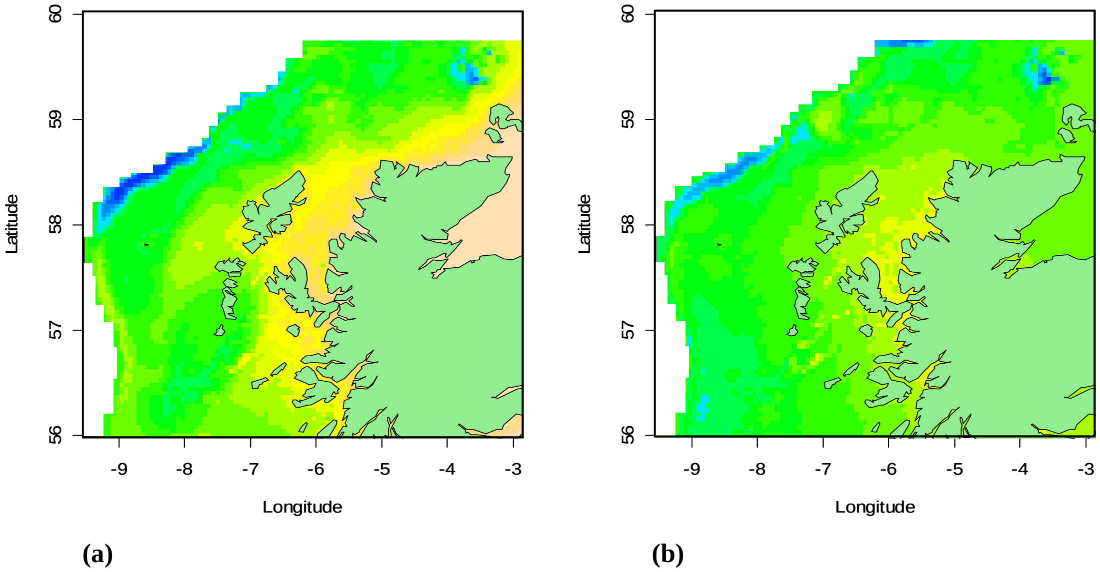
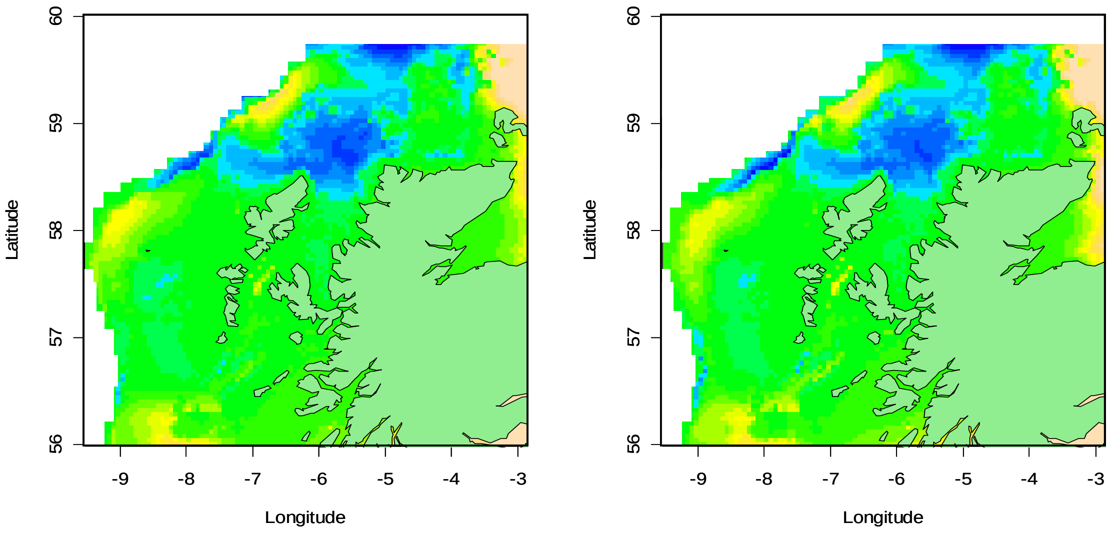


Figure 5.6 – Comparisons between the Multinomial Logit Model plots of correlation for 2004 with p_2 changed from the (a) potentially over-fitted model $p_2 \sim s(Lon,Lat,Time) + s(Depth)$, to (b) $p_2 \sim s(Lon,Lat) + s(Depth)$. The MLM correlation for the original model is shown for time category 4 (sunset). The colour scale ranges from blue (negative correlation) to green (no correlation) to yellow/white (positive correlation).

In the 2005 data set, the model for p_2 was also reduced from a potentially over-fitted model of $p_2 \sim s(Lon,Lat) + factor(Time) + s(Depth)$ with an estimated 37 degrees of freedom, to $p_2 \sim s(Lon,Lat) + factor(Time)$ with 32 degrees of freedom. This had no significant effect on the overall correlation between herring and delphinids.



(a) **(b)**

Figure 5.7 – Comparisons between the Multinomial Logit Model plots of correlation for 2005 with p_2 changed from the (a) potentially over-fitted model $p_2 \sim s(Lon,Lat) + factor(Time) + s(Depth)$, to (b) $p_2 \sim s(Lon,Lat) + factor(Time)$. The MLM correlation for both models are shown with time category 3 (afternoon). The colour scale ranges from blue (negative correlation) to green (no correlation) to yellow/white (positive correlation).

5.4 Discussion

5.4.1 Correlation between delphinids and herring

Few studies have attempted to incorporate *direct* variables such as prey distributions into models of cetacean distributions, and most of these have used an index of prey abundance such as acoustic backscatter rather than abundances of the prey species themselves (Fiedler et al 1997; Hooker 1999; Tynan et al 2005). When building habitat models of top predator distributions, habitat preferences are often hypothesised to be due to the habitat preferences of their prey (Ballance et al. 2006; Baumgartner & Mate 2005; Baumgartner et al. 2001; Cañadas et al. 2002; Gregr & Trites 2001; Ingram et al. 2007; Johnston et al. 2005; Macleod et al. 2004). For example, in the case of delphinids (Chapter 2) it is likely that their preference for warmer SST and deeper thermoclines is related to the distribution of their prey in off-shelf waters. However, such hypotheses, while logical, remain unproven. It would appear to be a logical next step to include prey distributions within the models of delphinid distributions, and to examine the spatial correlation between species.

Direct inclusion of herring occurrence and/or abundance showed that although herring was significant in explaining delphinid occurrence in 2005, it was not in 2004. In addition, in 2005 there was a visual sighting (pers. obs.) of common dolphins (*Delphinus delphis*) demonstrating foraging behaviour in the vicinity of a trawl on a known herring school. However, herring was only able to explain around 2% of the deviance, though not dissimilar to the proportion of deviance explained by individual environmental variables in the off-shore delphinid models (Chapter 2). As mentioned in the discussion of Chapter 2 (§2.4.3), this small amount of explained deviance may be due to the different species represented by the whistles (different species with different prey preferences), and detecting animals both during travel and foraging activities (Ballance et al. 2006).

A better insight into the correlation between delphinid and herring distributions, can be obtained by carrying out a spatially-explicit analysis of correlation (Beare et al. 2003). By examining the locations at which the two species show positive and negative correlations, it is possible to determine whether foraging of delphinids on herring is spatially localised. While this does not explain what proportion herring represents in the delphinid diet (since we have no data on other prey species), it does provide some indication of the locations in which foraging on herring is likely to occur.

The Multinomial Logit Model technique used by Beare et al. (2003) provides a valuable way of exploring the correlation between herring and delphinids, allowing comparison of patchy distributions of two species where there are a high proportion of zeros (around 80% of the delphinid data and 60% of the herring data). By nesting the four probabilities resulting from the combination of delphinid presence/absence and herring presence/absence, it is possible to model the nested probabilities *independently* within GAMs. This technique made it possible to analyse the correlation between species on both a temporal and spatial scale.

The models for the three different probabilities (p_1 equivalent to delphinid occurrence, p_2 equivalent to herring occurrence, and p_3 herring & delphinids present together) suggested that of all the predictor variables, depth was an important predictor of both dolphins and herring. This is supported by many other studies both for delphinids (Baumgartner et al. 2001; Cañadas et al. 2002; Davis et al. 2002; Gowans & Whitehead 1995; Hastie et al. 2005; Selzer & Payne 1988), and for herring (Maravelias 1999, 2001). For herring this preference has been linked to the location of the prey species, *Calanus finmarchicus* (Maravelias & Reid 1997; Maravelias 2001). For delphinids it is also believed that this preference for depth is also related to the aggregation of fish/celphalopod prey species (Beardsley et al. 1996; Davis et al. 2002). In this study, delphinid depth preferences were shown to overlap with the preferred depth of herring at 140 m depth, though were generally found to prefer deeper water than herring.

Using latitude and longitude together, however, was often a more important predictor than depth. However, depth was strongly correlated with longitude, mainly because the shelf edge is at a fairly consistent longitude. It was found that a two-way smooth of depth with longitude was an important predictor of delphinids with the species found preferentially in deep westerly waters, i.e. towards the shelf edge: similar to that found in Chapter 2. However, latitude and longitude together as predictors may summarise many of the environmental factors that influence the distribution of both herring and dolphins, even if it is the environmental factors that are a more direct influence on the animals through biology and ecology. Since the only environmental predictor available in this survey is depth, longitude and latitude provide a useful substitute, even if the models lack strength (most of the models explain less than 30% of the deviance).

In 2005, RoxAnn sediment data had been collected synoptically during the survey, however due to the difficulty of matching the RoxAnn measures of sediment type to an underlying grid of sediment data for making predictions over the whole shelf region; it had to be excluded from full spatial correlation analysis. There is some indication that inclusion of sediment type into the model increases the amount of deviance explained by environmental variables by around 15% for delphinids and 5% for herring (Appendix Table A4.1 & A4.2). This analysis also suggested that delphinids and herring overlapped in their preference for sand/gravel type substrate (Appendix Figure A4.2). Herring were also found to prefer sand-gravel type substrate in the studies carried out by Maravelias (1999, 2001), the type of substrate in which herring are known to spawn (Haegele & Schweigert 1985). Since the abundance surveys are scheduled to match the time at which herring aggregate into pre-spawning schools, it is perhaps not surprising that herring were shown to associate with the sand/gravel habitat of their spawning grounds. Despite the significance of sediment type to herring, it was only able to explain 5% of the deviance, perhaps because pre-spawning aggregations had not yet reached their spawning grounds which are generally found in shallower waters.

Time of day was only an important predictor in the models of p_2 herring distributions (Table 5.3 & 5.4); there were significantly more detections of herring during the day than during the sunrise categories. This is likely to be due to the diurnal behaviour of herring which aggregate in schools close to the bottom during the day (occasionally near the surface), but which disperse into 'scattering layers' at night (Maravelias et al. 2000). Fernandes et al. (2001) showed that this dispersion occurs at sunset, with the schools reforming at sunrise. In addition, they showed that school sizes were larger during these times of day, breaking up into more numerous smaller aggregations in the middle of the day. Time was not significant in explaining the detections of delphinids; despite several studies suggesting diurnal changes in vocalisation behaviour of dolphins (Goold 2000; Gordon et al. 2000; Hastie et al. 2005). Although in both of these studies, dolphin vocalisations peaked at sunrise and sunset, the reverse to the results of this study. Hastie et al. (2005) suggest that this diurnal variation in vocalisation rates may be related to feeding activity, so it may be that the dolphins in their study in the Faroe-Shetland Channel were feeding on different species than the dolphins in this study. The fact that there were more vocalisations during the middle of the day may suggest that the dolphins are feeding on prey that is more available during the middle of the day (such as herring).

The results of the MLM correlation analysis suggest that there was very little if any positive correlation between delphinids and herring in 2004 (Figures 5.4 & 5.6), but some significant positive correlation between delphinids and herring in 2005 along parts of the shelf edge and in the Minch (Figures 5.5 & 5.7). There was a consistent area of negative correlation between delphinids and herring along the shelf edge around 59°N, where herring were predicted to have high probability of occurrence but delphinids were predicted to be absent (Figures 5.4 & 5.5). Also in 2005, there was a large area of negative correlation to the north of the Outer Hebrides (Figure 5.5). However, due to hydrophone problems, this area had not been surveyed for delphinid occurrence during 2005, so little can be inferred from this prediction. Certainly, this area to the north of the Outer Hebrides is the core area of white-beaked dolphins (*Lagenhorhynchus albirostris*) during summer months (Northridge et al. 1995; Northridge et al. 1997), so had delphinid monitoring been carried out in this area it is probable that delphinids would have been detected. Therefore, based on the *grain* size used in this study (around 5 km); there was only significant correlation between delphinids and herring in patches along the shelf edge.

It is possible that delphinids were not foraging on herring to any great extent, and certainly the few diet studies of the species likely to be found on the west coast of Scotland show much evidence of herring in the diet (Santos et al. 1994; Santos 1998; Murphy pers. comm.). However, the main on-shelf species available within the water column at the time of the surveys was herring in the large pre-spawning aggregations that occur in these autumn spawning populations. So it would be odd if the delphinids did not make use of this abundant and available source of prey. Given the small number of strandings that occur on the west coast of Scotland, it is likely that a seasonal signal within the diet would be missed in stomach analyses if the strandings took place at a different time of year to that of the herring spawning aggregations.

The limited correlation shown between delphinids and prey could also be due to the scale (or *grain* size) at which the analysis was carried out. Many studies suggest that scale is important in studying predator-prey relationships, only finding correlations between predators and prey at larger rather than smaller scales (Fauchald et al. 2000; Guinet et al. 2001; Mehlum et al. 1999; Rose & Leggett 1990; Schneider & Piatt 1986). This is illustrated very clearly in a study carried out by Guinet et al. (2001) who found that there was a negative correlation between female Antarctic fur seals (*Arctocephalus gazella*) and prey density at a small *grain* size (< 18 km), but which changed to a positive correlation at a large *grain* sizes (> 36 km). Also, in a study of North Atlantic fish species, it was found that distributions of Atlantic cod (*Gadus morhua*) only correlated positively with their capelin prey (*Mallotus villosus*) at a scale larger than the aggregation dimensions, where aggregation dimension was 3-5 km (Rose & Leggett 1990). So this study may benefit from a more detailed analysis of delphinid-herring correlations at a range of scales from finer (given the availability of gridded environmental variables at a fine enough scale) to larger *grain* sizes.

A final difficulty in examining predator-prey relationships with mobile species such as delphinids is that they will be detected both when in transit and when foraging. Overlap between herring and delphinids may not necessarily mean that the delphinids are foraging on herring but just that they are travelling through an area. In the study of dusky dolphins (*Lagenorhynchus obscurus*) in Admiralty Bay carried out by Benoit-Bird et al. (2004), correlations were only found with prey when they were observed foraging. Similarly, Hastie et al. (2004) linked bottlenose dolphins (*Tursiops truncatus*) identified visually as exhibiting foraging behaviour to environmental variables (depth and slope) in an area associated with the salmon (*Salmo salar*) migration. Using passive acoustics for identifying dolphin foraging behaviour is not yet possible. However, there is some evidence that delphinids change vocalisation rates and patterns with different behaviours (Cook et al. 2004; Janik 2000; Jones & Sayigh 2002). Janik (2000) found that a specific type of whistle was produced just before bottlenose dolphin fed on salmon; however Jones and Sayigh (2002) found that vocalisation rates in bottlenose dolphins were generally less for feeding than for travelling and socialising. Passive acoustics also has the disadvantage of not knowing which species are being detected, making it difficult to determine differences in prey preferences between species. It is possible that species that preferentially forage at the shelf-edge (such as common dolphins or white-sided dolphins) are feeding on herring rather than the more inshore delphinids such as white-beaked dolphins which feed on species such as whiting, cod, haddock, and sandeels (Kinze et al. 1997; Santos et al. 1994).

Analysing the correlation between species using the Multinomial Logit Model, does however, appear quite robust. Wood's (2006a, b) MGCV method of fitting GAMs has been accused of over-fitting data (Kim & Gu 2004), however, using alternative GAM models that reduce the potential over-fit (Table 5.3) had little effect on the overall conclusions from the correlation analysis (Figures 5.6 & 5.7). The MLM model suggested a higher correlation between delphinids and herring in 2005 than in 2004, despite the 40% higher abundance in 2004 than 2005 (ICES 2006). There was both higher positive correlation and higher negative correlation in 2005 than in 2004. However, 2005 was a year of many anomalies in the marine environment off the west coast of Scotland, with clear reductions in the success of seabirds (puffins, kittiwakes and guillemots), and dramatic shifts in minke whale distribution (Stevick et al. 2007). So changes in correlation and distribution of both delphinids and herring may be linked to this ecosystem change that occurred at this time.

Overall, there was little correlation exhibited between the delphinids and herring at the *grain* size analysed, suggesting that herring may not be an adequate *direct* predictor of dolphin distributions on its own. With delphinids eating a wide range of prey species it would be interesting to include other prey species such as mackerel (*Scomber scombrus*) (which was also caught in trawls but mainly travels at the surface missed by active acoustic surveys), sandeels (*Ammodytes* spp.) (sometimes also seen acoustically in patches) and shelf-edge species such as blue whiting (*Micromesistius poutassou*). A wider range of prey species modelled at a range of *grain* sizes, may provide a better correlation with delphinid distributions, and provide better *direct* variables for inclusion in predictive models of their distributions.

5.4.2 Conclusions

This study analysed the spatial correlation between delphinid and herring distributions from simultaneously collected data. Overall, it was found that delphinids and herring were only correlated in 2005, and not in 2004. The main positive correlation was concentrated along the shelf edge in both years.

Given the high abundance and availability of herring in the shelf waters off the west coast of Scotland during the time of the surveys, it is likely that the correlation is actually higher but was obscured by a number of problems: (i) the use of whistles does not allow for the species of delphinid to be identified so individual species preferences may be masked; (ii) delphinids are not exclusively detected during foraging but also detected when travelling between foraging sites; and (iii) the correlation may occur at a larger scale similar to other studies of predator-prey correlations (Fauchald et al. 2000; Guinet et al. 2001; Mehlum et al. 1999; Rose & Leggett 1990; Schneider & Piatt 1986).

Therefore, although prey distributions may be useful *direct* predictors of predator distributions, they can not compensate for difficult predator data (no knowledge of species or behaviour), and may correlate better at a larger *grain* size than other more *indirect* predictor variables.

5.5 References

Anthony, J. A., D. D. Roby, and K. R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology **248**: 53-78.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling **157**:101.

Bailey, M. C., C. D. Maravelias, and E. J. Simmonds. 1998. Changes in the distribution of autumn spawning herring (Cupea harengus L.) derived from annual acoustic surveys during the period 1984-1996. ICES Journal of Marine Science **55**:545-555.

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

Baumgartner, M. F. and B. R. Mate. 2005. Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. Canadian Journal of Fisheries and Aquatic Sciences **62**: 527-543.

Baumgartner, M. F., K. Mullin, L. N. May, and T. D. Leming. 2001. Cetacean habitats in the northern Gulf of Mexico. Fishery Bulletin **99**:219-239.

Beardsley, R. C., A. W. Epstein, C. Chen, K. F. Wishner, M. C. Macaulay, and R. D. Kenney. 1996. Spatial variability in zooplankton abundance near feeding right whales in the Great South Channel. Deep-Sea Research II **43**:1601-1625.

Beare, D. J., D. G. Reid, and E. McKenzie. 2003. Fish schooling behaviour in the northwest North Sea: interspecific associations measured by acoustic survey. Aquatic Living Resources **16**:307-312.

Bellehumeur, C., P. Legendre, and D. Marcotte. 1997. Variance and spatial scales in a tropical rain forest: Changing the size of sampling units. Plant Ecology **130**:89-98.

Benoit-Bird, K. J., and W. W. L. Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behav Ecol Sociobiol **53**:364-373.

Benoit-Bird, K. J., B. Wursig, and C. J. McFadden. 2004. Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: active acoustic detection of dolphins and their prey. Marine Mammal Science **20**:215-231.

Bodholt, H., H. Ness, and H. Solli. 1989. A new echo-sounder system. Proceedings of the Institute of Acoustics **11**:123-130.

Bräger, S., J. A. Harraway, and B. F. J. Manly. 2003. Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). Marine Biology **143**: 233-244.

Brophy, J. T. 2003. The diet of the common dolphin (Delphinus delphis L.) in Irish waters. MSc Thesis. Department of Zoology. University of Cork.

Cañadas, A., R. Sagarminaga, and S. Garcia-Tiscar. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters of southern Spain. Deep-Sea Research I **49**:2053-2073.

Chambers, J. M., and T. J. Hastie 1991. Statistical Models. Chapman & Hall/CRC Press, Boca Raton.

Chivers, R. C., N. Emerson, and D. R. Burns. 1990. New acoustic processing for underway surveying. The Hydrographic Journal **56**:9-17.

Cook, M. L. H., L. S. Sayigh, J. E. Blum, and R. S. Wells. 2004. Signature-whistle production in undisturbed free-ranging bottlenose dolphins (Tursiops truncatus). Proceedings of the Royal Society of London Series B-Biological Sciences **271**:1043-1049.

Couperus, A. S. 1997. Interactions between dutch midwater trawl and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) southwest of Ireland. Journal of Northwest Atlantic Fishery Science **22**:209-218.

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

Davis, R. W., J. G. Ortega-Ortiz, C. A. Ribic, W. E. Evans, D. C. Biggs, P. H. Ressler, R. B. Cady, R. R. Leben, K. D. Mullin, and B. Wursig. 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. Deep-Sea Research I **49**:121-142.

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

Fernandes, P. G., L. MacDonald, R. Aukland, D. G. Reid, E. J. Simmonds, and A. Shanks. 2001. Changes in the availability of herring to the North Sea acoustic survey; the impact of diurnal migration. ICES CM 2001/Q:08. International Council for the Exploration of the Sea.

Fernandes, P. G., and E. J. Simmonds. 1996. Practical approaches to account for receiver delay and the TVG start time in the calibration of the Simrad EK500. Page 8. International Council for the Exploration of the Sea.

Fiedler, P. C., T. R. Barton, and T. Gerrodette. 1998. Dolphin prey abundance determined from backscatter data in eastern pacific surveys. Fishery Bulletin **96**:237-247.

Gontarek, S. 2005. STJG Tools for ArcGIS v9 - GIS Extract, SAMS, Dunstaffnage, Oban.

Goold, J. C. 2000. A diel pattern in vocal activity of short-beaked common dolphins, Delphinus delphis. Marine Mammal Science **16**:240-244.

Gordon, J. C. D., J. N. Matthews, S. Panigada, A. Gannier, J. F. Borsani, and G. Notarbartolo Di Sciara. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. Journal of Cetacean Research and Management **2**:27-36.

Gowans, S., and H. Whitehead. 1995. Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. Canadian Journal of Zoology **73**:1599-1608.

Gregr, E. J. and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **58**: 1265-1285.

Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J.-P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographical information systems. Marine Ecology Progress Series **219**:251-264.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147-186.

Haegele, C. W., and J. F. Schweigert. 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Can. J. Fish. Aquat. Sci. **42**:39-55.

Hafsteinsson, M. T., and O. A. Misund. 1994. Mapping the migration pattern of schooling fish by use of multibeeam sonar during conventional acoustic surveys. International Council for the Exploration of the Sea.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson, and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. ICES Journal of Marine Science **62**:760-770.

Hastie, G. D., B. Wilson, L. J. Wilson, K. M. Parsons, and P. M. Thompson. 2004. Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. Marine Biology **144**:397-403.

Hooker, S. K. 1999. Resource and habitat use of northern bottlenose whales in the Gully: ecology, diving and ranging behaviour. PhD Thesis. Dalhousie University, Halifax, Nova Scotia, Canada.

ICES. 2004. Report of the planning group for herring surveys. ICES CM 2004a/G:05. International Council for the Exploration of the Sea.

ICES. 2005. Report of the Planning Group for Herring Surveys. ICES CM 2005/G:G:04. International Council for the Exploration of the Sea.

ICES. 2006. Report of the Planning Group on Herring Surveys (PGHERS). ICES CM 2006/LRC:04. International Council for the Exploration of the Seas, Rostock, Germany.

Ingram, S. N., L. Walshe, D. Johnston, and E. Rogan. 2007. Habitat partitioning and the influence of benthic topography and oceanography on the distribution of fin and minke whales in the Bay of Fundy, Canada. Journal of the Marine Biological Association U. K. **87**: 149-156.

Janik, V. M. 2000. Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society London B **267**:923-927.

Johnston, D. W., L. H. Thorne, and A. J. Read. 2005. Fin whales *Balaenoptera physalus* and minke whales *Balaenoptera acutorostrata* exploit a tidally driven tidal wake ecosystem in the Bay of Fundy. Marine Ecology Progress Series **305**: 287-295.

Jones, G. J., and L. S. Sayigh. 2002. Geographic variation in rates of vocal production of free- ranging bottlenose dolphins. Marine Mammal Science **18**:374-393.

Kim, Y. J., and C. Gu. 2004. Smoothing spline gaussian regression: more scaleable computation via efficient approximation. Journal of the Royal Statistical Society, Series B **66**:337-356.

Kinze, C. C., M. J. Addink, C. Smeenk, M. G. Hartmann, H. W. Richards, R. Sonntag, and H. Benke. 1997. The white-beaked dolphin (*Lagenorhynchus albirostris*) and the white-sided dolphin (*Lagenorhynchus acutus*) in the North and Baltic Seas: review of available information. Report of the International Whaling Commission **47**: 675-681.

Lawson, J. W., A. M. Magalhães, and E. M. Miller. 1998. Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. Marine Ecology Progress Series **164**: 13-20

MacLennan, D. N., P. G. Fernandes, and J. Dalen. 2002. A consistent approach to definitions and symbols in fisheries acoustics. ICES Journal of Marine Science **59**:365-369.

MacLeod, C. D., C. R. Weir, C. Pierpoint, and E. J. Harland. 2007. The habitat preferences of marine mammals west of Scotland (UK). Journal of the Marine Biological Association of the UK **87**:157-164.

Macleod, K. 2001. The spatial and temporal distribution of cetaceans off the west coast of Scotland in relation to environmental factors: the implications for marine management. PhD Thesis. University of Greenwich.

Macleod, K., R. Fairbairns, A. Gill, B. Fairbairns, J. Gordon, C. Blair-Myers, and E. C. M. Parsons. 2004. Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull, Scotland. Marine Ecology Progress Series **277**: 263-274.

Maravelias, C. D. 1999. Habitat selection and clustering of a pelagic fish: effects of topography and bathymetry on species dynamics. Canadian Journal of Fisheries and Aquatic Sciences **56**:437-450.

Maravelias, C. D. 2001. Habitat associations of Atlantic herring in the Shetland area: influence of spatial scale and geographic segmentation. Fisheries Oceanography **10**:259-267.

Maravelias, C. D., and D. G. Reid. 1997. Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Marine Ecology Progress Series **147**:1-9.

Maravelias, C. D., D. G. Reid, and G. Swartzman. 2000a. Modelling spatio-temporal effects of environment on Atlantic herring, Clupea harengus. Environmental Biology of Fishes **58**:157-172.

Maravelias, C. D., D. G. Reid, and G. Swartzman. 2000b. Seabed substrate, water depth and zooplankton as determinants of the prespawning spatial aggregation of North Atlantic herring. Marine Ecology Progress Series **195**.

Mehlum, F., G. L. H. Jr, Z. Klusek, and M. B. Decker. 1999. Scale-dependent correlations between the abundance of Brunnich's guillemots and their prey. Journal of Animal Ecology **68**:60-72.

Northridge, S. P., M. L. Tasker, A. Webb, K. Camphuysen, and M. F. Leopold. 1997. White-beaked Lagenorhynchus albirostris and Atlantic white-sided dolphin L. acutus distributions in northwest European and US Atlantic waters. Report of the International Whaling Commission **47**:797-805.

Northridge, S. P., M. L. Tasker, A. Webb, and J. M. Williams. 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirostris* Gray), and minke whales (*Balaenoptera acutorostrata* Lacepede) around the British Isles. ICES Journal of Marine Science **52**:55-66.

Oswald, J. N., J. Barlow, and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. Marine Mammal Science **19**:20-37.

Oswald, J. N., S. Rankin, J. Barlow, and M. O. Lammers. 2007. A tool for real-time acoustic species identification of delphinid whistles. Journal of the Acoustical Society of America **122**:587-595.

Overholtz, W. J., and G. T. Waring. 1991. Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during spring 1989. Fishery Bulletin **89**:723-728.

Reeves, R. R., C. Smeenk, C. C. Kinze, R. L. Brownell, and J. Lien 1999. White-beaked dolphin Lagenorhynchus albirostris Gray, 1846. Academic Press, London.

Rendell, L. E., J. N. Matthews, A. Gill, J. C. D. Gordon, and D. W. Macdonald. 1999. Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. Journal of the Zoological Society of London **249**:403-410.

Rivoirard, J., J. Simmonds, K. G. Foote, P. Fernandes, and N. Bez 2000. Geostatistics for Estimating Fish Abundance. Blackwell Science, Oxford.

Rose, G. A., and W. C. Leggett. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. Ecology **71**:33-43.

Santos, M. B. 1998. Feeding ecology of harbour porpoises, common and bottlenose dolphins and sperm whales in the Northeast Atlantic. PhD Thesis. University of Aberdeen.

Santos, M. B., G. J. Pierce, H. M. Ross, D. G. Reid, and B. Wilson. 1994. Diets of small cetaceans from the Scottish coast. International Council for the Exploration of the Sea, Marine Mammal Committee. ICES CM 1994/N:11.

Schneider, D. C., and J. F. Piatt. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Marine Ecology Progress Series **32**:237-246.

Selzer, L. A., and P. M. Payne. 1988. The distribution of white-sided (Lagenorhynchus acutus) and common dolphins (Delphinus delphis) vs. environmental features of the continental shelf of the northeastern United States. Marine Mammal Science **4**:141-153.

Simmonds, E. J. 2003. Weighting of acoustic- and trawl-survey indices for the assessment of North Sea herring. ICES Journal of Marine Science **60**:463-471.

Simmonds, E. J., and D. N. MacLennan 2005. Fisheries acoustics: theory and practice. Blackwell Publishing, Oxford.

Simmonds, E. J., N. J. Williamson, F. Gerlotto, and A. Aglen. 1992. Acoustic survey design and analysis procedures: a comprehensive review of current practice. Co-operative Research Report. Report No 127. ICES.

Smout, S., and U. Lindstrøm. 2007. Multispecies functional response of minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. Marine Ecology Progress Series **341**:277-291.

Steiner, W. W. 1981. Species-specific differences in pure tonal whistle vocalizations of five western North Atlantic dolphin species. Behavioural Ecology and Sociobiology **9**:241-246.

Stevick, P. T., S. V. Calderan, C. Speedie, J. Shrimpton, and C. B. Embling. 2007. A trophic shift off west Scotland: minke whales and basking sharks in P. G. H. Evans, editor. 21st Annual Conference of the European Cetacean Society, San Sebastian, Spain.

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

Weir, C. R., C. Pollock, C. Cronin, and S. Taylor. 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. Continental Shelf Research **21**:1047-1071.

Wood, S. N. 2006a. Generalised Additive Models - An Introduction with R. Chapman and Hall/CRS, Boca raton, Florida.

Wood, S. N. 2006b. The mgcv package. R statistical group.

Chapter 6

General Discussion

6.1 Synthesis

Predictive modelling of species' distributions requires an understanding of the robustness of the model predictions to spatial variation (Araujo & Guisan 2006; Fielding & Haworth 1995; Guisan & Zimmermann 2000; Jimenez 2005; Moses & Finn 1997; Randin et al. 2006), temporal variation (Ferguson et al. 2006; Forney 2000; Gregr & Trites 2001; Hamazaki 2002; Hastie et al. 2005), autocorrelation (Aarts 2006; Mendes 2007; Scott-Hayward 2006; Stephenson et al. 2006), direct or indirect nature of variables (Fiedler et al. 1998; Guinet et al. 2001) and survey techniques. As yet, no assessment of the robustness of models to visual versus acoustic survey methodologies has been carried out. Also, most studies tend to evaluate predictive models based on only an evaluation of space or time or autocorrelation, but rarely a combination of these (Ferguson et al. 2006; Forney 2000; Gregr & Trites 2001; Hamazaki 2002; Hastie et al. 2005; Jimenez 2005; Moisen & Frescino 2002; Moses & Finn 1997). A search of the literature found no examples of models that have been evaluated using all measures of model robustness; yet to know whether a model is robust it is essential to evaluate the model performance on these criteria. This study is the first attempt to model cetaceans off the west coast of Scotland by assessing predictive model robustness over space (through *grain* size and *extent*), time (by month, year or groups of years), and survey methodology, whilst also assessing the influence of autocorrelation on model predictions, and the potential for prey species to be used as predictor variables.

The overall aim of this thesis was to produce environmental models of harbour porpoise (*Phocoena phocoena*), delphinid, and sperm whale (*Physeter macrocephalus*) distributions. The robustness of these models was assessed to ensure that the models would be able to reliably predict critical areas for each species such that the appropriate mitigation measures can be put into place in these areas to reduce risks to cetaceans from potentially harmful anthropogenic activities. This chapter is therefore constructed around three main aspects: the distribution and habitat use of cetaceans off the west coast of Scotland, evaluation of model robustness, and the applied use of the models in conservation planning and mitigating potentially harmful anthropogenic activities.

6.2 Distribution and habitat use

The oceanographic regimes of the Inner Hebrides and off-shelf waters are very different: the Inner Hebrides being driven mainly by tidal mixing and tidal oceanography, and the off-shore areas driven more by ocean and shelf-edge processes (Mann & Lazier 2006). The habitat variables important in describing the distributions of the different species reflect this difference in oceanographic regimes: harbour porpoise distributions were related most strongly to tidal variables such as tidal speed and position in the spring-neaps cycle; whereas dolphins and sperm whales were more closely related to the oceanographic variables that define their oceanic habitat such as topography, Sea Surface Temperature (SST) and depth or strength of the haloclines and thermoclines (Table 6.1).

Harbour porpoises were shown to be found in higher densities in areas with low tidal currents, and were seen more during spring tides than neap tides (Chapter 4). This is likely to be influenced mainly by scale: other studies found that harbour porpoises aggregated in relatively small areas of tidal current where tide is funnelled through channels (Calderan 2003) or around islands (Johnston et al. 2005). Such studies were carried out over small scales at single sites known to have high harbour porpoise density. At a larger scale (both of *grain* size and surveyed *extent*) such as that carried out in this study, harbour porpoises were found to associate preferentially with areas of low tidal current. This may be as a result of small-scale association between prey species in small areas of high tidal current, but not in large areas of high current such as that found off the west coast of Scotland to the west of Islay.

Table 6.1 – Comparison of predictive modelling results for the distributions of harbour porpoises, dolphins and sperm whales off the west of Scotland

	Core (porpoise)/ Full spatial & temporal *extent* model	Temporal scale	Spatial scale	Acoustic model (porpoise); All whistle model (delphinids)
Harbour porpoise sightings density (Chapter 4)	s(SeaState) ***7.7%***	s(SeaState) 2003-2005 ***6.5-18.2%***	s(SeaState) Full 2005: ***13.9%***	s(Noise): - linear ***5.9%*** s(Speed): - linear ***2.5%***
	s(MaxTideCur): - linear s(NeaptoSpring): spring s(TimeofDay): peak midday **8.2%**	Robust Robust Not robust 2003: s(TimeFrLW): slack+ebb s(Lon): east **25.2%** 2005: only s(MaxTideCur) **2.7%**	Not robust Not robust Not robust Full: s(SpringTideRange): +ve s(Slope): + linear **11.2%**	Not robust Not robust Not robust 2004-5: s(PctMud): >15% s(SpringTideRange): nl **5.6%**
Dolphin acoustic occurrence (Chapter 2)	s(Depth): + peak @ 1500m s(SST): + level @ 11.5ºC s(ThermoDepth): + linear **5.3%**	← Robust (2003-2005) ← Robust in 2003-2004 not 2005 ← Robust in 2005 not 2003-2004 Robust in October not May → Robust in May not October → Not robust → May FSC: s(HaloDepth): + linear	Not robust Robust Robust FSC: s(SST): + peak @11.5ºC s(ThermoDepth): + linear s(HaloStrength): strong **7.2%**	Robust but drops off >1500m Robust Robust All whistles: s(HaloStrength) strong **9.6%**
Sperm whale acoustic occurrence (Chapter 3)	s(Depth): + s(ThermoStrength): weak s(HaloStrength): strong **27.8%**	Not investigated	Not robust (*extent*); robust (*grain*) Robust (*grain* & Ellet); not (FSC) Robust (Ellet); not (FSC & *grain*) Ellet: s(HaloDepth): + s(SSS): bimodal **25.6%** FSC: s(SST): - linear s(SSS): + peak @ 35.27ppt s(Chl): + linear **33.9%**	

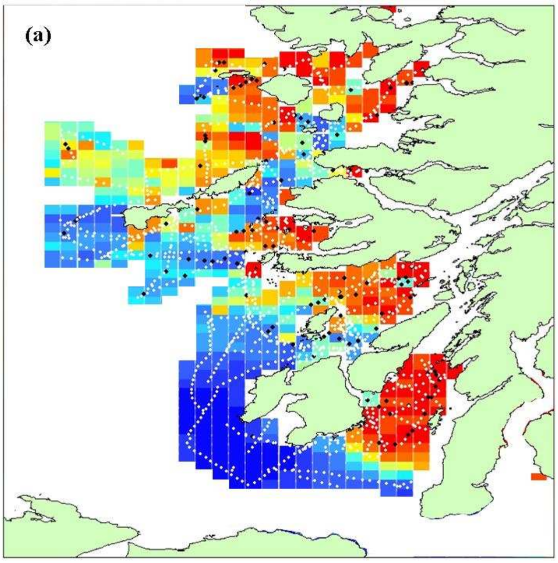
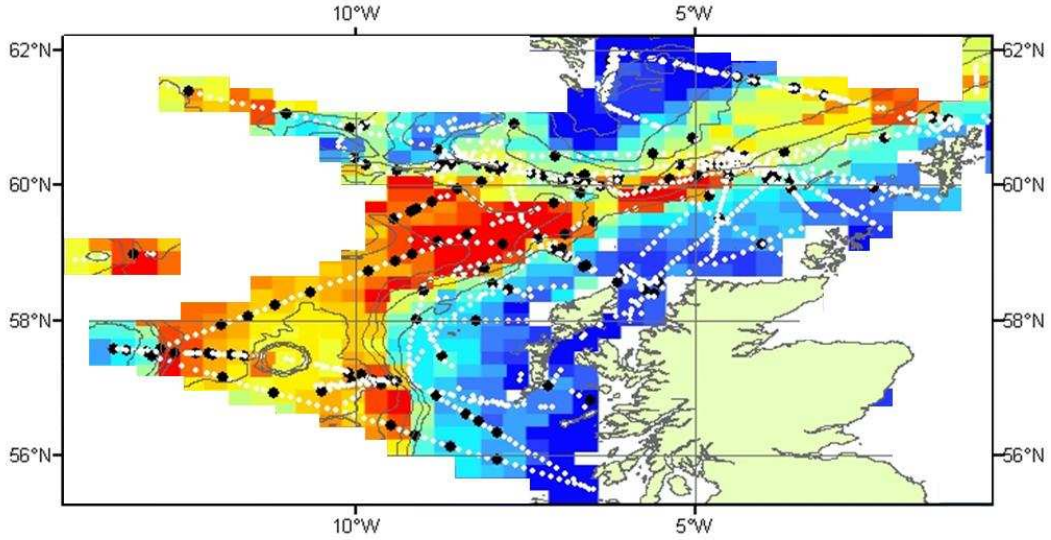
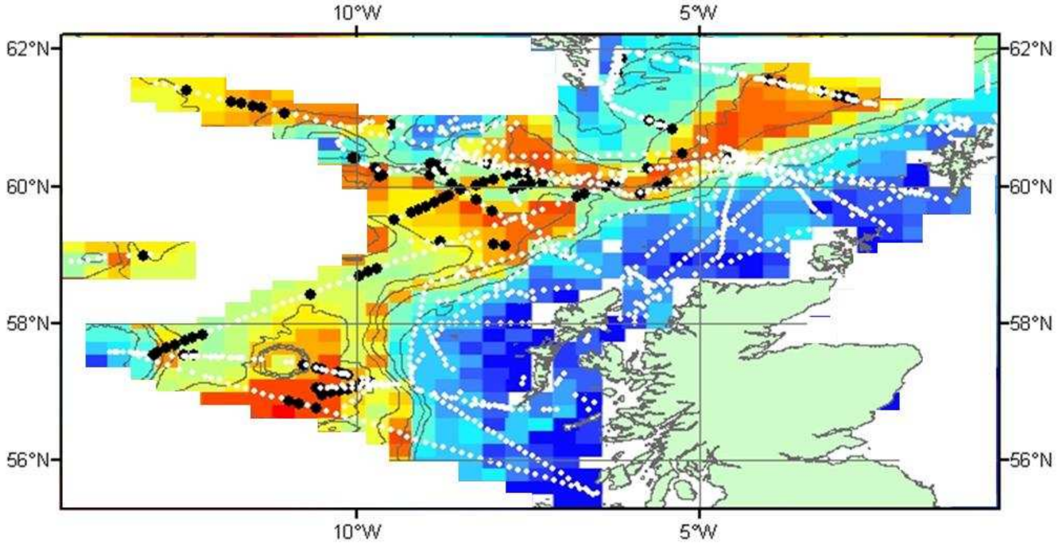


Figure 6.1 – Spatial predictions for (a) the core Southern Inner Hebrides harbour porpoise density model for visual data from 2003-2005; (b) the full survey area grouped dolphin occurrence model for passive acoustic data collected between July 2003 - October 2005; (c) the full survey area sperm whale occurrence model for passive acoustic data collected between July 2003 – October 2005.



(b)



(c)

The higher visual detection rates of harbour porpoises during spring tides was a new finding, certainly this is the first known study to investigate the effect of the spring-neaps cycle on harbour porpoises. There is evidence to suggest that prey is more aggregated during spring rather than neap tides (Alldredge & Hamner 1980; Cotte & Simard 2005; Coyle et al. 1992; St John et al. 1992; Zamon 2002, 2003), so it is hypothesised that the increased detection rates are related to more vigorous foraging behaviour during this tidal state, creating a stronger visual cue.

Unlike harbour porpoises, delphinids (Chapter 2) and sperm whales (Chapter 3) were more influenced by oceanic and shelf-edge oceanographic features (Table 6.1). For both species the main predictor variable was depth, with a preference for waters off the shelf. In delphinids this preference peaked at 1500 m depth, whereas sperm whale preference increased as depth increased above 1500 m. Sperm whales feed predominantly on squid, which in Scottish and Irish waters have been identified from stomach contents to be primarily: *Gonatus fabricii, Histioteuthis bonnelli, Teuthowenia megalops, Todarodes sagittatus* and *Haliphron atlanticus* (Santos et al. 1999; Santos et al. 2002). These are generally deep water species: the largest mature *G. fabricii* being found in water deeper than 400 m, and generally deeper than 1000 m in cooler North Atlantic waters (Bjørke 2001); both *H. bonnelli* and *T. sagittatus* are generally found in waters between 700–4600 m, and *T. megalops* in water depths of between 400-4500 m in the Rockall Trough (Collins et al. 2001). So sperm whales are likely to be associating with the deep water off the shelf in order to feed on these deep water species of cephalopods. Some of these species (namely: *G. fabricii* and *T. sagittatus*) also occur in the diet of long-finned pilot whales (*Globicephala melas*) (Desportes & Mouritsen 1993). Although pilot whales typically make shallower dives than sperm whales (Baird et al. 2002), they are the deepest diving of the delphinids found off the west coast of Scotland. They were generally heard and seen more frequently in the deeper waters further offshore than the other dolphin species. So of the delphinids, long-finned pilot whales were most likely to explain the peak in detections around 1500 m.

The similarity in habitat preferences between sperm whales and delphinids diverges after the inclusion of depth: with SST and thermocline depth being the main predictors of delphinids and halocline and thermocline strength being the main predictors of sperm whales. The higher detection rates of delphinids in warmer surface waters may be due to different factors in different species. For example, common dolphins (*Delphinus delphis*) appear to be limited in their northerly extent by SST (MacLeod et al. 2007; Macleod 2001). They are also shown to be allopatric to both white-sided dolphins (*Lagenorhynchus acutus*) (Selzer & Payne 1988), and white-beaked dolphins (*Lagenorhynchus alibirostris*) (MacLeod et al. 2007) with SST dividing the warm water preferences of common dolphins from the cold-water *Lagenorhynchus* species. Whether this preference for warmer water is due to inter-species competition or due to the habitat of their preferred prey species is not known. However, the warmer surface water is associated with the Gulf Stream, North Atlantic Water (NAW) travelling north from its origins in the equatorial waters near the Gulf of Mexico (Mann & Lazier 2006). This water has been associated with migration and transport of many species of fish (Bartsch & Coombs 1997; Borja et al. 2002; Ibaibarriaga et al. 2007; Shelton et al. 1997), and also high densities of non-migrating fish such as blue whiting (Armstrong pers. comm.). This current is also associated with a deep thermocline, especially from around the Wyville-Thompson Ridge (WTR) and along the Shetland side of the Faroe Shetland Channel (FSC). Thus, the higher detection rates of delphinids in warmer surface water and deeper thermoclines may partly reflect foraging preferences of delphinids.

Similarly, sperm whales’ preference for areas with weak thermoclines and strong haloclines is likely to reflect the habitat preferences of their cephalopod prey. Weak thermoclines were found in areas characterised by steep topography, such as around the Anton Dorhn seamount and around Wyville-Thompson Ridge. Steep topography tends to induce vertical movement of water around the slope, so increasing mixing between surface and deep waters and increasing productivity (Mann & Lazier 2006). If these areas allow for stable areas of mixing, then it is likely that they are favourable foraging locations for the sperm whale cephalopod prey. Steep topography has been shown in other studies to be a significant predictor of sperm whale distribution (Davis et al. 1998; Gregr & Trites 2001; Jaquet & Whitehead 1996; Kenney & Winn 1986; Whitehead et al. 1992). In this study, the higher detection rates of sperm whales observed in areas of weak thermocline strength is likely to be a more *proximal* variable than slope in explaining distributions of sperm whale prey.

Higher detection rates of sperm whales were also found in areas of strong haloclines. Strong haloclines are characteristic of the deep water of the Faroe-Shetland Channel (FSC) and of the Rockall Trough (RT), where the warm salty surface water lies above deep cold fresh Norwegian Sea Water (NSW) in the FSC, and above the cool fresh Labrador Sea Water (LSW) in the RT. This is the main habitat for some of the deepest species of squid such as *G. fabricii* in the FSC (Bjorke 2001), and *H. bonnelli* & *T. sagittatus* in the RT (Collins et al. 2001).

Overall, the models for delphinids and sperm whales predicted some overlapping areas of high density, such as the area just south of the Wyville-Thompson Ridge in a band between the Scottish shelf edge and Rosemary Bank (Figure 6.1). This may reflect some overlap in prey preferences between the squid-eating delphinids and sperm whales. However, differences in overall habitat preferences between delphinids and sperm whales probably reflect the different habitats of their prey species: shallower living cephalopods and fish species in delphinids and deep water cephalopods in sperm whales.

6.3 Evaluation of predictive models

6.3.1 Temporal scale

Temporal scale was examined for both harbour porpoises (Chapter 4) and delphinids (Chapter 2) at the yearly, two yearly and three yearly scales, whereas delphinids were also analysed at a smaller monthly scale. Only the harbour porpoise model was robust over time, with the same two variables being selected in every combination of years: maximum tidal current and position in the spring-neaps cycle (Table 6.1). This provides a good indication that this model will be able to reliably predict harbour porpoise distribution for this core survey *extent* around the Southern Inner Hebrides into the future. There are few examples of yearly analysis of habitat preferences to examine the robustness of habitat preferences over time, however in a study of dolphin habitat preferences in the tropical Pacific it was found that the same five variables were able to predict dolphin occurrence year on year (Ferguson et al. 2006). Such modelling is useful in the identification of boundaries for marine reserves. For marine reserves with static boundaries to be successful, the habitat needs to be important to the species over time (Cañadas & Hammond 2006; Cañadas et al. 2005; Hyrenbach et al. 2000). For example, high density of bottlenose dolphins (*Tursiops* *truncatus*) was predicted consistently over 11 years of survey data in the area around the sea mount 'Seco de los Olivos' in Spanish waters despite between year fluctuations in abundance (Cañadas & Hammond 2006). This area was also predicted to be of importance especially to common dolphins, and a wide range of other cetacean species, and was thus proposed as a Special Area of Conservation (Cañadas et al. 2005).

In contrast, delphinid models were different depending on month and year (Table 6.1), although the two key predictors were SST and thermocline strength. In years which had poor SST signal (i.e. low SST), thermocline strength was a more important predictor of delphinids (Table 6.1). The low surface SST signal in 2005 was likely to be due to wind-induced mixing of the surface waters during the poor weather conditions of that year (Gillibrand pers. comm.). However, the low SST signal during May is due to the loss of summer surface heat during the winter months, which only return to their warmest temperatures again in October (Mann & Lazier 2006). Despite some variation between years, both SST and thermocline strength appear to show some consistency in modelling delphinid distributions over different temporal scales. This shows a variation in predicted distributions dependent on whether SST or thermocline strength is influencing distributions. It is perhaps not surprising that delphinids show so much variation between years, or that so little variance is explained by the model (only around 5%), since they are likely to move with prey distributions depending on oceanographic variations within that year or season. However, the area around Rosemary Bank is consistently predicted to show high usage by delphinids both between years and months, so may provide some indication of an area that requires protection from harmful anthropogenic activities.

6.3.2 Spatial scale

The effect of changing the *extent* on the species-environment relationships and the spatial robustness of the models was investigated for each species group. For both harbour porpoises (Chapter 4) and delphinids (Chapter 2), models were build on data from the whole survey area and compared with models built on data from a restricted geographic area (the southern Inner Hebrides for harbour porpoises and the Faroe-Shetland Channel for delphinids). For sperm whales (Chapter 3), models were compared based on data from two completely different extents: for the Faroe Shetland

Channel survey data and for the Ellet Line (Rockall Trough) survey data. Only for delphinids was there any consistency in species-environment relationships as *extent* was varied. In this case, SST and thermocline depth had the same relationships with delphinid distributions in the models for the constrained *extent* (Faroe-Shetland Channel surveys) as for the full *extent* (Table 6.1).

If any model is to be used to predict species' distributions in areas where there is little or no data, the variables must be spatially robust (Araujo & Guisan 2006; Boyce et al. 2002; Fielding & Haworth 1995; Randin et al. 2006). Although caution must be exercised whenever any model is used for extrapolation or for predicting where there is little survey effort, areas predicted to have high usage allow for the direction of future field studies (Cañadas et al. 2005; Moses & Finn 1997). For example, predictions of medium to high density of bottlenose dolphins were predicted in an area off Malaga with little survey effort, highlighting the area for future fieldwork (Cañadas et al. 2005). For delphinids, the consistent higher detection rates of delphinids in areas of higher SST and deeper thermoclines may provide some indication of spatially important areas for the group.

For both sperm whales (Chapter 3) and harbour porpoises (Chapter 4), no variables were consistent in explaining the differences in detection rates over different *extents*. These studies are not unusual in showing differences in species-environment relationships between differing *extent* (Fielding & Haworth 1995; Jimenez 2005; Randin et al. 2006). For example, predictive models of Golden eagle (*Aquila chrysaetos*) nest sites off the west coast of Scotland, found that models based on data from the mainland did not predict nest sites in the North of Mull (Fielding & Haworth 1995). It was suggested that this may be due to differing availability of combinations of habitat variables that result in good nest site habitats. Highly mobile species, such as cetaceans are likely to be mainly influenced by their prey distributions, thus species-environment relations will change from area to area with changing habitats due to the changing availability of prey. This suggests exercising caution in using any of the sperm whale or harbour porpoise models for predicting species distribution outwith the surveyed *extent*.

The effect of *grain* size on the species-environment relationships and the variables selected was only investigated for sperm whales (Chapter 3). Increasing the *grain* size from 9 km to 18 km resulted in the same relationships at both scales but with one fewer variables in the 18km model, which may be related to the reduction in sample size due to increasing the *grain* size rather than a change in preference. *Grain* sizes of between 80 to 640 nm (150-1200 km) were used to evaluate sperm whale distributions in relation to environmental features in the South Pacific. This analysis only found correlations with steep topography and secondary productivity at *grain* sizes greater than 320 nm (600 km) (Jaquet & Whitehead 1996). So for sperm whales it is likely that much larger *grain* sizes may yield different species-environment relationships. Analysis at these scales was not possible within the limited *extent* of this study.

Changes in *grain* size can influence the predicted species-environment relationships quite significantly (Bailey 2006; Fauchald et al. 2000; Guinet et al. 2001; Jaquet & Whitehead 1996; Mehlum et al. 1999; Rose & Leggett 1990). For example, the relationship between female Antarctic fur seals (*Arctocephalus gazella*) and chlorophyll was found to be negative at a small spatial scale (< 1x1° or around 110x110 km) but positive at a larger spatial scale (>2x2° or around 220x220 km) (Guinet et al. 2001). This suggests that any model based on a certain *grain* size should only be used to predict distributions within that *grain* size, since relationships may change at different scales.

6.3.3 Direct versus indirect predictors

Indirect predictors were used for all the predictive models in this thesis (Chapters 2-4), namely: topographical and oceanographic predictors. This was partly driven by the fact that data for more direct predictors such as prey distribution and abundance were not available. But also by the desire to use environmental features which were non-variant or easily measurable for making predictions in the future. For the dolphin and harbour porpoise predictive models, indirect predictors were only able to explain small amounts of the deviance (Table 6.1). After compensating for survey effects, the full models were only able to explain 5.3% of the dolphin occurrence, and 8.2% of the harbour porpoise distribution (Table 6.1). Although, the harbour porpoise model for 2003 was able to explain as much as 25.2% of the deviance (Table 6.1). Similarly, the sperm whale models were able to explain as much as 33.9% of the deviance (Chapter 3, Table 6.1).

In part, the low proportion of deviance explained by each of the models is due to the limitations of the survey data. For delphinids, the combination of "whistling odontocetes" into a single group is likely to blur together the habitat preferences of the individual species. This results in general habitat preferences that are only able to explain the overall preferences of delphinids and thus little explained deviance. A similar study of delphinids in the eastern tropical Pacific Ocean using a similar range of environmental variables was similarly only able to explain 12% of the variance (Ferguson et al. 2006).

For visual survey methods, such as that used for modelling harbour porpoise distributions, the proportion of deviance explained by environmental variables is strongly influenced by sea state (Chapter 4 & Table 6.1). In years of poor weather conditions, the ability to model distributions of harbour porpoises is diminished due to the difficulty in detecting porpoises during high sea states. Thus, in years of poor sea state (2005), environmental variables were only able to explain 2.7% of the deviance of harbour porpoise distribution, and in years of good sea state (2003), environmental models were able to explain as much as 25.2% of the deviance. Sea state thus limits the ability to model environmental preferences of elusive species such as porpoises (Forney 2000).

Generally, both *indirect* and *direct* predictors assume that cetaceans' habitat preferences are related to foraging preferences. However, cetaceans are also likely to be detected while travelling between foraging locations, during which they may not be in their preferred habitat. Also, by combining season and years of data into a single model, any changes in habitat preferences linked to changes in prey distributions will be blurred. These reasons, and the previously stated difficulties of cetacean survey data explain, at least in part, why the models explain so little deviance.

However, the use of *indirect* predictors rather than *direct* predictors, or the use of *distal* rather than *proximal* predictors may also be one reason why it is difficult to model cetacean distributions and explain larger amounts of deviance. For example, in studies of large whale distributions off British Columbia, a species was considered to be not very closely linked to the oceanographic conditions if the model explained less than around 30% of the deviance (Gregr & Trites 2001). In this study, models explaining the distribution of fin whales (*Balaenoptera physalus*) and sei whales (*B.*

borealis) explained around 50% of the deviance, and were therefore considered to be quite closely associated to the indirect predictor variables they used in the models (depth, slope, SST and SSS). The highest explained variation can only occur if (i) all the variables that explain the species distribution are included (*proximal* or *distal*) and (ii) the variables are measured at the same temporal and spatial scale as the species distribution data. In a study of cetacean habitat use within the California Current System, simultaneous multidisciplinary mesoscale and fine-scale surveys of ocean and ecosystem structure were carried out (Tynan et al. 2005). Using this broad range of oceanographic and prey data, multiple logistic regression models of species' distributions were able to explain 94.4% of the variation in distribution of humpback whales (*Megaptera novaeangliae*), and between 70-79% of harbour porpoise distributions. In my study, it is also probable that the environmental variables are not *proximal* or *direct* enough to reliably predict the species' distributions, and that some variables may be missing from the model selection.

Alternatively, direct variables are often difficult to get hold of, especially at a similar temporal and spatial scale to the cetacean data. The herring (*Clupea harengus*) stock is monitored every year during a survey carried out in the shelf waters off the west coast of Scotland (Chapter 5) and by collaborating with FRS we were able to collect data on herring and delphinid distributions at the same time. A preliminary assessment of the correlation between dolphin and herring distributions was carried out in Chapter 5, to assess the ability of herring to be used as a *direct* predictor of dolphin distributions. Little correlation was found between the two species at the *grain* size analysed, suggesting that herring may not be an adequate *direct* predictor of dolphin distributions. However, the combination of "whistling odontocetes" into a single delphinid group blurring together individual species prey preferences, and the detection of animals during travel and foraging behaviours may hinder the ability to detect a correlation with prey distributions. Also, there is evidence to suggest that predators only correlate with prey at large *grain* sizes (Fauchald et al. 2000; Guinet et al. 2001; Mehlum et al. 1999; Rose & Leggett 1990; Schneider & Piatt 1986). So while, in theory, prey distributions should be a good *direct* predictors of cetacean distributions, the reality is more complex.

6.4 Survey effects on predictive models

6.4.1 Autocorrelation

Autocorrelation was evaluated by several different methods in different chapters: cross-validation (Chapter 3 & 4), direct removal of the autocorrelation (Chapter 2), the Wald-Wolfowitz test (Chapter 2 & 3), and with the use variograms (Chapter 5) or temporal autocorrelation functions (Chapter 5).

Autocorrelation in the data resulted from: (i) detecting the same animal over a large distance and hence over several segments (Chapter 2, 3 & 5), and/or (ii) aggregation of a species either due to underlying autocorrelated environmental features or due to some behavioural response (Chapter 3 & 5). Autocorrelation caused by detecting the same animal or group of animals over a large distance is measurable and was removed from the data by choosing a suitable sampling unit (Chapter 2 & 3). The effect of this autocorrelation was examined for delphinids, and illustrated clearly the overfitting of the model when autocorrelation was not removed: an additional variable was included in the model, and the environmental relationships changed slightly (Chapter 2). This is due to the inflated degrees of freedom resulting from autocorrelation resulting in variables being retained in the model when they are not actually significant (Aarts 2006; Borchers et al. 1997; Lennon 2000).

Including autocorrelation due to detecting the same animals over a large distance is likely to complicate the species-environmental relationship due to the difference in sound propagation under different oceanographic conditions: in deep stratified water such as that in the Rockall Trough, sounds travel much further than in mixed shelf and shelf-edge waters (Urick 1983). This results in different detection rates in different habitats, and cetaceans being heard over a larger number of segments in some habitats more than others, resulting in unequal distribution of autocorrelation over the whole survey *extent*. We can have more confidence in the statistical validity of models and resulting species-environment relationships after removal of this autocorrelation.

With the sperm whale models, even after the ‘acoustic autocorrelation’ was removed, the sperm whales were still significantly autocorrelated (Chapter 3). This suggested that there is still an environmental or behavioural variable missing from the model that explains this remaining autocorrelation. This flags up the need to include other environmental variables able to explain the autocorrelation or to explore modelling approaches such as Generalised Estimating Equations (GEEs) which are just recently being used to model autocorrelation directly within the modelling process in marine mammal biology (Bailey 2006; Hardin & Hilbe 2003; Scott-Hayward 2006). Despite this un-modelled autocorrelation, cross-correlation techniques (basing the model on 75% of the data and testing it on the remaining 25% of the data), suggested that the models were not overfitted.

6.4.2 Survey methodology

Detection rates for visual and passive acoustic survey methodologies for detecting cetaceans were different, with different variables affecting detection probabilities for each modality (Chapter 4). Visual detection is influenced by the surfacing pattern of the species (Okamura et al. 2006), group size (Barlow et al. 2001), weather conditions (Barlow et al. 2001; Palka 1996), behaviour (Palka & Hammond 2001), platform height (Barlow et al. 2001), and observer experience (Barlow et al. 2001). Acoustic detection is likely to be influenced by vocalisation rates, frequency of vocalisations, sound propagation in different habitats, natural ambient noise, vessel noise, and behaviour.

This was the first study to examine the difference both in detection rates and predictive models based on visual and passive acoustic survey data for harbour porpoises. Noise levels had a significant impact on the acoustic detection rates of harbour porpoises, with fewer detections at higher noise levels. This is similar to that found for the acoustic detection of other cetacean species (Gordon et al. 2000; Hastie et al. 2005). It was also shown that noise levels varied with a number of environmental features including: depth, sediment type, tidal state, boat speed and tidal current speed. Similarly, for visual survey data sea state had a significant impact on visual detection rates, reducing detection rates above sea state 1, and severely reduced in sea states >2. Sea state is also affected by the underlying environmental features: for example, sea state is higher in areas of high tidal current, and the area to the west of Islay characterised by the highest tidal currents is nearly always beset with high swell making visual surveys nearly impossible for harbour porpoises.

Despite compensating for survey effects, different environmental variables were selected to explain visual and acoustic detection rates. The visual model included maximum tidal current and position in the spring-neaps tidal cycle as the two main predictors, whereas the acoustic model included percentage of mud in the sediment and spring tidal range as the most important predictors (Table 2.1). Maximum tidal current was significantly negatively correlated to the percentage of mud in the sediment (r = -0.541) and spring tidal range (r = -0.325), and the predicted distribution maps were very similar. So despite the differences in the environmental predictors included in the models, somewhat similar predicted distribution surfaces were produced and the same high use areas highlighted.

The results of the modelling were able to highlight some of the uncertainties still remaining in the factors affecting detection rates both in visual and passive acoustic methodologies. Some of these warrant further investigation. Passive acoustic techniques have been shown in this study to be valuable in several ways: they are very effective for determining distribution of sperm whales with their long dive times; increasing the detection rates of harbour porpoises in this study and in the study carried out by Gillespie et al. (2005) by around 8 times that of visual methods if surveys are carried out in any sea states; and useful for determining delphnid distributions. They can be particularly useful on platforms off opportunity where space is limited making it impossible to accommodate teams of visual observers.

6.5 Future applications

The work detailed above has provided a suite of predictive models for the distribution of harbour porpoises, delphinids and sperm whales to be used as a baseline for future conservation work. It is hoped that these models will provide a framework from which to inform developers (such as oil and gas seismic operations and windfarm development), and the military of the critical habitats for the three species/groups of species. The data also provide a baseline for identifying potential future Marine Protected Areas.

The harbour porpoise model was shown to be robust over time (as evaluated over 3 years) so some confidence can be placed in using the model to predict cetacean distribution into the future. The areas predicted to be important high-use areas to harbour porpoises appear to be consistent over time. Such a result is not only useful for predicting areas where anthropogenic activities may worst affect harbour porpoise populations, but also provides information on which marine reserves for harbour porpoises may be based. As yet, there are no Special Areas of Conservation (SACs) for harbour porpoises in UK waters, even though this is a requirement of the EU Habitats Directive. However, the identification of high use areas with boundaries determined by oceanographic processes that are consistent over time (such as tidal currents) provides a good basis on which to inform the selection of SACs (Cañadas et al. 2005; Hooker & Gerber 2004). Habitat models were used as a basis on which to identify potential Special Areas of Conservation for cetaceans in Spanish waters (Cañadas et al. 2005). The west coast of Scotland has the second highest densities of harbour porpoises in Europe after Denmark (SCANS-II 2006), so would provide the optimum location for harbour porpoise SAC in UK waters.

One of the main threats to harbour porpoises in coastal waters off the west coast of Scotland is Acoustic Deterrent Devices (ADDs). Acoustic deterrent devices (ADDs) are used extensively on salmon farms throughout the west coast of Scotland to deter seals. The sounds they produce have been shown to deter harbour porpoises from their habitat (Johnston 2002; Olesiuk et al. 2002). For example, harbour porpoise abundance decreased significantly at ranges over 3.5 km from an active ADD in Retreat Passage, British Columbia (Olesiuk et al. 2002). To be able to monitor the effects of ADDs on cetacean distributions, long term studies of their habitat preferences are required (Morton & Symonds 2002). For example, a 15 year study of killer whale (*Orcinus orca*) distributions in British Columbia, showed significant displacement of the species from an area during the time in which ADDs were installed on salmon farms, but a return to the area after the ADDs were removed (Morton & Symonds 2002). Use of ADDs off the west coast of Scotland may therefore displace harbour porpoises from their preferred habitat. These models are able to predict high density areas in which harbour porpoises are most likely to be affected for future mitigation of ADD effects (Figure 6.2).

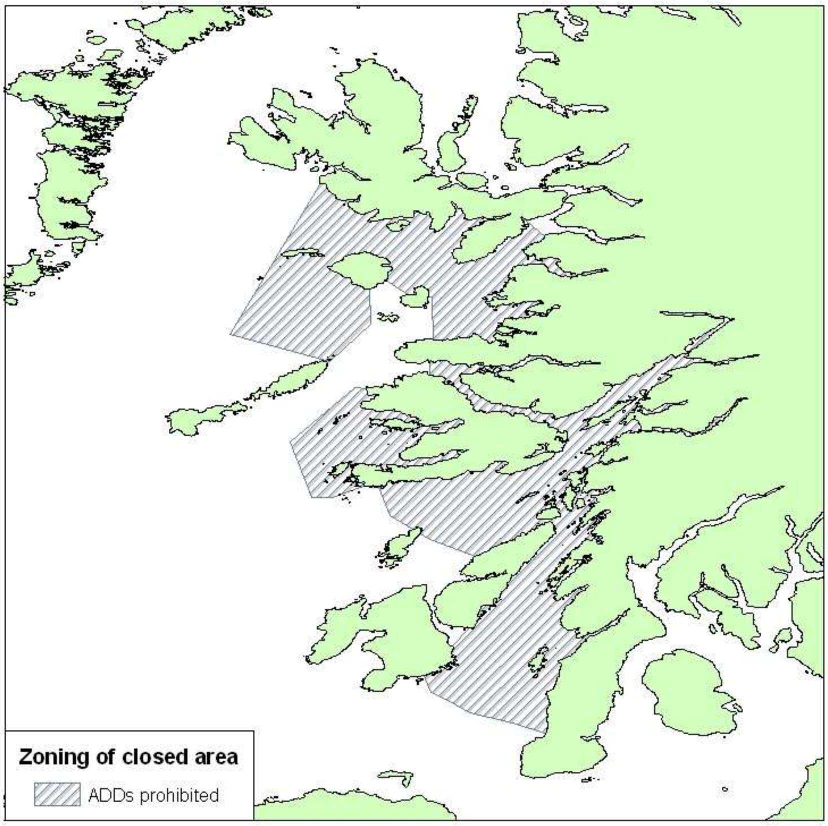


Figure 6.2 – Potential closed area for the management of Acoustic Deterrent Devices (ADDs) and their potential impact on harbour porpoises.

Generally the whole of the deep waters off the west coast of Scotland are important to both delphinids and sperm whales. Since the models of delphinid distributions are not temporally robust, nor the models of sperm whale distributions spatially robust, little can be predicted in terms of core high use areas. However, one area emerges as having consistently high usage for both species over space and time: the area just south of the Wyville-Thompson Ridge, stretching between the Hebridean shelf edge and Rosemary Bank (Figure 6.3). This would suggest that this area should be avoided during any military exercises when testing sonar, or when carrying out seismic surveys. These areas have in the past been used for such activities: the area around Rosemary Bank may have been used as a testing area for the new Low Frequency sonar (MacLeod et al. 2007), and mid-frequency sonar was heard in the Faroe-Shetland Channel during the October 2004 survey.

The whole west coast of Scotland is available for oil exploration (Macleod 2001). Macleod (2001) found that the Faroe-Shetland Channel had the highest diversity and abundance of a wide range of cetaceans in offshore waters, and recommended that the core area should be closed to seismic activities during the time at which fin and sei whales were present in significant numbers between July-September (Figure 6.3). Harwood & Wilson (2001) recommended that any seismic surveys should be avoided completely in high use areas. This study suggests that the closed area recommended by Macleod (2001) should also include the area to the north and east of Rosemary Bank, to mitigate the harmful effects of anthropogenic activities such as seismic surveys (Figure 6.3).

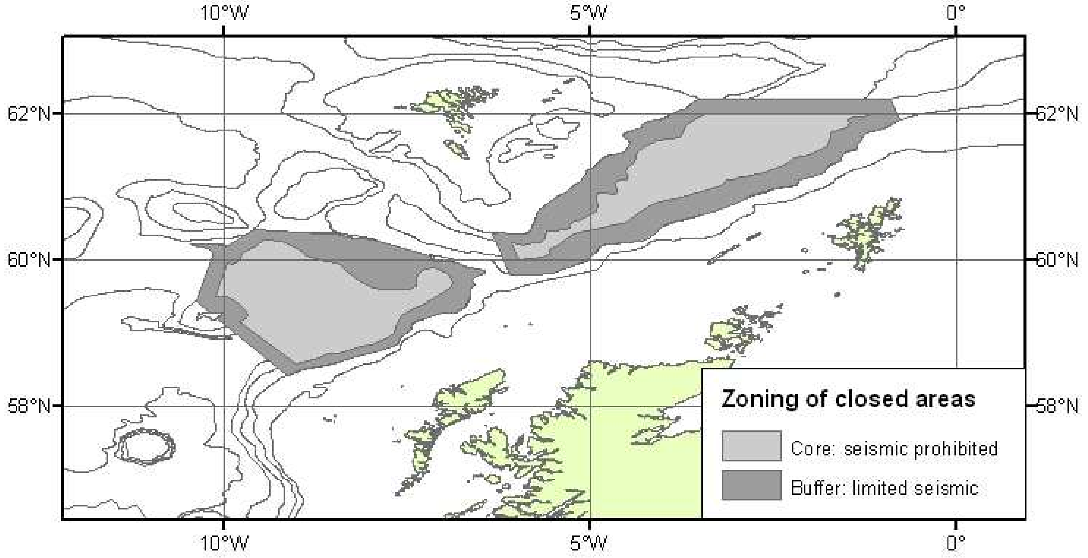


Figure 6.3 – Potential closed areas for management of seismic and military activities and its potential impact on fin whales (Macleod 2001), sperm whales and delphinids.

6.5.1 Recommendations

Conclusions and recommendations based on the model of harbour porpoise distribution:

- Limit the use of Acoustic Deterrent Devices (ADDs) and other anthropogenic activities likely to affect harbour porpoises within the predicted high use areas shown in Figure 6.2.
- Harbour porpoises were shown to be distributed throughout the whole of the Inner Hebrides (the models only explained 8.2% of the deviance), so any anthropogenic activities within their distribution may have the potential to disturb or harm harbour porpoises.

- The model is only able to predict high-use areas within the Argyll Islands and Small Isles, further survey effort would be required to determine the high use areas within the Minch and northern Hebrides.
- Models were only based on data from the summer months (May-September) so only valid in predicting high-use summer habitats. Further year-round survey effort would be required to investigate whether the same habitats are used year-round.
- Models are based at a 2 km scale, different habitat preferences may be obtained at a larger or smaller scale, as shown in other studies of harbour porpoises (Bailey 2006).

Conclusions and recommendations based on the models of delphinid and sperm whale distribution:

- Avoid carrying out seismic activities or testing military sonar within the two high use areas shown in Figure 6.3.
- Since both delphinids and sperm whales are distributed throughout the deep waters off the west coast of Scotland, extra precautions should be taken to ensure any anthropogenic activities do not harm cetaceans outwith the ‘closed areas’ (e.g. using acoustics to listen for the presence of delphinids or sperm whales & not operating sonar or seismics in their presence).
- The delphinid models showed a clear difference between distributions and habitat preferences between May and October, suggesting that season is important in explaining cetacean distributions off the west coast of Scotland. Therefore these models should not be used to infer distributions at other times of year, and further effort should be directed towards determining distributions and habitat preferences for the rest of the year.
- Some areas (especially the Rockall Trough) were surveyed very infrequently, with some areas only visited once in the whole data set, whereas the Faroe-Shetland Channel had more even and regular survey effort. Thus less confidence should be placed in the model predictions for the Rockall Trough than for the Faroe-Shetland Channel. Further survey effort is recommended in the Rockall Trough to increase the confidence in the predictions.

- Since the delphinid models showed a change in habitat preferences between years, further data is required to determine the environmental predictors explaining between-year changes in distribution and habitat preference and to determine if there is any pattern (e.g. whether SST is the main predictor in ‘good’ weather years and thermocline depth the main predictor in ‘bad’ weather years as hypothesised). Another 3-4 years data which covers both ‘good’ and ‘bad’ weather years may be adequate to produce models able to predict between-year changes in distribution. There is data available from the same Faroe-Shetland Channel surveys going back to 2001; however FOAM data was not available pre July 2003. Should this data be made available, another 3 years of data would be available for analysis with no extra survey effort required.
- Models are based at a 9 km or 18 km (sperm whales) scale, different habitat preferences may be obtained at a larger or smaller scale (e.g. Jaquet 1996). The models are also only valid for the environmental data sources used: data at a finer or coarser scale may result in different predictions.

And some overall conclusions and recommendations:

- All three (harbour porpoise, delphinid and sperm whale) models illustrate the difficulties of extrapolating beyond the survey area. Species may distribute themselves differently in different habitats, so changing the overall model predictions. Thus, all of the models in this thesis are only valid for the areas and times surveyed. Should the models be used to predict outwith the surveyed areas, effort should be directed to test the model predictions and to improve the models.

6.6 References

Aarts, G. 2006. Modelling space-use and habitat preference from wildlife telemetry data. PhD Thesis. School of Biology. University of St Andrews.

Alldredge, A. L., and W. M. Hamner. 1980. Recurring aggregation of zooplankton by a tidal current. Estuarine and Coastal Marine Science **10**:31-37.

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

Bailey, H. 2006. Distribution and habitat use of bottlenose dolphins (*Tursiops truncatus*) at varying temporal and spatial scales. PhD Thesis. Department of Zoology. University of Aberdeen.

Baird, R. W., J. F. Borsani, M. B. Hanson, and P. L. Tyack. 2002. Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. Marine Ecology Progress Series **237**:301-305.

Barlow, J., T. Gerrodette, and J. Forcada. 2001. Factors affecting perpendicular sightings distances on shipboard line-transect surveys for cetaceans. J. Cetacean Res. Manage. **3**:201-212.

Bartsch, J., and S. Coombs. 1997. A numerical model of the dispersion of blue whiting larvae, *Micromesistius poutassou* (Risso), in the eastern North Atlantic. Fisheries Oceanography **6**:141-154.

Bjorke, H. 2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. Fisheries Research **52**:113-120.

Borchers, D. L., S. T. Buckland, I. G. Priede, and S. Ahmadi. 1997. Improving the precision of the daily egg production method using generalised additive models. Can. J. Fish. Aquat. Sci. **54**:2727-2742.

Borja, A., A. Uriarte, and J. Egana. 2002. Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north-east Atlantic coasts of Europe. Fisheries oceanography **11**:116-127.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281.

Calderan, S. V. 2003. Fine-scale temporal distribution by harbour porpoise (*Phocoena phocoena*) in North Wales: acoustic and visual survey techniques. MSc Thesis. School of Biological Sciences. University of Wales, Bangor.

Cañadas, A., and P. S. Hammond. 2006. Model-based abundance estimates for bottlenose dolphin (*Tursiops truncatus*) off Southern Spain: implications for conservation. Journal of Cetacean Research and Management **8**:13-27.

Cañadas, A., R. Sagarminaga, R. De Stephanis, E. Urquiola, and P. S. Hammond. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conserv: Mar. Freshw. Ecosyst. **15**:495-521.

Collins, M. A., C. Yau, L. Allcock, and M. Thurston. 2001. Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom **81**:105-117.

Cotte, C., and Y. Simard. 2005. Formation of dense krill patches under tidal forcing at whale feeding hotspots in the St. Lawrence Estuary. Marine Ecology Progress Series **288**.

Coyle, K. O., G. L. J. Hunt, M. B. Decker, and T. J. Weingartner. 1992. Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. Marine Ecology Progress Series **83**:1-14.

Davis, R. W., G. S. Fargion, L. N. May, T. D. Leming, M. F. Baumgartner, W. E. Evans, L. J. Hansen, and K. Mullin. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. Marine Mammal Science **14**:490-507.

Desportes, G., and R. Mouritsen. 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Report of the International Whaling Commission **Special Issue 14**:305-324.

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

Ferguson, M. C., J. Barlow, P. Fiedler, S. B. Reilly, and T. Gerrodette. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling **193**:645-662.

Fiedler, P. C., T. R. Barton, and T. Gerrodette. 1998. Dolphin prey abundance determined from backscatter data in eastern pacific surveys. Fishery Bulletin **96**:237-247.

Fielding, A. H., and P. F. Haworth. 1995. Testing the generality of bird-habitat models. Conservation Biology **9**:1466-1481.

Forney, K. A. 2000. Environmental Models of Cetacean Abundance: Reducing Uncertainty in Population Trends. Conservation Biology **14**:1271-1286.

Gillespie, D., P. Berggren, S. Brown, I. Kuklik, C. Lacey, T. Lewis, J. Matthews, R. McLanaghan, A. Moscrop, and N. Tregenza. 2005. Relative abundance of harbour porpoises (*Phocoena phocoena*) from acoustic and visual surveys of the Baltic Sea and adjacent waters during 2001 and 2002. J. Cetacean Res. Manage. **7**:51-57.

Gordon, J. C. D., J. N. Matthews, S. Panigada, A. Gannier, J. F. Borsani, and G. Notarbartolo Di Sciara. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. Journal of Cetacean Research and Management **2**:27-36.

Gregr, E. J., and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Colombia. Canadian Journal of Fisheries and Aquatic Sciences **58**:1265-1285.

Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J.-P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographical information systems. Marine Ecology Progress Series **219**:251-264.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147-186.

Hamazaki, T. 2002. Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). Marine Mammal Science **18**:920-939.

Hardin, J. W., and J. M. Hilbe 2003. Generalized Estimating Equations. Chapman & Hall/CRC.

Harwood, J., and B. Wilson. 2001. The implications of developments on the Atlantic Frontier for marine mammals. Continental Shelf Research **21**:1073-1093.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson, and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. ICES Journal of Marine Science **62**:760-770.

Hooker, S. K., and L. R. Gerber. 2004. Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. BioScience **54**:27-39.

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

Ibaibarriaga, L., X. Irigoien, M. Santos, L. Motos, J. M. Fives, C. Franco, A. Lago de Lanzos, S. Acevedo, M. Bernal, N. Bez, G. Eltink, A. Farinha, C. Hammer, S. A. Iverson, S. P. Milligan, and D. G. Reid. 2007. Egg and larval distributions of seven fish species in north-east Atlantic waters. Fisheries Oceanography **16**:284-293.

Jaquet, N., and H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series **135**:1-9.

Jimenez, I. 2005. Development of predictive models to explain the distribution of the West Indian manatee *Trichechus manatus* in tropical watercourses. Biological Conservation **125**:491-503.

Johnston, D. W. 2002. The effect of acoustic harassment devices on harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada. Biological Conservation **108**:113-118.

Johnston, D. W., A. J. Westgate, and A. J. Read. 2005. Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. Marine Ecology Progress Series **295**:279-293.

Kenney, R. D., and H. E. Winn. 1986. Cetacean high-use habitats of the NE US continental shelf. Fishery Bulletin **84**:345-357.

Lennon, J. 2000. Red-shifts and red herrings in geographical ecology. Ecography **23**:101-113.

MacLeod, C. D., C. R. Weir, C. Pierpoint, and E. J. Harland. 2007. The habitat preferences of marine mammals west of Scotland (UK). Journal of the Marine Biological Association of the UK **87**:157-164.

Macleod, K. 2001. The spatial and temporal distribution of cetaceans off the west coast of Scotland in relation to environmental factors: the implications for marine management. PhD Thesis. University of Greenwich.

Mann, K. H., and J. R. N. Lazier 2006. Dynamics of marine ecosystems (3rd Edition). Blackwell Scientific Publications, Cambridge.

Mehlum, F., G. L. H. Jr, Z. Klusek, and M. B. Decker. 1999. Scale-dependent correlations between the abundance of Brunnich's guillemots and their prey. Journal of Animal Ecology **68**:60-72.

Mendes, S. 2007. Male sperm whales (*Physeter macrocephalus*) in the Northeast Atlantic: Insights into movements, distribution and foraging ecology. PhD Thesis. Department of Zoology. University of Aberdeen.

Moisen, G. G., and T. S. Frescino. 2002. Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling **157**:209.

Morton, A. B., and H. K. Symonds. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. ICES Journal of Marine Science **59**:71-80.

Moses, E., and J. T. Finn. 1997. Using Geographical Information Systems to Predict North Atlantic Right Whale (*Eubalaena glacialis*) Habitat. J. Northw. Atl. Fish. Sci. **22**:37-46.

Okamura, H., S. Minamikawa, and T. Kitakado. 2006. Effect of surfacing patterns on abundance estimates of long-diving animals. Fisheries Science **72**:631-638.

Olesiuk, P. F., L. M. Nichol, M. J. Sowden, and J. K. B. Ford. 2002. Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbour porpoises (*Phocoena phocoena*) in Retreat Passage, British Columbia. Marine Mammal Science **18**:843-862.

Palka, D. 1996. Effects of Beaufort sea state on the sightability of harbour porpoises in the Gulf of Maine. Report of the International Whaling Commission **46**.

Palka, D. L., and P. S. Hammond. 2001. Accounting for responsive movement in line transect estimates of abundance. Canadian Journal of Fisheries and Aquatic Sciences **58**:777-787.

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

Rose, G. A., and W. C. Leggett. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. Ecology **71**:33-43.

Santos, M. B., G. J. Pierce, P. R. Boyle, R. J. Reid, H. M. Ross, I. A. Patterson, C. C. Kinze, S. Tougard, R. Lick, U. Piatkowski, and V. Hernandez-Garcia. 1999. Stomach contents of sperm whales Physeter macrocephalus stranded in the North Sea 1990-1996. Marine Ecology Progress Series **183**:281-194.

Santos, M. B., G. J. Pierce, M. G. Hartmann, C. Smeenk, M. J. Addink, T. Kuiken, R. J. Reid, I. A. P. Patterson, C. Lordan, E. Rogan, and E. Mente. 2002. Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom **82**:501-507.

SCANS-II. 2006. The quarterly newsletter for project SCANS-II: Small Cetaceans in the European Atlantic and North Sea. Issue 7: June 2006.

Schneider, D. C., and J. F. Piatt. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Marine Ecology Progress Series **32**:237-246.

Scott-Hayward, L. A. S. 2006. Modelling the spatial distribution of sperm whales, *Physeter macrocephalus*, in the Gulf of Mexico. MRes Thesis. Department of Biology. University of St Andrews.

Selzer, L. A., and P. M. Payne. 1988. The distribution of white-sided (Lagenorhynchus acutus) and common dolphins (Delphinus delphis) vs. environmental features of the continental shelf of the northeastern United States. Marine Mammal Science **4**:141-153.

Shelton, R. G. J., W. R. Turrell, A. Macdonald, I. S. McLaren, and N. T. Nicoll. 1997. Records of post-smoult Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. Fisheries Research **31**:159-162.

St John, M. A., J. Stevenson MacDonald, P. J. Harrison, R. J. Beamish, and E. Choromanski. 1992. The Fraser River plume: Some preliminary observations on the distribution of juvenile salmon, herring and their prey. Fisheries oceanography **1**:153-162.

Stephenson, C. M., M. L. MacKenzie, C. Edwards, and J. M. J. Travis. 2006. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. Ecological Modelling **193**:747-758.

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

Urick, R. J. 1983. Principles of underwater sound. Peninsula Publishing, Los Altos, CA.

Whitehead, H., S. Brennan, and D. Grover. 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology **70**:912-918.

Zamon, J. E. 2002. Tidal changes in copepod abundance and maintenance of a summer *Coscinodiscus* bloom in the southern San Juan Channel, San Juan Islands, USA. Marine Ecology Progress Series **226**:193-210.

Zamon, J. E. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelgo depend on flooding tidal currents. Marine Ecology Progress Series **261**:243-255.

Appendix

Additional results for all chapters

A.1 Chapter 2 – delphinid model tables & figures

Table A1.1 – GAM forward step-wise model selection results for models of delphinid occurrence off the west of Scotland based on Faroe-Shetland Channel surveys carried out between September 2003 and October 2005 based on 9 km segment size. Smooths are shown in order of importance, with the estimated number of degrees of freedom for each smooth given in the parentheses. %dev is the percentage deviance explained by adding the term to the model, $\mathrm{UBRE}_{\mathrm{diff}}$ is the reduction in UBRE score caused by the addition of the variable to the model, and $\mathrm{AIC}_{\mathrm{eq}}$ is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 918. ThDpt = thermocline depth, SBS = halocline strength.

Parameter order	Faroe-Shetland Channel ***ungrouped***				Faroe-Shetland Channel ***grouped***			
		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$
1	s(Depth,2.3)	*10.6*	*0.11603*		s(SST,2.9)	*3.6*	*-0.37884*	
2	s(SST,3.2)	+4.7	-0.0453	-42	s(ThDpt,1)	+1.6	-0.0073	7
3	s(ThDpt,1)	+2.1	-0.0222	-20	s(SBS,2.7)	+2.0	-0.0053	5
total %dev		17.4				7.2		

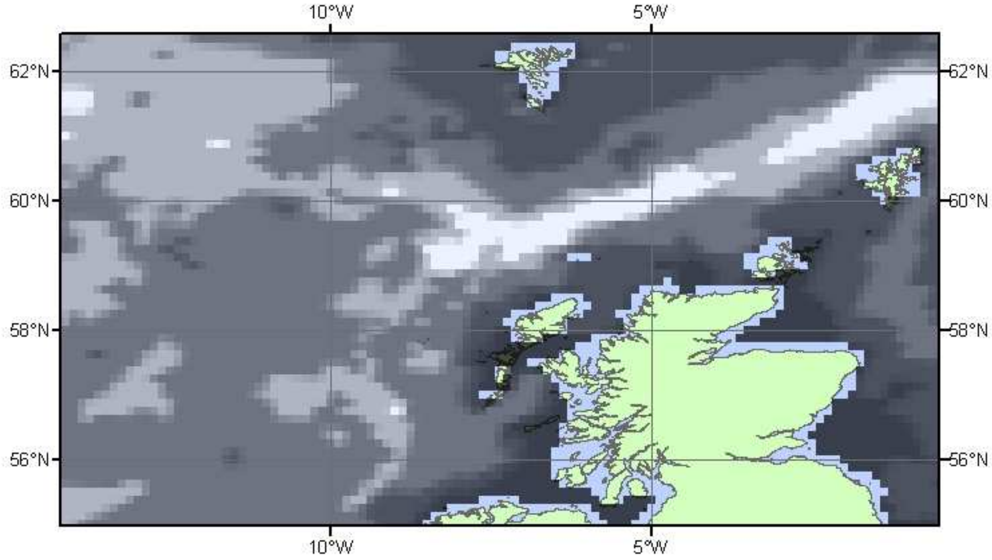


Figure A1.1 – FOAM modelled thermocline depth for 14 October 2004. Dark grey indicates shallow thermoclines and white indicates deep thermoclines.

Table A1.2 – Spearman-rank correlation test results for all variables for the dolphin oceanographic data off the west coast of Scotland from 2003-2005. Correlations are shown where p < 0.001, in red where the correlations are positive, and blue where the correlations are negative, NC where there is no significant correlation.

	Lon	Lat	Bt	wN	sN	rN	Spd	WSp	Tm	Mth	Yr	STw	STm	Clw	Clm	Dpt	BCS	SCS	Mix	SBD	SSD	Hal	SBS
Lat	0.506																						
Bt	0.492	0.556																					
wN	0.174	0.173	0.216																				
sN	NC	0.205	0.182	0.252																			
rN	0.175	NC	0.102	NC	0.108																		
Sp	0.092	0.224	0.373	0.463	0.446	0.114																	
WSp	0.144	0.101	0.249	0.472	NC	NC	0.362																
Tm	0.140	NC	0.206	NC	NC	0.104	NC	NC															
Mth	0.104	NC	0.224	NC	NC	NC	0.242	0.112	NC														
Yr	0.304	0.189	0.595	0.351	NC	NC	0.346	NC	0.230	0.526													
STw	0.382	0.491	0.557	0.139	NC	NC	0.287	NC	NC	0.709	0.671												
STm	0.300	0.442	0.542	NC	0.155	NC	0.330	0.137	NC	0.768	0.574	**0.875**											
Clw	0.261	0.398	0.441	NC	NC	NC	NC	NC	0.117	0.176	0.362	0.279	0.101										
Clm	0.212	0.323	0.460	0.276	NC	0.138	0.129	NC	0.206	NC	0.641	0.279	0.200	0.658									
Dpt	0.262	NC	0.277	0.469	0.368	NC	0.262	0.126	0.237	0.174	0.269	0.218	0.200	NC	0.126								
BCS	0.296	NC	0.338	0.128	0.210	0.196	0.148	0.287	0.137	NC	0.224	0.098	NC	0.293	0.151	NC							
SCS	0.127	NC	0.161	0.377	0.296	0.118	0.265	0.335	NC	NC	NC	NC	NC	0.235	0.111	0.391	0.613						
Mix	NC	0.148	0.468	0.153	NC	NC	0.180	NC	0.201	0.362	0.269	NC	NC	0.400	0.470	NC	0.149	NC					
SBD	0.188	NC	0.480	0.384	0.247	NC	0.323	NC	0.170	0.459	0.588	0.479	0.454	0.128	0.296	0.701	0.141	0.141	0.243				
SSD	0.209	0.381	0.547	0.141	NC	0.096	0.323	NC	NC	0.742	0.734	**0.879**	**0.826**	0.241	0.320	0.155	NC	0.112	0.097	0.498			
Hal	0.194	NC	NC	0.463	0.328	NC	0.270	0.297	0.108	NC	NC	NC	NC	0.110	NC	0.725	0.217	0.474	NC	0.474	NC		
SBS	0.144	0.173	NC	0.150	0.102	0.235	NC	0.095	0.091	0.114	NC	NC	NC	0.212	0.182	0.526	0.148	0.178	0.180	0.352	0.191	0.402	
SSS	0.171	0.444	0.211	0.138	0.111	NC	NC	0.234	0.145	0.196	0.193	NC	NC	NC	NC	NC	0.444	0.235	0.177	0.222	NC	0.290	0.159
Thm	NC	NC	0.531	NC	0.092	NC	0.133	NC	0.159	NC	0.578	0.251	0.192	0.405	0.533	NC	0.423	0.313	0.582	0.401	0.389	0.331	NC
SBT	0.174	0.105	0.397	0.381	0.238	0.106	0.271	NC	0.191	0.392	0.493	0.355	0.344	NC	0.229	0.750	0.160	0.169	0.199	**0.976**	0.355	0.533	0.513
SST	0.248	0.495	0.549	0.182	0.103	0.109	0.334	NC	NC	0.650	0.715	**0.879**	0.799	0.288	0.366	0.158	NC	NC	0.100	0.449	**0.970**	NC	0.174

	SSS	Thm	SBT	SST
Thm	0.470			
SBT	0.254	0.342		
SST	0.174	0.316	0.298	

Abbreviation definitions: Bt = vessel type (1=Scotia, 2=Poseidon, 3=Darwin); wN = water noise; sN = self boat noise; rN = remote vessel noise; Spd = boat speed; WSp = wind speed; Tm = time of day; Mth = month; STw = weekly SST (satellite); STm = monthly SST (satellite); Clw = weekly chlorophyll; Clm = monthly chlorophyll; Dpt = depth (measured from sea level); BCS = bottom current speed; SCS = surface current speed; Mix = mixed layer depth; SBD = mixed layer strength; SSD = surface density; Hal = halocline depth; SBS = halocline strength; SSS = surface salinity; Thm = thermocline depth; SBT = thermocline strength; and SST = FOAM modelled SST.

Table A1.3 – Summary statistics for the environmental variables for the oceanographic survey years grouped by all surveys, and Faroe-Shetland Channel (FSC) surveys off the west coast of Scotland. Results of a Mann-Whitney test to test between the two data sets environmental variable distributions are shown if significant, where * p<0.05; **p<0.01; and ***p<0.001.

Parameter		All data	FSC
Survey effort with environmental data available			
Distance surveyed (km)		11,178	8,262
Number of stations/segments		1242	918
Segments with dolphin whistles or clicks		138 (11.1%)	88 (9.6%)
Survey variables			
Vessel speed	range (knots)	3.3-13.7	3.3-13.7***
	mean (standard deviation)	9.7 (1.8)	9.9 (1.9)
WaterNoise	range	0-5	0-5
	median (IQR)	2 (1-2.5)	2 (1-2.5)
SurveyVesselNoise	range	0-4	0-.4
	median (IQR)	2.5 (2-3)	2.5 (2-3)
Topographical variables			
Depth	range (m)	15-2374	15-1641***
	median (IQR)	292 (121-940)	202 (116-626)
Satellite data			
SST	range (°C)	5.7-15.3	6.0-13.8***
	mean (standard deviation)	11.3 (1.8)	10.7 (1.4)
Chl	range (mg/m^3)	0.03-22.1	0.03-22.1
	median (IQR)	0.48 (0.25-1.02)	0.53 (0.29-0.99)
FOAM variables			
HaloDepth	range (m)	30-1335	30-815
	median (IQR)	100 (50-200)	100 (50-200)
SBS	range (psu)	-0.44-0.20	-0.38-0.15
	median (IQR)	0.0 (-0.10-0.03)	0.0 (-0.06-0.02)
SSS	range (psu)	35.0-35.4	35.0-35.4
	median (IQR)	35.26 (35.2-35.3)	35.26 (35.2-35.3)
ThermDepth	range (m)	20-774	30-774
	median (IQR)	95 (56-133)	85 (67-132)
SBT	range	-12.6-0.11	-12.5-0.11***
	median (IQR)	-1.7 (-4.2--0.3)	-1.1 (-2.8--0.1)
SurfCurSpd	range (m/s)	0.00-0.58	0.01-0.58
	median (IQR)	0.12 (0.07-0.20)	0.12 (0.07-0.20)
BotCurSped	range (m/s)	0.00-0.46	0-0.46***
	median (IQR)	0.07 (0.03-0.12)	0.08 (0.04-0.14)

Table A1.4 – Summary statistics for the environmental variables for the Faroe-Shetland Channel oceanographic surveys grouped by month. Results of a Mann-Whitney test to test between the two data sets environmental variable distributions are shown if significant, where * $p<0.05$; **$p<0.01$; and ***$p<0.001$.

Parameter		May Scotia data	October Scotia data
Survey effort with environmental data available			
Distance surveyed (km)		4,158	4,104
Number of stations/segments		462	456
Segments with dolphin whistles or clicks		40 (8.7%)	48 (10.5)
Survey variables			
Vessel speed	range (knots)	3.3-13.7	3.4-12.8***
	mean (standard deviation)	10.1 (2.2)	9.8 (1.5)
WaterNoise	range	0-5	0-4***
	median (IQR)	1.5 (1-2)	2 (1.5-2.5)
SurveyVesselNoise	range	0-4	0-4
	median (IQR)	2.5 (2-3)	2.5 (2-3)
Topographical variables			
Depth	range (m)	15-1641	21-1432**
	median (IQR)	254 (124-631)	182 (106-607)
Satellite data			
SST	range (°C)	6.0-11.2	8.9-13.8***
	mean (standard deviation)	9.7 (0.86)	11.8 (1.06)
Chl	range (mg/m^3)	0.16-9.7	0.03-22.1***
	median (IQR)	0.63 (0.39-1.02)	0.36 (0.20-0.93)
FOAM variables			
HaloDepth	range (m)	30-815	30-700***
	median (IQR)	133 (50-240)	95 (50-200)
SBS	range (ppt)	-0.31-0.15	-0.38-0.15***
	median (IQR)	0.00 (-0.08-0.02)	0.00 (-0.003-0.04)
SSS	range (ppt)	35.0-35.4	35.0-35.4***
	median (IQR)	35.30 (35.2-35.3)	35.20 (35.2-35.3)
ThermDepth	range (m)	30-774	40-346***
	median (IQR)	105 (76-165)	79 (61-113)
SBT	range	-8.25-0.00	-12.5-0.11
	median (IQR)	-1.1 (-2.2--0.5)	-1.1 (-4.3-0.0)
SurfCurSpd	range (m/s)	0.01-0.50	0.01-0.58***
	median (IQR)	0.10 (0.06-0.17)	0.14 (0.08-0.22)
BotCurSped	range (m/s)	0.00-0.37	0.00-0.46*
	median (IQR)	0.08 (0.04-0.13)	0.09 (0.05-0.16)

A.2 Chapter 3 – sperm whale model tables

Table A2.1 – GAM forward step-wise model selection results for models of sperm whale occurrence off the west of Scotland based on surveys carried out between July 2003 and October 2005 based on segment sizes 9 km or18 km. Smooths are shown in order of importance, with the estimated number of degrees of freedom for each smooth given in the parentheses. %dev is the percentage deviance explained by adding the term to the model, $\text{UBRE}_{\text{diff}}$ is the reduction in UBRE score caused by the addition of the variable to the model, and AIC_{eq} is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 930 for the 9 km model (based on a 75% training data set), and 615 for the 18 km model. SBT = thermocline strength, SBS = halocline strength.

Parameter order	9 km Full data set				18 km Full data set			
		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}
1	s(Speed,3.4)	*3.0*	*-0.42848*		s(Speed,3.4)	*3.9*	*-0.3057*	
2	s(Depth,2.9)	+22.0	-0.1175	-109	s(Depth,3.2)	+20.7	-0.1290	-79
3	s(SBT,3.4)	+3.9	-0.0123	-11	s(SBT,3.2)	+3.5	-0.0110	-7
4	s(SBS,1)	+1.9	-0.0095	-9				
total %dev		30.8				28.1		

Table A2.2 – GAM forward step-wise model selection results for models of sperm whale occurrence off the west of Scotland based on either Faroe-Shetland Channel surveys, or on Ellet Line surveys 9 km segments collected between July 2003 and October 2005. Smooths are shown in order of importance, with the estimated number of degrees of freedom for each smooth given in the parentheses. %dev is the percentage deviance explained by adding the term to the model, $\text{UBRE}_{\text{diff}}$ is the reduction in UBRE score caused by the addition of the variable to the model, and AIC_{eq} is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 918 for the Faroe-Shetland Channel model, and 321 for the Ellet Line model. HaloD = halocline depth, SBS = halocline strength, SBT = thermocline strength, SSS = Sea Surface Salinity.

Parameter order	9 km Faroe-Shetland Channel data				9 km Ellet Line data			
		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}
1	s(Speed,2.7)	*2.7*	*-0.5595*		s(Depth,3.6)	*14.8*	*-0.2486*	
2	s(Depth,3.6)	+22.6	-0.0884	-81	s(SST,1)	+5.7	-0.0215	-7
3	s(HaloD,2.2)	+2.5	-0.0059	-5	s(SSS,3.0)	+2.7	-0.0166	-5
4	s(SBS,1)	+3.0	-0.0095	-9	s(Chl,1)	+2.4	-0.0102	-3
5	s(SBT,2.7)	+3.6	-0.0105	-10				
6	S(SSS,2.5)	+2.2	-0.0040	-4				
total %dev		36.6				25.6		

A.3 Chapter 4 – harbour porpoise model tables

Table A3.1 - Results of forward model selection for the GAM of DC acoustic noise levels per 2km segment for the full area surveyed in 2004-2005 for those segments with topographical, tidal and sediment variables available. Smooths are shown in order of importance, with the estimated number of degrees of freedom for each smooth given in the parentheses. %dev is the percentage deviance explained by adding the term to the model, GCV_{diff} is the reduction in GDV score caused by the addition of the variable to the model. Sample size *n* is 1554 for 2004-2005.

Parameter order	2004-2005 (full area)		
		%dev	GCV_{diff}
1	s(Depth,3.6)	*15.8*	*1366.7*
2	s(%Gravel,2.0)	+5.1	-80.7
3	factor(EngineOn)	+3.6	-53.7
4	s(TimeFrLW,3.4)	+2.4	-36.1
5	s(Speed,1.9)	+2.0	-28.4
6	s(MaxTideCur,1.2)	+1.1	-16.7
total %dev		30.0	

Table A3.2 – Spearman's rank correlation of all the environmental variables for the 2004 dataset, where the figure shown is the correlation coefficient for all significant correlations (p>0.05), NC indicates that there is no significant correlation; bold figures indicate moderate correlation, and bold red figures indicate strong correlation.

	Lat	Lon	Spd	SeaS	Time	ClSW	FrLW	Dpth	Slpe	Sand	Mud	Grav	Mix	SBD	SSD	Halo	SBS	SSS	Ther	SBT	SST	SCD	MCD	BCD	SCH	MCH	BCH	Max	STR
Longitude	**-0.363**																												
Speed	-0.141	0.127																											
SeaState	-0.091	NC	-0.144																										
TimeSunrise	-0.092	NC	NC	**-0.359**																									
ClosetoSW	**-0.370**	-0.177	-0.177	0.093	0.109																								
TimeFrLW	-0.247	NC	NC	NC	NC	-0.128																							
Depth	NC	0.188	NC	NC	0.175	NC	NC																						
Slope	0.097	0.198	NC	NC	NC	NC	NC	NC																					
%Sand	-0.237	NC	-0.179	NC	0.093	NC	NC	NC	-0.186																				
%Mud	0.142	**0.399**	-0.092	-0.106	0.164	0.089	NC	**0.464**	0.134	NC																			
%Gravel	NC	-0.268	0.179	0.095	-0.156	NC	NC	**-0.325**	NC	**-0.469**	**-0.812**																		
MixedDepth	**-0.577**	NC	NC	0.212	NC	**-0.308**	0.128	0.147	-0.109	0.089	-0.179	NC																	
SBDensity	**0.532**	0.279	NC	**-0.302**	0.096	0.155	-0.188	NC	0.128	NC	**0.360**	-0.221	**-0.758**																
SurfDens	**-0.490**	-0.123	0.101	0.273	NC	-0.158	NC	0.125	NC	NC	-0.166	0.147	**0.636**	**-0.742**															
HaloDepth	-0.217	**-0.301**	NC	0.151	0.128	NC	NC	0.236	NC	NC	-0.106	NC	**0.588**	**-0.494**	**0.642**														
SBSalinity	0.245	**0.379**	NC	**-0.361**	0.212	NC	-0.109	NC	0.109	NC	**0.353**	-0.273	**-0.563**	**0.795**	**-0.651**	**-0.525**													
SSS	**-0.309**	**-0.428**	NC	0.202	NC	-0.089	0.181	0.090	-0.112	NC	**-0.308**	0.239	**0.629**	**-0.778**	**0.702**	**0.623**	**-0.841**												
ThermDepth	**-0.461**	NC	NC	NC	NC	**-0.429**	0.113	NC	NC	0.133	-0.153	NC	**0.719**	**-0.451**	0.260	0.254	-0.213	0.280											
SBT	**-0.552**	-0.201	0.109	0,164	NC	-0.285	0.225	-0.114	-0.103	0.122	**-0.397**	0.220	**0.656**	**-0.897**	**0.506**	0.276	**-0.570**	**0.597**	**0.538**										
SST	**0.574**	NC	-0.102	**-0.311**	NC	0.197	NC	-0.104	NC	NC	0.134	-0.106	**-0.605**	**0.685**	**-0.974**	**-0.591**	**0.572**	**-0.587**	-0.255	**-0.462**									
SurfCurDay	-0.232	-0.162	0.091	NC	**-0.313**	-0.142	NC	NC	NC	NC	**-0.323**	0.209	**0.313**	**-0.374**	NC	0.158	**-0.403**	**0.342**	**0.431**	**-0.449**	NC								
MidCurDay	-0.240	-0.276	NC	0.115	-0.248	NC	0.148	NC	NC	NC	**-0.330**	0.235	**0.438**	**-0.519**	0.211	**0.316**	**-0.487**	**0.452**	**0.406**	**0.552**	-0.161	**0.704**							
BotCurDay	-0.264	-0.093	NC	0.119	-0.180	NC	NC	NC	NC	NC	-0.251	0.176	**0.382**	**-0.367**	0.110	0.252	**-0.308**	0.290	0.293	**0.375**	-0.090	**0.517**	**0.834**						
SurfCurHr	-0.114	**-0.504**	NC	NC	-0.139	NC	0.280	NC	-0.148	NC	**-0.360**	0.229	**0.359**	**-0.554**	**0.321**	**0.323**	**-0.556**	**0.531**	0.287	**0.477**	-0.233	**0.430**	**0.406**	0.189					
MidCurHr	NC	**-0.562**	NC	NC	-0.115	0.116	0.134	-0.091	NC	-0.110	**-0.388**	**0.310**	**0.302**	**-0.516**	**0.323**	**0.355**	**-0.574**	**0.531**	0.223	**0.431**	-0.223	**0.408**	**0.429**	0.201	**0.880**				
BotCurHr	NC	**-0.541**	NC	NC	NC	0.113	NC	NC	NC	NC	**-0.352**	0.247	0.295	**-0.513**	**0.326**	**0.354**	**-0.541**	**0.518**	0.230	**0.436**	-0.223	**0.365**	**0.405**	0.232	**0.764**	**0.859**			
MaxTideCur	-0.132	**-0.523**	NC	NC	-0.210	-0.094	0.101	-0.225	-0.211	NC	**-0.541**	**0.357**	0.229	**-0.486**	0.261	0.215	**-0.480**	**0.430**	0.224	**0.482**	-0.199	**0.447**	**0.436**	0.219	**0.551**	**0.541**	**0.582**		
SWTideRge	**-0.815**	0.111	-0.122	NC	NC	0.234	-0.217	NC	0.147	-0.159	0.296	NC	**-0.647**	**0.715**	**-0.614**	**-0.433**	**-0.458**	**-0.620**	**-0.426**	**-0.677**	**0.602**	-0.271	**-0.399**	**-0.363**	**-0.317**	-0.269	-0.295	**-0.325**	
DCNoise	NC	NC	**0.309**	-0.273	NC	-0.167	NC	**-0.307**	NC	-0.138	**-0.310**	**0.341**	-0.156	0.099	-0.206	-0.154	0.191	NC	NC	NC	0.233	0.114	NC	0.127	NC	NC	NC	0.125	NC

Table A3.3 – Results of forward model selection for the GAM of the number of harbour porpoise groups detected visually per 2km segment for 2004, 2005, and 2004-2005. Smooths are shown in order of importance, with the estimated number of degrees of freedom for each smooth given in the parentheses. %dev is the percentage deviance explained by adding the term to the model, $\mathrm{UBRE}_{\mathrm{diff}}$ is the reduction in UBRE score caused by the addition of the variable to the model, and $\mathrm{AIC}_{\mathrm{eq}}$ is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 455 for 2004, 516 for 2005, and 972 for 2004-2005 (75% training set).

Param order	2004				2005				2004-2005			
		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$
1	s(SeaState,1.0)	*9.9*	*-0.53463*		s(SeaState,3.6)	*18.2*	*-0.55962*		s(SeaState,2.6)	*10.2*	*-0.5092*	
2	factor(EngineOn)	+2.3	-0.0054	-2.5	s(MaxTideCur,1)	+2.7	-0.0092	-4.7	factor(EngineOn)	+1.4	-0.0045	-4.3
3	s(MaxTideCur,1.6)	+7.9	-0.0298	-13.6					s(MaxTideCur,1)	+5.3	-0.0257	-25.0
4	s(ClosetoSW,1.0)	+5.6	-0.0157	-7.2					s(ClosetoSW, 2.6)	+2.6	-0.0063	-6.1
5									s(Slope,1.6)	+1.8	-0.0049	-4.7
%dev		25.7				20.9				21.3		

Table A3.4 - Results of forward model selection for the GAM of the number of harbour porpoise groups detected acoustically per 2km segment for 2004, 2005, and 2004-2005. Smooths are shown in order of importance, with the estimated number of degrees of freedom for each smooth given in the parentheses. %dev is the percentage deviance explained by adding the term to the model, $\mathrm{UBRE}_{\mathrm{diff}}$ is the reduction in UBRE score caused by the addition of the variable to the model, and $\mathrm{AIC}_{\mathrm{eq}}$ is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 455 for 2004, 516 for 2005, and 972 for 2004-2005 (75% training set).

Param order	2004				2005				2004-2005			
		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$		%dev	$\mathrm{UBRE}_{\mathrm{diff}}$	$\mathrm{AIC}_{\mathrm{eq}}$
1	s(DCNoise,1.0)	*6*	*-0.23013*		s(Speed,1.0)	*10*	*-0.27384*		s(DCNoise,1.0)	*5.9*	*-0.1602*	
2	s(Speed,2.3)	+ 3.6	-0.0172	-7.8	s(DCNoise,1.0)	+3.1	-0.0133	-6.9	s(Speed,1.0)	+2.5	-0.0160	-15.6
3	s(PctMud,2.2)	+6.4	-0.0466	-21.2	s(Depth,1.0)	+3.1	-0.0197	-10.2	s(PctMud,2.2)	+3.7	-0.0300	-29.2
4	s(TimeFrLW,1)	+1.5	-0.0049	-2.3	s(Lon,Lat,3.6)	+2.8	-0.0217	-11.2	s(SWTideRange,3.8)	+1.9	-0.0042	-4.0
%dev		17.5				19.0				14.0		

Table A3.5 - Results of forward model selection for the GAM of the number of harbour porpoise groups detected visually per 2km segment for 2003, 2004, and 2003-2004 for those segments with all variables available (including POLCOMS). Smooths are shown in order of importance, with d.f. in parentheses. $\text{UBRE}_{\text{diff}}$ is the reduction in UBRE score caused by the addition of the variable to the model, and AIC_{eq} is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 615 for 2003, 377 for 2004, and 996 for 2003-2004 (75% training set).

Param order	2003				2004				2003-2004			
		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}
1	s(SeaState,1.0)	*6.5*	*-0.53318*		s(SeaState,1.7)	*6.6%*	-0.60013		s(SeaState,2.9)	*5.9*	*-0.60056*	
2	s(SSS,2.1)	+9.5	-0.0360	-22.2	s(SurfCurDay,1.1)	+8.1	-0.0201	-7.6	s(MaxTideCur,1)	+8.9	-0.0284	-28.3
3	s(ClosetoSW,1.8)	+5.3	-0.0198	-12.2	s(Lon,1.0)	+2.3	-0.0061	-2.3	s(ClosetoSW,1)	+3.6	-0.0117	-11.7
4	s(PctMud,1.0)	+2.4	-0.0063	-3.9					s(Lon,1.0)	+1.3	-0.0049	-4.9
5									s(Depth,1.0)	+1.5	-0.0032	-3.2
6									s(PctSand,2.9)	+3.2	-0.0044	-4.4
%dev		23.7				17.0				24.4		

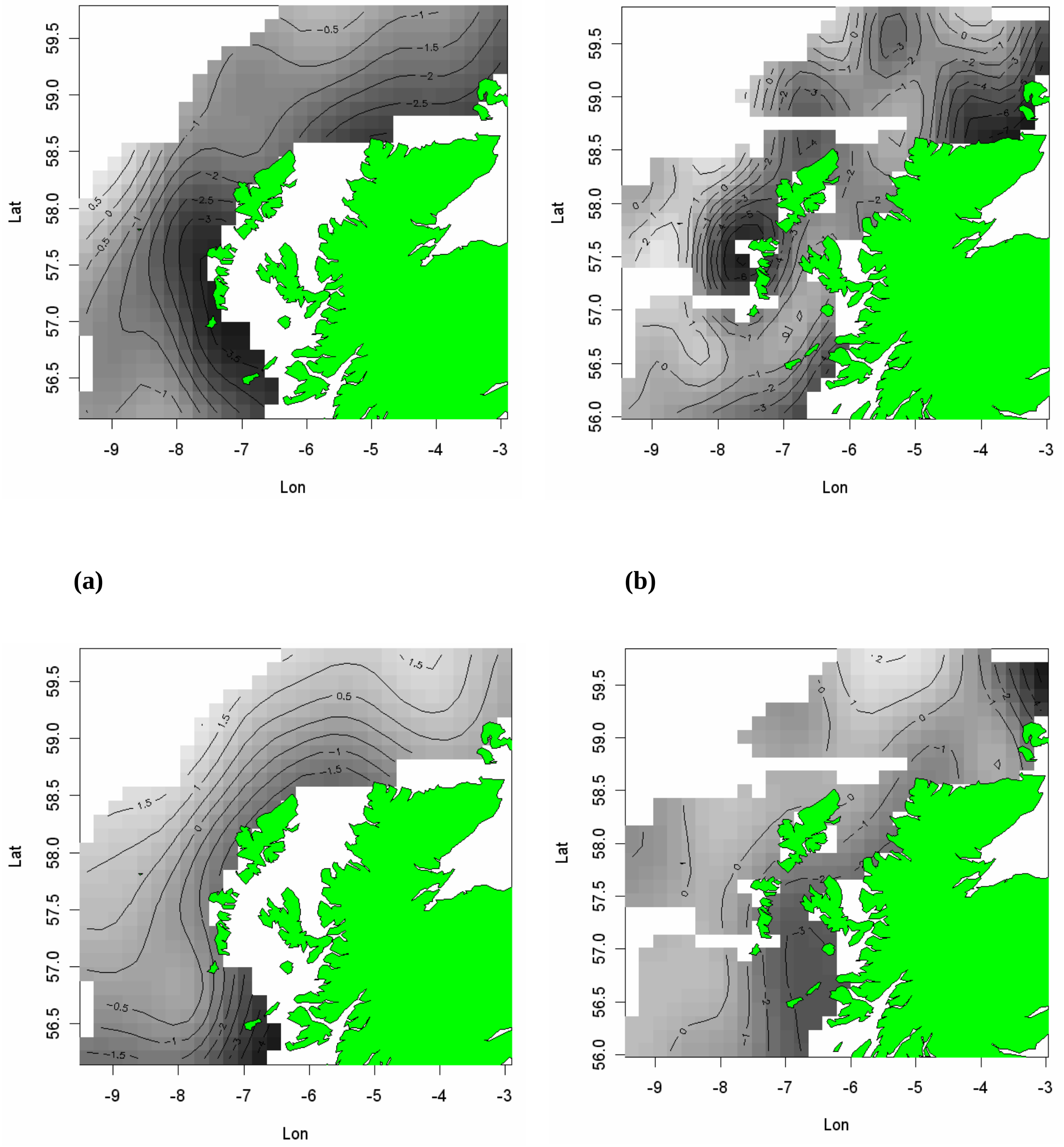
Table A3.6 - Results of forward model selection for the GAM of the number of harbour porpoise groups detected visually per 2km segment for 2003, 2004-2005, and 2003-2005 for those segments with topographical, tidal and sediment variables available. Smooths are shown in order of importance, with d.f. in the parentheses. $\text{UBRE}_{\text{diff}}$ is the reduction in UBRE score caused by the addition of the variable to the model, and AIC_{eq} is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 714 for 2003, 972 for 2004-2005, and 1712 for 2003-2005 (75% training set).

Param order	2003				2004-2005				2003-2005			
		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}		%dev	$\text{UBRE}_{\text{diff}}$	AIC_{eq}
1	s(Speed,2.6)	*3.7*	*-0.5472*		s(SeaState,2.6)	*10.2*	*-0.5092*		s(SeaState,2.6)	*7.7*	*-0.52167*	
2	s(SeaState,1.0)	+3.2	-0.0108	-8.0	factor(EngineOn)	+1.4	-0.0045	-4.3	s(MaxTideCur,1.5)	+5.0	-0.0238	-40.8
3	s(MaxTideCur,1)	+9.0	-0.0361	-25.8	s(MaxTideCur,1)	+5.3	-0.0257	-25.0	s(TimeSunrise,2.6)	+1.9	-0.0052	-8.9
4	s(ClosetoSW,1)	+6.3	-0.0210	-15.0	s(ClosetoSW, 2.6)	+2.6	-0.0063	-6.1	s(ClosetoSW,1.0)	+1.3	-0.0051	-8.7
5	s(TimeFrLW,5.5)	+8.9	-0.0166	-11.9	s(Slope,1.6)	+1.8	-0.0049	-4.7				
6	s(Lon,1.0)	+1.0	-0.0033	-2.3								
%dev		32.1				21.3				15.9		

Table A3.6 - Results of forward model selection for the GAM of the number of harbour porpoise groups detected visually per 2km segment for the full area surveyed in 2005, 2004-2005, and 2003-2005 for those segments with topographical, tidal and sediment variables available. Smooths are shown in order of importance. % dev is the percentage deviance explained by adding the term to the model, $UBRE_{diff}$ is the reduction in UBRE score caused by the addition of the variable to the model, and AIC_{eq} is the equivalent reduction in AIC (calculated by multiplying by the sample size *n*). *n* is 788 for 2005, 1243 for 2004-2005, and 2238 for 2003-2005 (75% training set).

Param order	2005 (full area)				2004-2005 (full area)				2003-2005 (full area)			
		%dev	$UBRE_{diff}$	AIC_{eq}		%dev	$UBRE_{diff}$	AIC_{eq}		%dev	$UBRE_{diff}$	AIC_{eq}
1	s(SeaState)	*13.9*	*-0.46423*		s(SeaState)	*10.5*	*-0.44206*		s(SeaState)	*8.2*	*-0.53577*	
2	factor(EngineOn)	+1.1	-0.0030	-2.4	factor(EngineOn)	+1.9	-0.0088	-11.0	s(SWTideRange)	+7.0	-0.0310	-69.3
3	s(SWTideRange)	+7.6	-0.0385	-30.3	s(SWTideRange)	+4.2	-0.0323	-40.2	factor(Month)	+3.0	-0.0106	-23.6
4	s(Slope)	+1.1	-0.0035	-3.1	s(PctGravel)	+1.9	-0.0052	-6.5	s(MaxTideCur)	+1.2	-0.0044	-9.8
%dev		23.7				20.5				19.4		

A.4 Chapter 5 – delphinid-herring tables & figures



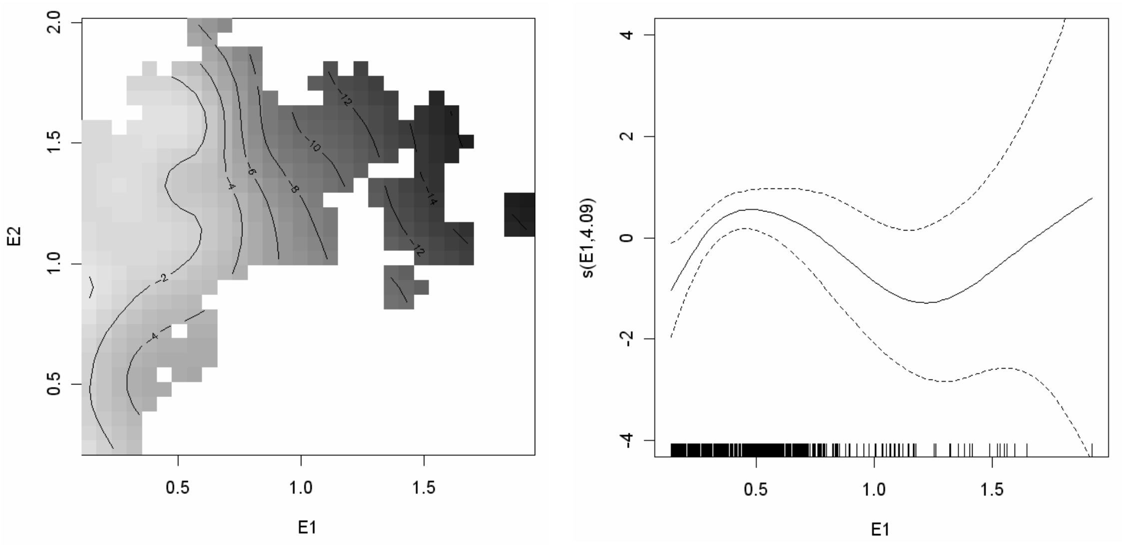
(a)

(b)

(c)

(d)

Figure A4.1 – Relationship of (a) & (b) delphinid and (c) & (d) herring occurrence with a two-way smooth of latitude and longitude for surveys carried out on the west coast of Scotland in (a) & (c) July 2004 and (b) & (d) July 2005 based on GAM models detailed in Table A4.1. Light grey show areas of high preference by herring/delphinids, and dark grey show areas of low preference by herring/delphinids. Lines show contours of equal probability, with 0 = no preference, <0 = negative preference, >0 positive preference.



(a)

(b)

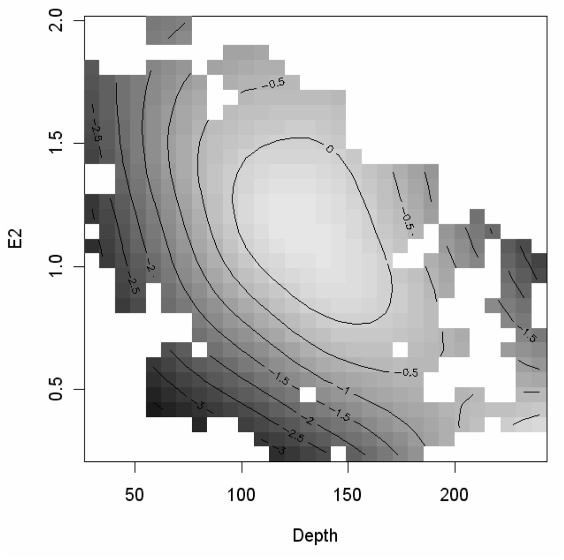
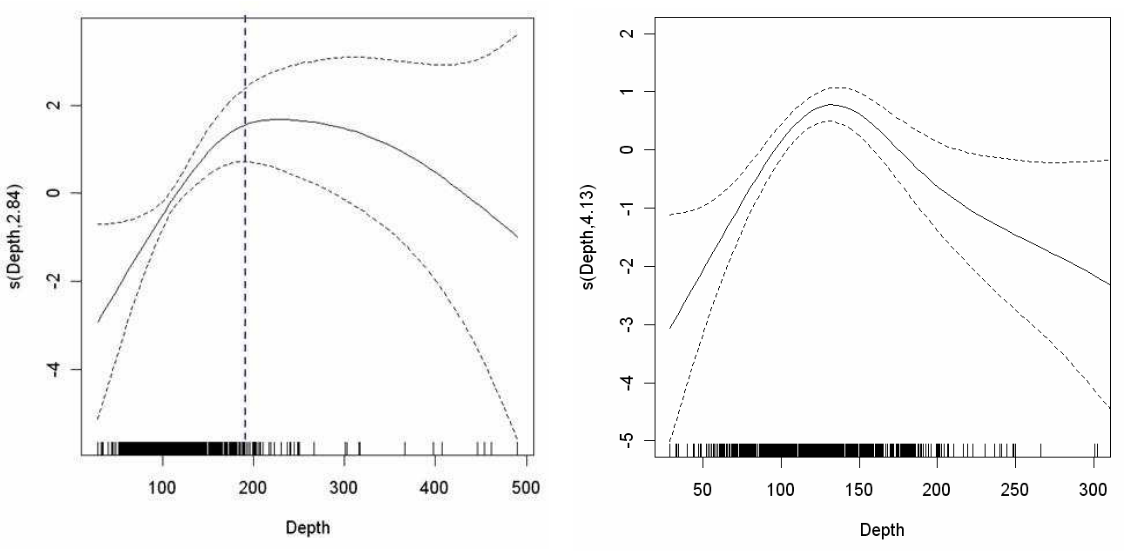


Figure A4.2 – Relationship between (a) delphinid occurrence and the interaction of E1 & E2, (b) herring occurrence and E1, (c) herring occurrence with the interaction between depth & E2 for surveys carried out on the west coast of Scotland in July 2005. E1 = roughness of the seabed (0 = smooth → 2 = rough), E2 = hardness of bottom (< 0.6 = silt/sand, 0.6-1.2 = sand/gravel, 1.2-1.5 = stony, > 1.5 = rocky). Light grey indicates areas areas of high preference to delphinids/herring, dark grey indicates areas of low preference. Lines show contours of equal probability, with 0 = no preference, <0 = negative preference, >0 positive preference.

(c)

Delphinids showed a significant preference for smooth sediments for sand/gravel type substrate (Figure A4.2a). Whereas, herring showed a significant preference also for smooth sediments (Figure A4.2b), but also sand/gravel/stony areas between 100-170 m depth, preferring sandier/gravier substrates in deeper water (Figure A4.2c).



(a) **(b)**

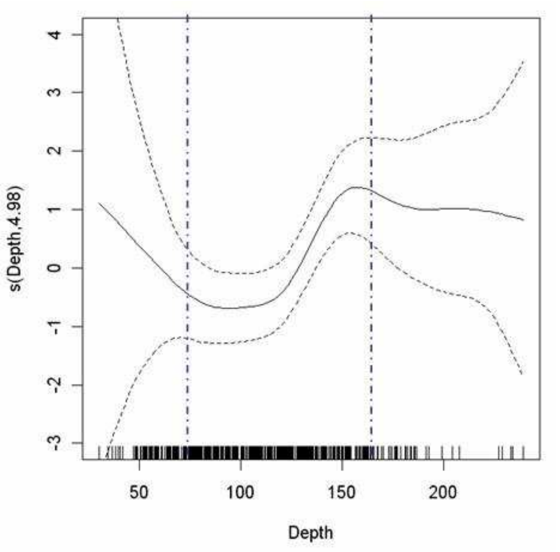


Figure A4.3 – Relationship between (a) & (c) delphinid occurrence and depth, and (b) herring occurrence and depth for surveys carried out off the west coast of Scotland in (a) & (b) July 2004, and (c) 2005. Tick marks above the x-axis indicate the distribution of observations in all segments. Dotted lines show 95% confidence intervals. Vertical dashed lines show limits of the ability of the model to model the relationship (confidence intervals too wide outside these lines).

(c)

In both years, delphinids showed a preference for the deeper water surveyed (Figure A4.3a&c), though confidence intervals were too wide to determine preference in shallow water (< 70 m) or in deep water (>170m). Herring showed a preference for water depths between 70-180 m, with a peak preference at 140 m (Figure A4.3b).

Table A4.1 – Best GAM models for delphinid presence/absence and herring presence/absence in 2004 and 2005 based on model selection by lowest UBRE score. The parameter smooths (spline s or tensor te) and the linear parameters (of day or time of day as factors) are shown in the order they were selected by forward stepwise model selection. Degrees of freedom for each smooth or linear predictor are given in the parentheses, %dev = the percentage explained deviance by adding the term to the model, and UBRE score for the addition of each parameter. The total % explained deviance is given at the bottom for each of the four models.

Param Order	Delphinids						Herring					
	2004	(%dev)	(UBRE)	2005	(%dev)	(UBRE)	2004	(%dev)	(UBRE)	2005	(%dev)	(UBRE)
1	s(Lon,Lat,24)	21.9%	-0.182	s(Lon,Lat,27)	26.5%	-0.231	s(Lon,Lat,15)	18.8%	0.155	s(Lon,Lat,27)	19.2%	0.157
2	s(Depth,3)	+2.9%	-0.217	s(E1,E2,26)	+19.5%	-0.309	s(Depth,4)	+3.4%	0.100	factor(Time,3)	+4.3%	0.121
3	factor(Day,15)	+7.4%	-0.220	-			factor(Day,15)	+3.6%	0.091	factor(Day,12)	+6.6%	0.095
4	-			-			-			s(E1,4)	+2.5%	0.077
5	-			-			-			te(Depth,E2,7)	+3.3%	0.059
Dev exp.		32.2%			46.0%			25.8%			35.9%	

Table A4.2 – Best GAM models for delphinid & herring presence/absence in 2004 & 2005 based on model selection by lowest UBRE score, but excluding latitude and longitude. The parameter smooths & the linear parameters are shown in the order they were selected by forward stepwise selection. Degrees of freedom for each smooth or linear predictor are given in the parentheses, %dev = the percentage explained deviance by adding the term to the model, and UBRE score for the addition of each parameter. The total % explained deviance is given at the bottom for each of the four models.

Parameter Order	Delphinids						Herring					
	2004	(%dev)	(UBRE)	2005	(%dev)	(UBRE)	2004	(%dev)	(UBRE)	2005	(%dev)	(UBRE)
1	s(Depth,4)	16.4%	-0.178	s(Depth,5)	13.5%	-0.195	s(Depth,4)	10.0%	0.219	te(Depth,E2,9)	10.7%	0.240
2	-			s(E1,E2,15)	+11.4%	-0.242	factor(Day,15)	+8.9%	0.143	factor(Day,12)	+8.1%	0.172
3	-			factor(Day,12)	+10.2%	-0.288	factor(Time,3)	+1.6%	0.128	factor(Time,3)	+2.4%	0.153
Dev exp.		16.4%			35.1%			20.5%			21.2%	