Spatiotemporal patterns of marine megafauna distribution in coastal waters off the west coast of Scotland

Basking shark (*Cetorhinus maximus*)

Common dolphins (*Delphinus delphis*)

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Word count: 9373

Contents

Abstract

The waters off the west coast of Scotland have long been known as an important area for a large marine species. Understanding the relationship between environmental variables and their distribution over time is an important aspect for the implementation of conservation measures and future developments. Here, sighting data collected by the Hebridean Whale and Dolphin Trust during dedicated vessel surveys from 2003 to 2012, were used to identify the effect of year and different environmental variables on the probability of sighting common dolphin (*Delphinus delphis),* basking shark (*Cetorhinus maximus*), harbour porpoise (*Phocoena phocoena*), minke whale (*Balaenoptera acutorostrata*) and white-beaked dolphin (*Lagenorhynchus albirostris)*. The results of generalised linear models suggest that year, depth, slope, and sediment type and some interactions significantly affect the probability of sighting these species. The probability of sighting these species fluctuated between the years. Common dolphins were more likely to be sighted in areas of deeper water, with a slightly less degree of slope and were there was an average of 39 per cent sand. Harbour porpoise presence increased in areas of higher percentage mud and higher percentage sand and where the seabed was deeper and more sloped. Similarly, the probability of sighting a minke whale was increased in areas of greater depth and a greater degree of slope, and in areas where sediment was made up of less per cent mud. The results indicate that basking sharks are present more often in shallow water, where the seabed is less sloped and where the sediment is made up of a majority sand and mud mix. White-beaked dolphins were more likely to be sighted in the deep waters, where there was a shallow degree of slope and in areas where the sediment was made up of less percentage mud. These patterns generally have consistent biological explanations, often relating to the availability of prey.

1. Introduction

A challenging but fundamental aspect of conservation is understanding the distribution and richness of species that use a particular habitat. The marine environment is under pressure from many human activities including fishing, tourism, and renewable energy developments. Management strategies of the marine environment have been put in place to mitigate the impact of human activities which includes implementing marine protected areas (MPAs) such as special areas of conservation (SACs) (Defra, 2006). The implementation of effective conservation measures, such as these, requires knowledge of habitat use and habitat preference at different spatial scales (Marubini et al., 2009). Importantly, monitoring the distribution and abundance of species is necessary to determine whether conservation objectives are fulfilled as a result of the implemented conservation measures (Cañadas and Hammond, 2008).

The marine environment off the west coast of Scotland is an essential habitat for many species of megafauna including basking sharks (*Cetorhinus maximus*) and cetaceans (whales, dolphins and porpoises). Basking sharks are frequently sighted in this area (Southall et al., 2005) and harbour porpoise (*Phocoena phocoena*) have been identified as the most common cetacean species on the west coast of Scotland (Reid et al., 2003). Minke whale (*Balaenoptera acutorostrata*) is another commonly sighted species (Macleod et al., 2004) and killer whales (*Orcinus orca*) are known to inhabit these waters (Bolt et al., 2009) as well as white-beaked dolphins (*Lagenorhynchus albirostris),* common dolphins (*Delphinus delphis)* (Weir et al., 2009) and bottlenose dolphins (*Tursiops truncatus*) (Cheney et al., 2012). Both harbour porpoise and bottlenose dolphin are listed on Annex II of the European Union’s Habitat Directive, which states that SACs must be established in areas in which they occur (European Commission, 1992). Data collected on the distribution of these species are therefore crucial to increase our understanding of the areas which these highly mobile species use but also to justify the continued implementation of MPAs.

In addition to understanding which species inhabit the water, it is necessary to understand the relationship between species distribution and environmental variables in order to identify habitat preferences and use (Spyrakos et al., 2011). Depth has been identified as an environmental factor related to the distribution of cetaceans and other marine mammals (Sleeman et al., 2007; Marubini et al., 2009). The relationship between harbour porpoise and depth in the waters off the west coast of Scotland has received a moderate amount of research effort. Booth (2010) found that peak sighting rates of harbour porpoise were observed at depths between 50m and 150m. In a study which included data from a larger area stretching off the continental shelf, MacLeod et al. (2007) found harbour porpoises were sighted most often in waters deeper than 60m. A further study, using a smaller study area, found a similar relationship between depth and harbour porpoise distribution, where a preference was shown for habitats at depths between 50m and 150m (Marubini et al., 2009). Goodwin and Speedie (2008) provide additional evidence that harbour porpoise distribution is related to depth, and they that most sightings occurred at depths between 50m and 100m. The effects of depth on cetacean distribution may be due to the distribution of cetacean prey such as cephalopods and fish, because areas of deep water may act to induce currents and upwelling which can influence the spatial distribution of prey through aggregating effects or transport (Davis et al., 1998; Cañadas et al., 2005). It is likely that prey distribution and abundance has a strong effect on cetacean distribution (Selzer and Payne, 1988) which drives the observed relationship between cetacean distribution and depth in the waters off the west coast of Scotland**.**

Less is known about the depth preferences of basking sharks as they are less well studied and understanding their distribution is more difficult compared to cetaceans (Eckert and Stewart, 2001). This is because, unlike cetaceans, they don’t need to come to the surface to breathe and their behaviour is comparatively quite different (Southall et al., 2005). Research using satellite tagging has revealed that basking sharks utilise a wide range of depths from 0m to 1000m (Sims et al., 2003). Although there is an increasing amount of recent research describing the areas in which basking sharks are seen (e.g. Witt et al., 2012; Speedie et al., 2009; Skomal et al., 2004) there is a paucity of literature describing their distribution specifically in relation to bathymetric variables.

The slope of the seabed is another environmental factor that has been found to influence marine mammal distribution. The encounter rate of bottlenose dolphins in the waters off the north east of Scotland increased in areas where the seabed gradient was less steep (Bailey and Thompson, 2009). Booth (2010) found that harbour porpoise sightings and acoustic detection rates were much higher in areas with a highly sloped seabed (up to a maximum angle of 6°). Consistent with this, Embling (2010) found slope to be a significant predictor of higher acoustic porpoise detection rates and found that porpoise detection rates increased with increasing slope. It is thought that areas with a highly sloped seabed may increase cetacean sightings because sloped regions provide an area of upwelling, as cold, nutrient rich water is forced to the surface (Kaiser et al., 2005). This increases productivity and prey densities which in turn attracts and supports larger numbers of predators such as cetaceans (Yen et al. 2004). Despite this, there have been studies which identified areas of high porpoise densities with areas of shallow seabed slope (an angle of <0.5°). Raum-Suryan and Harvey (1998) conducted a study using data collected from the waters off Washington State, USA and found that the highest densities of porpoise were in areas of very shallow sloped seabed. The authors attributed this contrasting observation to the fact that in their study area, areas of shallow slope coincided with areas of deep water which probably increased prey abundance and therefore cetacean presence (Raum-Suryan and Harvey, 1998).

Distance to land may act as a proxy for other features of the marine habitat such as salinity of the water (Mann and Lazier, 2006) or areas of shelter and this variable has been used in studies modelling habitat preference of cetaceans. MacLeod et al. (2007) found that distance from the land was the primary variable linked to the occurrence of minke whale, harbour porpoise and common dolphin in the waters off the west coast of Scotland. Booth (2010) found that density of harbour porpoise decreased steadily as distance to land increased and it was shown that the highest predicted relative densities were in areas of up to 20km from land, indicating a strong inshore distribution.

Sediment type has also been identified as an important environmental factor that has been linked to large marine species distribution. The seabed is made up of a variety of sediment types that can be broadly divided into mud, sand and gravel (Folk, 1980). Macleod et al. (2004) found that minke whale were more likely to be present in areas of higher sand or mud sediment types. A similar trend has been observed with harbour porpoises and sighting increased in areas where mud was between 20 per cent and 60 per cent (Booth, 2010). These patterns have been attributed to prey availability as it is known that flat fish, which are a common prey species of harbour porpoise, inhabit muddy sediment types (Herr et al., 2009). This suggests that the sediment type effects cetacean distribution by providing suitable habitats for prey so sediment type could therefore be a predictor for the areas in which cetaceans are sighted. Prey populations could be measured directly but this is relatively difficult compared to studying bathymetric features and it has been found that the inclusion of prey data as explanatory variables does not always improve predictions of cetacean habitat selection (Torres et al., 2008).

In order to generate models and understand the relationship between species distribution and habitat preference, reliable data needs to be collected. Dedicated surveys are rare because they are expensive and time consuming to carry out, so previous efforts often use opportunistic sighting data collected by observers on fishing vessels or on passenger ferries (e.g. Spyrakos et al., 2011; López et al., 2004; Williams et al., 2006) or data collected from aerial photographs (e.g. Chilvers et al., 2005). Although it is possible to generate models from such data, using data from dedicated surveys are easier to analyse and the certainty of a consistent methodology is increased.

Research using dedicated survey data sets in the waters off the west coast of Scotland has focused on a limited number of species. Common dolphin sightings increased in the 1980s and 1990s (Weir et al., 2001) and further studies of this species indicated that as common dolphin increased in north-western Scotland, the numbers of white beaked dolphins have declined (MacLeod et al., 2005). Longer term studies (up to 9 years) using dedicated survey effort have been carried out to model the habitat preference and distribution of harbour porpoise (Marubini et al., 2009) and minke whales (MacLeod et al., 2007) but these studies used data collected before 2000. There is a serious lack of long term (> 5 years) studies using more recently collected data on megafauna in the waters off the west coast of Scotland as there are no published studies of this sort.

To ensure effective conservation and management of different species, it is not only necessary to identify important habitat variables but also to determine the consistency of the patterns over space and time (Booth, 2010).The Hebridean Whale and Dolphin Trust (HWDT) is a charity that has been conducting dedicated research surveys in the waters off the west coast of Scotland for 10 years between 2003 and 2012. This current data set provides a rare opportunity to analyse data over an extensive time scale that has been collected using a consistent methodology.

This study will add to knowledge of spatiotemporal distributions of marine megafauna in the waters off the west coast of Scotland by using the most up to date sighting data collected by HWDT. The aims of this study are to describe the distribution of five species of megafauna (basking shark, common dolphin, harbour porpoise, minke whale and white-beaked dolphin) in the waters off the west coast of Scotland in relation to year, depth, slope, distance to land and seabed sediment type. By fulfilling the aims, important information about the areas in which different species are more likely to be present will be gained. Findings from previous studies suggest that some of these factors will have an effect on cetacean distribution (e.g. Marubini et al., 2009; MacLeod et al., 2007; Bailey and Thompson, 2009) so it is predicted that these factors will have an effect on the different species distributions and at least some will be retained in the minimum adequate models generated. The lack of studies on the distribution of basking shark in relation to environmental variables make predications of which environmental factors will influence their distribution difficult, but inferences can be made based on cetaceans studies, which suggest factors influencing the availability of prey will affect basking shark distribution.

2. Materials and methods

2.1. The study area

The study area (Figure 1) encompassed the waters of the inner and outer Hebrides on the western coast of Scotland, UK (55°45’00 - 58°45’00 N - 4°15’00 -8°45’00 W). The area has a complex topography which includes deep sea lochs and several islands of varying size (Marubini et al., 2009). The southern region is characterised by extensive areas with water <50 metres in depth but with some steep sided channels particularly close to the coastline, whereas in the north of the study site the water is generally deeper with steep sided fjords (Ellet and Edwards, 1983). In addition to this varied topography, the waters are on the boundary between cold temperate and warm temperate waters which provides a variety of potential habitats for cetaceans (MacLeod et al., 2007). Within these waters, a tidal mass flows in a northwards direction from the Atlantic Ocean until it reaches Scotland and there is also the Scottish Coastal Current which flows from the Irish Sea (Simpson et al., 1979). The high nutrient load which flows into the region in these water currents allows for high productivity in the area which provides potential suitable habitats for cetaceans and other large marine vertebrates.

2.2. Survey Methods

Data were collected between April and October between 2003 and 2012. Due to the surveys being weather dependant there were some days during this period when data were not collected. Despite this, during at least 5 months of every year, data were collected. The survey routes were limited by the constraints of the weather and location of safe anchorage points but the aim of the survey was to cover the area as evenly as possible over ten consecutive survey days.

Sightings and *in situ* environmental data were collected by trained volunteers, under the supervision of an experienced cetacean observer, from a 16m sailing vessel operated by the Hebridean Whale and Dolphin Trust (HWDT). During the survey, two observers were positioned at

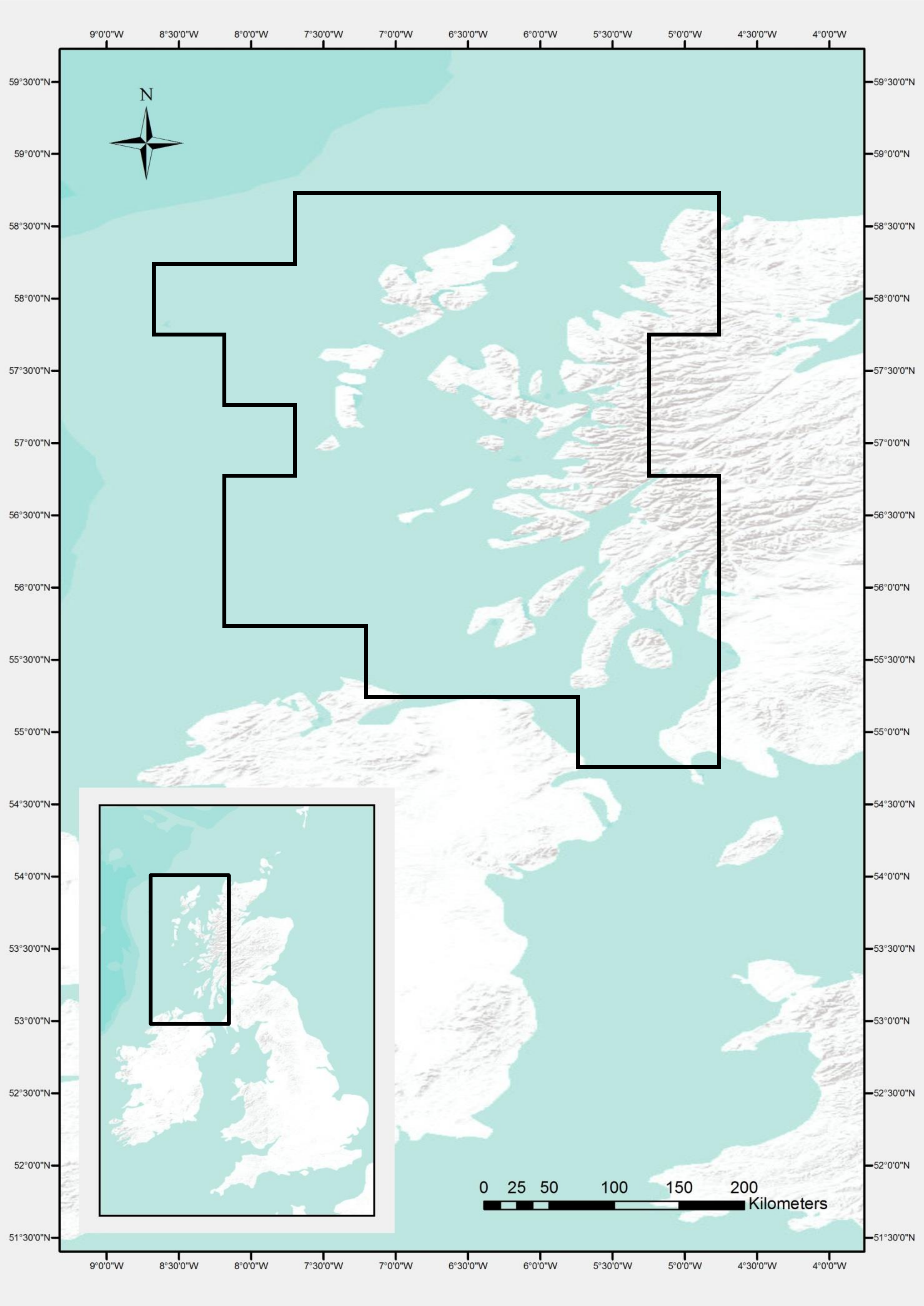


Figure 1. Map of the study area in the west coast of Scotland (black outline encloses the waters that were surveyed). Inset map: Western Isles of Scotland in relation to the UK. Source: created in ArcMap by Eryn Hooper.

two fixed points on the starboard and port sides of the vessel near the bow of the boat, 2m above sea level. Observers scanned an area from -5° to 90° on their side using a combination of the naked eye and 7 x 50 binoculars (Marine Opticron). When a cetacean was sighted, the vessel position, the species name and number of individuals were directly recorded into a computer running the International Fund for Animal Welfare (IFAW) software, Logger 2000 database. Because a large scale spatial was used in this study, the vessel position was used as a proxy for the location of the sighting. To avoid fatigue, observers changed sides after 30 minutes and were replaced by other trained volunteers after an hour had lapsed.

Surveys were carried out either under sail, when the weather conditions permitted, or under motor at an average speed of 6 knots. The vessel position was recorded every 10 seconds using the boat's global positioning system (GPS) and was automatically entered into the Logger 2000 database. Environmental data including Beaufort sea state and sightability were recorded and entered into the same database. Survey effort type (acoustic survey effort, visual survey effort or survey effort off) was also recorded whenever it changed.

2.3. Additional environmental data

Bathymetry data (seabed depth and slope) were sourced from Jisc-designated national data centre at the University of Edinburgh (EDINA) and imported using Manifold System. EDINA provided the best coverage of the surveyed area and at the highest resolution available (average depth and slope were calculated over a 200m x 200m grid). Seabed sediment data (percentage mud, percentage gravel and percentage sand) were obtained from the United Kingdom, Hydrographic Office (UKHO) and the Marine European Seabed Habitats (MESH) European Nature Information System (EUNIS) model and was added to the data set by the HWDT.

Table 1. Summary of covariates used in the analysis, showing details of information about the covariate, the temporal or spatial resolution, the units used and the source of the data. Those in bold are the additional environmental variables used in the GLMs. See main text for acronyms or abbreviations.

Covariate	Information	Resolution	Unit	Source
Date/time	Recorded in situ from vessel GPS	Every 10 seconds	Day, month, year. Hours, minutes, seconds.	*In situ*
Vessel position	Recorded in situ from vessel GPS	Every 10 seconds	Latitude and longitude	*In situ*
Sea state	Recorded by observers	Every 15 minutes	Beaufort scale	*In situ*
Sightability	Recorded by observers	Every 15 minutes	0 – 5 (where 1 is excellent and 5 is too poor to survey)	*In situ*
Distance from land	**Calculated in Manifold by HWDT and imported into the dataset**	**At every GPS location**	**Meters (m)**	**Manifold systems**
Depth	**Depth of sea bed below sea level. Imported using Manifold**	**0.2 km**	**Meters (m)**	**EDINA**
slope	**Change in depth over the 200m of sea bed. Imported using Manifold.**	**0.2 km**	**Degrees (°)**	**EDINA**
Percentage mud	**Imported using Manifold.**	**Variable**	**Percentage (%)**	**UKHO / MESH EUNIS**
Percentage gravel	**Imported using Manifold.**	**Variable**	**Percentage (%)**	**UKHO / MESH EUNIS**
Percentage sand	**Imported using Manifold.**	**Variable**	**Percentage (%)**	**UKHO / MESH EUNIS**

2.4. Data analysis

2.4.1. Pre-statistical analysis

Only data collected during visual search effort, in a Beaufort scale < 4, and where sightability was ≤ 4 were used for analysis. This was because cetacean sighting rates are significantly impacted by sea state (Palka, 1996) and sightablity impacts the area of water that can be seen by observers.

Only sightings of animals identified to the species level were included in the analysis. Due to the large data set, all species sighting data were pooled into 15 minute intervals. This gave a total number of animals sighted in 15 minutes, with the corresponding observed environmental data.

In order to analyse the data, the total number of animals sighted were converted into binary data. The encounter rate was categorised as either 0 or 1 which represented the absence or presence of a species, respectively, for each 15 minute interval. This meant that for each 15 minute interval, the data set provided information about the presence or absence of the species, rather than the absolute number of individuals seen.

The latitude and longitude of the data point at the end of each 15 minute interval was used in the analysis for the position of the boat corresponding to the sighting data recorded during that 15 minutes. The latitude and longitude of the data point at the end of the 15 minute interval was also used to import the corresponding additional environmental data.

To account for the difference in survey effort, grid squares of 30 minutes latitude by 30 minutes longitude were used to divide the study area into 47 cells of approximately 1670km^2 each (Figure 2). This provided a way to count the total amount of effort (15 minute intervals) and to calculate the proportion of 15 minute intervals in which species were seen.

Pivot tables in Microsoft Excel were used to provide a summary of the presence and absence of observed species in each 15 minute interval in each grid cell per year. The mean depth, mean percentage slope, mean percentage mud, mean percentage gravel and mean distance from land were calculated from the points at which each sighting was made. This resulted in a table of values that summarised the presence or absence of the species in each 15 minute interval by year, with the average environmental characteristics at the point at the end of the 15 minute interval, based on the values generated by the individual sightings. These values were used for the analysis.

2.4.2. Modelling

A common statistical method used to model large marine animal distribution and investigate habitat preference is to use generalised linear models (GLM) (e.g. Cañadas et al., 2005; Cañadas and Hammond 2008; Embling et al., 2010; Marubini et al., 2009). Sighting data such as this contains presence/absence data which results in non-normal distributions. There is often a non-linear relationship between species abundance and ecological variables such as depth (Oksanen and Minchin, 2002). GLMs are therefore particularly appropriate for large marine animal sighting data because they allow for non-normal distributions and non-linear relationships (Spyrakos et al., 2011)

GLMs assume that data points are independent but line transect surveys often result in non-independent data. This is because animals are detected at sequential sampling points along a survey route which means observations close in space or time are not random (Lennon, 2000). This results in autocorrelation which occurs when observations measured at neighbouring locations or times are more similar or less similar than randomly associated pairs of observations (Redfern et al., 2006). Including autocorrelated data in the analysis increases the risk of a type I error (the rejection of a true null hypothesis) so it is important to avoid using data of this type in the analysis (Dormann, 2007). It is difficult to avoid autocorrelation in large marine animal survey designs but it needs to be addressed when modelling the relationship between animal distribution and the environment (Keitt et al., 2002). This problem has been addressed here by categorising presence or absence of a species using 0 or 1 for each 15 minute interval, which removes sighting data that were made close in time.

All analyses were carried out using the statistical package R (64-bit version 2.15.2, R core development team, 2006). For the five species selected to model, a GLM was fitted initially with all the additional environmental variables (Table 1). Binomial models were originally fitted but where there was evidence that data were over dispersed, a quasibinomal model was fitted instead. In all models, year was treated as a factor variable whereas every other variable was assumed to be continuous. The results of an analysis of variance (ANOVA) were used to establish the order in which variables were removed from the model. The model was then simplified by backward deletion, removing variables that appeared to be of least importance first. Variables that had a significant impact (at the 95% confidence interval) on the ability of the model to explain variation were retained. The significant variables were then tested for pairwise interactions. If the interactions were significant they were retained in the model. This resulted in a minimum adequate model which contained variables that were significant at the 95% confidence interval.

3. Results

Between 2003 and 2012 a total of 5064 hours of dedicated visual search effort (under Beaufort scale < 4 and in conditions where sightability was ≤ 4) were carried out. Figure 2 shows the area sampled in each year and the resulting overall effort per grid square pooled over the ten years of surveys. The geographical area covered was approximately 78500km^2 but, as Figure 2 shows, effort was not distributed evenly because of weather and logistical constraints. The amount of dedicated visual search effort varied between the years with the least amount of effort (249 hours) in 2004 and the most amount of effort (675 hours) in 2011.

15 different species of marine mammals and large fish were recorded during the 10 years of surveys (Table 2). Observations of animals that were not identified to the species level were also recorded and Table 2 shows that the ability of observers to identify animals to the species level was not consistent over the years. Basking shark, bottlenose dolphin, common dolphin, common seal, grey seal, harbour porpoise and minke whale were all seen in every year. Rarely sighted species included the humpback whale which was sighted once in 2006 and the striped dolphin which was only sighted once in 2003. Relatively few sightings of killer whale were recorded (30 individuals) and fewer still of sunfish (23 individuals). White-sided dolphins were only seen in 2003 and 2004, and have not been sighted during a dedicated survey since.

Once all sighting data had been converted into a value that represented the presence or absence per 15 minute interval it was apparent that the sightings for some species had been clustered in time and presence per 15 minute interval was, as a result, relatively low. Five species that had higher presence per 15 minute interval were chosen to be analysed in relation to environmental factors using GLMs. These species were basking shark, common dolphin, harbour porpoise, minke whale and white-beaked dolphin.

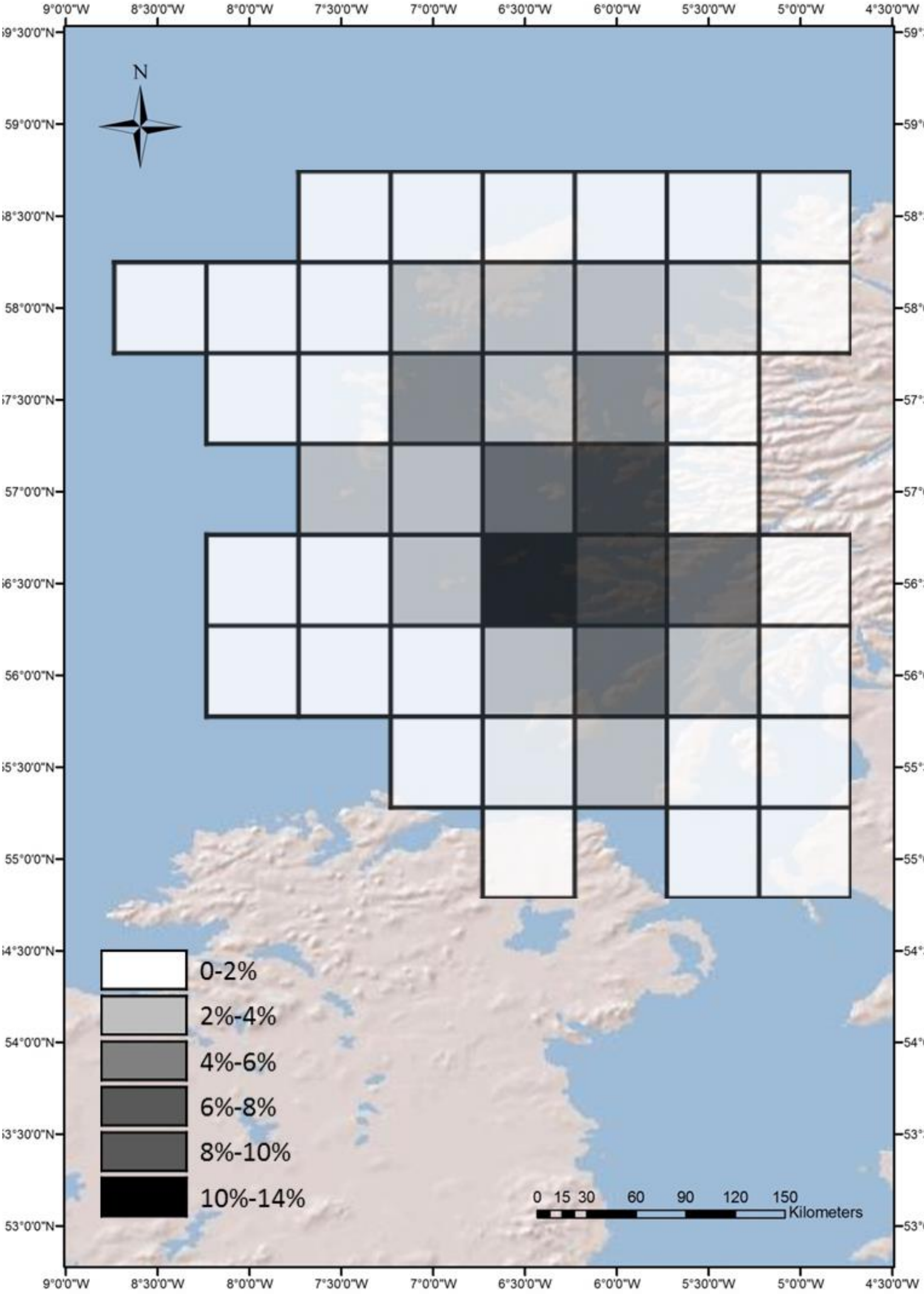


Figure 2. Map showing effort (15 minute intervals) spent in each grid cell (30 minute latitude by 30 minute longitude). Shading represents effort as a percentage of total effort for the 10 years of surveys. Source: Created in ArcMap by Eryn Hooper.

Table 2. Numbers of individuals recorded during dedicated visual searches from 2003 to 2012. Species in bold were analysed in relation to year and environmental factors using GLMs.

	Year										
Species	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**Totals**
Basking shark (*Cetorhinus maximus*)	**61**	**5**	**85**	**222**	**91**	**125**	**170**	**340**	**44**	**146**	**1289**
Bottlenose dolphin (*Tursiops truncatus*)	11	6	5	22	7	20	14	2	1	3	91
Common dolphin *(Delphinus delphis)*	**17**	**0**	**43**	**121**	**1207**	**213**	**423**	**314**	**695**	**165**	**3198**
Common seal (*Phoca vitulina*)	25	11	71	29	42	122	127	88	53	77	645
Fin whale (*Balaenoptera physalus*)	0	0	0	0	0	1	0	0	1	0	2
Grey Seal (*Halichoerus grypus*)	45	22	83	123	150	148	215	99	141	101	**1127**
Harbour porpoise (*Phocoena phocoena*)	**279**	**122**	**418**	**375**	**686**	**702**	**529**	**454**	**523**	**197**	**4285**
Humpback whale (*Megaptera novaeangliae*)	0	0	0	1	0	0	0	0	0	0	1
Killer whale (*Orcinus orca*)	1	6	0	0	6	8	4	0	0	5	30
Minke whale (*Balaenoptera acutorostrata*)	**56**	**24**	**19**	**35**	**37**	**43**	**53**	**40**	**56**	**26**	**389**
Rissos Dolphin (*Grampus griseus*)	27	0	7	3	21	14	20	0	15	2	109
Striped dolphin (*Stenella coeruleoalba)*	1	0	0	0	0	0	0	0	0	0	1
Sun fish (*Mola mola)*	0	1	8	1	4	2	2	2	1	2	23
White Beaked dolphin (*Lagenorhynchus albirostris*)	**0**	**0**	**0**	**18**	**53**	**68**	**82**	**30**	**118**	**11**	**380**
White sided dolphin (*Lagenorhynchus acutus*)	0	0	0	0	0	33	75	0	0	0	108
Shark	0	1	0	0	0	0	0	0	0	0	1
Turtle	0	0	0	0	0	0	0	0	1	0	1
Unidentified dolphin	1	7	4	15	26	3	1009	15	78	14	1172
Unidentified seal	18	27	31	31	37	65	89	69	89	27	483
Unidentified whale	1	0	0	1	0	0	4	0	1	1	8
Unknown species	3	1	5	8	14	11	10	12	6	4	74
Total of all sightings in each year	546	233	779	1005	2381	1578	2827	1465	1823	781	

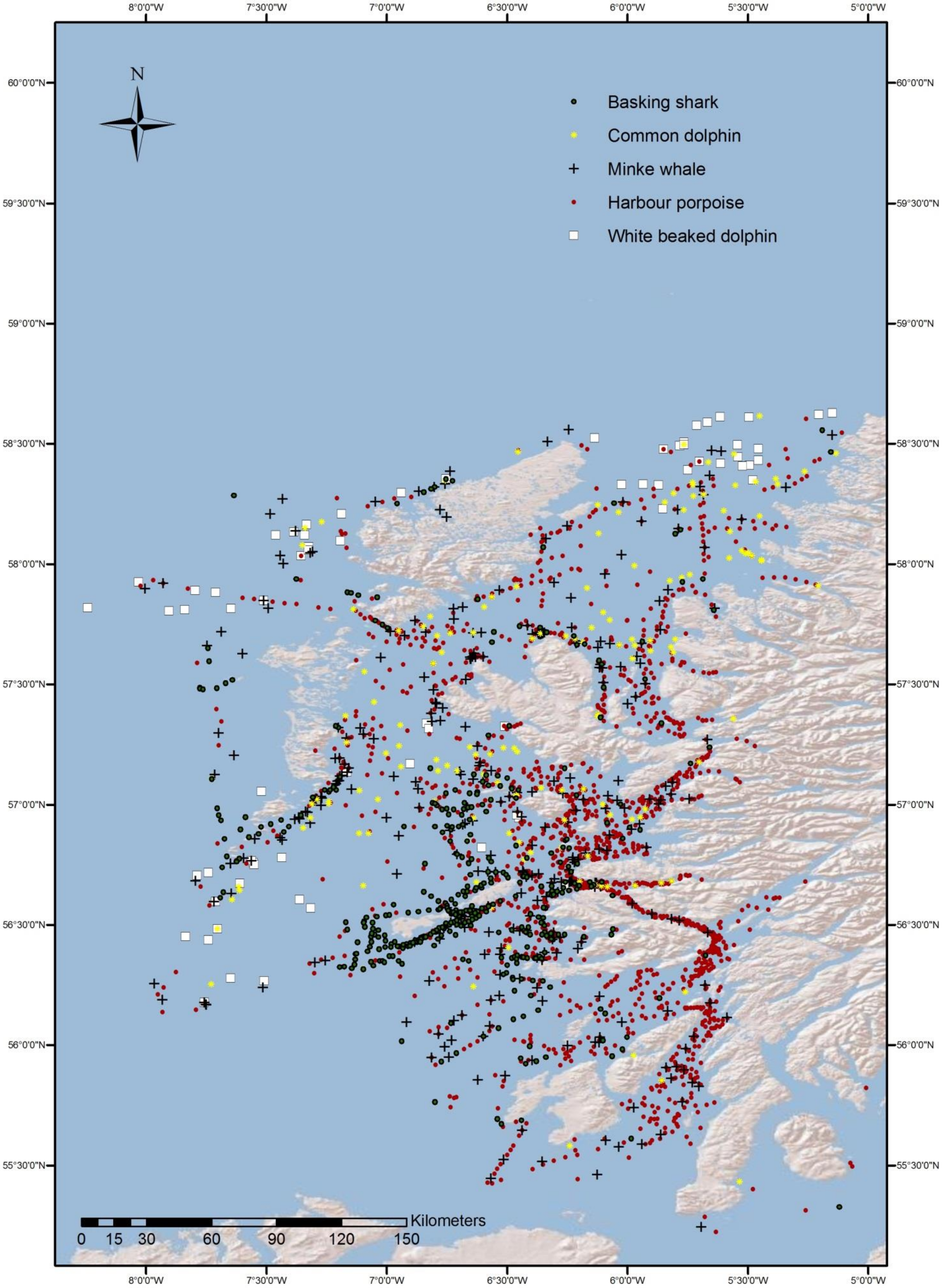


Figure 3. Map showing the areas in which basking sharks (black dots) common dolphin (yellow dots) minke whale (black crosses) harbour porpoise (red dots) and white beaked dolphin (white squares) were present per 15 minute interval, pooled over the 10 years of surveys. Source: created in ArcMap by Eryn Hooper.

3.1. Common dolphin

Common dolphin were the most frequently sighted dolphin in this survey area and 3198 individuals were sighted during dedicated search effort between 2003 and 2012. Sightings of common dolphin covered most of the survey area with fewer seen further south (Figure 3). There were no significant main effects of distance to land, percentage mud or percentage gravel (Table 2). The (binomial GLM) model that best captured common dolphin distribution included the main effects of year, depth, slope and percentage sand and the interaction between year and percentage sand and the interaction between depth and percentage sand. This was because removal of any of these main effects had a significant effect on the ability of the model to explain common dolphin distribution (Table 3) and the inclusion of these two pairwise interactions resulted in a significantly better fitting model (Table 4).

Common dolphins were more frequently sighted in areas of deeper water (Figure 4). Figure 5 shows that there was extensive overlap in the degree of slope in areas where common dolphins were present or absent.

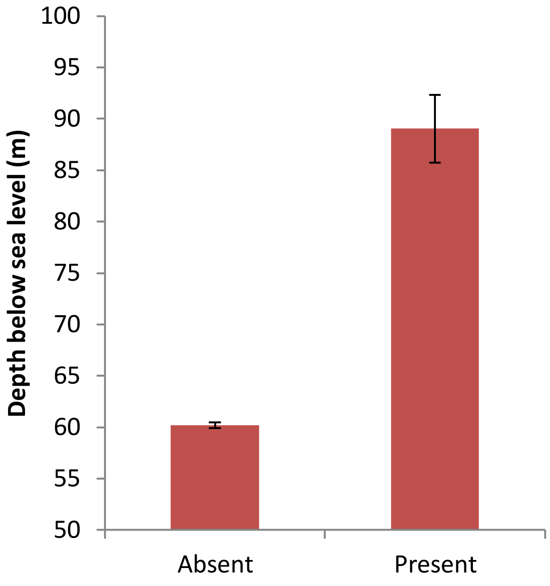


Figure 4. The average (mean) depth of the water in which common dolphins were absent and present. Error bars represent standard error.

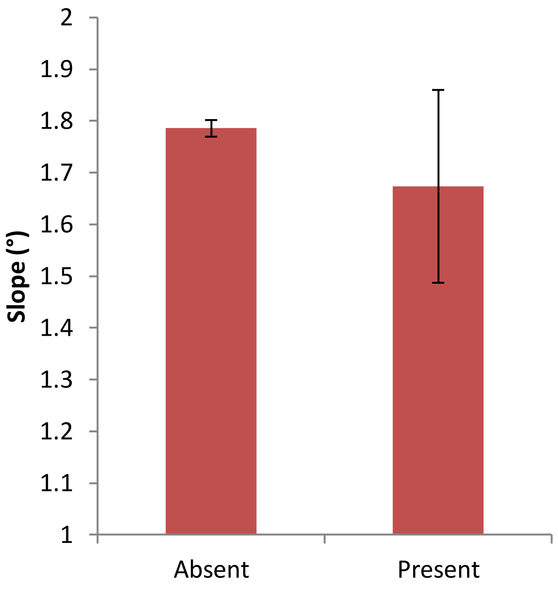


Figure 5. The average (mean) slope of the seabed in the areas where common dolphins were absent and present. Error bars represent standard error.

Although there is only a weak pattern, the average slope was slightly less where common dolphins were present (Figure 5). There was a large spread of percentage sand in the sediment in the areas that common dolphins were seen and the average percentage sand was similar in the areas that they were absent or present (Figure 6). The main effect of year was generally positive over the years except in 2006 and 2008 and also in 2004 when no common dolphins were present (Figure 7). Overall the presence per 15 minute interval increased over the 10 years of surveying.

Inspection of the coefficients of the significant interaction between percentage sand and depth show there was a small negative effect of percentage sand on the effect of depth. The coefficients of the interaction between percentage sand and year show that the effect of percentage sand varied from year to year with a negative relationship in 2003, 2004 , 2005, 2007 and 2012 and a positive relationship in all other years.

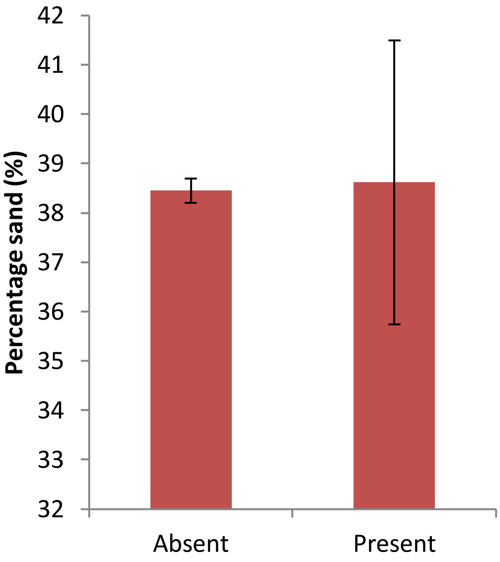


Figure 6. The average (mean) percentage sand in the sediment of the seabed, in areas where common dolphins were absent and present. Error bars represent standard error.

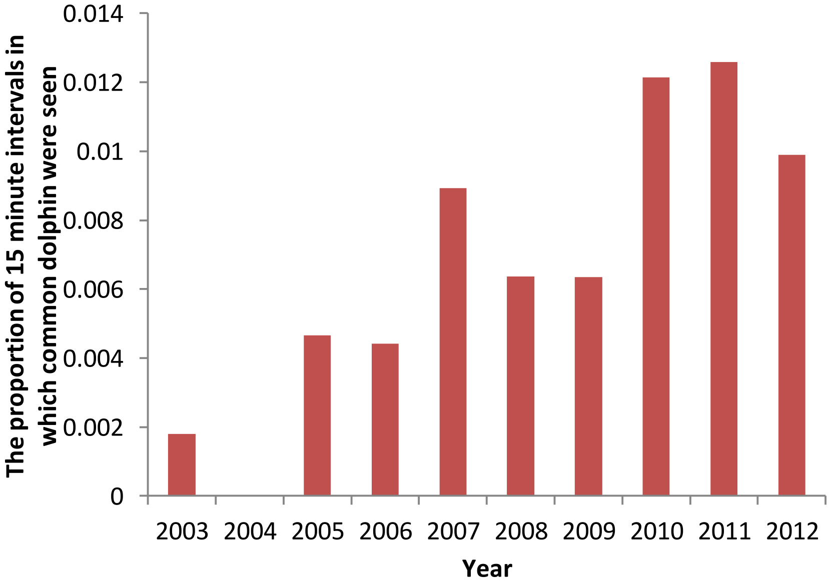


Figure 7. The change over the years in the proportion of 15 minute intervals in which at least one common dolphin was seen.

Table 3. Results of binomial or quasibinomial GLM testing the main effects of year and environmental variables on the probability of sighting common dolphin, basking shark, harbour porpoise, minke whale and white-beaked dolphin, all to 3 significant figures. d.f. (degrees of freedom), χ^2(chi-squared test), F (F test). Those in bold are significant. Significance *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

Species	Environmental variable	Test statistic (χ^2/F)	d.f.	*P value*
Common dolphin (*Delphinus delphis*)	**Year**	**34.431**	**9**	**>0.001 *****
	Depth	**63.412**	**1**	**>0.001 *****
	Slope	**8.106**	**1**	**0.004 ****
	Distance to land	1.009	1	0.315
	Percentage mud	0.037	1	0.847
	Percentage gravel	3.320	1	0.068
	Percentage sand	**4.446**	**1**	**0.035 ***
Basking shark (*Cetorhinus maximus*)	**Year**	**3.510**	**9**	**>0.001 *****
	Depth	**3.963**	**1**	**0.047 ***
	Slope	**16.308**	**1**	**>0.001 *****
	Distance to land	0.082	1	0.774
	Percentage mud	2.370	1	0.125
	Percentage gravel	**6.371**	**1**	**0.012 ***
	Percentage sand	0.536	1	0.465
Harbour porpoise (*Phocoena phocoena*)	**Year**	**2.012**	**9**	**0.038 ***
	Depth	**5.061**	**1**	**0.025 ***
	Slope	**30.762**	**1**	**>0.001 *****
	Distance to land	0.206	1	0.651
	Percentage mud	**5.818**	**1**	**0.017 ***
	Percentage gravel	0.428	1	0.514
	Percentage sand	**4.863**	**1**	**0.028 ***
Minke whale (*Balaenoptera acutorostrata*)	**Year**	**2.090**	**9**	**0.031 ***
	Depth	**14.166**	**1**	**>0.001 *****
	Slope	**3.912**	**1**	**0.049 ***
	Distance to land	1.627	1	0.203
	Percentage mud	**4.478**	**1**	**0.035 ***
	Percentage gravel	1.750	1	0.187
	Percentage sand	1.954	1	0.163
White-beaked dolphin (*Lagenorhynchus albirostris*)	**Year**	**3.145**	**9**	**0.001 ****
	Depth	**53.865**	**1**	**>0.001 *****
	Slope	**53.085**	**1**	**>0.001 *****
	Distance to land	0.499	1	0.480
	Percentage mud	**16.344**	**1**	**>0.001 *****
	Percentage gravel	1.708	1	0.192
	Percentage sand	1.147	1	0.285

Table 4. Results of binomial or quasibinomial GLM testing the pair wise interactions of year and environmental variables on the probability of sighting common dolphin, basking shark, harbour porpoise, minke whale and white-beaked dolphin, all to 3 significant figures. d.f. (degrees of freedom), χ^2(chi-squared test), F (F test). Those in bold are significant. Significance *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

Species	Pairwise interaction of environmental variables	Test statistic (χ^2/F)	d.f.	*P* value
Common dolphin (*Delphinus delphis*)	Year: depth	11.135	9	0.267
	Year: slope	6.384	9	0.701
	Year: percentage sand	**22.775**	**9**	**0.007 ****
	Depth: slope	0.001	1	0.972
	Depth: percentage sand	**6.134**	**1**	**0.013 ***
	Slope: percentage sand	1.716	1	0.190
Basking shark (*Cetorhinus maximus*)	Year: depth	0.429	9	0.919
	Year: slope	0.431	9	0.918
	Year: percentage gravel	1.081	9	0.377
	Depth: slope	2.390	9	0.123
	Depth: percentage gravel	0.009	9	0.924
	Slope: percentage gravel	1.177	1	0.279
Harbour porpoise (*Phocoena phocoena*)	Year: depth	0.907	9	0.519
	Year: slope	**2.829**	**9**	**0.003 ****
	Year: percentage mud	**3.188**	**9**	**0.001 ****
	Year: percentage sand	1.789	9	0.070
	Depth: slope	0.579	1	0.447
	Depth: percentage mud	1.457	1	0.229
	Depth: percentage sand	0.744	1	0.389
	Slope: percentage mud	0.003	1	0.958
	Slope: percentage sand	1.757	1	0.186
	Percentage mud: percentage sand	0.266	1	0.607
Minke whale (*Balaenoptera acutorostrata*)	Year: depth	1.083	9	0.376
	Year: slope	1.169	9	0.315
	Year: percentage mud	**3.592**	**9**	**>0.001 *****
	Depth: slope	1.557	1	0.213
	Depth: percentage mud	0.103	1	0.749
	Slope: percentage mud	>0.000	1	0.994
White-beaked dolphin (*Lagenorhynchus albirostris*)	Year: depth	1.272	9	0.252
	Year: slope	1.593	9	0.117
	Year: percentage mud	0.892	9	0.533
	Depth: slope	2.412	1	0.122
	Depth: percentage mud	0.256	1	0.614
	Slope: percentage mud	0.617	1	0.433

3.2. Basking shark

A total of 1289 individual basking sharks were sighted during dedicated search effort between 2003 and 2012. The best (quasibinomial GLM) model for the distribution of basking sharks included depth, slope, year and percentage gravel because removing these variables significantly affected the ability of the model to explain basking shark presence (Table 3).The interactions between the significant main effects were tested but none significantly improved the ability of the model to explain basking shark distribution (Table 4).

Basking sharks were more frequently sighted in areas of shallower water (Figure 8). The presence of basking sharks also increased in areas where there was a less degree of slope on the sea bed (Figure 9).

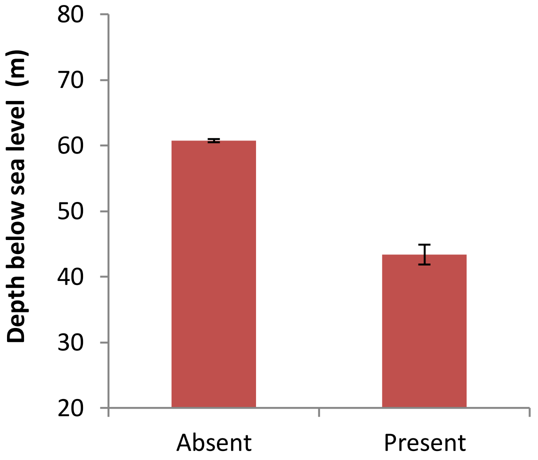


Figure 8. The average (mean) depth of the water in which basking sharks were absent and present. Error bars represent standard error.

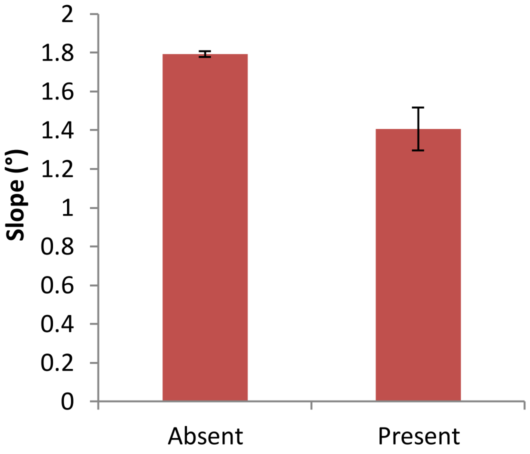


Figure 9. The average (mean) slope of the seabed in the areas where basking sharks were absent and present. Error bars represent standard error.

The sediment type also significantly affected the probability of basking shark presence (Table 3) and they were more likely to be present in areas where there was a higher percentage of gravel in the sediment (Figure 10). There was a significant effect of year on the presence of basking sharks (Table 3) and year had a positive effect on all years except in 2004 and 2011 where the effect of year was negative (Figure 11). Presence per 15 minute interval ranged from 0.005 in 2004 to 0.04 in 2006.

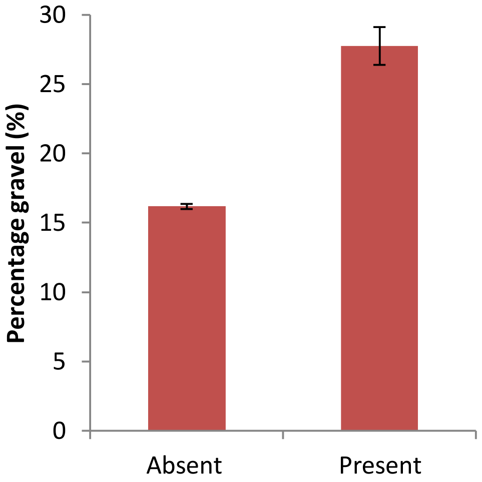


Figure 10. The average (mean) percentage gravel in the sediment of the seabed, in areas where basking sharks were absent and present. Error bars represent standard error.

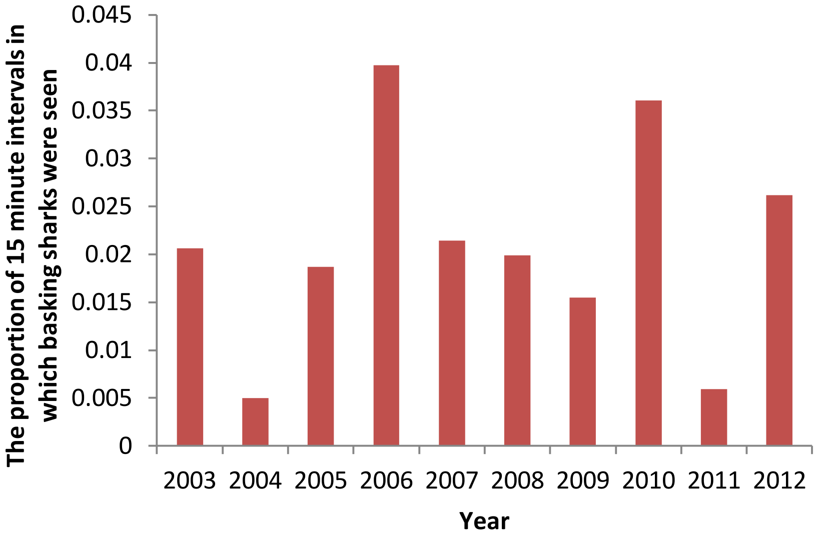


Figure 11. The change over the years in the proportion of 15 minute intervals in which at least one basking shark was seen.

3.3. Harbour porpoise

Overall the harbour porpoise was the species that had the most individual sightings and was recorded in every year during the 10 years of dedicated surveys (Table 1). However, once the number of sightings had been converted into presence or absence in a 15 minute interval, presence per 15 minute interval was much lower than less numerous species, such as the basking shark, indicating that harbour porpoise sightings were clustered close in time. Presence per 15 minute interval ranged between 0.06 in 2004 to 1.12 in 2008 (Figure 12). The significant effect of year was typically positive on the presence of harbour porpoise with the exception of years 2004, 2009 and 2012 where the effect of year was negative.

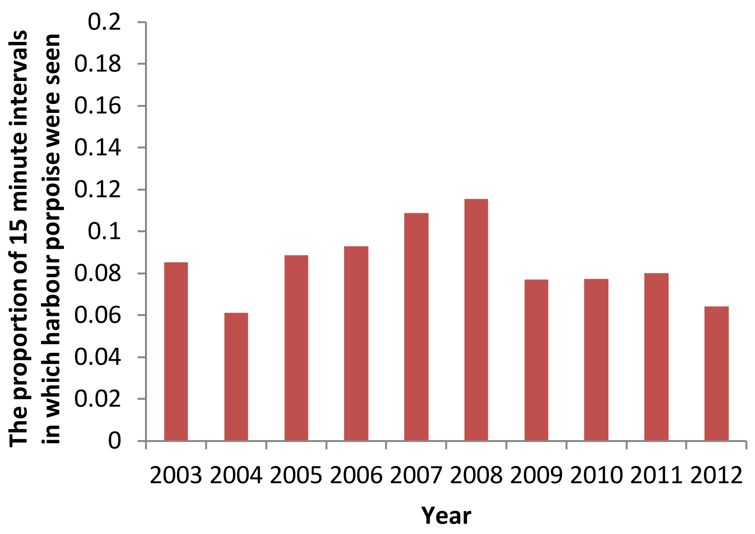


Figure 12. The change over the years in the proportion of 15 minute intervals in which at least one harbour porpoise was seen.

With the exception of distance to land and percentage gravel, all other variables included in the initial model significantly affected the ability of the (quasibinomial, GLM) model to explain the distribution of harbour porpoise (Table 2).

Harbour porpoise were present more often in areas where the sediment type had a higher percentage mud (Figure 13) and lower percentage sand (Figure 14).

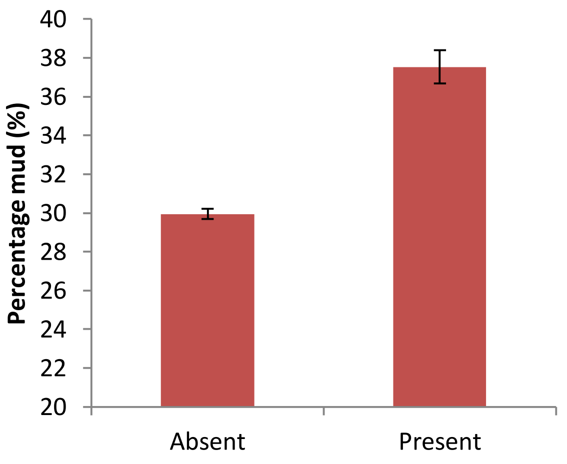


Figure 13. The average (mean) percentage mud in the sediment of the seabed, in areas where harbour porpoise were absent and present.

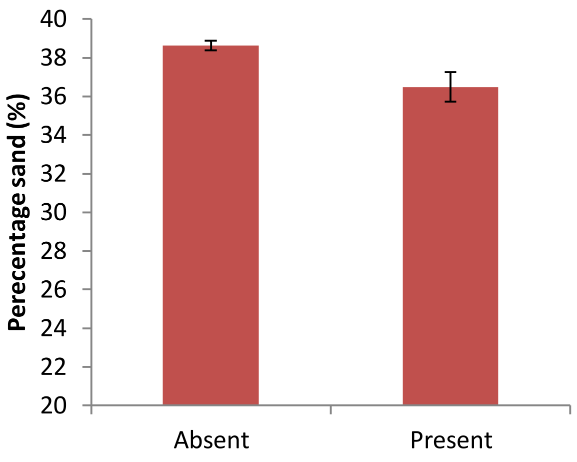


Figure 14. The average (mean) percentage sand in the sediment of the seabed, in areas where harbour porpoise were absent and present.

Harbour porpoise were more often present in deeper water and were sighted at an average depth of 67.4m (Figure 15). The main effect of slope was also significant and harbour porpoise were sighted more often in areas where there was a higher degree of slope (Figure 16).

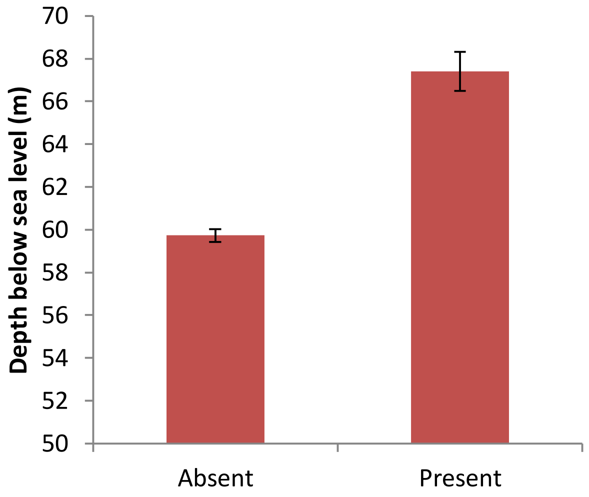


Figure 15. The average (mean) depth of the water in which harbour porpoise were absent and present. Error bars represent standard error.

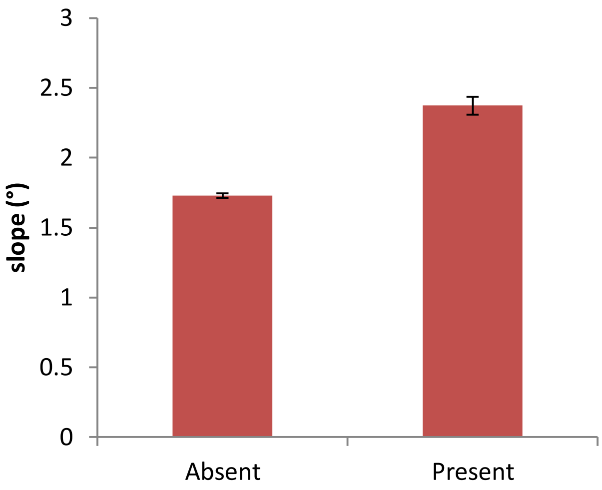


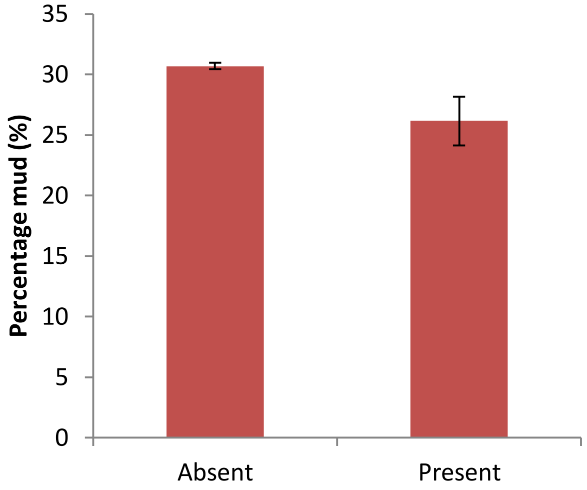
Figure 16. The average (mean) slope of the seabed in the areas where harbour porpoise were absent and present. Error bars represent standard error.

The pairwise interactions between year and slope and year and percentage mud were significant (Table 4). Inspection of the coefficients show that generally in most years there was a positive effect of slope but in 2008 it was strongest and 2003 there was a negative relationship. Examination of the coefficients of the interaction of year and percentage mud showed that there was a positive effect of slope in all the years which increased over the years with the strongest effect in 2010 and the weakest effect in 2009.

3.4. Minke whale

A total of 389 minke whales were recorded during dedicated search effort. The number of individuals recorded remained relatively consistent throughout the 10 years of surveys but the least number of individuals were sighted in 2005 (Table 2).

The minimum adequate (quasibinomial GLM) model for minke whale distribution retained the significant main effects of year, depth slope and percentage sand as well as the interaction of year and percentage mud because removal of these significantly affected the model to explain minke whale distribution (Table 3; Table 4). Minke whales were more likely to be present in areas where there is less mud in the sediment (Figure 17) and in deeper waters (Figure 18).



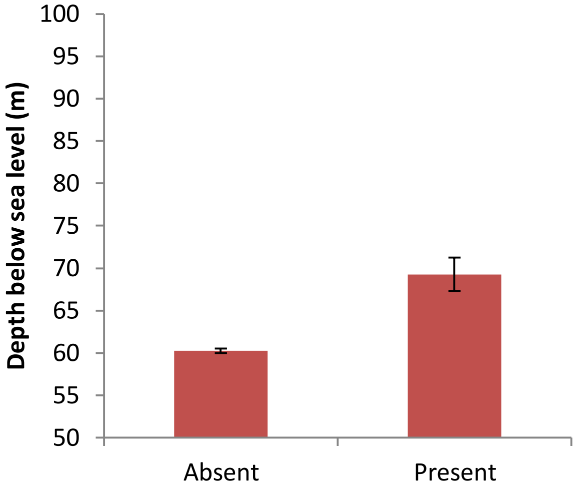
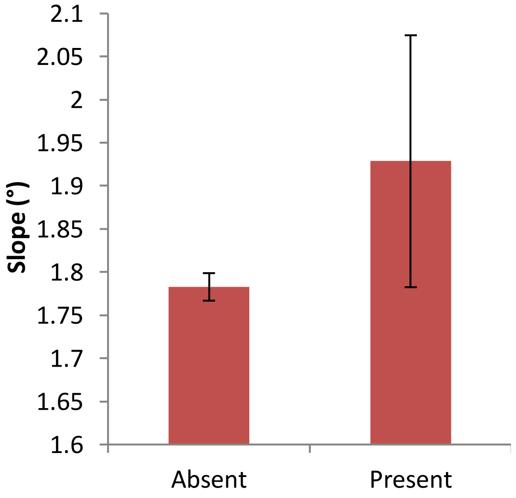


Figure 17. The average (mean) percentage mud in the sediment of the seabed, in areas where minke whales were absent and present. Error bars represent standard error.

Figure 18. The average (mean) depth below sea level in areas where minke whales were absent and present. Error bars represent standard error

The probability of sighting a minke whale increased where there was a greater degree of slope, although Figure 19 shows that there was a lot of variation in the degree of slope in the sites that minke whales were seen. There was a change in sighting rates over the years with a sudden decline from 2003 to 2004 and the most negative effect of year was in 2005 but generally after that the effect of year was positive (Figure 20).



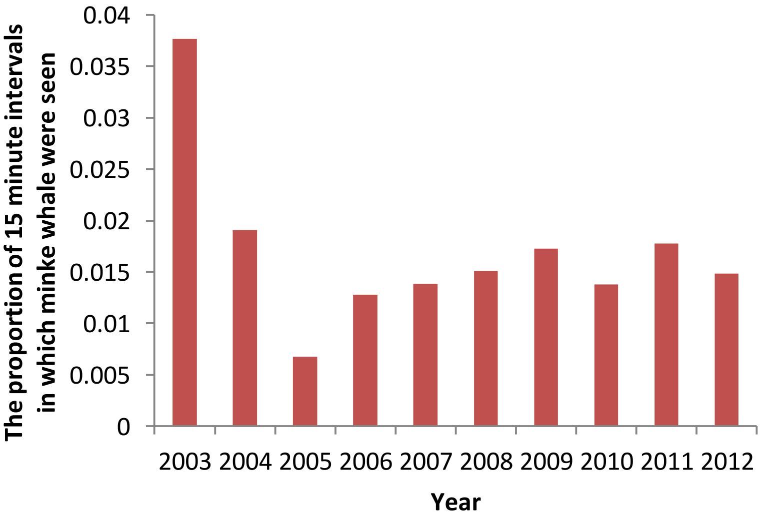


Figure 19. The average (mean) degree of slope in areas where minke whales were absent and present. Error bars represent standard error.

Figure 20. The change over the years in the proportion of 15 minute intervals in which at least one minke whale was seen.

The significant interaction of year and percentage mud varied between the years but inspection of the coefficients show that generally there was a negative effect of year on the effect percentage sand. In 2004, 2005, 2010 and 2011 there was a positive relationship between year and the effect of percentage mud with the strongest effect in 2005.

3.5. White-beaked dolphin

No white-beaked dolphins were recorded until 2006 after which a total of 380 individuals sighted during dedicated surveys. The main effects of year, depth, slope and mud all significantly affected the model to explain white-beaked dolphin distribution (Table 3). White-beaked dolphins were more likely to be sighted in areas of a shallower degree of slope (Figure 21). The average depth in which they were present was much deeper than in areas in which they were absent suggesting that white-beaked dolphins prefer areas of deeper water (Figure 22).

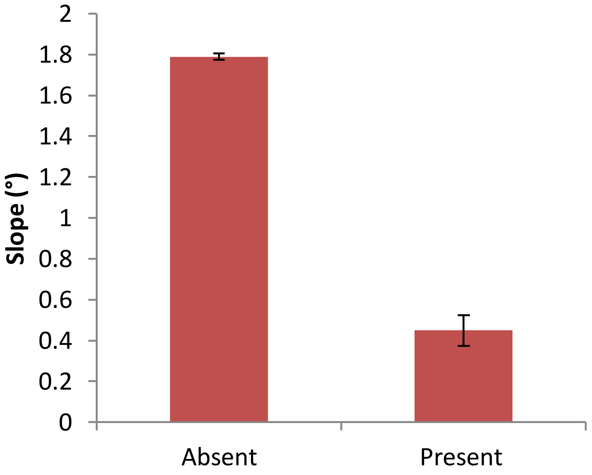


Figure 21. The average (mean) degree of slope in areas where white-beaked dolphins were absent and present. Error bars represent standard error.

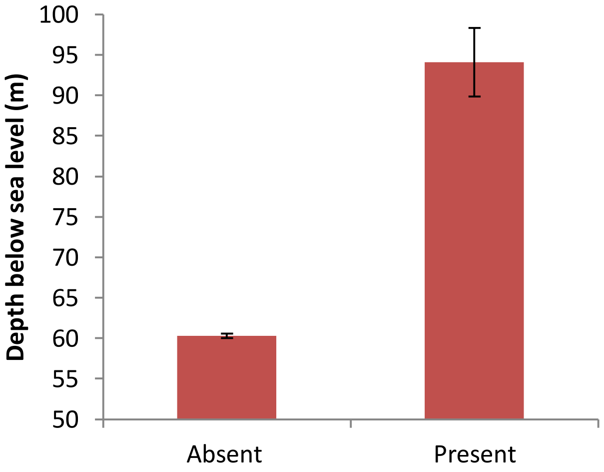


Figure 22. The average (mean) degree of slope in areas where white beaked dolphins were absent and present. Error bars represent standard error.

White beaked dolphins were more likely to be seen in areas where there was less mud in the seabed sediment (Figure 23).Over the years white beaked dolphin sightings generally increased with the highest presence per 15 minute interval in 2011 (Figure 24). Pairwise interactions were tested but none were significant (Table 4) so the best (quasibinomial GLM) model for white beaked dolphin distribution contained the main effects of year, depth, slope and mud.

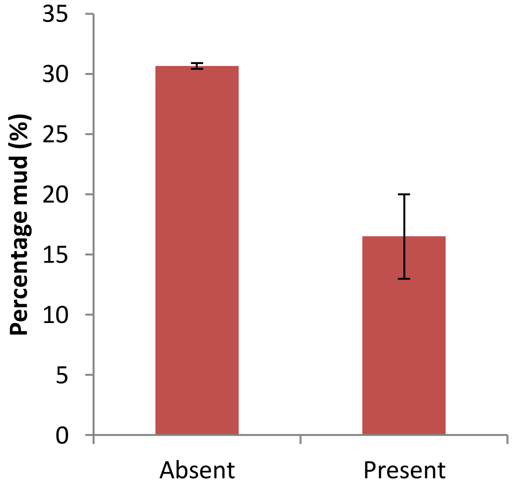


Figure 23. The average (mean) percentage mud in the sediment of the seabed, in areas where white beaked dolphins were absent and present. Error bars represent standard error.

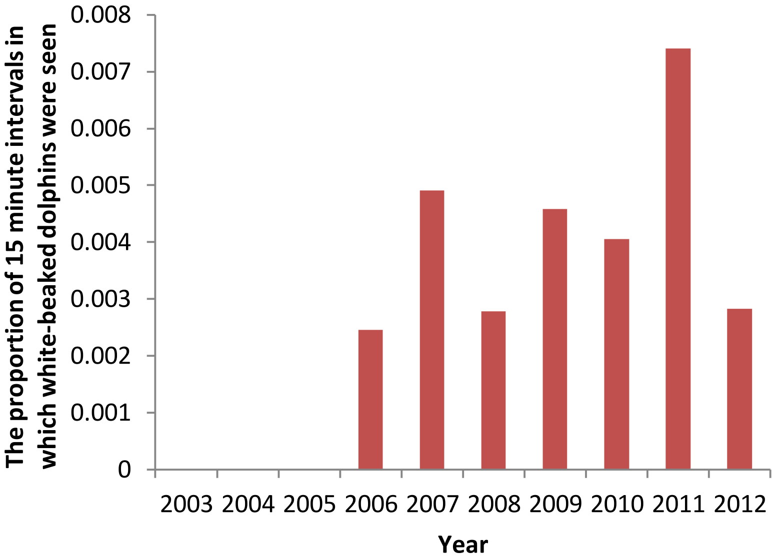


Figure 24. The change over the years in the proportion of 15 minute intervals in which at least one white-beaked dolphin was seen.

4. Discussion

15 large marine animals were identified in this study and harbour porpoise were the most frequently sighted cetacean species in the area. This result is in agreement with previous publications which show that harbour porpoise are the most common and widespread cetacean species in the shelf waters around the UK (Reid et al., 2003) and more specifically have been identified as most abundant cetacean species in the waters of the west coast of Scotland (Booth, 2010).

Enough sighting data was collected to model the distribution of five different large marine species in respect to year and environmental variables. In studies such as these, it is important to consider that although considerable effort was made to cover most of the study area, coverage of all possible ranges and combinations of habitat variables was probably not achieved, which means that the habitat preferences identified in this study are not absolute (MacLeod et al., 2007). Instead, the distribution and habitat preferences identified here are relative to the ranges and combinations of the habitats covered by the surveys.

In all the minimum adequate models for the different species, year, depth, slope and at least one sediment type were retained. The probability of sighting each species was affected differently by the variables tested; therefore the models of each species will be discussed in turn.

4.1. Common dolphin

There was a strong effect of depth on common dolphin distribution and they were more likely to be present in deeper waters. This is consistent with studies of common dolphin in Galician waters where a higher abundance of common dolphin was found in areas of deeper water (López et al., 2004). The average depth at which common dolphins were present was 89m which coincides with the range of depths (4m-120m) in which common dolphins were found in the western Atlantic Ocean (Jefferson et al., 2009). The apparent preferential use of deeper water may be due to the presence of available prey. Blue whiting (*Micromesistius poutassou*) is a main prey species of common dolphin and are known to live in depths of 160m-3000m although in summer months immature blue whiting are found in less deep waters (Bailey, 1982). The surveys were carried out between April and October which would have captured data throughout the summer months when immature blue whiting were in water of depths <160m, so this could provide an explanation for the preference of common dolphin in the depths at which they were seen.

Importantly, the interactions of percentage sand and year and the interaction of percentage sand and depth were included in the minimum adequate model. It is known that over time, due to the strong tidal currents in this area, sediment transportation occurs (Ellett and Edwards, 1983). This might explain the complicated interaction of year and percentage sand because in different years sediment may have been in different areas.

4.2. Basking shark

The areas in which there was a high presence of basking sharks (Figure 3) was very similar to what has been found in studies using older data sets. ‘Hot spots’ which describe areas with consistently high sighting rates have been identified in the areas between the islands of Coll and Tiree (Speedie et al., 2009) which were the same areas in which most basking sharks were observed in this study. The probability of sighting a basking shark increased in areas of shallower water and where there was a slightly less degree of slope. This may be explained by the way in which the topography of the sea bed influences the availability of basking shark prey. Basking sharks are ram filter feeders preying on zooplankton, predominantly copepods, such as *Calanus finmarchicus* and *C. helgolandicus* (Sims and Merrett, 1997). They must filter large amounts of plankton to sustain their energetic needs, which requires them to stay in areas with high zooplankton concentrations (Drewery, 2012). Tidal fronts, which are areas where different water bodies meet, are associated with a high abundance of zooplankton (Sims & Quayle, 1998). Previous studies found that in areas where these tidal fronts are well defined there are relatively more annual sightings of basking sharks (Sims, 2008). Tidal fronts generally form in shallow coastal waters (Simpson and Bowers, 1981) and this may be driving the patterns of basking shark distribution in shallower waters because of the increased abundance of food available that can support larger numbers of basking sharks. Interestingly, there was a higher presence of basking shark in areas where there was a slightly less degree of slope but tidal fronts normally form where there is variable sea bed topography (Simpson and Bowers, 1981) so it may be expected that more sightings would be made in areas of a larger degree of slope. Perhaps in this study area upwelling is influenced more by other variables not tested such as tides or currents that are known to be unique to this area (Simpson et al., 1979).

Rather than inferring the presence of tidal fronts based on bathymetric features it would be more appropriate to directly measure sea surface temperature (SST). SST can provide important information about the location of tidal fronts (Simpson and Pingree, 1978) and the distribution of basking sharks in relation to this environmental variable could be tested in future models if data was made available.

Sighting data may not have been the most appropriate data for studying the distribution of basking sharks because of their surfacing behaviour. Basking sharks move horizontally in the water column in relation to the availability of food (Sims et al., 2003) so in years where plankton were deeper, sighting data may give the impression that basking sharks were absent when in fact they were just too deep to be sighted. It is also not known how many of the population bask on the surface of the water or how often this behaviour is exhibited (Southall et al., 2005). Therefore, there is a significant bias associated with sighting data of basking sharks and is possible that this bias may explain the negative effect of year in 2004 and 2011.

In recent years satellite tags, which track the movement of the animals over a long period of time, have been utilised in trying to better understand basking shark movements and distribution

(Witt et al., 2012). Although it is more expensive, data from these sources, rather than sightings, may be a better method to understand temporal and spatial patterns in relation to environmental features.

4.3. Harbour porpoise

The model that best explained harbour porpoise distribution included the main effect of year, depth, slope, percentage mud and percentage sand as well as the interaction between year and percentage mud and the interaction between year and slope. This indicates that over the ten years studied, there was significant temporal variation between the years. There was no clear pattern between the years although there was a peak in the presence of harbour porpoise in 2008.

Fluctuations in the number of harbour porpoise sightings between years has been studied previously in this area (Booth, 2010) and changes in climatic or oceanographic conditions have been attributed to a change in harbour porpoise distribution (Stevick et al., 2008). Without investigating the climatic or oceanographic changes that occurred from year to year it is difficult to identify if these could cause the patterns shown in this study. Alternatively, it could be that the study area does not encompass the whole effective range of the observed harbour porpoises. The fluctuations could therefore be explained by movement in and out of the study area. A study encompassing waters much further south (Bay of Biscay, Spain) and further north than the study area (up to the Norwegian and Icelandic coasts) found that harbour porpoise populations between these regions consisted of a single population with no obvious ecological barrier to limit their dispersal (Fontaine et al., 2007). It is possible that the movement of animals within a larger range than the area studied could account for the significant temporal effect of year.

The interaction between year and slope and year and percentage sand may be explained by the different areas that were surveyed each year. In different years, the effect of slope or percentage mud may have had a different effect depending on the areas that were surveyed in each year.

The average depth of 67m in which harbour porpoise were present is consistent with previous studies that found an increase in harbour porpoise detections at depths between 50m – 150m (Booth, 2010; Marubini et al., 2009; MacLeod et al., 2007; Goodwin and Speedie, 2008). The effect of depth on harbour porpoise presence could be explained by the availability of prey especially juvenile whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius pollachius*) and saithe (*Pollachius virens)* as they form a major part of harbour porpoise diet (Santos et al., 2004). These species inhabit waters shallower than 200m and it is specifically known that whiting inhabit depths of between 40m and 200m (Persohn et al., 2009). The depths that these fish species inhabit may be driving the observed distribution of harbour porpoise observed in this study and could explain the importance of depth in increasing the probability of harbour porpoise presence.

Percentage mud and percentage sand both, singularly, had a significant effect on the probability of the presence of harbour porpoise. The result that harbour porpoise were present in areas with an average of 38 per cent mud and 36 per cent sand in the sediment may be explained by the habitat required of harbour porpoise prey species. Whiting are known to prefer muddy sandy sediments (Weng, 1986) and make up a large part of harbour porpoise diet (Santos et al. 2004). The increased prey available in muddy sandy areas may be attracting larger numbers of harbour porpoise and could explain why harbour porpoise are more likely to be present in areas of these sediment types.

Distance to land has been previously identified as an important variable in explaining harbour poripoise distribution (Booth, 2010) but this was not found in this study. Booth (2010) suggested that distance to land could act as a proxy for other unmeasured biologically significant features such as salinity, upwelling occurring closer to the shore and sheltered areas. However, the results presented here contrast with these previous findings and suggest that distance to land does not have a significant effect on harbour porpoise distribution, or indeed on any other species analysed.

4.4. Minke whale

Sediment influenced minke whale sightings and this is consistent with the findings of a study on a smaller area of the western coast of Scotland where the distribution of minke whale was strongly influenced by sediment type (Macleod et al., 2004). This could be linked to the presence of prey because certain prey species require certain habitat types. Sandeel (*Ammodytes* spp.) are a major prey source for minke whale, making up between 62%-87% by weight of their diet in this study area (Pierce et al., 2004). Sandeel are more available in the beginning of the summer because juveniles emerge from the seabed at the end of spring (MacLeod et al., 2004). Sandeel distribution is limited by the availability of appropriate sediment types in which their eggs can develop which includes coarse sand and gravel (Reay, 1970). It has been found that there is a strong correlation between prey availability and minke whale diet (Tamura and Fujise, 2002) so the association of sandeel with habitat type may explain the patterns of minke whale distribution. The main effects of sand or gravel were not significant when removed from the model but minke whales were more likely to be seen in areas where there was an average percentage mud of 26% which leaves the remaining average sediment made up of about 74% gravel and sand mix. The surveys were carried out between April and October so it is likely that their diet during the surveys consisted of sandeel (Tamura and Fujise, 2002). The habitat preference of sandeel could therefore indirectly explain minke whale distribution and their preference for areas of a lower percentage mud.

Depth and slope were both, singularly, influenced the spatial distribution of minke whale in this study. On the eastern coast of Scotland is has been observed that the majority of sightings between 2001 and 2006 occurred at steeply sloped areas and at depths between 20m and 50m (Robinson et al., 2009). The authors attributed this pattern in minke whale distribution to areas of increased upwelling of nutrient rich currents caused by the steep slopes and depths of the seabed (Robinson et al., 2009). In addition, it has been proposed that minke whale in the St. Lawrence estuary, Canada, use currents caused by seabed topography during feeding (Lynas and Sylvestre, 1998). The same processes could be happening in the waters of this study area because more minke whales were present in areas of greater degree of slopes and they preferred areas of deep water. It would be expected that an increase in nutrient rich currents caused by the change in depth may increase local productivity that would provide enhanced feeding opportunities for marine predators such as minke whale (Yen et al., 2004). The significant effect of depth and slope on minke whale distribution found here may therefore be explained by the interaction of seabed topography with prey availability.

Markedly, there was a strong negative effect of year in 2005 on the probability of minke whale observations which coincided with a reported significant change in the ecosystem in the waters off the west coast of Scotland in 2005 (Booth, 2010). Concurrently, there was a strong positive effect of year on the presence of basking sharks in 2005. A reduction in salinity was recorded from early 2005 to 2007 which suggests a reduced influence of water into the study area from the Atlantic (Baxter et al., 2011). Although it is unclear why, this change in water movement coincided with a regional change in available prey with a reduction in small schooling fish such as sandeels and herring (*Clupea harengus*) and an increase in large zooplankton (Stevick et al., 2007). The decline in sandeels and herring would have resulted in less available prey for the minke whale which may explain this pronounced decline in the presence of minke whale during 2005. Sandeels and herring rely on plankton as a main food source (Prokopchuk and Sentyabov, 2006; Christensen, 2010) so it could be reasoned that a reduction in these species may have reduced predation pressure on zooplankton. This, in turn, could have provided a more abundant prey resource for basking sharks, resulting in the observed increase in their numbers in 2005. Further investigation into the oceanographic changes that occurred during this time would allow for better conclusions to be drawn about the reasons behind the marked changes in minke whale and basking shark distribution changes in 2005.

4.5. White-beaked dolphin

Notably, white-beaked dolphins were first recorded in 2005 in this study. It is unlikely that they were absent because they were recorded during 2004 and 2005 (MacLeod et al., 2007). The absence of white-beaked dolphins recorded in this study is more likely to be a reflection of the change in survey effort over the years. Survey effort has increased to more northerly and westerly waters in recent years, which is where white beaked dolphins are more often sighted (Figure 3). This highlights one of the limitations of using data from an area so large because resources do not allow total coverage of the area in every year. Increasing survey effort or by collaborating many data sets would improve this.

Depth was identified as a significant predictor of white beaked dolphin presence and this is consistent with previous studies conducted in this area which found that depth was the primary variable linked to the occurrence of white beaked dolphin (MacLeod et al., 2007). They were more often sighted in areas to the west of the outer islands (Figure 3) which is reflected in an increased probability of presence with the shallowest slope and deepest waters of all the species analysed. In addition MacLeod et al. (2007) identified distance to land as an important variable but this was not found in this study. A possible reason that it was not found to be an important variable in describing white-beaked dolphin distribution in this study could be because of the time periods used. MacLeod (2007) looked at data from June and July in two consecutive years whereas this study used data from 10 years and over a much longer period of the season (April-October). It is known that during the summer there is a peak in white-beaked dolphin sightings closer to the shore (Canning et al., 2008; Reid et al., 2003). Pooling the data from all the months may have meant that the effect of distance to land appeared to not have an effect on white-beaked dolphin distribution because the effect of month had not been considered. To test for this, further analysis should be carried out which includes the effect of month in the models. Data were available on Julian day so seasonal variation could have been investigated but this is an area for further work.

5. Conclusions

Effective conservation will depend critically on our understanding of the relationship between the species and the habitats they use (Canadas and Hammond, 2008). Many of the environmental variables tested seem to have real biological reasons influencing the probability of megafauna distribution and this knowledge can help identify important areas in the waters off the west coast of Scotland.

Understanding that year, depth, slope and sediment type effect the distribution of a range of megafauna in the waters off the west coast of Scotland is highly relevant today because, with fossil fuels depleting, there is ever more demand for energy from alternative sources. Scotland has set a target of producing 100 per cent of its electricity requirements from renewable sources by 2020 (DECC, 2009) and the marine environment will no doubt play an important role in achieving this ambitious aim. Proposals have been made to use the waters of this study area for the production of renewable energy (Alexander et al., 2013) so background knowledge on the distribution of species that inhabit the waters off the west coast of Scotland are of paramount importance. The spatial and temporal patterns identified in this study, in combination with other studies, should be considered in plans for future conservation measures and developments in these waters.

Acknowledgements

Many thanks go to the HDWT who were so generous with their time and data which made this project possible. A big thank you to my supervisor, Tom Reader, who has taught me everything I know about R and introduced me to the wonders of pivot tables in Excel.

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