The role of fine-scale environmental variables in predicting the distribution of minke whales (*Balaenoptera acutorostrata*) in the Moray Firth, North East Scotland

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Marine Mammal Science

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“An understanding of the natural world and what's in it is a source of not only a great curiosity, but great fulfilment.”

-David Attenborough

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Abstract

Minke whales are the most abundant species of Balaenopteridae found in European waters, and act as important indicator species of ecosystem health. Understanding species-habitat relationships is essential to the success of conservation efforts. In the present study, minke whale presence and environmental data were collected during May to October, 2009 to 2013 inclusive. The distribution and relative abundance of whales in relation to environmental variables was investigated using a combination of GIS and generalised additive models (GAMs). Minke distribution showed distinct spatio-temporal variation, with the greatest abundances recorded in July (40%). Presence was strongly associated with chlorophyll concentration, photosynthetically active radiation and euphotic depth. Such variables are linked to primary productivity, suggesting a preference for highly productive areas. However, a time-lag between minke occurrence and peak chlorophyll is apparent. It is likely that arrival of minke whales is synchronised with the emergence of sandeels into the water column, yet prey aggregations induced by amplified productivity are also utilised by *B.acutorostrata*. Minke preferences for other productivity-inducing bathymetric features (e.g. shallow sea depths) also support this theory. The present study highlights the importance of habitat modelling to the conservation of marine ecosystems, and the reliability of environmental variables as predictors of species occurrence.

Key words: Minke whale, *Balaenoptera acutorostrata,* cetaceans, Moray Firth, distribution, habitat modelling, conservation, chlorophyll, photosynthetically active radiation.

1. Introduction

Understanding the interactions between cetaceans and the surrounding environment is an essential part of the conservation and management of their ecosystems (Tetley *et al.,* 2008; Baumgartner, 2011). Recent concerns regarding the impact of climate change on species-habitat relationships have been raised but such impacts are notoriously hard to detect in marine environments (Dalla-rosa *et al.,* 2012). Being high trophic level predators yet also vulnerable to anthropogenic activities, cetaceans are useful indicators of ecosystem health (Hooker and Gerber, 2004; Elith e*t al.,* 2006). Cetacean species across the world are exhibiting declines or alterations in their distribution patterns, in response to fluctuating prey populations due to pressures from climate change and exploitation. For example, thirty-five percent of all marine top predators worldwide are expected to experience significant changes in core habitat in response to climate change, resulting in a northward displacement of biodiversity (Lambert *et al.,* 2011; Hazen *et al.,* 2013). Therefore an understanding of the complex relationships dictating these changes is necessary to enable the successful protection of marine biodiversity, both present and future.

Habitat modelling is currently a priority in conservation, and has been used in the protection of terrestrial environments for many years (Gerber et al., 1999). However, its application to support the conservation of marine species, including the establishment of Marine Protected Areas (MPAs), is increasingly important (e.g. Embling et al., 2010). Models are constantly being developed and improved to enhance our understanding of species ecology, and also growing in their breadth and complexity (Gregr et al., 2013). Ecological modelling has multiple benefits including the prediction of species occurrence even when sufficient distribution data is unavailable (Zaniewski et al., 2002; Schweder, 2003).

The minke whale, *Balaenoptera acutorostrata* (figure 1), is the smallest and most common of all baleen whales found in European waters (Weir *et al.,* 2007). Within the north east Atlantic, *B.acutorostrata* occurs from Norway to France and throughout the North Sea (Hammond *et al.,* 2002). It is particularly abundant in Scottish waters, frequenting near shore areas <200m deep (Macleod *et al.,* 2004; Wall *et al.,* 2006; Robinson *et al.,* 2007). Sightings in the northern North Sea mainly occur from April to October, peaking in June and July (Northridge *et al.,* 1995; Macleod *et al.,* 2004; Robinson *et al.,* 2009; Weir*,* 2010) although in some locations sightings have been reported year round (Macleod *et al.,* 2004).

Minkes are opportunistic feeders, displaying temporal and spatial differences in diet according to the local availability of prey (Robinson and Tetley, 2007). Preferred food sources include shoaling fish, such as Cluepids (herring and sprat), sandeels, mackerel and Gadoids (Neve, 2000; Olsen and Holst, 2001; Lindstrom *et al.,* 2002; Pierce *et al.,* 2004). Comparisons of marked individuals from northeast Scotland and the Inner Hebrides have demonstrated that individuals switch between sites, most likely responding to annual shifts in the distribution of target prey species (Tetley *et al*., 2008). *B. acutorostrata* undertake seasonal migrations, moving from feeding grounds at lower latitudes to breeding sites at higher latitudes (Stevick *et al.,* 2002). The Moray Firth is an evidently important site for minkes, which are sighted in this area considerably more frequently than in adjacent waters (e.g. Macleod *et al.,* 2004; Canning, 2007). Since 2005, the inner region has been designated a Special Area of Conservation (SAC) on account of its resident bottlenose dolphin population, as well as their habitat and the submerged sandbank habitats (SNH, 2006). However, recent studies have highlighted the importance of the southern outer Firth for feeding minke whales (e.g. Robinson and Tetley, 2009). Whilst minke whales also form an integral component of the ecosystems that characterise Scottish waters, they are often overlooked (Clark *et al.,* 2010).

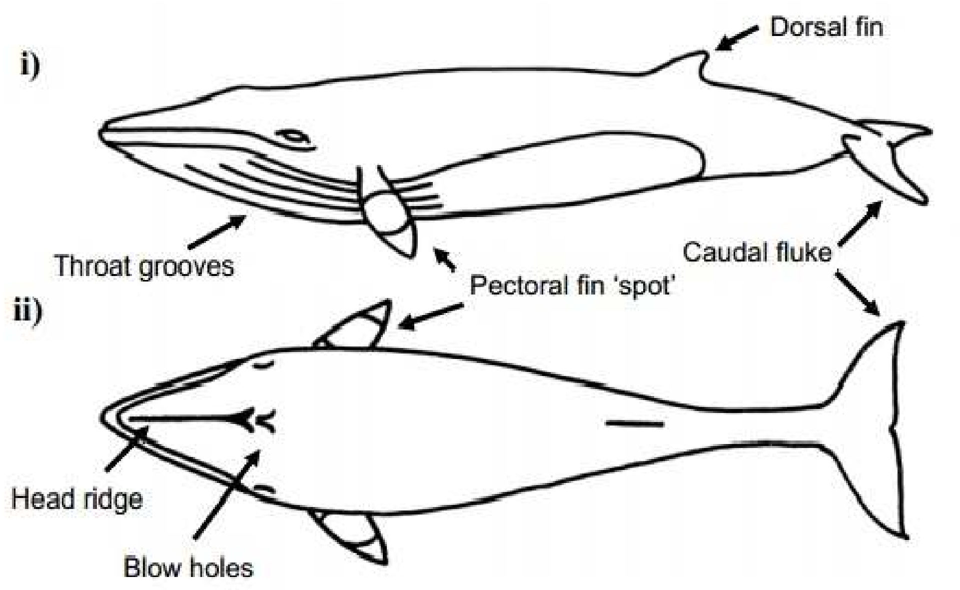


Figure 1: Diagram of the Northern Atlantic minke whale* Balaenoptera acutorostrata acutorostrata. *Labels indicate distinguishing characteristics of the species. Image i) lateral view; ii) dorsal view. Adapted from Tetley (2008).

B. acutorostrata is not currently endangered; population size in European waters was stated as 10,500 in 2005 (SCANS, 2005) and the frequency of sightings is increasing throughout the North Sea, particularly in the east and north of Scotland (Reid *et al.,* 2003). However, as with all cetaceans, the species is undoubtedly threatened by human activities such as climate change and over-exploitation; both from whaling (minkes are hunted off Norway and Iceland) and prey depletion due to fisheries (Parsons *et al.,* 2000; Gill *et al.,* 2001; Hurd, 2013). Typically knowledge regarding cetacean distribution is limited as these small rorqual whales are difficult to detect; they are visible only when surfacing and whilst in close proximity to the coast (Macleod *et al.,* 2004). Similarly, accurate data regarding prey distribution and abundance are scarce. One potential solution is to predict species occurrence using environmental variables (EVs), such as sea surface temperature, as a proxy for species abundance. Torres *et al.* (2008) indicated that compared to fish distribution data (which are difficult to collect and generally lack precision) EVs offer greater predictive power, with higher precision and accuracy for forecasting predator species distribution, at less expense.

Whilst studies in most recent years have been lacking, it has been previously shown that minke whale presence is influenced by a number of environmental factors such as sediment type, depth and slope gradient (Robinson *et al.,* 2009), sea surface temperature (Tetley, 2008) chlorophyll-a concentration (Anderwald *et al.,* 2012), sea ice extent (Ainley *et al.,* 2012) and tidal currents (Chenoweth *et al.,* 2011).

Broad and fine scale oceanographic and topographic variables likely determine prey abundance and distribution, and therefore are underlying reasons behind the presence of their predators (Torres *et al.,* 2008).

The aim of the present study is to quantify and model relationships between the distributions and abundance of minke whales and fine-scale environmental variables. The study will focus on the southern outer Moray Firth, spanning the period 2009 to 2013. This work will improve understanding of spatial and temporal variation in minke whale presence in the region and provide insight into the value of species distribution modelling as a tool for the conservation of cetaceans.

2. Materials and Methods

2.1) Study site

The Moray Firth (figure 2) is a large triangular embayment, spanning from Duncansby Head to Kinnaird's Head near Fraserburgh (Harding-Hill, 1993). The largest of its kind on the east coast of Scotland, the Moray Firth covers approximately 5, 320km² and incorporates the Dornoch, Cromarty and Inverness firths (Eleftheriou *et al.,* 2004). The entire area is divided into two sections. The inner firth is defined as the area to the west of a straight line drawn from Helmsdale to Lossiemouth (Wright *et al.,* 1998). The outer firth is the remaining body of water to the east of this outer limit, defined as a straight line drawn from Duncansby Head in the north to Kinnairds Head in the east (figure 2).

The Moray Firth is an 'open system', sharing water circulation patterns and other large-scale environmental characteristics with the North Sea basin and beyond, and forms an integral part of the North Sea system as a whole (Wright *et al.,* 1998; Eleftheriou *et al.,* 2004). The main input is provided by the Dooley current, which carries mixed cold water from the north and circulates it in a clockwise direction, shown in figure 2 (Adams and Martin, 1986;Wilson, 1995). Resulting frontal zones are characterised by strong horizontal gradients in surface and bottom temperatures (Reid e*t al.,* 2003). The current study was carried out across a 1, 280km² area of the southern outer firth coastline (see figure 2).

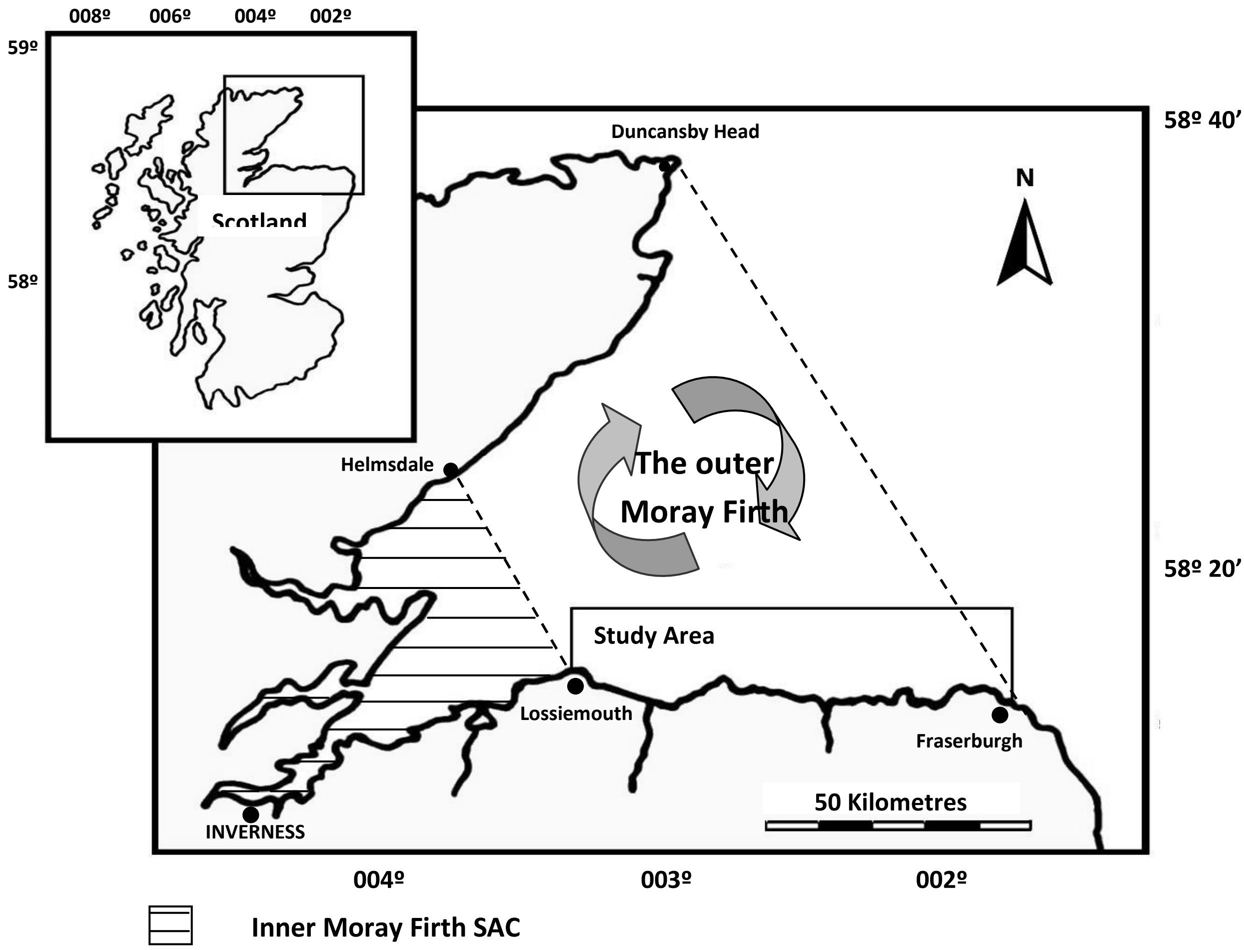


Figure 2: Map of the Moray Firth in north east Scotland, displaying the limits of inner and outer parts (dotted lines).The Special Area of Conservation is represented by the striped area, whilst the outlined area represents the extent of the 1,280km² CRRU study area from which the data was collected. From Tetley et al. (2008).

2.2) Minke whale sightings Data

The sightings data used in this study were collected during dedicated boat surveys by the Cetacean Research & Rescue Unit (CRRU) between the months of May and October from 2009 to 2013 inclusive. Surveys utilised a combination of dedicated offshore routes, opportunistic routes and one dedicated coastal route (figure 3). Survey effort for this study was largely opportunistic, as whilst surveys followed three offshore and one coastal route, once an animal was encountered the observers switched from “survey effort” to “encounter effort” (i.e. data on behaviour etc. were collected on the encountered animals, prior to resuming the survey) .

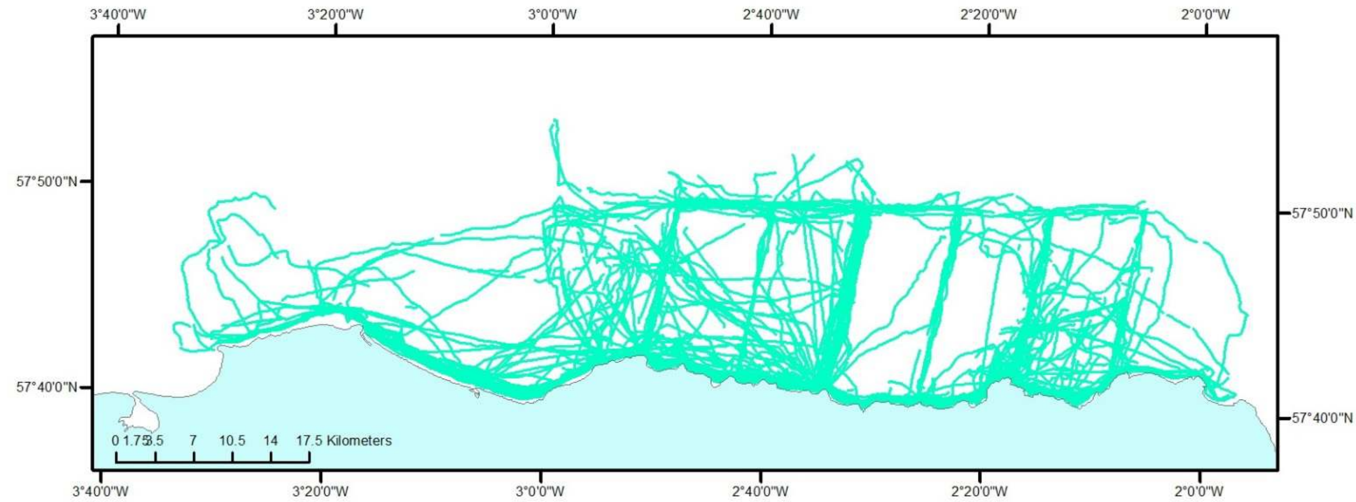


Figure 3: The southern outer coastline of the outer Moray Firth and the location of survey effort during dedicated and opportunistic boat surveys for the study period 2009 to 2013. Routes were notionally divided into three offshore routes and one inner coastal route.

All surveys were carried out using 5.4m Ridged Inflatable Boats (RIBs) powered by a 90hp, 2-stroke outboard engine and outfitted with Raymarine GPS/depth finder units and thermistor probes,. Boats travelled at a constant speed of between 10 to 18km/hr (7 to 10 knots). During all boat surveys, a continuous scanning method was employed, using two experienced observers and up to five trained observers. 7x50mm binoculars were used for scanning far from the boat. As weather conditions in the outer firth tend to be highly variable, the Beaufort Sea scale (see Robinson *et al.,* 2007) and visibility were used as guides to decide when observations should be carried out. If conditions were classified as three or above or visibility dropped below 1.5km, search efforts were deemed unfeasible and either suspended or aborted.

The day, month, time, survey type, latitude, longitude, sea state, swell and weather conditions were recorded throughout the survey. If at any point a minke whale was encountered, the total number of individuals was recorded along with the GPS location, depth and sea temperature at time of the survey. All data were later entered into a Microsoft excel spreadsheet.

2.3) Absence data

Data obtained from the CRRU were presence-only, however presence-absence datasets have a higher predictive ability (Macleod *et al.,* 2008). Absence data were generated in Microsoft Excel, using the presence of other cetacean species as pseudo-absences of minke whale. All non-minke whale sightings were assigned a random number using the Excel RAND function and records were sorted by year and random number. The first 300 values from each year were then used as the absence data set.

2.4) Environmental data

Oceanographic and bathymetry data for 2009-2013 were obtained from multiple online databases. The selection of variables used in the study was based upon the availability of data and the relevance of the variable to the purpose of the research. Sea surface temperature (SST), chlorophyll concentration (CHL), photosynthetic active radiation (PAR) and euphotic depth (ZEU) were attained from the Oceancolor Data website (Level-3 SMI-Standard Mapped Images, http://oceancolor.gsfc.nasa.gov) in HDF (hierarchal data format). Salinity (SAL) data were taken from the IRI/LDEO Climate Data Library website (http://iridl.ldeo.columbia.edu), NOAA-GODAS: Global Ocean Data Assimilation System in a GRIDASCII format. Bathymetry data including depth (DEP) were obtained from the GEBCO website (General Bathymetric Chart of the Oceans, http://www.gebco.net), in a GEBCO_08 gridded dataset in netCD (Network Common Data Form) Format. Bathymetry slope and aspect were calculated separately from the bathymetry data using ArcGIS tools.

Processing of satellite data was carried out in an ArcGIS Workstation environment. Different programming routines were developed in Arc Macro Language (AML) in order to convert HDF, GRIDASCII, and netCDF formats to ArcGIS grids. Then, a separate AML routine was developed to obtain the environmental satellite parameter values for each sighting point. Satellite data were interpolated to 1.4km at a resolution of 4km. A buffer of 2km was applied around each presence and absence point.

2.5) Data analysis

Exploratory data analysis was conducted to identify outliers and highlight any other potential issues that could reduce model performance (Zuur *et al.,* 2007). Inclusion of collinear explanatory variables can alter p-values, making it difficult to distinguish significant effects (Zuur e*t al.,* 2010). Pairplots were used to identify highly correlated explanatory variables. In the case of any variable pairs that gave a high Pearson's correlation coefficient ($r = >0.75$), only one could be used in models. Variance inflation factors (VIFs) were used as a measure of multiple collinearity. High VIF values indicate that the majority of variation shown by one variable can be explained by the set of other covariates. Among the variables shown to be highly correlated, that with the greatest VIF was dropped from further analyses. VIFs were then recalculated and the process repeated until all variables had VIF values of below 3.0 (Montgomery and Beck, 1992; Zuur *et al.,* 2010). Presence was then modelled as a function of the remaining environmental variables.

As the forms of the relationships with explanatory variables were unknown, generalised additive models (GAMs) were used. Since presence data comprised of just two values (1 and 0 respectively) binomial GAMs were used to model presence. Models were constructed using a forwards stepwise procedure (Akaike, 1973). Each explanatory variable was run against the response variable (presence) separately, selecting the most significant variable as the base for the second stage models, each of which contained the variable selected at step 1 and one other variable. This process was repeated until no further statistically significant variables could be added. The final model was that with the lowest Akaike information criterion (AIC), given that all of the explanatory variables retained were statistically significant and no clear patterns were apparent in the residual plots. To check whether the final model could be enhanced, I tested whether the AIC value was improved after adding any of the explanatory variables that had been excluded.

Based on niche theory and the range of conditions in the study area relative to the niche, most relationships between animal presence and environmental variables would be expected to be either monotonic or showing a single peak. Due to the tendency of GAMs to sometimes overfit, smoothers were constrained to a maximum k value of 4 (akin to 3 degrees of freedom). All models were fitted using BRODGAR 2.7.2 software (www.brodgar.com), a menu based R interface (used with R 3.0.2).

2.6) GIS analysis

Explanatory variables found to be significant by the GAM were plotted for visualisation by importing data into ArcGIS (vers. 10.0). Excel spreadsheets were first transformed into dbase (.dbf) files in Microsoft Access to allow for easier analysis. Environmental and sightings data were exported as shapefiles and imported as separate layers, set to the projected coordinate system WGS 1984 30_N. Data points were then displayed using the 'display xy data' function. Basemaps and bathymetric data were obtained from the Edina online database and set to the same coordinate system. Using the 'select by attributes' function, presence data for each year of the study period were exported as individual shape files and overlaid to a depth contours bathymetry map acquired from Edina.

To create a continuous raster image of environmental parameters, each shapefile was interpolated using the 'Kriging' tool in spatial analyst set to spherical with the default cell size applied by ESRI. Sightings data were then overlaid on the resulting raster image. Grids of latitude and longitude were applied to the map using the 'grids and graticules' function in the properties of the data frame. Symbology was adjusted accordingly to best represent the data shown.

2.7) Predictions

To test the predictive power of the hypotheses inferred by the model, predictions of minke occurrence were generated for each year using a version of the final model based on data from all the other years, and compared to the original presence data for the selected year. For this analysis, data for each year were removed from the complete data set and saved as a separate file in Microsoft Excel. The final model, based on data for all other years, was fitted using the 'gam' function in R, using the set of environmental variables previously shown to be retained in the final model. The relevant environmental data for the selected year were then used as the basis for predictions. Predictions of presence were generated using 'predict' function from the mgcv package v.3.0.1 in R. Results were then stored an exported as Excel spreadsheets.

Since binomial GAMs were used, with a logit link function, predicted data needed to be back-transformed prior to further analysis. Data were transformed using the equation for the inverse of a logit transformation:

$$\mathbf{EXP(n)/(1+EXP(n))}$$

The transformed data were then compared with the original presence data for each year using correlations and paired t-tests. If predicted and original minke occurrence for any one year were highly correlated ($r=>0.50$), the model for that year was supported. Similarly if results from the t-tests were insignificant ($p=>0.05$) it could be assumed that the differences between the two datasets were not statistically significant. However, little or no correlation ($r=<0.50$) or significant t-test results ($p=>0.05$) would indicate that the two datasets were statistically different and therefore that the model was relatively weak

3) Results

3.1) Distribution patterns

Across the 5-year study period, 234 surveys were carried out on 447 days. During this time, 114 minke whale encounters were recorded. The spatial distribution of these encounters is shown in figure 4. Distribution was relatively widespread along the Moray Firth coastline but, overall, the highest frequency of sightings was centred around 52º 92’ N, -2º 10’ W. Sightings appear to show a more concentrated distribution towards the coast, with larger groups of animals frequenting inshore areas. Contrastingly, the overall distribution of animals sighted offshore tended to be more widely spread (figure 4).

Distribution maps for each year show that annual minke distribution was highly variable (see figures 5 and 6). 2009 and 2010 had similar numbers of sightings (28 and 30 respectively) however distribution in 2010 can be observed shifting towards the west, slightly further offshore. During the years 2011 and 2012 the least minke whales were encountered (n=14). In 2012 animals were primarily located further offshore than in other years. In 2013, encounter rates were much higher and individuals progressed further offshore and to the west as the year advanced.

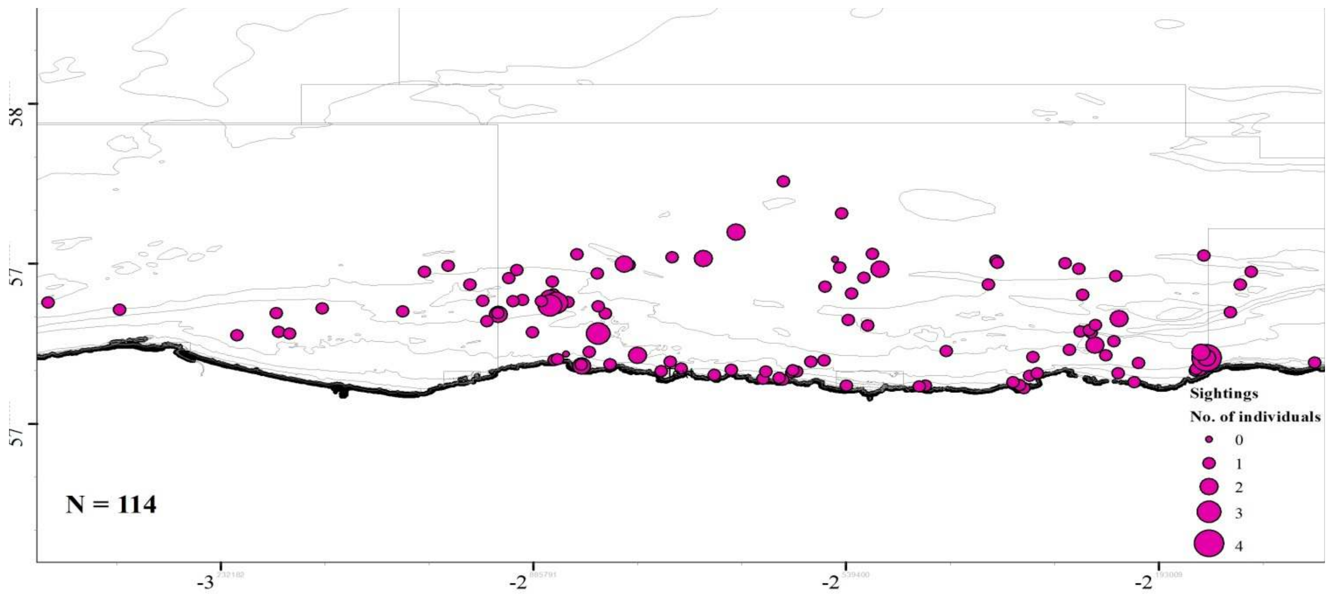


Figure 4: Sightings map of the southern outer Moray Firth, showing the spatial distribution of minke whales encountered across the 5-year study period from May to October 2009 to 2013 inclusive. Group sizes of whales (number of individuals) encountered are shown.

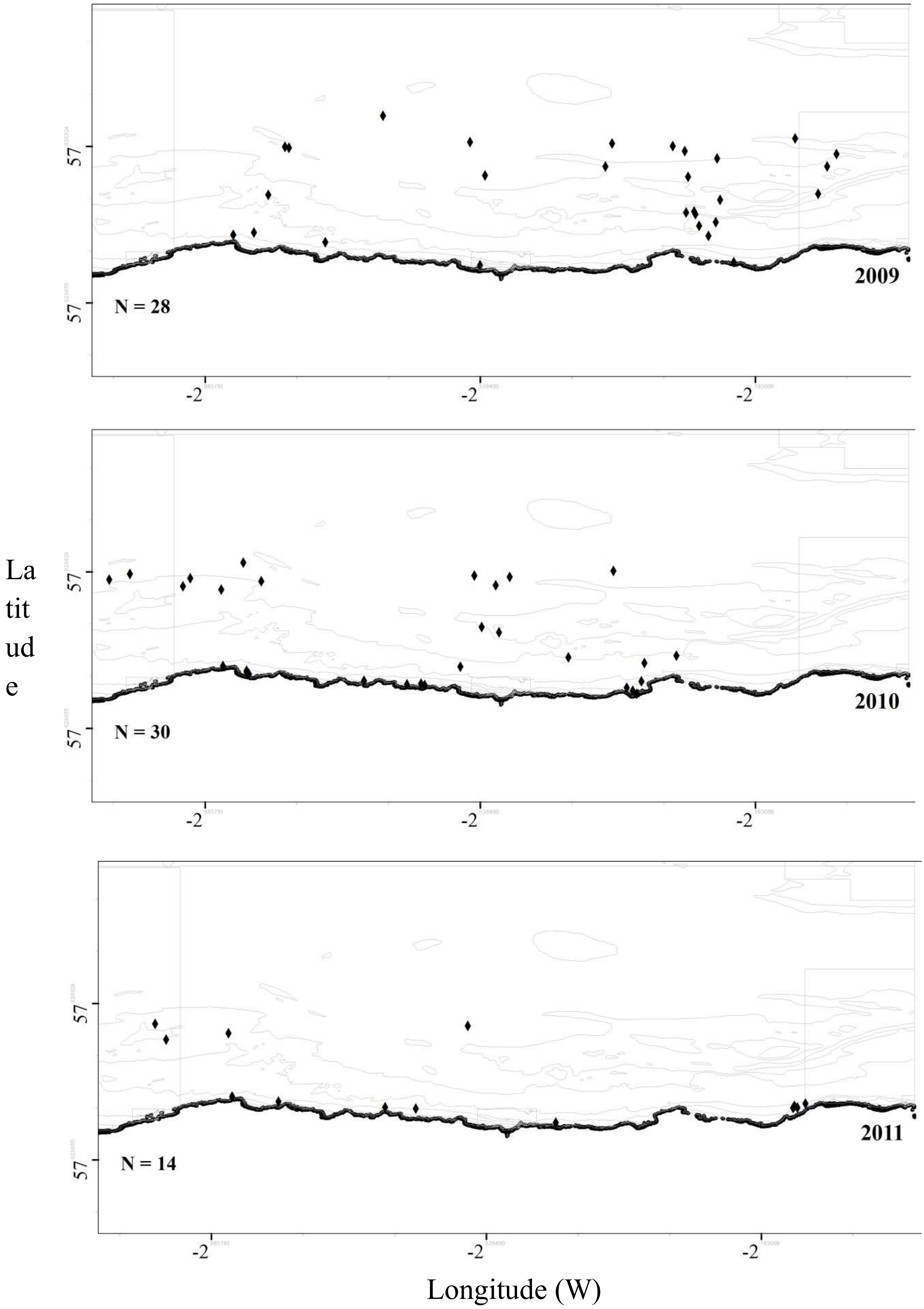


Figure 5: Sightings maps showing the annual distribution of minke whales recorded along the southern outer Moray Firth coastline for the years 2009, 2010 and 2011. Surveys carried out in the months between May to October. Depth contours shown.

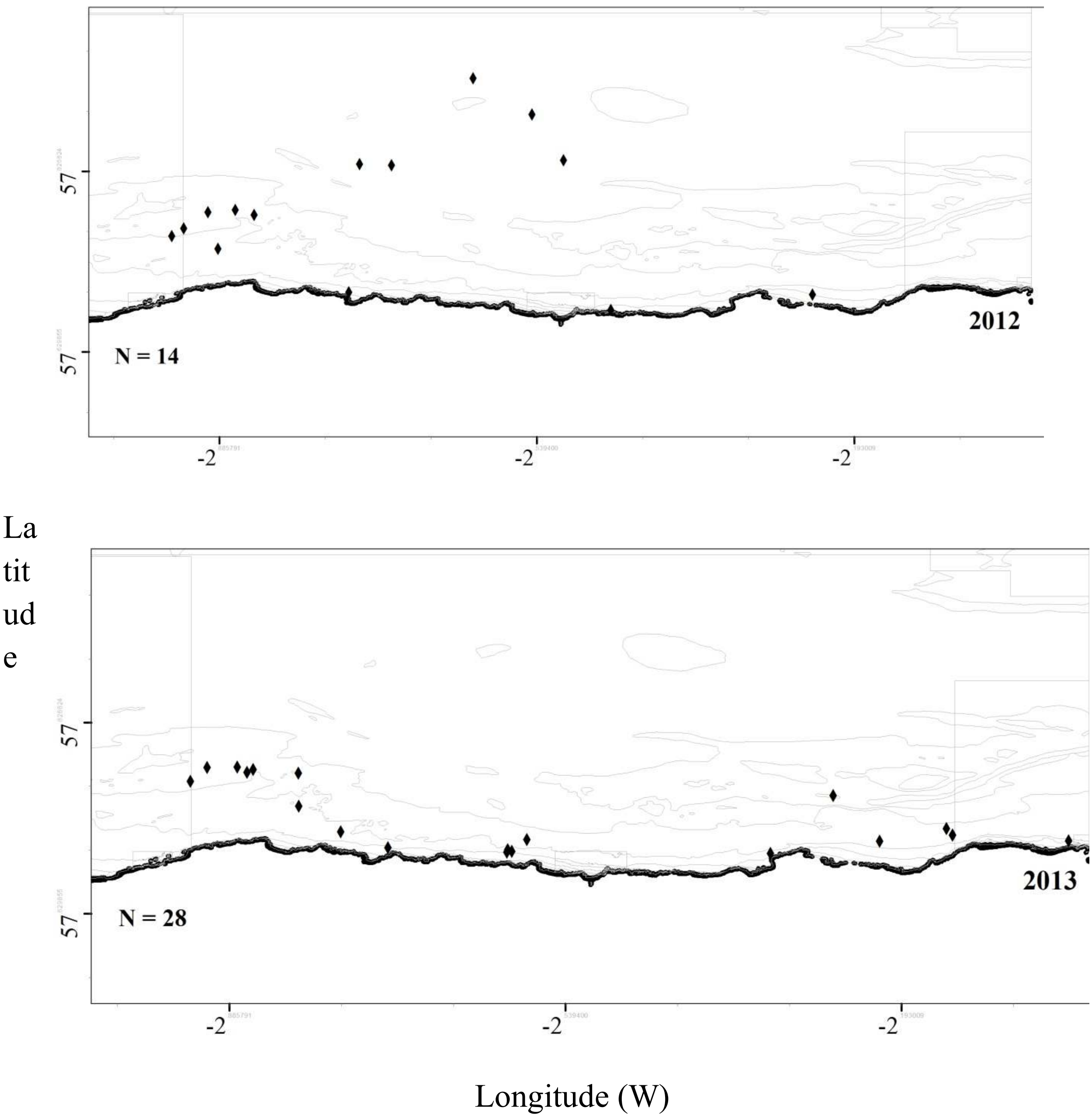


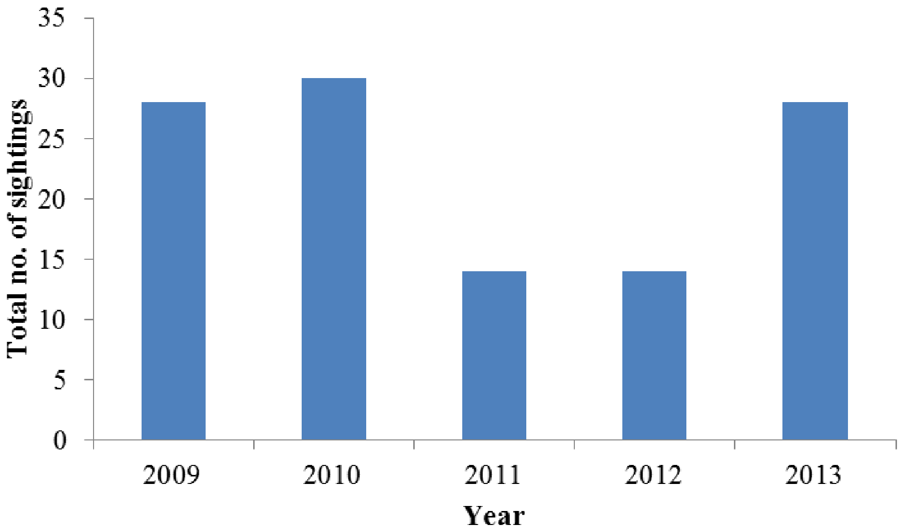
Figure 6: Sightings maps showing the annual distribution of minke whales recorded along the southern outer Moray Firth coastline for the years 2012 and 2013. Surveys carried out in the months between May to October. Depth contours shown.

3.2) Temporal trends in abundance and environmental conditions

Both minke abundance and environmental factors showed distinct temporal variation. Total sightings were also variable across all years in the study period. The lowest frequency of sightings occurred in 2011 and 2012, with 14 encounters recorded for both years. The year with the highest total of sightings was 2010 (30). 28 sightings were recorded for both 2009 and 2013 (see figure 7a).

Minke sightings were most frequent in June and July, decreasing throughout August and were lowest for May (figure 7b). A slight increase in sightings can be observed in September, before a decline in October. 40% of sightings occurred in July and 33.3% in June, whereas just 2.6% were sighted during May and October, although these findings may be influenced by low boat effort in these months.

a)



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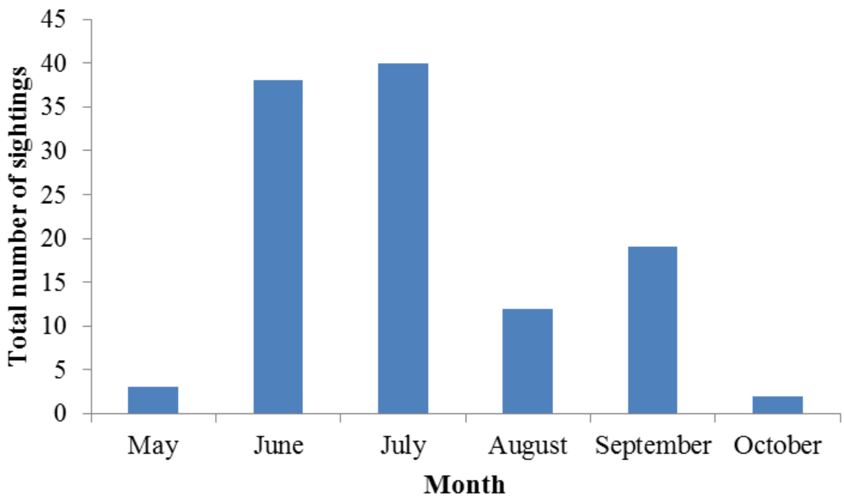


Figure 7: The total number of minke whale sightings recorded in each a) year and b) month. Totals for each month were caluclated as a sum of all records for that month across the study period. Calculated using presence data from line transect surveys of the southern outer Moray Firth from 2009-2013

As figures 8-10 indicate, levels of chlorophyll-*a*, photosynthetically active radiation and euphotic depth displayed temporal differences. Annual chlorophyll-*a* concentration was highest in 2009 (4.7mg/m^3), yet dropped substantially in 2010 and 2011 by approximately 3.1mg/m^3 (figure 8). Chlorophyll concentration then demonstrated a gradual increase during 2012 and 2013. Conversely, annual photosynthetically active radiation and euphotic depth were lowest in 2009 (31 E/m²/d and 29m, respectively) and peaked in 2013 (figure 9).

Chlorophyll-*a* peaked at 6.6 mg/m³ in May, and then demonstrated a steep decline throughout June to August (figure 10a). A second smaller peak in September (2.3mg/m³) can be observed. The opposite trend was shown in photosynthetically active radiation and euphotic depth; both variables were at their lowest levels in May (approx. 30.5 E/m²/d and 24.3m, respectively) and peaked in June, remaining at relatively high levels through to October (figure 10b).

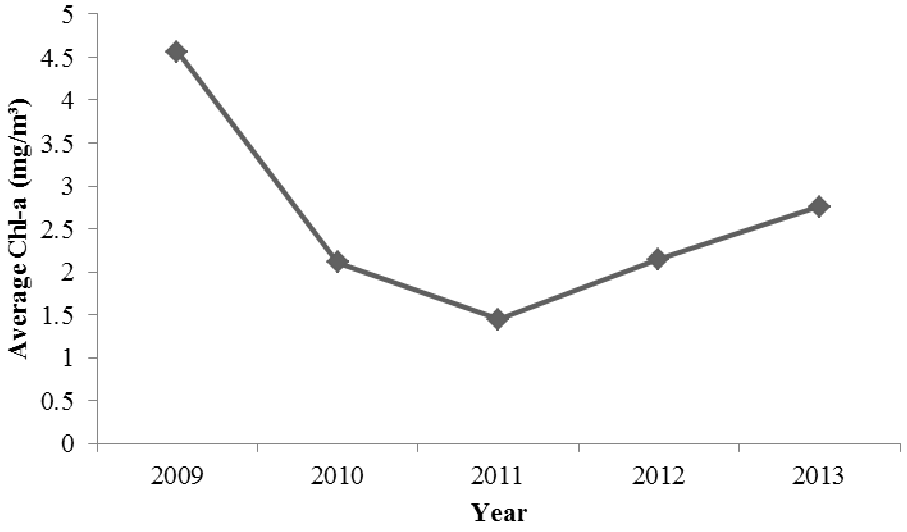


Figure 8: Average cholorophyll concentration (mg/m³) detected in surface waters of the southern outer Moray Firth for the years between 2009 to 2013. Data attained from the Oceancolor online database.

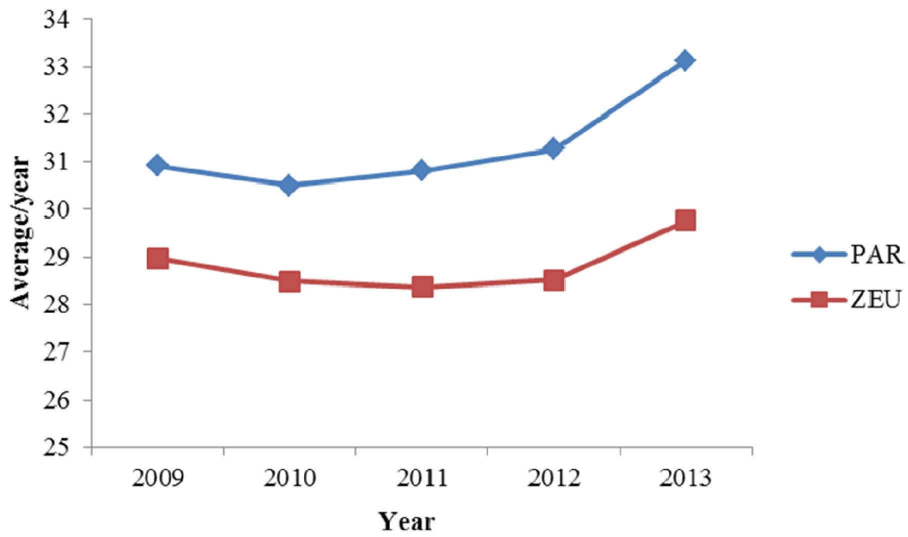
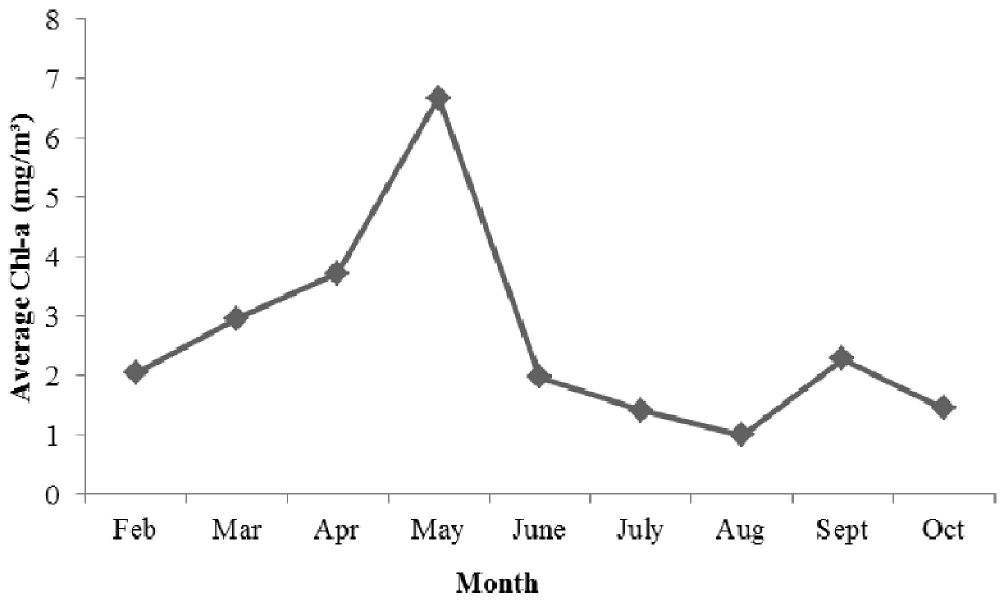


Figure 9: Average annual photosynthetically active radiation (E/m²/d) and euphotic depth (m) in the waters of the southern outer Moray Firth for the years between 2009 to 2013. Data for both parameters obtained from the Oceancolor online database.

a)



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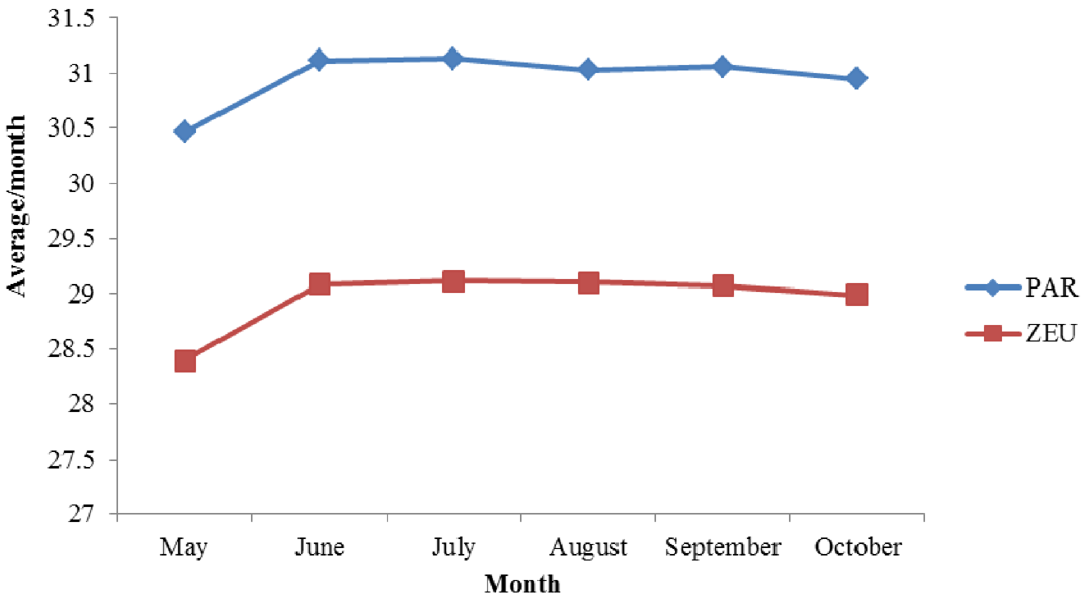


Figure 10: Monthly averages for a) chlorophyll concentration (mg/m³) and b) photosynthetically active radiation (E/m²/d) and euphotic depth (m). Data representative of the southern outer Moray Firth. Averages calculated from all data for each month across all years in the study period. Data for all parameters obtained from the Oceancolor online database.

Monthly averages from February to October demonstrate that chlorophyll concentration was greatest in May (see figure 11). This trend was consistent in all years, however May of 2009 showed the highest concentration of chlorophyll recorded within the study period (17mg/m³). July 2010 to March 2012 displayed relatively low levels of chlorophyll in comparison to other years. Minke whale sightings were most frequent in July 2009 and June 2013. The majority of years showed peaks in sightings in July, with the exception of 2011 which had the lowest overall encounter rate (see figure 12).

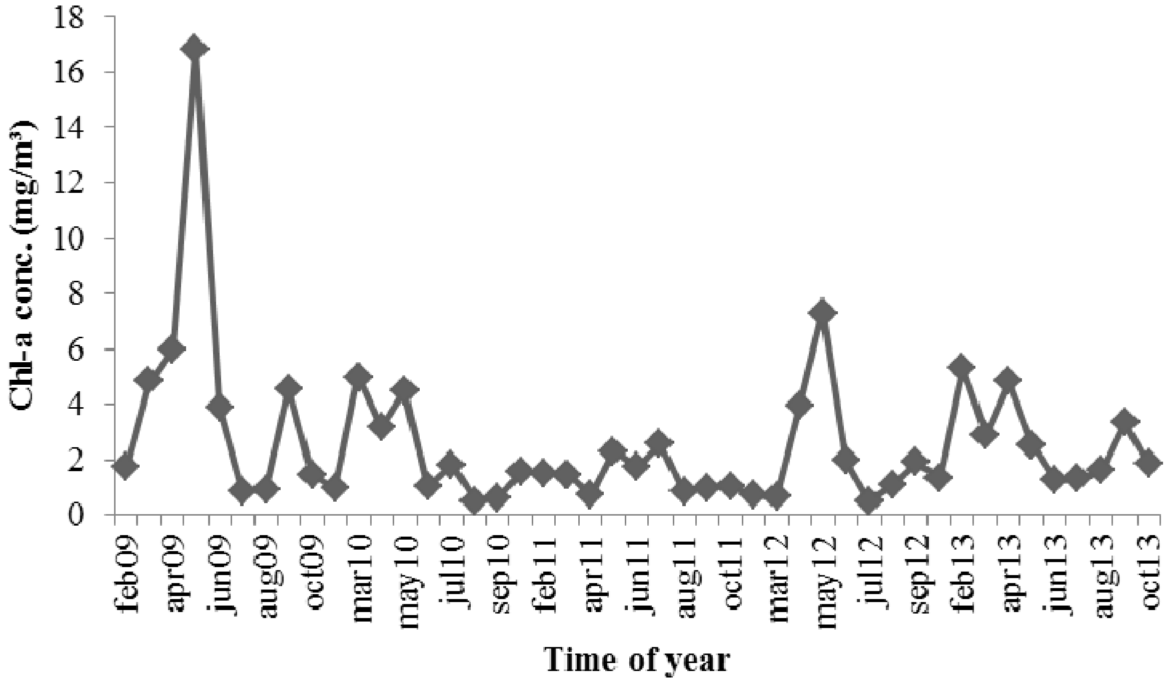


Figure 11: Monthly chlorophyll-a concentration (mg/m³) across the study period of 2009 to 2013 for the southern outer Moray Firth. Data obtained from the Oceancolor online database.

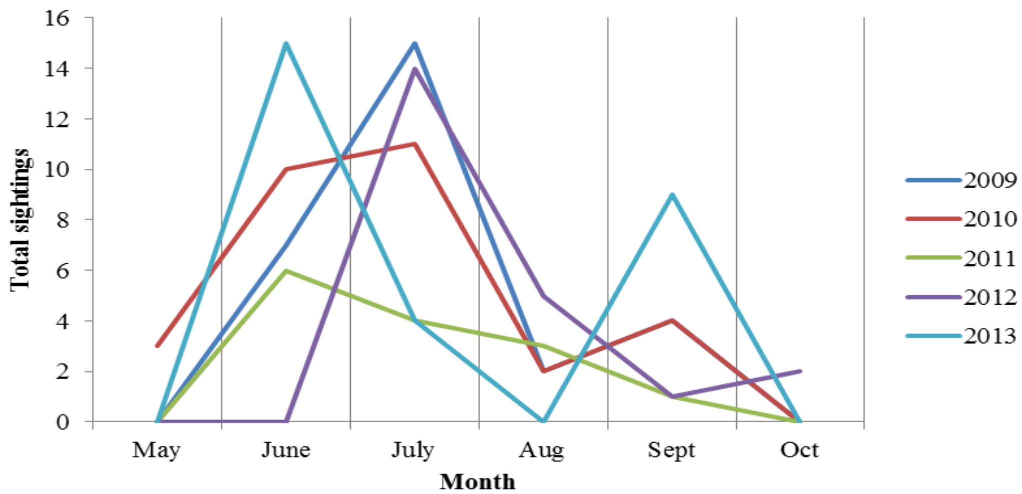


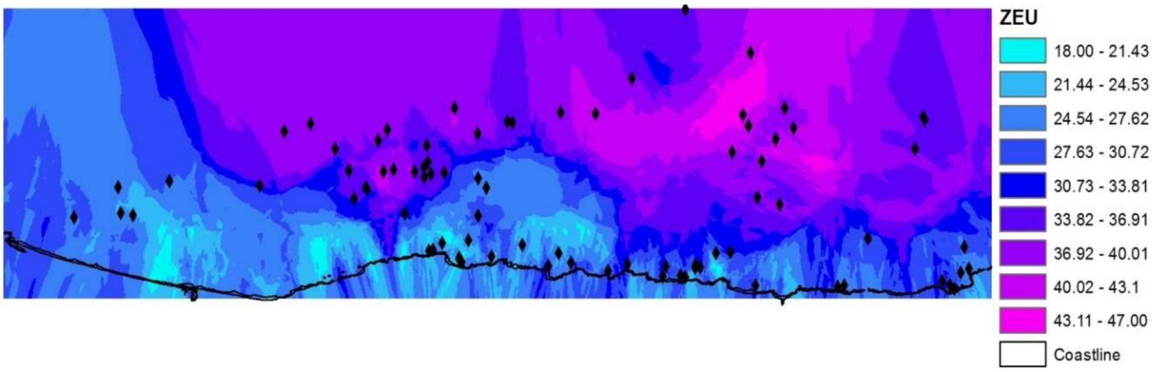
Figure 12: Total sightings recorded in the southern outer Moray Firth during the months May to June for all five years in the study period.

3.3) Minke distribution in relation to environmental parameters

GIS layouts for presence in relation to the environmental parameters found to be significant in the GAMs (see below) can be found in figures 13 and 14. Through the use of GIS it is possible to say that spatial distribution was not uniform; areas that harboured the greatest densities of minke whales were characterised by certain ranges of environmental variables. Whales preferred areas defined by euphotic depths of 33-37m, photosynthetically active radiation of 27-33 E/m²/d and 0.4-3mg/m³ chlorophyll-*a* concentration. Minkes were also most commonly sighted at sea depths of 30-40m (figure 14).

Spatial patterns of different parameters across the study site varied. Chlorophyll-*a* increased with increasing proximity to the coast, whereas photosynthetically active radiation and euphotic depth were greater with increasing distance from the coastline. Minke whale distribution appears to be more widespread further offshore, suggesting an inclination towards areas of higher photosynthetically active radiation and euphotic depths yet lower concentrations of chlorophyll-*a.*

a)



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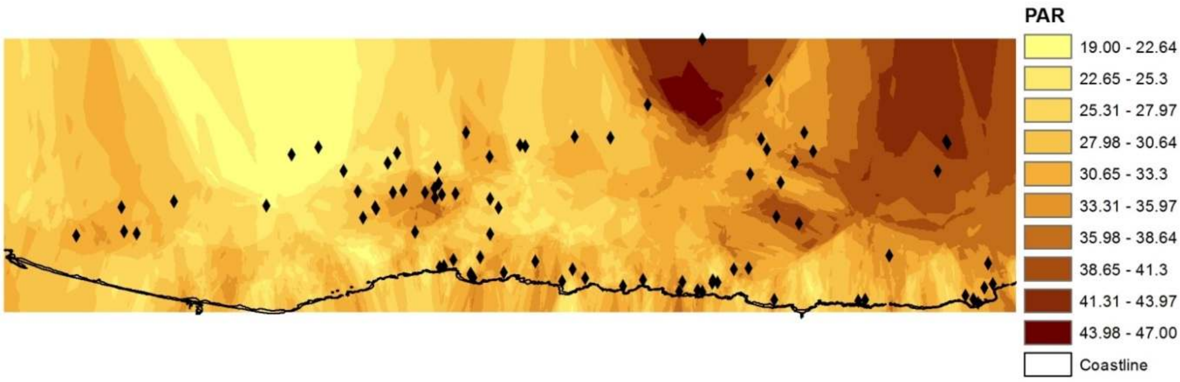

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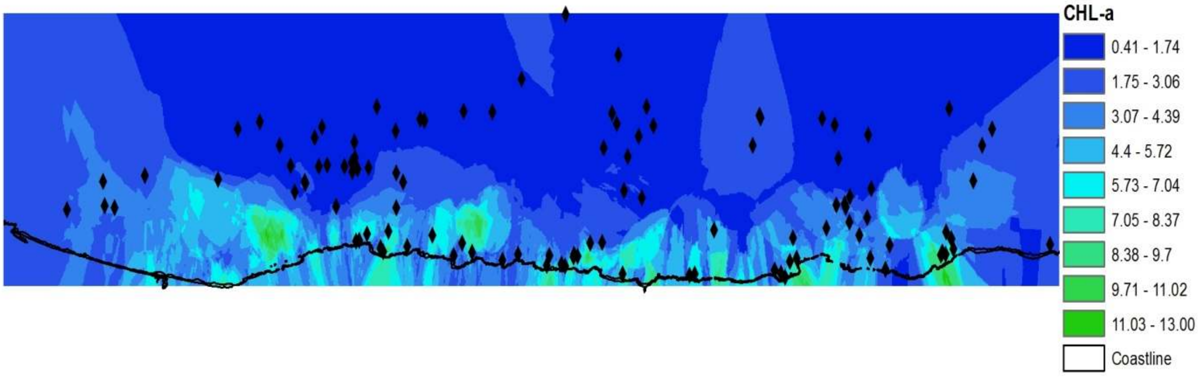

Figure 13: Minke distribution in relation to a) euphotic depth (ZEU), b) photosynthetically active radiation (PAR) and c) chlorophyll-a concentration (CHL). Data for sightings and environmental variables collected between 2009-2013 along the southern outer Moray Firth coastline. Maps created using ArcGIS.

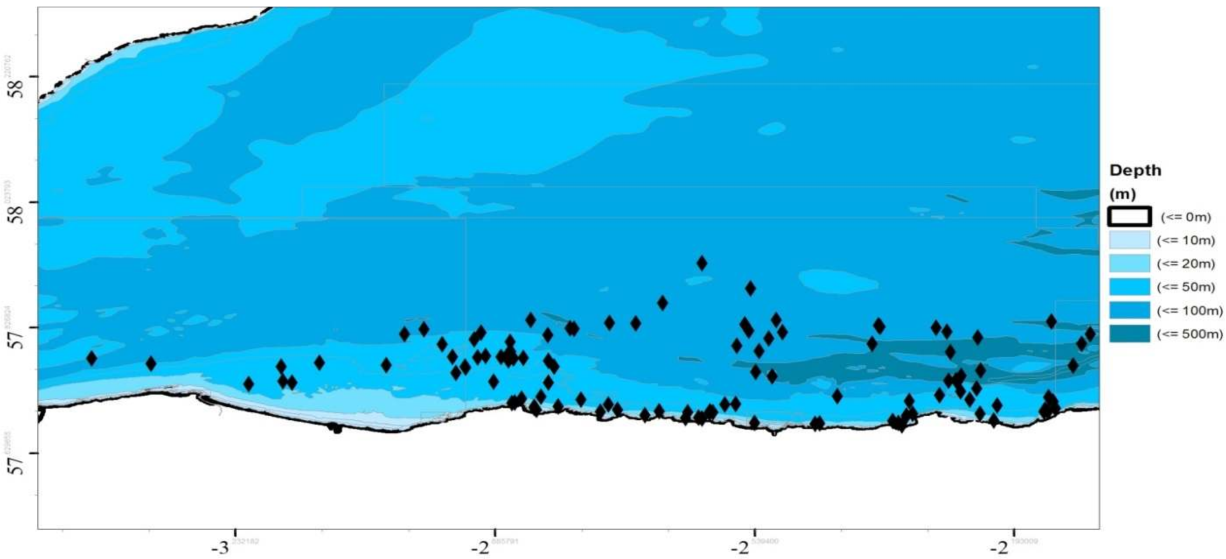

Figure 14: Minke distribution in relation to depth (m) in the southern outer Moray Firth across the years 2009-2013. Map created in ArcGIS (vers. 10).

3.4) Minke presence and environmental predictors

Generalized additive models for minke whale presence in relation to environmental parameters are summarized in table 1. The final environmental model for *B. acutorostrata* included 7 significant explanatory variables: photosynthetically active radiation, chlorophyll-*a* concentration, euphotic depth, depth, sea state and swell. The variables 'Month' and 'aspect_cos' were excluded from analysis after data exploration demonstrated strong co-linearity with other variables. Latitude and longitude were also excluded *a priori* from the analysis due to strong spatial correlation with other environmental variables. Effects of SST, day, year and salinity were not significant when run with the final model. Slope was significant (df = 1, p=<0.05), yet this model produced a higher AIC value (708.52) and was shown to make no real difference when both models were compared using an ANOVA (p=0.2528). The final model explained 19% of deviance (AIC = 707.88).

Relationships between explanatory variables and minke presence are demonstrated in figure 15. There was a clear tendency for the species to be sighted most frequently in areas where chlorophyll-*a* concentration is between 10-12 mg/m^3. Smoothing functions for both photosynthetically active radiation and euphotic depth displayed linear relationships with presence, with minke whale occurrence showing a positive relationship with both parameters. Depth was also significant; however the relationship shown is less clear in comparison to the other variables. Encounter rate seems to fluctuate between 140 to 40m, peaking between 30 and 40m. In shallower waters (above 25m) minke presence shows a steep decline. The results from the model also demonstrated significant effects of sea state and swells. Relatively moderate sea states (3) and swell (2 to 4) were shown to be significantly different from the base level (0), implying an association between presence and these levels.

Table 1: Results of the GAM demonstrating the relative significance of each environmental variable upon minke whale presence and absence in the Moray Firth. Variables are labelled as follows: CHL (Chlorophyll-a concentration), ZEU (euphotic depth), PAR (photosynthetically active radiation) and DEP (bathymetry depth). Significance levels of P-values are represented by: '.' = <0.05, '*'=<0.01, '**' = <0.001, '' = 0.0001. For categorical variables, significance refers to differences from the base level (0 in both cases).***

a) **Approximate significance of smooth terms:**

Variable	**Edf**	**Chi-sq**	**P-value**
CHL	3.726	30.908	2.29e-06 ***
ZEU	1.00	12.644	0.002210 **
PAR	1.00	9.367	<2e-16***
DEP	5.408	113.098	0.000377***

b) **Significance of parametric Coefficients:**

Variable	**Estimate**	**Standard error**	**P Value**
Sea state:			
1	-2.929e-01	1.865e-01	0.11635
2	-2.701e-01	2.084e-01	0.19506
3	-7.102e-01	2.658e-01	0.00754**
4	-1.339e+02	7.780e+06	0.99999
5	1.237e+00	1.085e+00	0.25414
Swell:			
1	-2.804e-01	3.986e-01	0.48179
2	-7.144e-01	4.091e-01	0.08077 .
3	-1.440e+00	4.508e-01	0.00140 **
4	-1.202e+00	5.718e-01	0.03548 *
5	-1.347e+02	1.370e+07	0.99999

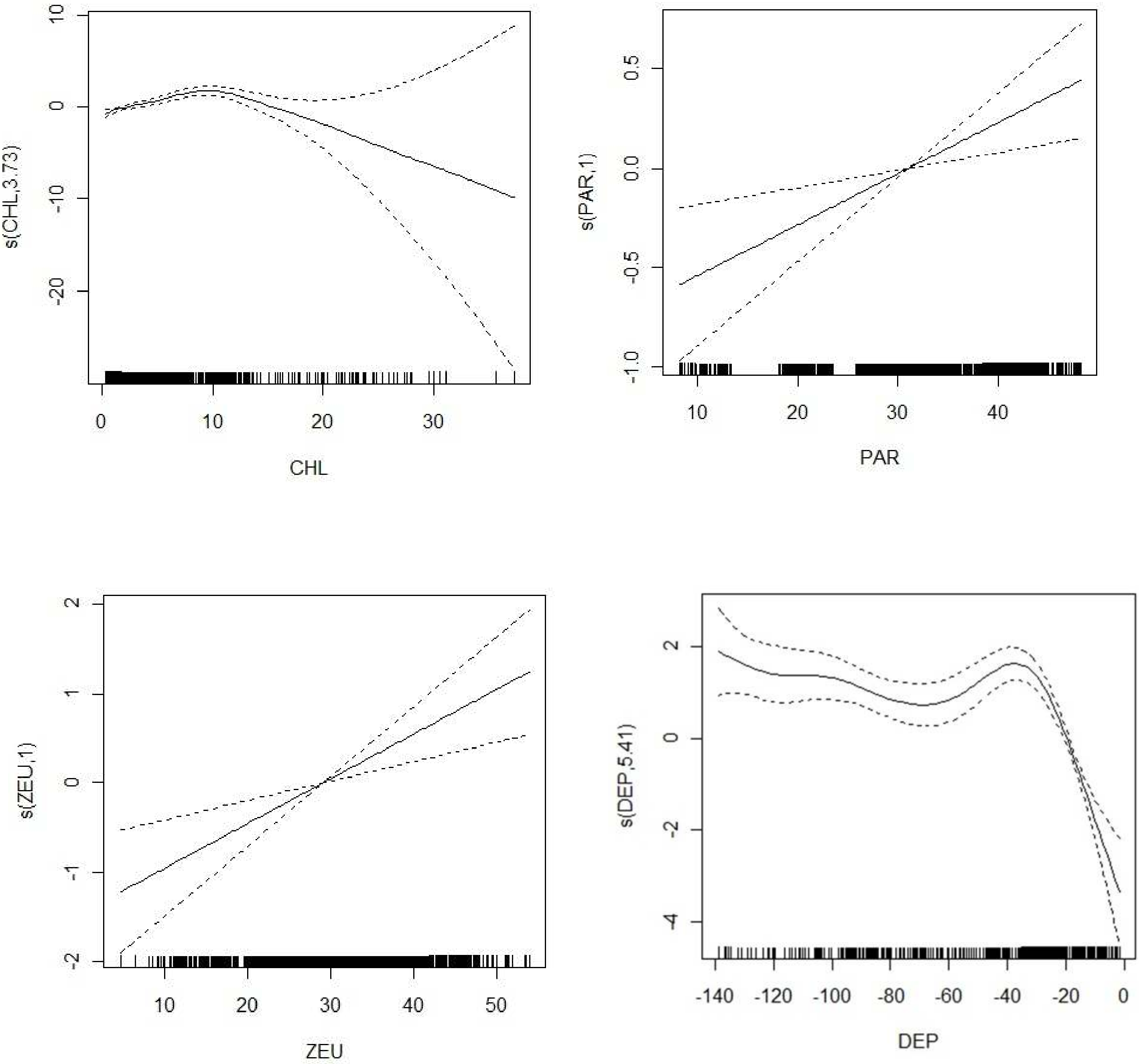

Figure 15: Fitted smoothing curves for partial effects (solid line) of explanatory variables and standard error bands (dashed lines) from GAMs fitted to whale occurrence. Plots show the marginal effect of each significant variable once effects of all other variables in the model have been taken into account: effects of chlorophyll concentration (CHL), photosynthetically active radiation (PAR), euphotic zone (ZEU) and depth on the presence of minke whales. Effects of sea state and swell were also accounted for. Units in the y axis correspond to the scaled fitted presences. Dashes along the X axis (the "rugplot") indicate the amount of data available.

3.5) Predictions

There were no strong correlations between predicted and original data for any year, implying that the model is not strongly supported (see table 2). Nevertheless all but one of the p-values from the t-tests were non-significant. The exception was 2011, for which the difference was small but significant. This indicates that whilst there is no obvious correlation, there are also no important differences between the observed and predicted data. Therefore the model is neither strongly supported nor opposed.

Table 2: Output of analysis on predictions of minke whale occurrence against original sightings data for each year. Pearson's correlation coefficient (r) shown for correlations. Values shown for both t-tests are p values.

Year	Correlation	Paired T-test	Unpaired T-test
2009	0.03	0.16	0.16
2010	0.202	0.10	0.12
2011	0.18	0.06	0.07
2012	0.09	0.41	0.41
2013	0.28	0.15	0.17

4) Discussion

The general aim of the present study was to ascertain whether there were any significant relationships between environmental predictors and minke whale distribution in the Moray Firth and to test whether these relationships were sufficiently consistent to be used to predict minke whale habitat. For the first time, minke habitat use in this area has been modelled using both physiographic and oceanographic parameters on a fine spatial scale. The analysis showed that minke presence varied spatially and temporally and was associated with a combination of variables: chlorophyll-*a*, photosynthetically active radiation, euphotic depth, sea depth, sea state and swell. It should be noted that the latter two variables may affect detection of minke whales by observers rather than affecting minke whales directly.

Models explained around 20% of deviance, an acceptable performance for ecological data (see Zuur et al. 2007), indicating the occurrence of significant spatiotemporal patterns in minke whale occurrence in the study area. Whilst predicted data did not correlate significantly with the observed data, differences between the two datasets were also not significant, thus predictions were neither strongly supported nor rejected. Good agreement between observed and predicted data would support the inference that the spatiotemporal patterns seen were based on direct or indirect causal relationships with environmental variables, which could thus be used to predict minke whale presence in future years or possibly in different locations. However, further work will be needed to develop a predictive model. The relatively small sample sizes may have been an issue, limiting the statistical power of the tests. It may be useful to introduce additional environmental variables and or investigate year-to-year changes the seasonal evolution of productivity in more detail. Minke whale presence reflects both the number of whales in the study area and their distribution; the former likely depend on cues occurring at a larger spatial scale or at least outwith the study area (see Visser et al 2011). Overall, however, the analysis lends an insight into minke whale habitat use in the Moray Firth.

4.1) Environmental variables associated with minke whale presence

4.1.1) Chlorophyll-a, photosynthetically active radiation and euphotic depth

Results indicate that minke whale distribution was strongly associated with photosynthetically active radiation, euphotic depth and chlorophyll-*a* concentration. Minkes, amongst many other cetaceans, are frequently found to exploit areas of high chlorophyll-*a* concentration (Kasamatsu *et al.,* 2000; Clark *et al.,* 2010; Anderwald *et al.,* 2012). Previously, Anderwald *et al.* (2012) found a significant correlation with minkes on the west coast of Scotland. Similarly, Pierce *et al.* (2010) demonstrated a preference in bottlenose dolphins for continental shelf areas in NW Spain with high levels of chlorophyll, presumably to support high levels of production and hence ultimately high abundances of blue whiting, a preferred prey source. Surface chlorophyll-*a* concentration is an indication of primary productivity, since it is present in phytoplankton (Dalpadado, 2006). Areas of heightened chlorophyll-*a* will subsequently be characterised by a greater biomass of phytoplankton, and thus larger concentrations of zooplankton. This, in turn, will attract predators, such as piscivorous fish, pinnipeds and cetaceans. However, whilst chlorophyll-*a* was a significant variable in the model, minke abundance was greatest at relatively low levels (10-12 mg/m^3) and appeared to drop at higher concentrations (see fig. 15). On a similar note, temporal patterns contrasted with the hypothesis suggested by Anderwald (2012) and others. Whilst month and year were not significant in the model itself (probably because temporal patterns are captured by the oceanographic variables), both seem to have an influence over minke distribution. Interestingly minke occurrence peaked in June and July, whereas chlorophyll-*a* concentration was highest in May, declining throughout the remaining months. A comparable pattern can be observed for annual abundance; sightings were more frequent in 2013, the year with the lowest concentration of chlorophyll. However, it is clear minke presence follows periods of high chlorophyll. Years that had high concentrations of chlorophyll in May were also characterised by a higher abundance of minkes in June or July (figures 11 and 12).

A number of studies have demonstrated similar time lags between amplified chlorophyll-*a* and cetacean presence. Many baleen whales - including blue and fin whales - display a time lag of up to several weeks following the spring phytoplankton bloom, to allow for zooplankton growth to reach a level suitable for feeding (Stafford *et al.,* 2009). Egg development and larval growth are initiated by the onset of the spring bloom, with high concentrations of phytoplankton providing ideal conditions for larvae (Tarling and Cuzin-roudy, 2003; Dalpadado, 2006). This growth period may take up to several weeks, during which chlorophyll-*a* stores are depleted by extensive photosynthesis (Longhurst, 2007). Consequently, baleen whale presence typically peaks three to four weeks following the bloom, when prey sources are of an optimal size. In the Azores, *B. acutorostrata* is commonly sighted in late summer when chlorophyll-*a* is lowest, following preferences for particular size classes of krill (Santora *et al.,* 2010; Visser *et al.,* 2011). It is more probable that in the Moray Firth, minke whale migration is timed appropriately to coincide with the point of productivity growth at which sandeels are nutritionally attractive. In concordance with the present findings, minkes in the Moray Firth are most frequent in the summer months (June to August), in synchrony with the emergence of juvenile sandeels into the water column (FRS, 2004; Robinson *et al.*, 2009; Anderwald *et al.,* 2011). The lesser sandeel constitutes 62-87% of minke diet (Pierce *et al*., 2004), reflected by a preference for areas consisting of sandy-gravel sediment types – optimal burrowing material for sandeels (Arnott and Ruxton, 2002; Robinson *et al.*, 2009). Hence, the study population responded to aggregations of sandeels following periods of high chlorophyll-*a,* not the bloom itself.

Conversely, minke abundance showed a distinctive positive correlation with both euphotic depth and photosynthetically active radiation. Photosynthetically active radiation relates to the amount of solar input to the system, and is directly related to rates of photosynthesis (Fritsen *et al.,* 2010). Increased radiation can have a 'cascading effect' upon the foodweb; more photosynthesis prompts higher quantities of phyto- and zooplankton, attracting organisms of higher trophic standing (Quentin *et al.,* 2007). Euphotic depth refers to the depth at which photosynthetically active radiation falls to 1% of its surface value, and is essentially a measure of water clarity (Lee *et al.,* 2007). The two are thereby tightly linked; the greater the extent of the euphotic depth, the more opportunity for photosynthesis. Sandeels will exploit areas of greater productivity to feast on phytoplankton in the summer (FRS, 2004). Hence, minkes in the Moray Firth apparently shift distribution according to areas of high productivity. Comparable studies on pygmy right whales *Caperea marginata* show similar patterns with "hotspots" of productivity, as groups follow abundances of mesoplankton (Matsuoka *et al.,* 2005; Kemper *et al.,* 2013). Present findings indicate equivalent synchrony between *B. acutorostrata* and productivity. The age class of the study population may also be a factor. The large majority of whales encountered in the study area are juveniles (Robinson, pers. comm.), which are probably less proficient at actively corralling prey. Instead, these animals likely take advantage of the ephemeral baitballs concentrated by predatory mackerel (Robinson and Tetley, 2007). In this respect, the number and abundance of mackerel are also thought to be indirectly significant to the availability of sandeel prey to young minkes and hence their respective annual occurrence along this coastline.

4.1.2) Depth

Minkes demonstrated a preference for relatively shallow water depths of 30-40m and appeared to frequent inshore areas. This is supported by findings from Robinson *et al.* (2009) from an earlier dataset, who also found increased whale abundances at depths between 20 to 50m. Coastal areas with shallow depths are characterised by higher productivity due to tidal mixing and the upwelling of nutrients into the euphotic zone (Robinson and Tetley, 2007; Kemper *et al.,* 2013). Minkes capitalise on the secondary productivity found along these depth thermocline upwellings. Juvenile *Ammodytes* require tidally active areas for oxygen transport within burrows, and prefer depths of 30-70m (Baumgartner, 2011). The utilisation of productivity-inducing bottom topography by baleen whales is well documented. In the St. Lawrence estuary, Canada, minkes are strongly associated with upwelling features associated with coastal topography (Lynas and Sylvestre, 1988). Similar behaviour has also been found in blue, fin and pygmy right whales (Kasamatsu *et al.,* 2000; Zanardelli *et al.,* 2003; Kemper *et al.,* 2013).

4.2) Feeding ecology

The fact that minkes are utilising areas of high productivity suggests a requirement for dense aggregations of prey. Habitat use typically reflects energy constraints (Mannocci *et al.,* 2014). Baleen whales need extensive amounts of prey in order to forage efficiently and thereby require areas of sufficient productivity (Friedlander *et al.,* 2006; Goldbogen *et al.,* 2011). Many feeding strategies echo this requirement. Minkes show evidence of both 'swallowing' and 'skimming' behaviours, although swallowing strategies are particularly common in UK waters (Hoelzel *et al.,* 1989; Gill, 1994). *B. acutorostrata* are designed for the consumption of substantial quantities of prey; specialised throat grooves allow maximum throat expansion whilst keratinous baleen plates act as filters (Woodward *et al.*, 2006). Behavioural studies have observed minkes aggregating prey towards the sea surface - either via bubble blowing or chasing – before an open mouth breach known as a lunge feed (Hoelzel *et al.,* 1989; Kuker *et al.,* 2005). On the same thread, minke whales are known to associate with foraging seabirds, exploiting groups of prey already aggregated. Such associations have been documented with gannets (*Morus bassanus*), kittiwakes (*Rissa iridactyla*), herring gull (*Larus argentatus*) razor bill (*Alea torda*) and guillemots (*Uria aalge*) (Wright and Begg, 1997; Garthe *et al.,* 2003; Robinson and Tetley, 2007). Manx shearwaters and minkes were found together in 34% of sightings in the Isle of Mull (Gill *et al.,* 2000). Top predators are commonly found to utilise different aspects of the same oceanographic feature, and therefore respond to the same prey aggregations (Scott *et al.,* 2010).

It is apparent minkes seek out areas of dense prey concentration, induced by a number of finescale oceanographic and bathymetric parameters. As mentioned earlier, juvenile minke whales are less efficient at aggregating prey themselves, and possibly take more of an advantage of such associations. Thus these behaviours could well have been operating during the current study.

4.3) Applications and implications for conservation

Studies such as this have highlighted the importance of understanding the complex interactions of marine mammals and their environments. Accurate fish abundance data are often lacking (certainly at the fine-scale relevant to predators), and therefore cannot be relied upon to predict cetacean distribution (Macleod *et al.,* 2004; Torres *et al.,* 2008). Our findings have demonstrated the strength of using both fine-scale oceanographic and physiographic variables as predictors of movements and presence for these coastal whales. By combining environmental parameters with data regarding species presence, it is possible to detect patterns even in the absence of previous information.

A deeper understanding of the dynamic environmental variables influencing species distribution is now recognised as a priority in the establishment of MPAs (Clark *et al.,* 2010). Previously MPA designations have been based upon stationary variables such as bathymetry and sediment type, leading to the fixation of MPA boundaries (e.g. Naud *et al.,* 2003; Yen *et al.,* 2004). However, this practice is unrealistic for highly mobile species. Recent shifts in the habitat use of the resident bottlenose dolphin population have raised concerns regarding the effectiveness of the current boundaries of the Moray Firth SAC (Clark *et al.,* 2010). MPAs need to allow for seasonal and temporal variations in species distribution by incorporating non-fixed ecological variables into site designation (Dalla-rosa *et al.,* 2012). Studying the fine-scale parameters that underlie these movements will help to develop protective boundaries that alter with season and the known distribution of prey. For example, Embling *et al.* (2010) used both bathymetric and hydrographic variables to build GAMs that identified suitable protected areas for the harbour porpoise around the Scottish western isles. This study has demonstrated that the same techniques can be applied for *B. acutorostrata,* and suggests the importance of the southern outer region for the species. Robinson *et al.,* (2007) also advocate the incorporation of broader scale research efforts in the management of the Moray Firth region.

The minke whale comprises an integral part of the marine ecosystem, acting as an important indicator species. Like all cetaceans, minkes are vulnerable to anthropogenic activities resulting in habitat loss and environmental degradation (Parsons *et al*., 2000; Gill *et al*., 2001), which have gained growing attention from a range of statutory bodies and NGOs including the likes of ASCOBANS, ACCOBAMS, Whale and Dolphin Conservation (WDC), and the International Whaling Commission (IWC). A particular problem in Scotland is entanglement of minkes in fishing lines; both stranded individuals and photo ID records exhibit evidence of rope-related injuries (Coram *et al.,* 2010). Additionally, the frequency range of pile driving noise (mid-low) is also in the range utilised by minke whales, possibly leading to behavioural disturbances and displacement (Bailey *et al.,* 2010). Given the increasing practice of renewable energy generation, this may become a serious issue in the Moray Firth and equivalent coastal areas.

Furthermore, combining sightings data with oceanographic information enables the production of predictive habitat maps (e.g. Hamazaki, 2002). In light of climate change, this will inevitably be a vital tool when planning future measures for UK cetacean species. The complex relationships between predators and prey will certainly be affected by the continued warming of our seas. In the North Sea, zooplankton distribution has already demonstrated a northward shift (Beaugrand *et al.,* 2010) and changes in the biodiversity of neritic cetacean species has been noted (Robinson & MacLeod, 2009; Robinson *et al.,* 2010). As this study shows, minkes and other cetaceans are highly responsive to the movements of prey. Further range shifts have been predicted for many species, as they attempt to remain within their respective thermal niche (Simmonds and Elliot, 2008; Lambert *et al.,* 2011, 2014). In the UK, numbers of baleen whales are expected to increase as more individuals over-winter in British waters (Hammond *et al.*, 2013). However, stratification of surface waters due to warming limits primary productivity by blocking the nutrients required for phytoplankton growth (Behrenfeld *et al.,* 2006). This was also suggested as the cause of recent failures in sandeel recruitment in the North Sea and, given the dependency of minke whales upon such fish, will possibly have had a significant impact upon current minke distribution and abundance (Arnott and Ruxton, 2002; Van deurs *et al.,* 2009). As such, the monitoring of *B. acutorostrata* and the parameters linked to its distribution is essential for successful conservation of the species.

4.4) Limitations

It has been acknowledged that the outcomes and interpretations of the present study may be hindered by several limitations. Arguably one of the greatest is the nature of the focal species. Minke whales – akin to most cetaceans - are notoriously difficult to detect and track, since they spend the majority of their lives beneath the ocean surface. Records of presence can only be obtained during surfacing events, limiting accuracy to the skill of the observer. Similarly, the encounter rates used herein are cumulative and cannot account for repeated sightings of the same individuals, although recaptures of distinctive "marked" adults are evidently few and far between in this region (Robinson, pers. comm.; Robinson *et al*., 2007).

False absences are also an obvious issue with any species that exhibits diving behaviour. Individuals that were present at the time of survey but did not surface may have remained undetected. Whilst mis-detections are inevitably unavoidable, they were accounted for by the random generation of absence data.

Further errors may have arisen from survey effort during sampling. Variable weather conditions offshore often restricted survey efforts to inner routes where conditions were more favourable. Although every effort was made to ensure outer routes were used as much as possible, this could still create perception bias (e.g. Pollock *et al.,* 2002). It may therefore be argued that the area sampled was not fully representative of the southern outer Firth. Equally, as minkes are a cosmopolitan species, it cannot be said that this association is apparent in other sites within their range. Being widely distributed and opportunistic feeders, the species experiences a broad variety of habitats and prey species. As a result strategies and behaviours may differ with region, so that it may not be possible to generalise predictions of minke habitat use across large areas. Nevertheless the methods used in this project can be applied to other areas, to gain a more broad-scale idea of minke distribution.

Studies akin to this can almost always be improved by increasing survey effort. Adding survey routes further offshore and assigning a higher priority to them will reduce sampling bias by levelling out the effort awarded to all areas within the firth. Similarly, research could be expanded to incorporate locations other than the firth. By doing so, we would be able to determine whether the same variables found to be significant in this study apply to other locations in the minke range. Comparisons could also be made between different areas, helping to inform management plans for *B. acutorostrata* on a larger scale.

5) Conclusions

The findings from this study suggest that minke whale distribution in the Moray Firth is related to the location of aggregations of suitable prey, predicted by the environmental variables underlying these groupings. Whilst previous studies on minke whales in the area have shown associations with bathymetric parameters such as depth and sediment type, this research has demonstrated for the first time a strong link with fine scale oceanographic and physiographic characters. It has been suggested that variables such as this are reliable predictors of species occurrence and that they are indeed better predictors than actual fish distribution data. The present study also highlights the spatial and temporal variation apparent in these parameters and therefore in the presence of *B.acutorostrata*. To ensure efficient conservation of marine ecosystems, it is vital that such variation is taken into account during the establishment of MPAs which should, ideally, have flexible boundaries. The methods used in this study are applicable globally, to a wide range of species, and represent an important tool for future management of our marine fauna.

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8) Appendices

Appendix A. Explanations of abbreviations used to describe units of Chlorophyll concentration, euphotic depth and photosynthetically active radiation.

Variable	Abbreviation	Units
Chlorophyll concentration	mg/m^3	Milligram per cubic metre
Euphotic depth	m	Metres
Photosynthetically active radiation	$E/m^2/d$	Einstein per square metre per day

Appendix B. Scale used to estimate sea state.

Sea state	Description
1	Slight
2	Moderate
3	Rough
4	Very rough

Appendix C. Scale used to estimate wave swell.

Swell	Description
Low	
1	Short/average
2	Long
Moderate	
3	Short
4	Average
5	Long
Heavy	
6	Short
7	Average
8	Long
9	Confused