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Title	Distribution, abundance and habitat use of deep diving cetaceans in the North-East Atlantic
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Publication date	2017-04-07
Original Citation	Rogan, E., Cañadas, A., Macleod, K., Santos, M. B., Mikkelsen, B., Uriarte, A., Van Canneyt, O., Vázquez, J. A. and Hammond, P. S. (2017) 'Distribution, abundance and habitat use of deep diving cetaceans in the North-East Atlantic', Deep Sea Research Part II: Topical Studies in Oceanography, 141, pp. 8-19. doi:10.1016/j.dsr2.2017.03.015
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1016/j.dsr2.2017.03.015
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Download date	2026-11-04 21:52:58
Item downloaded from	https://hdl.handle.net/10468/4064

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PII: S0967-0645(17)30091-7
DOI: http://dx.doi.org/10.1016/j.dsr2.2017.03.015
Reference: DSRII4219

To appear in: *Deep-Sea Research Part II*

Cite this article as: Emer Rogan, Ana Cañadas, Kelly Macleod, M. Begoña Santos, Bjarni Mikkelsen, Ainhize Uriarte, Olivier Van Canneyt, José Antonio Vázquez and Philip S. Hammond, Distribution, abundance and habitat use of deep diving cetaceans in the North-East Atlantic, *Deep-Sea Research Part II*, http://dx.doi.org/10.1016/j.dsr2.2017.03.015

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Distribution, abundance and habitat use of deep diving cetaceans in the North-East Atlantic

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ABSTRACT
In spite of their oceanic habitat, deep diving cetacean species have been found to be affected by anthropogenic activities, with potential population impacts of high intensity sounds generated by naval research and oil prospecting receiving the most attention. Improving the knowledge of the distribution and abundance of this poorly known group is an essential prerequisite to inform mitigation strategies seeking to minimize their spatial and temporal overlap with human activities. We provide for the first time abundance estimates for five deep diving cetacean species (sperm whale, long-finned pilot whale, northern bottlenose whale, Cuvier's beaked whale and Sowerby's beaked whale) using data from three dedicated cetacean sighting surveys that covered the oceanic and shelf waters of the North-East Atlantic. Density surface modelling was used to obtain model-based estimates of abundance and to explore the physical and biological characteristics of the habitat used by these species. Distribution of all species was found to be significantly related to depth, distance from the 2000m depth contour, the contour index (a measure of variability in the seabed) and sea surface temperature. Predicted distribution maps also suggest that there is little spatial overlap between these species. Our results represent the best abundance estimates for deep-diving whales in the North-East Atlantic, predict areas of high density during summer and constitute important baseline information to guide future risk assessments of human activities on these species, evaluate potential spatial and temporal trends and inform EU Directives and future conservation efforts.

Keywords: design-based abundance, model-based abundance, beaked whales, sperm whales, pilot whales, distribution, deep divers, habitat models

1. Introduction

Effective marine mammal conservation and management requires information on the abundance and distribution of species. Reliable abundance estimates are a crucial prerequisite to assess the impact that accidental or deliberate removals have on a population (Wade, 1998) or to evaluate

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its status and trends (Reeves et al., 2000). Quantifying abundance and distribution can be very challenging for cryptic and highly mobile species, especially over large spatial, and often, transnational scales. Understanding the relationship between species and habitat can help improve population estimates and can also help in the identification of marine protected areas (Cañadas et al., 2005; Mannocci et al., 2014; Forney et al., 2015; Breen et al., 2016; Becker et al., 2016).

Beaked whales (family Ziphiidae) are among the most diverse but least known marine mammals, with little information available on their distribution, ecology and population structure. Their oceanic habitat and a behaviour often consisting of long, deep dives followed by short surface intervals (e.g. Johnston et al., 2004, 2006; Aguilar de Soto et al., 2006, Tyack et al., 2006) have made these species very difficult to study. Other deep diving species include sperm whales (*Physeter macrocephalus*) and long-finned pilot whales (*Globicephala melas*). Despite a long history of commercial exploitation of sperm whales and northern bottlenose whales(*Hyperoodon ampullatus*) (whaling spanned several centuries), and an ongoing annual subsistence hunt (the *grindadráp*) of several hundred pilot whales in the Faroe Islands (Hoydal and Lastein, 1993; Fielding, 2010), little current information is available on the abundance of these species in the North-East Atlantic. With the exception of Cuvier's beaked whale (*Ziphius cavirostris*) which is listed as *least concern,* beaked whales and long-finned pilot whales are listed globally as *Data Deficient* and in the Atlantic, sperm whales are listed as *Vulnerable* under the IUCN Red List (IUCN, 2010).

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Globally, deep diving cetaceans are exposed to a wide variety of anthropogenic threats, including noise, ship strikes, contaminants, prey depletion, and entanglement in fishing gear (e.g. Whitehead, 2003; Aguilar de Soto et al., 2006; Read et al., 2006; Nowacek et al., 2007; Tyack, 2008; Jensen et al., 2009). An increase in ocean noise is of particular concern for these

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species. Beaked whales appear to be especially sensitive to mid-frequency sonar (Tyack et al., 2011; Miller et al., 2015), and a number of beaked whale mass stranding and multiple stranding events have occurred coincident with naval exercises (e.g. Simmonds and Lopez, 1991; Jepson et al., 2003; Fernandez et al., 2005; Cox et al., 2006). In addition, noise associated with seismic activity, hydrocarbon exploration and geophysical research is increasing both spatially and temporally, occurring in deeper waters and in most months of the year (Nowacek et al., 2015).

The European Union (EU) includes ocean noise (amongst other stressors) as an indicator of environmental quality under the Marine Strategy Framework Directive (MSFD, EU-COM, 2008) and is in the process of developing targets for achieving "good environmental status" for ocean noise and acute noise-producing activities. However, a poor understanding of beaked whale ecology has made assessing the potential risk of anthropogenic activity difficult (Hazen et al., 2011; Moore and Barlow, 2013); in particular, information on abundance and distribution of deep diving cetaceans in the North-East Atlantic is lacking.

All cetacean species are listed under Annex IV of the EU Habitats Directive (EU-COM, 1992), Article 12 of which obliges Member States to take measures to "establish and implement an effective system of strict protection". Subsequent guidelines on interpreting Article 12 of the Directive suggest that an adequate system of strict protection for Annex IV species consists of a "set of coherent and co-ordinated measures of a preventive nature" and that measures must "contribute to the aim of maintaining the species in the long term or restoring its population in its habitat." (Anon, 2007). Understanding abundance, distribution and habitat use can therefore be considered as core elements of the EU Habitats Directive. In addition, examining the spatial and temporal overlap between anthropogenic stressors, such as ocean noise, for example, and beaked whale distribution and habitat use should help with the implementation of the MSFD. More generally, this approach would also help in developing effective planning strategies for managing environmental risk associated with geophysical surveys, for example.

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In recent decades, large scale multinational surveys have collected data on the distribution and abundance of cetaceans in offshore and shelf waters of the North-East Atlantic in summer (SCANS, Hammond et al., 2002; SCANS-II; Hammond et al., 2013; CODA, CODA(2009); and NASS/T-NASS, Lockyer and Pike, 2007; Pike et al., 2008). These surveys used methodology specially designed to deal with failure to detect animals on the transect line (a particular problem for some deep diving species, Whitehead, 2002; Barlow and Taylor, 2005).

Here we analyse the combined data from SCANS-II, CODA and the Faroese block of T-NASS to generate design-based estimates of summer abundance of long-finned pilot whales (hereafter referred to as pilot whales), sperm whales and beaked whale species in waters of the North-East Atlantic. In addition, we fit models that estimate density as a function of relevant environmental variables to determine which of those variables most influenced abundance, to predict spatial distribution, to investigate habitat use and to generate model-based estimates of abundance. The results can be used to inform the conservation of these species and management of the human activities that impact them.

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2 Methods

2.1 Study area & survey data

The study area covered 3 023 280 km^2 in the North-East Atlantic; a vast area with complex hydrography (e.g. Pingree and Garcia-Soto, 2014; Marzocchi et al., 2015) and characterized by heterogeneous habitats, including continental shelf areas of varying extent, steep continental slopes and deep canyon systems. Productivity is also variable, with nutrient rich deep water brought to the surface in specific areas, such as off Galicia (NW Spain, Bode et al., 2009) and west of Ireland (Raine et al., 1990).

The Small Cetaceans in the European Atlantic and North Sea project (SCANS-II) surveyed the continental shelf waters of the North-East Atlantic in July 2005 using a combination of ships and

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aircraft (Hammond et al., 2013). The Cetacean Offshore Distribution and Abundance in the European Atlantic project (CODA) covered offshore waters off the Atlantic coasts of Spain, France, Ireland and Scotland by ship in July 2007(CODA, 2009). The Trans North Atlantic Sightings Survey (T-NASS) was also conducted by ship in July 2007 and covered large areas of the North Atlantic (Pike et al., 2008). The Faroese block of this survey was contiguous with the western and northern boundary of CODA (Fig. 1, Table 1, Supplementary Figure D).

All shipboard surveys were conducted using the same double platform line transect methods (detailed in Hammond et al., 2013). Two teams of experienced observers (referred to here as Primary observers and Trackers) were located on each survey vessel in a 'trial configuration' (Laake and Borchers, 2004) to collect data that could be used to account for animals missed on the transect line and potentially for any responsive movement. Sightings were identified to species level where possible. In some cases, identification was to a broader taxonomic level, such as unidentified large whale or unidentified beaked whale. Low, best and high estimates of group size were made (best estimates were used in analysis).

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2.2 Data processing

All on-effort transects were divided into segments with homogeneous sighting conditions. For all data combined, this gave a total of 8169 segments ranging from 0.1 to 17.6 km (mean = 5.84km, sd = 3.41km), totalling 47 225km on effort (Table 1).

2.3. Analytical methods

2.3.1. Estimation of detection functions

Detection functions were estimated for pilot whales, sperm whales, unidentified large whales (to allow sperm whale abundance to be adjusted to take account of unidentified sightings), and all beaked whales combined, using DISTANCE 6.0 software (Thomas et al., 2010). Data were

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truncated at a perpendicular distance from the transect line that balanced removing distant observations to improve model fit and retaining as much data as possible (Buckland et al., 2001).

For pilot whales and large whales, sample sizes were sufficient to fit Mark-Recapture Distance Sampling (MRDS) models to the double platform data (Laake and Borchers, 2004). As no evidence of responsive movement was found for any of these species, point independence mark-recapture models were used. For sperm whales and beaked whales there were insufficient duplicate sightings to carry out a double platform analysis, so Conventional Distance Sampling (CDS) models were used. Abundance for these latter species is therefore under-estimated to an unknown extent. Covariates available for fitting the detection functions are given in the Supplemental Appendix Table B. These included factors such as sightability, swell height, sea state (Beaufort scale), vessel and cue. Continuous variables included the height of the observer on the primary platform and group size.

The best functional form of the detection function (Half Normal or Hazard Rate model) and the covariates retained by the best fitting models for the detection functions were chosen based on standard model fitting diagnostics (AIC, goodness of fit tests, Q-Q plots, inspection of plots of fitted functions).

2.3.2. Estimating design-based abundance

Design-based estimates of abundance were generated using DISTANCE software. Estimates were calculated for sperm whales, pilot whales, unidentified large whales and all large whales and all beaked whales combined and for each species of beaked whale separately (including those unidentified to species), using the combined beaked whale detection function. As there was a slight overlap (3.5%) in the SCANS-II and CODA survey areas, all estimates from these surveys were corrected by dividing by 1.035.

Forty percent of the sightings of beaked whales were unidentified to species, so estimates for each identified species were also adjusted (by survey block) to include a proportion of unidentified beaked whale abundance, prorated according to the number of sightings:

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$$N_{adj} = N_{id} + p_{id} N_{unid}$$

where N_{id} is the abundance estimate from sightings identified to a given species in each block, N_{unid} is the estimate of abundance of unidentified beaked whales in each block and $P_{id}$is the number of sightings of a given species divided by the total number of identified beaked whales in each block.

The variance of the adjusted estimate was calculated as follows:

$$var\left[N_{adj}\right] = var\left[N_{id}\right] + p_{id}^{\ 2} N_{unid}^{\ 2} \left(CV_{p_{id}}^{\ 2} + CV_{N_{unid}}^{\ 2}\right)$$

The estimate for sperm whales was similarly adjusted to include a proportion of unidentified large whale abundance.

2.3.4 Estimating model-based abundance

Modelling to investigate the effect of environmental covariates on abundance and to examine habitat use followed Cañadas and Hammond (2008). A spatial grid of resolution 0.25 x 0.25 degrees was created covering the survey areas. This resolution was chosen as it was the coarsest resolution of the available environmental covariates. This yielded a total of 6830 grid cells within the study area. The width of a degree of longitude changes with latitude causing variation in the area of the grid cells, which ranged from 297.0km^2 in the northernmost grid cells to 618.4km^2 in the southernmost grid cells. Environmental data were assigned to the centre of each grid cell and the grid was used to provide values of environmental covariates for the effort segments and to predict abundance spatially.

Analysis was undertaken in two steps: first, modelling abundance of groups and, second, modelling group size. Cetacean abundance in each grid cell was obtained by multiplying the abundance of groups by the group size using the best fitting model in each case. Estimated abundance was summed over all grid cells to generate an estimate for the entire survey area. All

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modelling was carried out using statistical software R (R Core Team, 2015) using the *mgcv* package (Wood, 2006).

2.3.5. Environmental data

Environmental variables were derived from a number of sources (Supplemental Appendix Table B) and included water depth (m), distance to the 0m, 200m and 2000m contours (as proxies for coastal, continental shelf and oceanic habitats, respectively), slope and contour index (to give an index of benthic habitat and seafloor topography in the area). As indices of biological activity/primary productivity we included sea surface temperature (C°) and chlorophyll a (mgC/l).

2.3.6. Abundance of groups

The response variable in the modelling of abundance of groups was obtained using the Horvitz-Thompson estimator:

$$\hat{N}_i = \sum_{j=1}^{n_i} \frac{1}{\hat{p}_{ij}}$$

Where n_i is the number of detected groups in the i^{th} segment, and $\hat{p}_{ij}$ is the estimated probability of detection of the j^{th} group in segment i, obtained from the appropriate fitted detection function for the appropriate level or measurement of each covariate included in the detection function.

The abundance of groups was modelled using a Generalized Additive Model (GAM) with a logarithmic link function. Due to over-dispersion in the data, a quasi-Poisson error distribution was assumed, with variance proportional to the mean, and using the searched area of each segment as an offset. The general structure of the model was:

$$\hat{N}_i = exp\left[ln(a_i) + \theta_0 + \sum_k f_k(z_{ik}) \right]$$

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where the offset a_i is the search area for the i^{th} segment (calculated as the length of the segment multiplied by twice the truncation distance), θ_0 is the intercept, f_k are smoothed functions of the explanatory covariates, and z_{ik} is the value of the k^{th} explanatory covariate in the i^{th} segment.

For each species, the maximum number of covariates per model and the maximum number of "knots" (equivalent to degrees of freedom) for each covariate was limited to avoid excessive and biologically unrealistic "wiggliness" in the fitted smooth function. As a rule of thumb, the maximum total degrees of freedom in the model was not allowed to exceed 30-50% of the total number of non-zero observations to avoid over-fitting and to avoid problems when using bootstrap re-sampling of the data to estimate measures of precision of the estimates. Model selection was implemented manually based on three criteria: (a) the GCV (General Cross Validation score); (b) the percentage of deviance explained; and (c) the probability that each variable was included in the model by chance.

2.3.7. Group size

Group sizes were corrected to take account of likely error recorded on the Primary observation platform. Using duplicate detections, a correction factor for group size made by Primary was estimated as:

$$\hat{c}_s = \frac{\sum s_j(2)}{\sum s_j(1)}$$

Where $s_j(1)$ is the group size estimated by the Primary observers in duplicate sightings, and $s_j(2)$ is the group size estimated by the Tracker observers.

Group size was also modelled using a GAM with a logarithmic link function. The response variable was the number of whales counted in each group (s_j) and a quasi-Poisson error distribution was used, with the variance proportional to the mean, because of over-dispersion in the data. The general structure of the model was:

$$E(s_j) = exp\left[\theta_0 + \sum_k f_k(z_{jk})\right]$$

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where θ_0 is the intercept, f_k are smoothed functions of the explanatory covariates, and z_{jk} is the value of the k^{th} explanatory covariate in the j^{th} group. Manual selection of the models was done following the same criteria described for the models of abundance of groups.

2.4 Estimating model-based abundance and uncertainty

Cetacean abundance in each grid was obtained by multiplying the abundance of groups by the group size using the best fitting model in each case. Estimated abundance was summed over all grid cells. Where the best model included a temporally varying covariate (e.g. sea surface temperature) the prediction chosen was 2007 when most of the data were collected. A section to the west end side of the Faroese block was not included in the grid because the covariates were not available for that section. The original estimate obtained for the Faroese block was therefore proportionally increased to take account of that missing section (27.2% of the Faroese block), by multiplying the abundance estimate of this block by 1.3739.

The modelling process was replicated in 600 non-parametric bootstrap re-samples to obtain the coefficient of variation (CV) for this part of the analysis. The re-sampling unit used was the combination of day and transect (each line of the zig-zag survey track), so each day was considered a unit but was further divided if it encompassed segments of two or more transects. Each re-sampling unit therefore corresponded to either a transect or a piece of transect surveyed over a single day. The re-sampling process was stratified by survey region (SCANS-II, CODA, Faroese block of T-NASS) as far as data allowed.

For each bootstrap resample, the models for abundance of groups and for group size were run (or mean group size calculated if including covariates in the model did not improve estimation), and the degree of smoothing of each model term was chosen by the *mgcv* package, within the maximum number of knots allowed for each covariate, thus incorporating some model selection uncertainty in the variance.

The CV of animal abundance for the entire area for each species was obtained by combining the model CV and the CV of detection probability. Percentile-based 95% confidence intervals were obtained assuming the estimates of abundance were log-normally distributed.

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3 Results

A total of 47 225km of transect line was surveyed by the three surveys, mainly by shipboard effort (Table 1). There were 187 sightings of deep diving species, comprising at least five species (Table 2, Supplemental Appendix Table C). Of these, sperm whales (34%) and pilot whales (33%) were the most frequently sighted species, with fewer sightings of Cuvier's (9%) and Sowerby's (3%) beaked whales and northern bottlenose whale (8%). An additional 25 sightings of beaked whales could not be identified to species level. During the surveys, a substantial number of sightings of large whales were made and based on those identified to species, were believed mostly to be fin whales (*Balaenoptera physalus*) but some could have been sperm whales (Supplemental Appendix Table C).

3.1 Sperm whales

All sperm whale sightings (n = 65) occurred in the deeper waters of the North-East Atlantic (Figure 2a). The fitted detection functions for all species/species groups are shown in the Supplemental Appendix Fig. E. The calculated group size correction factor was 1.11. The design-based estimate of total abundance of sperm whales was 3267(CV = 0.23) individuals. Adjusting this estimate to include a proportion of the unidentified large whale sightings, we obtained an abundance estimate of 7035(CV = 0.28) sperm whales (Supplemental Table C). The component for identified sperm whales is not corrected for animals missed on the transect line. The final model for abundance of groups included depth, SST and contour index, while SST and depth were the only variables retained in the final model for group size (Table 3). The selected models predicted that abundance of groups was highest in waters between 1000 and 4000m, over a wide temperature range mostly between 10°C and 20°C, where the contour index varied between 0 (steeply sloping) and 80 (gently sloping) (Supplemental Appendix Fig. Fa). Group size was predicted to increase as SST increased and to be higher in waters less than 2000m deep

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(Supplemental Appendix Fig. Ga). The model-based estimate of abundance (unadjusted for a proportion of unidentified large whale sightings) was 3424 (CV = 0.27) individuals. Sperm whales were predicted to concentrate in the southern areas of the surveyed region, in the oceanic deep waters off Galicia (NW Spain) and in the Bay of Biscay (Figure 3).

3.2 Pilot whales

Pilot whale sightings (n = 59) were distributed widely along the continental shelf edge and in oceanic waters, extending from the Straits of Gibraltar to the deep waters of the Rockall Trough around 60°N (Figure 2b). No pilot whales were sighted in the North Sea or the Irish Sea. The calculated group size correction factor was 1.61. The design-based estimate of total abundance was 172 195 (CV = 0.35) individuals (Table 2).

Depth, distance to the 2000 m depth contour and latitude were found to be important in predicting pilot whale abundance of groups while depth and contour index were retained in the best model for group size (Table 3). Abundance of groups was predicted to be highest in water depths >1000m, was strongly associated with the 2000m depth contour and showed geographic variation with latitude, with a peak at 55°W (Supplemental Appendix Fig. Fb). Group size was predicted to be smaller in deeper waters, and higher at contour index values of 30-50, indicating that that they occur in waters over moderately steep slopes (Supplemental Appendix Fig. Gb). The model-based estimate of pilot whale abundance was 152 071 (CV = 0.32) whales. Results suggest that the steep slopes on both sides of the Rockall Trough are important areas for pilot whales in the North-East Atlantic, along with an area further west on the Rockall plateau (Figure 3b).

3.3 Beaked whales

At least three species of Ziphiidae were sighted during the surveys: northern bottlenose whale, Cuvier's beaked whale and Sowerby's beaked whale (*Mesoplodon bidens*). Northern bottlenose

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whales (n=15) and Sowerby's beaked whales (n=6) were only sighted in offshore waters but Cuvier's beaked whales (n=17) and unidentified beaked whales (n=25) were also seen on the continental shelf area during the SCANS-II survey (Figure 2c). Most sightings of northern bottlenose whales occurred in the northern part of the survey area. Sowerby's beaked whale showed a similar pattern, although one individual was sighted off northwest Spain. In contrast, most sightings of Cuvier's beaked whales occurred in the southern Bay of Biscay, with other sightings widely distributed, from Portugal to northwest Ireland and the Rockall Trough.

Abundance estimates were calculated for each beaked whale species separately (Table 2) and combining all the adjusted estimates for species with the unidentified beaked whale category, gave a total beaked whale estimate of 29 154 (CV 0.27). These estimates are not corrected for animals missed on the transect line and therefore total abundances are underestimated.

All species of beaked whales were modelled together because of the small number of sightings. The final model for abundance of groups included depth, latitude, distance to the 2000 m depth contour and longitude. For group size, the best model retained latitude and the interaction between depth and the contour index (Table 3). The abundance of beaked whale groups was predicted to decline steeply east of longitude 0°, to peak at latitudes 45°N and 60°N and depths of 1000m and 4000m, and to be strongly associated with the 2000m depth contour (Supplemental Appendix Fig. Fc). Group size was predicted to be highest in the north of the study area (Supplemental Appendix Fig. Gc). The model-based estimate of abundance for all beaked whale species (uncorrected for animals missed on the transect line) was 29 205 (CV = 0.23). Beaked whales were predicted to concentrate in the north-western part of the surveyed area and in the deeper waters of the central part of the Bay of Biscay (Figure 3c).

4 Discussion

4.1 Abundance estimates

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Surveys designed to achieve equal coverage probability will, if executed correctly, provide design- based unbiased estimates of abundance, the precision of which primarily depends on the number of sightings and the distribution of encounter rate among transects but also on the fit of the detection function and the distribution of group sizes. Model-based estimates of abundance depend on the validity of the model and are therefore not necessarily unbiased. However, they have the potential to improve precision if the model covariates explain variability in the data (Redfern et al., 2008; Cañadas and Hammond, 2008; Hammond, 2010) and these models have the advantage of providing additional information on species-habitat relationships.

To derive abundance estimates for deep diving species, we used data from three different surveys, which used the same data collection methodology to ensure consistency across the entire surveyed region. Although the SCANS-II survey occurred two years prior to the CODA and T-NASS surveys, 90% of the sightings of deep diving species were made during the 2007 offshore surveys. In addition, there is no reason to believe that any directional shift occurred in distribution and abundance during the period between surveys. The effect of any random changes in distribution does not cause bias but may increase the variance of the abundance estimates, so-called additional variance or "process error" - see, for example, the Norwegian six year cycle of "mosaic" surveys to estimate minke whale abundance in the North-East Atlantic (Solvang et al., 2015). Thus, our estimates of abundance should be unbiased but the variance could be underestimated.

Our design-based and model-based abundance estimates for sperm whales were very similar but the design-based estimate was slightly more precise. For some large whale species, uncertainty in species identification can be an issue, especially if blows are the main cue. We attempted to address this in the analysis, by including a proportion of large whales not identified to species level. As a result, the adjusted design-based estimate is twice as large.

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Gunnlaugsson et al. (2009) derived an estimate for sperm whales, corrected for availability bias, from NASS 2001 data of 11 185 (CV = 0.34) animals for the central North Atlantic including the area around the Faroe Islands. The availability bias was estimated as 0.71, while the uncorrected sperm whale abundance estimate was about 7900 individuals. Data from Norwegian surveys covering the northeastern North Atlantic obtained a figure (uncorrected for availability bias) of 6375 (CV = 0.22) sperm whales (Øien, 2009). These estimates give uncorrected densities of 0.0035 and 0.0020 sperm whales/km^2 for the central and eastern North Atlantic, respectively. Our uncorrected estimates of 3267-7035 animals represent a comparable density of 0.0021-0.0044 whales/km^2. There is little overlap in these surveyed areas and summing the uncorrected estimates gives a conservative figure of around 20000 sperm whales in the central and eastern North Atlantic. Applying the Gunnlaugsson et al. (2009) value of availability bias, would give an estimate close to 30000 whales.

For pilot whales, the model-based estimate of abundance was considerably more precise but 11% smaller than the design-based estimate. Buckland et al. (1993) estimated a total of 778 000 (CV = 0.295) pilot whales in 1989, in a large area (~4.4 million km^2) of the central and eastern North Atlantic, including the offshore waters of our study area. Our model-based estimate, which (unlike the 1989 estimate) accounts for animals missed on the transect line, is 152 071 (CV = 0.25). Comparison of these estimates is limited by methodological differences, but despite the apparently large difference, they are not inconsistent if differences in area covered are taken into account.

Using a common detection function for all beaked whales combined together with species-specific encounter rates allowed design-based estimates to be derived for each species even though there were small numbers of sightings. These small numbers of observations meant that it was only possible to develop models for all beaked whale species combined. For all beaked whales combined (including those unidentified to species), the model-based estimate was practically identical to the design-based estimate, but slightly more precise.

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Information from strandings programmes (e.g. Berrow & Rogan, 1997) and opportunistic sightings surveys in the North-East Atlantic suggest that three additional beaked whale species occur in this area: True's beaked whale (*M. mirus*), Gervais' beaked whale (*M. europeaus*) and Blainville's beaked whale (*M. densirostris*). There were no positive identifications of these species during the surveys but distinguishing species within the genus *Mesoplodon* can be difficult (Reeves et al., 2002) and therefore it is possible that some of our unidentified beaked whale sightings included sightings of these species. If this was the case, the adjustment for a proportion of unidentified beaked whale abundance could have caused an over-estimation of Cuvier's and Sowerby's beaked whale and northern bottlenose whale abundance. However, because both sightings and stranding records of these additional species are rare, it is likely that they would not represent a large proportion of the unidentified beaked whale category.

An alternative methodology that has been successfully implemented for sperm whales is the use of towed hydrophones to record echolocation clicks (sperm whales click almost continuously, during deep dives therefore effectively eliminating availability bias) and generate acoustic-based estimates of abundance (Barlow and Taylor, 2005; Lewis et al., 2007). Beaked whales also echolocate (e.g. Johnson et al., 2004) but estimating abundance using passive acoustic methods is considerably more challenging for these species (Klinck et al., 2012). A combined visual and acoustic approach may help refine abundance estimations and better elucidate habitat use for these species.

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4.2 Habitat modelling

Habitat modelling is a valuable tool that can help identify factors structuring a species distribution, abundance and even behaviour, on a wide range of temporal and spatial scales (Cañadas and Hammond , 2008; Redfern et al., 2008; Forney et al., 2015). Most studies use physical and environmental variables to help predict distribution, density or biodiversity (e.g.

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Ingram and Rogan 2002; Ballance et al. 2006; Ferguson et al. 2006; Barlow and Forney 2007; Skov et al., 2008; Praca et al., 2009; Whitehead et al., 2010). Habitat modelling is also a valuable tool for identifying areas of high density and can thus provide the information needed for the development of spatially explicit management strategies, which are particularly difficult to establish for highly mobile marine megafauna species such as cetaceans (e.g. Cañadas et al., 2005; Cañadas and Hammond, 2006; Redfern et al., 2008; Embling et al., 2009; Hazen et al., 2011). Identifying habitat requirements and habitat predictors for deep diving species can support environmental risk assessments and can be incorporated into a risk management framework (Azzellino et al., 2011; Brown et al., 2013).

The environmental feature likely to have most influence on the distribution and abundance of cetacean (and other) species is the distribution and abundance of their prey (see, for example, Hátun et al., 2009). However, obtaining prey distribution data at the spatial and temporal resolution needed to make meaningful comparisons with top predator distribution has proven challenging, with the exception of some cetacean and bird species feeding on pelagic fish species (e.g. Certain et al., 2011). Therefore, as with many other studies on habitat use of marine organisms and specifically beaked whales (Ferguson et al., 2006) and sperm whales (Skov et al., 2008), environmental variables such as SST, fine-scale frontal and topographic features, and depth are used as proxies of the actual driving forces for habitat selection.

The scale at which many remotely sensed variables are available, both spatially and temporally, can be highly variable (Becker et al., 2016; Scales et al., 2017) and may influence the fine scale resolution of predictive models. In our study, the size of the grid cells was determined by the scale at which data for some environmental variables were available. Given that the overall area exceeds 3 million km^2 it is likely that fine scale habitat use has been overlooked. A more in-depth examination of some "high use" areas in particular, may elucidate such fine scale habitat use. Predicting species distributions for management and conservation decisions can be tailored to suit a range of decision making contexts (e.g. Guisan et al., 2013). Risk assessments of

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anthropogenic threats are frequently carried out on relatively large spatial scales, given the wide scale nature of some threats, such as bycatch (e.g. Breen et al., 2016) and in the case of noise, where the sphere of influence may be very large, using a slightly coarser scale to predict habitat use may be sufficient to carry out a preliminary risk assessment.

4.2.1 Sperm whales

Our results indicate that although sperm whales appear widely distributed in offshore European Atlantic waters, the highest densities were predicted to concentrate in the deep water areas off Galicia (NW Spain) and in the southeastern part of the Bay of Biscay, an area which includes the Santander Canyon, previously reported as being important for the species (Kiska et al., 2007). Surveys in the central and northeastern North Atlantic have detected most sperm whales in deep waters west and southwest of Iceland but found the highest densities between Iceland and northern Norway in the Norwegian Sea (Gunnlaugsson et al., 2009; Øien, 2009).

Female sperm whales and their calves remain in the warmer lower latitudes, while so called "bachelor herds" and large bulls distribute themselves further north when not breeding (Teloni et al., 2007). This sexual segregation means that the animals encountered in our surveys were likely males and that our results reflect male sperm whale abundance and distribution.

4.2.2 Pilot whale

Although recorded in inshore waters and on the continental shelf, the pilot whale is mostly considered an oceanic species. Results from our study show that pilot whales are distributed throughout the study area and that the steep slopes on both sides of the Rockall Trough are important areas, along with an area further west on the Rockall Plateau. Important areas highlighted in previous studies also include the Rockall Trough (Ó Cadhla et al., 2001), the Faroe-Shetland channel (Macleod et al., 2003) and the Bay of Biscay (Kiska et al., 2007). In NW Spain they are regularly sighted off the shelf (López et al., 2003) although some individuals have also been sighted from the coast (Pierce et al., 2010).

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4.2.3 Beaked whales

Beaked whales have become the focus of much research because of strandings associated with naval mid frequency sonar in parts of their range (e.g. Frantzis, 1998; Jepson et al., 2003). As a taxonomic grouping, new species are still being described (Dalebout et al., 2002) and very little is known about habitat preferences, although work in specific geographical areas has produced some insights into diving behaviour (Tyack et al., 2006), feeding ecology (e.g. Santos et al., 2007; Wenzel et al., 2013), and distribution (e.g. Azzelino et al. 2008; Gannier, 2011). There is also evidence to suggest that Cuvier's beaked whale and *Mesoplodon* spp. are declining in parts of their range (Moore and Barlow, 2013).

Avoidance of beaked whale habitats could provide a means for reducing the potential effects of mid-frequency sonars and geophysical sound sources (Barlow and Gisiner, 2006; Fernandez et al., 2013). To achieve this, accurate predictions of densities of sensitive species are needed (Azzellino et al., 2011). Our maps of predicted distribution highlight important areas in the north-western part of the surveyed area, although it should be noted that sightings of individual species showed very different distribution patterns. Northern bottlenose whales had a predominantly northern distribution, primarily in the Faroese T-NASS survey area. Sightings of Sowerby's beaked whale were also predominantly in the northern part of the survey area; whereas Cuvier's beaked whales were almost exclusively sighted in the southern part.

Within the North-East Atlantic, the importance of the southern Bay of Biscay, and in particular the Santander canyon, to Cuvier's beaked whales has been previously highlighted (e.g. Kiska et al., 2007) and is consistent with the distribution reported here. Our model suggests that the Rockall Trough margin is also an important area for beaked whales. Both the Santander canyon area and the Rockall Trough margin could be considered sensitive areas. More research focussed at a range of spatial and temporal scales, and risk assessments for military sonar and seismic exploration, is strongly recommended.

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Northern bottlenose whales have previously been sighted in deeper oceanic waters and are thought to occasionally use shelf areas and coastal areas such as the Irish Sea (MacLeod et al., 2004, Rogan and Hernandez, 2011), which may possibly be associated with prey movement (Whitehead and Hooker, 2012). The high density of northern bottlenose whales predicted in the Faroese T-NASS survey area, and additional sightings further east on the north of the Rockall Trough suggest that this is an important area for bottlenose whales in the summer.

Most sightings of Sowerby's beaked whale occurred in the northern part of the surveyed area. Sightings of this species have also been reported in the Atlantic Frontier and the Faroes-Shetland Channel to the west and North of Scotland (Pollock et al., 2000; Macleod et al., 2003). Of the two predicted high use areas for beaked whales to the NW of Ireland/Scotland; the eastern cluster likely represents, or at least includes, Sowerby's beaked whales.

4.3 The deep diving cetacean community

The predicted distribution of these deep diving species suggests that there is little spatial overlap in the high use areas among species, at least in summer. Some overlap is apparent between sperm and beaked whales off northern Spain but otherwise, the predicted concentrations of animals are separated into fairly distinct non-overlapping areas. Differences in habitat use among sperm whales and beaked whales have been noted elsewhere (e.g. Tepsich et al., 2014).

Reasons for this separation may include differences in prey preferences, prey availability, foraging specializations, prey capture techniques and perhaps physiological constraints, such as diving capabilities. Knowledge of the feeding ecology of sperm whales, beaked whales and pilot whales (e.g. Santos et al. 2001, 2002, 2007; MacLeod et al., 2003; de Stephanis et al., 2008; Fernandez et al., 2014) is based mainly on the analysis of stomach contents of stranded individuals, and indicates that they feed predominately on oceanic cephalopod species. Resource partitioning has been shown in deep water cetacean assemblages (e.g. MacLeod et al.,

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2003, Whitehead et al., 2003; Spitz et al. 2011, Chouvelon et al., 2012) and differences in prey capture techniques, including differences in suction feeding capabilities and prey size selection (e.g. MacLeod et al., 2006) may also explain differences in distribution.

Whatever the underlying drivers for habitat separation, our analysis has provided the first large-scale abundance estimates of the deep diving cetacean species in the North East Atlantic, and identified at least three separate areas in this region where the summer density of these species is high. Refinement of the environmental variables available for modelling, together with future studies of deep diving cetaceans, will help to improve our understanding of the ecology of these species. Better information will also improve our ability to identify areas of potential overlap with threatening industries to establish conservation risk. Year round spatial density maps of sensitive species can inform spatial planning and management of oil and gas exploration, fishing, ship traffic, offshore renewable industry sites and military exercises, providing an invaluable tool to help conservation of these species.

Conclusion

We present the most comprehensive and robust estimates of abundance available for deep diving cetaceans in the North East Atlantic, and describe a first examination of which features of the environment most influence their distribution and abundance. Model predictions have generated maps that give an unprecedented illustration of how sperm whales, pilot whales and beaked whales are distributed in the North East Atlantic in summer. Our results will help inform EU Member States reporting under the Habitats Directive and the MSFD, and also the deliberations of international organisations such as the IUCN, ICES and IWC. The lack of data from other seasons precludes extending our inferences beyond summer but nevertheless this information is an important addition to our knowledge of the ecology of deep diving species that will inform future conservation efforts.

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Acknowledgements

This project would not have been possible without the help and dedication of the many observers who participated in the surveys, and the ships' captains and crews. CODA was funded with contributions from UK Department for Environment, Food & Rural Affairs; UK Department for Trade & Industry; Irish Department of the Environment, Heritage & Local Government; Irish Bord Iascaigh Mhara and the Spanish Ministry of the Environment and Rural and Marine Affairs via the Spanish Cetacean Society. Ship and personnel time was contributed by the Instituto Español de Oceanografía, AZTI Tecnalia, Marine Nationale France and University College, Cork. SCANS-II was funded by the EU LIFE Nature programme under Project LIFE04NAT/GB/000245 and by the governments of all range states: Belgium, Denmark, France, Germany, Ireland, Netherlands, Norway, Poland, Portugal, Spain, Sweden and UK. The survey in the Faroese block of T-NASS was funded by the Faroese government. We would like to thank Trish Breen for help in preparing Fig. 1 and two anonymous reviewers and the associate editor for their insightful comments, which helped improve the manuscript.

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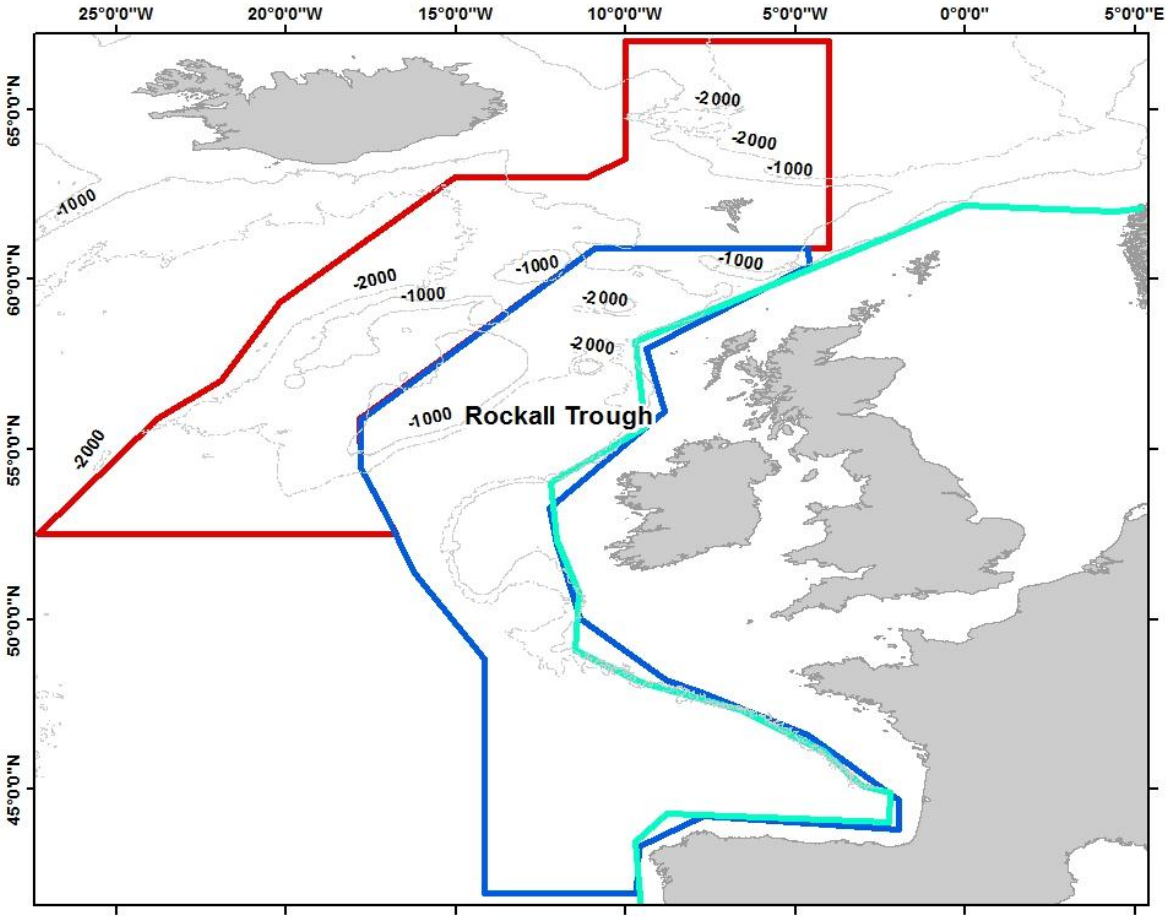
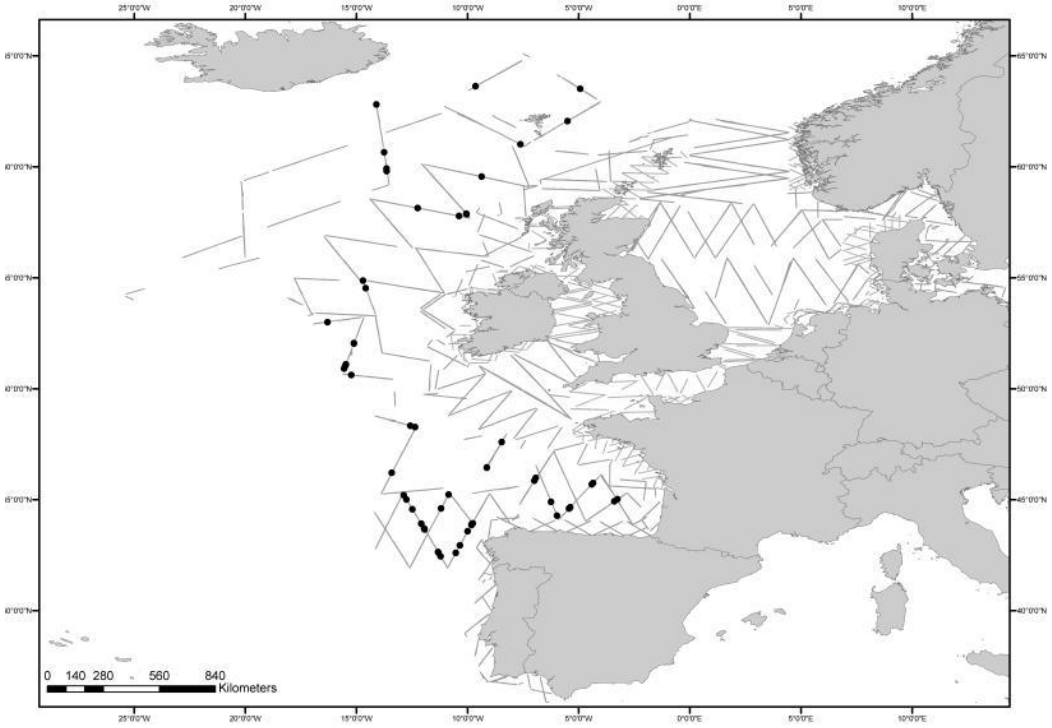


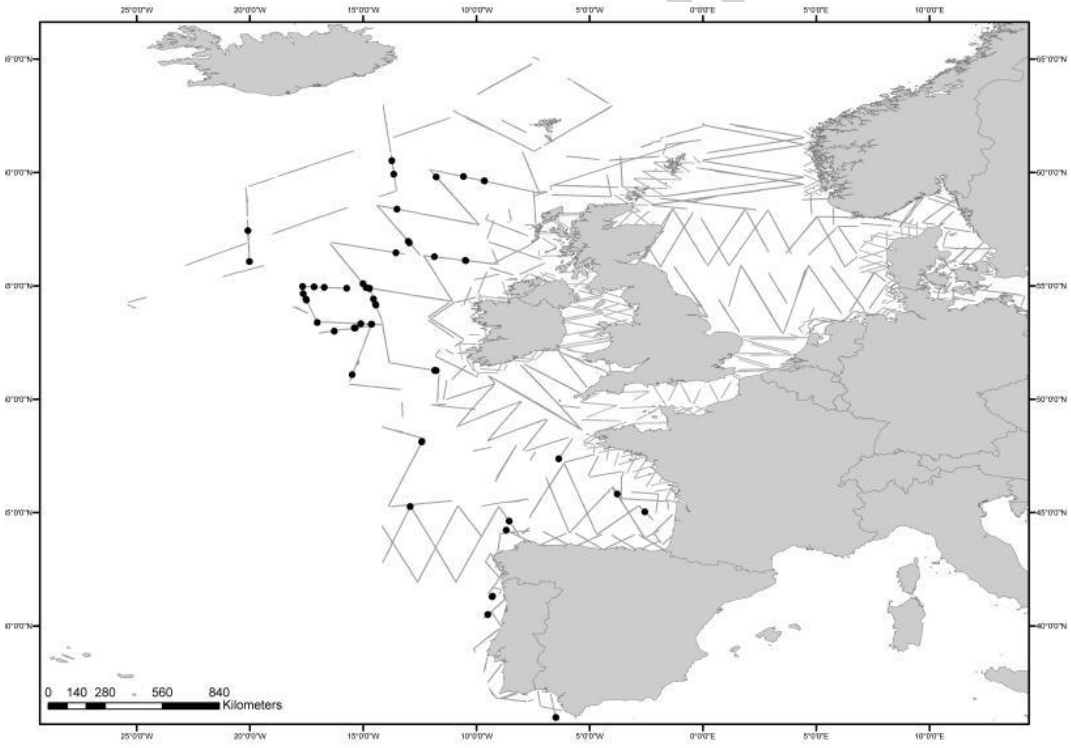
Figure 1. Survey areas: SCANS-II 2005 (outlined in cyan), CODA 2007 (outlined in blue), and the Faroese block of TNASS 2007 (outlined in red) and underlying bathymetry (showing 1000 and 2000m isobaths)

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a) Sperm whales



b) Pilot whales



c) Beaked whales

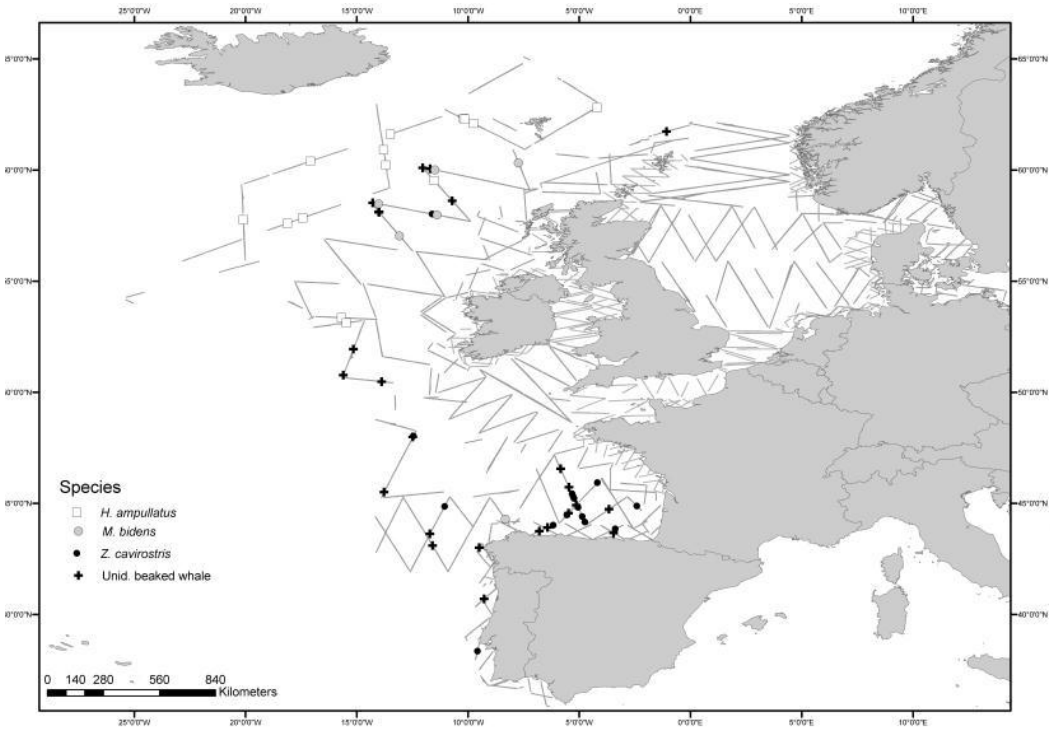
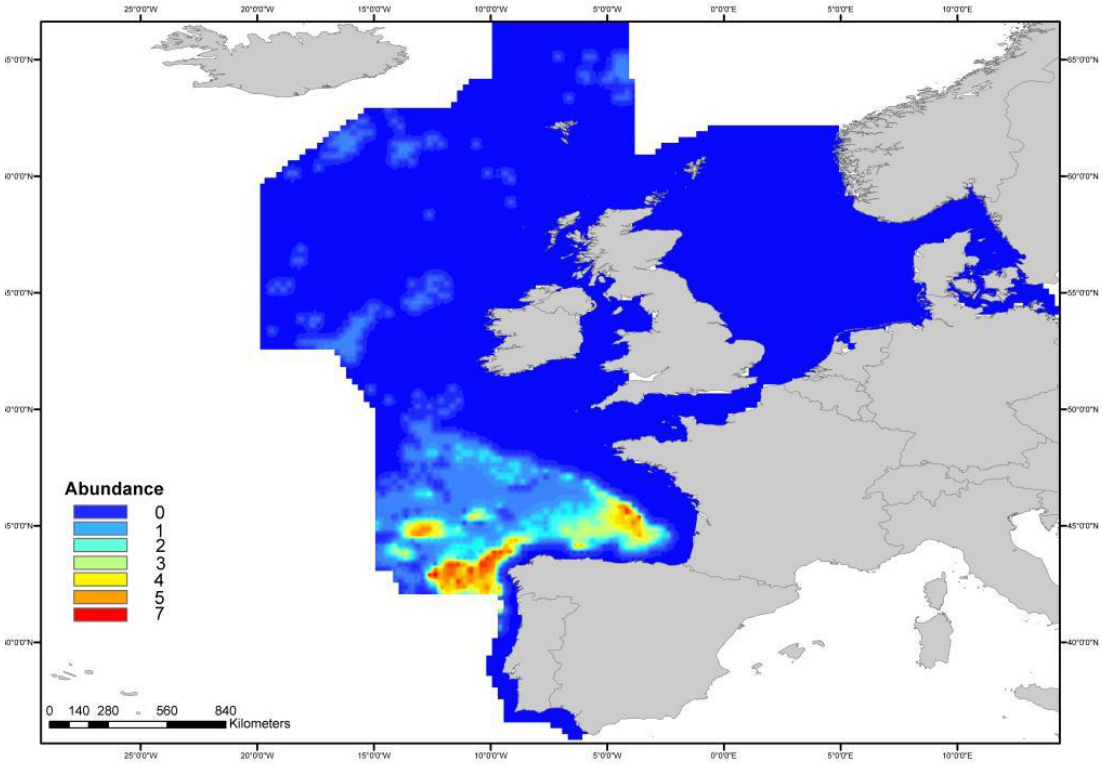


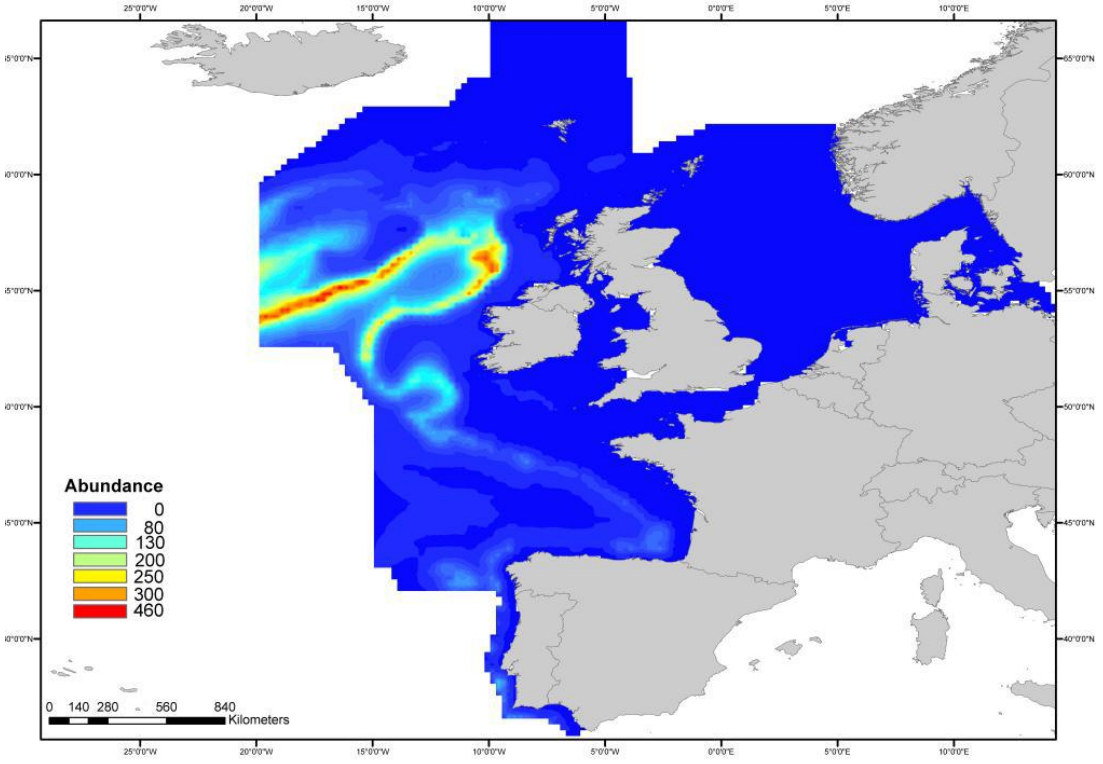
Figure 2. Distribution of survey effort and sightings of a) sperm whales, b) Long-finned pilot whales and c) beaked whales in the survey area

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a) Sperm whales



b) Pilot whales



c) Beaked whales

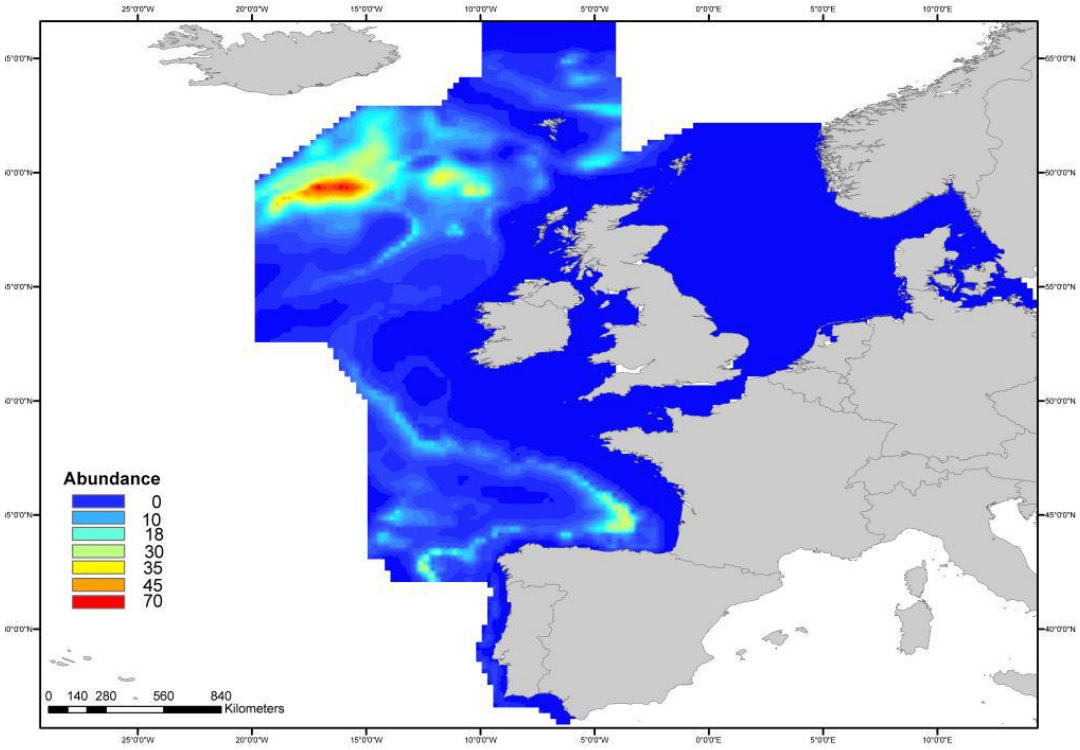


Figure 3. Surface maps of smoothed predicted abundance (numbers/km^2) of a) sperm whales, b) long-finned pilot whales and c) beaked whales

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Table 1. Areas and length of transect searched in each survey region. Data are for surveys in Beaufort sea states 0-4 for SCANS-II (ship), CODA and T-NASS, and for good and moderate conditions for SCANS-II (air) (equivalent to Beaufort 0-2).

Region	**Area (km^2)**	**Transect (km)**
SCANS-II (ship)	1,005,743	19,614
SCANS-II (air)	364,371	15,802
CODA	967,538	9,491
TNASS (Faroes)	685,628	2,318
Total area	**3,023,280**	**47,225**

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Table 2. Design- and model- based estimates of abundance for deep diving species.

Species	No. obs	Design based Animal abundance [95% confidence interval]	CV (%)	Model based Animal abundance [95% confidence interval]	CV (%)
Sperm whale	65	3267 [2103 – 5076]	0.23	3424 [1925 – 5487]	0.27
Pilot whale	59	172,195 [88,194 – 336,206]	0.35	152,071 [75,862 – 256,575]	0.25
Cuvier's beaked whales	17	2286 [942 – 5552]	0.48		
Northern bottlenose whale	15	19,539 [9921 – 38,482]	0.36		
Sowerby's beaked whale	6	3518 [1570 – 7883]	0.43		
Unidentified beaked whale	25	3811 [2322 - 6254]	0.26		
Total beaked whale	38	29,154 [17,478 – 48,629]	0.27	29,205 [16,909 – 41,514]	0.23

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Table 3. Covariates retained in the final models for (a) abundance of groups and (b) group size for each species or species combination including the maximum number of knots allowed in each smooth function, the estimated degrees of freedom (approximately the number of knots used in the model - 1), the probability of each covariate being included in the model by chance (*p*) and the deviance explained by the model. Covariates include Depth(m), Sea Surface Temperature (SST), Contour Index (CI), Distance to the 2000m contour (Dist2000), Latitude (Lat) and Longitude (Lon).

(a) Abundance of groups

Covariate	Max. knots allowed	Estimated d of f	*p*	Deviance explained
Sperm whale				
Depth	6	4.98	<<0.001	33.8%
SST	6	4.86	<<0.001	
CI	6	4.93	<<0.001	
Beaked whales				
Depth	6	4.97	<<0.001	30.6%
Lat	6	4.98	<<0.001	
Dist2000	5	3.95	<<0.001	
Lon	5	3.99	<<0.001	
Long-finned pilot whale				
Depth	5	3.92	<<0.001	32.0%
Dist2000	4	2.95	<<0.001	
Lat	5	3.99	<<0.001	

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(b) Group size

Covariate	Max. knots allowed	Estimated d of f	*p*	Deviance explained
Sperm whale				
SST	10	1	0.003	19.8%
Depth	10	2.34	0.064	
Beaked whales				
Depth:CI	20	4.71	0.762	26.8%
Lat	8	3.89	0.449	
Long-finned pilot whale				
Depth	5	1.83	0.081	27.5%
CI	5	2.30	0.007	

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