Abundance and distribution of beaked whales in the European Atlantic

CAÑADAS, A.[1], KELLY MACLEOD[2], MIKKELSEN, B.[3], ROGAN, E.[4], URIARTE. A.[5], JOSÉ ANTONIO VÁZQUEZ [6], VAN CANNEYT, O. [7] & HAMMOND, P.S.[2]

[1] *ALNILAM, Cándamo 116, 28240 Hoyo de Manzanares, Madrid, Spain. anacanadas@alnilam.com.es*
[2] *Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St. Andrews, Fife, KY16 8LB, UK.*
[3] *Faroese Museum of Natural History, FO-100 Tórshavn, Faroe Island*
[4] *Department of Zoology, Ecology and Plant Science, University College, Distillery Fields, North Mall, Cork, Ireland*
[5] *AZTI Tecnalia, Marine Research Division, Herrera kaia, Portualdea z/g, Pasaia, E-20110, Spain*
[6] *Spanish Cetacean Society, Cabeza de Manzaneda 3, Pelayo Algeciras 11390, Spain*
[7] *CRMM, UMS 3419 Université de La Rochelle/CNRS, 5 allées de l'océan, 17000 La Rochelle, France*

INTRODUCTION

The abundance and distribution of cetaceans in offshore waters of the European Atlantic is not well known. The series of North Atlantic Sightings Surveys (NASS) in 1987-2001, T-NASS in 2007 and the Norwegian Independent Line Transect Surveys (NILS) in 1995-2007 have provided much information on abundance for the North Atlantic as a whole but these surveys have focussed primarily on the northern and central North Atlantic; European waters have not received much coverage.

The Cetacean Offshore Distribution and Abundance in the European Atlantic (CODA) project conducted shipboard surveys in July 2007 to obtain data for the estimation of abundance of cetaceans in offshore waters of the UK, Ireland, France and Spain, outside continental shelf waters that had been surveyed in 2005 (SCANS-II 2008). In this paper, we analyse the data on beaked whales from the CODA surveys combined with data from SCANS-II and the Faroese block of T-NASS to generate the most comprehensive possible abundance estimates for the Cuvier´s and Sowerby's beaked whales and Northern bottlenose whales in European Atlantic waters.

This paper updates the preliminary abundance estimates for beaked whales presented in Macleod *et al*. (2008) previously presented to the Scientific Committee (SC/60/O2).

METHODS

Data sources

The following survey datasets were analysed here: SCANS-II 2005, CODA 2007 and the Faroes block of TNASS 2007. Details of the SCANS-II and CODA surveys are given in SCANS-II (2008) and CODA (2009). The TNASS survey followed the same design and protocol as the CODA survey. The areas covered by these surveys are shown in Figure 1.

The SCANS-II data included shipboard and aerial survey data; CODA and the Faroes block of TNASS were shipboard surveys. Shipboard surveys were all conducted in "double platform" mode in which a Tracker observation platform searches far ahead to detect animals/groups before they may respond to the approaching ship and a Primary observation platform searches conventionally closer to the ship. Duplicate observations allow the probability of detection on the transect line to be estimated and to take account of responsive movement, as appropriate (Laake & Borchers 2004). Figure 2 shows the effort tracks and the sightings of all identified and unidentified species of beaked whales.

There was one sighting of a bottlenose whale in the SCANS-II aerial survey but we ignore this here.

Data processing

All shipboard survey effort and sightings data were processed into the same format, appropriate for entry into analysis software DISTANCE (Thomas *et al.* 2006) for estimating detection functions. SCANS-II aerial survey data were not reanalyzed to estimate detection probabilities. All the data (shipboard and aerial) were organized into a common format for conducting the spatial modelling in statistical software R (R Development Core Team 2009).

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 in the available environmental covariates. This yielded a total of 6,830 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, ranging from 297.0 km^2 in the northernmost grid cells to 618.4 km^2 in the southernmost grid cells.

This grid was populated with the covariates described in Table 1 that were also used in the spatial modelling analysis.

All on effort transects were divided into small segments with homogeneous sighting conditions along them. It was assumed that there would be little variability in physical and environmental features within these segments. Each segment was assigned to a grid cell based on the mid point of the segment and values of covariates for each grid cell were associated with the segment.

Methods of analysis

Design-based estimates of abundance

Detection function fitting

Detection functions were fitted combining all beaked whale sightings because of their similar characteristics with respect to detection and to increase sample size. Data were truncated at a perpendicular distance from the transect line determined by a balance between removing distant observations to improve model fit and retaining as much data as possible (Buckland *et al.* 2001). There were not enough duplicates to perform a double-platform analysis, so a single observer mode was used instead.

Covariates available for fitting the detection functions are given in Table 2.

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

Estimates of abundance

Estimates of abundance were obtained in DISTANCE 6 for all beaked whales (including beaked whales unidentified to species level) and for each particular species.

Because there was a slight (3.5%) overlap in the SCANS-II and CODA survey areas, all estimates from these surveys were corrected by dividing by 1.035.

<u>Adjusting estimates to account for sightings unidentified to species</u>

Because 40% of the sightings were unidentified beaked whales, estimates for each species were also adjusted to include a proportion of unidentified beaked whale abundance, prorated according to the number of sightings. This process was done by block:

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

where N_{id} is the abundance estimate of each species from sightings identified to species in each block,

N_{unid} is the estimate of abundance of unidentified beaked whales in each block, and

p_{id} , was estimated as the number of sightings of each species divided by the total number of identified beaked whales in each block.

The variance of the adjusted estimate was estimated as:

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

Density Surface modelling

Density surface modelling methods broadly followed Cañadas & Hammond (2008) and was undertaken in two steps: first, modelling the abundance of groups and, second, modelling the group size. The estimated abundance of animals was obtained by multiplying the results from the two steps. Modelling was undertaken with statistical software R (R Development Core Team 2009) using the 'mgcv' package (Wood 2006).

Modelling abundance of groups

Estimation of number of groups per segment

The response variable in the modelling of abundance of groups was estimated abundance of groups in each segment. This 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.

The probability of detection for each group encountered was obtained from the appropriate fitted detection function for the appropriate level or measurement of each covariate included in the detection function.

Model fitting

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:

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

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.

The maximum number of covariates per model and the maximum number of "knots" (equivalent to degrees of freedom) for each covariate allowed in model fitting was limited to avoid excessive and unrealistic "wiggliness" in the fitted smooth function. As a rule of thumb from experience, the maximum total number of knots allowed in the model should not 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 the CV of the estimates (see below).

Automated model selection using a stepwise procedure cannot be implemented for GAMs in the version of R used (2.10.1). Therefore, manual selection of the models was done using three criteria: (a) the GCV (General Cross Validation score); (b) the percentage of deviance explained; and (c) the probability that each variable is included in the model by chance.

Modelling group size

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:

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

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.

Estimating abundance

Abundance of animals of beaked whales as a group in each grid cell was obtained by multiplying the abundance of groups predicted by the best fitting model by the group size predicted by the best fitting model (or mean group size) for each grid cell in the survey area. Estimated abundance was summed over all grid cells in the survey areas. There was a section on the west end side of the Faroese block that was not included in the grid because the covariates were not available for that section. Therefore, the original estimate obtained for the Faroese block was proportionally increased to take account of that missing section (around 25% of the Faroese block).

Estimating uncertainty

The density surface modelling 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 a transect or a piece of transect surveyed over a single day.

For each bootstrap resample, the models for abundance of groups and for group size were run (or mean group size calculated if no model was selected), 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 Delta method was used to obtain the final CV by combining the CV obtained from the models through the bootstrap and the CV of detection probability. 95% confidence limits were obtained assuming the estimates of abundance were log-normally distributed.

Results

Effort data

There was a total of 8,169 segments ranging from 0.1 to 17.6 km (mean = 5.84 km, sd = 3.41 km), totalling 47,718 km on effort. For each segment a “search area” was calculated by multiplying the length of each segment by twice the truncation distance used for the detection function. Table 3 gives the areas and transect lengths surveyed in SCANS-II (ship and aerial), CODA and TNASS (Faroese block).

Sightings data

Beaked whale sightings included Sowerby’s beaked whale (*Mesoplodon bidens*), Cuvier’s beaked whale (*Ziphius cavirostris*), northern bottlenose whale (*Hyperoodon ampullatus*) and unidentified beaked whale.

The number of sightings used in analysis in each survey region (and the truncation distance used to limit data for analysis) are given in Table 4.

Probability of detection

The best-fitting model was a conventional single platform half-normal detection function fitted to all data from both platforms, with a truncation at 1000m and with covariate "cue2" (factor for conspicuous or inconspicuous cue) as the only significant covariate.

Figure 3 shows the detection function. The estimated average probability of detection was 0.367 (CV=0.135).

Spatial models for estimating abundance

The covariates retained in the final models for abundance of groups and group size are given in Table 5. Plots of the fitted smooth functions for each covariate in the final models for abundance of groups and group size are shown in Figure 4.

Estimates of abundance

Design-based estimates of animal abundance and associated uncertainty are given in Table 6. Estimates of abundance for beaked whale species unadjusted and adjusted for the addition of a proportion of unidentified beaked whale abundance are given in Table 7.

The model-based estimate of animal abundance from density surface modelling, once corrected for the missing Faroese section, was 28,711 (CV = 0.232, 95%CI = 22,835-36,098). The model-based estimates of animal abundance from density surface modelling are shown by survey area in Table 8. The total estimated abundance for the whole area is smaller than the sum of the three survey areas because the total takes account of the small overlap between CODA and SCANS-II survey areas.

A map of smoothed predicted abundance of animals is shown in Figure 5.

DISCUSSION

Comparison of the design-based and model-based results

The point estimates of abundance of animals for the two methods are very similar. However, the estimates of uncertainty, i.e. coefficients of variation and 95% confidence intervals, are smaller and narrower, respectively, for the model-based than for the design-based estimates (Tables 6 and 8). This may be because the density surface modelling has been able to account for some variability in the data, despite the fact that this model encompasses beaked whales as a group, in which at least three different species have been pooled together: Cuvier's beaked whale, Northern bottlenose whale and Sowerby's beaked whale, plus various sightings of beaked whales not identified to species level.

Unfortunately, the sample size for individual species did not allow the spatial modelling of each species individually. Therefore, no proration was possible for the model-based abundance estimates to assign the unidentified to species sightings to particular species, in the same way as was done for the design-based estimates.

Patterns in the modelled distribution of beaked whales

The model-predicted (Figure 5) gives an unprecedented illustration of where beaked whales are distributed in summer in the European Atlantic. According to the results of this analysis, there are clearly two high use areas for beaked whales in the study area in summer: the most south-eastern section (the Gulf of Biscay), and the most north-western section (see Figure 5). These widely separated areas probably correspond to different species or groups of species. In CODA Block 1 and the Faroese block of TNASS, where the north-western predicted high use area is, most sightings of beaked whales identified to species were of Sowerby's beaked whales (5) and Northern bottlenose whale (14), with only one sighting of Cuvier's beaked whale. In the Gulf of

Biscay all sightings identified to species were of Cuvier's beaked whale (there was one sighting of Sowerby's beaked whales in block 3, outside the predicted high use area in block 4). The model also highlights the area to the southwest of Ireland in the deep water over the Rockall Trough as being important.

The Gulf of Biscay, and particularly its south-eastern part, is known from previous surveys in the more coastal waters of Spain and from the observations from the ferries crossing from the UK to Spain (e.g. SCANS-II, 2008; Williams et al., 1999; Cresswell & Walker 2001, 2003; Walker et al., 2004; Smith et al. 2007) as an important habitat for beaked whales, especially Cuvier's beaked whales. The results presented here support this.

References

Buckland, ST, Anderson, DR, Burnham, KP, Laake, JL, Borchers, DL & Thomas, L (2001). *Introduction to distance sampling: estimating abundance of biological populations.* Oxford University Press, Oxford.

Cañadas, A. & Hammond, P.S. 2008. Abundance and habitat preferences of the short-beaked common dolphin (*Delphinus delphis*) in the South-western Mediterranean: implications for conservation. Endangered Species Research 4: 309-331.

CODA (2009). Cetacean Offshore Distribution and Abundance in the European Atlantic. Available from http://biology.st-andrews.ac.uk/coda/.

Cresswell, G. and Walker, D. (Eds.) 2001. A Report on the whales, dolphins and seabirds of the Bay of Biscay and English Channel. Organisation Cetacea, No. 1.

Cresswell, G. and Walker, D. (Eds.) 2003. ORCA. The Annual Report of the Organisation Cetacea. Brunton Business Publications. 45pp.

Hammond, PS, Berggren, P, Benke, H, Borchers, DL, Collet, A, Heide-Jørgensen, MP, Heimlich, S, Hiby, AR, Leopold, MF & Øien, N 2002. Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. Journal of Applied Ecology 39: 361-376.

Laake, JL & Borchers, DL (2004). Methods for incomplete detection at distance zero. In: Buckland, ST, Anderson, DR, Burnham, KP, Laake, JL, Borchers, DL & Thomas, L (2004). *Advanced distance sampling: estimating abundance of biological populations*. Oxford University Press.

R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

SCANS-II (2008). Small Cetaceans in the European Atlantic and North Sea. Final Report to the European Commission under project LIFE04NAT/GB/000245. Available from http://biology.st-andrews.ac.uk/scans2/.

Smith, J., Brereton, T., Macleod, C., Martin, C. & Tyler, P. 2007. Spatial and temporal distribution of cuvier's beaked whale,ziphius cavirostris, influenced by depth and sea surface temperature, in the bay of biscay. 21st Annual Conference of the European Cetacean Society, San Sebastian, Spain.

Thomas, L, Laake, JL, Rexstad, E, Strindberg, S, Marques, FFC, Buckland, ST, Borchers, DL, Anderson, DR, Burnham, KP, Burt, ML, Hedley, SL, Pollard, JH, Bishop, JRB and Marques, TA (2006). Distance 6.0. Release 4. Research Unit for Wildlife Population Assessment, University of St Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/

Walker, D., Telfer, M., and Cresswell, G. 2004. The status and distribution of beaked whales (Ziphiidae) in the Bay of Biscay. Pp. 278-282. In: European Research on Cetaceans – 15 (Eds. P.G.H. Evans and E. O'Boyle). Proc. of the 15th Ann. Conf. of the European Cetacean Society, Rome, Italy, 6-10 May 2001. European Cetacean Society, Kiel, Germany. 478pp.

Williams, A.D., Brereton, T.M. and Williams, R. 1999. Seasonal variation in the occurrence of beaked whales in the southern Bay of Biscay. Pp. 275-280. In: European Research on Cetaceans – 13 (Eds. P.G.H. Evans, J. Cruz and J.A. Raga). Proc. of the 13th Ann. Conf. of the European Cetacean Society, Valencia, Spain, 5-8 April 1999. European Cetacean Society, Valencia, Spain. 484pp.

Wood, SN (2006). Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC. Boca Raton, FL, USA.

Table 1. Covariates used in the modeling analysis and to populate the spatial grid for prediction.

Name	Description	Source
depth	Average depth in the grid cell	2-Minute Gridded Global Relief Data (ETOPO2v2). National Geophysical Data Center (NGDC). NOAA Satellite and Information Service.
depthsd	Standard deviation of the depth data points within the grid cell	Derived from ETOPO2 bathymetric data
dist0	Distance to the 0 m depth contour (coast), in decimal degrees	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
dist200	Distance to the 200 m depth contour, in decimal degrees	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
dist2000	Distance to the 2000 m depth contour, in decimal degrees	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
slope	Slope of the sea floor in m per km, calculated as follows: $\frac{\left(\frac{depth_{max} - depth_{min}}{distance\ in\ km_{(depth_{max} - depth_{min})}}\right)}{10}$	Derived from ETOPO2 bathymetric data
ci	Contour index of the sea floor, calculated as follows: $\frac{(depth_{max} - depth_{min})}{depth_{max}} * 100$	Derived from ETOPO2 bathymetric data
ssh	Average Sea Surface Height Anomaly for the months of June to August 2005 and 2007, calculated as the difference between measured SSH and the expected mean SSH.	Altimetry Sensors on multiple spacecrafts (JASON-1, TOPEX/POSEIDON, ENVISAT, GFO, ERS 1/2, GEOSAT). Resolution: 0.25 degrees. NOAA CoastWatch Program
sst	Average Sea Surface Temperature for the months of June to August 2005 and 2007.	Sensor: Moderate Resolution Imaging Spectroradiometer (MODIS) on Aqua, Advanced Very High Resolution Radiometer (AVHRR) on POES, Imager on GOES, Advanced Microwave Scanning Radiometer (AMSR-E) on Aqua. Resolution: 0.1 degrees. NOAA CoastWatch Program
sst_sd	Standard deviation of Sea Surface Temperature for the months of June to August 2005 and 2007.	Derived from NOAA CoastWatch Program sea surface temperature data.
chla	Average Chlorophyll-a concentration for the months of June to August 2005 and 2007.	Sensor: Sea-viewing Wide Field-of-view Sensor (SeaWiFS). Resolution: 0.1 degrees. NOAA CoastWatch Program
chla_sd	Standard deviation of Chlorophyll-a concentration for the months of June to August 2005 and 2007.	Derived from NOAA CoastWatch Program Chlorophyll-a concentration data.

prpr	Average primary productivity for the months of June to August 2005 and 2007.	Measurement of primary productivity based on the following satellite measurements: Chlorophyll-a concentration and photosynthetically available radiation (PAR) measurements from the SeaWiFS sensor aboard the GeoEye spacecraft, SST measurements from the NOAA Pathfinder Project and from the Reynolds Optimally-Interpolated SST (OISST) v2 product from NOAA's National Climatic Data Center (NCDC). Resolution: 0.1 degrees. NOAA CoastWatch Program
prpr_sd	Standard deviation of primary productivity for the months of June to August 2005 and 2007.	Derived from NOAA CoastWatch Program primary productivity data.
lat	Latitude in decimal degrees	
lon	Longitude in decimal degrees	

Table 2. Covariates available for fitting detection functions.

Name	Description	Type	Levels
sightability	Qualitative measure of the searching conditions for detecting dolphins (including sea state, glare, visibility, etc)	factor	0 – Excellent 1 – Good 2 – Moderate 3 – Poor
swell	Height and length of the swell	factor	0 – No swell 1 – Low <1m short/average 2 – Low <1m long 3 – Moderate <2m short/average 4 – Moderate <2m long 5 – Big <2-4m short/average 6 – Big <2-4m long 9 - Confused
swellf	Height of swell condensed in three levels	factor	0 – No swell 1 – Low <1m 2 – Moderate-Big >1m 3 – Confused
platfactor	Height of the Primary platform	factor	1 – < 6m 2 – > 6-8m 3 - > 8m
platheight	Height of the Primary platform (m)	continuous	
beaufort	*Ad hoc* scale of sea state	factor	0 - glassy mirror-like 0.5 - glassy & ripple patches 1 - scale ripples 2 - small wavelets 2.5 - rare whitecaps 3 - whitecaps, 1 - 5/sector 4 - frequent whitecaps
vessel	Vessel	factor	GO - Gorm IN - Investigador MC - Mars Chaser SK - Skagerak VH - Victor Hensen WF - West Freezer ZI - Zirfaea GE - Germinal RA - Rari CS - Cornide de Saavedra
size	Group size	continuous	
cue	Cue that caused the detection	factor	BL - Blow SP - Splash JU - Jump/Breach SL - Slick BY - Body FL - Flash AW - Assoc wildlife SB - Seabirds SD - Sound
cue2	Cue that caused the detection, condensed into two levels	factor	UC – inconspicuous (BY + FL) C – conspicuous (rest of levels)

Table 3. Areas and length of transect searched for each survey region used in analysis. Data are for sea state Beaufort 0-4 for SCANS-II (ship), CODA and TNASS (Faroes), and for good and moderate conditions for SCANS-II (air) (equivalent to Beaufort 0-2). Data for sea state Beaufort 0-2 only were used in harbor porpoise analysis.

Region	Area (km^2)	Transect (km)	Transect (km) Beaufort 0-2
SCANS-II (ship)	1,005,743	19,614	9,085
SCANS-II (air)	364,371	15,802	15,802
CODA	967,538	9,491	4,313
TNASS (Faroes)	685,628	2,318	810
Total area	3,023,280	47,225	30.010

Table 4. Number of sightings of each species in each survey region used in analysis (after truncation).

Species	SCANS-II	CODA	Faroese T-NASS	All
Ziphius cavirostris	3	14	0	17
Hyperoodon ampullatus	0	3	12	15
Mesoplodon bidens	0	6	0	6
Unidentified beaked whale	7	18	0	25
TOTAL	10	41	12	63

Table 5. Covariates retained in the final models for abundance of groups and for group sizes, including the maximum number of knots allowed, the estimated degrees of freedom (approximately the number of knots used in the model - 1), the probability of that covariate being included in the model by chance (*p*) and the deviance explained by the model. The symbol ":" means "interaction with".

Covariate	Max. knots allowed	Estimated degrees of freedom	p	Deviance explained
Abundance of groups				
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	
Group sizes				
Depth:Ci	20	4.71	0.762	26.8%
Lat	8	3.89	0.449	

Table 6. Design-based estimates of abundance for each species and block with coefficient of variation (CV) and 95% confidence limits calculated assuming the estimates are log-normally distributed.

	Survey block	Primary sightings	Abundance of animals	CV	Lower 95% CL	Upper 95% CL
Z. cavirostris	CODA 1	1	**101**	0.98	20	503
	CODA 2	1	**148**	0.95	31	717
	CODA 3	1	**219**	0.97	44	1,078
	CODA 4	11	**1,456**	0.74	400	5,301
	CODA total	14	**1,924**	0.58	695	5,327
	SCANS-II	3	**362**	0.58	126	1,042
	T-NASS (Faroes)	0				
	Total	**17**	**2,286**	**0.49**	**942**	**5,552**
H. ampullatus	CODA 1	2	**3,106**	0.73	865	11,152
	CODA 2	1	**148**	1.01	29	767
	CODA 3	0				
	CODA 4	0				
	CODA total	3	**3,254**	0.70	982	10,781
	SCANS-II	0				
	T-NASS (Faroes)	12	**16,284**	0.41	7,560	35,077
	Total	**15**	**19,539**	**0.36**	**9,921**	**38,482**
M. bidens	CODA 1	5	**3,190**	0.48	1,311	7,761
	CODA 2	0				
	CODA 3	1	**328**	1.07	59	1,819
	CODA 4	0				
	CODA total	6	**3,518**	0.44	1,570	7,883
	SCANS-II	0				
	T-NASS (Faroes)	0				
	Total	**6**	**3,518**	**0.44**	1,570	7,883
All species	**TOTAL**	**38**	**24,792**	**0.30**	**14,706**	**43,675**
Unid. beaked whales	CODA 1	6	911	0.48	374	2,221
	CODA 2	5	1,354	0.53	510	3,597
	CODA 3	2	219	0.63	70	682
	CODA 4	5	956	0.54	352	2,594
	CODA total	18	3,441	0.29	2,006	5,900
	SCANS-II	7	370	0.46	161	852
	T-NASS (Faroes)	0			-	-
	Total	**25**	**3,811**	**0.26**	**2,322**	**6,254**
Total beaked whales	CODA 1	14	7,309	0.37	3,654	14,617
	CODA 2	7	1,651	0.45	714	3,817
	CODA 3	4	766	0.55	282	2,081
	CODA 4	16	2,412	0.63	780	7,456
	CODA total	41	12,137	0.26	7,445	19,787
	SCANS-II	10	732	0.42	339	1,584
	T-NASS (Faroes)	12	16,284	0.41	7,560	35,077
	Total	**63**	**29,154**	**0.25**	**18,042**	**47,110**

Table 7. Estimates of abundance for beaked whale species unadjusted and adjusted for the addition of a proportion of unidentified beaked whale abundance.

	Survey block	Unadjusted abundance of animals	CV	Proportion of identified	Adjusted abundance of animals	CV	Lower 95% CL	Upper 95% CL
Z. cavirostris	CODA 1	**101**	0.98	0.13	**221**	4.79	7	7,276
	CODA 2	**148**	0.95	0.50	**825**	1.15	136	4,999
	CODA 3	**219**	0.97	0.50	**328**	3.70	13	8,170
	CODA 4	**1,456**	0.74	1.00	**2,412**	0.54	901	6,458
	CODA total	**1,924**	0.58		**3,787**	0.60	1,275	11,243
	SCANS-II	**362**	0.58	1.00	**684**	0.39	327	1,429
	T-NASS (Faroes)							
	Total	**2,286**	**0.49**		**4,471**	0.51	1,735	11,519
H. ampullatus	CODA 1	**3,106**	0.73	0.25	**3,346**	0.71	952	11,766
	CODA 2	**148**	1.01	0.50	**825**	1.15	136	5,007
	CODA 3							
	CODA 4							
	CODA total	**3,254**	0.70		**4,171**	0.62	1,372	12,683
	SCANS-II							
	T-NASS (Faroes)	**16,284**	0.41	1.00	**16,284**	0.41	7,560	35,077
	Total	**19,539**	**0.36**		**20,456**	0.35	10,553	39,650
M. bidens	CODA 1	**3,190**	0.48	0.63	**3,790**	0.43	1,704	8,426
	CODA 2							
	CODA 3	**328**	1.07	0.50	**438**	2.85	24	8,073
	CODA 4							
	CODA total	**3,518**	0.44		**4,227**	0.48	1,725	10,356
	SCANS-II							
	T-NASS (Faroes)							
	Total	**3,518**	**0.44**		**4,227**	0.48	1,725	10,356
All species	**TOTAL**	**24,792**	**0.30**		**29,154**	**0.27**	**17,478**	**48,629**

Table 8. Model-based estimates of abundance for beaked whales as a group per survey area with coefficient of variation (CV) and 95% confidence limits obtained from bootstrap.

	Survey area	Primary sightings	Abundance of animals	CV	Lower 95% CL	Upper 95% CL
Beaked whales	CODA	41	11,104	0.23	7,284	17,504
	SCANS-II	10	1,245	0.28	672	1,984
	T-NASS (Faroes)	12	17,159	0.34	10,638	39,038
	Total	**63**	**28,711**	**0.23**	**22,835**	**36,098**

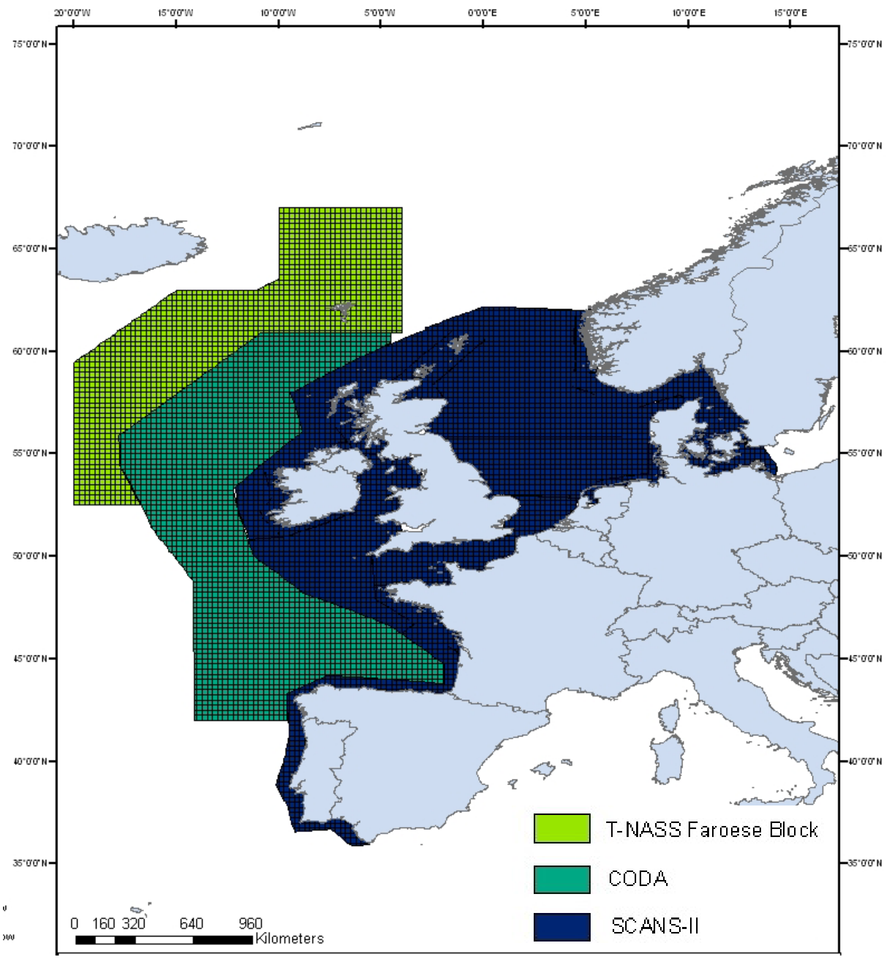

Figure 1. Survey areas: SCANS-II 2005, CODA 2007 and the Faroese block of TNASS 2007.

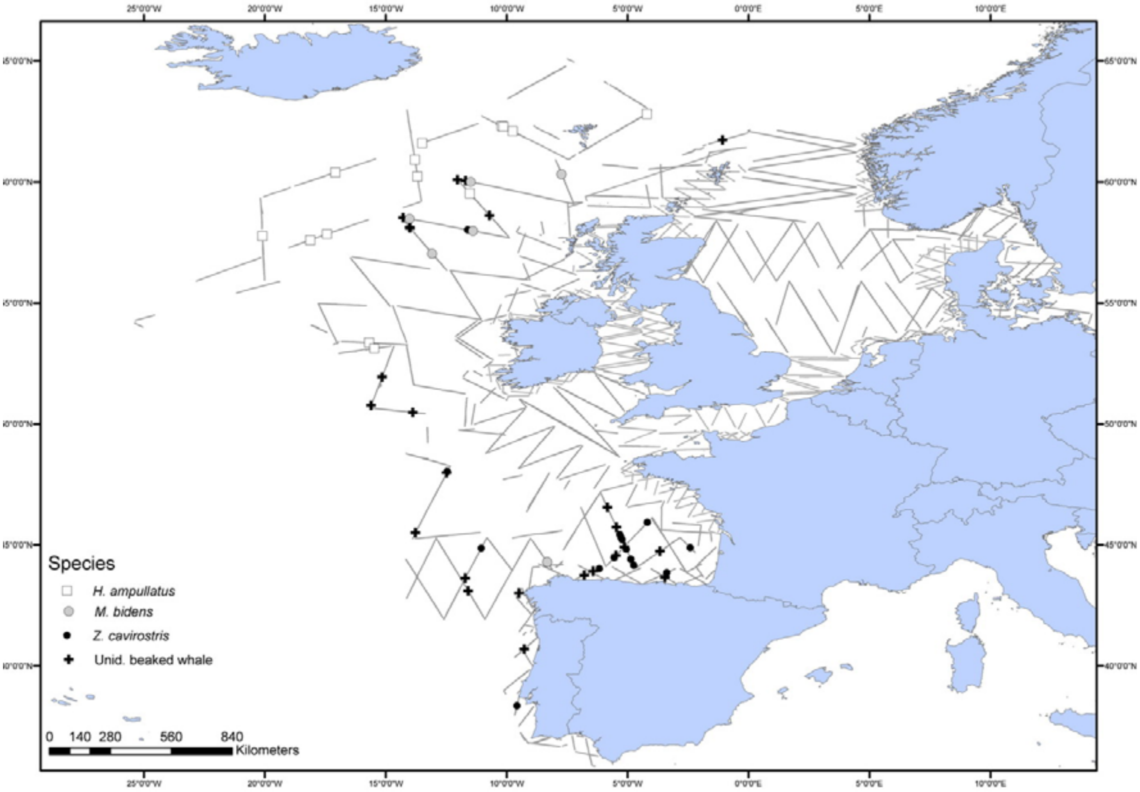

Figure 2. Effort tracks and sightings of beaked whales

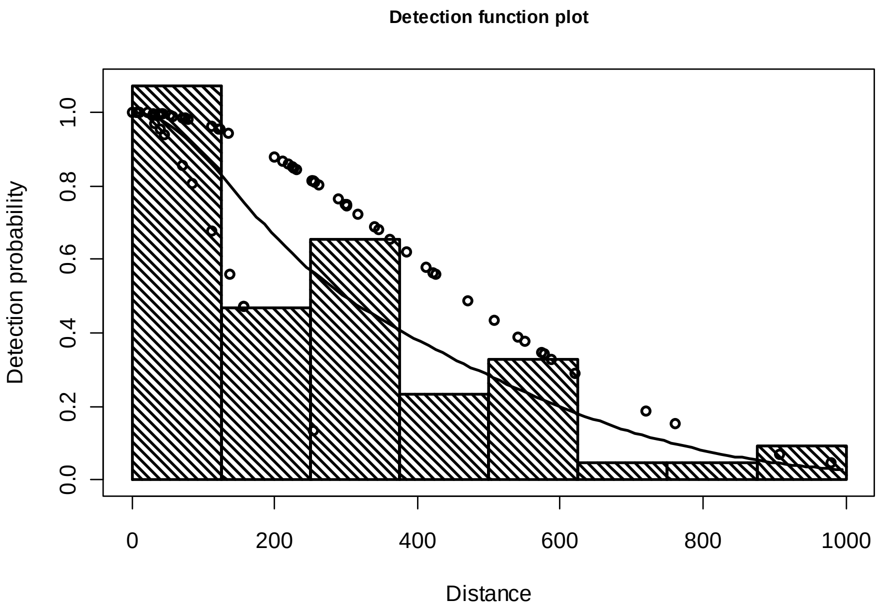

Figure 3. Detection function for beaked whales. The open circles are the data. The line is the fitted function. The histogram show the frequency of all sightings.

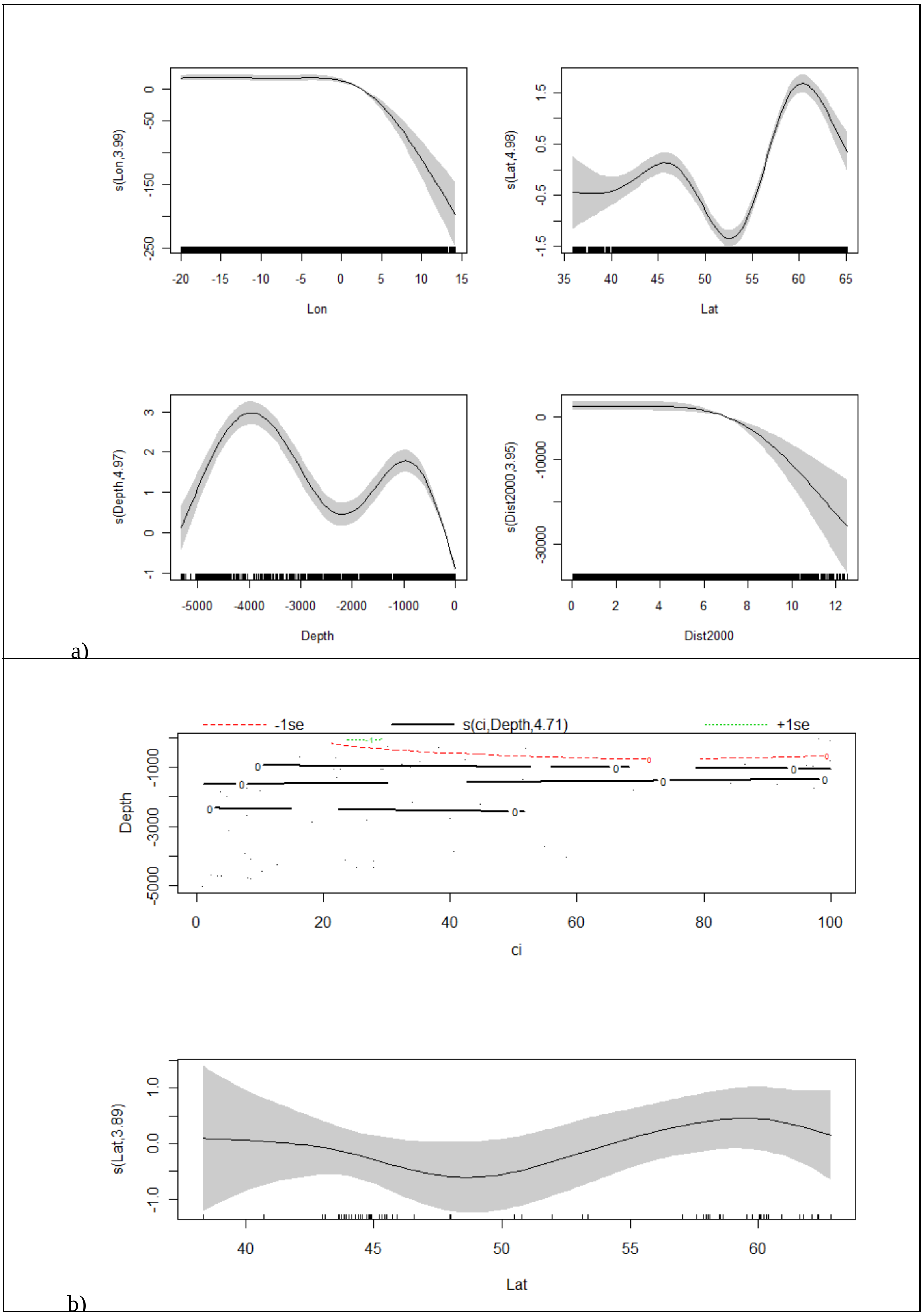

Figure 4. Fitted smooth functions for each covariate in the final models for (a) abundance of groups and (b) group size.

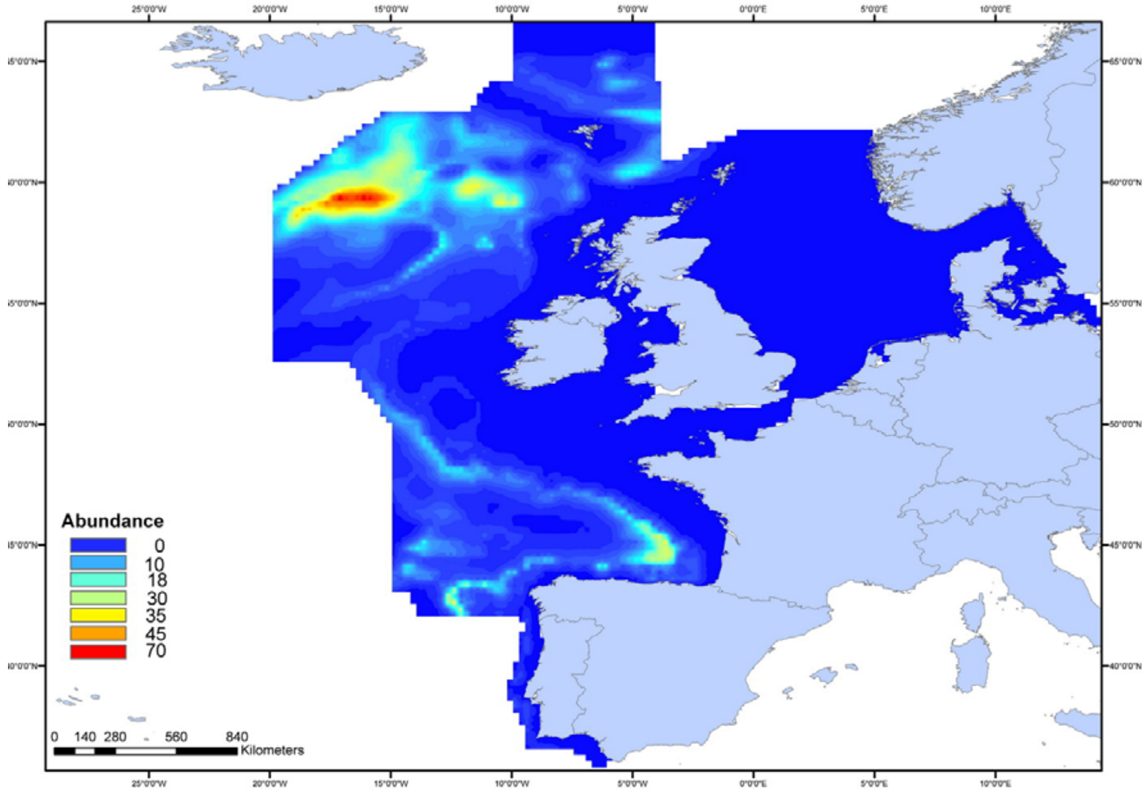

Figure 5. Predicted density surface of beaked whales in the European Atlantic