The challenge of habitat modelling for threatened low density species using heterogeneous data: the case of Cuvier's beaked whales in the Mediterranean

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ABSTRACT

The Mediterranean population of Cuvier´s beaked whale (*Ziphius cavirostris*), a deep-diving cetacean, is genetically distinct from the Atlantic, and subject to a number of conservation threats, in particular underwater noise. It is also cryptic at the surface and relatively rare, so obtain robust knowledge on distribution and abundance presents unique challenges. Here we use multiplatform and multiyear survey data to analyse the distribution and abundance of this species across the Mediterranean Sea. We use a novel approach combining heterogeneous data gathered with different methods to obtain a single density index for the region. A total of 594,996 km of survey effort and 507 sightings of Cuvier’s beaked whales, from 1990 to 2016, were pooled together from 24 different sources. Data were divided into twelve major groups according to platform height, speed and sea state. Both availability bias and effective strip width were calculated from the sightings with available perpendicular distance data. This was extrapolated to the rest of the sightings for each of the twelve groups. Habitat preference models were fitted into a GAM framework using counts of groups as a response variable with the effective searched area as an offset. Depth, coefficient of variation of depth, longitude and marine regions (as defined by the International Hydrographic Organization) were identified as important predictors. Predicted abundance of groups per grid cell were multiplied by mean group size to obtain a prediction of the abundance of animals. A total abundance of 5799 (CV=24.0%) animals was estimated for the whole Mediterranean basin. The Alborán Sea, Ligurian Sea, Hellenic Trench, southern Adriatic Sea and eastern Ionian Sea were identified as being the main hot spots in the region. It is important to urge that the relevant stakeholders incorporate this information in the planning and execution of high risk activities in these high-risk areas.

KEYWORDS: Cuvier’s beaked whales; abundance; distribution; conservation; density surface modelling; correction factor; Mediterranean Sea

1. INTRODUCTION

The Cuvier´s beaked whale (*Ziphius cavirostris*) is the only member of the Ziphiidae family with a regular occurrence in the Mediterranean Sea, inhabiting both the western and eastern basins (Notarbartolo di Sciara 2016; Podestà et al. 2016). Much of the early knowledge of this species in the Mediterranean has come from stranding data (Figure S10 in Supplementary Material). In total 316 animals were found between 1986 and 2003 (Podestà et al. 2006). However, stranding data are potentially subject to severe bias because the location of the strandings might be more related to the regional currents and the stranding place might be far away from where the animals actually were, so they cannot be used alone to make strong inferences about at-sea distribution (Peltier et al. 2014). The lack of more quantitative distribution and abundance data has certainly contributed to the current ‘Data Deficient’ IUCN listing for this species (Cañadas 2006), which means that there was insufficient information available to assess the conservation status, and no Red List Category could be assigned.

Cuvier’s beaked whales seem to be relatively abundant in the eastern Ligurian Sea, off southwestern Crete and in the Alborán Sea, especially over and around canyons (Cañadas and Vázquez 2014; D'Amico et al. 2003; Frantzis et al. 2003). They appear to be regular inhabitants of the western Ligurian Sea (Azzellino et al. 2008), the Hellenic Trench (Frantzis et al. 2003), the southern Adriatic Sea (Holcer et al. 2007) and the eastern section of the Alborán Sea (Canadas et al. 2005; Cañadas and Vázquez 2014). They also occur in the central Tyrrhenian Sea (Marini et al. 1992) and in Spanish Mediterranean waters (Raga and Pantoja 2004); M. Castellote, pers. comm.). However, survey effort and the efficiency of stranding networks vary greatly across the region, with little or no effort to record sightings or to detect strandings in some areas, particularly in the southern and eastern parts of the basin, except for Syria and Israel (Aharoni 1944; Gonzalvo and Bearzi 2008; Kerem et al. 2012). In addition, they are very difficult to detect reliably because of their long dive times (over 60 min; (Baird et al. 2006; Baird et al. 2008; Cañadas and Vázquez 2014; Tyack et al. 2006) and usually inconspicuous and brief appearances at the surface (Heyning 1989). As a result, knowledge of the abundance and population trends in this population is severely limited. In the Gulf of Genova (eastern Ligurian Sea) mark-recapture analysis (2002-2008) yielded estimates between 95 (CV=9%) and 98 (CV=10%) using open population models (Podestà et al. 2016; Rosso et al. 2009). In the Alborán Sea, off Southern Spain, spatial modelling of line transect data (1992–2009) yielded an abundance estimate of 429 individuals (CV=22%, corrected for availability bias; Cañadas and Vázquez 2014).

This species face multiple threats, of which the most significant are anthropogenic noise, fishery interactions and shipping. Firstly, underwater acoustic pollution is recognized as a threat for marine fauna, including deep diving species (Cox et al. 2006; Filadelfo et al. 2009). Beaked whales appear especially vulnerable, with recorded cases of mortality as a consequence of high-intensity noise in areas including the Mediterranean, Canary Islands, United States, Bahamas and Japan, (Arbelo et al. 2008; Balcomb III and Claridge 2001; Fernández et al. 2012; Frantzis 1998; Podestà et al. 2006). They have also shown behavioural responses at sound levels well below those previously thought to affect this group (Cox et al. 2006; Fernández et al. 2012; Filadelfo et al. 2009; Pirotta et al. 2012; Tyack et al. 2011). The numerous cases where mass-strandings of beaked whales followed (and where related to) naval exercises (Balcomb III and Claridge 2001; Filadelfo et al. 2009; Frantzis 1998) have resulted in these species becoming indicators for the effects of high intensity anthropogenic noise.

Secondly, fishery interactions are a consistent threat to all Mediterranean cetaceans (Reeves and Notarbartolo di Sciara 2006), and this includes Cuvier’s beaked whales. Fourteen were reported as having been captured incidentally between 1972 and 1982 (11 in French waters and 3 in Spanish waters (Northridge 1984)) and two more in Italian waters in subsequent years (Notarbartolo di Sciara 1990). Entanglement in fishing gear and other marine debris have also been recorded (Cañadas and Vázquez 2014; Podestà et al. 2016), but actual occurrence is unknown.

Finally, the Mediterranean is one of the busiest shipping regions in the world. Large cetaceans are vulnerable to ship strikes and increased sea ambient noise. While there are no data on ship strikes on Cuvier's beaked whales in the Mediterranean, Carrillo and Ritter (2010) reported that 12% of the strandings with signs of ship strikes in the Canary Islands correspond to beaked whales. Additionally, shipping increases ambient noise, with the potential to mask the ultrasonic echolocation signals of beaked whales and thereby interfere with their sensory biology (Aguilar Soto et al. 2006).

Increasing awareness of numerous and synergistic threats to cetaceans in the Mediterranean Sea led, in part, to the creation of ACCOBAMS (Agreement for the Conservation of Cetaceans in the Black Sea, Mediterranean Sea and Atlantic contiguous waters), under the auspices of the Convention on migratory species. The Fourth meeting of the Scientific Committee of ACCOBAMS (Monaco, November 2006) addressed the issue of the impact of anthropogenic noise on marine mammals in the Mediterranean, and noted that in the specific case of Cuvier's beaked whales, fundamental information on their distribution and habitat use in the Mediterranean waters was scarce. The Committee agreed that information on the distribution and habitat use of Cuvier's beaked whales in the region should be made available to interested parties and stakeholders to prevent the production of high intensity noise in areas of high density for this species. Given that appropriate data on distribution and relative (or absolute) abundance of Cuvier's beaked whales in the Mediterranean were lacking, the Committee recommended that a habitat modelling exercise should be attempted for the Mediterranean Sea.

The use of multiplatform and multiyear survey data from multiple sources to estimate the distribution and abundance of cetacean species is extremely challenging, but made necessary by the paucity of data and large scale objectives of the study. For species which are threatened, rare and difficult to detect, whose spatial range encompasses both international and waters of multiple nations, pooling together all available information is the only option for increasing knowledge. Heterogeneity in factors such as the data collection procedures, height and speed of the platforms, observer experience, and so forth, can easily lead to biased results (Jewell et al. 2012). Pooling together large amounts of multiplatform data to yield a single result per species has been previously achieved using both line transect data (Jewell et al. 2012; Roberts et al. 2016) and presence only data (Kaschner et al. 2006; Ready et al. 2010). Combining heterogeneous effort related data from both line transect data *and* non-line transect data (i.e. with and without perpendicular distances) to obtain a single density index has not however been done before to our knowledge. Here we present the results of an effort to pool such data on Cuvier's beaked whales in the Mediterranean region. We adopted a novel approach to combine heterogeneous data into a single habitat preference model. This was based on stratification by platform type, extrapolation of perpendicular distance data according to such stratification, and the application of correction factors to take into account availability bias according to platform type.

2. METHODS

2.1 Data collection and compilation

Twenty four institutions contributed data, totalling 594,996 km of survey effort in good to moderate visual conditions (sea state of Beaufort 3 or less). This survey effort yielded 507 sightings of Cuvier's beaked whales with a total of 1,166 individuals, covering a time span from 1990 to 2016 (Table S1 in the Supplementary Material; Figure 1). These data are divided by time period and platform type in the online supplementary material (Figures S1-6).

Areas with a low research effort and areas with no research effort were due to lack of funding and/or lack of permits in some countries.

It was not possible to constrict the data used to a single platform type (e.g. ships *vs* airplanes, large ships *vs* small ships) because none of them cover all the areas, so very large portions would remain empty of effort and the purpose of this collaborative and integrating effort would be meaningless. However, to minimise the potential bias created by using different platforms, a correction factor is fundamental (see point 2.2.2 below).

2.2 Data organization

2.2.1 Sampling units

A grid of 7287 cells with a resolution of 0.2º (22.2 km) was built (with an average size of 494 km^2, ranging from 403 km^2 in the northern part of the area to 455 km^2 in the South). The size of the grid was chosen as a trade-off between limiting the number of grid cells for computational reasons and the resolution of the available covariates. A number of geographical and environmental covariates were associated to each grid cell. These were of three types: (a) Geographic: latitude and longitude, and Marine Region; (b) Fixed: depth, distance from the 200, 1000 and 2000 m isobaths, coefficient of variation of depth, slope, contour index ((max depth-min depth)*100/max depth), aspect (orientation of sea floor in 360º), factor with classification into three levels: Abyss, Slope and Shelf (Ab-Sl-Sh), factor with classification into three levels: Canyon, Escarpment, or None (Cany-Escarp-None), distance from the slope area (steep area between the continental shelf and the abyss plains), from canyons and escarpments, and from sea mounts; (c) Dynamic: SST_All (mean annual sea surface temperature 1990-2015) and SST.SD_All (Inter-annual standard deviation of the annual sea surface temperature 1990-2015). The covariate 'Marine Regions' (see Figure S7 in supplementary material), is a subdivision of the Mediterranean basin into smaller areas, obtained from the International Hydrographic Organization (IHO 1953). The large Libyan-Levantine basin was subdivided into Libyan and Levantine according to the ICES ecoregions (ICES 2004). The Hellenic Trench was added as a separate region (IHO 2016). Figure S11 shows the depth contours in the Mediterranean Sea.

Search effort was divided into segments fitting grid cells, with the tool *Identity* in ArcGis. In this way, each segment of search effort track was assigned to a grid cell, and the covariates associated with that grid cell were then associated to that segment, as well as the source (data owner), type of survey (aerial, ferry, large research ship or small ship/boat), day and sea state. This resulted in a total of 107,393 segments. These segments were aggregated in each grid cell according to source and year, totalling 16,554 units of source-year-cell, which constituted the sampling units, with total effort (in km), number of sightings, and number of animals associated with unit. The total number of grid cells containing effort was 4449, representing 61.0% of the total Mediterranean Sea.

No stratification was possible by season or year (nor was the temporal aspect included as a covariate) due to the high heterogeneity in coverage and platforms used among seasons and among years. Areas with year-round effort, such as the Alborán Sea (Cañadas and Vázquez 2014) and Ligurian Sea (Rosso et al. 2011), have sightings of this species in the same areas in all seasons, suggesting that major seasonal changes in distribution do not occur, although it must be noted that these data pertain only to a sub-section of the study area.

2.2.2 Correction for availability

There was considerable heterogeneity in survey platforms (and therefore observer height and platform speed). Platforms included aerial surveys (fast speed and pre-designed routes), ferries (high observation point and speeds, usually around 30 km/h), research and whale watching ships or boats (speed ranging between 6 and 14 km/h, and observer heights between 3 and 15 m). Platform speed was either provided directly or measured from the GPS data for all segments. While in most cases the approximate height of the observation platform (an approximation to the height of the observer's eye) was available, in some cases it was assumed based on the characteristics of the vessel.

Density estimates from line transect surveys are usually subject to availability bias, due to animals not always being available for detection (e.g. actually surfacing) while within detectable range (Buckland et al. 2004), and perception bias due to observers failing to detect animals even though they are available to be detected (Buckland and Elston 1993). For beaked whales, both sources of bias are known to be important (Barlow 1999, 2006; Borchers et al. 2013; Cañadas and Vázquez 2014). Correcting for perception bias typically requires some form of double platform approach, and was not possible here because no such data were available. However, we were able to take steps to mitigate the effect of availability bias.

As no radial or perpendicular distances were available for most datasets, abundance could not be estimated with the distance sampling method (Buckland et al. 2001). However, such distances were available for some of the datasets, allowing the estimation of an availability bias. The availability bias was used as a correction factor to minimize the heterogeneity in platforms and the large spatial differences in coverage by different platform types, which could yield a bias in the density surface modelling. Laake et al. (1997) developed a correction factor, $\hat{a}$, to correct estimates for availability bias. This factor takes into account the average duration of the availability (animals present at surface) and unavailability (animals underwater) and the time an animal is within a detectable range. The detectable range was estimated by dividing the maximum forward distance at which animals are expected to be detected by the platform's speed. The average duration of availability and unavailability was estimated using data on focal follows of Cuvier's beaked whales collected during surveys in the Alborán Sea in 2008 and 2009 (Cañadas and Vázquez 2014). For the datasets with available radial distances, these were used to estimate the forward distances for the sightings. Subsequently the particular correction factor for availability bias for a range of platform speeds for those datasets were estimated, using a cut-off point of 80% of the forward distances to avoid outliers (Cañadas and Vázquez 2014). The range of speeds used was between 1 and 50 km/h (depending on the range of each platform, and at intervals of 0.1 km/h) and 185 km/h for aircraft. For other datasets without radial distance, the correction factors of the platforms with similar attributes of type and height were assigned. Given that the potential maximum radial distance of detection depends largely on the height of the observation platform (as proxy to height of observer eye), data were divided into twelve major groups according to the platform height, speed and sea state following Cañadas and Vázquez (2014)(Table 1).

2.2.3 Correction for effective searched area

A similar procedure was used to estimate an effective strip width (*esw*) which was associated with all segments of effort. Using the known perpendicular distances where available, specific detection functions were created for all the platform groups. The particular *esw* for each platform type was estimated from their detection function and used for all platforms in that group. An effective search area was calculated for each segment (included in the models as offset), as *L*2*esw* where L is the length of the segment (in kilometres). The mean speed for all segments of a particular platform and year was used to obtain a mean $\hat{a}$ and *esw* for each platform/year. Finally, the calculated effective search area for each segment was multiplied by the appropriate mean $\hat{a}$ to obtain the effective search area corrected for availability bias. This was then used as the final offset in the spatial models (Table 1).

We assumed that for similar platform type, height and speed, and similar sea state conditions, the mean availability bias and mean *esw* were similar. Other factors that might affect estimates of availability bias and *esw* include observer experience, the number of observers and searching protocols. However, as these could not rigorously be corrected for these factors, we assumed that the main sources of variability associated with platform height and speed were taken into account.

2.3 Data analysis

2.3.1 Spatial models and abundance estimate

The response variable used to formulate the spatial models of abundance of groups was the count of groups (N) in each sampling unit (Hedley et al. 1999). The abundance of groups was modelled using a Generalized Additive Model (GAM) with a logarithmic link function. Overdispersion was tested in models with a Poisson distribution using the Poisson Pearson residuals ($\sum \text{residuals}^2/(N-p)$ where N is the sample size of effort and p is the number of parameters of the model). The results was 7.3, way above the acceptable limit of 1.5 for a Poisson distribution. Therefore, a Tweedie error distribution was used, with a parameter p of 1.1, very close to a Poisson distribution but with some over-dispersion.

The general structure of the model was:

$$\hat{N}_i = \exp\left[\ln(a_i) + \theta_0 + \sum_k f_k(z_{ik})\right] \qquad (2)$$

where the offset a_i is the search area for the i^{th} sampling unit (corrected for availability bias), 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.

Models were fitted using package ‘mgcv’ version 1.7-22 for R (Wood 2011). Model selection was done manually using three diagnostic indicators: (a) the GCV (Generalised Cross Validation score, an approximation to AIC; Wood 2000); (b) the percentage of deviance explained; and (c) the probability that each variable was included in the model by chance (p-value of the covariate in the model). Only one of the collinear covariates was used in each iteration of model selection, unless the collinearity was weak and the inclusion of the two covariates improved the model. Table S2 (Supplementary Material) shows the Pearson's product-moment correlation among pairs of all continuous covariates.

The model returned a prediction for the abundance of groups in each grid cell. A model for group size was attempted but there were no significant results, so we assumed there was no systematic variation in group size across the study area. Therefore, we multiplied the predicted number of groups in each grid cell by the mean group size of the Marine Region to which the cell belonged (Figure S7 in Supplementary Material). The point estimate of total abundance was then obtained by summing the abundance estimates of all grid cells over the study area and plotted as a density surface map in ArcGis 10.0.

Finally, a non-parametric bootstrap with replacement with 400 iterations was used to generate the model coefficient of variation (CV) and 95% confidence intervals for the resulting habitat use prediction maps and abundance estimates. To obtain a total CV, the model CV was combined with the overall *esw* CV and mean $\hat{a}$ CV through the Delta method (Seber 1982).

3. RESULTS

All the group size records ranged between 1 and 8 individuals, with only one large group of 20 animals in the Alborán Sea. Mean group sizes ranged between 1.6 in the Libyan Sea and 2.5 in the Ionian Sea. Figure S11 (Supplementary Material) shows the detection functions for all the combinations for which data were available, to obtain a measure of *esw*.

A total of 60 models were tried with different combinations of covariates. The best model for abundance of groups, according to the diagnostics, included four covariates: depth, coefficient of variation of depth, longitude and marine region, with a total deviance explained of 34% (Table 2; Figure 2). All the other models either had smaller deviance explained, larger GCV, non-significant covariates or edge-effect issues.

The total abundance estimate obtained through modelling, once the correction factor for the effective searched area was applied, was 5799 animals in the whole Mediterranean (4261 when excluding the area south of 34.3ºN and the Aegean Sea), with a total CV of 24.0% (CV_{model}=11.5%; CV_{esw}=14.7%; $CV_{\hat{a}}$=15.0%) and a 95% CI of 4807 – 7254. This would equate to an overall density of 0.00223 animals per km^2 for the whole Mediterranean.

Figure 2 shows the smoothed functions of the continuous covariates selected in the final model. Cuvier's beaked whales show a highest density between 1000 and 1500m. Density declines sharply in waters shallower than 1000m. There is also a preference for areas with medium to high variability in bottom depth (CV of depth). However, the areas with highest CV of depth are associated with low data density, so have a large prediction uncertainty and results for these areas should therefore be interpreted with caution. The smooth term associated with longitude has a lower density around 14ºE-18ºE, including the northern Adriatic, eastern Tyrrhenian Sea and southeast of Sicily, and a much less pronounced area of low density between 4ºE-7ºE (Figure 3) between France and Algeria.

The predicted abundance of Cuvier's beaked whales in the Mediterranean (Figure 3) shows two areas marked with diagonal lines: the area south of 34.3ºN and the Aegean Sea, where reliability is low due to the very low effort (Figure 1). Figures S8 and S9 (Supplementary Material) show the lower and upper 95% confidence intervals. Figure S10 (Supplementary Material) shows the beaked whale sighting and stranding locations overlying this prediction.

4. DISCUSSION

Little or no data were available for large portions of the region, so it is necessarily the case that the conclusions we draw here regarding distribution and abundance need to be taken with caution. Therefore, the results presented here ideally need to be validated by a systematic and region-wide survey of the Mediterranean Sea.

4.1 Habitat preferences

Cuvier's beaked whales show a clear habitat preference for areas with depths over 1000m, and medium to high variability in bottom depth (CV of depth), which would usually include escarpments, canyons and sea mounts. This coincides with previous descriptions of the habitat of this species in the Mediterranean and the Northeast Atlantic as a predominantly oceanic species often associated with steep slope habitat and a marked preference for submarine canyons and escarpments (D'Amico et al. 2003; Frantzis et al. 20013; MacLeod 2005; Podestá et al. 2006; Azzellino et al. 2008). Also in the Eastern Tropical Pacific habitat modelling on this species show a preference for depths over 1000m (Ferguson et al. 2006), as does an habitat-cetacean relationship study in the Gulf of Mexico (Davis et al. 1998), among other studies.. The lower density around 14ºE-18ºE detected by the smoothed term of Longitud, coincides with shallower areas of the northern Adriatic and the southeast of Sicily. Considering that there is generally good effort coverage in this region it suggests that this is a genuine area of relatively low density. In contrast, there is little effort between France and Algeria (4ºE-7ºE, less pronounced area of low density), especially in the south, so this apparent gap in distribution should be treated with caution.

It is interesting to look at the effect of other covariates explored. The factor "Cany_Escarp", with three levels: Canyon, Escarpment or None, explained 7% of the deviance and had a positive effect (higher density) for Escarpment and negative for None, with respect to Canyon (which was the intercept). Its associated covariate "Dist_c_e" (distance from canyons and escarpments) explained 8.3% of the deviance and predicted higher numbers with declining distances from canyons and escarpments. The distance from sea mounts (Dist_mounts explained 9.2% of the deviance, and showed a strong positive effect at the closest distances, and a second, smaller peak at long distances. Distance from the slope (Dist_Slope) explained 6% of the deviance and had a more positive effect at closer distances from the slope area. The same happened with "Dist_1000", explaining 9% of the deviance. This information is consistent with existing knowledge about habitat use by Cuvier's beaked whales (a preference for deep waters and steep floors; e.g. Cañadas and Vazquez 2014; Arcangelli et al. 2016; Podestà et al. 2016), suggesting that areas of high bathymetric relief are important for Cuvier's beaked whales.

The main influence of the physical environment over cetacean distribution is most probably the aggregation of prey species (Baumgartner 1997; Davis et al. 1998). For beaked whales main prey species, cephalopods, sea floor physiography could play an indirect role through mechanisms such as topographically induced up-welling of nutrients (Guerra 1992; Rubin 1997), increased primary production, and aggregation of zoo-plankton due to the enhanced secondary production or convergence of surface waters (Rubin 1994). This would be in total accordance with the patterns described above for Cuvier's beaked whales.

4.2 High-use areas

The best model highlighted six high density areas for beaked whales: Ligurian Sea, Alborán Sea, Hellenic Trench, northern Ionian Sea, southern Adriatic Sea and northern Tyrrhenian Sea (listed in decreasing order of density). These areas, particularly the first three, are supported by a large proportion of the available sightings, giving more confidence that these are genuinely high-use areas. All these areas are also well represented in the predicted map of lower 95% confidence interval (Figure S8, Supplementary Material). This map is useful to show which areas are the minimum hot spots for which we are certain at a 95% level of confidence. Most of these areas, with the exception of the Levantine and Libyan basins, have previously been reported as high-use areas by Cuvier's beaked whales (Arcangeli et al. 2016; Cañadas and Vázquez 2014; Rosso et al. 2009).

Akkaya Bas et al. (2014) reported sightings of Cuvier's beaked whales in Antalya Bay, Turkey. In this area, where a deep canyon and steep escarpment exist, there is also one stranding (Podestà et al. 2016). Low to medium model predictions of density in this area, despite poor information available for the model, suggests that further research effort may be worthwhile here.

Much less confidence can be accorded to many areas of low predicted density because of insufficient effort. These include the south-eastern Mediterranean, the Aegean Sea, the waters north of Algeria and the Gulf of Lion. Additional survey effort should be made to assess the occurrence of Cuvier's beaked whales in these regions. More generally, predictions in areas of little or no effort are useful only in an exploratory region-wide context. This is why results for the whole section south of 34.3ºN and the Aegean Sea should be considered with caution (Figure 3).

4.3 Abundance estimate

The lack of data on perpendicular distances from the trackline in most datasets meant that our estimate of abundance relied heavily on the correction factors applied and the extrapolation of the estimated *esw* from the available data according to the characteristics of the platforms. However, we still consider it worthwhile to contribute an estimate of the population size of Cuvier's beaked whales in the Mediterranean, given the concern regarding its conservation. The abundance estimate provided here, of approximately 5800 individuals, should be taken with caution as it only provides a tentative order-of-magnitude estimate for the population size of Cuvier's beaked whales in the Mediterranean.

We were able to explore the reliability of our method by comparing with the only two available abundance estimates of Cuvier's beaked whales in the Mediterranean: the Alborán Sea (Cañadas and Vázquez 2014) and the Ligurian Sea (Rosso et al. 2009). When comparing the Alborán Sea, by summing up the grid cells corresponding to the area for which an abundance estimate was provided (Cañadas and Vázquez 2014), results are very similar. The original abundance estimate of Cañadas and Vázquez (2014) was 429 individuals (CV=22%), in both cases taking into account the correction factor for availability bias. For the same area, in the current modelling exercise the estimate was 417 individuals. Similarly, when comparing the area of the Ligurian Sea, by summing up the grid cells corresponding to the area for which an abundance estimate from photo-identification exists (Rosso et al. 2009), the results are comparable. Rosso et al. (2009) calculated the abundance estimate to be 95-98 (SD=9-10) individuals. For the same area, in the current modelling exercise the estimate was 94 individuals.

Additionally, an abundance estimate was attempted with ISPRA-Tethys aerial surveys in the Ligurian Sea and Central and South Tyrrhenian Seas from 2009 to 2014, with all seasons pooled together. There were only nine sightings of Cuvier's beaked whales. Despite this, a detection function could be fitted given the pattern of the distance data for this species with good diagnostics of goodness of fit (this abundance estimate should only be considered in the framework of this exploration, as sample size was too small). An abundance estimate of 59 individuals was obtained, which, corrected by the availability bias estimated for this survey (0.078; see Table 1), yielded an estimate of 756 animals (CV=56.6%). When comparing the area corresponding to this survey using the same methods as for the Alboran Sea and Ligurian Sea results are once again similar. In the current modelling exercise the estimate was 755 individuals for the same area. Of course, the data from the surveys that generated these figures were included in the present analysis, so it is not a genuinely independent test, but it does indicate that the modelling approach we adopted is comparable to more standard approaches.

Given that our estimate was obtained through an unorthodox process, a full basin-wide survey with line transect data collection is needed to obtain reliable estimates of abundance. Until then, the preliminary information provided here could be used as a baseline. This analysis used a compilation of 27 years of data, collected from a variety of survey platforms, by observers with variable experience, with heterogeneous geographic coverage, under both good and moderate sighting conditions. Little or no data were available for large portions of the region. Therefore, the results presented here ideally need to be validated by a systematic and region-wide survey of the Mediterranean Sea. Such a line transect survey would also confirm the validity or otherwise of the approach used here for analysing multiplatform, multiyear, heterogeneous data covering large areas for which no systematic surveys exist

4.4 Strandings and mass strandings

A further check of our results can be made by comparing with independent observations of stranding events. Making inferences from strandings is problematic because carcasses may end up stranding at a point on the coast which is actually distant from where the animal died. Regardless, stranding records often compare well with sightings records (Maldini et al. 2005; Peltier et al. 2014). Mass strandings can provide more useful information because these events concern animals that strand alive or very fresh, potentially close to the area where they suffered the stress that made them strand. Most mass stranding events reported by Podestà et al. (2016) coincide with, or are very close to areas, where our model predicted higher densities of Cuvier's beaked whales (Figure S10 in Supplementary Material).

The southern portion of the Mediterranean lacks stranding data. This does not, however, mean that there are no strandings in that area, but rather that information is unavailable. Numerous stranding records, including one mass stranding reported off the coast of Israel (Kerem et al. 2012; Podestà et al. 2016) suggest that these events may also occur in surrounding areas, but remain unreported.

There have been a few mass strandings in the Balearic region, where the predicted density is not particularly high. This corresponds with the fact that there are very few sightings in this region, however, most of the surveys have been aerial, and the probability of detecting long divers like Cuvier's beaked whales is rather low. Therefore, given the amount of strandings in this area, coincident with the presence of some sightings and a medium density prediction, it would be advisable to survey this region with a platform that allows for easier detection of deep divers.

4.5 Implications for conservation and management

Assuming the abundance estimate is on the correct order of magnitude, our results could contribute toward an IUCN Red List assessment and upgrading of the Mediterranean subpopulation of Cuvier's beaked whales, currently classified as Data deficient (Cañadas 2006).

The areas of predicted high density, together with the areas of concentration of atypical mass strandings, constitute aeras of concern for conservation of the Mediterranean Cuvier's beaked whales population (Figures 3 and S10 in Supplementary Material). These maps concur with long-held opinions of the scientific and regulatory community: that there are a number of Mediterranean areas where Cuvier's beaked whales are often found and can be considered to be at risk of exposure to high intensity anthropogenic noise, such as the Alboran Sea, the Ligurian Sea and the Hellenic Trench. The other areas are not risk free, but rather of unknown risk, where data are required to assess beaked whale presence prior to, and during, human activities of potential impact (ACCOBAMS 2010; Kendra 2009). We know of multiple mass strandings associated with intense anthropogenic noise production (Frantzis 1998; Podestà et al. 2016), but mortality of Cuvier's beaked whales could be much higher considering that the probability of finding a carcass of a deep diving species can be as low as 3% (Williams et al. 2011).

Therefore, it is important to recommend caution in these high-risk areas of the Mediterranean, and urge that the relevant bodies incorporate this information in the planning and execution of high risk activities, such as naval excercises and seismic surveys.

Avoiding the production of high levels of noise within the areas with predicted higher density of Cuvier's beaked whales identified here (Figure 3) will undoubtedly reduce the risk of exposure and consequent mortalities for a significant part of the Mediterranean population of this species. Mitigation should include dedicated surveys and monitoring efforts. Additionally, mitigation requirements should be incorporated into national regulations and incorporated into the planning, consultation and permitting processes whenever the use of high-intensity noise is planned in the Mediterranean.

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Table 1. Mean speed (km/hr), associated mean correction factor for availability bias ($\hat{a}$), and estimated *esw* (km) per group of platform type/height/sea state, total track length (km) total area searched before correction (L*2**esw*, km^2), and total area searched after correction (L*2**esw**$\hat{a}$, km^2). Large ships of more than 15m platform height used BigEyes binoculars (usually more than 20x magnification), while large or medium ships of more than 10m platform height did not use BigEyes binoculars. Small ships could either use crow's nest platform (10-12 m height), deck (3-4.5 m) or both/undefined (3-12m). Sea state "0-3" means it was undefined but less than 4 Beaufort.

Platform type	**Platform height (m)**	**Sea state**	**Mean speed**	**Mean $\hat{a}$**	**Estimated *esw***	**Track length**	**Search area (not corrected)**	**Search area (corrected)**
Large ship	>15	0-1	10.15	0.8677	2.280	1134	5173	4496
		2-3	10.02	0.7778	1.930	2676	10320	8055
Large or medium ship	>10	0-1	25.92	0.6582	1.410	7497	21141	10376
		2-3	38.26	0.4053	1.440	15296	44051	15048
		0-3	26.08	0.6710	1.460	17176	50153	32046
Small ship	10 - 12	0-1	8.77	0.6715	1.080	30313	65476	43911
	3 - 4.5	0-1	9.12	0.4654	0.480	24440	23462	10602
		0-3	13.05	0.3388	0.350	204190	142933	51076
	3 - 12	0-1	11.71	0.4519	0.980	19240	37711	17100
		2-3	10.31	0.2521	0.250	61391	30696	7688
		0-3	9.67	0.4392	0.780	18478	28862	12807
Aircraft		0-3	185	0.0781	0.615	193168	237597	18622
TOTAL			**63.43**	**0.3016**	**0.573**	**594996**	**697538**	**231826**

Table 2. Covariates selected in the model, their estimated degrees of freedom (approximately number of knots in the smoothed function - 1) and their p-value (probability that their inclusion in the model is by chance).

Covariates	*Estimated degrees of freedom*	*P value*
Depth	4.87	<<0.0001
Depth CV	4.99	<<0.0001
Longitude	8.83	<<0.0001
Marine Regions (factor)	***Coefficient***	***P value***
(Intercept – Adriatic Sea)	-3.4714	0.0079
Aegean Sea	-3.7951	0.0188
Alborán Sea	-8.3304	0.0033
Balearic Sea	-9.4726	<<0.0001
Hellenic Trench	-1.8803	0.0417
Ionian Sea	-1.2692	0.0732
Levantine Basin	-3.4277	0.0822
Libian Basin	-1.5717	0.1255
Ligurian Sea	-5.5045	0.0005
NorthWestern Basin	-8.5522	<<0.0001
SouthWestern Basin	-10.9357	<<0.0001
Tyrrhenian Sea	-4.5613	0.0014

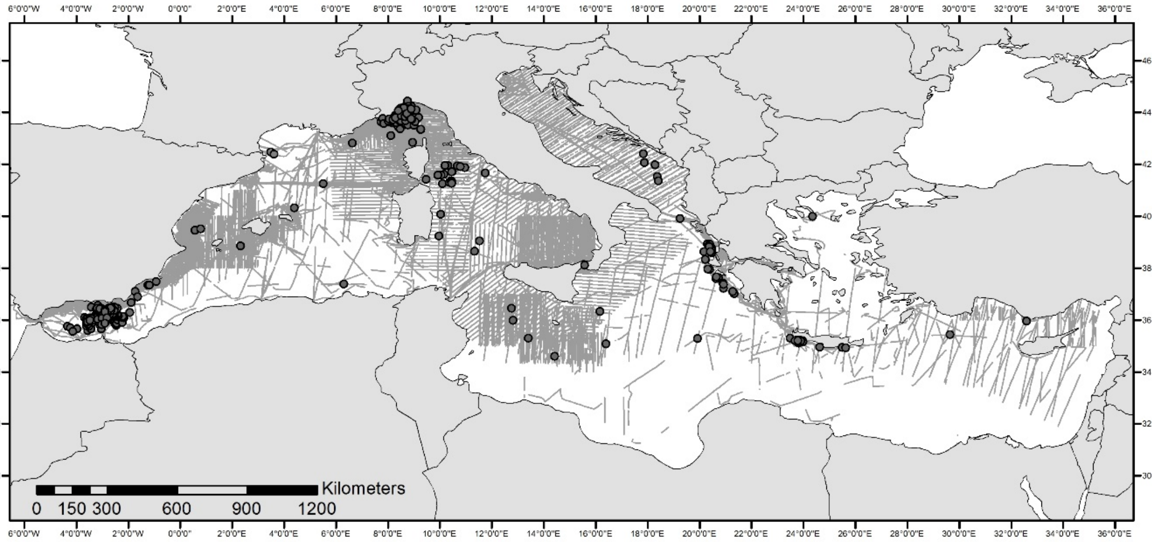

Figure 1. Searching effort (track lines) and sightings of beaked whales from 1990 to 2016.

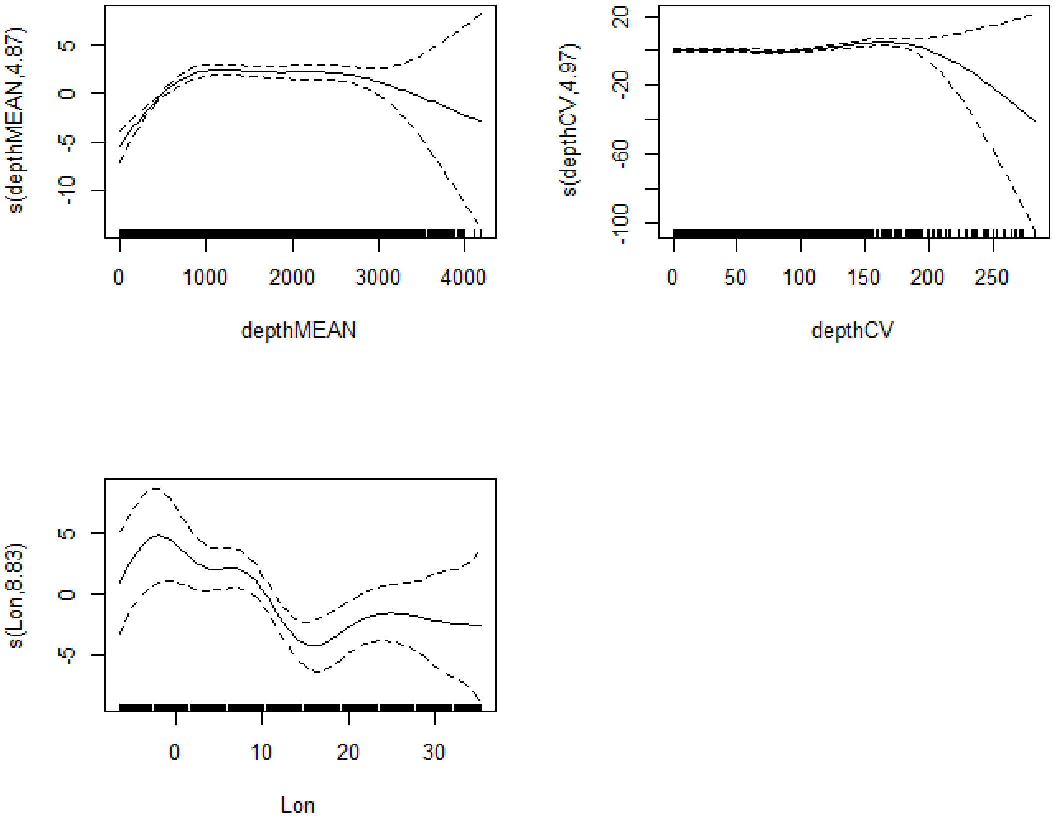

Figure 2. Smoothed functions of the continuous covariates selected in the final model of abundance of groups: depth, depth CV and longitude. The ticks on the x axis show the distribution of the sample data used in the model for each covariate. The dashed lines represent ±1 se. The y-axis represents an index of relative density. When the fitted line of the smooth function is greater than 0, the covariate has a positive effect and *vice versa*.

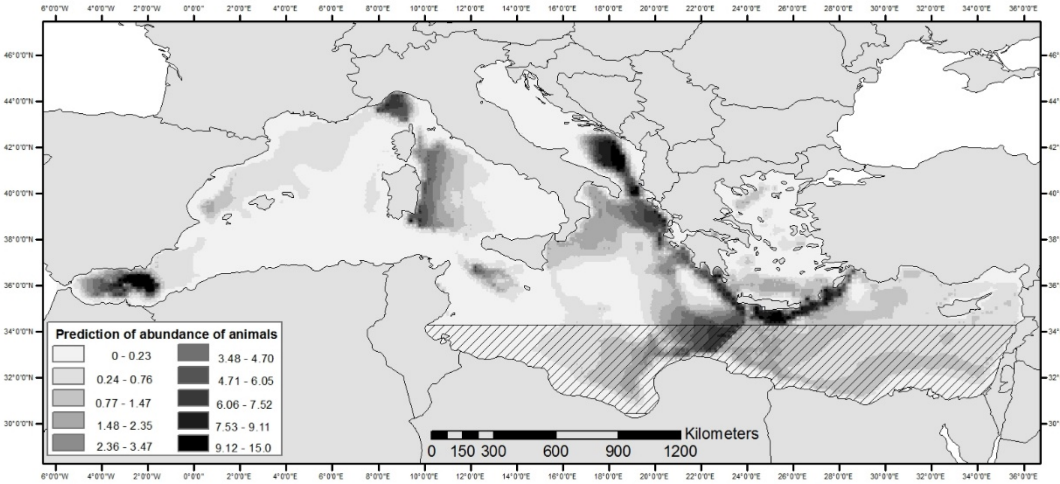

Figure 3. Predicted abundance of beaked whales in the whole Mediterranean (the grey scale represent the number of animals predicted in each grid cell). Results in striped areas (Aegean Sea and South-eastern Mediterranean) are not very reliable due to very small sample size.