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Original Article

Integrating passive acoustic and visual data to model spatial patterns of occurrence in coastal dolphins

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Fine-scale information on the occurrence of coastal cetaceans is required to support regulation of offshore energy developments and marine spatial planning. In particular, the EU Habitats Directive requires an understanding of the extent to which animals from Special Areas of Conservation (SAC) use adjacent waters, where survey effort is often sparse. Designing survey regimes that can be used to support these assessments is especially challenging because visual sightings are expected to be rare in peripheral parts of a population's range. Consequently, even intensive visual line-transect surveys can result in few encounters. Static passive acoustic monitoring (PAM) provides new opportunities to extend survey effort by using echolocation click detections to quantify levels of occurrence of coastal dolphins, but this does not provide information on species identity. In NE Scotland, assessments of proposed offshore energy developments required information on spatial patterns of occurrence of bottlenose dolphins in waters in and next to the Moray Firth SAC. Here, we illustrate how this can be achieved by integrating data from broad-scale PAM arrays with presence-only data from visual surveys. Generalized estimating equations were used with PAM data to model the occurrence of dolphins in relation to depth, distance to coast, slope, and sediment, and to predict the spatial variation in the cumulative occurrence of all dolphin species across a 4 × 4 km grid of the study area. Classification tree analysis was then applied to available visual sightings data to estimate the likely species identity of dolphins sighted in each grid cell in relation to local habitat. By multiplying these probabilities, it was possible to provide advice on spatial variation in the probability of encountering bottlenose dolphins from this protected population at a regional scale, complementing data from surveys that estimate average density or overall abundance within a region.

Keywords: cetaceans, habitat association modelling, marine spatial planning.

Introduction

Robust data on the population size and distribution of cetaceans are required to support a wide range of management and conservation issues (Evans and Hammond, 2004; Dawson *et al.*, 2008). Over the last 25 years, the requirement for these data has driven important developments in survey design and analytical methods that have greatly enhanced both our understanding of cetacean ecology and our ability to assess and manage threats to their populations (Kaschner *et al.*, 2006; Hammond, 2010). These new approaches have been particularly successful in supporting management of issues such as harvesting and bycatch (Slooten *et al.*, 2006; Williams *et al.*, 2006). In such cases, the highly mobile nature of cetacean species means that conservation and management strategies must be considered at very large scales, typically involving collaboration across different national and international waters (Smith *et al.*, 1999; Hammond *et al.*, 2002). However, the results from broad-scale studies of this kind can be of more limited use when data are required to underpin the assessment and management of smaller scale, regional, and site-specific activities (Cubero-Pardo *et al.*, 2011).

The need for finer-scale data on the extent to which cetaceans use coastal and shelf waters is becoming increasingly important following new conservation and marine spatial planning initiatives (Rees *et al.*, 2013). In particular, better information is often required on temporal patterns of occurrence in relatively small areas (Vanderlaan *et al.*, 2009; Dolman and Simmonds, 2010; Harris *et al.*, 2012). In contrast, while available aerial and ship-based line-transect data typically provide good broad-scale spatial coverage, they generally represent only a single period or integrate data collected over longer time-scales (Jewell *et al*., 2012; Hammond *et al.*, 2013). Data do exist at finer spatio-temporal scales for some resident or semi-resident populations of coastal cetaceans (e.g. Rayment *et al.*, 2010; Gnone *et al.*, 2011; Wiseman *et al.*, 2011), but, even in these cases, information on temporal patterns of occurrence in other parts of their range are often lacking. For example, in several European countries, bottlenose dolphins show high levels of fidelity to core-areas that have subsequently been designated as Special Areas of Conservation (SAC) under the EU Habitats Directive (Ingram and Rogan, 2002; Wilson *et al.*, 2004). Focused studies within these areas have provided information on local distribution and abundance. However, individuals using these sites can range widely across neighbouring waters (Ingram and Rogan, 2002; Wilson *et al.*, 2004), and much less is known about the extent of movements into more offshore areas. This uncertainty has constrained Habitat Regulations Assessments (HRA) required to assess whether new developments may impact populations that use a particular SAC. In the northeast of Scotland, for example, uncertainty over the range of the bottlenose dolphin population that uses the Moray Firth SAC recently delayed licencing of seismic surveys for oil exploration in the region, and additional studies have been required to assess whether this population may use areas proposed for offshore wind farm developments (Figure 1). Designing survey programmes that can be used to support these assessments is especially challenging because visual sightings are expected to be rare in peripheral parts of a population's range. Consequently, even intensive visual line-transect surveys can result in few encounters (Dawson *et al.*, 2008), resulting in rather uncertain information on population distribution, and little or no understanding of temporal patterns in the way that animals use different parts of their range.

Static acoustic monitoring techniques provide opportunities to collect higher temporal resolution data on temporal patterns of occurrence in selected areas (Van Parijs *et al.*, 2009). The comparatively low cost of TPODs and CPODs, passive acoustic monitoring (PAM) devices that have been designed to detect odontocete echolocation clicks, now permits the deployment of large arrays of these instruments (Verfuss *et al.*, 2007; Brookes *et al.*, 2013). These arrays can collect data for several months, allowing the detection of rare visits to different sampling sites and the collection of presence–absence data in weather and light conditions that would be unsuitable for visual surveys (Thompson *et al.*, 2010; Rayment *et al.*, 2011; Teilmann and Carstensen, 2012). However, these devices are unable to distinguish between echolocation clicks from different species of small odontocetes. In European waters, for

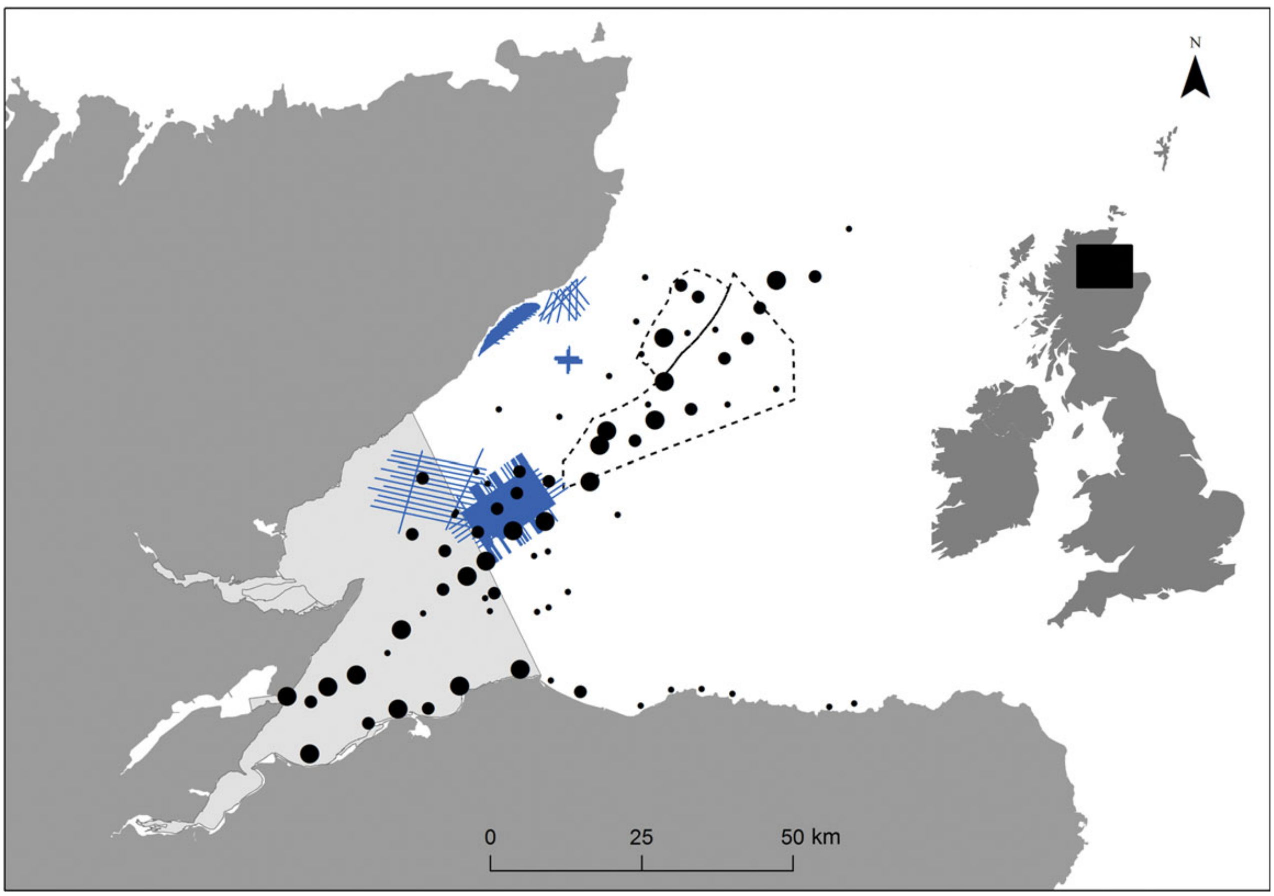

Figure 1. Map of the study area showing all CPOD sites used in the study. The size of each marker is related to the number of years for which data are available (1 – 3 years). The area within the Moray Firth Special Area of Conservation is shaded, and the map also shows the location of recent seismic surveys undertaken to support oil and gas developments (solid lines (in blue online)) and consented wind farm development areas (dashed outlines).

Table 1. The number of sightings used from each of the datasets included in the classification tree analysis of visual sightings.

Dataset	Year(s)	Survey method	$n_{sightings}$	Source
1	1980–1998	Boat and helicopter-based line transect	45	JNCC Seabirds at Sea Database (see Reid *et al.*, 2003)
2	1998–2006	*Ad hoc* boat-based observations	23	JNCC Database of observations from seismic vessels (see Stone and Tasker, 2006)
3	2010	Boat-based line transect	8	Moray Offshore Renewables Ltd Environmental Statement
4	2009/2010	Aerial visual and video line transect	4	The Crown Estate enabling actions
5	2001	Boat-based line transect	4	University of Aberdeen (see Hastie *et al.*, 2003)
6	2009	Boat-based line transect	1	University of Aberdeen, unpublished data
7	2010	Aerial visual line transect	29	University of Aberdeen, unpublished data
8	2004/2005	Boat-based line transect	41	University of Aberdeen (see Bailey and Thompson, 2009)
9	1990–2010	Photo-ID boat-based survey	828	University of Aberdeen (Cheney *et al.*, 2013)

example, while high-frequency clicks from harbour porpoises (*Phocoena phocoena*) can be discriminated from mid-frequency dolphin clicks (Bailey *et al.*, 2010; Simon *et al.*, 2010; Brookes *et al.*, 2013), it is not currently possible to use this approach to discriminate between species such as bottlenose (*Tursiops truncatus*), white-beaked (*Lagenorhynchus albirostris*), common (*Delphinus delphis*), and Risso's dolphin (*Grampus griseus*), all of which are likely to occur in many coastal areas in the Northeast Atlantic (Reid *et al.*, 2003).

The relative strengths and weaknesses of visual survey and acoustic monitoring data are complementary, highlighting the potential for integrating these approaches to provide more robust data on spatio-temporal patterns of occurrence of small cetaceans in particular areas of interest. In this paper, we illustrate this potential by combining data from arrays of static acoustic monitoring devices and a variety of different visual survey platforms. Our general approach was to use acoustic data in a habitat association model to predict spatial variation in the probability of occurrence of dolphins (Redfern *et al.*, 2006; Soldevilla *et al.*, 2011). Available data on visual sightings were then used in a classification tree analysis (De'ath and Fabricius, 2000) to assess the likely species identity of dolphins detected in different areas. The resulting data on spatial variation in the occurrence of bottlenose dolphins could then be used to characterize the baseline distribution required to assess the spatial overlap between bottlenose dolphins from the Moray Firth SAC and proposed developments in the offshore waters surrounding this protected area.

Material and methods

Passive acoustic data collection

Acoustic data were collected using a dispersed array of echolocation detectors (CPOD, Chelonia Ltd, UK) that were deployed across the Moray Firth between July and October 2009, 2010, and 2011 (Figure 1). CPODs continuously monitor the 20–160 kHz frequency range for possible cetacean echolocation clicks, and record the centre frequency, frequency trend, duration, intensity, and bandwidth of each click. CPODs were moored in the water column, ~5 m from the seabed, typically with a surface marker, although acoustic releases were used at some sites in 2011. Once recovered, data were downloaded and processed using version 2.025 of the custom CPOD software (Chelonia Ltd). This software first uses the recorded click parameters to differentiate cetacean echolocation clicks from other high-frequency sounds such as boat sonar. It then uses the frequency characteristics to identify which of those clicks are likely to have been made by harbour porpoises, whose clicks occur in a narrow high-frequency band that is centred near 130 kHz. The remaining wideband and lower frequency cetacean detections could be produced by a variety of dolphin species, whose relative likelihood of detection and identity remains uncertain. The output indicated the level of confidence in classification of the detection of these other cetacean echolocation click trains by classing each as CetHi, CetMod, or CetLow. Only click trains categorized as CetHi or CetMod were used in subsequent analyses. These output files were used to determine whether or not dolphins (of any species) were detected in each hour within each of these deployments.

Visual survey data collection

Visual identifications of dolphins and estimates of group sizes were extracted from all publically available survey datasets from the Moray Firth. These included observations made between 1982 and 2010 from a variety of surveys, that each covered different subsections of our overall study area (Table 1). The minimum requirement was that surveys were carried out using experienced observers, and recorded the location, species, and number of animals sighted. Surveys included both effort-related and non-effort-related (presence-only) data, and observations of bottlenose, white-beaked, Risso's, and common dolphins (see the Results section).

Modelling spatial variation in the occurrence of dolphins using PAM data

Following the approach used to model porpoise and harbour seal distribution within the same study area (Brookes *et al.*, 2013; Bailey *et al.*, 2014), raster grids for depth (SeaZone Hydrospatial Bathymetry) and polygon shapefiles for sediment type (SeaZone Seabed Sediment) were imported into ArcGIS 9.3. Slope, in degrees, was calculated from the depth data and distance to coast was calculated from a shapefile of the UK coastline. Data were summarized into 4 × 4 km grid cells, with a value for each cell of the mean depth, mean slope, mean distance from coast, the longitude and latitude of the centre of each cell, and sediment type. In our model of PAM data, we characterized sediment type based on the total proportion of the cell's area that was made up of sand and/or gravelly sand; a key prey habitat that had been shown to influence the distribution of harbour porpoises using this area (Brookes *et al.*, 2013). ArcGIS 9.3 was then used to extract habitat variables for each of the grid cells containing CPOD sampling sites. There were few data at steeper slopes, and transformations were unsuccessful, so slope was converted into a categorical variable where 0–0.25 = 1; 0.25–0.5 = 2; 0.5–1.5 = 3; and 1.5–3.0 = 4. These static habitat variables were then combined with temporal data on hour of the day, Julian day, and year (as a categorical variable) to explore which factors influenced variation in the probability of dolphins being detected within each hourly sample of acoustic data. Owing to the temporal correlation in dolphin detections between hours of the day at each POD site, data were analysed using a binomial generalized estimating equation (GEE; Photopoulou *et al.*, 2011; Bailey *et al.*, 2013). The autoregressive correlation structure (ar1) was chosen as this specifies correlation as a function of time, meaning that if dolphins are present in 1 h, they are more likely to be present in the following hours, although with a declining probability, allowing correlation in the model residuals. A unique number was applied to hourly data within each day at a particular site in a particular year, specifying the temporal correlation within groups (clusters), giving a cluster size of 24. As the GEE can only accommodate a single stratum of correlation and not a nested structure, the model assumed that different days and sites were independent. However, including a time covariate in the model accounted for the temporal variation in detections, which might be expected to occur as a result of some correlation between adjacent days.

We ran models with additive effects of distance to coast, sediment, slope, depth, longitude, Julian day (with and without a quadratic function), year, and hour of the day, as well as the interactions between distance to coast and sediment, slope and depth, distance to coast and slope, and depth and sediment. Julian day with a quadratic function represents a mid-season peak in dolphin occurrence (see Bailey *et al.*, 2013). Latitude was not included in any of the models as this was highly collinear with several of the other variables, including those such as distance to coast, and depth, which are considered more important parameters when predicting dolphin occurrence. Analyses were carried out using the package geepack within R version 2.12.1, and model selection was carried out based on QIC scores. Model fit was explored by plotting residuals and fitted values against spatial coordinates to investigate spatial autocorrelation. The effect size of individual parameters from the top model was assessed by their 95% confidence limits, whereby confidence limits that did not overlap zero indicated a significant effect.

Modelling spatial variation in the identity of dolphins species using presence-only visual data

The presence-only data from visual surveys were used within a classification tree to assess the likely species identity of dolphins that might be detected within each 4 × 4 km grid cell, based upon the habitat available within that cell. Habitat variables included depth, sediment type, seabed slope, distance from coast, and the latitude and longitude of the centre of the cell. In this analysis, considering sediment as a categorical variable based upon the dominant sediment type in each grid cell was found to be more informative. Individual sightings of each dolphin species were used in the classification tree. First, each of the sightings was assigned the habitat values averaged for the 4 × 4 km grid cell that it occurred within. The tree was then built using R version 2.12.1 and the tree package (Ripley, 2010). This involved repeatedly splitting the dataset in two, based on the value of a particular variable, until most animals were assigned to a unique species group. A tree, similar to a phylogeny was produced, weighted by the count of animals in each sighting. This allowed predictions to be made of the proportion of each species that might be expected in each 4 × 4 km grid cell within our study area, given its habitat characteristics.

Integrating visual and PAM data to predict spatial variation in the occurrence of different dolphin species

As the predictions from the classification tree are based upon presence-only data from patchily distributed survey effort, they cannot be used to estimate either the probability that dolphins might occur in a particular grid cell or the number of animals that might be expected to be in that cell. Instead, the classification tree provides an estimate of the likely species composition that one would find in a cell if dolphins were present. In contrast, the analysis of PAM data provides an estimate of the probability that dolphins might occur in a given cell within a particular hour, but cannot be used to make inference about the likely species identity or numbers of dolphins occurring in that cell. We therefore integrated these two model outputs using the predictions from the GEE for PAM data to estimate the probability that dolphins would occur in each grid cell within a given hour, and multiplied this by the output from the classification tree to predict the probability of bottlenose dolphins occurring within each grid square in the study area.

Results

Passive acoustic data

Dolphin echolocation clicks were detected during all deployments across the study area. There was large spatial variation in the level of detection across sites, but this was fairly consistent between years (Figure 2). At certain coastal sites, dolphins were detected on most days, for up to 21 h d^{-1}. In contrast, detections sometimes occurred only once every few weeks at offshore sites, and typically occurred only within 1 or 2 h on those days.

The GEE analysis revealed two top models, which were both 78 QIC scores better than all other models (Table 2). These models included the interactions between distance to coast and sediment (proportion of sand and/or gravelly sand), and slope and depth. They also included the longitude of the cell, Julian day with a quadratic function that represented seasonal variation, and year. The simpler model [Equation (1)], without hour of the day, was used to predict the likelihood of dolphin presence in all grid cells across the study area standardized for Julian day 248 of 2010 (Figure 3).

$$\begin{aligned}&\text{Dolphin detection} \sim \text{DistCoast} + \text{Sediment} + \text{Slope} + \text{Depth}\\&+ \text{Longitude} + \text{JulianDay} + \text{I(JulianDay}^2) + \text{Year} + \text{DistCoast}\\&\times \text{Sediment} + \text{Slope} \times \text{Depth}, \text{family} = \text{binomial},\\&\text{corstr} = \text{AR1}, \text{id} = \text{Unique Number}.\end{aligned} \tag{1}$$

Modelling spatial variation in the identity of dolphin species using presence-only visual data

Overall, there were 988 sightings of dolphin groups that were identified to species, involving a total of over 7000 individuals (Table 3). Most sightings were of bottlenose dolphins (Table 3) during coastal boat-based photo-identification surveys (Table 1). The other species recorded were white-beaked, common, and Risso's dolphin, and these were more typically observed in offshore areas (Figure 4).

The classification tree based upon these data had 21 terminal nodes, and used depth, slope, distance to coast, sediment type, and latitude to identify likely species composition in different parts of the study area. The misclassification rate was 0.014, which equated to 111 animals out of 7870 being wrongly classified, and the residual mean deviance was 0.0925. Predictions from this tree indicate that any dolphins encountered along the coastal strip are most likely to be bottlenose dolphins, but that those encountered

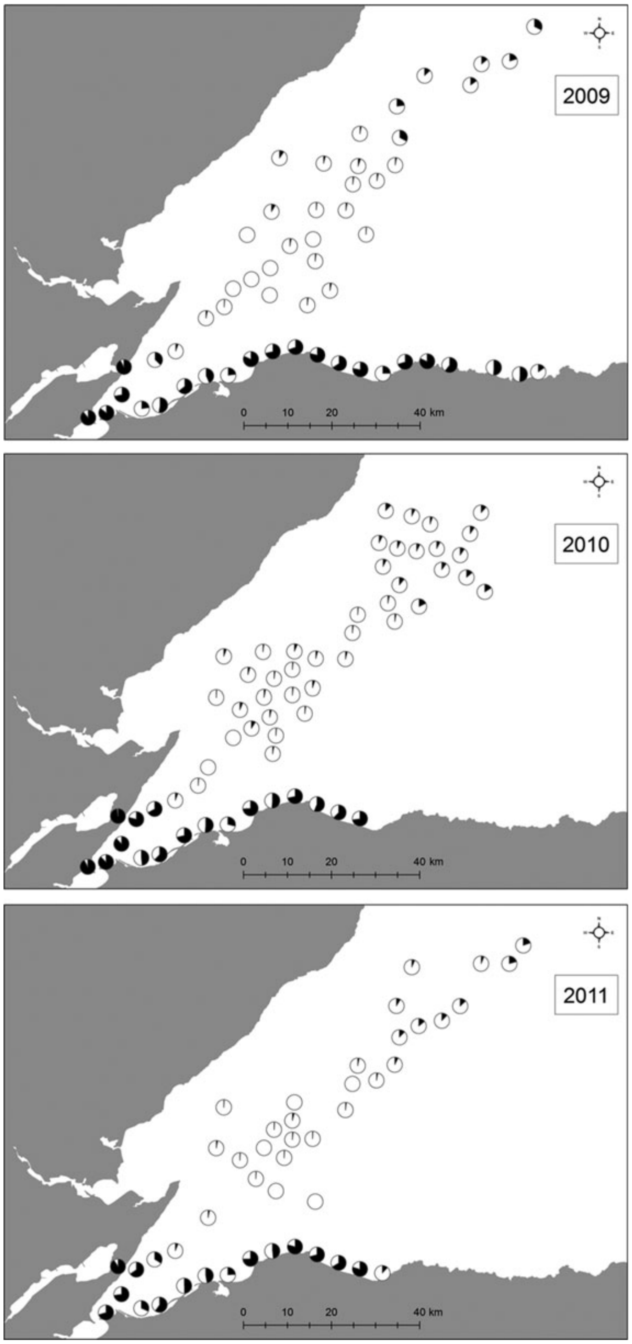

Figure 2. Variation in the occurrence of dolphins at different PAM sites in August, September, and October 2009, 2010, and 2011. Each site is represented with a pie chart, with the filled section of the pie chart representing the proportion of days that dolphins were detected.

in offshore areas were, in general, more likely to be other species (Figure 5).

Integrating visual and PAM data to predict the distribution of different dolphin species

The predicted probability of dolphin occurrence from the GEE (Table 2 and Figure 3) was multiplied by the predicted probability that detections were bottlenose dolphin (from the classification tree; Figure 5) to predict the probability of encountering bottlenose dolphins in different parts of the study area (Figure 6).

Table 2. Parameter estimates and confidence intervals from the top model.

Parameter	Estimate	Lower 95% CI	Upper 95% CI
Intercept	**−2.65000**	−5.72720	0.42720
Julian_day	**−0.04660**	−0.06444	−0.02876
Julian_day^2	**0.00009**	0.00005	0.00013
Year(2010)	**0.30100**	0.20280	0.39920
Year(2011)	**0.19300**	0.08579	0.30021
Longitude	**0.00001**	0.00001	0.00001
Dist_coast	**−0.00016**	−0.00020	−0.00011
Sediment	**−0.37800**	−0.63084	−0.12516
Depth	**−0.04220**	−0.04881	−0.03559
Slope(2)	**−0.58500**	−0.75944	−0.41056
Slope(3)	**−2.37000**	−2.82080	−1.91920
Slope(4)	**4.15000**	3.72860	4.57140
Dist_coast × sediment	**0.00007**	0.00003	0.00011
Depth × slope(2)	**0.01760**	0.01117	0.02403
Depth × slope(3)	**0.02200**	0.00473	0.03927
Depth × slope(4)	**−0.08900**	−0.10035	−0.07765

Confidence intervals that do not overlap zero indicate a significant effect (bold text).

Discussion

Data on spatio-temporal patterns of the distribution of cetacean populations are often unavailable at the scales required to assess current management issues. In the Moray Firth, for example, patchy survey effort in offshore areas resulted in uncertainty over the extent to which protected bottlenose dolphins may occur in areas being considered for offshore energy developments (Figure 1). Here, we collected new acoustic data, and integrated these with available information on cetacean sightings to model regional variation in the occurrence of bottlenose dolphins. These analyses built on the strengths of these two survey techniques. The acoustic data demonstrated that dolphins occurred only rarely in offshore areas (Figure 3), while visual sightings indicated that dolphins in those areas were most likely to be offshore species such as white-beaked, common, and Risso's dolphin rather than bottlenose dolphins (Figures 4 and 5). Critically, this approach provided a transparent and quantitative framework for predicting spatial variation in the probability of encountering protected bottlenose dolphins in offshore areas (Figure 6).

Typically, additional information to meet these management needs would have been sought through the collection of more visual survey data. However, boat and aircraft-based surveys in offshore areas such as these are expensive and logistically challenging, and sightings rates are typically low (Dawson *et al.*, 2008). Furthermore, as one moves to finer and finer spatial scales, it is more likely that cetaceans occupy sites of interest only temporarily, and frequent visual surveys would be required to detect rare visitors. While temporal changes in occurrence could be assessed through repeated visual surveys, sufficiently intensive survey campaigns are only likely to be practical within relatively small inshore sites. At the regional scales relevant to our study system, systematic regular visual surveys alone would be unlikely to produce the data required to satisfy other stakeholders that bottlenose dolphins were rarely encountered around offshore developments sites.

We used GEEs to model the PAM data and classification trees to model species composition, thus predicting how each varied in relation to different habitat characteristics. However, this general approach could be developed using alternative modelling tools. A GEE

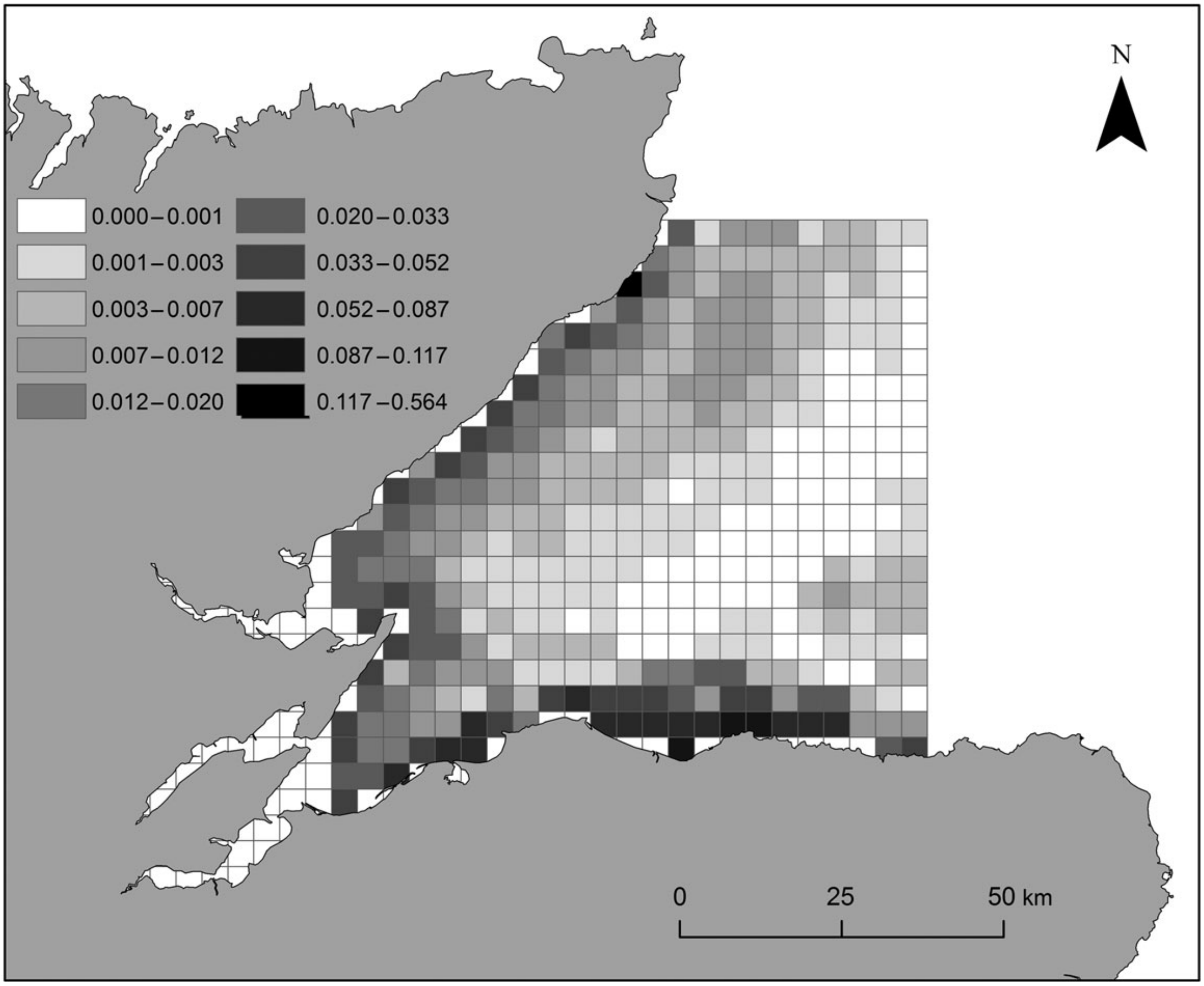

Figure 3. Predicted spatial variation in the probability of detecting dolphins (of all species) across the Moray Firth. Predictions are based on the GEE analysis of passive acoustic data, and are standardized for Julian day equal to 248 and year equal to 2010.

Table 3. The number of sightings and counts of individuals of each of the four species of dolphin observed on the visual sightings and included in the classification tree analysis.

Species	$n_{sightings}$	$n_{animals}$
Bottlenose dolphin	915	7 465
Common dolphin	14	231
Risso's dolphin	4	6
White-beaked dolphin	50	168

framework was chosen here because it was recognized that the PAM data were likely to be temporally autocorrelated. However, the GEE could not be used with a nested correlation structure. Thus, while we found no evidence of spatial autocorrelation in our acoustic data, it would be valuable to explore alternative frameworks that could cope with more complex correlation structures. The data that we have used in our analysis are available to encourage further exploration of alternative modelling frameworks.

Similarly, while the classification tree provided a convenient method for integrating the data sources available to us in this study area, alternative approaches might be more suitable in other cases. For example, Reid *et al.* (2003) used data from a variety of different effort-based surveys to provide an indication of the relative abundance of different cetacean species in UK waters. Data from this publication could be used as an alternative to the classification tree analysis in other areas. We chose not to take this route because there have been a number of relevant studies in the Moray Firth since Reid *et al.*'s (2003) analysis (Table 1), and we required regional scale analysis that incorporated all these data. Our use of the classification tree analysis also allowed us to include additional non-effort-based data that provided valuable information on the likely species identity of dolphins seen in different parts of the Moray Firth. The use of a framework that could incorporate these diverse data sources is particularly valuable because there were few sightings of species other than bottlenose dolphins and relatively few sighting of any dolphin species in offshore areas. This framework increases the potential to use alternative approaches to extend these datasets. For example, given the increasing availability of high-quality digital cameras and GPS receivers, geo-referenced verifiable records of sightings from recreational sailors and other marine users could also provide a valuable source of data for these studies. In future, it may also be possible for this step of the process to incorporate

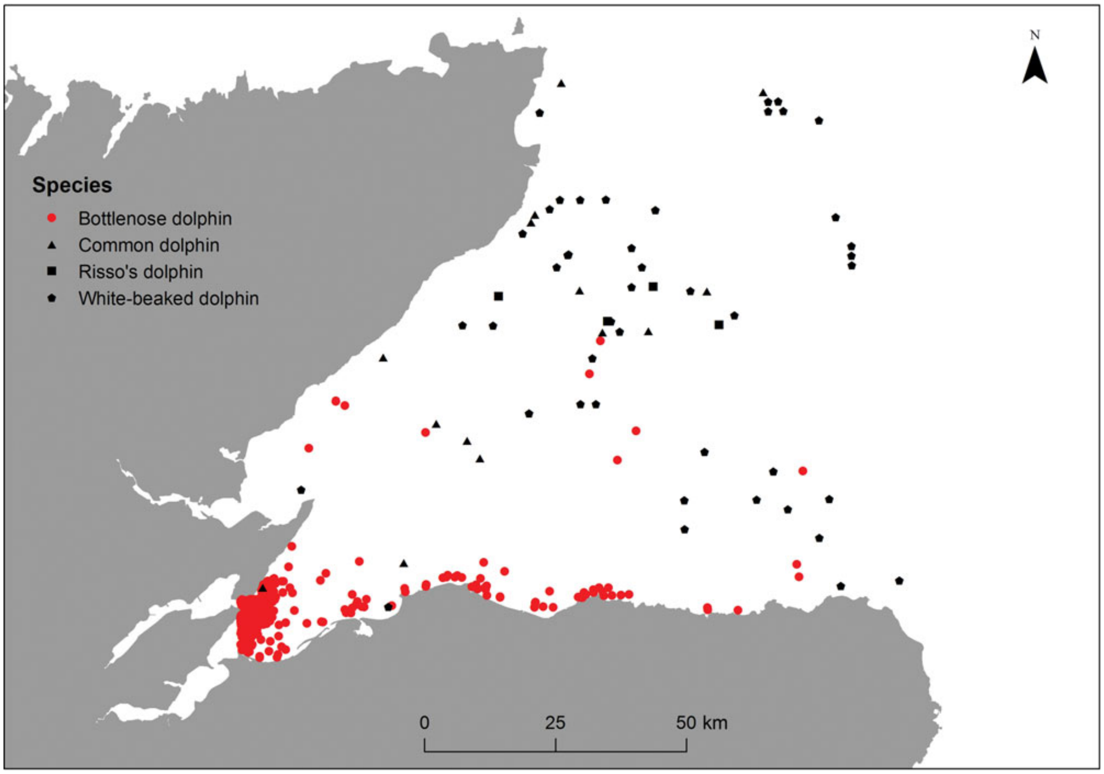

Figure 4. Locations of all the sightings of different dolphin species used in the classification tree. Data are from the sources listed in Table 1.

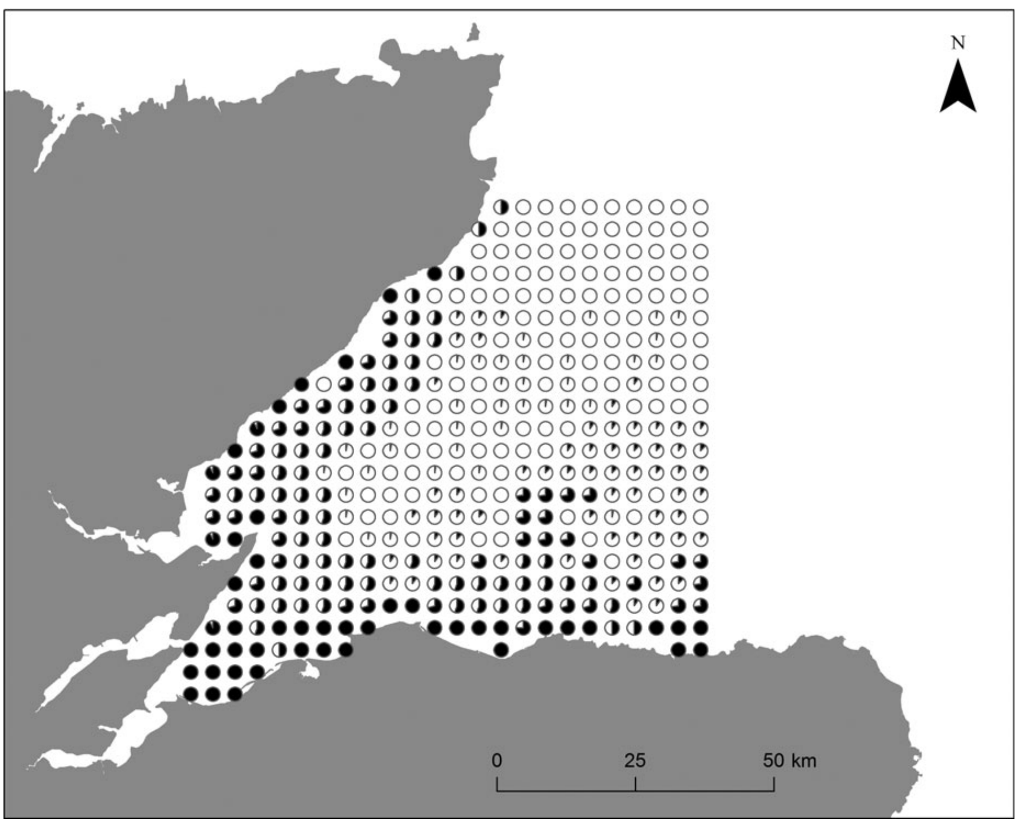

Figure 5. Classification tree-based predictions of the probability (black portion of pie chart) that dolphins encountered in each 4 × 4 km grid cell were likely to be bottlenose dolphins.

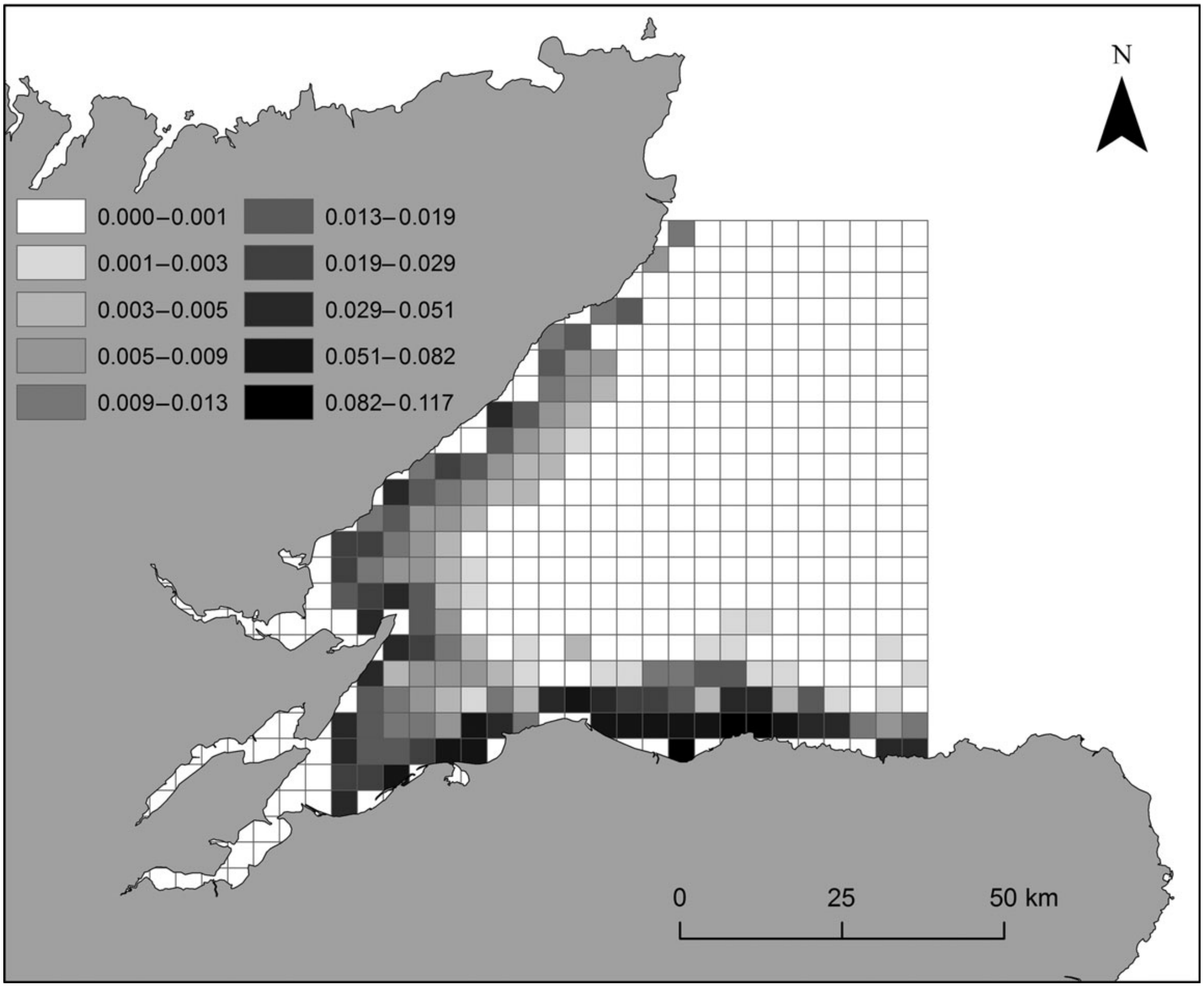

Figure 6. Spatial variation in the predicted probability of bottlenose dolphin occurrence across the Moray Firth. Predictions for each cell are based on the outputs from both the GEE and the classification tree analyses, and represent the probability of bottlenose dolphins occurring in that cell in any given hour. Spatial variation was similar across periods, but absolute values for predictions are standardized for Julian day 248 of 2010.

data on dolphin species composition in different UK waters from the Joint Cetacean Protocol (http://jncc.defra.gov.uk/page-5657); a national database of cetacean line-transect survey data that will update and extend information provided in Reid *et al.* (2003).

Our study was based upon a PAM array that had been designed for other purposes (see Thompson *et al.*, 2013). This meant that we were unable to detect variation in occurrence over some of the variables that might be expected to influence bottlenose dolphins. Most notably, latitude was not included in any of our GEE models, although this study area represents the northern extreme of this population's range (Wilson *et al.*, 1999). This was not included as our array design resulted in co-variation between latitude and other key variables such as distance from shore. As a result, our final model appears to over-predict the importance of the north coast of the Moray Firth for bottlenose dolphins compared with the south coast when compared with other available data (Reid *et al.*, 2003). Future studies that aim to refine these models would benefit from additional sampling in areas such as the inshore waters along the north coast, and year-round PAM studies that could explore whether these patterns persist in other seasons. Similarly, such studies could use deployments of broadband acoustic data loggers to complement the visual data by providing information on dolphin species identity through analysis of whistle characteristics (Oswald *et al.*, 2007; Soldevilla *et al.*, 2011).

In conclusion, these analyses highlight the potential for integrating PAM and visual survey data to characterize spatial variation in the occurrence of coastal dolphins. Although our study design did not allow us to fully characterize variation in their use of different coastal waters, these analyses brought together available data to inform the management of offshore energy developments that required information on the relative occurrence of bottlenose dolphins in inshore and offshore areas. The approach developed in this study complements broader scale efforts to estimate abundance or density using other techniques such as mark-recapture or DISTANCE analysis (Hammond, 2010). Such methods provide an indication of abundance over larger regions, but cannot be used to assess how often these animals occur in particular subareas within those regions. In contrast, our study provides a framework that can be used to predict how often animals may be encountered in different subareas, but provides no information on the number of individuals involved. The use of these complementary approaches will be increasingly important as new marine spatial planning frameworks require better information on spatio-temporal patterns of occurrence to assess and mitigate risks from interactions between coastal dolphins and human activities such as fisheries and marine energy developments.

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