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Predictions from harbor porpoise habitat association models are confirmed by long-term passive acoustic monitoring[a]

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Survey based habitat association models provide good spatial coverage, but only a snapshot in time of a species' occurrence in a particular area. A habitat association model for harbor porpoises was created using data from five visual surveys of the Moray Firth, Scotland. Its predictions were tested over broader temporal scales using data from static passive acoustic loggers, deployed in two consecutive years. Predictions of relative abundance (individuals per kilometer of survey transect) were obtained for each 4 km × 4 km grid cell, and compared with the median number of hours per day that porpoises were acoustically detected in those cells. There was a significant, but weak, correlation between predicted relative abundance and acoustic estimates of occurrence, but this was stronger when predictions with high standard errors were omitted. When grid cells were grouped into those with low, medium, and high predicted relative abundance, there were similarly significant differences in acoustic detections, indicating that porpoises were acoustically detected more often in cells where the habitat model predicted higher numbers. The integration of acoustic and visual data added value to the interpretation of results from each, allowing validation of patterns in relative abundance recorded during snapshot visual surveys over longer time scales.

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I. INTRODUCTION

Habitat association models have been widely used to investigate species' ecological requirements, to identify key conservation areas (e.g., Ingram and Rogan, 2002; Cañadas *et al.*, 2005; Louzao *et al.*, 2006; Bailey and Thompson, 2009; Embling *et al.*, 2010; Péron *et al.*, 2010), and to support spatial planning in order to minimize interactions with human activities (e.g., Brambilla *et al.*, 2010; Gontier *et al.*, 2010; Forcey *et al.*, 2011; Muhling *et al.*, 2011). These models may use either survey or telemetry data to identify habitat characteristics that influence the distribution or abundance of animals, and then predict over areas where data are sparse or absent (e.g., Nur *et al.*, 2011). One fundamental assumption of these models is that the predictor gradients have been adequately sampled (Elith and Leathwick, 2009), and it is recognized that predictions outside this range of environmental variables will have increased errors. However, because independent data sets are rarely available for comparison, the predictive power of these models, even within the range of environmental variables studied, often remains uncertain.

Harbor porpoises *Phocoena phocoena* are widely distributed across European waters (Reid *et al.*, 2003), occurring in a variety of habitats that range from offshore sandbanks in open waters (Hammond *et al.*, 2002; Todd *et al.*, 2009) to complex tidal streams around island archipelagos (Marubini *et al.*, 2009; Shucksmith *et al.*, 2009; Embling *et al.*, 2010). Their protected status under the European Habitats Directive (ECC, 1992), frequent interactions with fisheries (e.g., Vinther and Larsen, 2004; Leeney *et al.*, 2008), and use of areas identified for offshore energy developments (Bailey *et al.*, 2010b; Thompson *et al.*, 2010; Scheidat *et al.*, 2011) have led to a number of studies that have used habitat association modeling to identify key management areas (Bailey and Thompson, 2009; Embling *et al.*, 2010). Most of these studies have been carried out in inshore waters, and indicate that the likelihood of porpoises being present increases in areas with bathymetric or oceanographic features associated with increased productivity and prey aggregation. Such features include increased tidal flow (Marubini *et al.*, 2009) or fronts (Johnston *et al.*, 2005; Shucksmith *et al.*, 2009), but the detail varies between sites.

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[a] Portions of these data were previously published in Bailey, H., and Thompson, P. M. (**2009**). "Using marine mammal habitat modeling to identify priority conservation zones within a marine protected area," Mar. Ecol. Prog. Ser. **378**, 279–287.

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Offshore, fewer studies have been carried out due to the logistic difficulties of surveying these areas, although studies using static passive acoustic devices have found that porpoises are likely to be foraging on the Dogger Bank in the central North Sea (Todd *et al.*, 2009).

Habitat association models are often based on line transect survey data, which can only provide a snapshot in time. Consequently, these models are often unable to account for diel, inter-annual or seasonal changes in distribution, or habitat use. For example, two large-scale surveys carried out a decade apart reported marked differences in harbor porpoise distribution in the North Sea (Hammond *et al.*, 2002; Hammond, 2006). However, it was not clear whether these differences represented a genuine long-term range shift, or an interaction between slight changes in survey timing and a shorter-term seasonal change in distribution.

Static passive acoustic monitoring (PAM) offers the potential to study changes in the occurrence of animals over longer temporal scales, since devices can be deployed to record continuously for several months. Harbor porpoise have been shown to echolocate almost constantly (Akamatsu *et al.*, 2007; Linnenschmidt *et al.*, 2013), so it is likely that animals that are present will be detected acoustically. However, these techniques suffer the converse problem to that of habitat association modeling, of limited spatial coverage. Comparison of the results from survey based habitat association modeling with PAM within a particular area therefore provides an opportunity to explore whether predicted variations in spatial distribution are consistent over longer time scales. Here, we use visual survey data to develop a model of harbor porpoise habitat association in the Moray Firth, NE Scotland, and compare these predictions with PAM data collected from the same area over a 2 year period.

II. METHODS

A. Data collection

1. *Study site*

The Moray Firth is a large triangular embayment of over 6000 km^2. Water depths gradually shelve from the coast, but in the central Moray Firth, there is a shallow sand bank of 40 to 50 m depth called the Smith Bank, a minimum of 15 km offshore. Along the east of the southern coast is a trench with depths of up to 200 m (Fig. 1). The slope is rarely more than 1°, except in the areas around the southern trench, where it reaches a maximum of 6.5°. Sediment types within the firth are generally sandy and gravelly, with some muddy sediments in the southern, deeper areas. The Smith Bank has historically been known to support sandeel *Ammodytes marinus* populations (Hopkins, 1986) and although no recent surveys have been carried out, fishery landings data (ICES, 2007), and analysis of diets of other predators (Greenstreet *et al.*, 1998) suggest that this is still the case.

2. *Survey methods*

This study was based upon harbor porpoise sightings and counts collated from five different survey datasets. Four datasets were from boat-based line transect surveys, and one was from an aerial line transect survey. All data were collected between April and October, from 2004 to 2010 (Table I), with some datasets covering most or all months in that period, while the aerial survey dataset covered only August and September. Each dataset was collected using standard protocols for marine mammal surveys and aimed to spread survey effort evenly through the survey windows presented in Table I. Boat based surveys used the European Seabirds at Sea (ESAS) methodology (Webb and Durinck, 1992; Camphuysen *et al.*, 2004) and aerial surveys were conducted using the methodology described for the SCANS-II surveys (Hammond, 2006). Both aerial and boat surveys collected effort data in the format of transect distance surveyed. All surveys recorded the location, species, and number of animals sighted and did not deviate from the track line when animals were sighted. For boat based surveys animal location was determined by combining the boat's GPS data with measurements of distance and angle from the trackline. For aerial surveys, animals were recorded at the moment they were abeam of the aircraft, the time of which was compared with the onboard GPS and the declination angle to the water was used to calculate distance from the trackline. Some details, such as vessel type, survey speed, the number of observers (Table I), and the area surveyed varied between datasets (Fig. 2). In surveys where only one observer was present, the observer scanned a 180° arc forward of the vessel, while in surveys with two observers, each observer scanned a 90° arc abeam to forward of the vessel. The vast majority of data were collected in Beaufort sea state 3 or less, but occasionally conditions deteriorated during a survey and some small sections were surveyed in Beaufort sea state 4.

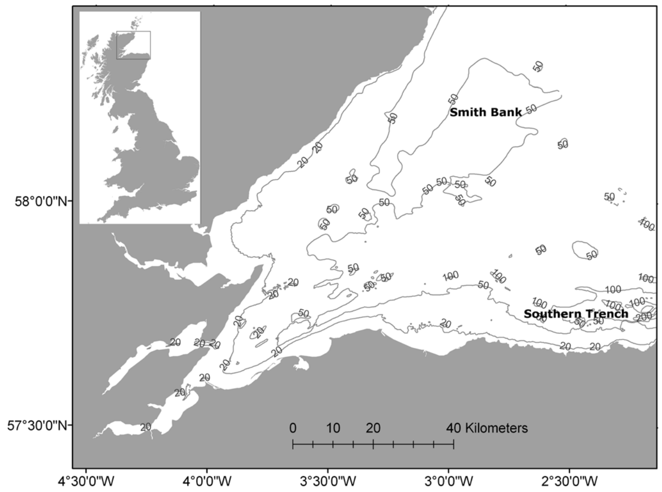

FIG. 1. Map showing the bathymetry and location of the Moray Firth. The 50 m depth contour in the center of the firth demarks the Smith Bank.

3. *Passive acoustic monitoring*

Acoustic loggers (CPOD, Chelonia Ltd. UK) were deployed across the Moray Firth (for locations see Sec. III) throughout the period from April to October in 2009 and 2010. CPODs continuously monitor the 20–160 kHz

TABLE I. Details of five survey datasets of harbor porpoise, collected in the Moray Firth and used in habitat association modeling. Dataset a contains data previously published in Bailey and Thompson (2009).

Dataset	Years	Total survey days	Months of survey	Total trackline surveyed	Total porpoise count	Survey Vessel	Number of mammal observers	Survey speed	Survey platform height
A	2004	10	August to October	251 km	62	Boat	1	7 knots	3.5 m
	2005	15	April to July	1029 km					
B	2009	14	June, August to October	1618 km	131	Boat	2	8 knots	≥5 m
C	2010	24	April to October	3015 km	362	Boat	1	10 knots	≥5 m
D	2010	14	April to September	1390 km	177	Boat	1	10 knots	3 m
E	2010	13	August and September	4493 km	341	Airplane	2	100 knots	183 m

frequency range for possible cetacean echolocation clicks, and record the center frequency, frequency trend, duration, intensity, and bandwidth of each click. They are capable of detecting porpoise clicks within an omnidirectional range of up to 300 m (Chelonia Ltd., 2012a). The loggers were moored in the water column, approximately 5 m from the seabed. Once recovered, data were downloaded and processed using version 1.054 of the custom CPOD software (Chelonia Ltd., 2012b) to differentiate between dolphin and porpoise echolocation clicks and other high frequency sounds such as boat sonar. The output indicated the level of confidence in classification of the detection as a cetacean echolocation click train by classing each as CetHi, CetMod, or CetLow. Only click trains categorized as CetHi or CetMod were used in analyses.

B. Habitat association model

Raster grids for depth (6 arc min grid, approximately equivalent to 180 m grid) and polygon shapefiles for sediment type (1:250 000 scale) were used to provide habitat variables (SeaZone Solutions Ltd., 2005a,b), which were

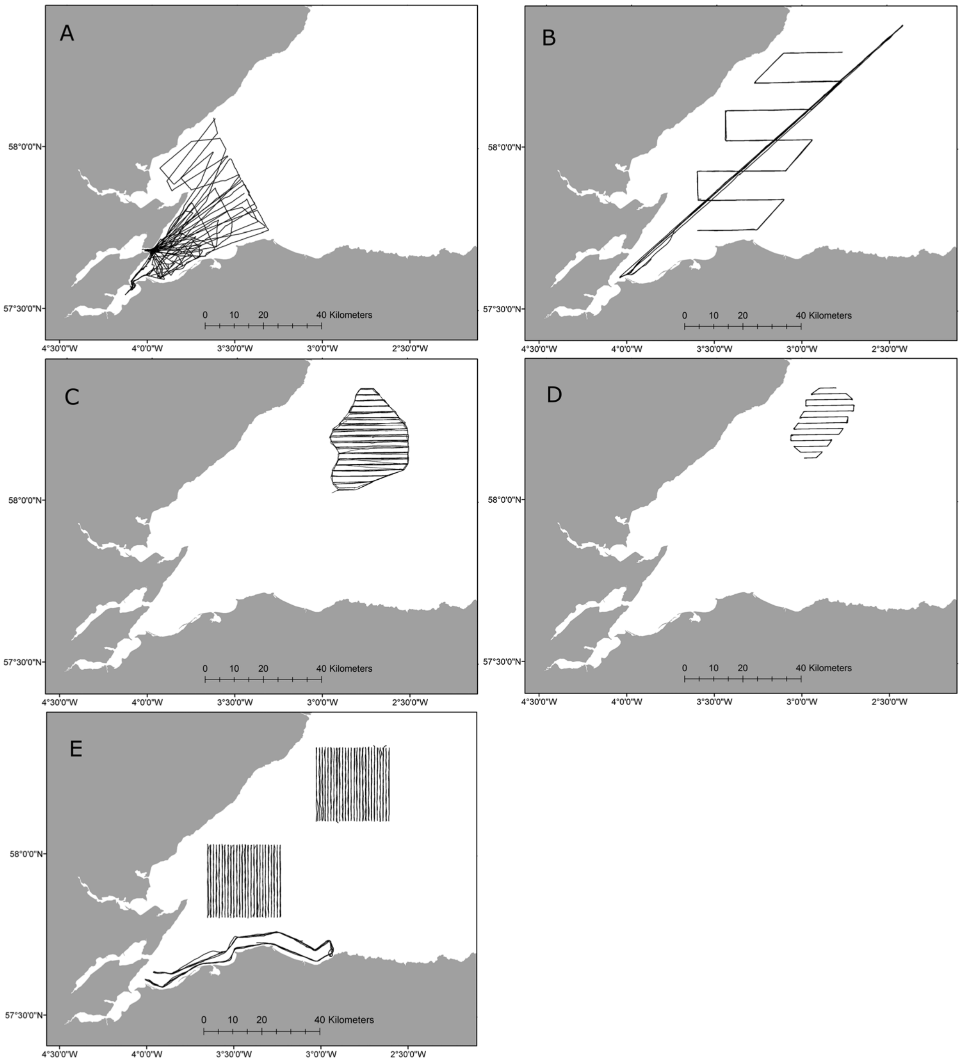

FIG. 2. Spatial extent of effort from four boat based surveys (a to d), and one aerial survey (e) carried out in the Moray Firth in (a) 2004 (August, September, October) and 2005 (April, May, June, July), (b) 2009 (June, August, September, October), (c) 2010 (April, May, June, July, August, September, October), (d) 2010 (April, May, June, July, August, September) and (e) 2010 (August, September).

processed using ArcGIS 9.3. Data were summarized into 4 km × 4 km grid cells as in Bailey and Thompson (2009), with a value for each cell of mean depth, mean slope, mean distance from coast, and the proportion of the area of the cell containing sand and gravelly sand sediment types (Fig. 3). This sediment variable was used because it is most likely to account for the suitability of the habitat for sandeels, which prefer fine and coarse sands (Holland *et al.*, 2005) and along with whiting (*Merlangius merlangus*), which prefer sandy sediments (Atkinson *et al.*, 2004), are key prey species for harbor porpoises (Santos and Pierce, 2003; Santos *et al.*, 2004). Frequency histograms of the habitat variables within grid cells that had been surveyed showed that the distribution of depth was strongly right skewed and so cells with depth values greater than 80 m were excluded from the analysis.

The total number of harbor porpoises sighted and the total effort (meters of survey track) in each cell were calculated separately for each of the five datasets. In many cells, both effort and sightings were available from multiple datasets, so a mixed model approach was taken to account for correlation between observations within the same cell. The relationship between porpoise counts and depth was nonlinear, so generalized additive modeling was used. Generalized Additive Mixed Models (GAMMs) were created using the mgcv package (Wood, 2008) in R version 2.12.1 (R Development Core Team, 2010). Models were constructed with a count of animals in each 4 km × 4 km grid cell for each dataset as the response variable, along with a value for each habitat variable as explanatory variables. The log of the total transect length within each grid cell from each dataset was used as an offset variable. The use of different survey platforms means that is possible that sightings rates differed between the five data sets. If they exist, such differences are most likely between boat-based and aerial surveys, so we explored potential differences in sighting rate between these two main survey types by including method (aerial versus boat-based) as a variable in the model. Models were weighted by the ratio of effort to the maximum value of effort, thereby allowing cells with more effort to have more influence on the estimated values from the model. Cell identity was included as a random effect to account for correlation between observations within the same cell. The resulting model was then used to predict the number of harbor porpoises in each grid cell across the whole Moray Firth. This included the area surveyed, which was used to construct the model, and other areas outside of this where the cells had habitat variables that fell within the range of those used in the model. We applied a standard value for effort to allow comparisons to be made across cells which had received different levels of survey effort. This value of 1 km of transect line per grid cell, provided a relative index of porpoise abundance which we express as porpoise sightings per kilometer of trackline (porpoises km^{-1}).

C. Model comparison with acoustic data

In 2009 and 2010, between April and October, 69 CPODs (Chelonia Ltd., UK) were deployed within grid cells for which we were able to predict porpoise relative abundance from the habitat association model. Data from these CPODs were exported in four ways, summarizing the data over different time scales: The number of minutes per day that porpoise click trains were detected (porpoise positive minutes; PPM), the number of hours per day that porpoise click trains were detected (porpoise positive hours; PPH), the number of days on which porpoise clicks trains were detected (porpoise positive days; PPD) and the waiting time between detections (waiting time). The minimum waiting time allowed was one minute, so the data reflect new trains of porpoise clicks rather than the very short intervals between clicks within a train. Data were then pooled for 2009 and 2010, for the entire April to October sampling period for each site. The median value was calculated for PPM, PPH and waiting time, while the proportion of PPD was reported. If more than one CPOD was concurrently present within the cell, the device with the longest time series was used. The minimum duration of data collection at a site was 56 days. These data were then compared with the habitat association model predictions using a Spearman's rank correlation test between each of the acoustic metrics for the grid

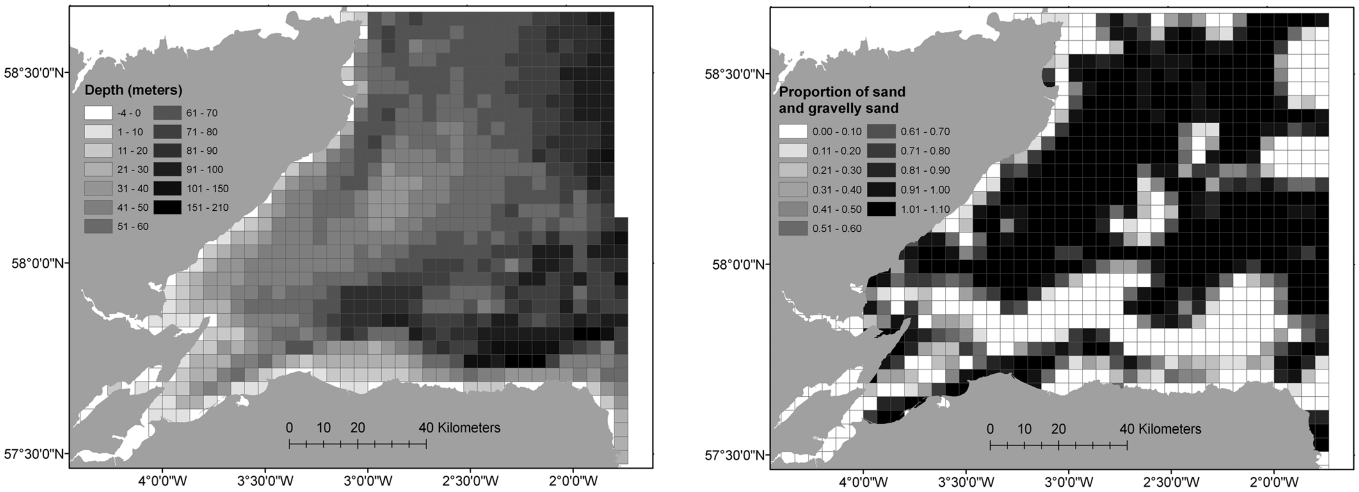

FIG. 3. Habitat variables (depth and sediment type) summarized over a 4 × 4 km grid. Sediment type is coded as the proportion of the area of the cell that was classified as sand or gravelly sand. © Crown Copyright/SeaZone Solutions Ltd. All Rights Reserved.

cells in which the CPODs were positioned and the modeled relative abundance predictions.

This analysis was carried out on the full dataset, and also on a dataset that excluded cells in which the model predictions had high standard error values. The full dataset of 69 observations had a mean standard error of 1.32, and a median of 1.23, with values ranging from 1.14 to 2.64. In our reduced dataset, removing observations with standard errors greater than 1.40 reduced the dataset by 15 observations but brought the mean standard error much closer to the median, with values of 1.22 and 1.21, respectively, effectively removing the tail of the distribution.

For the acoustic metric with the strongest correlation, we also grouped all cells in which there were acoustic data into three categories to represent areas in which model predictions of relative porpoise abundance were low, medium, or high. The groups were of equal width of predicted values, with each group accounting for approximately a third of the range of predictions. The low group contained 26 cells containing CPODs, with predicted porpoises km^{-1} of 0.000–0.039. The medium group contained 33 cells with predicted porpoises km^{-1} of 0.040–0.079 and the high group contained ten observations from cells with predicted porpoises km^{-1} of 0.080–0.130. We then compared the selected acoustic metric for sites in each of these groups using a Kruskal Wallis test. Where a significant effect was found, *post hoc* Wilcoxon tests were used to determine which groups were different from each other. This analysis was also carried out on the reduced dataset. The number of observations in the low, medium and high groups was 16, 29, and 9 respectively in this reduced dataset.

III. RESULTS

In total, 1073 porpoise sightings were included in the model (Table I). These were generally clustered in offshore areas where there were large amounts of survey effort (Fig. 4).

A. Habitat association model

Data exploration indicated that depth and distance from the coast were highly collinear, so distance from the coast was removed from the model since its relationship with porpoise count was somewhat weaker. Initial models were found to be overdispersed when using a Poisson distribution, and the final models therefore used a negative binomial distribution (O'Hara and Kotze, 2010). The initial model included the explanatory variables depth, the proportion of

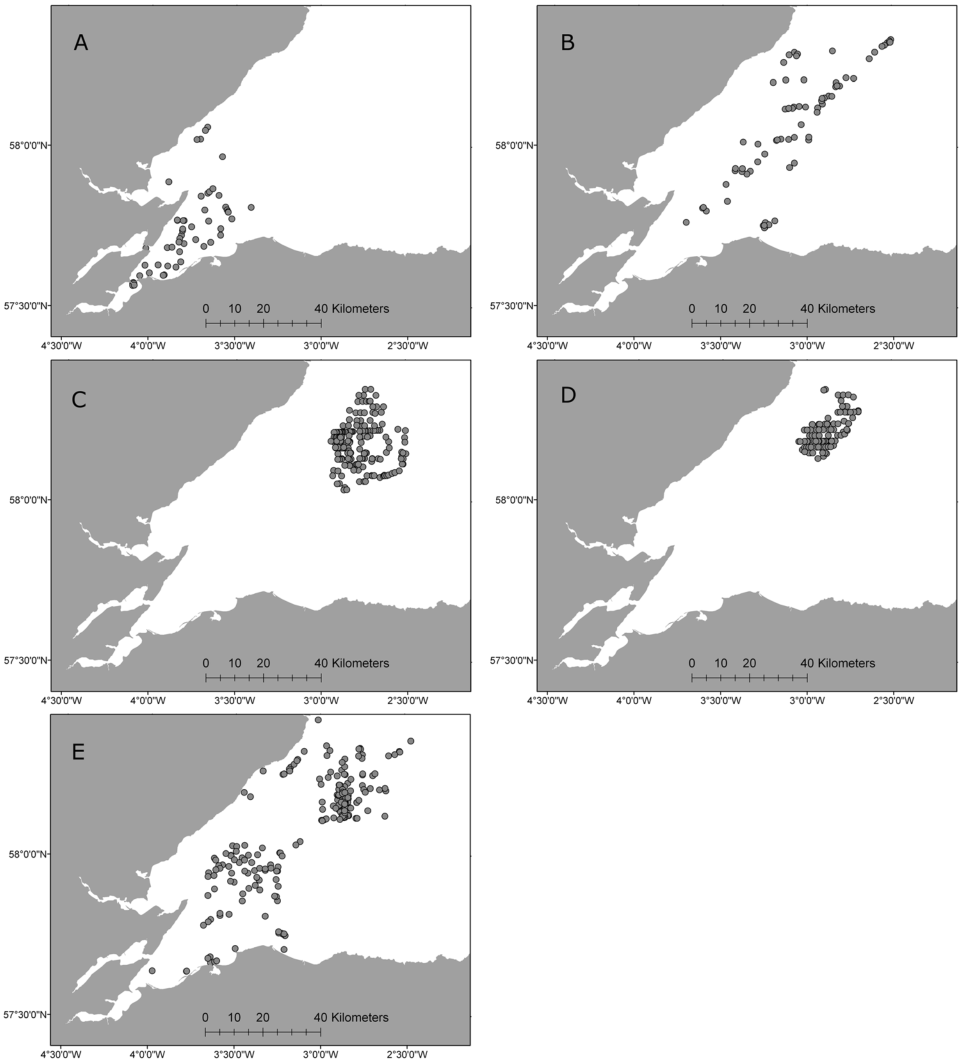

FIG. 4. Location of harbor porpoise sightings from four boat based surveys (a to d) and one aerial survey (e) in the Moray Firth between 2004 and 2010.

the sediment that was sand or gravelly sand, slope, survey method, and the log of effort length as an offset. Model selection, based on AIC scores (Akaike, 1974), resulted in the removal of slope, but retained a smoother, which was a 2D surface describing the relative abundance of porpoises using an interaction between depth and the proportion of sand and gravelly sand sediments (Fig. 5, Table II). Survey method did not improve the AIC score of the model, so was not included in the final model, which contained only the 2D smoother and the effort offset as fixed effects, and cell identity as a random effect. The r^2 value of this model was 0.381.

The random effect in the model showed that there was a relatively strong correlation of 0.69 between observations from the same cell. This was calculated as

$$a^2/(a^2+b^2), \tag{1}$$

where a is variance of the random intercept and b is variance of the residual term (Zuur *et al.*, 2009). In this case, $a = 0.710$ and $b = 0.481$.

The final model was then used to predict spatial variation in the relative abundance of porpoises across the Moray Firth (Fig. 6).

B. Model comparison with acoustic data

The CPODs used in this analysis were deployed for a median of 106 days. All of the metrics showed similar variation in the occurrence of porpoises across the Moray Firth between April and October, with lower detection rates in coastal regions (Table III). The four acoustic metrics (PPM, PPH, PPD, and waiting time) derived from the CPOD data were compared with the predictions from the habitat association model for the cell in which they were deployed, using a Spearman's rank correlation (Table III). For both the full dataset and the reduced dataset, only PPH [Fig. 7(a)] was significantly correlated with the model predictions. This metric was therefore preferred in further analyses (Fig. 8). Comparison of data from the 30 sites where data were available in both 2009 and 2010 indicate that this spatial variation in median PPH was consistent between years [Spearman's rank correlation: $R = 0.834$, $S = 744$, $P < 0.001$; Fig. 7(b)].

TABLE II. Results of a negative binomial GAMM used to analyze harbor porpoise counts, using a tensor smoother, with an interaction term between depth and the proportion of sand and gravelly sand.

	Parametric coefficients			
	Estimate	Standard error	t	P
Intercept	−3.010	0.084	−35.86	<0.001
	Smooth terms			
	Estimated degrees of freedom	Reference degrees of freedom	F	P
2D smoother for depth and proportion of sand and gravelly sand	6.679	6.679	6.274	<0.001

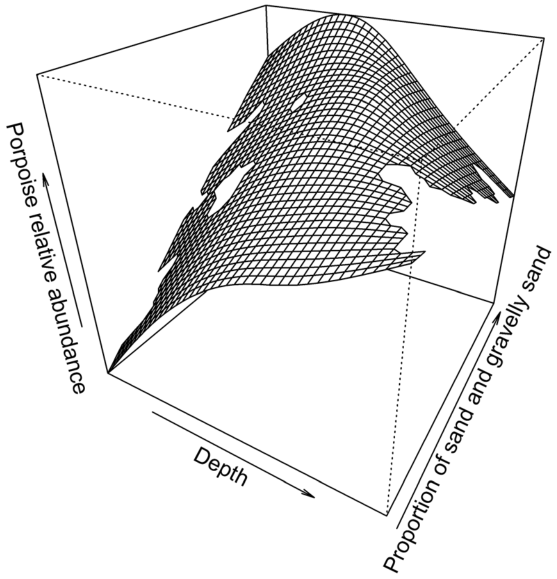

FIG. 5. Two dimensional smoother used in the porpoise habitat association model to describe the interaction between depth and the proportion of sediments that were sand or gravelly sand, and the relationship between these habitat variables and harbor porpoise relative abundance.

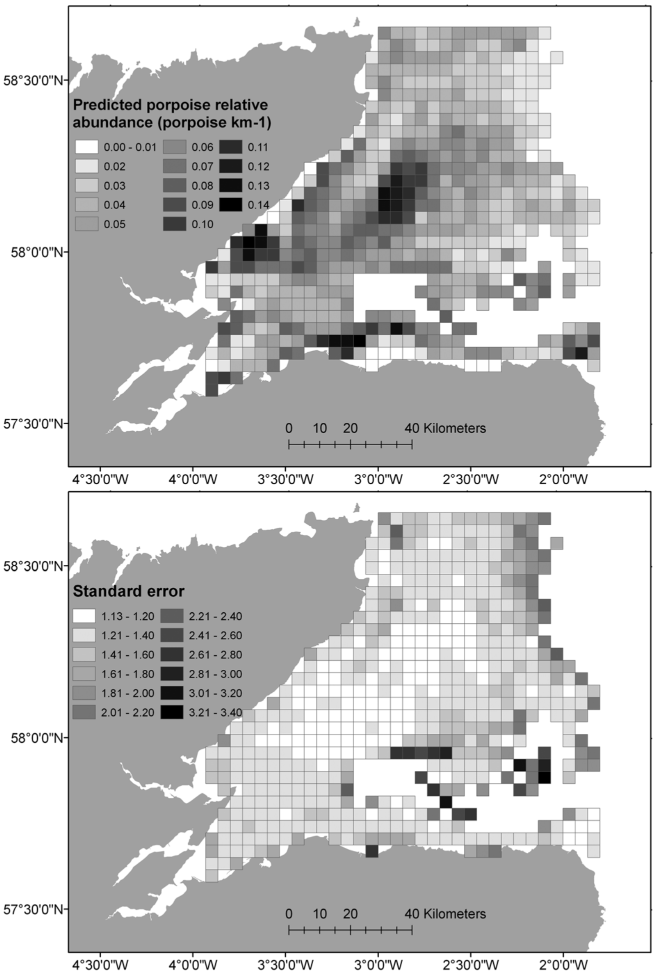

FIG. 6. Maps of predicted relative abundance of porpoises (porpoise km^{-1}) and the standard error of the prediction, from a GAMM with depth and the proportion of sand and gravelly sand sediments, given 1 km of effort in each cell. Predictions were not made in cells where depth was greater than 80 m because no survey data were available to inform these predictions (white areas in the figures).

TABLE III. Comparison of CPOD metrics used in correlation analyses with the porpoise habitat association model, from 69 CPODs deployed from April to October of 2009 and 2010. PPD is the proportion of porpoise positive days, PPH is median porpoise positive hours per day, PPM is median porpoise positive minutes per day and waiting time is the median number of minutes between successive porpoise detections. Correlations are Spearman's rank, on the full and reduced datasets. Coastal CPOD locations are within 10 km of land.

	Coastal N = 20			Offshore N = 49				
Metric	Min	Max	Median	Min	Max	Median	Correlation (all data)	Correlation (SE < 1.40)
PPD	0.0667	1	0.8390	0.2056	1	0.99	R = 0.148, S = 46628, p = 0.224	R = 0.229, S = 20233, p = 0.096
PPH	0	8	2.5	0	17	6	R = 0.239, S = 41681, p = 0.048	R = 315, S = 17973, p = 0.020
PPM	0	60	8	0	178.5	29	R = 0.169, S = 45493, p = 0.169	R = 0.255, S = 19534, p = 0.062
Waiting time	19	6546	86	7	127	39	R = −0.054, S = 57686, p = 0.661	R = −0.164, S = 30534, p = 0.235

Using the pooled data from both years, there were significant differences in median PPH at sites within cells with low, medium and high predicted densities [Fig. 9(a); Kruskal Wallis, $\chi^2 = 7.979$, d.f. = 2, P = 0.019]. *Post hoc* analysis with Wilcoxon tests showed that there was a significant difference between the low and medium groups (W = 255.5, P = 0.008). Analysis of the reduced dataset [Fig. 9(b)], also showed an overall significant effect of the groups (Kruskal Wallis, $\chi^2 = 10.810$, d.f. = 2, P = 0.005). *Post hoc* analysis with Wilcoxon tests showed that there was a significant difference between the low and medium predicted relative abundance groups (W = 102.5, P = 0.002), and also between the low and high groups (W = 34.5, P = 0.035).

IV. DISCUSSION

Both habitat association modeling and static acoustic monitoring are well established methods of studying cetaceans (e.g., Bailey and Thompson, 2009; Bailey *et al.*, 2010a), with habitat modeling providing good spatial coverage, and static acoustics providing good temporal coverage. Clearly, both techniques have weaknesses as well as strengths; visual survey are reliant on porpoises being visible at the surface, which is affected by sighting conditions, as well as the length of time they are under the water and acoustic data rely on animals echolocating in the vicinity of the devices to be detected. For harbor porpoise, the likelihood of this is high as they have been shown to produce high rates of echolocation clicks, particularly when foraging (Akamatsu *et al.*, 2007; Linnenschmidt *et al.*, 2013). Combining and comparing these complementary techniques in this study allowed us to determine whether spatial patterns observed in snapshot surveys were consistent over time.

The area covered by visual surveys was predominantly offshore, and the data used to build the habitat association model reflect this. Consequently, we were unable to determine whether harbor porpoises in the Moray Firth are associated with areas of high tidal strength or areas around islands which other studies have shown to be important (Marubini *et al.*, 2009; Shucksmith *et al.*, 2009; Embling *et al.*, 2010). Instead, as expected from studies of other predators in this region (Mudge and Crooke, 1986; Greenstreet *et al.*, 1998), we found high numbers of harbor porpoise sightings over areas such as the Smith Bank, which are likely to contain suitable habitat for potential prey such as sandeels (Hopkins, 1986; ICES, 2007). Sighting rates of harbor porpoise further inshore may also be affected by the presence of bottlenose dolphins *Tursiops truncatus* in coastal areas (Culloch and Robinson, 2008; Cheney *et al.*, 2013), due to the risk of aggressive interactions between the two species (Ross and Wilson, 1996; Thompson *et al.*, 2004; Simon *et al.*, 2010).

The pattern of higher visual sightings in offshore areas remained clear even when effort was taken into account. We therefore modeled distribution based upon depth and the availability of sand and gravelly sand, a habitat that is likely to be favored by potential prey. Modeling species distribution using these static variables to some extent allowed us to

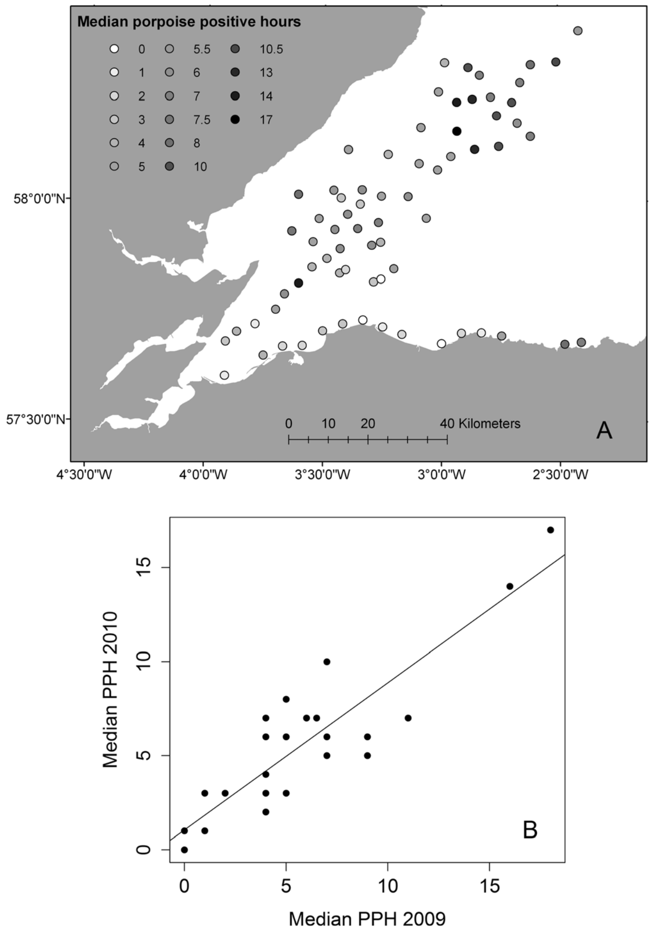

FIG. 7. (a) Spatial variation in median PPH detected on acoustic loggers deployed April to October in 2009 and 2010. Loggers less than 10 km from the coast are considered to be "coastal," while those further from coast are considered to be "offshore." (b) Comparison of detection rates in 2009 and 2010 at the 30 sites where data were available from both years. Median PPH for the sites in both years is shown, along with the line of best fit from a linear model for illustration.

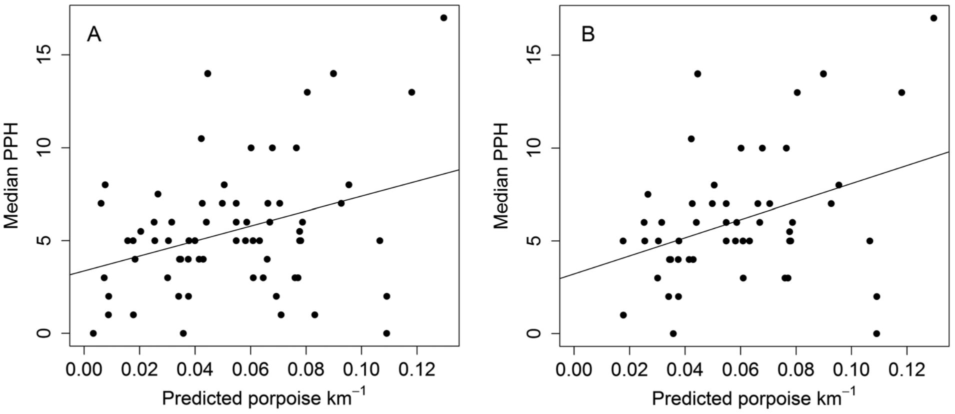

FIG. 8. Plots of the predicted porpoises km^{-1} from the habitat association model, against the median hours porpoises were detected acoustically within the same cell. (a) Data are included from all cells; (b) only cells where the standard error of the predicted number of porpoises was less than 1.4 are included. The line of best fit from a linear model is plotted for illustration.

avoid problems of trophic mismatch between environmental covariates and animal habitat preference that have been shown when using dynamic variables such as sea surface temperature and chlorophyll-*a* concentration (Grémillet *et al.*, 2008). While such dynamic variables, which influence prey availability over tidal, diel, and seasonal time-scales, can influence the distribution of both harbor porpoises and other marine top predators that they may interact or compete with (Scott *et al.*, 2010), they generally do not directly influence marine predator distributions and instead tend to be used as proxies for prey availability.

Habitat association models allow species distribution to be predicted over large areas, but effort and sightings in even the highest density areas are typically low. In some studies in which dynamic variables have been included in habitat association models using visual survey data (e.g., Forney *et al.*, 2012), survey effort has been divided into track line segments, but this requires then having to use interpolation and/or smoothing of the resulting model predictions to obtain values across the entire study area. This can introduce additional errors as it generally involves a distance-weighted interpolation that does not take into consideration the habitat characteristics in the areas not surveyed between the track lines. We instead used the approach of first gridding the data and then using the habitat characteristics of each grid cell to make predictions based on the habitat association model. Since our response variable was the sum of the number of porpoises for each survey, and these surveys generally occurred over several months, the values in each grid cell do not correspond to a single point in time. It was therefore not possible to match the number of sightings with a corresponding value for dynamic variables that would have changed over the course of the survey periods.

The standard error around predictions was particularly high in cells with habitat variables at the extremes of those surveyed, although the dataset used to build the model potentially contained additional sources of variability, such as the difference in numbers of observers used on surveys, observer experience, and the broad time scale over which surveys were carried out. In particular, we anticipated that sighting rates may differ between aerial and boat based surveys. However, the method of data collection did not contribute to a lower AIC value, and we therefore pooled data from all surveys in the final model. While there may also have been some differences in sighting rates between the different boat based surveys, efforts to evaluate this were constrained by sample size and the limited spatial overlap between boat surveys. In practice, this between-survey variability should have been reduced by following standardized ESAS methodology and ensuring that most surveys were carried out in Beaufort sea state 3 or less.

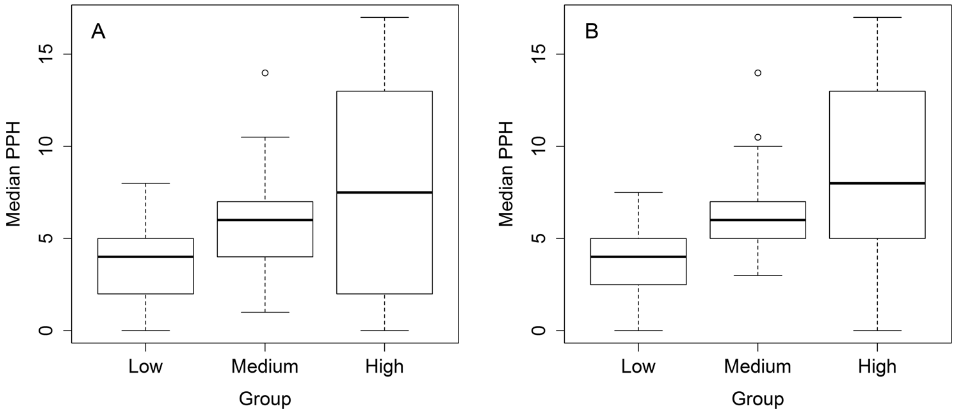

FIG. 9. Box plots of median number of detection positive hours from CPODs grouped by (a) predicted porpoise numbers for all cells in a habitat association model from visual survey data (N = 69) and (b) for cells with predictions with standard errors less than 1.4 (N = 54). The low group contains predicted porpoises km^{-1} values ranging from 0 to 0.039, the medium group contains values from 0.04 to 0.079 and the high group contains values from 0.08 to 0.13. Boxes represent the limits of the second and third quartile, while the bold central line represents the median. The range of the data (first and fourth quartiles) is shown by the dotted lines and outlying observations are represented by circles.

The spatial pattern of acoustic detections also showed that porpoises were detected more often in offshore waters than in coastal areas (Table III), with particularly high levels of detection around the Smith Bank area [Fig. 7(a)]. These acoustic data were collected at a resolution that allowed us to assess a range of metrics that have been used in previous studies (e.g., Carstensen *et al.*, 2006; Brandt *et al.*, 2011). When compared with habitat association model predictions, the strongest correlation was obtained using PPH as a metric. It is likely that PPD is too coarse to describe porpoise distribution since a porpoise need only be close to a device for a few seconds in a given day for it to record a positive value. Conversely, the broad scale of the habitat association model may not be captured when compared with finer scale variability in waiting times and PPM. Using PPH is also likely to reduce temporal auto-correlation, and previous studies using TPODs, the precursor to the CPOD, indicated that any impacts from slight differences in the sensitivity of individual devices were reduced when data were analyzed at the hour scale (Bailey *et al.*, 2010a). Comparison of acoustic data collected in 2009 and 2010 suggest that this spatial variation in median PPH was consistent in the 2 years of our study [Fig. 7(b)]. Acoustic data from this broad suite of sites were not available earlier than 2009, but a 3-year data set collected at a single site on the Smith Bank between 2005 and 2007 also found consistently high levels of detections in this offshore area (Thompson *et al.*, 2010).

When using only visual survey data, a portion of the original survey data are commonly held back and used to validate habitat association models (e.g., Marubini *et al.*, 2009), but this reduces the number of sightings available to build the model, which may reduce its power. It is therefore valuable to identify other sources of data which can be used to test model predictions. Embling (2007) compared the predicted core areas of porpoise abundance from models built on boat based survey sightings data with models built using passive acoustic detections. In that case, both visual and acoustic data were collected simultaneously from the same vessel. Models constructed with the two different types of data supported the use of different predictor variables, but the two models still predicted similar core areas (Embling, 2007). Sveegaard *et al.* (2011) took this one stage further, using independent data from mobile passive acoustic surveys to test the predictions of habitat association models built using tracking data from satellite tagged porpoises.

Our study also made use of independent data, which used different methods for detecting porpoises, to improve our understanding of spatial and temporal patterns in habitat association. Overall, the correlation between habitat model predictions and acoustic detections was significant, but not especially strong. However, some cells had large standard errors around the predictions, often because they had habitat variables that were at the extremes of those used to build the model or because a limited amount of survey effort had been concentrated on that particular combination of habitat variables. Further survey work could be targeted toward those habitats or water depths that were poorly represented to improve the precision of the model. Removing data associated with cells with high standard errors improved this fit, but the association was still relatively weak. This is likely to be partly due to differences in the type of data collected, with the acoustic data representing the presence or absence of porpoises within an hour, and visual surveys recording numbers of animals within an area. Nevertheless, at a coarser scale, where model predictions were grouped as low, medium, and high porpoises km^{-1} for each cell, significant differences were evident in median PPH between the low group and the medium group (Fig. 9). The high group was more variable, largely due to its smaller sample size, but when cells with a high standard error were excluded, this was also significantly different from the low group. Overall, many of the passive acoustic monitoring locations that had the highest rates of detection [Fig. 7(a)] were within areas where the model predicted high numbers of porpoises km^{-1} (Fig. 6). Similar analyses carried out by Sveegaard *et al.* (2011) showed that there were also more acoustic detections in the key areas predicted by telemetry data.

Overall, the integration of passive acoustic data and visual surveys can add value to the interpretation of the results of each. Visual survey techniques remain important where measures of absolute density are required (e.g., Hammond *et al.*, 2002), and although there is an ongoing effort to establish methods for using C-POD data to estimate animal density (Marques *et al.*, 2013), at present it is not possible to determine how variations in acoustic detections on these devices are influenced by the numbers of individuals present around the site. In this study we have demonstrated that passive acoustic techniques now offer the opportunity to collect data over broad temporal and spatial scales. Collection of year-round acoustic data is currently ongoing to assess how spatio-temporal variation in the occurrence of porpoises relates to a range of habitat characteristics, including both static and dynamic variables.

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Akaike, H. (**1974**). "A new look at the statistical model identification," IEEE Trans. Autom. Control AC**19**, 716–723.

Akamatsu, T., Teilmann, J., Miller, L. A., Tougaard, J., Dietz, R., Wang, D., Wang, K. X., Siebert, U., and Naito, Y. (**2007**). "Comparison of echolocation behaviour between coastal and riverine porpoises," Deep Sea Res. Part II **54**, 290–297.

Atkinson, C. J. L., Bergmann, M., and Kaiser, M. J. (**2004**). “Habitat selection in whiting,” J. Fish Biol. **64**, 788–793.

Bailey, H., Clay, G., Coates, E. A., Lusseau, D., Senior, B., and Thompson, P. M. (**2010a**). “Using T-PODs to assess variations in the occurrence of coastal bottlenose dolphins and harbour porpoises,” Aquat. Conserv. Mar. Freshwater. Ecosys. **20**, 150–158.

Bailey, H., Senior, B., Simmons, D., Rusin, J., Picken, G., and Thompson, P. M. (**2010b**). “Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential effects on marine mammals,” Mar. Poll. Bull. **60**, 888–897.

Bailey, H., and Thompson, P. M. (**2009**). “Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area,” Mar. Ecol. Prog. Ser. **378**, 279–287.

Brambilla, M., Casale, F., Bergero, V., Bogliani, G., Crovetto, G. M., Falco, R., Roati, M., and Negri, I. (**2010**). “Glorious past, uncertain present, bad future? Assessing effects of land-use changes on habitat suitability for a threatened farmland bird species,” Biol. Conserv. **143**, 2770–2778.

Brandt, M. J., Diederichs, A., Betke, K., and Nehls, G. (**2011**). “Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea,” Mar. Ecol. Prog. Ser. **421**, 205–216.

Camphuysen, C. J., Fox, A. D., Leopold, M. F., and Petersen, I. K. (**2004**). “Towards standardised seabirds at sea census techniques in connection with environmental impact assessment for offshore wind farms in the UK: A comparison of ship and aerial sampling methods for marine birds, and their applicability to offshore wind farm assessments,” Collaborative Offshore Wind Research Into the Environment, London. COWRIE-BAM-02-2002, http://jncc.defra.gov.uk/pdf/Camphuysenetal2004_COWRIEmethods.PDF (Last viewed 24 May 2012), p. 39.

Cañadas, A., Sagarminaga, R., de Stephanis, R., Urquiola, E., and Hammond, P. S. (**2005**). “Habitat preference modelling as a conservation tool: Proposals for marine protected areas for cetaceans in southern Spanish waters,” Aquat. Conserv. Mar. Freshwater. Ecosys. **15**, 495–521.

Carstensen, J., Henriksen, O. D., and Teilmann, J. (**2006**). “Impacts of offshore wind farm construction on harbour porpoises: Acoustic monitoring of echolocation activity using porpoise detectors (T-PODs),” Mar. Ecol. Prog. Ser. **321**, 295–308.

Chelonia Ltd. (**2012a**). “C-POD specification,” www.chelonia.co.uk/cpod_specification (Last viewed 24 May 2012).

Chelonia Ltd. (**2012b**). “CPOD.exe: A guide for users,” http://www.chelonia.co.uk/downloads/CPOD.doc (Last viewed 24 May 2012).

Cheney, B., Thompson, P. M., Ingram, S. N., Hammond, P. S., Stevick, P. T., Durban, J. W., Culloch, R. M., Elwen, S. H., Mandleberg, L., Janik, V. M., Quick, N. J., Islas-Villanueva, V., Robinson, K. P., Costa, M., Eisfeld, S. M., Walters, A., Phillips, C., Weir, C. R., Evans, P. G. H., Anderwald, P., Reid, R. J., Reid, J. B., and Wilson, B. (**2013**). “Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters,” Mammal Rev. **43**, 71–88.

Culloch, R. M., and Robinson, K. P. (**2008**). “Bottlenose dolphins using coastal regions adjacent to a Special Area of Conservation in north-east Scotland,” J. Mar. Biol. Assoc. U.K. **88**, 1237–1243.

EEC (**1992**). “Council Directive on the conservation of natural habitats and of wild fauna and flora,” in *92/43/EEC*, http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CONSLEG:1992L0043:20070101:EN:PDF (Last viewed 23 May 2012).

Elith, J., and Leathwick, J. R. (**2009**). “Species distribution models: ecological explanation and prediction across space and time,” Annu. Rev. Ecol. Evol. Syst. **40**, 677–697.

Embling, C. B. (**2007**). “Predictive models of cetacean distributions off the west coast of Scotland,” PhD Thesis, University of St. Andrews, UK, pp 278.

Embling, C. B., Gilibrand, P. A., Gordon, J., Shrimpton, J., Stevick, P. T., and Hammond, P. S. (**2010**). “Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*),” Biol. Conserv. **143**, 267–279.

Forcey, G. M., Thogmartin, W. E., Linz, G. M., Bleier, W. J., and McKann, P. C. (**2011**). “Land use and climate influences on waterbirds in the Prairie Potholes,” J. Biogeogr. **38**, 1694–1707.

Forney, K. A., Ferguson, M. C., Becker, E. A., Fiedler, P. C., Redfern, J. V., Barlow, J., Vilchis, I. L., and Ballance, L. T. (**2012**). “Habitat-based spatial models of cetacean density in the eastern Pacific Ocean,” Endangered Species Res. **16**, 113–133.

Gontier, M., Mörtberg, U., and Balfors, B. (**2010**). “Comparing GIS-based habitat models for applications in EIA and SEA,” Environ. Imp. Assess. Rev. **30**, 8–18.

Greenstreet, S. P. R., McMillan, J. A., and Armstrong, E. (**1998**). “Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: A response to variation in prey abundance?,” ICES J. Mar. Sci. **55**, 121–133.

Grémillet, D., Lewis, S., Drapeau, L., van Der Lingen, C. D., Huggett, J. A., Coetzee, J. C., Verheye, H. M., Daunt, F., Wanless, S., and Ryan, P. G. (**2008**). “Spatial match-mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions?,” J. Appl. Ecol. **45**, 610–621.

Hammond, P. S. (**2006**). “Small cetaceans in the European Atlantic and North Sea (SCANS-II),” in *EC LIFE Project LIFE04NAT/GB/000245*, http://biology.st-andrews.ac.uk/scans2/documents/final/SCANS-II_final_report.pdf (Last viewed 10 May 2012), p. 55.

Hammond, P. S., Berggren, P., Benke, H., Borchers, D. L., Collet, A., Heide-Jørgensen, M. P., Heimlich, S., Hiby, A. R., Leopold, M. F., and Øien, N. (**2002**). “Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters,” J. Appl. Ecol. **39**, 361–376.

Holland, G. J., Greenstreet, S. P. R., Gibb, I. M., Fraser, H. M., and Robertson, M. R. (**2005**). “Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment,” Mar. Ecol. Prog. Ser. **303**, 269–282.

Hopkins, P. J. (**1986**). “Exploited fish and shellfish populations in the Moray Firth,” Proc. R. Soc. Edin. [Biol.] **91B**, 57–72.

ICES (**2007**). “Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak (WGNSSK), 5–14 September 2006,” Report (ICES, Copenhagen, Denmark), pp. 1160.

Ingram, S., and Rogan, E. (**2002**). “Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*,” Mar. Ecol. Prog. Ser. **244**, 247–255.

Johnston, D. W., Westgate, A. J., and Read, A. J. (**2005**). “Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy,” Mar. Ecol. Prog. Ser. **295**, 279–293.

Leeney, R. H., Amies, R., Broderick, A. C., Witt, M. J., Loveridge, J., Doyle, J., and Godley, B. J. (**2008**). “Spatio-temporal analysis of cetacean strandings and bycatch in a UK fisheries hotspot,” Biodivers. Conserv. **17**, 2323–2338.

Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R., and Miller, L. A. (**2013**). “Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*),” Mar. Mammal Sci. **29**, 77–97.

Louzao, M., Hyrenbach, K. D., Arcos, J. M., Abello, P., de Sola, L. G., and Oro, D. (**2006**). “Oceanographic habitat of an endangered Mediterranean Procellariiform: Implications for marine protected areas,” Ecol. Appl. **16**, 1683–1695.

Marubini, F., Gimona, A., Evans, P. G. H., Wright, P. J., and Pierce, G. J. (**2009**). “Habitat preferences and interannual variability in occurrence of the harbour porpoise *Phocoena phocoena* off northwest Scotland,” Mar. Ecol. Prog. Ser. **381**, 297–310.

Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Moretti, D. J., Harris, D., and Tyack, P. L. (**2013**). “Estimating animal population density using passive acoustics,” Biol. Rev. Camb. Philos. Soc. **88**, 287–309.

Mudge, G. P., and Crooke, C. H. (**1986**). “Seasonal changes in the numbers and distribution of seabirds at sea in the Moray Firth, northeast Scotland,” Proc. R. Soc. Edin. [Biol.] **91B**, 81–104.

Muhling, B. A., Lee, S. K., Lamkin, J. T., and Liu, Y. (**2011**). “Predicting the effects of climate change on bluefin tuna (*Thunnus thynnus*) spawning habitat in the Gulf of Mexico,” ICES J. Mar. Sci. **68**, 1051–1062.

Nur, N., Jahncke, J., Herzog, M. P., Howar, J., Hyrenbach, K. D., Zamon, J. E., Ainley, D. G., Wiens, J. A., Morgan, K., Ballance, L. T., and Stralberg, D. (**2011**). “Where the wild things are: Predicting hotspots of seabird aggregations in the California Current System,” Ecol. Appl. **21**, 2241–2257.

O’Hara, R. B., and Kotze, D. J. (**2010**). “Do not log-transform count data,” Methods Ecol. Evol. **1**, 118–122.

Péron, C., Delord, K., Phillips, R. A., Charbonnier, Y., Marteau, C., Louzao, M., and Weimerskirch, H. (**2010**). “Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island,” Mar. Ecol. Prog. Ser. **416**, 267–284.

R Development Core Team (**2010**). “R: A language and environment for statistical computing, version 2.12.1” (R Foundation for Statistical Computing, Vienna, Austria.).

Reid, J. B., Evans, P. G. H., and Northridge, S. P. (**2003**). *Atlas of Cetacean Distribution in North-West European Waters* (Joint Nature Conservation Committee, Peterborough, UK), p. 82.

Ross, H. M., and Wilson, B. (**1996**). "Violent interactions between Bottlenose Dolphins and Harbour Porpoises," Proc. R. Soc. Lond. **263**, 283–286.

Santos, M. B., and Pierce, G. J. (**2003**). "The diet of harbour porpoise (*Phocoena phocoena*) in the northeast Atlantic," Ocean. Mar. Biol. **41**, 355–390.

Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Ross, H. M., Patterson, I. A. P., Reid, D. G., and Beare, D. (**2004**). "Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003," Mar. Mamm. Sci. **20**(1), 1–27.

Scheidat, M., Tougaard, J., Brasseur, S., Carstensen, J., Petel, T. V., Teilmann, J., and Reijnders, P. (**2011**). "Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea," Environ. Res. Lett. **6**, 025102.

Scott, B. E., Sharples, J., Ross, O. N., Wang, J., Pierce, G. J., and Camphuysen, C. J. (**2010**). "Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll," Mar. Ecol. Prog. Ser. **408**, 207–226.

SeaZone Solutions Ltd. (**2005a**). "6 arcsecond grid tiles: NW25600020, NW25600040, NW25600060, NW25800040," Hydrospatial bathymetry [gridded bathymetry].

SeaZone Solutions Ltd. (**2005b**). "1:250,000 scale tiles: NW25600020, NW25600040, NW25600060, NW25800040," Seabed sediment [shapefile geospatial data].

Shucksmith, R., Jones, N. H., Stoyle, G. W., Davies, A., and Dicks, E. F. (**2009**). "Abundance and distribution of the harbour porpoise (*Phocoena phocoena*) on the north coast of Anglesey, Wales, UK," J. Mar. Biol. Assoc. U.K. **89**, 1051–1058.

Simon, M., Nuuttila, H., Reyes-Zamudio, M. M., Ugarte, F., Verfuß, U. K., and Evans, P. G. H. (**2010**). "Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning," J. Mar. Biol. Assoc. U. K. **90**, 1539–1545.

Sveegaard, S., Teilmann, J., Berggren, P., Mouritsen, K. N., Gillespie, D., and Tougaard, J. (**2011**). "Acoustic surveys confirm the high-density areas of harbour porpoises found by satellite tracking," ICES J. Mar. Sci. **68**, 929–936.

Thompson, P., White, S., and Dickson, E. (**2004**). "Co-variation in the probabilities of sighting harbor porpoises and bottlenose dolphins," Mar. Mammal Sci. **20**, 322–328.

Thompson, P. M., Lusseau, D., Barton, T., Simmons, D., Rusin, J., and Bailey, H. (**2010**). "Assessing the responses of coastal cetaceans to the construction of offshore wind turbines," Mar. Poll. Bull. **60**, 1200–1208.

Todd, V. L. G., Pearse, W. D., Tregenza, N. C., Lepper, P. A., and Todd, I. B. (**2009**). "Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations," ICES J. Mar. Sci. **66**, 734–745.

Vinther, M., and Larsen, F. (**2004**). "Updated estimates of harbour porpoise (*Phocoena phocoena*) bycatch in the Danish North Sea," J. Cetacean Res. Manage. **6**, 19–24.

Webb, A., and Durinck, J. (**1992**). "Counting birds from ship," in *Manual for Aeroplane and Ship Surveys of Waterfowl and Seabirds*, edited by J. Komdeur, J. Bertelsen, and G. Cracknell, Special Publication 19 (International Waterfowl and Wetlands Research Bureau, Slimbridge, UK), pp. 37.

Wood, S. N. (**2008**). "Fast stable direct fitting and smoothness selection for generalized additive models," J. R. Statist. Soc. (B) **70**, 495–518.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (**2009**). *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York), pp. 101–142, 323–342.