Habitat use of a coastal delphinid population investigated using passive acoustic monitoring

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Abstract

- The population of bottlenose dolphins in eastern Scotland has undergone significant range expansion since the 1990's, when a special area of conservation was established for the population.
- Distribution of this population is well described within areas of its range, where intensive work has been carried out, such as the inner Moray Firth, St Andrews Bay, and the Tay estuary area. However, elsewhere in their range, habitat use is less well understood.
- In this study, a large-scale and long-term passive acoustic array was used to gain a better understanding of bottlenose dolphin habitat use in eastern Scottish waters, complementing and augmenting existing visual surveys.
- Data from the array were analysed using a three-stage approach. First, acoustic occupancy results were reported; second, temporal trends were modelled; and third, a spatial-temporal-habitat model of acoustic occupancy was created.
- Results from the acoustic occupancy are in agreement with visual studies that found areas near known foraging locations were consistently occupied. Results from the trend

analysis were inconclusive. Habitat modelling showed that, throughout their range, bottlenose dolphins are most likely to be detected closer to shore, and, for a constant distance to shore, in deeper water.

Keywords: Ocean, coastal, habitat management, Marine Protected Area, protected species, mammals

1. Introduction

Bottlenose dolphins (*Tursiops truncatus*) are a cosmopolitan species with populations found in tropical and temperate waters worldwide (Connor, Wells, Mann, and Read, 2000). Presently, the International Union for Conservation of Nature lists the species as 'Least concern' indicating a low risk of extinction. However, they are also listed under Appendix 2 of the Convention on the Conservation of Migratory Species of Wild Animals indicating a need for, or benefit from, international co-operation on conservation efforts. Off the eastern coast of Scotland, there is a population of bottlenose dolphins consisting of approximately 200 individuals (Cheney et al., 2013). The population is protected by a variety of national and international regulations, including Annexes II and IV of European Union Habitats Directive (92/43/EEC), Wildlife and Countryside Act (1981), and Joint Nature Conservation Committee UK Post-2010 Biodiversity Framework. In 2005, as part of these conservation efforts, a Special Area of Conservation (SAC) was established in the Moray Firth to protect habitat important to this population. The Moray Firth SAC covers approximately 1500 km^2 extending west from the Beauly Firth, north to Helmsdale, and east to Lossiemouth (http//:www.jncc.defra.gov.uk; Figure 1). The management of the SAC has been implemented in such a way that the population is protected throughout its range, whereby any activity which could have an adverse effect on the integrity of the site (i.e. the protected features) is subject to a Habitats Regulations Appraisal (Arso Civil et al., 2019).

The range of this population extends well outside of the bounds of the SAC, with animals commonly sighted along more than 200 km of coastal habitat (Paxton, Scott-Hayward, Mackenzie, Rexstad, & Thomas, 2016). Both within and outside the SAC, animals are known to aggregate at certain locations, often associated with the mouths of rivers or estuaries (Hastie, Wilson, & Thompson, 2003, 2006; Hastie, et. al, 2004; Mendes, Turrell, Lütkebohle, & Thompson, 2002; Pirotta et al., 2014; Sargeant, Mann, Berggren, & Krutzen, 2005; Wilson, Thompson, & Hammond, 1997). Because of the high encounter rates at these locations, some have become focal areas for boat-based survey efforts, most notably the inner Moray Firth and Firth of Tay. In some of these locations, henceforth termed points of aggregation, dolphins are known to exploit tidal cycles and local bathymetry to maximise foraging efficiency (Hastie et al., 2004). This is the case at two locations within the inner Moray Firth SAC: Chanonry Point near the River Ness, and the entrance to the Cromarty Firth (Figure 1). At these locations deep channels result in higher prey density at low tides and therefore may represent increased foraging success for marine mammals (Thompson, Pierce, Hislop, Miller, & Diack, 1991). Outside of the Moray Firth SAC, points of aggregation have been observed around the mouth of the River Dee (Sini, Canning, Stockin, & Pierce, 2005), the Firth of Tay, and St Andrews Bay (Arso Civil et al., 2019). While foraging activity has been observed at some of these locations, the underlying factor(s) resulting in the higher occurrence are less clear for others. For example, dolphins are commonly sighted in and around St Andrews Bay, which is a shallow water area with a small estuary (Arso Civil et al., 2019; Quick & Janik, 2012).

Despite the large population range, most survey effort has focused on the Moray Firth and specifically on well-established areas of high usage (Arso Civil, 2014; Arso Civil et al., 2019; Bailey et al., 2010; Bailey & Thompson, 2006; Hastie et al., 2006; Hastie et al., 2003; Janik & Thompson, 1996; Pirotta et al., 2014; Thompson, Brookes, & Cordes, 2015; Wilson et al., 1997). While these areas clearly represent key habitat for this population (Cheney et al., 2013), effective conservation requires knowledge of habitat use throughout the population's range. Even in foraging hotspots, bottlenose dolphin sightings are often not predictable (Culloch & Robinson, 2008).

Since 2000, there have been a handful of regional scale surveys covering a large portion of the population's habitat (Cheney et al., 2013). These include a compilation of visual and sightings data from land and boat-based surveys (Thompson et al., 2011); a series of line transect surveys between the Firth of Forth and the river Dee (Arso Civil, 2014), as well as some passive acoustic studies (Cheney et al., 2013) . Together, results from these studies suggest that bottlenose dolphins use the entirety of the coastal habitat, though less frequently outside of the Moray Firth SAC than within it, and that animals are more likely to be sighted in waters within a few kilometres of the shore. However, the relative lack of survey effort in other parts of the population's range (Paxton et al., 2016) limits understanding of how these areas are used and their relative importance to the population.

This lack of understanding has potential implications for the Habitats Regulations Appraisals undertaken as part of the licensing of marine activities in the region, including the development of offshore wind energy. Of particular concern is the lack of data in the regions most likely to receive noise from wind farm construction activities, along with a lack of understanding of how far offshore bottlenose dolphins range in these regions. Thompson, Brookes & Cordes (2015) used a combination of fixed passive acoustic, and presence only visual survey data to model usage of offshore areas by bottlenose dolphins. While they showed that it was unlikely that the species used areas close to construction activities, the lack of data in the areas of concern reduced stakeholder confidence in the findings.

To address these issues, the East Coast Marine Mammal Acoustic Study (ECoMMAS) (Marine Scotaland Science, 2013) was started in 2013 to improve understanding of bottlenose dolphin use of the east coast of Scotland, with effort spread more evenly throughout the region, including data collection further offshore. The study uses fixed passive acoustic monitoring to complement existing visual surveys in coastal and high-use areas. The data presented here were collected during the first three years of the study.

C-PODs are commercially available echolocation click train detectors widely used for monitoring cetaceans. The instruments are sold with a proprietary click train detector that discriminates between 'noise' and the echolocation click trains (series of echolocation clicks) produced by dolphins and porpoises. Over the last decade, studies using these devices have contributed to our understanding of the behaviour and habitat use of the Moray Firth bottlenose dolphin population (Graham et al., 2017; Pirotta, Merchant, Thompson, Barton, & Lusseau, 2015; Pirotta et al., 2014).

Where multiple species are present however, discriminating between target (e.g. bottlenose dolphin) and non-target species constitutes a major and ongoing challenge in the field of marine passive acoustic monitoring. This is especially pertinent for studies using logging devices like C-PODS that collect few acoustic features from which to classify the detections. To account for this, users typically either deploy the instruments in habitats where only a single species is expected (Jaramillo-Legorreta et al., 2017) or assume the contribution of non-target species detections to the analysis is limited (Pirotta et al., 2014; Thompson et al., 2011). Due to the scale of the ECoMMAS array, neither assumption was applicable in this study. Throughout the survey area, multiple species have been known to occur (Anderwald et al., 2010; Arso Civil, 2014; Hammond et al., 2017). There is therefore a need to incorporate both acoustic classifiers and classifier uncertainty into the analysis (Caillat, 2013).

In this research, a heuristic approach was taken to misclassification wherein species uncertainty is built into the model response. An acoustic classification system (Palmer, Brookes, & Rendell, 2017) was applied to C-POD detections in order to group detections into one of three classes: broadband, frequency banded or unknown. The broadband category represents click trains matching bottlenose dolphin and common dolphin (*Delphinus spp.*) click characteristics and the frequency banded category represents click trains matching white-beaked (*Lagenorhynchus albirostris*) and Risso's (*Grampus griseus*) dolphin click characteristics (Calderan, Wittich, Harries, Gordon, & Leaper, 2013; Soldevilla et al., 2008). This analysis used the probability that each echolocation click was broadband as the predictor for bottlenose dolphin presence, thereby reducing the influence of non-target species on the model results.

Monitoring occupancy rates provides baseline data for future studies seeking to understand changes in distribution over long timescales. In Scottish waters, long-term acoustic studies of have been used to investigate the spatial and temporal distribution of harbour porpoises and bottlenose dolphins, as well as model the potential impacts of anthropogenic activities (Brookes, Bailey, & Thompson, 2013; Harris et al., 2017; Simon et al., 2010; Williamson et al., 2016) . In these studies, the presence of an acoustic signal characteristic of the animal (e.g. click or whistle) is used as a proxy for true occupancy (P. Thompson et al., 2011).

We expected to find low acoustic occupancy rates and the potential for misclassification was high, so this research took a three-stage approach. In the first stage, two acoustic occupancy rates are reported: proportion of acoustically monitored days containing acoustic encounters, and the proportion of acoustically monitored days containing one or more broadband acoustic encounters. The proportion of days with echolocation encounters is reported for the first three years of the ECoMMAS survey.

The second stage of the study modelled temporal trends in acoustic occupancy from the first three years of the ECoMMAS. As with baseline acoustic occupancy rates, identifying patterns in annual occupancy trends should be of interest to regulators seeking to manage the effects of offshore activities on dolphin habitat and behaviour.

The third stage of the analysis determined whether and to what extent it is possible to produce spatial-temporal habitat models of broadband acoustic occupancy using ECoMMAS C-POD data alone. In this portion of the analysis a model containing all available spatial and temporal covariates was fitted to acoustic detections aggregated from the first three years of the ECoMMAS study.

2. Methods

Data Collection

Data in this study were collected by 30 C-POD (version 1) echolocation click detectors (Chelonia, Ltd, UK). Deployment locations were spread across the region of interest, in ten groups of three; each group of three radiated out from the coast at approximately 5km intervals to provide data at increasing distance offshore (figure 1). The 30 deployment locations are identified by the combination of the group name (based on the nearest settlement on land) and distance from shore (e.g. Cro_05 for the Cromarty nearshore location).

The entire array was deployed each spring and recovered in the fall. Precise deployment and recovery times depended on ship availability and weather conditions (Table 1). With the exception of the first deployment in 2015, which was recovered prior to battery exhaustion, all C-PODS ran continuously until either storage or battery capacity was exhausted.

Data Quality

Acoustic Data Processing

C-POD data from 2013-2015 were processed with the accompanying KERNO classifier version 2.042 (www.chelonia.co.uk) for the presence of high or moderate quality "other cetacean" click trains. The KERNO classifier annotates impulsive detections as narrow-band high frequency (NBHF) click trains, 'Other cetacean' click trains and 'sonar'. NBHF detections are primarily produced by porpoises. 'Other cetacean' click trains may be indicative of a variety of dolphin species (Sarnocinska, Tougaard, Johnson, Madsen, & Wahlberg, 2016). After processing for the presence of 'other cetacean' clicks, click trains were grouped into acoustic encounters. Each acoustic encounter consisted of all high or moderate quality 'other cetacean' click trains starting within 20 minutes of the end of another click train. Acoustic encounters were subsequently processed with the categorization system described in Palmer et al. (2017). This system categorises each acoustic encounter into one of the following three categories; 'broadband', 'frequency banded', or 'unknown'. Thus, only acoustic encounters considered by the system to be at least five times more likely to be either broadband or frequency banded were categorised. Encounters that failed to meet the classification threshold for either taxonomic group were classified as unknown.

To incorporate classifier uncertainty into the analysis, the probability that broadband clicks were detected (P(*Broadband*)) was used as the response variable in the acoustic occupancy models (Palmer et al 2017; supplementary material). Broadband click detection probability was defined as the probability that broadband clicks were actually present, given the category produced by the classification system. For days when no acoustic encounters were detected, *P(Broadband)* was set to 0. Days when only broadband acoustic encounters (as determined by the classification system) were reported, *P(Broadband)* was set to 0.79, reflecting the known error rate as determined by the classification confusion matrix. Similarly, for days when only frequency-banded clicks were reported, P(Broadband) was 0.08. For days when both broadband and frequency banded click encounters were reported, complete uncertainty was assumed by setting *P(Broadband)* to 0.5.

Temporal Covariates

The way temporal covariates were included in the models differed between the modelling stages. For the second stage temporal models, time of the year was measured as the Julian day (1-365) and included as a smooth continuous variable. For the third stage spatial-temporal model, there were insufficient detections to incorporate time as a smoothed variable and thus, season was included in the model as a three-level factor (Spring, Summer, or Autumn). Spring was defined as the months between April and May (March data was not available), Summer (June to August) and Autumn (September to November). No data were collected over the winter season. For both analyses, year was included as a three-level categorical predictor (2013, 2014 or 2015).

Spatial Covariates

As with temporal covariates, spatial covariates were included as either continuous or factor variables. Previous studies have identified the following spatial covariates as potential predictors for the presence of bottlenose dolphins: distance to nearest point of aggregation (e.g. Cromarty Firth and River Dee), distance to shore, the gradient of the seabed (henceforth slope), and depth (Thompson et al., 2015).

Distance to the nearest point of aggregation was included as a continuous variable in the spatial-temporal model. Known points of aggregation have previously been shown to drive spatial and temporal distribution of animals in this population and, in some areas, have been linked to foraging (Hastie, Wilson, Wilson, Parsons, & Thompson, 2004). Given the spatial and temporal scale of this study, estuaries that may represent important habitat for animals either transiting between the established points of aggregation or contemporaneous with local and/or ephemeral prey sources were included. Known points of aggregation included the Cromarty Firth, Firth of Tay, and the rivers Ness and Dee (Cheney et al., 2013; Hastie et al., 2004; Quick et al., 2014). To the known points of aggregation, the mouths of the rivers Spey, North Esk, and Tweed were added. River estuaries were selected from the Atlantic Salmon Rivers Database (http://www.nasco.int/RiversDatabase.aspx). Distance to nearest point of aggregation was reported as a continuous variable and was measured by calculating the distance between each C-POD and the nearest point of aggregation.

Distance to shore was measured as either a three-level factor corresponding to whether each C-POD was deployed in nearshore (05), midshore (10), or offshore (15) habitat, or as a continuous predictor. For the spatial-temporal model of acoustic occupancy, distance to shore was reported as the continuous range between the deployment location and the distance to the nearest 0 m isobath (Pante & Simon-Bouhet, 2013).

Deployment depth (in meters) was recorded from the ship at the time of deployment. Additional spatial covariate data were obtained from the NOAA ETOPO1 database (Amante, 2009), with 1 arc-second resolution (~30m) and processed using the 'marmap' R package (Pante & Simon-Bouhet, 2013). Slope was calculated in radians using the Fleming and Hoffer algorithm through the 'raster' R package (Fleming & Hoffer, 1979; Hijmans & van Etten, 2014). Depth and slope were modelled as continuous predictors (see supplemental information for covariate details).

Site-specific temporal trends

Generalized estimating equations with splines (GEE-GAMs) were fitted to each of the ten deployment groups based on *a priori* knowledge that bottlenose dolphin behaviour changes throughout their range, depending on whether they are or are not near foraging areas (Hastie et al., 2004; Pirotta et al., 2014; Thompson et al., 2013). GEE-GAMs were chosen for their flexible modelling structures capable of handling binary data. Only data from C-PODs that returned at least two days with 'other cetacean' detections were included in the temporal models. Temporal autocorrelation in detections across consecutive days was accounted for by including in the models an autoregressive correlation structure (*ar1*) to detections from each individual C-POD deployment (Box, Jenkins, Reinsel, & Ljung, 2015).

For this analysis, model selection focused on estimating the form of the relationship between the probability of detecting a broadband acoustic encounter and the Julian day of the year. For each deployment, four models were investigated. Predictor variables for all models included ShoreDist, a three level factor for distance from shore of the deployment location (05, 10, 15), a three level factor for survey year (2013, 2014 or 2015) and an integer for Julian day of year.

The first model (Equation 1) assumed an interaction between the shore distance and Julian day of year, and that the pattern in detections throughout the year could be modelled by a cubic B-spline. The second model (Equation 2) assumed an interaction between the cubic B-spline and the survey year. The third model (Equation 3) had no interactions between the cubic B-spline and the shore distance or survey year, and the fourth model (Equation 4) assumed a parametric linearrelationship between the daily probability of detecting a broadband echolocation click train, P(*Broadband*), and the Julian day of year. In accordance with previous studies using cubic spline models a single knot was set at the median of each C-POD record (Pirotta, Matthiopoulos, MacKenzie, Scott-Hayward, & Rendell, 2011). It was not possible to include more than one knot in the spatial models, as the lost degrees of freedom prevented model convergence. All models were fitted in R v.3.3.2 using the ‘geepack’ package (Halekoh, Højsgaard, & Yan, 2006). B-splines were added to the models using the ‘splines’ package (R Core Team, 2016).

$$P(Broadband) \sim Year + ShoreDist * bs\big(JulianDay, knots = median(JulianDay)\big)$$

Equation 1

$$P(Broadband) \sim ShoreDist + Year * bs(JulianDay, knots = median(JulianDay)) \quad \text{Equation 2}$$

$$P(Broadband) \sim ShoreDist + Year + bs(JulianDay, knots = median(JulianDay)) \quad \text{Equation 3}$$

$$P(Broadband) \sim ShoreDist + Year + JulianDay \quad \text{Equation 4}$$

Akaike's Information Criterion (AIC) scores are commonly used to select between candidate GAM or GLM models (Akaike, 1974). However, because GEE's are not likelihood-based models, AIC scores cannot be calculated. Instead a quasi-likelihood criterion (QIC; Pan 2001) was used to select between the four temporal acoustic occupancy models. Quasi-likelihood criterion model selection mirrors AIC-based selection in application, but is appropriate for selecting between GEE models.

Assessing how well the selected model fitted the data followed previous methods (Pirotta et al., 2011; Thompson et al., 2013). For each deployment group, the model with the lowest QIC was used to predict the probability of detecting a broadband echolocation click across the range of the predictors. Receiver operating curves (ROCs; Fawcett, 2006) were then created to determine the relationship between the detection threshold, and the false positive and false negative rates for each model. ROC curves show the relationship between the proportions of true positive detections, here the proportion of days with broadband echolocation click trains accurately predicted, and the proportion of false positive detections or the proportion of days the model inaccurately predicted the presence of broadband echolocation click presence. True and false positive rates are then plotted for each threshold. The threshold at which the trade-off between true and false positive rates is approximately equal is referred to as the optimum threshold. Using the ROC, an optimal detection threshold was selected above which broadband echolocation clicks were assumed to be detected and below which they were not. Using optimum threshold, confusion matrices were then created to measure the proportion of detection-positive and detection-negative days correctly identified by the model. The area under the ROC curve (AUC) was used to describe the model goodness-of-fit. AUC scores represent a measure of how well the model predicts the data. AUC values of 0.5 indicate that the model correctly predicted 50% of the observations and therefore, for a binomial model, values of 0.5 represent models that performed as well as would be expected by chance alone. Considering the variation in the data, it was relevant to determine how well each model fit all locations in the group. Thus, in addition to assessing how well the selected model fit each deployment group, how well the winning model fit the data from each C-POD deployment location was also investigated. Through this process AUC scores were calculated for each model for each deployment group, as well as for all 30 individual deployment locations (Figure 1). These analyses were done in R using the 'ROCR' v1.0-7 and 'PresenceAbsence' v1.19 packages (Freeman, 2007; Sing, Sander, Beerenwinkel, & Lengauer, 2005). The relationship between *P(Broadband)* and Julian day was then plotted for each of the deployed C-PODs and years (Figures 3-5).

Spatial-Temporal Habitat Modelling

Bottlenose dolphins are known to move along the east coast of Scotland for foraging and other purposes (Cheney et al., 2013; Thompson et al., 2013). The full model presented in this study included independent factors for slope, distance to point of aggregation, depth, and distance to shore. Temporal covariates included only season as a factor (spring, summer, and autumn).

For this analysis, a generalized additive mixed model (GAMM; Wood 2006) that incorporated both spatial and temporal variables was fitted to the data. Because smooth terms are centred using the MGCV package, smooth terms were also added as a main effect, as per package recommendations. As with the temporal models, an autoregressive correlation structure with detections grouped by deployment site was included (Box et al., 2015). Only the 'ar1' autocorrelation structure was investigated, based on biological understanding that acoustic encounters spanning several days were unlikely to be driven by the same underlying factor.

The limited degrees of freedom in the data precluded fitting multiple models. Rather, a full model was fitted that included at least one form of all spatial and temporal covariates. Model covariates were investigated for collinearity using variance of inflation factors (VIF), and any covariates with VIF scores greater than two were considered collinear (Craney & Surles, 2002). As the goal of this analysis was to produce a comprehensive model for habitat use, model selection was limited to excluding variables with estimated degrees of freedom less than 1. Adjusted r-squared and AUC scores were used to describe model fit.

The resulting model was used to predict the presence of broadband acoustic encounters in the Scottish North Sea. A grid size of 1 km^2, the approximate detection range of the C-PODs (Nuuttila, Thomas, et al., 2013) was used. The prediction space was restricted to habitats that fell within the parameters covered by the C-POD deployments including depth (103.0 - 9.3 m), distance to nearest point of aggregation (2.3 - 67.17 km), and distance to shore (0.35 - 17.9 km).

3. Results

Acoustic Occupancy Rates

Throughout the three years of survey reported in this study, 11,663 days of C-POD recordings were collected. At only16 deployment sites, devices were retrieved in all three years (Figure 2 and Supplemental Material). C-PODs deployed at the Fraserburgh 10 site were not recovered in 2013 and 2014 and did not detect any acoustic encounters in 2015. C-PODs at the Spey Bay 10 and Helmsdale 10 locations returned data for two of the three years but failed to document two or more days with dolphin echolocation click trains. The C-PODs deployed at the St Andrews 10 location were successfully recovered in all three years but failed to detect dolphin echolocation click trains on two or more days.

The C-POD deployed nearest to Cromarty Firth showed the highest acoustic occupancy rate, with 78% of the days containing at least one broadband detection in 2013, and 83% in 2015 (Table 2). There was wide variation in the acoustic occupancy rate and broadband occupancy rate across the array. C-PODs deployed at the northern and southern ends of the survey area (Latheron and St Abbs) had very low (<5%) broadband occupancy rates for all survey years. Broadband occupancy rates at the nearshore (05) deployment locations were typically greater than the more offshore (10 or 15) locations. The mean broadband occupancy rates for the 05, 10 and 15 locations were 0.12, 0.03 and 0.02 detections/day respectively. Excluding the Cromarty 05 C-POD, the occupancy rate for the nearshore deployments was 0.06 detections/day, nearly twice that of the mid or offshore locations (Table 2).

C-PODs in the Stonehaven deployment group were notable for having the second highest acoustic occupancy rates behind the Cromarty group. Both broadband and frequency branded acoustic encounters were documented at these sites with similar frequency (Figure 2). The C-PODs in this group detected echolocation click encounters on more than 15% of the survey days and broadband encounters on at least 10% of the survey days.

Site-Specific Temporal Trends

Deployments at the Helmsdale 15, St Andrews 10, Fraserburgh 10, and Spey Bay 10 sites failed to detect broadband clicks on at least two days and were removed from the temporal analysis.

Delta-QIC scores for temporal model selection were less than 3.5 for half of the deployment groups indicating some uncertainty in model selection. Furthermore, AUC scores at some individual deployment sites less than 0.5 (Table 3): equal to what would be expected by chance alone. Even at sites with high AUC scores, the ability to predict days with broadband acoustic encounters was 0.53, indicating that nearly half the detections could not be explained by the model. The lowest AUC score among the ten deployment groups was at the St Abbs group (AUC = 0.62, Table 3), indicating it performed only slightly better than would be expected by chance alone. The highest AUC was 0.93 determined for both the Helmsdale and Cromarty groups. When model fit was investigated at each of the 30 deployment sites, AUC ranged from 0.2 at the Cruden Bay 10 location to 0.99 at the Latheron 10 location (Table 2).

Low acoustic occupancy rates across most sites meant that the temporal models generally did well at predicting periods without detections, but were poor at predicting detection-positive days. Across the dataset, 43% of the days without broadband detections were accurately predicted, with the exception of Cruden Bay, where 30% were correctly classified. Apart from the

Cromarty group, no model was able to predict more than 20% of the broadband detection-positive days.

Large (>3) ΔQIC and high (>0.75) AUC scores indicated a more confident model selection and better model fit at the Latheron 10, St Andrews 15, Stonehaven 15, Spey Bay 10, and Helmsdale 15 sites. Of these, only the Stonehaven 15 location contained broadband echolocation click trains on greater than 1 % of the days. Thus, high AUC scores at the other locations were influenced by the correct prediction of days without dolphin detections.

For sites with the highest acoustic occupancy of broadband click trains, e.g. Cromarty 05 and Stonehaven 15, GEE-GLM models suggested peaks in the probability of detecting broadband echolocation encounters in August and July, respectively. At other locations, including deployment sites in the Fraserburgh, Arbroath and St Andrews groups, temporal trends in acoustic occupancy were highly stochastic. Poor model fits (AUC <0.50) at the deployment sites within these groups make it difficult to identify the presence and/or persistence of patterns in daily acoustic occupancy (Figures 3-5).

Spatial-Temporal Habitat Modelling

VIF scores for spatial covariates were less than three and subsequently all spatial variables were retained. In the full model the estimated degrees of freedom (EDF) for slope were less than one, and the predictor was removed. In the final model, all terms were significant except season (Table 4). The AUC score of the final model was 0.86. Modelling results suggested that the probability of detecting broadband echolocation click train encounters decreased with increasing distance to shore and increasing distance to the nearest point of aggregation. However, across the extent of the array, the probability of detecting broadband echolocation encounters increased with increasing depth (Figure 6).

When the GAMM was projected over the available habitat, higher broadband occupancy was predicted near the Inner Moray Firth and Dee river estuaries. The GAMM also predicted that C-PODs deployed in nearshore areas were more likely to detect broadband encounters than those deployed further offshore. Finally, deeper (>60m) offshore areas were projected to have a higher probability of broadband occupancy than shallow areas (Figure 7; see supplemental material for projections of the confidence intervals as well as projections for Spring and Autumn).

4. **Discussion**

The primary goal of this study was to improve understanding of the patterns of habitat use by this coastal bottlenose dolphin population throughout its range. A three-step approach was taken to the analysis. First, daily acoustic occupancy rates were reported for all sites and for both unfiltered acoustic encounters and echolocation click encounters identified as 'broadband' by the classification system (Palmer et al., 2017). Second, models investigating temporal trends were fitted to the available data to investigate seasonal occurrence patterns. Third, a spatial-temporal model was fitted to the data to predict the animals' habitat use.

The study faced two main challenges: low acoustic occupancy rates and species classification uncertainty. Low acoustic occupancy rates limited detection sample size. The autocorrelation structure in the temporal model accounted for correlation within acoustic encounters, but further limited the remaining degrees of freedom to model spatial and temporal trends in acoustic occupancy. For half of the deployment groups, model selection techniques (ΔQIC) did not strongly favour one temporal model over another. This is indicative of variation not accounted for by any of the models in the set. Larger amounts of acoustic data will be needed to produce robust model estimates in future studies. For example, Pirotta et al. (2014) used data from eight years of continuous surveys to produce estimates for dolphin foraging rates within the Moray Firth SAC. In addition to having a longer sample period, echolocation detectors in Pirotta et al. (2014) were deployed in areas of high use and therefore registered a higher rate of detections. Future deployments of the ECoMMAS will address some of the temporal modelling issues this work encountered, as gaps in data coverage are reduced through multiple annual deployments, as was done in 2015.

Despite their lack of species resolution, C-PODs remain widely used instruments for passive acoustic monitoring (Cox et al., 2017; Jaramillo-Legorreta et al., 2017; Nuuttila, Meier, et al., 2013; Williamson et al., 2016; Wilson, Benjamins, & Elliott, 2013). Nearly all studies that use the instruments simply assume that the target species, here bottlenose dolphins, are responsible for the preponderance of the detections. This study improves to some degree on that assumption by applying a secondary classification system to the detections. This system is unable to discriminate between some species of dolphins and enhanced taxonomic resolution is unlikely to be achievable with these devices. Even with full spectrum recordings, it is exceptionally difficult to discriminate between echolocation clicks of common and bottlenose dolphins (Soldevilla et al., 2008).

Species discrimination was improved over the Chelonia classifier, but perfect dolphin classification is impossible for any passive acoustic study, regardless of the recording device or sample frequency (Caillat, 2013; Roch et al., 2011). As such, these findings emphasise the need to combine long term data from visual and acoustic surveys. In doing so, researchers will be able to provide robust data on long-term trends in dolphin occurrence throughout the habitat and for areas of ecological or commercial interest (Thompson et al., 2011).

This is the first acoustic study that approximates the entire geographic range of this population. The ECoMMAS, in combination with Arso Civil et al. (2019), provides critical information about baseline habitat use. Such information is needed to monitor change in habitat use through time (Bailey et al., 2010). A novel classification algorithm on the ‘other cetacean’ detections reported by the C-POD software was used. The additional information produced by the classification algorithm enabled both the temporal and spatial-temporal model to more closely focus on the species of interest. Thus, this research required fewer assumptions about the impact of non-target species detections on the resulting models.

Patterns in broadband acoustic occupancy rates were generally consistent with previous research suggesting the bottlenose dolphins are more likely to be observed in coastal waters, within 5 km of shore (Arso Civil, 2014). While most instruments were deployed in less than 30m of water, broadband acoustic occupancy rates throughout the survey were generally higher for C-PODs closer to the shoreline (Table 3; Figure 2). This supports the work of Thompson, Brookes & Cordes (2015) and increases the confidence that bottlenose dolphins are unlikely to be present in areas that may be exposed to significant construction noise from offshore wind farms.

Acoustic occupancy rates and habitat modelling highlight the waters between Stonehaven and Aberdeen as a potential area of high occupancy. Instruments deployed in the Stonehaven group showed the second highest acoustic occupancy rates behind the Cromarty group. In 2013 and 2015, the Stonehaven 15 and 05 (respectively) C-PODs documented dolphin presence on at least 30% of the monitored days (Table 3). Moreover, both broadband and frequency banded click trains were documented at these sites at nearly equal rates, suggesting a potential hotspot important for multiple species. Previous studies have shown that dolphins are present in coastal waters north and south of Stonehaven year-round (Thompson et al., 2011). Historically, white-beaked and bottlenose dolphin sightings have been common in visual surveys (Anderwald et al., 2010; Arso Civil, 2014; Weir, Stockin, & Pierce, 2007). Thus, further research to determine whether the area constitutes a biological hotspot is warranted.

Modelling efforts for temporal trends across the spatial and temporal extent of the array were challenged by few detections and gaps in data coverage. As such, the inference that can be made from the models is highly limited. Despite these challenges, the model for the Cromarty group did fit well and indicated a peak in broadband detections consistent with earlier visual surveys (Thompson et al., 2011). The novel approach to classification uncertainty reduced the number of days with echolocation encounters in the dataset. While this conservative approach hindered modelling efforts in this research, it will provide more robust estimates of dolphin species distributions as the survey matures (Pirotta et al., 2014).

Spatial-temporal habitat selection modelling was more successful and generally agreed with previous studies linking smaller distances to shore with increased probability of detecting bottlenose dolphins (Arso Civil, 2014; Pirotta et al., 2014; Quick et al., 2014). The spatial modelling suggested that broadband acoustic encounters were more likely to be detected in deeper water and predicted a slight increase in detections >15 km from shore (Figures 5-6). Without concurrent visual confirmation residual uncertainty remains regarding whether and to what extent echolocation encounters detected at offshore locations represented common dolphins. The spatial-temporal model indicated that distance to the nearest selected point of aggregation and depth were also important predictors of broadband occupancy. Unfortunately, there were not enough detection data to model the spatial and temporal covariates together (e.g. Julian day of year and depth).

Bottlenose dolphins are commonly sighted in St Andrews Bay (Arso Civil et al., 2019; Quick et al., 2014), so the low number of detections at the St Andrews survey location nearest the bay (St Andrews 05) was somewhat unexpected. There are several possible reasons for this. One possibility is that the area may represent habitat associated with rest or socializing rather than foraging, so there are fewer clicks to detect. Previous studies have found lower detection rates for groups of animals, travelling and socializing animals, than single animals or foraging animals (Nuuttila, Thomas, et al., 2013). If animals near the Fife Ness survey sites were primarily travelling or socializing, they may not have been detected at rates comparable to foraging animals. These results reinforce the need to integrate visual and acoustic surveys when managing highly mobile species.

Unfortunately, the limited taxonomic resolution of the acoustic data means that it is not possible to say with a high degree of certainty which of the broadband or frequency banded species were present at these locations. Delphinid species classification is an issue that other studies using C-PODs have not typically had the tools to address. This study uses improved classification measures to more reliably discriminate between the various species present in the area. Furthermore, the maximum acoustic occupancy probability of 0.79 for broadband acoustic encounters is not a direct representation of true bottlenose dolphin occupancy. Thus, conservative interpretation of these results, including relative occupancy between the survey locations, is prudent.

In situations where species classification remains an outstanding problem it is appropriate to combine inferences from multiple survey methodologies (Cheney et al., 2013; Thompson et al., 2015). In this survey region, visual surveys provide evidence that the majority of the broadband echolocation encounters detected at the near-shore deployments originated from bottlenose dolphins (Anderwald et al., 2010; Arso Civil, 2014; Arso Civil et al., 2019; Thompson et al., 2013). Considerable uncertainty remains regarding broadband detections from offshore areas that lack consistent visual survey effort. Where there are increased broadband detections at the offshore locations, the data warrant further investigation, but classification is not possible. These areas would benefit from either increased visual survey effort or more advanced acoustic techniques that have recently shown promise in discriminating between common and bottlenose dolphins (Frasier et al., 2017).

Data presented here also represent a small spatial sample, and acoustic data are lacking from many important sites such as the River Dee and Tay estuary. In these, shipping activity has restricted the use of acoustic moorings which may present a potential navigational hazard. Thus, it has not been possible to deploy acoustic recorders in some known points of aggregation. Appropriate sampling methods for investigating temporal and spatial trends are diametrically opposed. If the continued goal of the ECoMMAS array is to relate habitat data to acoustic occupancy, managers should consider changing deployment locations at each recovery and re-deployment. However, if the goal is to maintain a historical record of the trends in acoustic occupancy at these locations it is important that the deployment locations remain consistent.

From a conservation and management perspective, knowledge of where animals are is equally as valuable as knowledge of where they are not. The ECoMMAS provides continuous survey coverage for areas where consistent visual surveys are untenable. The first ecological results of

ECoMMAS are consistent with visual sightings highlighting the importance of particular high-usage areas to the population (Arso Civil et al., 2019). Similarly, daily acoustic occupancy rates in areas between established points of aggregation were an order of magnitude lower. In sites other than Cromarty 05, there was no clear trend in temporal detections. Thus, by themselves, these results do not suggest the need to change any of the existing regulatory framework for this population of bottlenose dolphins.

Bottlenose dolphins are highly mobile and adaptable generalists, capable of exploiting changing environments (Santos et al., 2001). The areas currently considered to be critical habitat for this population (e.g. the SAC) may shift with changing climate or other anthropogenic impacts. For example, the point of aggregation near the Cromarty Firth has conclusively been linked with foraging (Hastie et al. 2003). If the area no longer provides optimal foraging habitat, dolphins will likely move elsewhere. Under such dynamic systems fixed protected areas may not provide optimal conservation solutions for either protected species or human users. Dynamic ocean management plans represent a flexible conservation approach that mirror the spatial and temporal variability present in marine systems (Maxwell et al., 2015). Such management plans have been implemented in North America where vessel speed restrictions may be triggered when critically endangered North Atlantic right whales (*Eubalaena glacialis*) are visually or acoustically detected near shipping lanes (Spaulding et al., 2009; Van Parijs et al., 2009). These dynamic management areas are designed to provide maximum protection from anthropogenic mortality while limiting additional regulatory burden on users. In a changing regulatory landscape, there may be opportunities to rethink the implementation of conservation measures for highly mobile species. Since the establishment of the Moray Firth SAC, the population has grown and is now observed using the entire coastline (Cheney et al., 2013; Arso Civil et al.

2019). This range expansion over a relatively short period might be reflected in a dynamic management plan that considers variation in animal presence and the timing of ecological features (e.g. diadromous fish runs or seasonal patterns in habitat use). Under dynamic management plans, surveys like the ECoMMAS would be invaluable in providing detailed information about habitat over longer periods than can be provided by visual surveys alone.

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Tables

Table 1. Deployment and recovery months of the ECoMMAS array in the three years of data collection used in this study. In 2015 two consecutive deployments were undertaken.

Year	Deployment	Recovery
2013	June and July	October
2014	May	November
2015	April July	July November

Table 2. Daily acoustic occupancy rates (number of days with detections/days with acoustic coverage) for unprocessed C-POD data (All) and detections classified as “broadband” by the classification system. Ninety-five percent binomial confidence intervals in parenthesis. Black areas indicated C-PODs that were not recovered or failed to record data.

	2013		2014		2015	
	Occ. Rate (All)	Occ. Rate (Broadband)	Occ. Rate (All)	Occ. Rate (Broadband)	Occ. Rate (All)	Occ. Rate (Broadband)
Lat_05	0.19 (0.12 - 0.28)	0.00 (0.00- 0.04)	0.00 (0.00 - 0.04)	0.00 (0.00- 0.04)	0.20 (0.15 - 0.26)	0.00 (0.00- 0.03)
Lat_10	0.03 (0.01 - 0.08)	0.01 (0.00- 0.05)			0.04 (0.02 - 0.08)	0.01 (0.00- 0.04)
Lat_15	0.04 (0.01 - 0.09)	0.01 (0.00- 0.05)			0.02 (0.01 - 0.05)	0.00 (0.00- 0.02)
Hel_05	0.05 (0.02 - 0.12)	0.00 (0.00- 0.04)	0.12 (0.08 - 0.17)	0.03 (0.01 - 0.06)	0.14 (0.09 - 0.20)	0.07 (0.04 - 0.12)
Hel_10	0.00 (0.00 - 0.03)	0.00 (0.00- 0.03)			0.02 (0.01 - 0.06)	0.00 (0.00- 0.03)
Hel_15	0.01 (0.00 - 0.05)	0.00 (0.00- 0.03)	0.01 (0.00 - 0.06)	0.00 (0.00- 0.04)	0.00 (0.00 - 0.02)	0.00 (0.00- 0.02)
Cro_05	0.89 (0.80 - 0.94)	0.78 (0.68 - 0.86)			0.95 (0.91 - 0.97)	0.83 (0.77 - 0.87)
Cro_10	0.32 (0.17 - 0.52)	0.12 (0.04 - 0.30)	0.35 (0.26 - 0.46)	0.25 (0.17 - 0.35)	0.37 (0.27 - 0.48)	0.28 (0.19 - 0.39)
Cro_15	0.02 (0.01 - 0.08)	0.02 (0.01 - 0.08)	0.00 (0.00 - 0.04)	0.00 (0.00- 0.04)	0.04 (0.02 - 0.08)	0.03 (0.01 - 0.06)
SpB_05	0.22 (0.15 - 0.32)	0.13 (0.08 - 0.22)	0.21 (0.11 - 0.38)	0.09 (0.03 - 0.24)	0.14 (0.10 - 0.19)	0.08 (0.05 - 0.13)
SpB_10	0.00 (0.00 - 0.03)	0.00 (0.00- 0.03)			0.00 (0.00 - 0.05)	0.00 (0.00- 0.05)
SpB_15			0.01 (0.00 - 0.05)	0.01 (0.00- 0.05)	0.03 (0.01 - 0.06)	0.02 (0.01 - 0.05)
Fra_05	0.13 (0.08 - 0.21)	0.00 (0.00- 0.04)	0.21 (0.13 - 0.33)	0.20 (0.12 - 0.31)	0.11 (0.07 - 0.16)	0.06 (0.03 - 0.10)

Fra_10					0.00 (0.00 - 0.03)	0.00 (0.00- 0.03)
Fra_15			0.04 (0.02 - 0.10)	0.03 (0.01 - 0.08)	0.08 (0.05 - 0.13)	0.05 (0.03 - 0.09)
Cru_05	0.19 (0.13 - 0.26)	0.02 (0.00- 0.06)	0.04 (0.02 - 0.10)	0.01 (0.00- 0.05)	0.13 (0.07 - 0.22)	0.01 (0.00- 0.07)
Cru_10			0.15 (0.09 - 0.23)	0.04 (0.02 - 0.10)	0.00 (0.00 - 0.43)	0.00 (0.00- 0.43)
Cru_15	0.16 (0.11 - 0.23)	0.06 (0.03 - 0.10)	0.15 (0.09 - 0.23)	0.03 (0.01 - 0.09)		
Sto_05	0.17 (0.11 - 0.25)	0.10 (0.06 - 0.16)			0.36 (0.30 - 0.44)	0.27 (0.21 - 0.34)
Sto_10			0.12 (0.06 - 0.21)	0.05 (0.02 - 0.13)	0.07 (0.04 - 0.12)	0.04 (0.02 - 0.07)
Sto_15	0.30 (0.23 - 0.37)	0.11 (0.07 - 0.16)	0.10 (0.06 - 0.19)	0.01 (0.00- 0.06)	0.12 (0.06 - 0.20)	0.06 (0.03 - 0.14)
Abr_05	0.17 (0.11 - 0.26)	0.07 (0.03 - 0.14)	0.11 (0.06 - 0.18)	0.05 (0.02 - 0.12)	0.27 (0.18 - 0.38)	0.09 (0.04 - 0.17)
Abr_10	0.02 (0.01 - 0.08)	0.00 (0.00- 0.04)	0.02 (0.01 - 0.09)	0.00 (0.00- 0.05)	0.04 (0.02 - 0.08)	0.02 (0.01 - 0.06)
Abr_15	0.18 (0.13 - 0.25)	0.05 (0.03 - 0.10)			0.03 (0.01 - 0.06)	0.02 (0.01 - 0.05)
StA_05	0.18 (0.12 - 0.27)	0.09 (0.04 - 0.16)	0.07 (0.03 - 0.16)	0.03 (0.01 - 0.10)	0.07 (0.04 - 0.11)	0.03 (0.02 - 0.07)
StA_10	0.00 (0.00 - 0.04)	0.00 (0.00- 0.04)	0.01 (0.00 - 0.06)	0.01 (0.00- 0.06)	0.02 (0.01 - 0.09)	0.01 (0.00- 0.07)
StA_15	0.03 (0.01 - 0.08)	0.01 (0.00- 0.05)	0.02 (0.01 - 0.07)	0.01 (0.00- 0.06)	0.00 (0.00 - 0.05)	0.00 (0.00- 0.05)
Stb_05	0.05 (0.02 - 0.10)	0.02 (0.01 - 0.07)	0.06 (0.03 - 0.12)	0.02 (0.01 - 0.07)	0.04 (0.01 - 0.10)	0.04 (0.01 - 0.1)
Stb_10	0.03 (0.01 - 0.09)	0.01 (0.00- 0.06)	0.02 (0.01 - 0.07)	0.02 (0.01 - 0.07)	0.02 (0.01 - 0.05)	0.01 (0.00- 0.04)
Stb_15	0.04 (0.02 - 0.08)	0.02 (0.01 - 0.06)			0.01 (0.00 - 0.07)	0.00 (0.00- 0.05)

Table 3 Temporal model selection results for the 10 deployment groups (Group). Formula indicates the final model form selected via QIC for each deployment group (Equations 1-4). Response for all models was P(Broadband). ShoreDist represents the three-level factor for the near (05), mid (10), and offshore (15) deployment locations. Year is the two or three level factor each survey year (2013, 2014 or 2015), Delta QIC is the difference in QIC scores between selected model and the next best performing model. Group AUC is the area under the ROC curve for each model applied to deployment groups. Group presence (Pres.) and absence (Abs.) are the proportion of presences and absences correctly identified by the model for each group. Unit is the location of each C-POD within the group and each individual deployment location (Dep) AUC, Pres. and Abs. are the area under the curve and proportion of presences and absences correctly predicted by the model for each of the C-POD locations. Dashes indicated locations were modelling was not possible due to either low numbers of detections or failure to recover the C-PODs deployed at that location.

Group Name	Formula Selected	Delta QIC	Group AUC	Pres.	Abs.	Dep. Name	Dep. AUC	Dep. Pres.	Dep Abs.
Latheron	P(*Broadband*) ~ ShoreDist + Year * bs(JulianDay, knots = mean(JulianDay))	13.83	0.85	0	0.88	Lat_05	0.99	0.00	0.99
						Lat_10	0.82	0.01	0.59
						Lat_15	0.98	0.00	0.97
Helmsdale	P(*Broadband*)~ ShoreDist +	3.51	0.93	0.01	0.77	Hel_05	0.82	0.02	0.78

	Year + JulianDay								
						Hel_10	0.94	0.00	0.93
						Hel_15			
Cromarty	P(*Broadband*)~ ShoreDist + Year + bs(JulianDay, knots = mean(JulianDay))	1.22	0.93	0.28	0.6	Cro_05	0.62	0.53	0.10
						Cro_10	0.61	0.19	0.30
						Cro_15	0.78	0.01	0.80
Spey Bay	P(*Broadband*)~ Year + ShoreDist * bs(JulianDay, knots = mean(JulianDay))	5.34	0.81	0.04	0.63	SpB_05	0.63	0.05	0.63
						SpB_10			
						SpB_15	0.75	0.01	0.55
Fraserburgh	P(*Broadband*)~ ShoreDist + Year + JulianDay	2.52	0.75	0.04	0.48	Fra_05	0.70	0.03	0.81
						Fra_10	0.99	0.00	0.98
						Fra_15	0.54	0.04	0.40
Cruden Bay	P(*Broadband*)~ ShoreDist + Year + JulianDay	1.85	0.63	0.03	0.33	Cru_05	0.64	0.01	0.72
						Cru_10	0.22	0.03	0.13
						Cru_15	0.61	0.02	0.82
Stonehaven	P(*Broadband*)~ Year + ShoreDist * bs(JulianDay,	5.73	0.79	0.06	0.77	Sto_05	0.71	0.13	0.63

	knots = mean(JulianDay))								
						Sto_10	0.63	0.02	0.67
						Sto_15	0.81	0.05	0.82
Arborath	P(*Broadband*)~ Year + ShoreDist * bs(JulianDay, knots = mean(JulianDay))	1.39	0.82	0.03	0.51	Abr_05	0.61	0.04	0.58
						Abr_10	0.98	0.01	0.96
						Abr_15	0.76	0.03	0.49
St Andrews	P(*Broadband*)~ ShoreDist + Year * bs(JulianDay, knots = mean(JulianDay))	8.46	0.85	0.02	0.82	StA_05	0.83	0.04	0.72
						StA_10	0.81	0.00	0.72
						StA_15	0.63	0.00	0.51
St Abbs	P(*Broadband*)~ ShoreDist + Year + JulianDay	3.06	0.62	0.01	0.63	Stb_05	0.51	0.02	0.18
						Stb_10	0.63	0.00	0.92
						Stb_15	0.60	0.01	0.36

Table 4 GAMM summary for the parametric and smooth coefficient estimates, standard errors, estimated degrees of freedom (EDF), reference degrees of freedom (Ref.df), F, t and p-values for the final habitat model. Smooth factors (Distance to nearest Point Of Aggregation and Distance to Shore) are added as a main effect.

Model Formula

P(*Broadband*)~ s(DistToPOA, bs = "ts", k = 3) + s(Depth, bs = "ts") + s(DistToShore, bs = "ts") + POIName + Season+ DistToPOA+ DistToShore

Parametric coefficients				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-2.70586	0.17708	-15.281	<.001
Dee	-0.63122	0.34879	-1.81	0.070
Esk	-1.02055	0.31654	-3.224	0.001
Spey	-1.24386	0.27673	-4.495	<.001
Tay Firth	-0.64207	0.35049	-1.832	0.067
Tweed	-2.41157	0.44156	-5.461	<.001
SeasonSpring	-0.06665	0.16495	-0.404	0.686
SeasonSummer	0.03319	0.12101	0.274	0.784

Approximate significance of smooth terms				
	EDF	Ref.df	F	p-value
s(DistToPOA)	1.917	2	55.264	<.001
s(Depth_m)	4.686	9	6.233	<.001
s(DistToShore)	4.961	9	9.094	<.001

R-sq.(adj) = 0.322 , Scale est. = 1 , n = 9181

Figures

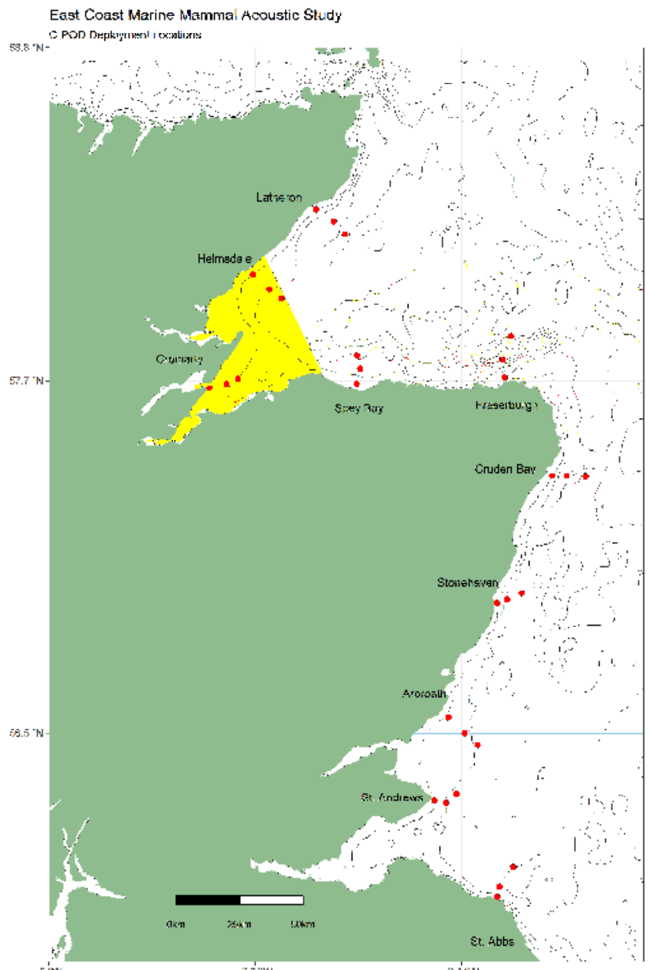


Figure 1. Study area including the Moray Firth Special Area of Conservation (yellow) and deployment locations of the East Coast Marine Mammal Acoustic Study (red points) and associated deployment group names.

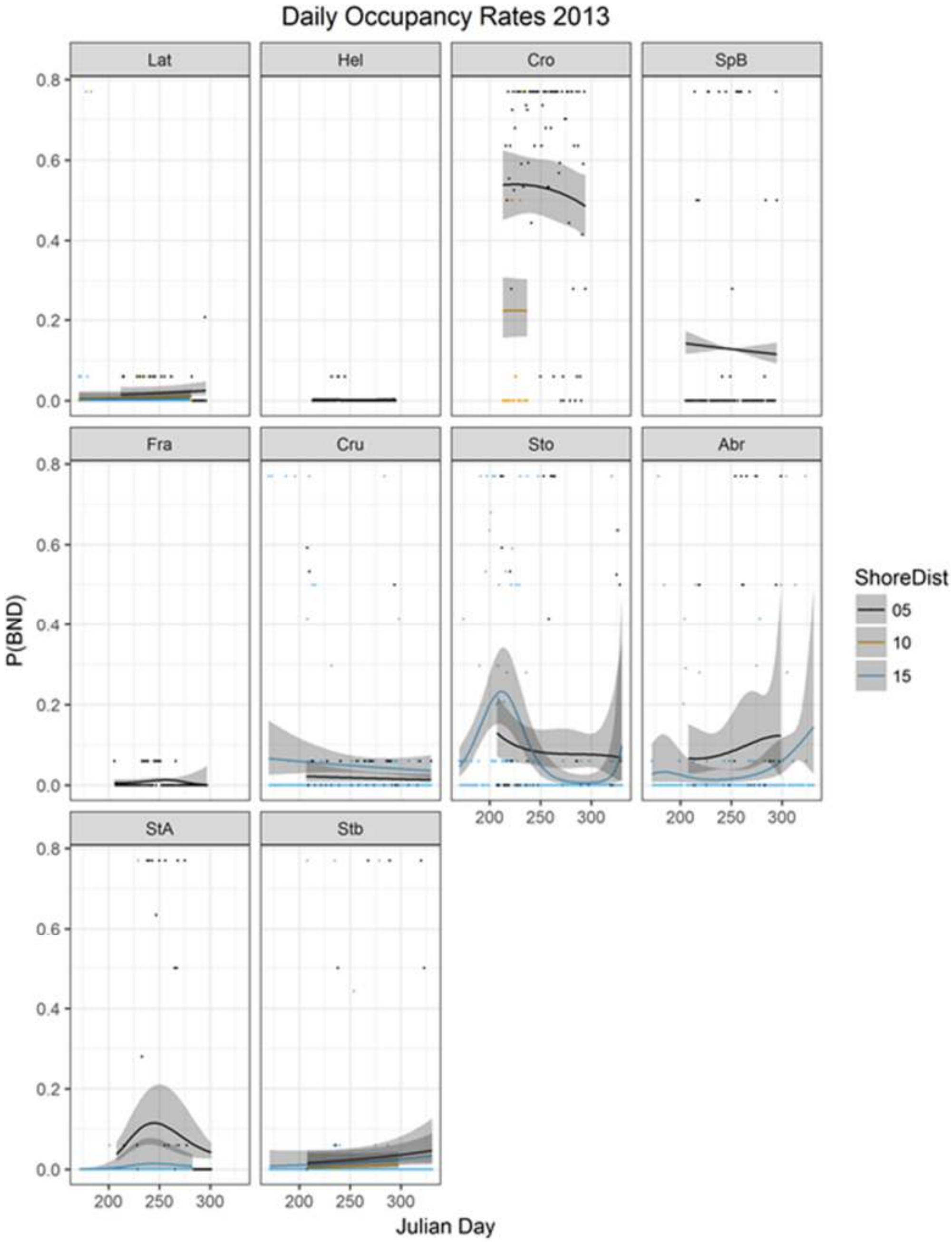


Figure 2. Observed (points) and 95% confidence interval of the modelled occupancy (shaded) for the 2013 near (05) mid (10) and offshore (15) deployment sites (panels). Colour indicates distance from shore as a factor.

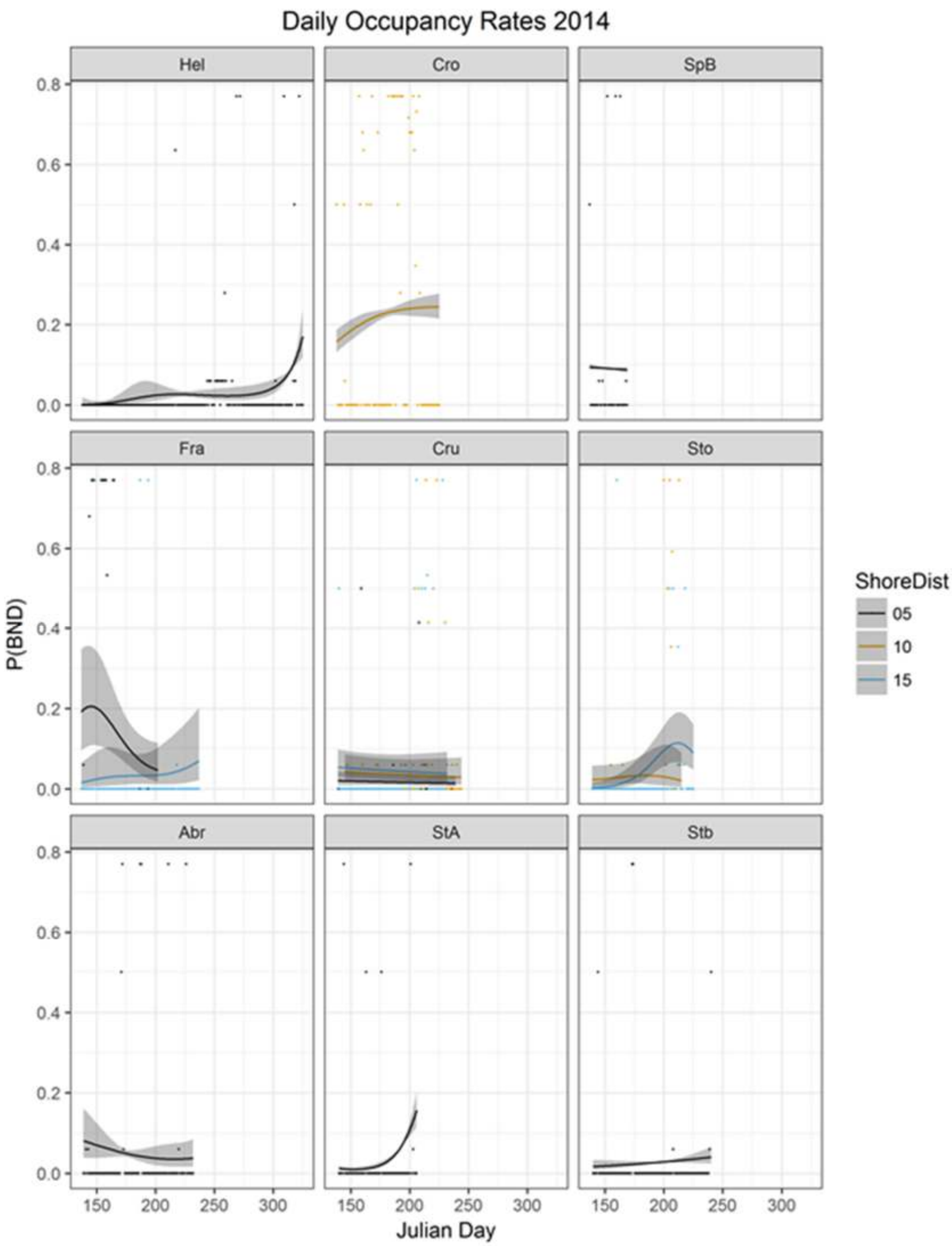


Figure 3. Observed (points) and 95% confidence interval of the modelled occupancy (shaded) for the 2014 near (05) mid (10) and offshore (15) deployment sites (panels). Colour indicates distance from shore as a factor.

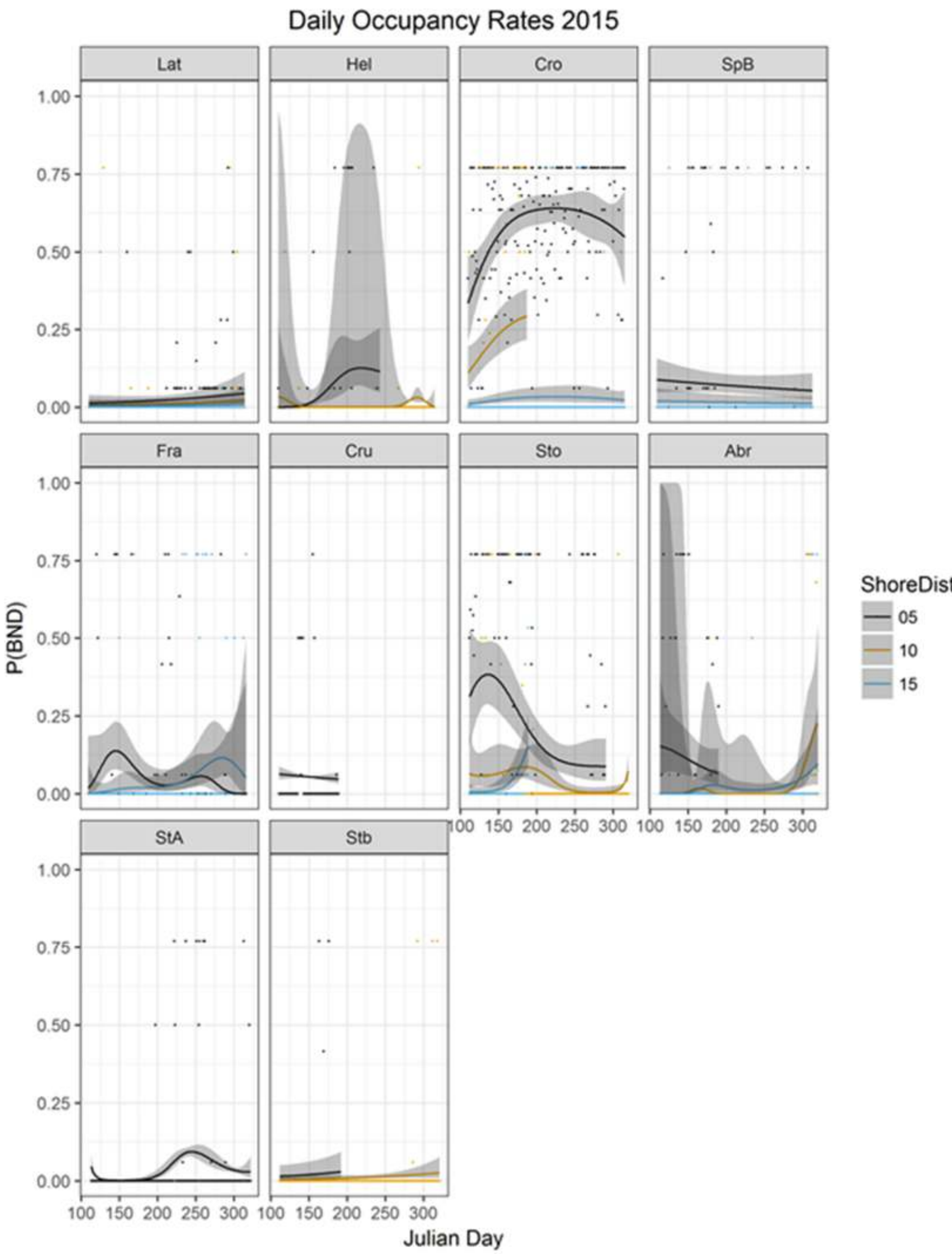


Figure 4. Observed (points) and 95% confidence interval of the modelled occupancy (shaded) for the 2015 near (05) mid (10) and offshore (15) deployment sites (panels). Colour indicates distance from shore as a factor.

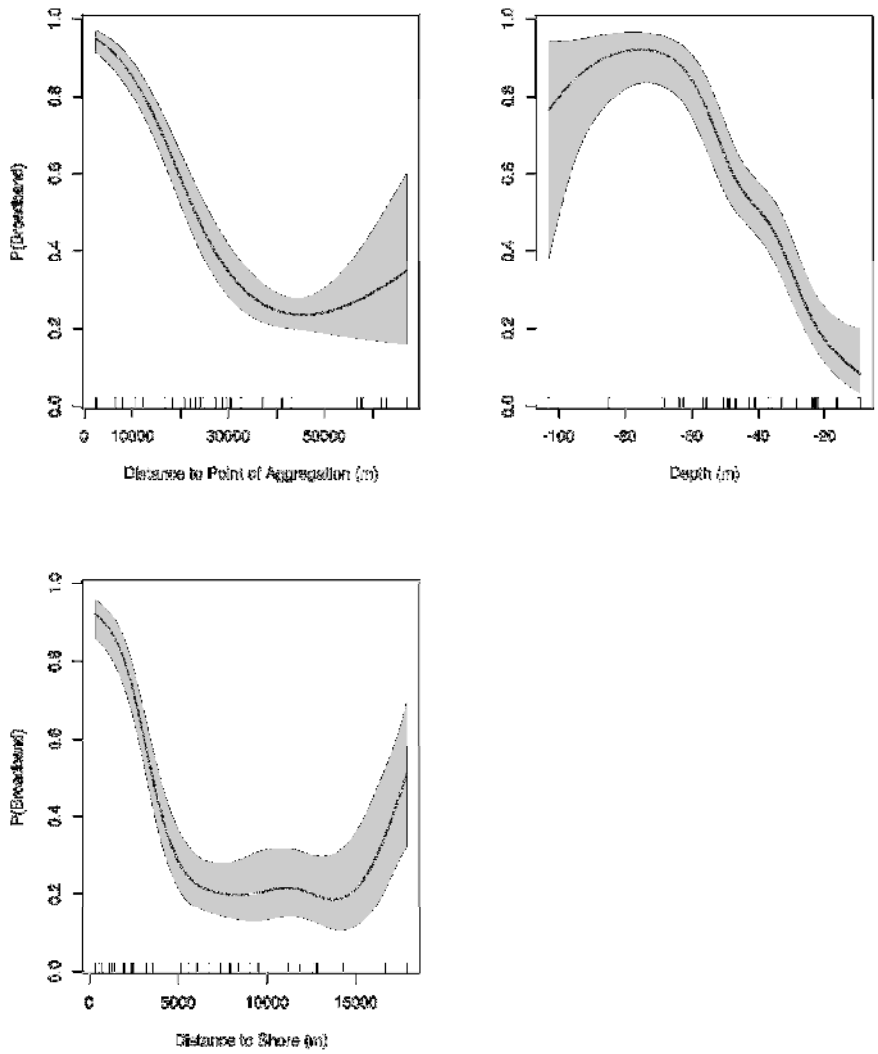


Figure 5. Two dimensional representations of the binomial smooths for the habitat GAMM. Shaded area represents the probability of detecting a broadband echolocation click train on a given C-POD as a function of the CPOD's distance to the nearest point of aggregation (top left), deployment depth (top right) and distance to shore (bottom). Shaded areas represent 95% confidence intervals and dashes on X-axis are rug plot of deployment variables.

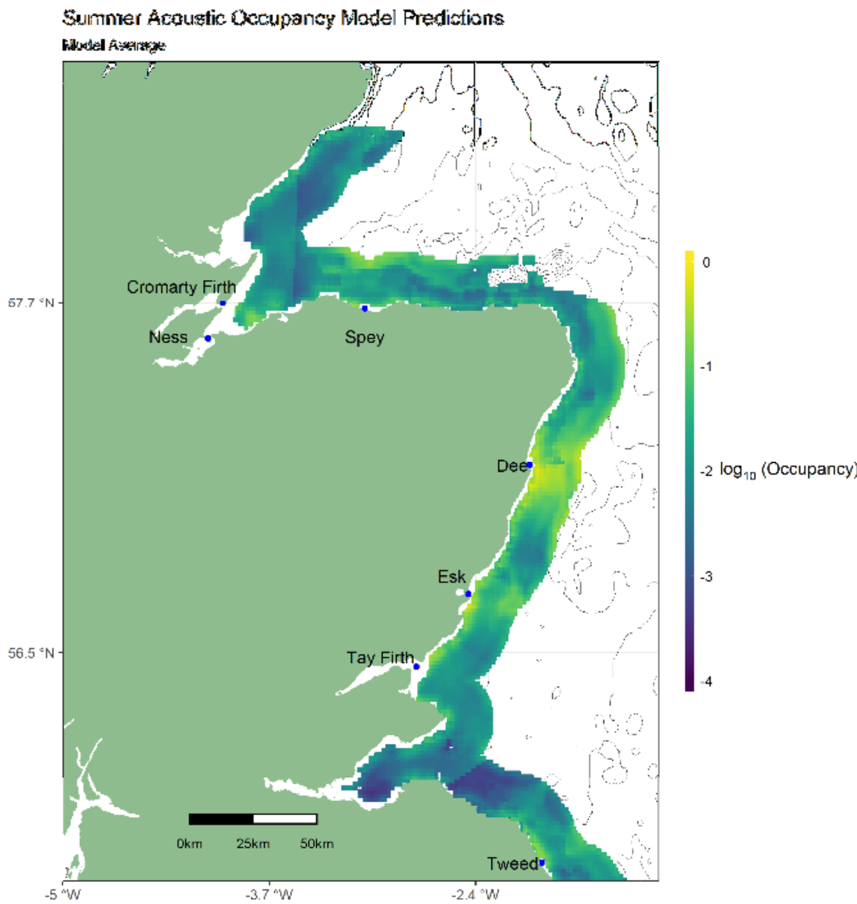
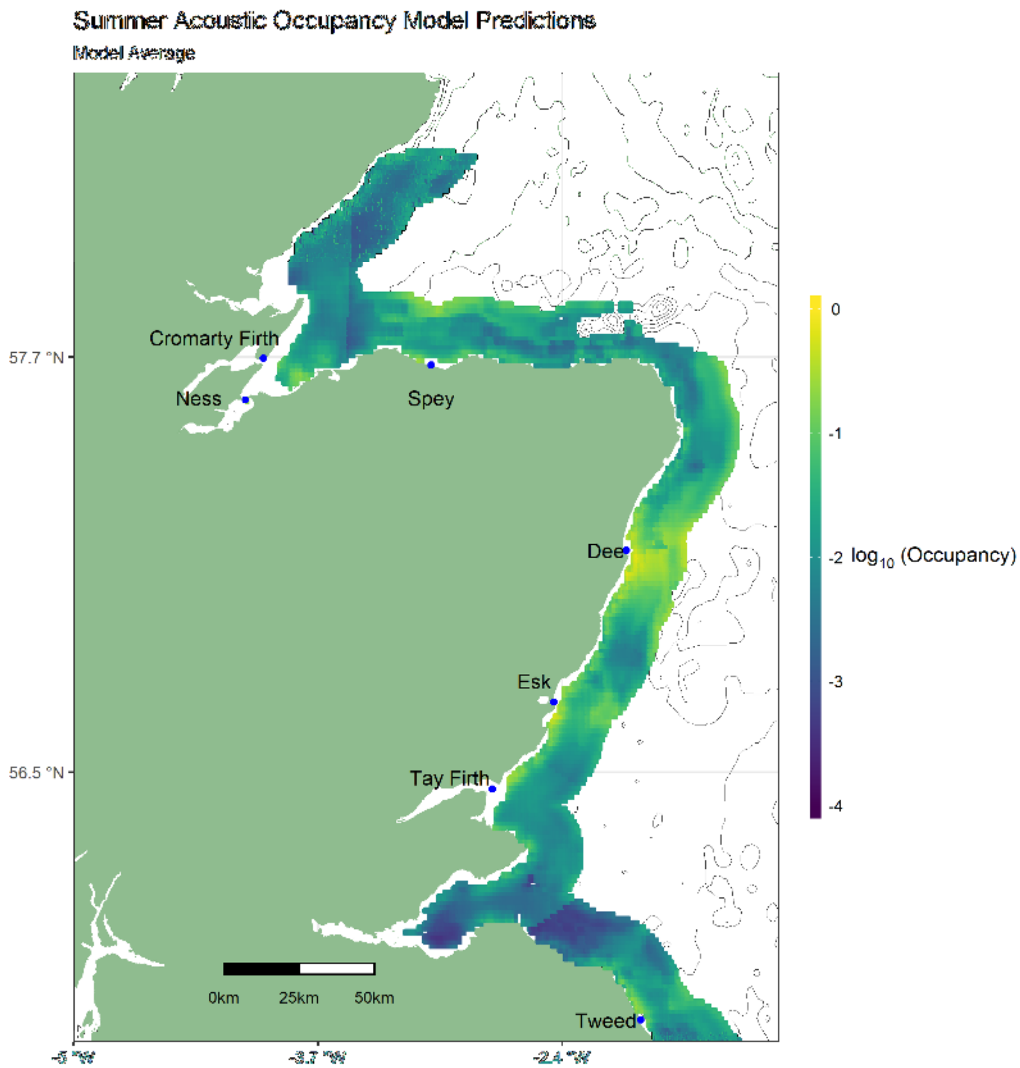


Figure 6. Predicted broadband occupancy throughout the east coast habitat. Predictions based on GAMM analysis of CPOD acoustic records from 2013-2015. Data are standardized to year 2015

and season is set to summer


Summer Acoustic Occupancy Model Predictions
Model Average
Cromarty Firth
Ness
Spey
Dee
Esk
Tay Firth
Tweed
0km
25km
50km
57.7 °N
56.5 °N
-5 °W
-3.7 °W
-2.4 °W
0
-1
-2
-3
-4
log10 (Occupancy)