# Changing distribution of the east coast of Scotland bottlenose dolphin population and the challenges of area-based management

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| Journal: | *Aquatic Conservation: Marine and Freshwater Ecosystems* |
| Manuscript ID | AQC-18-0287.R2 |
| Wiley - Manuscript type: | Supplement Article |
| Date Submitted by the Author: | n/a |
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| Broad habitat type (mandatory) select 1-2: | coastal < Broad habitat type, estuary < Broad habitat type |
| General theme or application (mandatory) select 1-2: | Special Area of Conservation < General theme or application, conservation evaluation < General theme or application |
| Broad taxonomic group or category (mandatory, if relevant to paper) select 1-2: | mammals < Broad taxonomic group or category |
| Impact category (mandatory, if relevant to paper) select 1-2: | |
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**Title**: Changing distribution of the east coast of Scotland bottlenose dolphin population and the challenges of area-based management.

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**Abstract**

1. The efficacy of marine protected areas (MPAs) depends on clear conservation objectives and ecologically meaningful boundaries. The east coast of Scotland bottlenose dolphin population expanded its distributional range during the 1990s beyond the boundaries of the Special Area of Conservation (SAC) in the Moray Firth, originally proposed to contain their core area of distribution. Two decades on, this study assesses the importance for this population of St Andrews Bay and the Tay estuary, 300 km south of the SAC.

2. Photo-identification data from 2009 to 2015 were analysed using mark-recapture models to investigate the proportion of the population that uses St Andrews Bay and the Tay estuary. Habitat models were fitted to bottlenose dolphin presence-absence data to identify areas of high use.

3. The estimated number of dolphins using St Andrews Bay and the Tay estuary during the summer increased from 91 (95% CI 78-106) in 2009 to 114 (95% CI 95-137) in 2015, representing, on average, 52.5% of the total estimated east coast population for that period. Spatial mixing of individuals during the summer between St Andrews Bay and the Tay estuary and the Moray Firth SAC was estimated to be a minimum of ~6% per year and ~30% over the study period. The entrance to the Firth of Tay and waters around Montrose were identified as areas of consistent high use.

4. The importance of St Andrews Bay and the Tay estuary reconfirms that effective monitoring of the population requires dedicated effort in both this area and the SAC. The results lead to consideration of the wider context of area-based management for the conservation/management of highly mobile wide-ranging species and human activities that might impact them.


**Keywords**: coastal, conservation evaluation, estuary, mammals, Special Area of Conservation.

## 1. Introduction

The designation of marine protected areas (MPAs) is a widely advocated approach in the conservation of many marine taxa (Halpern, 2003; Hooker & Gerber, 2004), supported under a number of conservation frameworks (e.g. Natura 2000 under the EU Habitats Directive (92/43/EEC); Convention on the Conservation of European Wildlife and Natural Habitats (1979); IUCN Important Marine Mammal Areas; Scottish Government MPA network) (Council of the European Communities, 1992; Council of Europe, 2018; Marine Mammal Protected Areas Task Force, 2018; Scottish Government, 2017). Area-based management approaches are intended to protect both the species of interest and other key components of the ecosystem, and their effectiveness relies in part on the ability to identify boundaries that are ecologically meaningful given the spatio-temporal distribution of the population of interest (Cañadas, Sagarminaga, De Stephanis, Urquiola, & Hammond, 2005; Hooker & Gerber, 2004) .

MPAs are typically designed with fixed boundaries, which present a challenge for the targeted conservation of highly mobile species, for migratory populations, for offshore oceanic species with extensive ranges that may vary seasonally and for more discrete populations that might still display wide ranging movements (Reeves, 2000; Wilson, 2016). The biological information leading to the designation of an MPA may be limited, and thus an adaptive approach during the early phases of management to incorporate information on the use of the MPA by the population of interest, as it becomes available, is recommended (Silva et al., 2012; Williams, Lusseau, & Hammond, 2009).

For a species-based MPA to be effective, clear conservation objectives are needed for the focal population. These objectives may vary depending on the characteristics of the population and its interaction with anthropogenic activities within the area. Management actions could include restricting or banning certain activities to reduce mortality (Gerrodette & Rojas-Bracho, 2011; Gormley et al., 2012) or to protect key life-history processes (Ashe, Noren, & Williams, 2010; Williams et al., 2009). Monitoring the long-term effectiveness of an MPA is essential to assess how well it is meeting its objectives (Gormley et al., 2012; Rayment, Dawson, & Slooten, 2010).

Under a framework known as Natura 2000, the EU Habitats Directive (92/43/EEC) requires the designation of Special Areas of Conservation (SACs) to make a significant contribution to the conservation of species listed under Annex II, which includes the bottlenose dolphin (*Tursiops truncatus*). As part of the UK's response, a candidate Special Area of Conservation (cSAC) in the inner Moray Firth (NE Scotland) was proposed in 1996 to protect the only known resident population of bottlenose dolphins in the North Sea. The cSAC boundary encompassed the core area of occurrence of the population as known at that time, based on data from the 1980s to the early 1990s (Curran, Wilson, & Thompson, 1996; Mudge, Crooke, & Barrett, 1984), and was eventually designated in 2005. During the 1990s, however, the population's distributional range expanded into areas to the south of the Moray Firth (Wilson, Reid, Grellier, Thompson, & Hammond, 2004). Long-term monitoring of this population shows that individuals currently occur along the east coast of Scotland, between the Moray Firth and the Firth of Forth (Cheney et al., 2013, Quick et al., 2014), which we term here the *main* distributional range of the population. Bottlenose dolphins do occur beyond this range, however. Sightings have become more frequent in recent years further south in north-east England (Sea Watch Foundation, 2018), where photo-identification data show matches with the study population catalogue (Aynsley, 2017; Thompson et al., 2011). North of the SAC, occasional public sightings of individuals from this population have been reported, but no systematic surveys or dolphin-watching boat tours occur in this region.

Current knowledge of the distribution, abundance and habitat use of bottlenose dolphins within the SAC is extensive, based on long-term monitoring over almost three decades (e.g. Cheney, Graham, Barton, Hammond, & Thompson, 2018; Hastie, Wilson, & Thompson, 2003; Pirotta et al., 2014; Wilson, Thompson, & Hammond, 1997). Data from other areas of the main distributional range, including the southern outer Moray Firth, Aberdeenshire, and St Andrews Bay and the Tay estuary are more limited (Cheney et al., 2013; Culloch & Robinson, 2008; Quick, 2006; Weir, Canning, Hepworth, Sim, & Stockin, 2008). During the range expansion (Wilson et al., 2004), surveys started to be conducted in St Andrews Bay and the Tay estuary, an area towards the southern end of the population's main distributional range (Figure 1). Consistent dedicated surveys have been conducted in this area every year since 2009, and have continued beyond the study presented here.

Under the Habitats Directive, each Member State must report every six years on the site condition of designated SACs, and on the Favourable Conservation Status in national waters for species listed under Annex IV, which includes all cetacean species. SAC site condition is assessed on the basis of a set of targets for specified attributes. The attributes of the Moray Firth SAC for bottlenose dolphins include the number of dolphins using the SAC and the frequency of occurrence of dolphins within the SAC. Atypically, a third attribute is trends in the population, with the target to maintain a stable or increasing population, and a prescription (method) to use all available data (not only data from within the SAC) (see Annex 4 in Cheney et al., 2018). This attribute was included by Scottish Natural Heritage (SNH), the Scottish Government's statutory adviser on nature conservation, at a time when data from outwith the SAC were starting to become available. It was deemed expedient to formalize this as a site attribute in order to make use of these data, which were considered important to put SAC monitoring into a wider context (Morven Carruthers, pers. comm., November 2018). Between 2001 and 2016, abundance within the SAC has been stable while the overall population has increased and the proportion of the population using the SAC therefore declined by an average of around 7% per year (Cheney et al. 2018). However, because the targets of the attributes regarding the use of the SAC by the population are met, the current condition status of the SAC is assessed as "favourable (recovered)" (Cheney et al., 2018).

Under Habitats Directive Article 6, a planned human activity for which a "significant effect" on the SAC in view of its conservation objectives cannot be ruled out requires a so-called appropriate assessment of the impact of the activity. Consent should only be given if it is determined that the activity will not compromise the conservation objectives. For the Moray Firth SAC, these can be summarized as avoiding deterioration of the habitats of, or significant disturbance to, the bottlenose dolphins associated with the SAC (see Conservation Objectives document in SiteLink Scottish Natural Heritage, 2018). Regulatory authorities are required to assess whether any planned development may have a significant effect on these conservation objectives. Because animals present in the SAC commonly occur along the east coast of Scotland to the south (Cheney et al. 2013; Quick et al. 2014), connectivity is established throughout this main distributional range. Scottish Natural Heritage guidance is therefore that any planned development that could affect bottlenose dolphins anywhere within the population's range is likely to have a significant effect on the SAC and will require an appropriate assessment (SNH Natura Casework Guidance, 2018). Examples of such developments are the Aberdeen harbour expansion and the Forth and Tay windfarm developments (Marine Scotland Information, 2018; Scottish Government, 2014). Thus, although Wilson et al. (2004) suggested that the range expansion in the 1990s might potentially diminish the protection originally envisioned for the Moray Firth SAC, the way in which the Habitats Directive is implemented in this specific case means that the SAC effectively provides protection for the population throughout its range.

Here the importance of St Andrews Bay and the Tay estuary for this population of bottlenose dolphins is assessed, more than a decade after the population's range expansion was documented by Wilson et al. (2004). To investigate the proportion of the population that uses this area, photo-identification data collected during consistent dedicated surveys (2009 to 2015) in this area are analysed and compared to data from this and other parts of the current main distributional range over the same time period. These data are also used to estimate the minimum proportion of identifiable animals seen in both the Moray Firth SAC and the St Andrews Bay and the Tay estuary area every summer and over the 2009-2015 study period. This provides some information on the spatial mixing of individuals across the population range and adds to current knowledge of the degree of connectivity of the population. Habitat modelling techniques are applied to bottlenose dolphin presence-absence data collected during surveys in 2012 and 2013 in St Andrews Bay and the Tay estuary to investigate a subset of available environmental features that may explain relative abundance in this area and to identify areas of high use.

The implementation of Natura 2000 for the east coast of Scotland bottlenose dolphin population via the Moray Firth SAC is envisaged to provide protection for the population throughout its range. However, this is an atypical application of the Habitats Directive and, more generally, of area-based management, and this population provides an interesting basis for wider consideration. Therefore, the results are discussed in the context of the conservation of highly mobile marine species that can range widely, in general, with the intention that this may be informative to other situations involving area-based management to help protect such species.

## 2. Methods

### 2.1 Data collection

Boat-based surveys were conducted off the east coast of Scotland between 2009 and 2015 in the summer months (May to September) to collect photo-identification data of bottlenose dolphins. Sampling effort was consistent (regular surveys throughout May-September) in all years in the two main survey areas: St Andrews Bay and the Tay estuary (extending from Fife Ness to Montrose), and the Moray Firth SAC (Figure 1). In other parts of the population's range, survey effort was variable and more limited: in the outer Moray Firth fewer surveys occurred between 2009 and 2015, and in the Firth of Forth and between Montrose and Aberdeen surveys only occurred in 2012 and 2013 (Figure 1).

Photo-identification data were collected following standardized protocols (see Cheney et al., 2014 for details) during encounters with groups of bottlenose dolphins, defined as one or more individual dolphins in close proximity and engaging in similar behaviour (e.g. traveling, foraging). Individual dolphins were identified from high quality photographs (Wilson, Hammond, & Thompson, 1999) based on unique markings on the dorsal fin (Würsig & Jefferson, 1990), and matched against a catalogue of previously identified bottlenose dolphins from the east coast of Scotland (Cheney et al., 2013). Capture histories of marked (i.e. dolphins with distinctive long-lasting nicks on the trailing edge of the dorsal fin) individual dolphins were compiled to estimate the abundance of animals: (1) using the sub-area of St Andrews Bay and the Tay estuary, and (2) using the population's main distributional range (i.e. between the Moray Firth and the Firth of Forth, using photo-identification data collected across the range including the outer Moray Firth, between Aberdeen and Montrose, and the Firth of Forth) (Figure 1). To investigate the movements of animals between areas at the extremes of the main range, St Andrews Bay and the Tay estuary to the south; and the Moray Firth SAC to the north, the number of marked individuals identified every summer, and over the study period in each and both areas were compared.

Bottlenose dolphin presence/absence data collected during the photo-identification surveys conducted in 2012 and 2013 in St Andrews Bay and the Tay estuary (Figure 1) were used to model habitat use. Survey lines were designed to provide even coverage over a 1 km grid within each month. Effort was divided into search effort (i.e. when following survey lines searching for dolphins) and follow effort (during an encounter with dolphins). For the duration of each survey, the boat position, sea surface temperature and depth were recorded *in situ* every minute using a Garmin GPS Map 551s GPS/Plotter/Sounder and a temperature sensor. Data collection protocols were designed to minimize any behavioural response of the encountered animals to the boat, i.e. attraction or avoidance. Bow riding (i.e. attraction behaviour) was discouraged by reducing boat speed or completely stopping the boat if necessary; the encounter was only resumed if/when animals where observed behaving independently from the boat (e.g. traveling, foraging). If a group of dolphins split during an encounter, a decision was made to follow the main group of dolphins followed up to that point in the encounter. If the composition of the group changed substantially, a new encounter was started, following the general photo-identification protocol. Finally, in the event of time/light constraints, both search and follow effort were suspended, meaning any further presence/absence data were excluded from the analysis.

## 2.2 Abundance of marked animals

Simple conventional mark-recapture models used to estimate abundance assume an equal probability of capture among animals on any one sampling occasion (Hammond, 2010). The combination of a large distributional range, limited sampling effort, and variability in the movement patterns among individuals (Cheney et al., 2013) can result in individuals being available for sampling on some occasions but not on others (i.e. temporary emigration; Kendall, Nichols, & Hines, 1997), which may introduce bias to estimates of animal abundance (Kendall, 1999). The robust design (RD) model framework (Kendall et al., 1995, 1997; Pollock, 1982) combines open and closed population models with estimators that incorporate temporary emigration to produce unbiased estimates of abundance, 185 and has been increasingly applied in cetacean population studies (e.g. Cantor, Wedekin, Daura-Jorge, Rossi-Santos, & Simões-Lopes, 2012; Smith, Pollock, Waples, Bradley, & Bejder, 2013; Verborgh et al., 2009).

188 In our application of the RD model framework, each annual field season represented a primary sampling occasion, and calendar months within each season (May to September), secondary sampling occasions. The latter provided a balance of adequate sample size within relatively short secondary sampling occasions separated by some days to allow mixing of the population. The RD applies closed population models to data from secondary sampling occasions (calendar months) within each primary sampling occasion (year) to derive estimates of capture probability (*p)* and population size ($\hat{N}$). Open population models are applied to the data from primary occasions (years) to estimate the probability of apparent survival (φ) and temporary emigration γ" and γ', defined as the probabilities of an animal being outside the sampling area in a year conditional on it being inside or outside the sampling area, respectively, during the previous year. γ" is thus the probability of temporary emigration and 1- γ' is the probability of re-immigration. Temporary emigration can be random, in which the probability of emigrating does not depend on whether or not an animal was previously available (γ" = γ'), or Markovian, in which the probability of emigrating depends on whether or not an animal was previously available (γ" ≠ γ').

202 A candidate set of models was fitted to capture histories of dolphins for each defined sampling area (i.e. St Andrews Bay and the Tay estuary, and the population's main range). Survival was constrained to be constant in all models. Capture probabilities were allowed to vary between and within years because preliminary analysis showed less support for models restricting capture probabilities to be constant over the study period, or to vary among years but not among months. Models allowing for individual heterogeneity in capture probabilities were also included using Pledger (2000) mixture models, in which the population is assumed to comprise a mixture of two or more types of individuals with different probability of capture, defined by mixture parameters (π). The number of types was limited to two to avoid over-parameterization of the models. Note that this does not imply that there are actually two distinct types of animal, simply that the use of such a mixture can reduce bias caused

by assuming homogeneity of capture probabilities (Pledger & Phillpot 2008). Random and Markovian temporary emigration parameters were allowed to be constant or time-dependent, with constraints being applied to allow identifiability of parameters (Kendall et al., 1997). Models without movement ( $\gamma'' = \gamma' = 0$) were also included.

There is no goodness-of-fit test available for the RD modelling approach. Instead, prior to model fitting, program U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009) was used to explore the key assumptions about the probability of capture (Lebreton, Burnham, Clobert, & Anderson, 1992) and to calculate the variance inflation factor ($\hat{c}$), which is indicative of over-dispersion of the data when > 1 and can be used to adjust model statistics and confidence intervals around the estimated parameters. To do so, data within each year from both data sets were pooled together into single annual sampling occasions in a Cormack-Jolly-Seber (CJS) framework (e.g. Pollock, Nichols, Brownie, & Hines, 1990). The assumptions regarding the probability of capture were satisfied in both data sets, and results found no evidence of over-dispersion in either of the two data sets ($\hat{c} < 1$) so model selection was based on the Akaike Information Criterion (Akaike, 1973) adjusted for small sample size (Burnham & Anderson, 2002). Model structures and parameters were specified and run using the package RMark (Laake, 2013) in R (R Core Team, 2016), and program MARK (White & Burnham, 1999).



### 2.3. Total abundance of animals

Estimates of abundance from mark-recapture models relate to animals with distinctive long-lasting marks (marked animals) and must be inflated to the total number of animals (i.e. marked and unmarked individuals) by the proportion of marked individuals in the population, $\theta$. Because unmarked individuals may not be identified from both sides, $\theta$ was calculated separately for each side as the number of marked individuals photographed from the right and the left sides in each trip divided by the total number of individuals photographed from each side, respectively. Generalized Linear Models (GLMs) with a binomial distribution and a logit link function were then fitted to data from St Andrews Bay and the Tay estuary and to data from the population's main range to estimate the annual proportion of marked individuals in each of the areas. In the models, the proportion of marked animals from both sides in each trip and area was the response variable and year was the explanatory variable, to account for variations in the estimated proportion of marked animals from year to year due to variation in sampling effort.

Estimates of the total number of animals, $\hat{N}_{total}$, were calculated by dividing each estimate of annual abundance of marked individuals ($\hat{N}$) from the best RD model by the corresponding annual proportion of marked individuals (θ):

$$\hat{N}_{total} = \frac{\hat{N}}{\theta}$$

with variance derived using the delta method:

$$var\left(\hat{N}_{total}\right) = \hat{N}^2_{total}\left(\frac{var(\widehat{N})}{\hat{N}^2} + \frac{var\left(\hat{\theta}\right)}{\hat{\theta}^2}\right)$$

Log-normal confidence intervals were derived for total abundance estimates following Burnham, Anderson, White, Brownie, and Pollock (1987). The lower and upper limits of the 95% confidence interval were calculated as $\hat{N}_{total}/C$ to $\hat{N}_{total} \cdot C$, where C is calculated as follows:

$$C = \exp\left(1.96\sqrt{\ln\left(1 + CV^2_{\hat{N}_{total}}\right)}\right)$$

## 2.4 Habitat use

### 2.4.1. Presence/absence data processing

The GPS fixes taken every minute were used as the sample data to model the habitat use of bottlenose dolphins. Only on-effort points were included in the analysis (i.e. during search and follow effort), excluding all other points (off-effort). On-effort points included in the analysis were restricted to favourable sighting conditions (Beaufort scale 0 to 3). All on-effort points recorded during follow effort (i.e. during the collection of photo-identification data) were classed as 1 = presence, and all other on-effort points recorded during search effort were classified as 0 = absence.

### 2.4.2. Environmental data

Values of available environmental variables were extracted for each GPS fix to use as covariates in models of bottlenose dolphin presence. Depth was collected *in situ* at each GPS fix, and any missing values were extracted from EDINA Marine Digimap, at a resolution of 200 m (SeaZone Hydrospatial Bathymetry). Slope (average depth gradient, measured in degrees) and aspect (orientation of the slope in degrees) were computed in Manifold (Manifold System Release 8.0, 2013). Sediment type was provided as a categorical variable by EDINA Geology Digimap / British Geological Survey and re-classified into four new categories: rock, sand, muddy-sand, and gravelly sediment. The shortest distance to land and to the entrance of the Tay estuary were computed in Manifold. Sea surface temperature (SST) was collected *in situ*, and any missing values were averaged from all available *in situ* temperature values taken in that same month within a 500 m cell around the missing value. Four categories were defined for tidal state (low, rising, high, and falling), each representing a 3 hour block of the tide cycle, based on tidal data extracted from POLTIPS-3 (Version 3.4.0.3/10, Proudman Oceanographic Laboratory Applications Group) for the nearest tidal port to each GPS fix. Current speed, level and direction were obtained using POLPRED (NERC National Oceanography Centre, Liverpool, UK). Tidal data sourced from POLPRED were not available in areas very close to the coast due to limitations of the tidal model to predict in those locations. Consequently, a subset of the presence/absence data excluding missing values for tidal covariates was used to model the presence of bottlenose dolphins. Year and month were also included as potential covariates in order to investigate temporal variation in the probability of presence of bottlenose dolphins across years and months.

2.4.3. Modelling approach

The presence/absence of bottlenose dolphins was modelled at each GPS fix using Generalized Additive Models (GAMs) (Wood, 2006), with a binomial distribution for the error structure and a logit link function. Following the analytical approach developed in Pirotta, Matthiopoulos, MacKenzie, Scott-Hayward, and Rendell (2011), autocorrelation in GAM residuals was visualized by means of an autocorrelation function (ACF) plot. Preliminary analysis showed that sub-setting the data (i.e. data-thinning) did not eliminate the autocorrelation in GAM residuals. Instead, Generalized Estimating Equations (GEEs) (Liang & Zeger, 1986) were used to account for the observed autocorrelation. Models were fitted using the R library geepack (Halekoh, Højsgaard, & Yan, 2006) together with the library splines (Bates & Venables, 2012) to extend the GEE-GLMs to GEE-GAMs. Presence/absence data points were grouped into follow (i.e. consecutive presence points) and searching (i.e. consecutive absence points) blocks, and a correlation structure within block was selected based on the quasi-likelihood under the independence model criterion (QIC; Pan, 2001). Multicollinearity among the covariates was inspected by means of Pearson's correlation coefficients and generalized variance inflation factors (GVIF). Non-categorical covariates could enter the models as a linear term, as a B-spline with four degrees of freedom (d.f.) (with one internal knot at the average value of that covariate) or as a B-spline with five d.f. (with two internal knots, positioned at the lower and upper quartiles of that covariate), and the $QIC_u$ (an approximation of the QIC; Pan, 2001) was used to compare the different forms. A manual backwards stepwise selection based on the $QIC_u$ was used to select the best subset of covariate predictors to model the presence of bottlenose dolphins.

All covariates retained in the final model based on the $QIC_{u,}$ improved the model fit and were thus used to predict the presence of bottlenose dolphins. The goodness-of-fit of the final model was evaluated by a confusion matrix of observed and predicted bottlenose dolphin presence/absence values (Fielding & Bell, 1997), shown as the percentage of correctly classified presences/absences by the fitted model. The cut-off probability for classification was chosen based on a receiving-operating characteristic (ROC) curve (Pearce & Ferrier, 2000; Pirotta et al., 2011; Praca, Gannier, Das, & Laran, 2009). The ROC curve evaluates the proportion of correctly and incorrectly classified predictions over a range of thresholds (Swets, 1988; Zweig & Campbell, 1993), and the area under the ROC curve (AUC) provides a measure of overall accuracy of model predictions (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). The library 'ROCR' (Sing, Sander, Beerenwinkel, & Lengauer, 2005) was used to build the ROC curve plot, calculate the AUC and extract the best cut-off probability, and the library PresenceAbsence (Freeman & Moisen, 2008) was used to compute the confusion matrix. Additionally, the significance of each retained covariate in the best model was assessed using repeated Wald's tests (Hardin & Hilbe, 2003; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) by excluding the least significant covariate each time (p-value > 0.05).

To visualize the results, the final model was used to predict the probability of presence of bottlenose dolphins in the sampling area, based on a 1 km cell grid with associated values for the retained covariates. Values of dynamic covariates (e.g. tidal covariates) were averaged for each cell at the temporal scale of interest retained in the final model (e.g. tidal state, month, or year), to generate prediction maps of the presence of dolphins at different temporal scales. The presence of dolphins at each location was predicted on the response scale (i.e. a value between 0 and 1) using the function 'predict' in R, and visualized by means of a smoothed surface of probabilities across the area.

## 3. Results

### 3.1. Photo-identification data

A total of 254 photo-identification surveys were conducted between 2009 and 2015 across the population's main distributional range, of which 79 surveys occurred in St Andrews Bay and the Tay estuary (Table 1). Overall, there were 1,139 encounters of bottlenose dolphin groups, of which 275 occurred in St Andrews Bay and the Tay estuary. Good quality photographs resulted in the identification of 128 marked dolphins of which, 82 were identified in St Andrews Bay and the Tay estuary between 2009 and 2015, with 33 to 52 individuals identified annually (Table 1).

The total number of animals identified in the sub-areas of St Andrews Bay and Tay estuary and/or the Moray Firth SAC in any given year ranged between 74 and 99 over the study period (Table 2). Of these, between 34.8% and 46.5% were seen only in St Andrews Bay and the Tay estuary (i.e. not seen in the same year in the Moray Firth SAC) and 47.5% to 57.1% were seen only in the Moray Firth SAC (Table 2 and Figure 2). On average, 5.6% (range 0% to 10.9%) of the total number of marked animals were seen in both areas in any one year, with no overlap in 2014. Over the study period, 35.2% of the marked animals were seen only in St Andrews Bay and the Tay estuary, 35.9% were seen only in the Moray Firth SAC, and 28.9% were seen in both areas.

### 3.2. Abundance of animals

For the population's main range dataset, model selection favoured models incorporating Pledger (2000) heterogeneity mixture parameters over models without it (Table 3), out of 18 candidate models. The most supported model, based on the lowest $AIC_c$ value, included time-varying heterogeneity mixture parameter and time-varying random temporary emigration, with an average probability of emigrating of 0.017 (range 0.00 to 0.044). The annual proportion of marked individuals ranged between 0.49 (CV = 0.028) and 0.55 (CV = 0.023) for encounters in the population's main range (Table 4). Once scaled up by the estimated annual proportion of marked individuals, the estimated total number of bottlenose dolphins using the population's main distributional range varied from 165 (95% CI 156-175) animals in 2009 to 209 (95% CI 189-230) in 2015 (Table 4).

For the St Andrews Bay and the Tay estuary dataset, models incorporating constant temporary emigration (random and Markovian) and no-movement models received some support from the data (Models 9 to 12, ΔAICc < 4, Table 3). The most supported model, representing half of the AICc weight, included random temporary emigration, with a low constant probability of emigrating of 0.106 (95% CI 0.056-0.192) and time-varying heterogeneity mixture parameter (model 9 in Table 3). The annual proportion of marked individuals in St Andrews Bay and the Tay estuary ranged between 0.47 (CV = 0.087) and 0.52 (CV = 0.051) (Table 4). Once scaled up by the estimated annual proportion of marked individuals, the estimated total number of bottlenose dolphins using St Andrews Bay and the Tay estuary ranged from a minimum of 85 (95% CI 77-93) animals in 2011 to a maximum of 121 (95% CI 84-173) animals in 2014 (Table 4). On average, the estimated number of animals using St Andrews Bay and the Tay estuary represented 52.5% percent of the estimated total population (i.e. using the population's main range).

## 3.3. Habitat use

### 3.3.1. Habitat model fitting, selection and evaluation

In total, 3,782 km of survey effort were conducted in 2012 and 2013 during the photo-identification surveys in St Andrews Bay and the Tay estuary. Bottlenose dolphins were encountered 128 times, resulting in 325 km of follows (Table 5). The resulting subset of data excluding data with missing values for tidal covariates included 7,758 GPS fixes with 2,739 presence points and 5,019 absence points, grouped into 120 follow (presence) blocks and 185 searching (absence) blocks.

A full model with all available explanatory variables did not show signs of multicollinearity (GVIF < 2). A working independence structure was preferred to an autocorrelation structure of order 1 (AR1) or to an exchangeable autocorrelation structure based on QIC values. The manual backwards stepwise selection based on the $QIC_u$ retained distance to the Tay, current speed, current direction, temperature, month and year in the final model. Dolphin presence increased close to the entrance of the Tay estuary, and decreased away from it except for a second presence peak 30 km away, corresponding to the waters around Montrose (Figure 3a). Predicted dolphin presence increased with current direction flowing towards the NE (i.e. 10 to 60 degrees) or towards the WSW (i.e. 220 to 300 degrees) (Figure 3b), associated with higher current speeds based on the tidal data. A higher probability of presence of bottlenose dolphins was associated with the lowest (0.0 to 0.15 m/s) and highest (0.5 to 0.8 m/s) current speeds occurring in St Andrews Bay and the Tay estuary during data collection for this study (Figure 3c). The probability of dolphin presence was slightly higher in September, when SST was between 12 and 15 degrees and in 2012 (Figures 3d-e-f). The 95% confidence intervals around the modelled relationships between the response variable and the retained covariates were generally wide. The final model correctly predicted 70% of the presence/absence observations and the area under the ROC curve was 0.741, which is indicative of good performance of the final model (AUC>0.7). Repeated Wald's test confirmed that the presence of dolphins was significantly related to distance to the Tay (*p*-value <0.05).

3.3.2. Predicted presence of bottlenose dolphins

The probability of presence of dolphins was predicted at different range values of the retained tidal covariates (current speed and direction). Based on the visual inspection of the raw tidal data and the modelled relationships between the probability of presence of dolphins and those two tidal covariates (Figure 3b-c), current direction was divided into 10 to 60 degrees, 60 to 220 degrees, 220 to 300 degrees, and 300 to 10 degrees, and current speed was divided into 0 to 0.15 $ms^{-1}$, 0.15 to 0.5 $ms^{-1}$, and >0.5 $ms^{-1}$. Values for each combination of current speed and current direction were averaged for each 1 km grid cell. SST was averaged across months, and the year and month with the highest coefficient values were selected for the predictions.

The prediction maps identified the entrance of the Tay as an area with high probability of presence of bottlenose dolphins in all value ranges of current direction and current speed (Figures 4 and 5). The area around Montrose was also predicted to have a high probability of presence of bottlenose dolphins, while the southern half of St Andrews Bay and the waters between Carnoustie and north of Arbroath had a lower probability of presence of dolphins. Within those identified areas of high probability of dolphin presence, the prediction maps showed that dolphin presence was lowest when the tidal flow was between 60 and 220 degrees and that the area with higher predicted probability of dolphin presence shifted slightly along the entrance to the Tay estuary at different current directions (Figure 4). The entrance of the Tay was identified as a high probability of dolphin presence at the highest current speeds (>0.5 $ms^{-1}$). Bottlenose dolphins were predicted to be present at the entrance to the Tay and around Montrose even at the lowest current speeds (0 to 0.15 $ms^{-1}$) (Figure 5).

## 4. Discussion

At the time the SAC for bottlenose dolphins on the east coast of Scotland was proposed, the only known concentration of animals was in the Moray Firth. However, during the 1990s, the population expanded its distributional range to areas outside the Moray Firth (Wilson et al., 2004). Here it is shown, more than a decade after Wilson et al. (2004) documented the range expansion, that St Andrews Bay and the Tay estuary was consistently used by half of the estimated population every summer. Furthermore, over the entire 2009-2015 period, around one-third of the population was seen only in this area, 300 km from the Moray Firth SAC. The results also show that dolphin presence in this area is focused on the entrance to the Firth of Tay and waters around Montrose.

### 4.1. Population context of St Andrews Bay and the Tay estuary

The estimated total population over the 7-year period was variable, but increased from 165 (95% CI 156-175) animals in 2009 to 209 (95% CI 189-230) in 2015. This estimate of an increasing population, from robust design analyses making use of data at a finer temporal scale within years from across the population's range, confirms previous work by Cheney et al. (2018) that used annual summaries of these sightings within a state space population model. Recent work by Arso Civil et al. (in press) identified an increase in juvenile and adult survivorship in this population, most likely driven by a change in juvenile survival, and Cheney (2017) found an increasing trend in reproductive rates and in calf survival for animals using the Moray Firth SAC. These results appear to explain the population's overall increase in size (Cheney et al., 2018) and may be a result of the previous range expansion (Wilson et al., 2004). It remains unknown, however, whether there is an influence of area on survival and fecundity rates. To explore this, especially in the context of the importance of St Andrews Bay and the Tay estuary identified in this study, annual data collection in both areas is required.

The estimated abundance of dolphins using St Andrews Bay and the Tay estuary during the summer over the same period was also variable and, similarly, increased overall from 91 (95% CI 78-106) in 2009 to 114 (95% CI 95-137) in 2015. The percentage of the total population using St Andrews Bay and the Tay estuary in summer during 2009-2015 averaged 52%. The percentage of the population using the Moray Firth SAC in summer declined from 2001 to 2015 but averaged more than 50% over this period (Cheney et al., 2018). The percentage of marked animals seen only in one area or the other during 2009-2015 was also equivalent at 35%. These results lead us to conclude that the St Andrews Bay and Tay estuary area is equally as important, in terms of simple presence of individuals, to the population in summer as the Moray Firth SAC. Assessing the importance of these (and other) areas in terms of how individuals use them temporally and spatially requires further work.

Animals in this population are highly mobile across the population's main distributional range and also show high individual variability in movement patterns, both spatially and temporally (Cheney et al., 2013; Quick et al., 2014). Analysis of photo-identification data collected across the population's main distributional range in 2006 and 2007 showed that the number of individuals seen in more than one area varied spatially, with the highest numbers between the geographically closest areas (within the Moray Firth) and lowest between the most distant ones (between the Grampian /Fife coast, where St Andrews Bay and the Tay estuary are located, and the Moray Firth SAC) (Cheney et al., 2013).

Comparison of photo-identification data collected from 1997 to 2007 in St Andrews Bay and the Tay estuary and in the Moray Firth SAC has shown that some animals were present in both areas within a single summer and others were present in one area for one or more years before being sighted in the other area the next year(s) (Quick et al., 2014).

The results show that the percentage of marked dolphins observed in both the Moray Firth SAC and in St Andrews Bay and the Tay estuary is small (average 5.6%) in any single summer and that during the 7-year study period fewer than 30% of these marked animals were seen in both areas, while around 35% were seen only in St Andrews Bay and the Tay estuary and 35% only in the SAC.

Making inferences from these results about spatial mixing of individuals in the population is limited by the fact that photo-identification effort included in this study only occured in certain areas within the population’s main distributional range, leaving other areas such as between the outer Moray Firth and Aberdeen with no information on the spatio-temporal presence of individuals from the population. Given the extensive distributional range, and in accordance with differences in individual movements between close and distant areas within the range (Cheney et al., 2013), it is conceivable that there is a cline in individual ranging behaviour.

Making inferences about spatial mixing at the population level also requires making two technical assumptions. First, it needs to be assumed that marked individuals are representative of the population. Bottlenose dolphins acquire permanent markings with age and males acquire more marks than females (e.g. Marley, Cheney, & Thompson, 2013) so bias could be introduced if younger animals and/or females are more or less likely to move between these two areas. In an analysis of data including animals with and without long-lasting permanent marks, Quick et al. (2014) found patterns that suggested a tendency for males to move more frequently than females between the Moray Firth SAC and St Andrews Bay and the Tay estuary. The inclusion of animals without long-lasting permanent marks in this analysis makes it difficult to make clear comparisons with our results and it remains unknown whether the results for animals with long-lasting permanent marks are representative of the population.

Second, it needs to be assumed that individuals seen in both areas in a summer season have the same probability of being observed (captured) as individuals seen in only one area or the other. Capture probability over an entire summer is very high in St Andrews Bay and the Tay estuary and in the Moray Firth SAC. Over the period 2009-2015, annual capture probability (calculated simply as number of marked animals observed divided by estimated total number of marked animals) varied from 0.88 to 1.0 in St Andrews Bay and the Tay estuary, except in 2014 (0.58), and from 0.91 to 0.98 in the Moray Firth SAC (Cheney et al., 2012, 2018). Nevertheless, it is possible that the number of animals seen in both areas may be greater if capture probability is higher. The number seen in both areas each summer was positively correlated with capture probability in St Andrews Bay and the Tay estuary but negatively correlated with capture probability in the Moray Firth SAC. We conclude that any bias introduced by variation in capture probability is likely to be small.

If these assumptions are met, the results indicate that individuals within the population display differential use of these areas within the population's main distributional range, at least in summer. To extrapolate beyond the summer, it has to be assumed that the observed levels of spatial mixing of individuals are similar at other times of the year. There are few photo-identification data outside the summer months, primarily because of adverse conditions for surveys. Incidental sightings of dolphins along the Fife coast (including St Andrews Bay, the Tay estuary and the Firth of Forth) are recorded throughout the year, and acoustic data have shown that bottlenose dolphins are present between the Moray Firth and St Andrews Bay in winter (Thompson et al., 2011). But it remains unknown whether the levels of spatial mixing of individuals observed in summer are representative of the whole year.

Information about the spatial mixing of individuals over the range of a population has potential implications for conservation, as described above. The overall connectivity within the east coast of Scotland bottlenose dolphin population is well-established. The results presented here provide a rough approximation of the temporal scale at which that connectivity operates. Assuming that the level of spatial mixing of individuals observed in summer is representative of the whole year and remains the same over time, a crude extrapolation of the 28.9% of animals seen in both areas over the 7-year study period implies that it would take around 25 years, about a generation (assuming 21 years, Taylor, Chivers, Larese, & Perrin, 2007), for the population to mix completely over its range. This supports the need to continue to obtain data from both areas to monitor the population effectively and gives an indication of the temporal scale at which the impact of human activities in one area may be manifest in the other area.

4.2. Identification of high use areas

Bottlenose dolphins were seen in all surveyed months (May to September) in 2012 and 2013, when bottlenose dolphin presence/absence data were collected, in line with the rest of the surveyed summers in this study and past survey effort during the summer in St Andrews Bay and the Tay estuary (Cheney et al., 2013). However, the predicted presence of bottlenose dolphins was not uniform across the study area. In particular, the models identified high use areas at the entrance of the Firth of Tay and in the waters around Montrose. The sandwich-based variance estimators used in the GEEs produced robust standard errors which ensured the retained covariates in the final model based on the $QIC_c$ were important predictors of dolphin presence (Hardin & Hilbe, 2003). Interpretation of the relationship between dolphin presence and the retained covariates in the final model was however difficult given the resulting wide 95% confidence intervals (e.g. Pirotta et al., 2011), and suggest a much more complex picture. Despite these limitations, the resulting prediction maps identified these high use areas consistently across different current speeds and current directions.

Temporal and spatial variability in the presence of bottlenose dolphins off the east coast of Scotland has previously been discussed in the context of the availability of food resources (Bailey, Corkrey, Cheney, & Thompson, 2013; Hastie, Wilson, Wilson, Parsons, & Thompson, 2004; Mendes, Turrell, Lutkebohle, & Thompson, 2002). In the Moray Firth, the peak in bottlenose dolphin presence in the summer months coincides with seasonal migrations of salmonids (Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*) through the area (Wilson et al., 1997). Salmonids are known to be important prey for bottlenose dolphins based on the analysis of stomach contents (Santos et al., 2001), and direct observations of foraging events (Hastie et al., 2004; Janik, 2000; Wilson et al., 1997). During the course of this study bottlenose dolphins were also observed foraging on salmonid species, as well as flatfish and mackerel, in St Andrews Bay and the Tay estuary. Other prey species important in the diet

526 of bottlenose dolphins from this population include cod, saithe, whiting, haddock and cephalopods
527 (Santos et al., 2001), all found in the waters off south-east Scotland (Callaway et al., 2002).

528 The river Tay and the rivers North Esk and South Esk by Montrose are important for migrating
529 salmon and sea trout in Scotland (ASFB & RAFTS, 2014; Marine Scotland Science, 2012), and
530 salmon and sea trout that do not migrate upstream also approach the Tay estuary at different stages of
531 their life cycle (Mills, 1986). It is thus likely that salmonids are an important prey species for
532 bottlenose dolphins in these areas, at least during the summer months, as has also been found for
533 harbour seals in the Tay estuary in summer and autumn, albeit with high uncertainty (Sharples,
534 Arrizabalaga, & Hammond, 2009).

535 Tidal dynamics influenced dolphin presence, which varied at different current speeds and directions.
536 Because these covariates vary together throughout the tidal cycle, it is impossible to completely
537 separate their effect on the predicted dolphin presence. Dolphins were more likely to be present in
538 areas with low or high current speeds, compared to intermediate values, and when the current was
539 flowing approximately towards the NE or WSW (falling and rising tides), but also towards the NNW.

540 There is dynamic and complex tidal mixing at the entrance to the Tay estuary, influenced by offshore
541 tidal currents and by the estuarine currents, which have different phase relationships with respect to
542 high water (Ferrier & Anderson, 1997). The outer part of the Tay estuary channel is characterized by
543 depths that range from 2 to 20 metres, with a generally flat sea bed (0° to 3° slope). The entrance to
544 the channel is delimited by two sandbars about 1 km apart which are exposed at low tide. Thus,
545 despite the relatively shallow waters and a flat sea bed, the area experiences fast and complex tidal
546 currents (Ferrier & Anderson, 1997), reaching spring tidal flows greater than 1.2 $ms^{-1}$ and a spring
547 tidal range of 4.4 meters at the entrance to the Tay (Hansom et al., 2011).

548 There is no fine-scale information on the distribution and availability of bottlenose dolphin prey at the
549 entrance of the Tay estuary. However, this dynamic and complex tidal mixing may accumulate prey
550 and improve the foraging efficiency of dolphins in the area, as suggested for the narrow channels in
551 the inner Moray Firth with similar highly complex tidal dynamics (e.g. Bailey & Thompson, 2006;
552 Hastie et al., 2004; Mendes et al., 2002). The sandbars may also increase foraging efficiency at low

tide by confining and concentrating prey in the area or acting as a physical barrier that the dolphins can use to herd fish. During the course of this study, individual dolphins were observed on many occasions next to the exposed sandbar, especially on the south side of the estuary entrance, displaying feeding behaviour (i.e. long dives at the same spot, chasing prey underwater, tossing fish at the surface and/or with fish in their mouths). Individuals were also seen over or next to the sandbar at other stages of the tide when it was covered by water.

A large proportion of the population uses both St Andrews Bay and the Tay estuary and the Moray Firth SAC in the summer months (see above) and high use areas have been identified in both areas. However, further work is required to assess the relative importance of specific areas across the population's main range.



### 4.3. Wider-context considerations of area-based management

Wilson (2016) has discussed the limitations of area-based management for highly mobile, wide-ranging species such as cetaceans and questioned some of the reasons behind its implementation; that is, whether it is the right tool for these species. Nevertheless, protected areas in the form of SACs are a legal requirement under the Habitats Directive for bottlenose dolphin and harbour porpoise and this is the primary management framework that is used in Europe to protect these species. The case of the east coast of Scotland population of bottlenose dolphins is an interesting and potentially informative example of how the challenges of imposed area-based management have been tackled.

The SAC proposed in 1996 in the Moray Firth encompassed the core area of occurrence of the population as known at that time. During the range shift in the 1990s (Wilson et al., 2004), research to study the population in southern parts of its range increased. As described above, the availability of new data outwith the SAC led to a change in the attributes and targets for the SAC so that the additional data fed into the site condition assessment to evaluate population trends. This paper, using data from regular surveys in St Andrews Bay and the Tay estuary since 2009, shows that half of the population uses this area every summer, with incomplete spatial mixing of individuals in the short term between this area and the Moray Firth SAC. This re-confirms that assessing the conservation status of the east coast of Scotland bottlenose dolphin population requires data from across the population range. Because the population is highly mobile within its main distributional range, Scottish Natural Heritage guidance is that a planned development that could impact bottlenose dolphins anywhere within the population's range is likely to have a significant effect on the SAC in view of its conservation objectives and that such plans need to be considered in appropriate assessments under Article 6 of the Habitats Directive (SNH Natura Casework Guidance, 2018).

Thus, although Wilson et al. (2004) suggested that the range expansion in the 1990s might diminish the protection originally envisioned for the Moray Firth SAC, the way in which Natura 2000 is implemented under the Habitats Directive in this specific case means that the SAC provides protection for the population throughout its range, and not just in the relatively small Moray Firth SAC. This management approach can therefore be seen as an effective way of maintaining favourable conservation status for this particular population.



However, this is not really area-based management as conventionally considered. Article 3 of the Habitats Directive states that: "For aquatic species which range over wide areas, such sites [SACs] will be proposed only where there is a clearly identifiable area representing the physical and biological factors essential to their life and reproduction". It is therefore clear that SACs should be in areas that are important to a population. However, as described above, they are also a proxy for monitoring and protecting the entire population if there is connectivity between SACs and the rest of the population's range. The photo-identification techniques used to study the east coast of Scotland bottlenose dolphin population demonstrate connectivity of individuals across the population's range. In this sense, the location of the SAC is not critical because the same level of protection exists across that range. As long as a site met the definition above, i.e. it was located in an area important to the population and connectivity between the site and the rest of the range was demonstrated, the SAC could be anywhere in the population's range and the same protection would result. The site condition of the Moray Firth SAC is favourably assessed because it meets the targets of the attributes regarding the use of the SAC by the population, even though the proportion of the population using the SAC is declining (Cheney et al., 2018). This further illustrates that it is not just the SAC itself that is of primary importance but the way in which the SAC management framework is implemented to protect the entire population. That half the population is observed in St Andrews Bay and the Tay estuary each summer confirms that protecting the population everywhere is more important than protecting an area at one end of the population's range.

The results presented here confirm that the east coast of Scotland population of bottlenose dolphins has shown a marked change in distribution. These new analyses further support Cheney et al.'s (2018) findings that the population is increasing, and raise the possibility that it is continuing to expand and further shift its distribution, supported by recently increasing sightings of bottlenose dolphins south of the Firth of Forth. Estimates of the number of animals using St Andrews Bay and the Tay estuary have increased at around 5% per year ($p=0.0157$) between 2009 and 2015. Although there is no significant trend in the number of animals using the Moray Firth SAC in the same period, if there is a southerly drift in the population in future it may be pertinent to consider whether current management still provides adequate protection.

It is also worth considering how the way in which the east coast of Scotland population of bottlenose dolphins is assessed and protected may be relevant to the conservation of other populations of highly mobile wide-ranging species. For example, the UK and Scottish governments recently proposed a number of SACs for harbour porpoise (JNCC, 2017; Scottish Government, 2016), a widely distributed species in shelf waters of the European Atlantic (Hammond et al., 2013) and the only other species of cetacean requiring SACs under Natura 2000. Population-wide photo-identification of harbour porpoises is unfeasible but telemetry studies have provided some indications of connectivity of individuals (Sveegaard et al., 2011, 2015). The proposed SACs in UK waters are large, reflecting the highly-mobile wide-ranging nature of the species and they cover a large proportion of English and Welsh waters over which connectivity of individuals may reasonably be assumed. Thus, monitoring and management equivalent to that implemented for the Moray Firth SAC for bottlenose dolphins may allow assessment of conservation status and provide protection for harbour porpoise throughout most of its range in these waters. However, this is unlikely to be true in Scottish waters because the single SAC west of Scotland is far from the majority of the distribution of harbour porpoises around the Northern Isles and east of Scotland, where there is no proposed SAC, and connectivity of individuals could not reasonably be assumed.

The conclusion here is that management using SACs as a proxy for monitoring and protecting highly mobile wide-ranging populations is only likely to succeed if the SACs cover a large proportion of the population distribution and that connectivity of individuals throughout the distributional range can be established. This has been feasible for the bottlenose dolphin populations using photo-identification data but the lack of knowledge about the connectivity within other populations of highly mobile species, including most cetaceans and seabirds, means that area-based management to conserve populations remains a considerable challenge.

Spatial and temporal variability in cetacean distributions poses challenges in the designation of protected areas (e.g. Embling et al., 2010) and calls for a flexible approach and adaptive management to ensure continued effectiveness of protected sites (Rayment et al., 2010; Silva et al., 2012). Area-based conservation/management of highly mobile wide-ranging species and human activities that might impact them can be effective, as illustrated by how it is applied to the east coast of Scotland bottlenose dolphin population. But whether this approach is generally the most appropriate way to monitor and protect populations of such species is not clear, for the reasons outlined by Wilson (2016). Monitoring over the main distributional range is clearly needed but the way in which anthropogenic pressures and threats are managed needs to be considered carefully.



**Acknowledgments**

MAC received funding from the Department of Energy and Climate Change (DECC) (now Department for Business, Energy and Industrial Strategy) UK, and the MASTS (Marine Alliance for Science and Technology for Scotland) pooling initiative. MASTS is funded by the Scottish Funding Council (grant reference HR09011) and contributing institutions. Annual surveys were funded by DECC, Scottish Natural Heritage (SNH), Beatrice Offshore Windfarm Ltd., Moray Offshore Renewables Ltd, Marine Scotland, The Crown Estate, Highlands and Islands Enterprise and the Universities of St Andrews and Aberdeen. All fieldwork was carried out under SNH Animal Scientific Licences to PMT and PSH. The authors have no conflict of interest to declare.

We thank John Baxter for helpful discussions about the implications for conservation and management while drafting this manuscript, and Morven Carruthers for her advice on the site condition monitoring for the Moray Firth SAC. This manuscript benefited from the helpful comments of two anonymous reviewers.

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**Tables**

Table 1. Photo-identification survey effort conducted between 2009 and 2015 in the overall study area (top) and in St Andrews Bay and the Tay estuary (bottom, also included in the overall effort). Details on survey effort dates, number of secondary sampling occasions (i.e. calendar months), number of surveys and encounters, and number of marked animals (total and new) identified from good quality photographs in each year are shown. The overall study area includes the Moray Firth SAC and St Andrews Bay and the Tay estuary (both surveyed annually), the outer Moray Firth (surveyed more occasionally), and the Firth of Forth and Montrose to Aberdeen area (both only surveyed in 2012 and 2013). Note that this difference in survey area accounts for the higher number of marked animals in certain years compared to Table 2.

| Year | Effort | Secondary occasions | No. Surveys | No. Encounters | Marked animals | New animals |
|---|---|---|---|---|---|---|
| *Overall study area* | | | | | | |
| 2009 | 06 May-30 Sep | 5 | 42 | 137 | 89 | - |
| 2010 | 05 May-21 Sep | 5 | 32 | 160 | 92 | 8 |
| 2011 | 03 May-29 Sep | 5 | 31 | 145 | 89 | 3 |
| 2012 | 02 May-27 Sep | 5 | 41 | 172 | 102 | 9 |
| 2013 | 02 May-27 Sep | 5 | 50 | 218 | 103 | 7 |
| 2014 | 02 May-22 Sep | 5 | 29 | 161 | 85 | 7 |
| 2015 | 08 May-30 Sep | 5 | 29 | 146 | 99 | 5 |
| *St Andrews Bay and the Tay estuary* | | | | | | |
| 2009 | 15 Jun-24 Aug | 3 | 7 | 30 | 43 | - |
| 2010 | 17 Jun-1 Sep | 4 | 8 | 39 | 42 | 9 |
| 2011 | 6 Jun-31 Aug | 3 | 10 | 38 | 42 | 4 |
| 2012 | 9 May-27 Sep | 5 | 17 | 48 | 42 | 6 |
| 2013 | 7 May-27 Sep | 5 | 20 | 70 | 43 | 6 |
| 2014 | 13 May-9 Sep | 4 | 8 | 26 | 33 | 7 |
| 2015 | 23 May-30 Sep | 4 | 9 | 24 | 52 | 7 |

Table 2. Number of marked animals identified in the sub-areas of St Andrews Bay and the Tay estuary, and/or in the Moray Firth SAC between 2009 and 2015. Annual proportions of the total number of marked animals seen only in each of the two sub-areas or in both sub-areas are given next to the number of marked animals seen.

| Year | Number of marked animals | St Andrews Bay and Tay estuary | Moray Firth SAC | St Andrews Bay and the Tay estuary only | Moray Firth SAConly | Both areas |
|---|---|---|---|---|---|---|
| 2009 | 89 | 43 | 53 | 36 (40.4%) | 46 (51.7%) | 7 (7.9%) |
| 2010 | 92 | 42 | 60 | 32 (34.8%) | 50 (54.3%) | 10 (10.9%) |
| 2011 | 87 | 42 | 52 | 35 (40.2%) | 45 (51.7%) | 7 (8.0%) |
| 2012 | 98 | 42 | 59 | 39 (39.8%) | 56 (57.1%) | 3 (3.1%) |
| 2013 | 91 | 43 | 51 | 40 (44.0%) | 48 (52.7%) | 3 (3.0%) |
| 2014 | 74 | 33 | 41 | 33 (44.6%) | 41 (55.4%) | 0 (0%) |
| 2015 | 99 | 52 | 53 | 46 (46.5%) | 47 (47.5%) | 6 (6.1%) |
| 2009 to 2015 | 128 | 82 | 83 | 45 (35.2%) | 46 (35.9%) | 37 (28.9%) |

Table 3. Model selection for the robust design models to estimate the abundance of marked animals in the overall study area (top) and in St Andrews Bay and the Tay estuary (bottom). Parameters estimated: survival probability ($\phi$), capture probabilities (p), temporary emigration probabilities (ɣ), and Pledger's mixture parameter for two types ($\pi$). In the model description: (.) = constant; (t) = time-specific for primary sampling occasions; (txs) = time-specific for primary (t) and secondary (s) sampling occasions; for temporary emigration ɣ`` = ɣ` = 0 = no emigration; ɣ``(x) = ɣ`(x) = random emigration; ɣ``(x) ɣ`(x) = Markovian emigration. Models are ordered from smallest to largest AICc.

Models not incorporating heterogeneity ($\pi$) did not receive support in the overall study area dataset and are not shown. Only the top 13 models are shown for the St Andrews Bay and the Tay estuary dataset (the others received less support)

| Model no. | Model | No. parameters | AICc | ΔAICc | $AIC_c$ weight | Deviance |
|---|---|---|---|---|---|---|
| *Overall study area* | | | | | | |
| 1 | $\phi_{(.)}\gamma''_{(t)} = \gamma'_{(t)}\, p_{(txs)}\, \pi_{(t)}$ | 57 | -437.22 | 0.00 | 0.792 | 2932 |
| 2 | $\phi_{(.)}\gamma'' = \gamma' = 0\ p_{(txs)}\, \pi_{(t)}$ | 52 | -434.51 | 2.71 | 0.204 | 2946 |
| 3 | $\phi_{(.)}\gamma'' = \gamma' = 0\ p_{(txs)}\, \pi_{(.)}$ | 46 | -426.64 | 10.57 | 0.004 | 2966 |
| 4 | $\phi_{(.)}\gamma''_{(t)}\ \gamma'_{(.)}\, p_{(txs)}\, \pi_{(t)}$ | 58 | -409.02 | 28.20 | 0.000 | 2958 |
| 5 | $\phi_{(.)}\gamma''_{(.)} = \gamma'_{(.)}\, p_{(txs)}\, \pi_{(t)}$ | 53 | -408.85 | 28.36 | 0.000 | 2969 |
| 6 | $\phi_{(.)}\gamma''_{(t)} = \gamma'_{(t)}\, p_{(txs)}\, \pi_{(t)}$ | 54 | -405.00 | 32.22 | 0.000 | 2971 |
| 7 | $\phi_{(.)}\gamma''_{(.)}\ \gamma'_{(t)}\, p_{(txs)}\, \pi_{(t)}$ | 58 | -402.60 | 34.62 | 0.000 | 2965 |
| 8 | $\phi_{(.)}\gamma''_{(t)}\ \gamma'_{(t)}\, p_{(txs)}\, \pi_{(t)}$ | 62 | -401.22 | 36.00 | 0.000 | 2958 |
| *St Andrews Bay and the Tay estuary* | | | | | | |
| 9 | $\phi_{(.)}\gamma''_{(.)} = \gamma'_{(.)}\, p_{(txs)}\, \pi_{(t)}$ | 46 | 87.77 | 0.00 | 0.524 | 992 |
| 10 | $\phi_{(.)}\gamma''_{(.)}\ \gamma'_{(.)}\, p_{(txs)}\, \pi_{(t)}$ | 47 | 89.83 | 2.06 | 0.187 | 992 |
| 11 | $\phi_{(.)}\gamma''_{(.)}\ \gamma'_{(.)}\, p_{(txs)}$ | 38 | 90.66 | 2.89 | 0.124 | 1014 |
| 12 | $\phi_{(.)}\gamma'' = \gamma' = 0\ p_{(txs)}\, \pi_{(t)}$ | 45 | 90.77 | 3.00 | 0.117 | 998 |
| 13 | $\phi_{(.)}\gamma''_{(t)} = \gamma'_{(t)}\, p_{(txs)}\, \pi_{(t)}$ | 50 | 94.87 | 7.10 | 0.015 | 990 |
| 14 | $\phi_{(.)}\gamma''_{(t)}\ \gamma'_{(.)}\, p_{(txs)}\, \pi_{(t)}$ | 51 | 95.79 | 8.02 | 0.009 | 989 |
| 15 | $\phi_{(.)}\gamma''_{(t)} = \gamma'_{(t)}\, p_{(txs)}$ | 41 | 96.06 | 8.29 | 0.008 | 1012 |
| 16 | $\phi_{(.)}\gamma''_{(t)}\ \gamma'_{(.)}\, p_{(txs)}$ | 42 | 97.28 | 9.51 | 0.005 | 1011 |
| 17 | $\phi_{(.)}\gamma''_{(.)}\ \gamma'_{(t)}\, p_{(txs)}\, \pi_{(t)}$ | 51 | 97.33 | 9.56 | 0.004 | 990 |
| 18 | $\phi_{(.)}\gamma''_{(.)}\ \gamma'_{(t)}\, p_{(txs)}$ | 42 | 97.39 | 9.62 | 0.004 | 1011 |
| 19 | $\phi_{(.)}\gamma'' = \gamma' = 0\ p_{(txs)}\, \pi_{(.)}$ | 39 | 99.01 | 11.24 | 0.002 | 1020 |
| 20 | $\phi_{(.)}\gamma''_{(t)}\ \gamma'_{(t)}\, p_{(txs)}\, \pi_{(t)}$ | 55 | 102.59 | 14.82 | 0.000 | 986 |
| 21 | $\phi_{(.)}\gamma''_{(t)}\ \gamma'_{(t)}\, p_{(txs)}$ | 46 | 103.43 | 15.66 | 0.000 | 1008 |

Table 4. Annual estimates of abundance of animals using the overall study area (top) and St Andrews Bay and the Tay estuary (bottom) with associated precision. θ = proportion of marked animals; $\hat{N}$ = abundance of marked animals; $\hat{N}_{total}$ = total abundance of animals; percentage = percentage of the total estimated population using St Andrews Bay.

| **Year** | **$\hat{N}$** | **CV ($\hat{N}$)** | **$\hat{\theta}$** | **CV ($\hat{\theta}$)** | **$\hat{N}_{total}$ (95% CI)** | **CV ($\hat{N}_{total}$)** | |
|---|---|---|---|---|---|---|---|
| *Overall study area* | | | | | | | |
| 2009 | 91 | 0.019 | 0.55 | 0.023 | 165 (156-175) | 0.030 | |
| 2010 | 92 | 0.000 | 0.53 | 0.024 | 175 (167-183) | 0.024 | |
| 2011 | 91 | 0.019 | 0.53 | 0.026 | 171 (161-182) | 0.032 | |
| 2012 | 102 | 0.011 | 0.49 | 0.028 | 208 (196-220) | 0.030 | |
| 2013 | 104 | 0.011 | 0.53 | 0.025 | 194 (184-205) | 0.028 | |
| 2014 | 103 | 0.069 | 0.51 | 0.031 | 202 (175-233) | 0.076 | |
| 2015 | 107 | 0.040 | 0.51 | 0.030 | 209 (189-230) | 0.051 | |
| *St Andrews Bay and the Tay estuary* | | | | | | | **Percentage** |
| 2009 | 47 | 0.063 | 0.52 | 0.051 | 91 (78-106) | 0.081 | 55.18 % |
| 2010 | 42 | 0.000 | 0.47 | 0.050 | 89 (81-98) | 0.050 | 50.66 % |
| 2011 | 42 | 0.000 | 0.50 | 0.049 | 85 (77-93) | 0.049 | 49.45 % |
| 2012 | 47 | 0.082 | 0.49 | 0.047 | 95 (80-114) | 0.095 | 45.80 % |
| 2013 | 48 | 0.110 | 0.48 | 0.058 | 100 (80-126) | 0.124 | 51.72 % |
| 2014 | 56 | 0.181 | 0.47 | 0.087 | 121 (84-173) | 0.201 | 59.92 % |
| 2015 | 59 | 0.069 | 0.52 | 0.068 | 114 (95-137) | 0.097 | 54.76 % |

Table 5. Summary of survey effort, photo-ID follows and number of encounters in 2012 and 2013 in St Andrews Bay and the Tay estuary.

| | 2012 | | | 2013 | | |
|---|---|---|---|---|---|---|
| Month | On-effort (km) | Follow (km) | No. Encounters | On-effort (km) | Follow (km) | No. Encounters |
| May | 376 | 34 | 6 | 414 | 37 | 10 |
| June | 358 | 20 | 5 | 602 | 45 | 17 |
| July | 628 | 90 | 21 | 402 | 25 | 13 |
| August | 225 | 15 | 5 | 243 | 16 | 18 |
| September | 214 | 30 | 7 | 320 | 13 | 26 |
| Total | 1801 | 189 | 44 | 1981 | 136 | 84 |
| Total 2012/13 | | | | 3782 | 325 | 128 |

**Figure Legends**

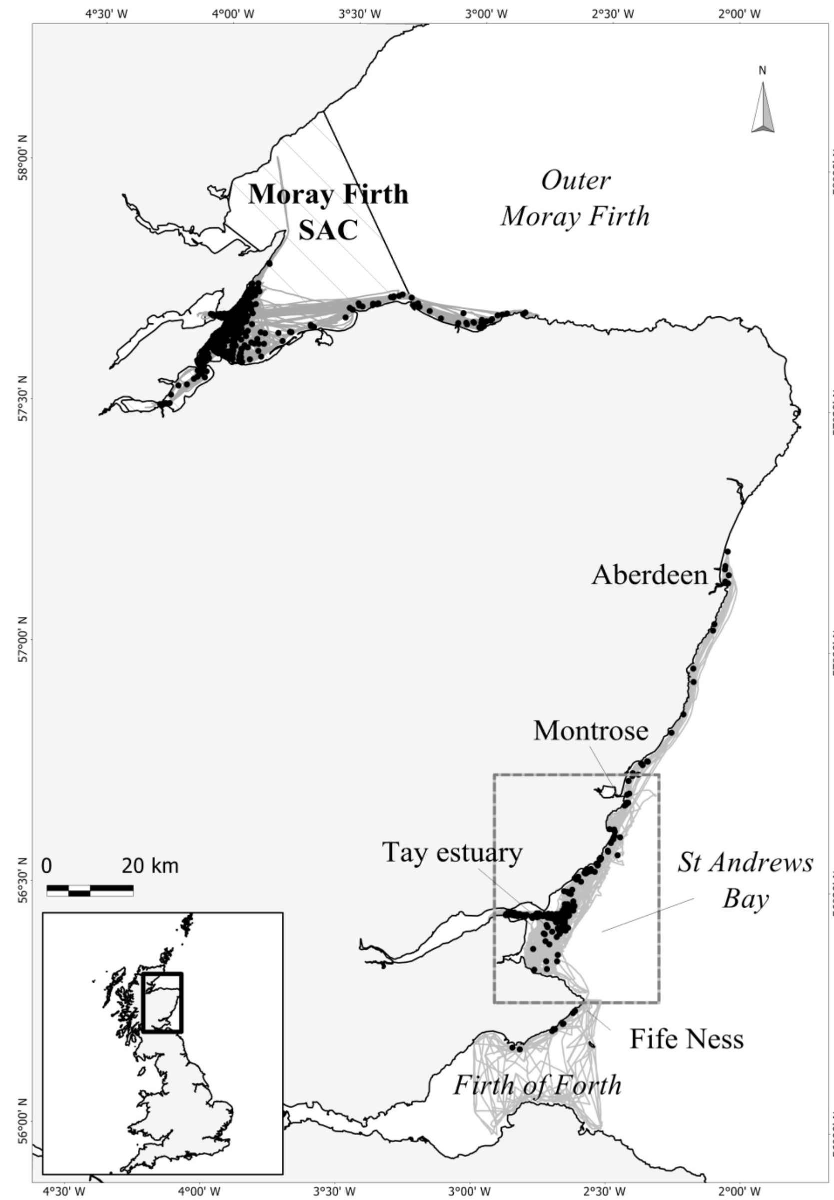
Figure 1. Overall sampling area along the east coast of Scotland between the Moray Firth and the Firth of Forth, covering the current population's main distributional range, including the sub-areas of St Andrews Bay and the Tay estuary (dashed box), and the Moray Firth SAC. Survey effort conducted from 2009 to 2015 is shown (grey lines) with locations of bottlenose dolphin encounters (black dots).

Figure 2. Proportion of marked dolphins seen only in St Andrews and the Tay Esturay (black), only in the Moray Firth SAC (dark grey), or seen in both areas (light grey) every year (May to September) and overall between 2009 and 2015.

Figure 3. Partial residual plots of the relationship between presence of bottlenose dolphins (on the link scale) and the retained covariates (a) distance to the Tay (meters), (b) current direction (0-360 degrees), (c) current speed (m/s), (d) month, (e) sea surface temperature (°C) and (f) year. The shaded areas are the GEE-based 95% confidence intervals and a rug plot with the actual data values is shown at the bottom of each plot.

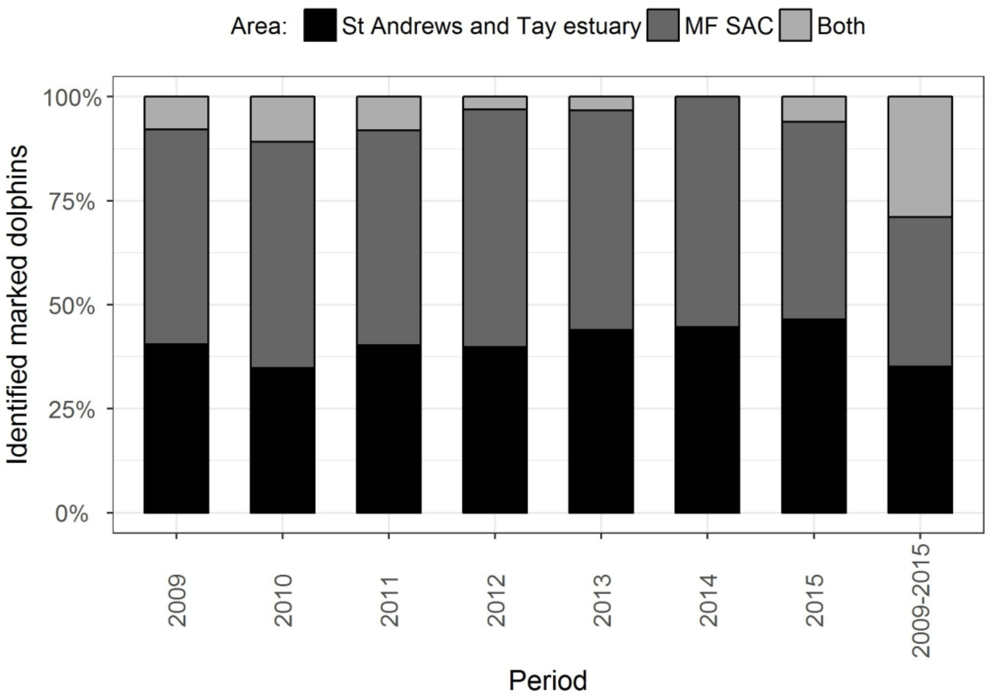
Figure 4. Prediction maps of probability of presence of bottlenose dolphins for different current directions (10-60 degrees, 60-220 degrees, 220-300 degrees and 300-10 degrees), with associated bottlenose dolphin presence points recorded during follows in each corresponding tidal condition.

Figure 5. Prediction maps of probability of presence of bottlenose dolphins for low (0-0.15 $ms^{-1}$), intermediate (0.15-0.5 $ms^{-1}$) and high (>0.5 $ms^{-1}$) current speeds, with associated bottlenose dolphin presence points recorded during follows in each corresponding tidal condition. Note that high current speeds (>0.5 $ms^{-1}$) did not occur in the entire surveyed area, compared to low or intermediate current speeds.



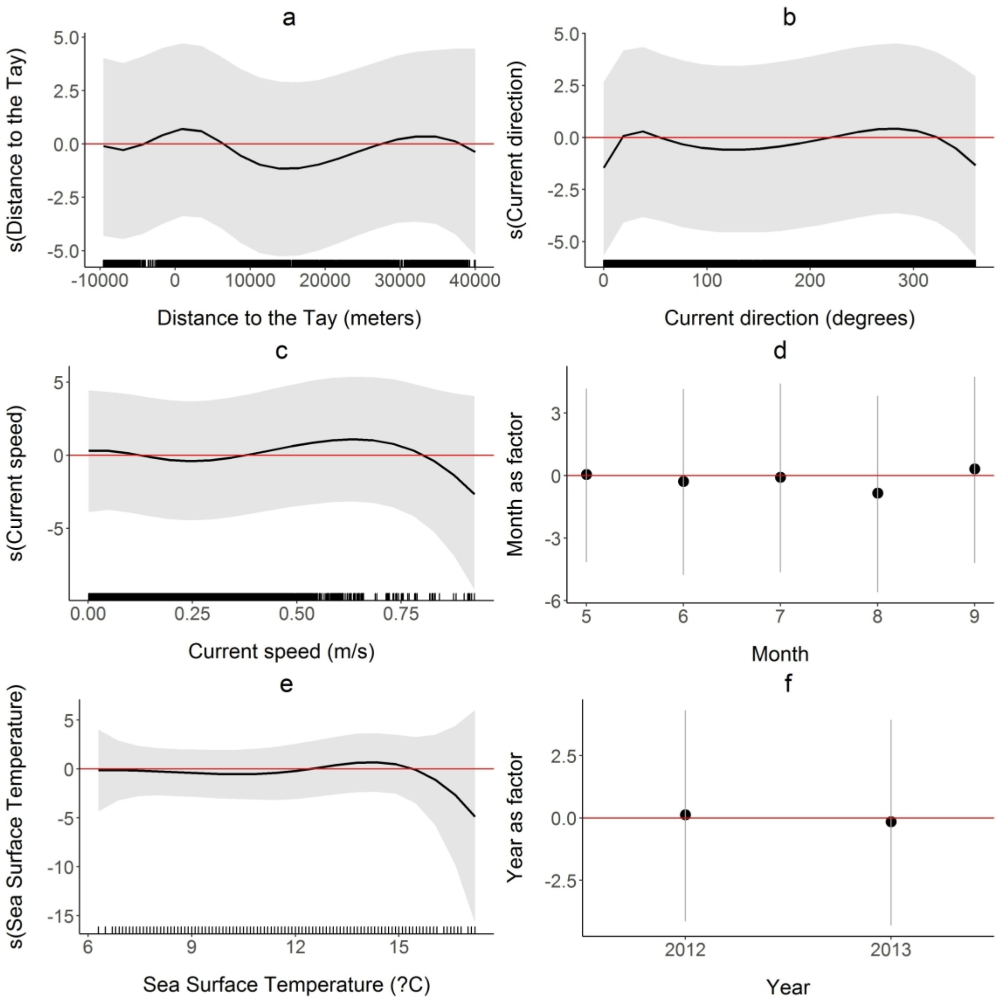

Overall sampling area along the east coast of Scotland between the Moray Firth and the Firth of Forth, covering the population's main distributional range, including the sub-areas of St Andrews Bay and the Tay estuary (dashed box), and the Moray Firth SAC. Survey effort conducted from 2009 to 2015 is shown (grey lines) with locations of bottlenose dolphin encounters (black dots).

201x288mm (300 x 300 DPI)



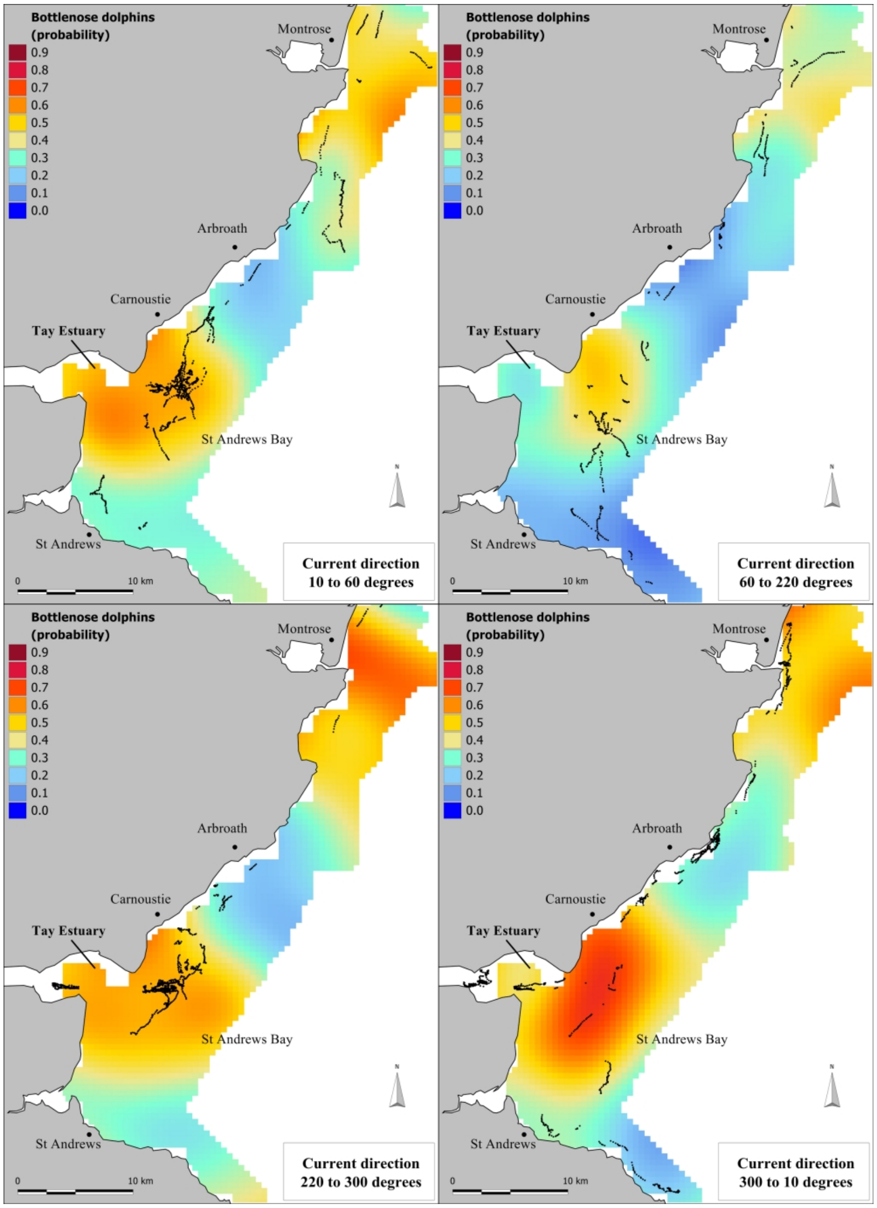

Proportion of marked dolphins seen only in St Andrews and the Tay Esturay (black), only in the Moray Firth SAC (dark grey), or seen in both areas (light grey) every year (May to September) and overall between 2009 and 2015.

177x127mm (300 x 300 DPI)



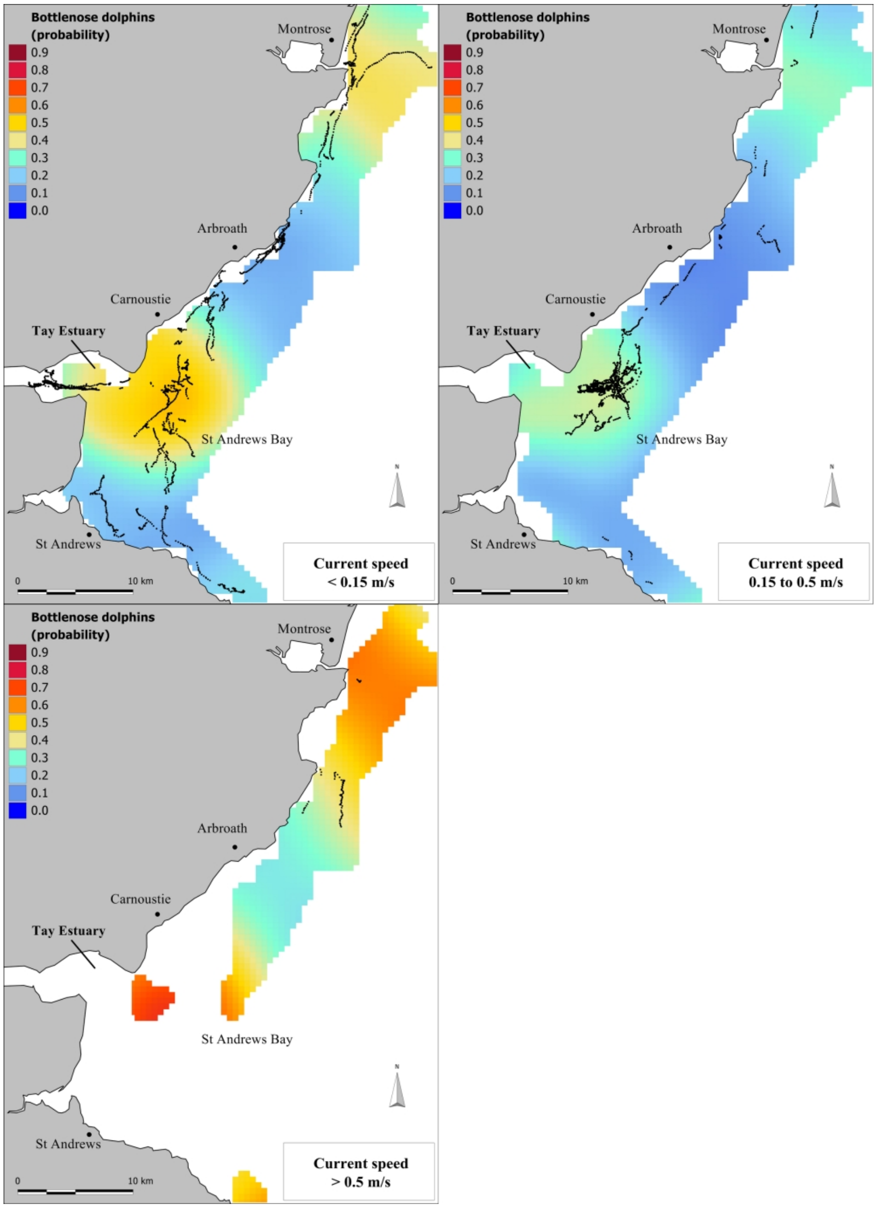

Partial residual plots of the relationship between presence of bottlenose dolphins (on the link scale) and the retained covariates (a) distance to the Tay (meters), (b) current direction (0-360 degrees), (c) current speed (m/s), (d) month, (e) sea surface temperature (°C) and (f) year. The shaded areas are the GEE-based 95% confidence intervals and a rug plot with the actual data values is shown at the bottom of each plot.

304x304mm (300 x 300 DPI)




Prediction maps of probability of presence of bottlenose dolphins for different current directions (10-60 degrees, 60-220 degrees, 220-300 degrees and 300-10 degrees), with associated bottlenose dolphin presence points recorded during follows in each corresponding tidal condition.

848x1170mm (72 x 72 DPI)




Prediction maps of probability of presence of bottlenose dolphins for low (0-0.15 ms-1), intermediate (0.15-0.5 ms-1) and high (>0.5 ms-1) current speeds, with associated bottlenose dolphin presence points recorded during follows in each corresponding tidal condition. Note that high current speeds (>0.5 ms-1) did not occur in the entire surveyed area, compared to low or intermediate current speeds.

848x1170mm (72 x 72 DPI)