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Improving understanding of bottlenose dolphin movements along the east coast of Scotland

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Improving understanding of bottlenose dolphin movements along the east coast of Scotland

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4 Executive Summary

This report provides a summary of the photo-identification surveys conducted by the Sea Mammal Research Unit (SMRU) in the summers of 2017 to 2019 in the Tay estuary and adjacent waters, supported by the European Offshore Wind Development Centre. The survey data were used to estimate the abundance of animals using this area since 2009, and compared to the total east coast of Scotland population, estimated using part of the long-term photo-identification dataset collected by the University of Aberdeen and SMRU (2009-2019). In addition, this collaborative long-term dataset (1989 - 2019) was used to provide estimates of survival and fecundity rate, as well as analyse the movement of animals between the Tay estuary and adjacent waters and the Moray Firth Special Area of Conservation (SAC).

A total of 63 boat-based photo-identification surveys were conducted in the Tay estuary and adjacent waters across the three-year study period between May and September each year. These resulted in 54 encounters with bottlenose dolphin groups, and a total of 154 different individuals from all age classes identified from high quality photographs.

The estimated abundance of animals in the Tay estuary and adjacent waters ranged between 84 dolphins (95% CI 77 - 93) in 2011 to 138 dolphins (95% CI 110 - 173) in 2016. On average, the number of animals using this area between 2009 and 2019 represented 53.8% of the estimated total population using the main range between the Moray Firth SAC and the Firth of Forth.

A total of 230 identified juvenile or adult bottlenose dolphins were included in the analysis to estimate survival rate between 1989 and 2019. A total of 105 females gave birth at least once during that time period and were used to estimate birth rate, defined here as the annual probability of a reproductive female having a calf. The estimated apparent survival probability for juveniles/adults was 0.944 (95% CI 0.933 - 0.953) based on the most supported model. The expected inter-birth interval for the population was estimated at 3.95 years (95% CI 3.63 - 4.20), resulting in an estimated birth rate of 0.253 (95% CI 0.238 - 0.275).

A continuous time hidden Markov model was used to assess movement patterns of male and female bottlenose dolphins between the Moray Firth SAC and the Tay estuary and adjacent waters. Between 2017 and 2019, 112 individuals were only seen in the Moray Firth SAC, 103 were only seen in the Tay estuary and adjacent waters and 51 were seen in both areas. Of the 51 seen in both areas, 40 were seen in both areas within the same year. Model results for the period 1990 - 2019 indicated that movement between the two sites is infrequent but that, despite the clear individual heterogeneity, there is a seasonal movement pattern that is directional and consistent over years. The transition

intensities (movement rates) were highest from the Tay estuary and adjacent waters towards the Moray Firth SAC in early summer and from the Moray Firth SAC to the Tay estuary and adjacent waters in late summer. This pattern was consistent across individuals of both sexes, but male dolphins had higher transition intensities than females leading to differences in estimated mean sojourn times spent in one area or the other. It is unclear what drives different individuals to move between these two locations.

5 Introduction

The common bottlenose dolphin (*Tursiops truncatus*) is an important species in waters around Scotland and the rest of the UK, and is protected at national and international levels. It is listed under Annexes II and IV of the EU Habitats Directive (92/43/EEC), meaning that it is a European Protected Species and that Member States are required to designate Special Areas of Conservation (SAC) under the Natura 2000 programme. Furthermore, any planned development that could affect the conservation objectives of an SAC (e.g. significant disturbance to bottlenose dolphins associated with the SAC) requires an appropriate assessment of the impact of the activities before it can be consented.

The population of bottlenose dolphins off the east coast of Scotland has been studied since 1989 as part of a collaborative project between the University of Aberdeen's Lighthouse Field Station and the Sea Mammal Research Unit at the University of St Andrews (Wilson et al. 1999, Wilson et al. 2004, Cheney et al. 2013, Arso Civil et al. 2019b, Cheney et al. 2019). This population has undergone considerable changes in its distributional range over the last three decades. In the late 1980s and early 1990s the inner Moray Firth was believed to be the core area of occurrence, and this was the basis for designating the boundaries of the Moray Firth SAC (see Figure 1 in section 6.3), which was implemented in 2005. However, during the 1990s the population range expanded to the south, (Wilson et al. 2004) and surveys of the Tay estuary and adjacent water over the past 10 years from May to September have shown that around 50% of the population use this area during the summer months (Arso Civil et al. 2019b). In recent years, there has been an increase in sightings of individuals from this population in the Firth of Forth and as far south as the coast of northern England (Sea Watch Foundation 2018).

Over the last 20 years, the size of the population has increased (Cheney et al. 2014, 2018). While the number of animals using the Moray Firth SAC has remained stable (based on data between 2001 and

2016; Cheney et al. 2018), the number using the Tay estuary and adjacent waters has increased at around 5% per year between 2009 and 2016 (Arso Civil et al. 2019b). There is a high connectivity within the population, characterised by individual and sex-specific variability in movement patterns across the population's main distributional range (between the Moray Firth SAC and the Firth of Forth) (Cheney et al. 2013, Quick et al. 2014).

This study, supported by the European Offshore Wind Deployment Centre (EOWDC), builds on previous research into population size, survival and birth rates, and movement patterns. In particular, it develops a new method to incorporate more data and explore seasonal variability in movement. It aims to:

- Improve the understanding of movement patterns of individual bottlenose dolphins across the population range by combining data collected in the Tay estuary and adjacent waters, and data collected in the Moray Firth SAC;
- Provide estimates of the number of bottlenose dolphins using the Tay estuary and adjacent waters between 2009 and 2019;
- Update estimates of total population size, and survival and birth rates using long-term data collected by the University of Aberdeen Lighthouse Field Station and SMRU from across the population's main range.

The study included intensive sampling in the Tay estuary and adjacent waters in the summers of 2017, 2018 and 2019. This report includes a summary of these photo-identification survey trips conducted by the Sea Mammal Research Unit during this period. The data from these years have been added to the time-series of data collected since 1989 though a collaboration between the University of Aberdeen Lighthouse Field Station and SMRU to underpin analyses to meet the project aims.

6 Methods

6.1 Field surveys (2017-2019)

Photo-identification boat-based surveys were conducted in the Tay estuary and adjacent waters between May and September in 2017, 2018 and 2019. Surveys were done weekly, weather permitting, with the survey day of that week selected based on the weather and wind forecasts to ensure sea conditions between Beaufort 0 and 3, and dry days. Surveys were conducted from one of six different small boat platforms, depending on availability:

- A 7.4 m aluminium planing hull cruiser with 225 horse power (hp) outboard engine (SMRU);

- A 7.0 m aluminium hard collar rigid inflatable boat (RIB) with a jet engine (SMRU);
- A 10.0 m planing hull cabin RIB with 2 x 150 hp outboard engines (David Anderson Marine);
- A 12 m cabin RIB with 2 x 300 hp outboard engines (David Anderson Marine);
- A 6.0 m planing hull open RIB with a 100 hp outboard and an 8 hp auxiliary outboard (David Anderson Marine); or
- A 7.4 m planing hull open RIB with a 200 hp outboard engine (Pirate Boats).

Surveys were designed to maximise the chances of encountering bottlenose dolphins and obtaining high quality photographs. Depending on the tide and boat availability, surveys started from St Andrews, Newport-on-Tay or (occasionally) Broughty Ferry. From all starting locations, surveys generally covered the area between Newport-on-Tay out to the entrance of the Firth of Tay, and from there south to St Andrews and/or north to Arbroath. Some surveys extended further north to Lunan Bay and Montrose (see Figure 3 in section 7 for detailed tracks of the surveys). Surveys were conducted by at least two crew members: the skipper and the photographer, with additional observers on some trips.

For the duration of each trip, the boat position was recorded every minute using a Garmin eTrex GPS. When available onboard, a Garmin GPS Map 551s GPS/Plotter/Sounder was used as the primary source of positioning and depth data. Approximately every 15 minutes, the position of the boat, activity of the crew (i.e. searching for dolphins, in an encounter with dolphins, or off effort) and the weather conditions were manually logged into a paper survey effort data form. When animals were encountered, information on group size and the presence of new-born individuals and older calves was recorded, as well as the time, location, water depth and sea conditions on the Beaufort scale at the start and end of each encounter. All surveys were conducted under SNH licence no. 98465 to PSH.

6.2 Photo-Identification data processing (2017-2019)

Photo-identification data were collected using a Canon EOS 50D, Canon EOS 70D or a Canon EOS 7D, with a 70-200 mm f2.8 USM Canon lens. Standardised protocols taken from the long-running east coast of Scotland bottlenose dolphin research programme (Cheney et al. 2013) carried out by the University of Aberdeen Lighthouse Field Station (UoA) and SMRU at the University of St Andrews were used at all times. This ensured all data were standardised with and could be incorporated into the long running dataset for bottlenose dolphins on the east coast of Scotland managed by the UoA.

As per standardised protocols, each individual photographed dorsal fin was graded for photographic quality following criteria adapted from Wilson et al. (1999) (see Figure 9 in the Appendix). Individual dorsal fins were matched to the most current catalogue of known bottlenose dolphins off the east coast of Scotland. More information on this catalogue can be found on this UoA website. The best (quality grade 3) photographs from the right (R) and left (L) sides of each identified individual in each encounter were selected, and the individual IDs confirmed by a second experienced researcher.

6.3 Long-term photo-ID dataset (1989-2019)

Data collected in the Tay estuary and adjacent waters from 2017 - 2019 were integrated with recent data collected under the Moray Firth Marine Mammal Monitoring Programme (MMMP) (Graham et al. 2017) and incorporated into the long-term bottlenose dolphin research programme managed by UoA.

Survey effort to collect bottlenose dolphin photo-ID data for the long-term dataset focussed mainly on the summer season (May - September). Survey effort by the UoA has been consistent within the Moray Firth SAC since 1989, albeit with a change from a fixed route within the SAC during 1990 - 2000 to a more flexible survey route since 2001 to maximise sighting probability given changes in the distribution of animals in that area (Cheney et al. 2014). Since 2014, this work has been carried out under the MMMP developed to meet consent conditions for offshore windfarm developments in the region. Outside the Moray Firth SAC, surveys have been conducted in the Outer Moray Firth, along the Grampian coastline, in the Tay estuary and adjacent waters, and in the Firth of Forth (see Figure 1). In the Tay estuary and adjacent waters, data collection started in 1997 but was sporadic until the initiation of consistent survey effort in 2009. Survey effort in the Firth of Forth has been limited except in 2012 and 2013.

The long-term dataset is the basis of the analyses on survival and fecundity rates and on the movement of animals (see below). The survival estimation and movement analysis also include data collected during two PhD projects based at the University of St Andrews in 2003 – 2004, and 2006 - 2007. The estimation of abundance is based on data from 2009 - 2019 to encompass the time period with consistent survey effort in the two main study areas (Moray Firth SAC and the Tay estuary and adjacent waters).

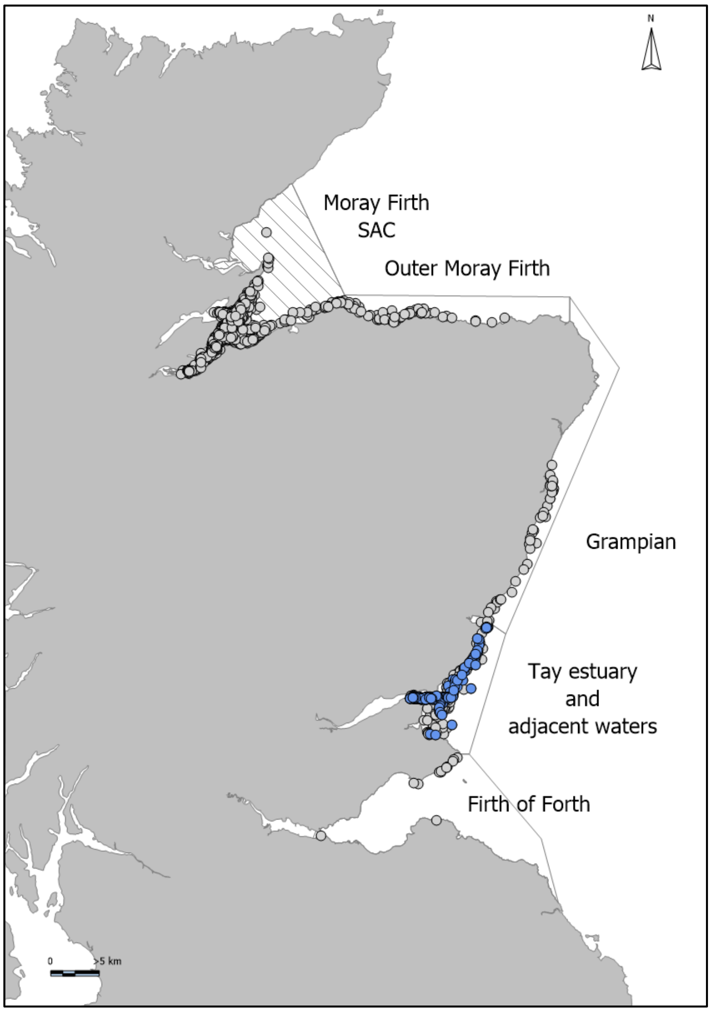

Figure 1. Main survey areas along the east coast of Scotland, from the Moray Firth SAC (hatched area) to the Firth of Forth. Locations of bottlenose dolphin encounters between 1990 and 2019 collected by UoA and SMRU are shown in grey, and those collected by SMRU between 2017 and 2019 in the frame of this project shown in blue.

6.4 Abundance estimation

We estimated the number of bottlenose dolphins using the Tay estuary and adjacent waters based on photo-ID data collected consistently between May and September in 2009-2019. We also estimated the size of the overall Scottish east coast population for the same time period; this analysis required all data collected by SMRU and UoA between the Moray Firth SAC and the Firth of Forth (Figure 1). These estimates update those published by Arso Civil et al. (2019b), which were based on the study period of 2009 to 2015. The analytical method follows that used in Arso Civil et al. (2019b) and is detailed below.

6.4.1 Model framework and fitting

Conventional mark-recapture models used to estimate abundance of animals from individual recognition (including photo-identification data) assume that all animals are available to be captured in each sampling occasion (Hammond 2010). This assumption is often violated because animals range outside the main surveyed areas and display variability in their movement patterns (Cheney et al. 2013). This can result in individuals being available for sampling on some occasions but not on others, a phenomenon known as temporary emigration (Kendall et al. 1997) which, if not accounted for, leads to bias in abundance estimates (Kendall 1999). We used so-called robust design models (Pollock 1982, Kendall et al. 1997, Kendall 1999) to model temporary emigration and produce unbiased estimates of abundance. Note that this same modelling framework was used to estimate survival rates (see section 6.5).

Under the robust design modelling framework, data were organized hierarchically into two levels: each annual field season represents a primary sampling occasion, and months within each year (May to September) constitute secondary sampling occasions. Closed population models were applied to data from secondary sampling occasions (months) within each year to derive estimates of capture probability p and population size N. Open population models were applied to data from primary sampling occasions (years) to estimate the probability of apparent survival (ϕ) and two temporary emigration probability parameters (γ'' and γ') between years. Apparent survival (henceforth referred to simply as survival) indicates that this incorporates permanent emigration as well as true survival, which cannot be distinguished from the data. The parameter γ'' represents the probability of temporarily emigrating outside the sampling area between years. The parameter γ' represents the probability of remaining outside the sampling area (i.e. remaining an emigrant); thus 1- γ' represents the probability of re-immigration. These probabilities were considered as either random, when the probability of emigrating does not depend on whether or not an animal was previously available (modelled as $\gamma'' = \gamma'$), or Markovian, when the probability of emigrating depends on whether or not an animal was previously available (modelled as $\gamma'' \neq \gamma'$).

Goodness-of-fit tests are not available for the robust design modelling framework. Instead, tests were run in program U-CARE (Choquet et al. 2009) using data from the primary (annual) sampling occasions to investigate if the key assumptions about the probability of capture (Lebreton et al. 1992) were met. U-CARE was also used to calculate the variance inflation factor, $\hat{c}$, which is indicative of over-dispersion in the data when $\hat{c} > 1$, and was used, if necessary, to adjust the model statistics and confidence intervals around the estimated parameters by inflating the estimated sampling variances.

Monthly capture histories were constructed for all marked individuals (i.e. with permanent marks on the dorsal fin such as nicks and notches) photographed with a quality grade 3 photograph. A candidate set of models was fitted to data for (a) the Tay estuary and adjacent waters, and (b) the whole population to determine which combination of model parameters best described each dataset. Survival probability was kept constant in all models. Capture and recapture probabilities were assumed to be equal because photo-identification does not involve handling of the animals and is not expected to cause any change in capture probability following first capture. Capture probabilities were allowed to vary: (a) between years and between months within each year, or (b) between years but not between months within each year. To explore whether models needed to account for individual variation in capture probabilities, which could lead to bias in the estimated parameters if not accounted for, Pledger (2000) mixture models were also fitted. In these models, the population was assumed to comprise a mixture of two groups of animals each with different probabilities of capture. Random and Markovian temporary emigration parameters were allowed to be constant or time (year) dependent, and models without temporary emigration ($\gamma'' = \gamma' = 0$) were also included for comparison.

Model selection was based on the Akaike Information Criterion (AIC; Akaike 1973) corrected for small sample size (Burnham and Anderson 2002) in the absence of over-dispersion ($\hat{c} < 1$), and on the quasi-AIC (QAIC) in the presence of over-dispersion ($\hat{c} > 1$). Models were constructed in the RMark package (Laake 2013) in R (R Core Team 2019), and fitted using MARK software (White and Burnham 1999).

6.4.2 Total abundance of animals

The resulting estimates of abundance from the robust design mark-recapture models refer only to the number of permanently marked animals in the population. To obtain the total number of animals (i.e. including marked and unmarked individuals), the estimates of abundance were inflated by the proportion of permanently marked individuals in the population (θ). This proportion was calculated for each trip by dividing the number of marked animals photographed by the total number of animals (marked and unmarked) photographed. This was done separately for each side of the dorsal fin because unmarked animals with only temporary marks (e.g. scars, skin lesions) may not be identified from both sides. The proportions from all trips were modelled using generalized linear models (GLMs) to obtain annual proportions of permanently marked animals for each dataset (i.e. the Tay estuary and adjacent waters, and the overall population).

The total number of animals $\hat{N}_{total}$ was calculated as:

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

with associated variance calculated using the delta method:

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

From this, 95% Confidence Intervals (CI) around the total number of animals were derived following Burnham et al. (1987), with the lower and upper limits calculated as $\hat{N}_{total}/C$ and $\hat{N}_{total} * C$, where C is calculated as:

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

6.5 Survival rates

Data collected by UoA and SMRU between 1989 and 2019 across the distributional range were used to estimate survival probabilities of juvenile/adult dolphins (i.e. non-calf individuals ≥ 4 years). Data were also included from two PhD projects based at the University of St Andrews which collected photo-ID data in the Tay estuary and adjacent waters in 2003 - 2004 (Quick 2006) and 2006 - 2007 (Islas-Villanueva 2009). Calves under the age of 4 years were excluded from the dataset, based on their year of birth (see section 6.6). Only those individuals with permanent marks on the dorsal fin (marked animals) were retained in the dataset. Capture histories were then constructed for all marked juvenile/adult individuals, based on whether or not they were captured in each month (May to September) between 1989 and 2019.

Models of survival probabilities (Pollock et al. 1990) rely on a number of assumptions regarding the probability of capture (Lebreton et al. 1992). One of these assumptions is that any emigration from the study area is permanent (Kendall et al. 1997); this is violated if so-called “transient” animals transiting through the area are captured once but are then unavailable for subsequent recapture (Pradel et al. 1997), or when there is temporary emigration. To allow this assumption to be relaxed, we applied the same robust design mark-recapture modelling framework that was used to estimate abundance.

Program U-CARE (Choquet et al. 2009) was used to estimate the over-dispersion factor ($\hat{c}$). Survival probability was set to be constant in all models to obtain an estimate of average survival for juveniles/adults over the whole time period. Capture probabilities were allowed to be constant or to vary by primary and/or secondary sampling occasion. Models with and without temporary emigration were fitted (both random and Markovian), and Pledger (2000) mixture models were included to account for heterogeneity in the capture probabilities. Additionally, and based on the results shown in Arso Civil et al. (2019a), a model was fitted to explore a trend in survival probability over the study period. Model selection was based on QAIC ($\hat{c} > 1$) (Burnham and Anderson 2002). Model structures were specified and run using RMark (Laake 2013) in R (R Core Team 2019) and program MARK (White and Burnham 1999).

6.6 Birth rates

Annual birth rates were estimated for the overall population following the method described by Arso Civil et al. (2017), which is summarized below. The data used were collected between 1989 and 2019 by UoA and SMRU and comprised the annual sighting histories of reproductive females and their reproductive histories, i.e. the year(s) in which they were known to have had a calf.

Sighting and reproductive histories for all known reproductive females (i.e. animals known to have calved at least in one year) were generated for the period 1989 to 2019. The data consisted of a string of 1s, 2s, and 0s to define whether, in each year, each female was (1) seen without a calf born that year (young of the year), (2) seen with a young of the year or (0) not seen. Mother-calf pairs were determined based on repeated observations of a calf with an adult individual in two or more trips. Young of the year were distinguished from older calves by their small size, coloration, prominent foetal folds and an almost constant association with an adult assumed to be the mother (see Figure 2). The year of birth could still be determined for calves first seen as one- and two-year olds, based on their relative size and foetal folds, which in this population can be visible at least during the first two years (Arso Civil et al. 2017). We assumed birth intervals <2 years were not possible, as they have never been observed in this population and are generally rare in bottlenose dolphins. With this assumption, females not seen in years before or after a known birth were assumed to be alive and without a young of the year, as long as the female was seen in subsequent years (Arso Civil et al. 2017).

Figure 2. Female #773 with her young of the year in 2012 which has the characteristic prominent foetal folds for that age, paler coloration and smaller size.

Birth rate, defined here as the annual probability of a reproductive female giving birth to a calf, was estimated based on conditional probabilities of birth; i.e. the probability that a female will give birth 1, 2 … *t* years after a previous birth. Following Arso Civil et al. (2017), the first step in analysis used a generalized linear mixed model framework to model these conditional probabilities of birth. This approach is appropriate when data contain repeated measures of individuals over time, so that one can account for variability to estimate the parameter of interest (in this case the population birth rate) over a period of time (e.g. Ward et al. 2009). The response variable took two possible values: 1 if a female was seen in a year with a young of the year, and 0 if a female was seen without a young of the year. Explanatory variables included the number of years since previous birth, included in models as a linear and/or as a quadratic term (to account for a possible non-linear relationship), and year and female ID, included as random effects. Models were fitted using the lme4 package (Bates et al. 2015) in R (R Core Team 2019), with a binomial error distribution and a logit link function (Bolker et al. 2009). The most supported model was selected as the one with the lowest AIC.

The second step obtained an expected mean inter-birth interval (IBI) for the population, i.e. the estimated number of years between consecutive calves in mature females in the population. The expected IBI was estimated from the probabilities of giving birth after 1, 2, …, *t* years, back-transformed from the most supported model coefficients (see Arso Civil et al. 2017 for details).

The third and final step was to estimate the annual birth rate as the reciprocal of the expected IBI. 95% confidence intervals (CI) around the estimated IBI and birth rate were generated using a parametric bootstrap (see Arso Civil et al. 2017 for details).

6.7 Animal movements

Estimates of population size, and survival and birth rates are most informative for conservation and management at regular intervals, for example annually. Mark-recapture studies therefore collect data at regular intervals suitable for analyses to estimate these quantities. Animal movements, however, need to be studied over shorter periods but data for analysis are not available at this finer time scale on a regular basis because the constraints of weather prevent surveys from occurring regularly. Methods for investigating animal movements that utilise data from capture occasions that are irregularly spaced in time do not currently exist.

In order to utilise the data available, i.e. irregular boat trips over several decades, to investigate individual-based movements between the Moray Firth SAC and the Tay estuary and adjacent waters, we developed a new method in which the capture histories of the individual dolphins are a realisation of a partially hidden Markov model in continuous time. Continuous time models are conceptually superior for dealing with irregularly spaced encounter histories but are mathematically more challenging than discrete-time models. This approach enables us to model traditional capture-recapture data, where an individual is documented as captured or not on each survey (boat trip), and allows us to use all the data available on every sighting of every individual from data that are fixed, but irregularly spaced, in time. It allows us to model the movement of individuals between the Moray Firth SAC and Tay estuary and adjacent waters at the resolution of a day, thus providing movement information per day of the year.

6.7.1 Data used in this study

Photo-identification data of individual dolphins beginning in 1990 in the Moray Firth SAC and 1997 in the Tay estuary and adjacent waters were used in this analysis. Any record of a dolphin sighted in either place was considered. The data frame included a column for each day between the first and last day of the entire dataset, i.e. from 13 January 1990 until 30 September 2019. This included a total of 10,853 potential capture occasions. All days were included and coded for effort as: 0 = no trips in either area, 1= a trip in the Moray Firth SAC, 2 = a trip in the Tay estuary and adjacent waters and 3 = trips in both areas on the same day. Sighting histories were then coded for each individual for each of the 10,853 days as: 0 = not sighted, 1 = sighted in the Moray Firth SAC and 2 = sighted in the Tay estuary and adjacent waters. In total, sighting histories of 855 individuals from a total of 1,236 boat trips (Moray Firth SAC: 1,017 trips; the Tay estuary and adjacent waters: 219 trips) were considered. The number of sightings per individual varied from 1 to 242.

Sex was assigned in three ways: 1. Based on photographs of the genital area; 2. Females were assigned based on association with calves; 3. Males were assigned based on long terms records when seen for longer than 10 years (as an adult) without a known association with a calf. Individuals of unknown sex could be included as a third category, but this can introduce bias in analysis because the more times an animal is observed the more chances there are to assign sex to that individual. As a result, sighting histories of individuals of unknown sex are generally shorter and lead to a greater probability (in the model – see below) of an individual dying. In the data, individuals of unknown sex were sighted much less than individuals of known sex (462 unknown sex individuals were sighted less than 6 times in total) and these individuals were thus excluded from analysis. This left 217 individuals (98 males and 119 females) in the analysis. For these individuals, the number of sightings ranged from 2 to 242 with a median of 46 sightings. Removing unknown sex individuals focussed analysis on differences between known sex individuals and ensured more robust results.

6.7.2 Modelling approach

A novel modelling approach was developed to assess movement patterns of male and female dolphins between the Moray Firth SAC and Tay estuary and adjacent waters. A hidden Markov model (HMM) allows inference of unobservable events or states underlying incomplete or indirect observations (Zucchini et al 2016). A HMM has two processes: one describes the data that are observed (the observation process), and the other describes the latent or hidden state (the state process) which is the process to be understood, for example, the location of a dolphin as determined by its movement behaviour. The two main assumptions are that the observations are reflective of the underlying state or behaviour and the state process fulfils the Markov condition of the probability of a state at time t depends only on the state at t-1. In this study, the individual dolphin sightings on survey trips are the observations, which reflect the animal's state, i.e. its location, defined as:

1 = seen in the Moray Firth SAC

2 = seen in the Tay estuary and adjacent waters

0 = not seen at all

A capture history for a single individual may thus appear as, for example:

Individual ID 746: 1001020011….

In this capture history, individual 746 was seen on four trips in the Moray Firth SAC, one trip in the Tay estuary and adjacent waters and not at all on five trips.

In the model, a dolphin is defined as being in one of three states (the state process):

1. In the Moray Firth SAC (represented as state 1);
2. In the Tay estuary and adjacent waters (represented as state 2);
3. Presumed dead (represented as state 3).

This HMM is termed partially hidden because the location of an observed dolphin is known (either in the Moray Firth SAC or in the Tay estuary and adjacent waters) so is not hidden, but when a dolphin is not observed its location is unknown, so it is hidden.

The irregularity of trips (capture occasions) over time requires the state process to be modelled using a continuous time Markov chain. To provide state-specific survey effort, information is included in the sighting histories of when all trips took place to calculate the time between capture occasions (Table 1).

Table 1. Example of a capture history with associated days since first capture

Capture history	1	0	0	1	0	2	0	0	1	1
Days since first capture	0	10	12	20	22	30	35	45	67	75

In the model, the state process is governed by a transition intensity matrix of the rates (Ra) at which animals transition between states (1 = Moray Firth SAC, 2 = the Tay estuary and adjacent waters). Ra_{11} = the rate at which individuals remain in state 1 (i.e. the Moray Firth SAC between two time periods). Ra_{12} = the rate at which individuals move between the Moray Firth SAC (state 1) and the Tay estuary and adjacent waters (state 2). Ra_{13} = the rate at which an animal transitions from state 1 (the Moray Firth SAC) to state 3 (presumed dead). The second row, Ra_{21}, Ra_{22} and Ra_{23}, describe the same rates for animals transitioning from state 2 (the Tay estuary and adjacent waters). The third row consists only of zeros because animals in state 3 (presumed dead) cannot transition back to the other states.

$$\begin{matrix} Ra_{11} & Ra_{12} & Ra_{13} \\ Ra_{21} & Ra_{22} & Ra_{23} \\ 0 & 0 & 0 \end{matrix}$$

The observation process is characterised by the state-specific recapture (or detection) probabilities, which are allowed to vary between the Moray Firth SAC and Tay estuary and adjacent waters, but are assumed to be constant over time. In particular, the probabilities of either observing a dolphin in one of the two areas or not observing a dolphin depend on the individual's state s_t at survey occasion t, which is only partially known, as well as the survey effort (i.e. whether a boat trip occurred in the area or not). For example, a dolphin is observed with probability p_1 or p_2 in the Moray Firth SAC and Tay estuary and adjacent waters, respectively, given that the area was searched while the dolphin was there. The probability that a dolphin is not observed, even though the area was searched, and the dolphin was there, is $1-p_1$ or $1-p_2$, respectively. The probability that a dolphin is not observed because it was not located in the searched area or because it is dead is 1.

To assess movement patterns over time we modelled the transition intensities between states (i.e. the rates at which animals moved between the Moray Firth SAC and the Tay estuary and adjacent waters) in relation to time of year (day) and sex (male or female). The model generates different transition intensities (movement rates) for each day of the year. Therefore, for any particular day we can calculate an expected mean sojourn time (i.e. the time spent in a state). If we choose the day with the highest transition intensity, we can calculate an expected mean sojourn time for this particular day as a lower boundary. For all the other days with lower transition (i.e. movement) intensities the mean sojourn time per day would be longer, as animals are transitioning less. We also included interactions between time of year and sex to model different movement patterns of males and females over time. Including sex as a covariate also enabled modelling of sex-specific apparent mortality rates (and hence apparent survival rates), as the transition into state 3 (presumed dead). We assumed that mortality rates were equal in the Moray Firth SAC and in the Tay estuary and adjacent waters and that they were constant over time.

Individual-specific state sequences given the encounter histories and the fitted model can be calculated to show survival status and spatial position throughout the observation period. Using the Viterbi algorithm (Forney 1973) it is possible to compute the most likely states for each individual dolphin, even during survey occasions when the individual was not observed. This approach supplements the encounter histories by inferring movements between sites even when an individual is rarely observed (i.e. when recapture probabilities are less than 50%) and can be used to look at longer individual movement across the whole temporal study period. Furthermore, the state sequence provides information on when a dolphin may have died (moved to state 3) or left an area.

Full model details are available in Mews et al. (in review) or at this arXiv website.

7 Results

7.1 Field surveys (2017-2019)

In total, 63 boat-based photo-identification trips were conducted between 2017 and 2019 in the Tay estuary and adjacent waters; 19 trips in 2017, 21 trips in 2018 and 23 trips in 2019. Boat tracks and location of encounters with bottlenose dolphins and other cetaceans are summarised for each year in Figure 33. During seven trips, sea conditions reached Beaufort 4 to 5 during search effort or during an encounter with dolphins, which made animals difficult to spot when on search effort, and/or difficult to spot and follow during an encounter, affecting the quality of the photographs taken (once in 2017, on four trips in 2018 and on two trips in 2019).

Bottlenose dolphins were encountered on 54 of the 63 trips in 157 separate encounters (Table 2). Most encounters occurred between Broughty Ferry and the Tay estuary, with fewer encounters in St Andrews Bay and north to Lunan Bay (Figure 3). Estimated group sizes during field observations ranged from 1 to 50 animals in the encountered groups, with an average group size of 11 animals (2017 = 16 animals, 2018 = 10 animals, 2019 = 8 animals). The exact locations and estimated group sizes are given in Table 5, Table 6, and Table 7 in the Appendix.

Harbour porpoise(s) were encountered on 42 separate occasions (2017 = 8, 2018 = 18, 2019 = 16), generally alone or in pairs, but in 2019 a group of approximately 20 individuals was observed in a single encounter. Minke whales were encountered on four occasions (2017 = 1, 2018 = 0, 2019 = 3), and an unidentified whale was seen on one occasion in 2018 (Figure 3).

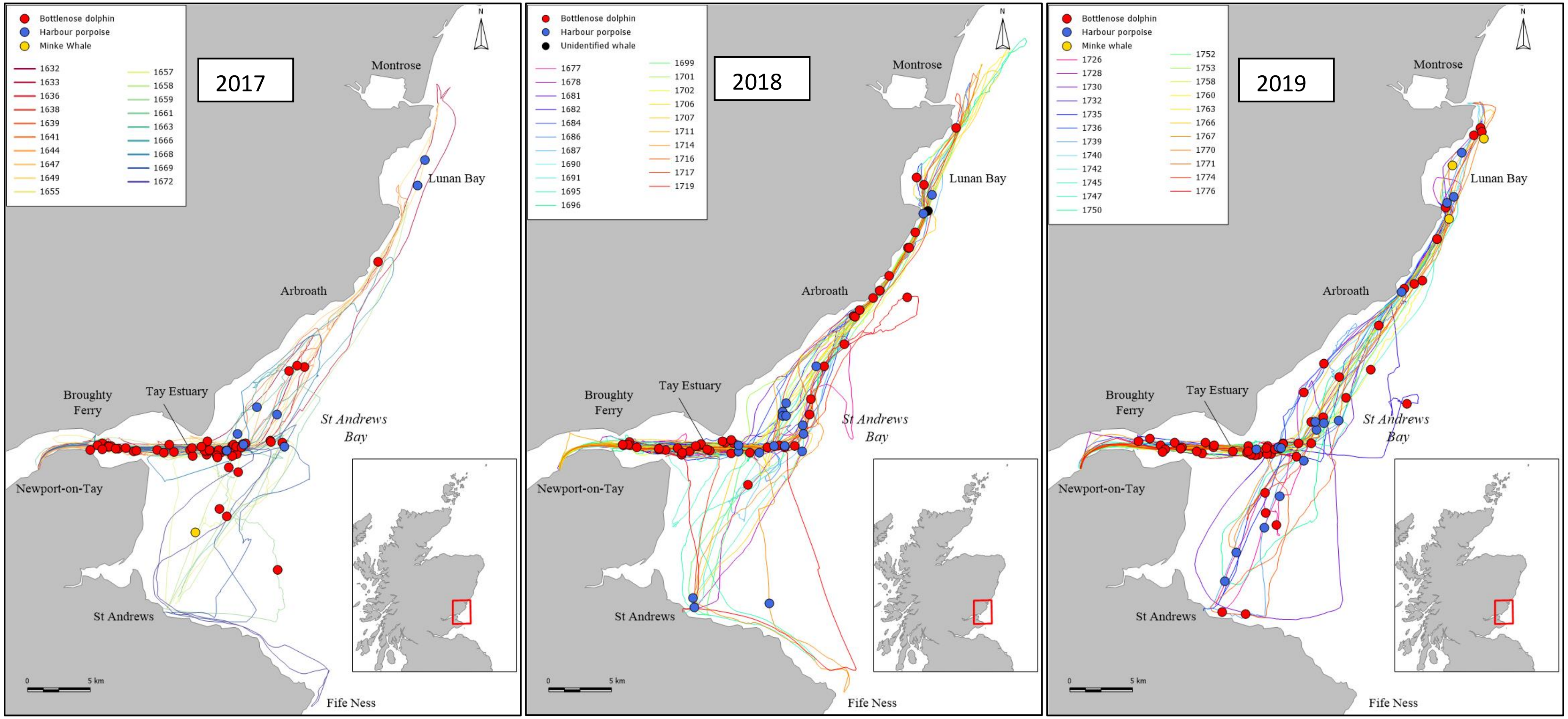

Figure 3 Survey effort in the Tay estuary and adjacent waters in 2017, 2018 and 2019 (lines coloured by trip) and bottlenose dolphin (red dots), harbour porpoise (blue dots), minke whale (yellow dots) and unidentified whale (black dot) encounters.

Table 2. Summary of survey time and encounters with bottlenose dolphins in the Tay estuary and adjacent waters.

Year	Trip #	Month	Date	Survey Time (hrs)	No. of Encounters	Time on encounters (hrs)	Group size (min-max)	Average group size
2017	1632	May	10-May-17	3.87	3	1.9	5-20	11
2017	1633	May	17-May-17	6.5	2	1.3	2-11	7
2017	1636	May	25-May-17	4.47	6	2.9	8-26	15
2017	1638	June	02-Jun-17	4.93	5	3.3	5-25	13
2017	1639	June	14-Jun-17	6.85	8	2.5	2-12	6
2017	1641	June	20-Jun-17	7.2	2	3.1	4-30	17
2017	1644	July	04-Jul-17	4.72	3	2.4	15-20	18
2017	1647	July	18-Jul-17	5.6	3	2.1	6-10	9
2017	1649	July	25-Jul-17	7.35	4	2.1	3-20	11
2017	1655	August	02-Aug-17	4.2	1	2.4	40	40
2017	1657	August	08-Aug-17	8.67	6	3.8	3-14	7
2017	1658	August	15-Aug-17	6.72	1	0.9	20	20
2017	1659	August	21-Aug-17	5.78	4	3.6	5-30	16
2017	1661	August	24-Aug-17	7.38	4	3.0	6-19	10
2017	1663	September	01-Sep-17	4.97	1	2.5	50	50
2017	1666	September	13-Sep-17	4.52	1	0.7	9	9
2017	1668	September	19-Sep-17	4.88	0	0	-	-
2017	1669	September	21-Sep-17	3.97	0	0	-	-
2017	1672	September	28-Sep-17	5.05	0	0	-	-
2018	1677	May	02-May-18	7.57	1	0.62	3	3
2018	1678	May	07-May-18	5.32	1	0.27	2	2
2018	1681	May	14-May-18	7.37	4	2.35	2-20	8
2018	1682	May	23-May-18	7.12	3	2.37	7-15	12

Year	Trip #	Month	Date	Survey Time (hrs)	No. of Encounters	Time on encounters (hrs)	Group size (min-max)	Average group size
2018	1684	May	28-May-18	6.75	2	2.40	5-18	11
2018	1686	June	07-Jun-18	8.30	3	2.22	4-20	10
2018	1687	June	11-Jun-18	5.78	1	0.97	14	14
2018	1690	June	22-Jun-18	5.57	3	2.55	5-15	9
2018	1691	June	25-Jun-18	6.25	3	2.27	2-20	9
2018	1695	July	04-Jul-18	7.12	1	1.57	25	25
2018	1696	July	10-Jul-18	7.65	4	3.63	4-40	13
2018	1699	July	18-Jul-18	7.38	0	0.00	-	-
2018	1701	July	19-Jul-18	4.95	3	2.52	8-15	10
2018	1702	July	24-Jul-18	7.35	5	3.08	1-24	8
2018	1706	August	03-Aug-18	8.10	3	2.58	9-15	12
2018	1707	August	07-Aug-18	8.20	1	0.20	3	3
2018	1711	August	20-Aug-18	6.88	2	1.10	5-12	8
2018	1714	August	30-Aug-18	7.27	2	0.82	1-7	4
2018	1716	September	04-Sept18	7.43	0	0.00	-	-
2018	1717	September	18-Sep-18	6.30	0	0.00	-	-
2018	1719	September	28-Sep-18	7.57	5	2.57	4-28	12
2019	1726	May	01-May-19	3.53	3	0.85	10-15	12
2019	1728	May	06-May-19	6.17	3	1.36	1-10	5
2019	1730	May	13-May-19	6.00	1	0.36	2	2
2019	1732	May	20-May-19	6.53	3	2.28	2-15	8
2019	1735	May	29-May-19	4.92	2	0.95	5-12	9
2019	1736	June	04-Jun-19	5.42	2	1.73	8-10	9
2019	1739	June	19-Jun-19	8.52	3	2.13	3-8	5
2019	1740	June	26-Jun-19	7.35	3	2.58	7-9	8

Year	Trip #	Month	Date	Survey Time (hrs)	No. of Encounters	Time on encounters (hrs)	Group size (min-max)	Average group size
2019	1742	July	08-Jul-19	4.03	3	2.40	3-20	12
2019	1745	July	15-Jul-19	5.23	3	1.81	6-11	9
2019	1747	July	19-Jul-19	5.35	2	1.03	5	5
2019	1750	July	26-Jul-19	7.70	3	1.03	4-6	5
2019	1752	August	01-Aug-19	2.47	2	0.70	1-2	1.5
2019	1753	August	02-Aug-19	3.73	4	1.96	3-16	7
2019	1758	August	08-Aug-19	7.65	5	2.56	1-40	14
2019	1760	August	12-Aug-19	7.33	5	2.01	5-15	9
2019	1763	August	20-Aug-19	6.57	0	0.00	-	-
2019	1766	August	26-Aug-19	4.68	1	0.08	1	1
2019	1767	August	27-Aug-19	3.58	5	1.26	1-15	9
2019	1770	September	10-Sep-19	5.30	0	0.00	-	-
2019	1771	September	18-Sep- 19	7.10	0	0.00	-	-
2019	1774	September	27-Sep-19	3.87	1	2.03	17	17
2019	1776	September	30-Sep-19	3.63	2	2.15	7-8	8
		Total	Year	Survey Time (hrs)	No. of Enc.	Time on Enc. (hrs)	Group size (min-max)	Average group size
			2017	100.23	54	35.88	2-50	16
			2018	146.2	47	34.07	1-40	10
			2019	126.67	56	31.33	1-40	8
		Total	2017-2019	373.10	157	101.28	1-50	11

7.2 Photo-identification data (2017-2019)

In total, 20,197 photographs (2017 = 5,052, 2018 = 7,802, 2019 = 7,343 photographs) were taken during encounters with bottlenose dolphins between 2017 and 2019 by SMRU in the Tay estuary and adjacent waters, each photograph containing one or multiple individual dorsal fins.

In total, 154 different individuals from all age classes were identified from good quality (Q3) photographs over the three-year survey period (2017 = 117 individuals from 1,675 photographs, 2018 = 105 individuals from 1,875 photographs, 2019 = 82 individuals from 1,105 photographs). These included 17 animals born during the period 2017 to 2019.

7.3 Abundance estimation (2009-2019)

In total, 383 photo-identification trips were conducted by SMRU and UoA between 2009 and 2019 across the population's main distributional range (Figure 1). Of these, 133 trips occurred in the Tay estuary and adjacent waters. Based on the good quality photographs, 151 marked individuals were included to estimate abundance, of which 105 individuals were seen in the Tay estuary and adjacent waters.

Goodness-of-fit tests revealed a small level of over-dispersion in the Tay estuary and adjacent waters dataset ($\hat{c} = 1.21$), as well as some evidence for trap-dependence (p-value = 0.03), confirming the need for models to incorporate temporary emigration and heterogeneity in capture probabilities. Consequently, model selection was based on QAIC and the inflation factor ($\hat{c}$) used to correct model outputs. The capture probability assumptions were met for the total population dataset, which showed no evidence of over-dispersion, and thus no correction was needed to the variances of the estimated parameters.

7.3.1 Number of dolphins in the Tay estuary and adjacent waters

Model selection favoured models incorporating Pledger (2000) heterogeneity mixture parameters over models without it. Out of 18 candidate models, the most supported model based on the lowest QAICc and representing 62% of the QAICc weight was a model with constant Markovian temporary emigration and time-varying capture probability. This model showed a low probability of temporarily emigrating γ'' of 0.09 (95% CI 0.05 - 0.15), and a probability of remaining an emigrant γ' of 0.41 (95% CI 0.19 - 0.68). The next most supported model, at ΔQAIC of 1.96 and thus receiving some support from the data, differed only in that the temporary emigration was modelled as random and produced a similarly low probability of emigrating of 0.10 (95% CI 0.06 - 0.16).

The estimated annual proportion of marked individuals in the Tay estuary and adjacent waters ranged between 0.47 (CV = 0.064) and 0.52 (CV = 0.051). Once scaled up by these estimated proportions of marked animals, and based on the most supported model, the estimated total number of bottlenose dolphins using the Tay estuary and adjacent waters in summer between 2009 and 2019 ranged from a minimum of 84 dolphins (95% CI 77 - 93) in 2011 to 138 dolphins (95% CI 110 - 173) in 2016 (see Table 3 and Figure 4). On average, the number of animals using this area represented 53.8% of the estimated total population using the main range between the Moray Firth SAC and the Firth of Forth (see next section).

7.3.2 East coast of Scotland population size

When using data across the main distributional range to estimate total population size, model selection also favoured models incorporating heterogeneity. The most supported model, accounting for 91% of the AICc weight, was a model with low constant random temporary emigration (0.012, 95% CI 0.002 - 0.062) and time-varying capture probability. The estimated annual proportion of marked animals in the overall population ranged from 0.44 (CV=0.03) to 0.55 (CV=0.02). Once scaled up by the estimated annual proportion of marked individuals, the estimated total number of animals using the population's main distributional range varied from 164 dolphins (95% CI 156 - 175) in 2009 to 243 dolphins (95% CI 214 - 277) in 2016 (see Table 3 and Figure 44).

Table 3. Annual estimates of abundance of animals using the overall study area (top) and the Tay estuary and adjacent waters (bottom), with associated precision. $\widehat{N}$: abundance of marked animals; CV: coefficient of variation; $\widehat{\theta}$: proportion of marked animals; $\widehat{N}_{total}$: total abundance of animals; CI: confidence interval; Percentage: percentage of the total estimated population using the Tay estuary and adjacent waters.

Year	$\widehat{N}$	CV ($\widehat{N}$)	$\widehat{\theta}$	CV ($\widehat{\theta}$)	$\widehat{N}_{total}$ (95% CI)	CV ($\widehat{N}_{total}$)	Percentage (%)
Overall study area							
2009	90	0.018	0.55	0.023	165 (156 – 175)	0.030	
2010	92	0.000	0.53	0.024	175 (167 – 183)	0.024	
2011	91	0.022	0.53	0.026	172 (161 – 184)	0.034	
2012	102	0.010	0.49	0.028	208 (196 – 220)	0.030	
2013	104	0.011	0.53	0.025	194 (184 – 205)	0.028	
2014	104	0.063	0.51	0.031	204 (179 – 234)	0.071	
2015	110	0.038	0.51	0.030	214 (195 – 234)	0.048	
2016	112	0.060	0.46	0.033	244 (214 – 277)	0.068	

Year	$\hat{N}$	CV ($\hat{N}$)	$\hat{\theta}$	CV ($\hat{\theta}$)	$\hat{N}_{total}$ (95% CI)	CV ($\hat{N}_{total}$)	Percentage (%)
2017	105	0.021	0.46	0.029	230 (215 – 247)	0.036	
2018	94	0.050	0.44	0.031	213 (190 – 238)	0.059	
2019	98	0.064	0.46	0.031	213 (186 – 244)	0.071	
Tay estuary and adjacent waters							
2009	47	0.063	0.52	0.051	91 (78 – 106)	0.081	55.2
2010	42	0.000	0.47	0.050	89 (81 – 98)	0.050	50.7
2011	42	0.000	0.50	0.049	85 (77 – 93)	0.049	49.1
2012	45	0.064	0.49	0.047	92 (79 – 107)	0.079	44.4
2013	48	0.107	0.48	0.058	101 (80 – 126)	0.122	51.9
2014	59	0.200	0.47	0.087	125 (85 – 184)	0.218	61.4
2015	62	0.070	0.52	0.068	120 (100 – 144)	0.098	56.2
2016	64	0.103	0.47	0.064	138 (110 – 173)	0.122	56.6
2017	65	0.069	0.49	0.045	132 (113 – 154)	0.083	57.2
2018	59	0.113	0.50	0.048	117 (94 – 147)	0.123	55.2
2019	57	0.134	0.50	0.056	114 (88 – 149)	0.145	53.7

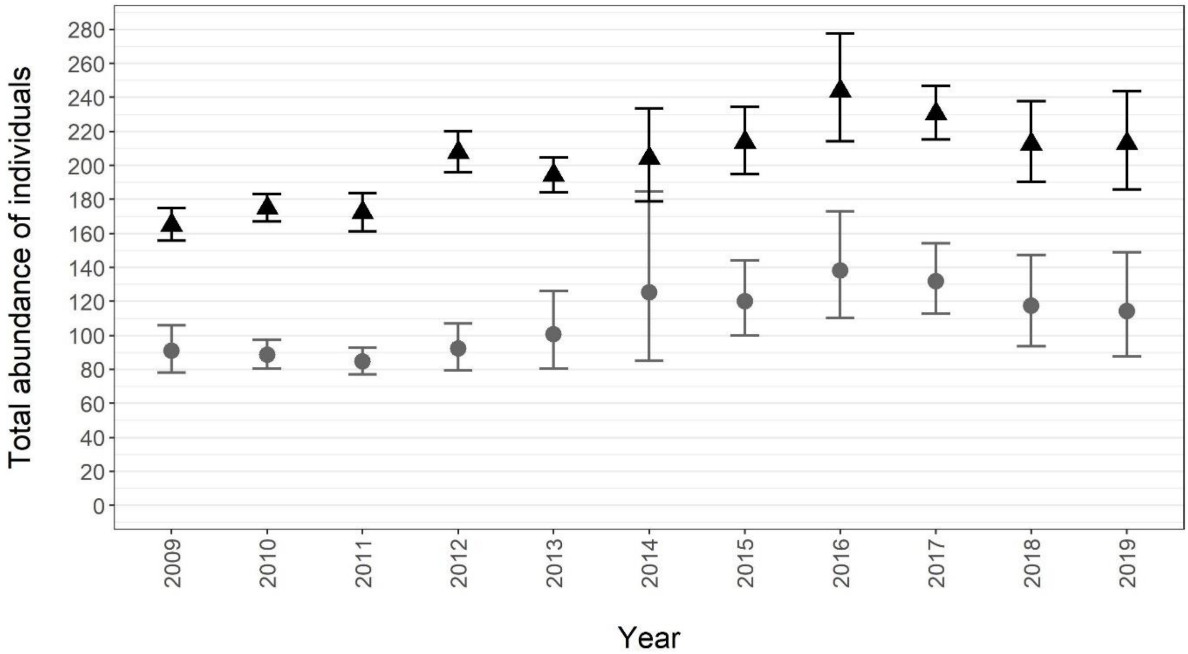

Figure 4. Total abundance of individuals using the Tay estuary and adjacent waters (grey dots) and the main distributional range (black triangles) with associated 95% CI.

7.4 Apparent survival rates

Between 1989 and 2019, a total of 230 juvenile/adult marked bottlenose dolphins were identified and included in the analysis to estimate apparent survival rate. This dataset showed a small level of over-dispersion ($\hat{c}$ = 1.55) and indication of trap-dependence and transience (p-value < 0.05). As with the models fitted to data from 2009 to 2019 to estimate abundance, models incorporating Pledger (2000) heterogeneity mixture parameters were favoured over those without it. The most supported model, representing 85% of the QAICc weight, had constant Markovian temporary emigration with a very low constant probability of emigrating, γ'', of 0.02 (0.01 - 0.04) and a high probability of remaining an emigrant γ' of 0.62 (0.36 - 0.82). Including a trend in the survival probability did not improve the model fit (ΔQAICc = 3.53) but accounted for the remaining QAICc weight. The estimated survival probability for juveniles/adults was 0.944 (95% CI 0.933 - 0.953) based on the most supported model.

7.5 Birth rates

Between 1989 and 2019, 105 females gave birth to a total of 248 identified calves, after removing two females that only calved in 2019. Four calves were first seen in 1989 (when photo-ID effort started) when aged 1 or 2 years. Each female gave birth to between 1 and 7 calves over the study period (mean = 2.36, SD = 1.4). The number of young of the year associated with females varied between 0 and 21 each year (mean = 8.12, SD = 6.22). This variation is likely to be partially caused by varying sampling effort because years with less effort will offer fewer opportunities to detect births. Additionally, some calves were recorded but could not be assigned to a particular female with enough confidence. Observed inter-birth intervals (IBI) ranged between 2 and 9 years (mean = 3.61, SD = 1.30, n =143).

The most supported model included linear and quadratic terms of the number of years since previous birth, and female identity and year as random effects. This model had an AIC score > 3 units compared to any other fitted model and was thus chosen to estimate the conditional probabilities of birth. Estimated conditional probabilities of birth increased from 1 to 5 years since previous birth and then decreased. Estimated IBI probability peaked at 4 years (Table 4). Based on these results, the expected IBI for the population was estimated at 3.95 years (95% CI 3.63 - 4.20 years), which results in an estimated annual birth rate per mature female of 0.253 (95% CI 0.238 - 0.275).

Table 4. Estimated conditional probability of birth 1, 2, ..., t YSPB and estimated probability of each observed IBI in the population. YSPB = years since previous birth; IBI = Inter-birth interval

YSPB	Conditional probability of birth	IBI (years)	Probability of IBI
1	0.012	1	0.012
2	0.081	2	0.080
3	0.276	3	0.251
4	0.497	4	0.327
5	0.605	5	0.200
6	0.585	6	0.076
7	0.438	7	0.024
8	0.204	8	0.006
9	0.048	9	0.001
		∑	0.976

7.6 Animal movements

The continuous time capture-recapture model showed a clear seasonal pattern in dolphin movements. Animals were estimated to have higher rates of movement (transition intensities) from the Tay estuary and adjacent waters to the Moray Firth SAC in early summer, and higher rates of movement from the Moray Firth SAC to the Tay estuary and adjacent waters in late summer (Figure 5). This pattern was consistent across individuals of both sexes, but males had higher movement rates than females on most days. These higher movement intensities translate to lower expected mean sojourn times (i.e. expected times remaining in state) for males on any given day compared to females. For example, females displayed expected sojourn times of 305 days in the Moray Firth SAC and 189 in the Tay estuary and adjacent waters compared to 207 days in the Moray Firth SAC and 138 days in the Tay estuary and adjacent waters for males. In general, our model indicates that there is no difference between the mortality rates of males and females with expected apparent survival times of about 25 years for both sexes.

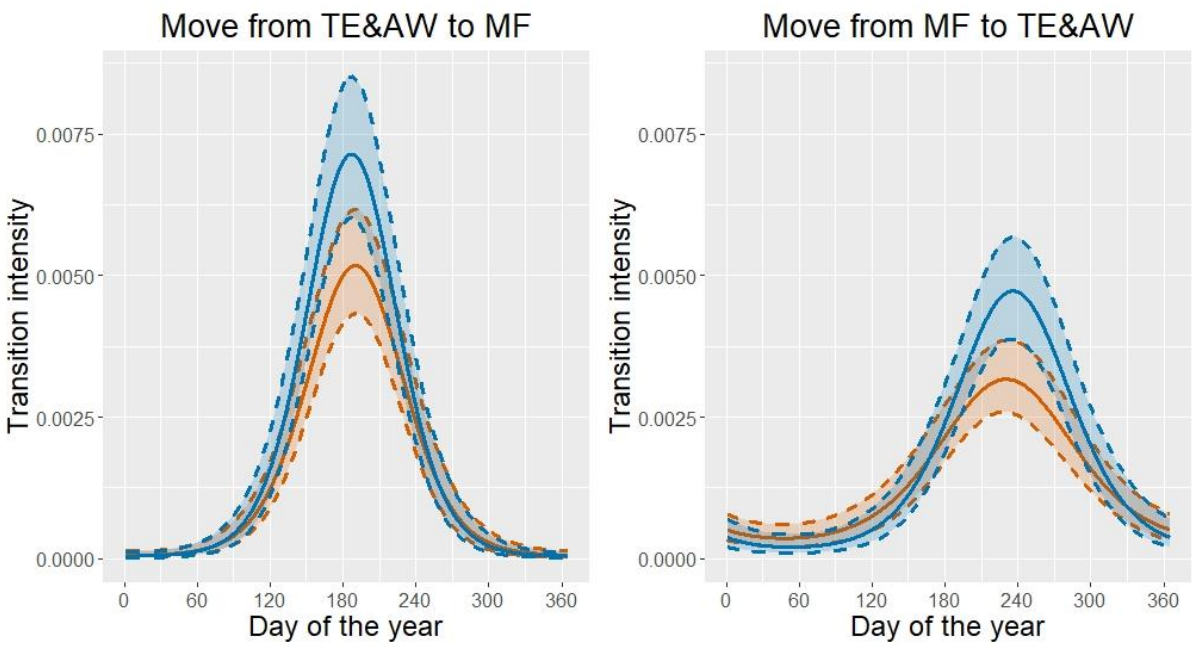

Figure 5. Estimated transition intensities (mean and 95% CI) as a function of the covariate day of the year. Left plot shows the transition intensities for moving from the Tay estuary and adjacent waters (TE&AW) to the Moray Firth SAC (MF) and right plot shows the intensities for moving from the Moray Firth SAC to the Tay estuary and adjacent waters. Blue is for male dolphins and orange for females. The large majority of the data are from May to September. Model-predicted intensities outside this period are therefore based on little information and results from October to April should be interpreted with caution.

7.6.1 Long-term versus short-term patterns

Individual-specific state sequences show the recaptures of an individual as well as the most likely state at times when an individual is not observed. This allows comparison of movement patterns over the course of this study (2017-2019) and over the longer-term dataset (1989-2019). An example of a state-specific sequence is shown in Figure 6, for female 932. This individual was captured in the Moray Firth SAC in July 2017 and 2018, but then transitioned to the Tay estuary and adjacent waters in late summer 2018. This individual is then predicted to have stayed in the Tay estuary and adjacent waters for the rest of 2018, until the end of the dataset. A matrix of individual dolphin sighting histories per area per year, coded for known sex of individual for 2017-2019 is shown in Table 8 in the Appendix. During these three years, 112 individuals were only seen in the Moray Firth SAC, 103 were only seen in the Tay estuary and adjacent waters and 51 were seen in both areas. Of the 51 seen in both areas, 40 were seen in both areas within the same year. Of the individuals of known sex, 11 males and 16 females were seen in both areas within the same year.

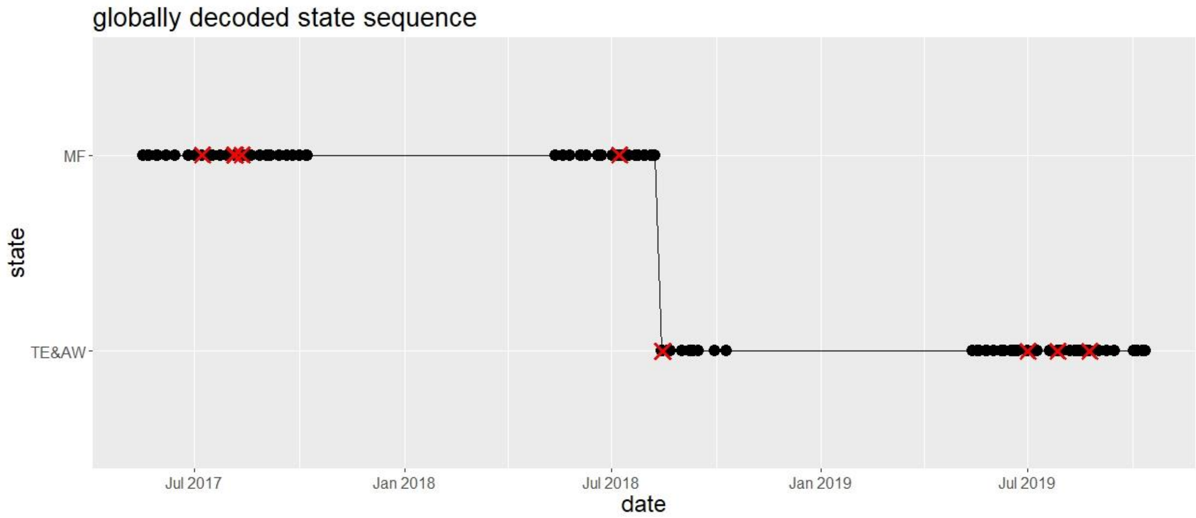

Figure 6. Example of an individually specific state sequence for female dolphin 932, showing the globally decoded states for the duration of this study 2017 - 2019. The red crosses indicate recapture of the dolphin. The black dots show likely state at times when the animal is not captured. MF = Moray Firth SAC and TE&AW = Tay estuary and adjacent waters

The individual state sequences provide an opportunity to compare how an individual moves between the two states over the entire course of their sighting history, and over the three years of this study. Figure 7 and 8 show the state allocation (i.e. likely area) for two well-known females (ID numbers 805 and 30) and two well-known males (1 and 908) during the three years of data collection for this project (2017-2019) and for the entirety of their sighting history. Females 805 and 30 (Figure 7) show multiple captures in both areas. A probability of 1 indicates the animal is predicted to be in the Tay estuary and adjacent waters, whilst a probability of zero indicates the animal is predicted to be in the Moray Firth SAC. Both females demonstrate less predicted movement over years than males 1 and 908 (Figure 8) and tend to show greater times in a state (area). The red crosses showing actual recaptures demonstrate how capture occasions are clustered over time and that individuals are usually captured in close temporal proximity when in one state (area). Male dolphin number 1 (Figure 8) is predicted to have had a higher probability of being in the Moray Firth SAC at the start of the dataset, but in the most recent three years (this study) has only been predicted to be in the Tay Estuary and adjacent waters. Individual 908 is predicted to have changed its movement pattern with most recent data predicting increased time in the Tay estuary and adjacent waters. Note that comparison of the patterns in predicted state probabilities of the different individuals in Figures 7 and 8 needs to take account of the lack of survey effort in the Tay estuary and adjacent waters prior to 2000 and differences in the period of each individual’s recapture history.

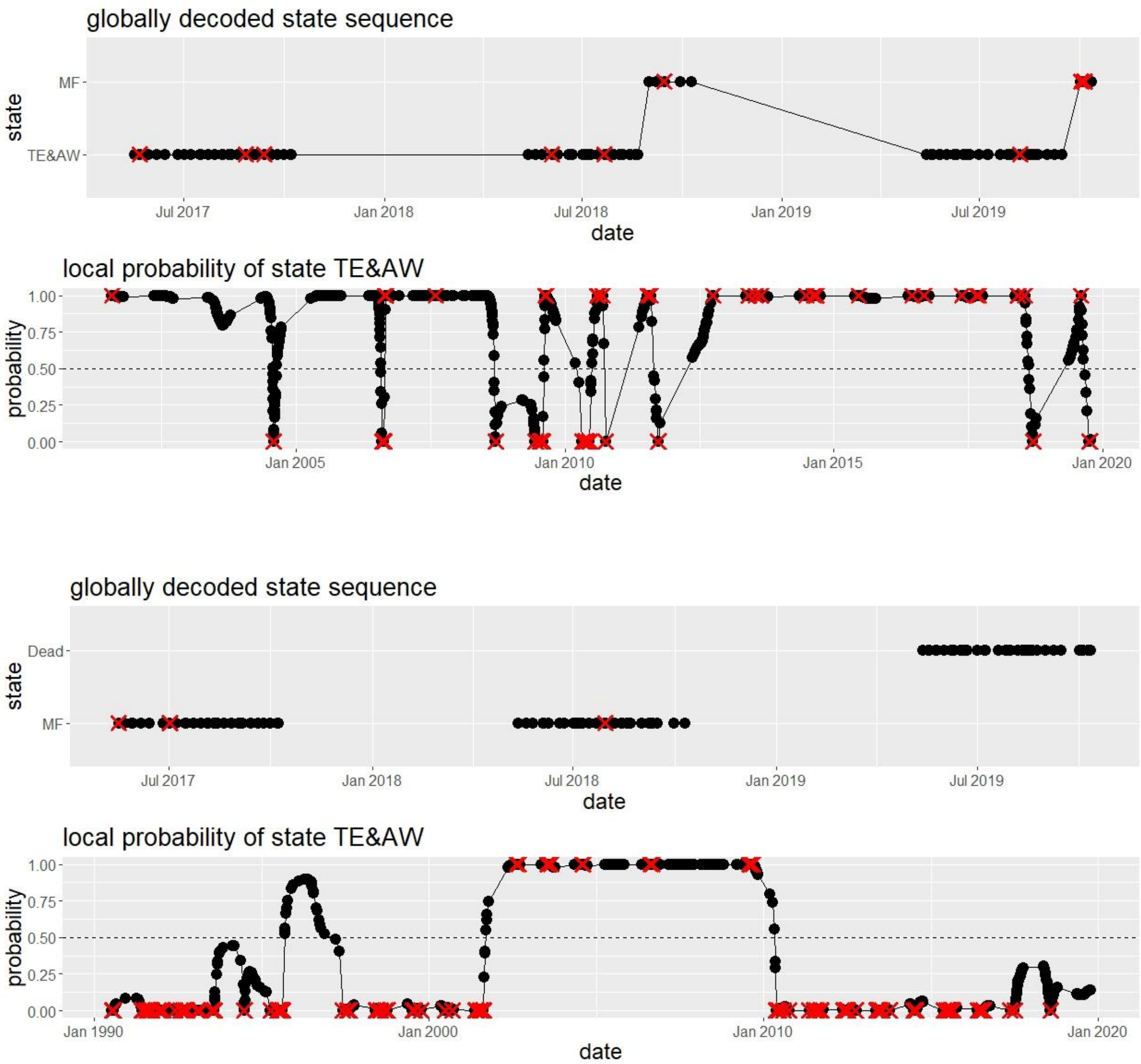

Figure 7. Females 805 (top two panels) and 30 (bottom two panels). Globally decoded state sequence shows the likely state (location) of the individual over the study period (2017-2019). Local probability of state shows the probability the individual is in the Tay estuary and adjacent waters from time of first sighting. A probability of one indicates the animal is predicted to be in the Tay estuary and adjacent waters, a probability of zero indicates the animal is predicted to be in the Moray Firth SAC. The red crosses indicate recapture of the dolphin. The black dots show likely state at times when animal is not captured.

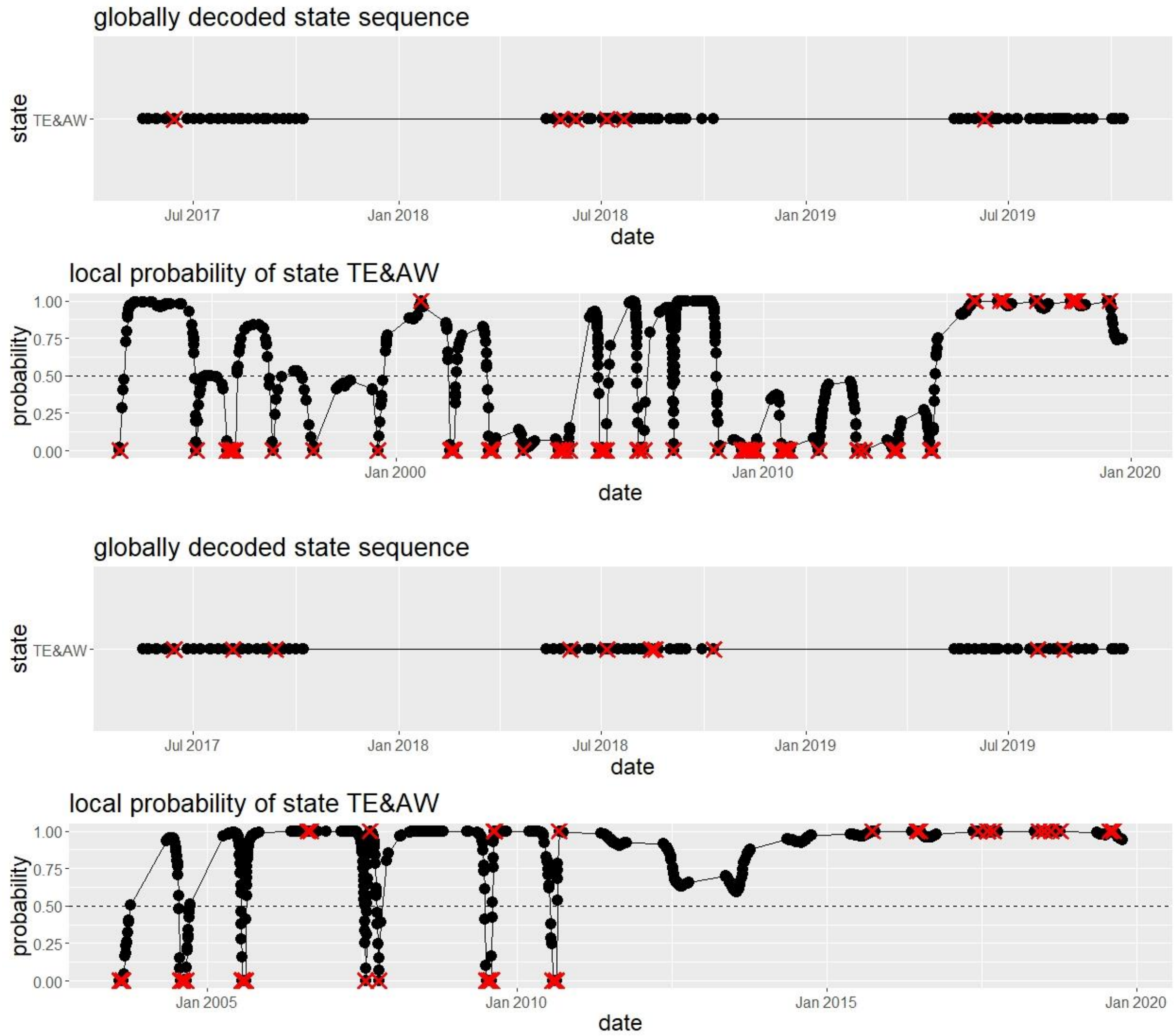

Figure 8. Males 1 (top two panels) and 908 (bottom two panels). Globally decoded state sequence shows the likely state (location) of the individual over the study period (2017-2019). Local probability of state shows the probability the individual is in the Tay estuary and adjacent waters from time of first sighting. A probability of one indicates the animal is predicted to be in the Tay estuary and adjacent waters, a probability of zero indicates the animal is predicted to be in the Moray Firth SAC. The red crosses indicate recapture of the dolphin. The black dots show likely state at times when animal is not captured.

8 Discussion

8.1 Abundance of animals

The number of animals estimated for the overall east coast of Scotland population varied among years but generally increased, from 165 (95% CI 156-175) animals in 2009 to 213 (95% CI 186-244) in 2019. This same trend was observed in the estimated number of animals using the Tay estuary and adjacent waters, which increased from 91 (95% CI 78-106) animals in 2009 to 114 (95% CI 88-149) animals in 2019. These increasing abundance estimates are in line with recent results by Arso Civil et al. (2019b) applied to a shorter time series (2009-2016), and by Cheney et al. (2018) for the overall population using data from 2001-2015 and a Bayesian state-space population model. The results thus continue to support an overall increase in population size, as previously indicated by Cheney et al. (2014).

This extended analysis of data shows that the area of the Tay estuary and adjacent waters continues to be used by more than half of the total estimated population every summer (53% on average). The number of animals estimated to be using this area has increased by around 4.3% per year ($p = 0.0052$) between 2009 and 2019, which is similar to the rate of increase for the period 2009-2016 (~5% annual increase; Arso Civil et al. 2019b). This supports the need to continue to obtain data from across the distributional range to effectively monitor the population (Arso Civil et al. 2019b).

The east coast of Scotland population of bottlenose dolphins has undergone a marked change in distribution since the early 1990s (Wilson et al. 2004, Arso Civil et al. 2019b) and photo-identification data show a highly mobile population across its distributional range. There is evidence of limited mixing of animals in the short term between distant areas within the range, but an overall high connectivity within the population (Cheney et al. 2013, Arso Civil et al. 2019b). As suggested by Arso Civil et al. (2019b), it is likely that changes in the distributional range are continuing with a further southern range expansion, given the increase in sightings of animals from this population south of the Firth of Forth. This highlights the need to increase knowledge of where and when animals are seen along the east coasts of Scotland and England to get a better understanding of their movements to inform their monitoring. Efforts are currently underway to increase photo-ID effort within the Firth of Forth as part of the regular monitoring of the population, as well as integrate any available photo-ID information from areas south of the Firth of Forth that are not regularly surveyed.

The number of individuals identified during surveys in the Tay estuary and adjacent waters declined from 117 individuals in 2017 to 82 individuals in 2019, and the abundance estimates for those years went from 132 (95% CI 113-154) to 114 (95% CI 88-149). This may simply be a result of inter-annual variation in the number of animals present in the area during the summer. However, it could also reflect a decrease in the number of animals using this area if part of the population is increasingly using other areas to the south. The continued collection of photo-ID data in the Tay estuary and adjacent waters, and an improved knowledge of which individuals are seen in other areas of the distributional range will help understand these variations in abundance of animals in different parts of the distributional range.

8.2 Survival rate

The addition of 2017-2019 data did not result in a significant change in survival rate of juveniles and adults (0.944, 95% CI 0.933-0.953) compared to that estimated by Arso Civil et al. (2019a) using data up to 2016 (0.948, 95% CI 0.933-0.959). This consistency in results is not surprising given only 3 years of data were added to the previous analysis of 27 years of data and there was no indication, based on the photo-identification data from across the distributional range, of a change in the number of identified animals that could have been indicative of a change in mortality rates. The time-invariant estimated survival rate translates into an annual mortality rate for juveniles and adults of 5.6% (95% CI 4.7%-6.7%) for this population. These rates are comparable to estimates of survival reported for the same age classes in other coastal bottlenose dolphin populations (e.g. Speakman et al. 2010, Nicholson et al. 2012, Smith et al. 2013).

Arso Civil et al. (2019b) found an increase in juvenile/adult annual survival over the study period between 1989 and 2016. Here we fitted a model with a trend in survival to investigate if it was still supported, but model selection instead favoured a model with a constant survival over time. The most supported model explained 85% of the AICc weight, while the model with a trend in survival explained 15% of the AICc weight. These percentages can be interpreted as the probability of each model to be the best description of the data, given a candidate set of models (Symonds and Moussalli 2011). This change in balance between a model with a positive trend and one without a trend is indicative of lower survival rates in recent years. This may be caused, at least in part, by the lower probability of sighting animals in the regularly monitored range, apparently because of an expansion of range to the south (see section 8.1). This reinforces the need to collect data across the whole range, and it is important to continue to study survival rates and how they may change in the future.

Information on demographic rates such as survival and birth rate (see below) is a key component in the assessment of conservation status and the impact that anthropogenic activities might have on populations of coastal cetaceans such as bottlenose dolphins. This updated estimate of survival helps understand how this population might be changing over time in response to changes in the environment.

8.3 Inter-birth interval and birth rate

The estimated inter-birth interval of 3.95 yr (95% CI 3.63-4.20 yr) is smaller than previously estimated with data up to 2012 only (4.49 yr, 95% CI = 3.94 - 4.93 yr for the period 1989 - 2012; Arso Civil et al. 2017). However, it is still larger than the observed average inter-birth intervals reported from the south coast of the Moray Firth, within this population's range (3.80 ± 1.4 yr; Robinson et al. 2017), and for common bottlenose dolphins in North Carolina, USA (2.9 yr, SD = 1.19 yr, range: 2–7 yr; Thayer 2007), and in Cardigan Bay, Wales (3.3 yr, range: 2–6 yr; Feingold and Evans 2013). The estimated inter-birth interval is, however, smaller than the observed mean inter-birth interval in Indo-Pacific bottlenose dolphins (*T. aduncus*) from Shark Bay, Australia (4.25 ± 0.10 yr; Karniski et al. 2018). These differences in reported observed inter-birth intervals between populations could reflect genuine differences in the reproductive histories of populations but are also likely to reflect common biases when using observed inter-birth intervals. Inter-birth intervals tend to be positively biased when births are missed if animals are not seen every year or if calves die before they are sighted, and negatively biased in shorter studies that do not allow for the observation of longer birth intervals (Barlow and Clapham 1997, Arso Civil et al. 2017).

The estimated annual birth rate for the period 1989 to 2019 of 0.253 (95% CI 0.238-0.275) is larger than previously estimated with data up to 2012 only (0.222, 95% CI = 0.218 - 0.253; Arso Civil et al. 2017), reflecting the difference in the estimated inter-birth intervals (see above). We do not know whether or not the difference in the new estimates reflect an increase in the birth rate of the population because the method used here did not explore temporal variation in reproductive rates. Previous estimates of birth rates for females sighted in the SAC are similar (0.23) but cannot be directly compared due to differences in the modelling approach used (Cheney et al. 2019). However, Cheney et al.'s (2019) analyses do provide evidence of an increase in birth rate within the SAC, from 0.16 (95% CI = 0.11-0.24) in 2001 to 0.28 (95% CI = 0.22-0.36) in 2016.

Including an additional seven years of reproductive data to an existing > 20 year dataset could have increased the accuracy (i.e. reduced bias) of the estimates in two ways. The longer dataset increases the probability of capturing longer inter-birth intervals, which could lead to an increase in estimated inter-birth interval and a decrease in birth rate. Conversely, the longer dataset extended the consistent survey effort in the Tay estuary and adjacent waters, which started in 2009, leading to increased capture probability compared to the early part of the time series; this could have decreased the overall proportion of missed births, thus leading to a decrease in estimated inter-birth interval and an increase in birth rate. In addition, the number of observed inter-birth intervals to which the model was fitted is larger and this increased the precision of the new estimates. Thus, the new estimates of inter-birth interval and annual birth rate are improvements over the previously published estimates (0.222, 95% CI = 0.218 - 0.253; Arso Civil et al. 2017).

8.4 Animal Movements

The results from the analysis suggest that movement between the two sites is infrequent, but that there is a seasonal movement pattern that is directional and consistent over years. This seasonal pattern was characterised by a higher intensity of movement from the Tay estuary and adjacent waters to the Moray Firth SAC in early summer, and from the Moray Firth SAC to the Tay estuary and adjacent waters in late summer.

During the three years of this study, 51 individuals were seen in both areas with 40 individuals seen in both areas within the same year. However, 112 individuals were only seen in the Moray Firth SAC and 103 were only seen in the Tay estuary and adjacent waters during these three years . Despite this clear individual heterogeneity, pooling all the data collected over 10,853 days did reveal a seasonal pattern, suggesting a general trend in movement. However, this pattern is not followed consistently every year by every individual. This may mean that there are differences among individual dolphins or sub-groups of dolphins within the population in how they utilise areas over different temporal scales.

Heterogeneity in individual ranging behaviour is well-documented for this species (Wilson et al. 2004, Arso Civil et al. 2019b), but it is unclear what drives the movement of different individuals. This seasonal pattern of a higher intensity of movement from the Tay estuary and adjacent waters to the Moray Firth SAC in early summer months, and from the Moray Firth SAC to the Tay estuary and adjacent waters in late summer could be driven by environmental and biological factors. It has been shown that these two areas share topographically distinct characteristics with increased observations of dolphins foraging (Wilson et al 1997, Hastie et al 2004). Seasonal changes in prey presence over variable temporal scales throughout the year may therefore enable dolphins to exploit these areas within their range at different times. Understanding fluctuations in prey availability in both areas over years may also help to understand why some individuals move some years and not others.

Social bonds and connections to close associates may also determine how animals move between locations. Stable male or female alliances have not been documented in this population, unlike populations in other areas (Connor et al 2000, Smolker et al 1992, Wells 1991), and it is unclear whether male and female dolphins move individually or as part of a group. Further information on the social structure of this population would help delineate socially driven movements and to determine whether individuals that were commonly associated in one area were similarly associated in the other area.

Although both sexes followed the seasonal pattern, males on average stayed for a shorter time (sojourn time) in both locations, (207 days compared to 305 for females in the Moray Firth SAC and 138 days compared to 189 for females in the Tay estuary and adjacent waters) making more frequent movements between sites. These differences in sojourn times between sexes may suggest that the two locations are important in different ways for different sexes. Males exhibiting more frequent movements is a common pattern in many mammals (Greenwood 1980). This pattern may aid avoidance of inbreeding, which is an important driver for sex differences in dispersal (Greenwood 1980), and is also consistent with other bottlenose dolphin populations in Sarasota Bay, Florida and Shark Bay, Western Australia. In these populations, both sexes are philopatric (Smolker et al. 1992, Connor et al. 2000) but demonstrate high fission-fusion dynamics where group composition changes frequently and individuals demonstrate variation in ranging patterns over a wider resident area (Smolker et al. 1992, Wells 1991). These differences in movement between sexes support the results from the study by Quick et al (2014).

Individual-specific state sequences and probability of occurrence in the Tay estuary and adjacent waters highlight the heterogeneity in individual movement patterns and also show how movement between locations is infrequent. Computing the most likely states for individuals, even at times when they are not captured, provides extra utility to the data set. Two well-known females (number 30 and 805) that were the focus of an individual analysis had periods when their sojourn time was extended in the Tay estuary and adjacent waters: in 2013-2017 for individual 805 and in 2002-2009 for individual 30. In contrast, the two male dolphins (numbers 1 and 908) that were the focus of an individual analysis appear to show more frequent movement between the two sites. Although all four individuals were seen in both areas at some point in their sighting history, assessment of only three years of data (2017-2019) shows that state allocation over a three-year time scale is not truly representative of the longer-term individual movement patterns exhibited by these individuals and highlights the need for long-term data collection on these long-lived mobile mammals.

Distance between the two locations is large (400km) and the investment to move from one area to the other may be dependent on many factors, including individual health status, resource availability and social structure. The implications of these large-scale movements include potential differences in the levels of exposure to disturbance from marine developments. As males move between sites more frequently, they have an increased risk of exposure to any disturbance events occurring along the coast. There are also potential implications for increased levels of disturbance in areas of transit between the two sites at different times of year, although animals appear to be moving up and down the coast throughout the summer. Our conclusions about movement patterns only relate to those months when data collection occurs in both areas (May-September). Understanding movement patterns for the months of October through April is a big data gap for this population and may show further differences in how individuals utilise different areas.

The continuous time formulation used in this analysis (Mews et al., in review) provides a more conceptually appealing approach than that used by Quick et al (2014), because this reflects the movement of animals in continuous time. The models presented here can accommodate different temporal scales and irregular sampling, and are thus more applicable than previous models, but they are technically more challenging to apply. The modelling also presented here highlights the need for methods development to answer applied research questions on disturbance using existing long-term datasets.

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11 Copyright

12 Appendix

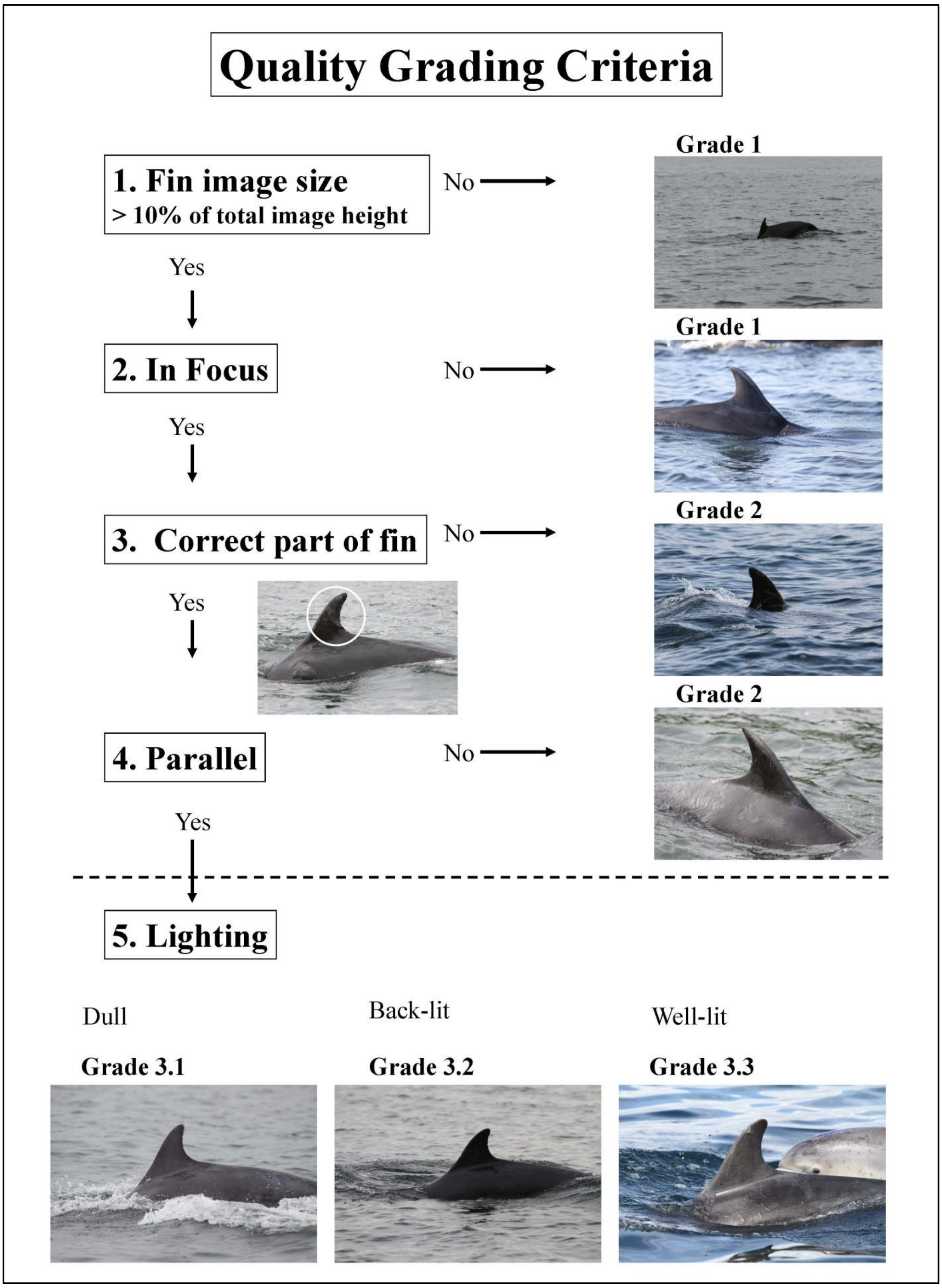

Figure 9. Criteria for grading pictures based on photographic quality, Cheney et al (2012), adapted from Wilson et al. (1999)

Table 5. Location, date and number of bottlenose dolphin individuals encountered per group in summer 2017 in the Tay estuary and adjacent waters.

Location					
Latitude	Longitude	Date	Trip	Encounter	Number of individuals
56.45492	-2.85567	10/05/2017	1632	3810	8
56.51097	-2.62153	10/05/2017	1632	3811	5
56.45311	-2.79163	10/05/2017	1632	3812	20
56.45677	-2.69473	17/05/2017	1633	3813	2
56.45549	-2.72953	17/05/2017	1633	3814	11
56.45759	-2.86328	25/05/2017	1636	3832	12
56.45562	-2.85533	25/05/2017	1636	3833	8
56.45553	-2.85138	25/05/2017	1636	3834	11
56.45372	-2.84199	25/05/2017	1636	3835	10
56.45216	-2.82166	25/05/2017	1636	3836	22
56.45709	-2.77647	25/05/2017	1636	3837	26
56.45159	-2.71628	02/06/2017	1638	3842	12
56.45169	-2.70894	02/06/2017	1638	3843	18
56.45386	-2.71213	02/06/2017	1638	3844	7
56.4547	-2.6927	02/06/2017	1638	3445	25
56.45328	-2.74952	02/06/2017	1638	3446	5
56.45767	-2.69279	14/06/2017	1639	3847	12
56.45003	-2.72751	14/06/2017	1639	3848	2
56.44972	-2.71416	14/06/2017	1639	3849	5
56.45075	-2.68856	14/06/2017	1639	3850	5
56.44953	-2.69472	14/06/2017	1639	3851	6
56.45613	-2.68947	14/06/2017	1639	3852	4
56.45794	-2.68101	14/06/2017	1639	3853	3
56.45499	-2.85459	14/06/2017	1639	3854	10
56.5136	-2.60179	20/06/2017	1641	3866	30
56.58948	-2.50746	20/06/2017	1641	3867	4
56.45583	-2.8691	04/07/2017	1644	3884	15
56.4518	-2.77018	04/07/2017	1644	3885	20
56.45275	-2.72771	04/07/2017	1644	3886	20
56.45272	-2.81887	18/07/2017	1647	3896	6
56.45871	-2.67718	18/07/2017	1647	3897	10
56.45987	-2.72668	18/07/2017	1647	3898	10
56.45306	-2.70268	25/07/2017	1649	3912	12
56.45328	-2.72973	25/07/2017	1649	3913	3
56.45379	-2.72438	25/07/2017	1649	3914	7
56.4541	-2.83279	25/07/2017	1649	3915	20
56.45916	-2.62992	02/08/2017	1655	3937	40
56.43782	-2.68614	08/08/2017	1657	3946	14
56.45598	-2.73448	08/08/2017	1657	3947	7
56.44915	-2.74567	08/08/2017	1657	3948	3

Location					
Latitude	Longitude	Date	Trip	Encounter	Number of individuals
56.45111	-2.78301	08/08/2017	1657	3949	6
56.45486	-2.7468	08/08/2017	1657	3950	5
56.45319	-2.8626	08/08/2017	1657	3951	9
56.45588	-2.68276	15/08/2017	1658	3952	20
56.44819	-2.71353	21/08/2017	1659	3953	30
56.41123	-2.70989	21/08/2017	1659	3954	5
56.40621	-2.70066	21/08/2017	1659	3955	20
56.36812	-2.63444	21/08/2017	1659	3956	8
56.4608	-2.64498	24/08/2017	1661	3959	19
56.45977	-2.64392	24/08/2017	1661	3960	6
56.4524	-2.87856	24/08/2017	1661	3961	9
56.4536	-2.84563	24/08/2017	1661	3962	7
56.44102	-2.69882	01/09/2017	1663	3964	50
56.51488	-2.61107	13/09/2017	1666	3974	9

Table 6. Location, date and number of bottlenose dolphin individuals encountered per group in 2018 in the Tay estuary and adjacent waters.

Location					
Latitude	Longitude	Date	Trip	Encounter	Number of individuals
56.45834	-2.85508	02/05/2018	1677	3994	3
56.45136	-2.72309	07/05/2018	1678	3995	2
56.45299	-2.80875	14/05/2018	1681	4006	6
56.55050	-2.56587	14/05/2018	1681	4007	2
56.57958	-2.52056	14/05/2018	1681	4008	20
56.54981	-2.56452	14/05/2018	1681	4009	5
56.45330	-2.81740	23/05/2018	1682	4010	7
56.56329	-2.54119	23/05/2018	1682	4011	15
56.59977	-2.49662	23/05/2018	1682	4012	15
56.45606	-2.76504	28/05/2018	1684	4018	5
56.64505	-2.47638	28/05/2018	1684	4019	18
56.45895	-2.73139	07/06/2018	1686	4023	7
56.45562	-2.67705	07/06/2018	1686	4024	20
56.45198	-2.69905	07/06/2018	1686	4025	4
56.42889	-2.70087	11/06/2018	1687	4026	14
56.45609	-2.86325	22/06/2018	1690	4041	8
56.44962	-2.78757	22/06/2018	1690	4042	15
56.56898	-2.53228	22/06/2018	1690	4043	5
56.45461	-2.79248	25/06/2018	1691	4044	2
56.45385	-2.81693	25/06/2018	1691	4045	20
56.45250	-2.77724	25/06/2018	1691	4046	5
56.45838	-2.71963	04/07/2018	1695	4056	25
56.45617	-2.85459	10/07/2018	1696	4057	4

Location					
Latitude	Longitude	Date	Trip	Encounter	Number of individuals
56.45751	-2.76218	10/07/2018	1696	4058	5
56.61084	-2.48678	10/07/2018	1696	4059	5
56.64997	-2.48599	10/07/2018	1696	4060	40
56.45450	-2.84576	19/07/2018	1701	4078	15
56.55470	-2.55885	19/07/2018	1701	4079	8
56.45128	-2.78701	19/07/2018	1701	4080	8
56.45668	-2.85702	24/07/2018	1702	4081	5
56.45606	-2.76912	24/07/2018	1702	4082	3
56.45953	-2.73498	24/07/2018	1702	4083	1
56.59965	-2.49508	24/07/2018	1702	4084	24
56.46083	-2.72342	24/07/2018	1702	4085	7
56.56894	-2.53244	03/08/2018	1706	5002	9
56.68564	-2.43463	03/08/2018	1706	5003	15
56.45666	-2.86377	03/08/2018	1706	5004	12
56.45288	-2.75156	07/08/2018	1707	5005	3
56.45369	-2.75500	20/08/2018	1711	5012	12
56.45720	-2.66148	20/08/2018	1711	5013	5
56.45580	-2.65441	30/08/2018	1714	5025	7
56.49080	-2.62083	30/08/2018	1714	5026	1
56.45690	-2.64128	28/09/2018	1719	5035	7
56.47954	-2.62227	28/09/2018	1719	5036	28
56.51406	-2.60404	28/09/2018	1719	5037	4
56.53020	-2.57775	28/09/2018	1719	5038	8
56.56404	-2.49660	28/09/2018	1719	5039	12

Table 7. Location, date and number of bottlenose dolphin individuals encountered per group in 2019 in the Tay estuary and adjacent waters.

Location					
Latitude	Longitude	Date	Trip	Encounter	Number of individuals
56.42294	-2.70605	01/05/2019	1726	5046	10
56.40873	-2.70502	01/05/2019	1726	5047	10
56.39988	-2.69105	01/05/2019	1726	5048	15
56.44930	-2.66578	06/05/2019	1728	5055	10
56.51598	-2.63163	06/05/2019	1728	5056	1
56.45839	-2.68356	06/05/2019	1728	5057	5
56.45890	-2.64669	13/05/2019	1730	5061	2
56.48793	-2.52318	20/05/2019	1732	5066	2
56.60603	-2.48539	20/05/2019	1732	5067	6
56.45613	-2.84186	20/05/2019	1732	5068	15
56.62893	-2.47494	29/05/2019	1735	5072	12
56.49538	-2.65725	29/05/2019	1735	5073	5
56.54378	-2.56091	04/06/2019	1736	5074	8
56.57368	-2.51472	04/06/2019	1736	5075	10

Location					
Latitude	Longitude	Date	Trip	Encounter	Number of individuals
56.33720	-2.75996	19/06/2019	1739	5090	3
56.33595	-2.72998	19/06/2019	1739	5091	3
56.50656	-2.61130	19/06/2019	1739	5092	8
56.68594	-2.42988	26/06/2019	1740	5093	9
56.68089	-2.43871	26/06/2019	1740	5094	8
56.60610	-2.48543	26/06/2019	1740	5095	7
56.45509	-2.77310	08/07/2019	1742	5102	3
56.45262	-2.72780	08/07/2019	1742	5103	20
56.45810	-2.82384	08/07/2019	1742	5104	12
56.45887	-2.87083	15/07/2019	1745	5110	6
56.47745	-2.63158	15/07/2019	1745	5111	11
56.45486	-2.81398	15/07/2019	1745	5112	9
56.03928	-2.67187	19/07/2019	1747	5117	5
56.45467	-2.68783	19/07/2019	1747	5118	5
56.45058	-2.78774	26/07/2019	1750	5126	6
56.45157	-2.72964	26/07/2019	1750	5127	5
56.45643	-2.72807	26/07/2019	1750	5128	4
56.45033	-2.71538	01/08/2019	1752	5140	2
56.45653	-2.70294	01/08/2019	1752	5141	1
56.45078	-2.69889	02/08/2019	1753	5142	16
56.44993	-2.71930	02/08/2019	1753	5143	3
56.45087	-2.70426	02/08/2019	1753	5144	3
56.45030	-2.72498	02/08/2019	1753	5145	5
56.45235	-2.74811	08/08/2019	1758	5151	1
56.49164	-2.60227	08/08/2019	1758	5152	2
56.57040	-2.52790	08/08/2019	1758	5153	3
56.47441	-2.64721	08/08/2019	1758	5154	25
56.45430	-2.69339	08/08/2019	1758	5155	40
56.45258	-2.72822	12/08/2019	1760	5158	5
56.57623	-2.50452	12/08/2019	1760	5159	10
56.51200	-2.57001	12/08/2019	1760	5160	8
56.45348	-2.83612	12/08/2019	1760	5161	8
56.45415	-2.81578	12/08/2019	1760	5162	15
56.68321	-2.42804	26/08/2019	1766	5167	1
56.45836	-2.78362	27/08/2019	1767	5168	15
56.45130	-2.83976	27/08/2019	1767	5169	4
56.46081	-2.85640	27/08/2019	1767	5170	11
56.45649	-2.77300	27/08/2019	1767	5171	1
56.45210	-2.79535	27/08/2019	1767	5172	15
56.45818	-2.68365	27/09/2019	1774	5184	17
56.45509	-2.70488	30/09/2019	1776	5192	7
56.45894	-2.66326	30/09/2019	1776	5193	8

Table 8. Matrix of sighting histories per year for all three years of the study. MF = Moray Firth SAC; TE&AW = Tay estuary and adjacent waters. Grey shading shows individual present in that area for that year. Yellow shading shows individuals only seen in the Tay estuary and adjacent waters, green shows individual only seen in the Moray Firth SAC and blue shows individuals seen in both areas during this study. Presumed M refer to individuals seen for at least 10 years as an adult without a calf so are assumed to be male and used in the analysis.

Dolphin ID	2017		2018		2019		Sex
	MF	TE&AW	MF	TE&AW	MF	TE&AW	
1							Presumed M
11							F
23							M
30							F
31							F
52							F
102							M
105							M
240							F
344							F
430							F
433							F
440							F
571							F
573							M
578							F
580							F
732							F
744							F
745							F
748							M
760							M
769							M
773							F
800							F
805							F
809							F
815							M
816							F
817							M
820							F
832							F
856							Presumed M
866							F
872							F
880							F
881							M
882							M
886							M
901							M
904							M
907							M
908							M
909							F
913							F
914							M
932							F
963							F
964							M
965							F

Dolphin ID	2017		2018		2019		Sex
	MF	TE&AW	MF	TE&AW	MF	TE&AW	
969							F
970							Presumed M
972							M
973							F
985							F
989							M
990							M
991							F
992							Presumed M
993							Presumed M
997							Presumed M
999							Presumed M
1000							Unknown
1002							F
1006							F
1007							M
1011							Unknown
1012							Unknown
1015							F
1016							F
1018							F
1020							F
1022							M
1023							F
1024							F
1025							M
1026							F
1027							F
1028							F
1029							F
1030							F
1031							Unknown
1032							F
1033							M
1036							Unknown
1037							M
1038							Presumed M
1039							Unknown
1040							Presumed M
1042							M
1043							F
1047							M
1048							Unknown
1049							M
1050							Unknown
1051							Unknown
1052							Unknown
1053							Unknown
1055							Presumed M
1056							F
1060							F
1061							Presumed M
1062							F
1063							Presumed M
1064							F
1065							Unknown

Dolphin ID	2017		2018		2019		Sex
	MF	TE&AW	MF	TE&AW	MF	TE&AW	
1068							F
1069							F
1070							Unknown
1073							F
1074							Presumed M
1075							F
1076							F
1077							M
1079							M
1084							F
1086							F
1087							Unknown
1089							Unknown
1091							M
1092							F
1093							Presumed M
1095							Presumed M
1097							Unknown
1098							Unknown
1099							Unknown
1100							F
1101							F
1102							Unknown
1103							Unknown
1104							Unknown
1105							Unknown
1108							Unknown
1109							F
1110							F
1113							M
1114							Unknown
1115							Unknown
1116							Unknown
1117							Unknown
1118							F
1119							Unknown
1120							Unknown
1121							Unknown
1124							Unknown
1125							Unknown
1126							F
1128							F
1129							M
1130							F
1132							M
1134							F
1135							Unknown
1137							M
1140							Unknown
1141							M
1143							F
1144							Unknown
1147							Unknown
1153							Unknown
1159							Unknown
1160							Unknown

Dolphin ID	2017		2018		2019		Sex
	MF	TE&AW	MF	TE&AW	MF	TE&AW	
1164							Unknown
1167							Unknown
1168							Unknown
1172							Unknown
1174							Unknown
1175							Unknown
1176							Unknown
1177							Unknown
1178							Unknown
1179							Unknown
1180							Unknown
1181							Unknown
1182							F
1183							Unknown
1184							Unknown
1185							Unknown
1186							M
1187							M
1189							Unknown
1190							Unknown
1191							Unknown
1192							Unknown
1193							Unknown
1194							Unknown
1195							Unknown
1196							M
1197							Unknown
1198							Unknown
1200							Unknown
1201							M
1202							F
1203							Unknown
1205							Unknown
1206							Unknown
1208							Unknown
1209							Unknown
1211							Unknown
1212							Unknown
1213							Unknown
1215							M
1216							Unknown
1217							Unknown
1221							Unknown
1222							Unknown
1223							Unknown
1224							Unknown
1225							Unknown
1226							Unknown
1227							Unknown
1229							Unknown
1230							Unknown
1231							Unknown
1232							Unknown
1233							Unknown
1234							Unknown
1235							Unknown

Dolphin ID	2017		2018		2019		Sex
	MF	TE&AW	MF	TE&AW	MF	TE&AW	
1236							Unknown
1237							Unknown
1238							Unknown
1239							Unknown
1240							Unknown
1241							M
1242							Unknown
1243							Unknown
1244							Unknown
1245							Unknown
1246							M
1247							Unknown
1248							F
1249							M
1250							Unknown
1251							Unknown
1252							Unknown
1253							Unknown
1254							Unknown
1255							Unknown
1256							Unknown
1257							Unknown
1258							Unknown
1259							Unknown
1261							Unknown
1262							Unknown
1263							Unknown
1264							Unknown
1265							Unknown
1268							Unknown
1269							Unknown
1270							Unknown
1271							Unknown
1272							Unknown
1273							Unknown
1274							Unknown
1275							Unknown
1277							Unknown
1278							Unknown
1279							Unknown
1280							Unknown
1281							Unknown
1282							Unknown
1283							Unknown
1284							Unknown
1285							Unknown
1286							Unknown
1287							Unknown