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Improving estimates of seabird body-mass survival rates

Scottish Marine and Freshwater Science Vol 11 No 13

F Daunt, Z Fang, R Howells, M Harris, S Wanless, K Searle and D Elston

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Improving estimates of seabird body-mass survival relationships
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Executive summary

- The Scottish Government has set a target of 100% of Scottish demand for electricity to be met by renewable sources by 2020. Offshore renewables have the potential to make a significant contribution to achieving this target. However, the Scottish Government has a duty to ensure that offshore renewable developments (ORDs) are achieved in a sustainable manner, by protecting habitats and species from adverse impacts.
- ORDs may negatively affect seabirds, in particular due to collisions with turbine blades, displacement to less favourable habitats and barrier effects to movement. Many so-called 'sub-lethal effects', whereby individuals birds are not killed instantaneously by an interaction with the wind farm, but behaviour is affected in the short term, may have knock on effects on energetic budgets and, in turn, demographic rates such as survival and productivity.
- A key potential process linking sub-lethal effects of ORDs and demography is the relationship between adult body condition at the end of the breeding season and survival probability the following winter. However, our understanding of this relationship is limited. To date only two empirical studies have quantified this relationship in the key seabird species that the Scottish Government are tasked with protecting, one on Atlantic puffins *Fratercula arctica* (hereafter "puffin") in northern Norway and one on black-legged kittiwakes *Rissa tridactyla* (hereafter "kittiwake") in Shetland. There is a concern that the relationships derived in these studies may not reflect the situation in key regions of Scotland for ORDs, notably the Forth/Tay region.
- Accordingly, the objective of this project was to use local data to estimate the relationship between mass at the end of breeding season and over-wintering survival probability for four key species in the Forth/Tay region: kittiwake, puffin, common guillemot *Uria aalge* (hereafter "guillemot") and razorbill *Alca torda*. To our knowledge, this is the most comprehensive study of its kind in terms of a) the size of data sets used (both the sample sizes of birds and years covered for each species) and b) the complexity of modelling undertaken.
- We formatted and pre-processed five data sets for survival analysis, two obtained using a capture-recapture protocol (puffins and kittiwakes) and three using capture-resightings (guillemots, razorbills and a subset of kittiwakes). Data were collected as part of the UK Centre for Ecology & Hydrology’s (hereafter “UKCEH”) long-term study of seabird populations on the Isle of May National Nature Reserve in the Forth Islands SPA, a Key Site in the Seabird Monitoring Programme.
- For each species, we developed linked statistical models for mass and body size, and used these to predict body mass at the end of the breeding season each year, taking account of varying breeding phenologies of species across

years by using data on median laying dates. We then developed statistical models for the recapture/resighting histories of each bird, making allowance for variation in recapture/resighting rates to estimate the probabilities of birds in the breeding population surviving from the end of one breeding season to the start of the next. These survival probabilities were modelled as a function of individual-specific body mass at the end of the preceding breeding season, the latter being imputed from the model of mass.

- Our models were contingent on a number of assumptions of the type usually adopted in analyses of similar data sets. Estimates of survival probabilities of kittiwakes based on recaptures were markedly lower than those derived from mark/resighting data suggesting that they were unreliable. Accordingly, we used the latter data set that enabled us to obtain more biologically plausible estimates of survival rates.
- Sample sizes of birds and span of years were as follows: kittiwake: 498 (1997-2018); puffin: 2,043 (1973-1985); guillemot: 341 (1982-2018); razorbill: 93 (1982-2018).
- For each species, parameters, missing values and other unknowns were estimated using Markov chain Monte Carlo methods in a Bayesian hierarchical framework with mildly informative priors using the statistical package OpenBugs.
- For puffins, we found evidence for a strongly positive relationship between individual-specific body mass at the end of the breeding season and the probability of survival to the start of the next breeding season. In contrast, in kittiwakes, guillemots and razorbills, the posterior mean estimated effect sizes were considerably smaller. For puffins, the 95% credible interval for the model coefficient relating survival to mass did not contain zero. In the case of the other species even 50% credible intervals contained zero which can be considered as analogous to statistical non-significance, in that there is no strong statistical evidence about the qualitative (positive or negative) nature of the relationship between survival and body mass. Whilst this lack of evidence about the qualitative nature of a relationship may be taken as evidence to ignore the relationship altogether by setting the regression coefficient of mass in the model of survival to zero, in risk based decision situations it may be more appropriate to consider all parameter values defining the modelled effect of mass on survival which have adequate support from the data. In particular, this would mean considering the mass-survival relationships as defined by the limits of the credible intervals formed from the appropriate posterior distributions.
- Differences in the relative sizes and natures of data sets available affected our ability to estimate effects reliably. Relative to the data set for puffins, a particular limitation in the data set for kittiwakes was the high variability in observed mass from day to day for the same bird in the same year, whilst for guillemots and razorbills the main limitation was the low numbers of birds with repeated mass observations.

- Our results on puffins give mass-survival effects somewhat smaller than in a previous study on the effects of mass on survival undertaken on a population in Norway, and our results on kittiwakes were substantially different to those estimated in a previous study undertaken on a Shetland population. However, comparison is challenging because of the differences in methods adopted.
- In conclusion, using the best available UK data and employing advanced methods of statistical analysis, we found evidence for a positive relationship between end-of-breeding season body mass and the survival of puffins with less evidence of an effect in kittiwakes, guillemots and razorbills. We consider these estimates more suitable for use, especially in a UK context, than relationships estimated from other studies. In ORD assessments, however, caution should still be applied. One issue is that effects of mass on survival may be masked by the exclusion of adult non-breeders from the analyses. Furthermore, sub-lethal effects of ORDs may be apparent on other demographic rates, such as productivity and immature survival. A future research priority is therefore to quantify sub-lethal effects on all key demographic rates so that a comprehensive assessment of population-level impacts can be made. In the context of ORDs, this entails achieving accurate estimates of the effects of sub-lethal effects such as displacement and barrier effects on energetics and knock-on effects on demography.

1 Introduction

The Scottish Government has set a target of 100% of Scottish demand for electricity to be met by renewable sources by 2020. The marine environment offers considerable potential with respect to harvesting renewable energy, through wind, wave and tidal stream energy generators. Offshore renewables have the potential to make a significant contribution to the Scottish Government’s target for the equivalent of 100% of Scotland’s gross annual electricity consumption to be met from onshore and offshore renewables by 2020. However, the Scottish Government has a duty to ensure that offshore renewable developments (ORDs) are achieved in a sustainable manner, by protecting the natural environment from adverse impacts in accordance with the requirements of the Marine Strategy Framework Directive (EC/2008/56), the Habitats Directive (EC/92/43) and the Birds Directive (EC/79/409).

Crucially, offshore renewable developments (ORDs) may affect seabirds from collisions with turbine blades, displacement to less favourable habitats, barrier effects to movement, disturbance during construction and operation, contamination, noise and indirect effects via impact of developments on seabird prey (Drewitt & Langston 2006; Larsen & Guillemette 2007; Masden et al. 2010; Grecian et al. 2010, Langton et al. 2011, Scottish Government 2011). These potential effects are particularly important for breeding seabirds that, as central place foragers, are constrained to obtain food within a certain distance from the breeding colony (Daunt et al. 2002; Enstipp et al 2006; Thaxter et al. 2012). Seabirds breed in internationally important numbers in Scotland, and many colonies are designated as Special Protection Areas under the EU Birds Directive. Habitat Regulation Appraisals and Strategic Environmental Assessments require assessment of the potential impact of any planned development on interest features of SPAs, such as an adverse effect on protected marine bird populations.

Many of these effects are so-called ‘sub-lethal effects’, whereby individuals birds are not killed instantaneously by an interaction with the wind farm (as is generally considered to be the case with collisions), but behaviour is affected in the short term in ways that can have knock on effects on, in turn, energetic budgets, demographic rates (including survival) and population size. The two sub-lethal effects of principal concern in assessments of ORDs are displacement and barrier effects. To date, a range of approaches have been used to quantify impacts, including a displacement matrix approach which assumes a certain proportion of individual birds die (Joint SNCB 2017) and Individual-based models (Searle et al. 2014; 2018). The latter approaches are the most sophisticated with the greatest potential for approximating reality. They are highly flexible allowing incorporation of complex baseline behaviours and changes in behaviour resulting from an offshore development. However, where these models rely on input data obtained from different locations, there is a concern that estimates of changes in demographic rates may not be accurate. Ensuring evidence is based on the most of up to date and geographically relevant data will improve the licensing and consenting decision making process. As such, analyses should be prioritised on local data sets where they exist.

To date, assessments have focussed on three main demographic processes that may be affected by displacement and barrier effects, mediated by changes in energetic budgets of adult birds:

(a) increased probability of chick mortality, either from starvation or from higher unattendance rates of adults, leading to higher predation risk or exposure to conspecific attack and severe weather

(b) increased reduction in adult body condition during the breeding season, leading to a higher probability of adult mortality by the end of the breeding season

(c) increased reduction in adult body condition by the end of the breeding season, leading to a higher probability of mortality in the following winter.

The aim of this project is to focus on this third process, using individual-specific variations in body mass as the measure of body condition. Of the two potential sources of adult mortality arising from sub-lethal effects outlined above, (c) is considered the most important because, although a decline in body condition during the breeding season is normal in seabirds (Golet & Irons 1999), adult mortality during the breeding season arising from this process is considered to be extremely rare. We expect that body condition at the end of the breeding season is a key determinant of whether birds are able to cope with the decline in food availability, shortened day length and adverse weather conditions that occur in winter (Daunt et al 2006; Fig 1).

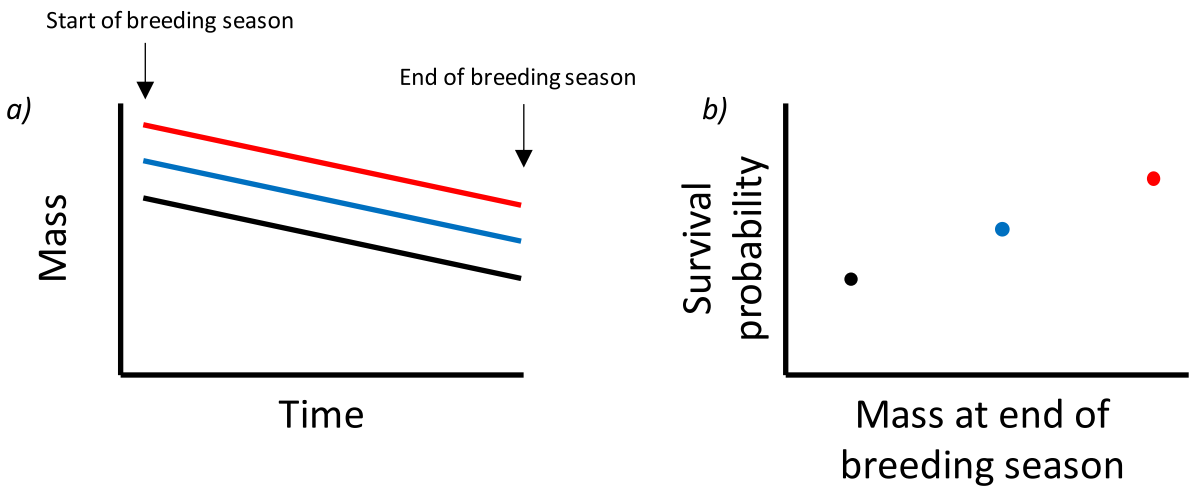

Figure 1: Schematic of a) declining body condition during the breeding season of three individuals that end the breeding season at different body masses, as typically occurs in seabirds (Golet & Irons 1999); and b) the relationship between mass at the end of the breeding season and over-winter survival probability. Individuals that are in poorer condition at the end of the breeding season (black line in a)) are expected to have lower survival probability the following winter (black dot in b); Oro & Furness 2002; Erikstad et al. 2009).

The most comprehensive assessments of the population-level consequences of displacement and barrier effects on chick and adult survival has been undertaken by Searle et al. (2014, 2018). This analysis focussed on the kittiwake, puffin, guillemot and razorbill, the four species that are the focus of this project, in the Forth/Tay region. In these assessments, relationships between adult body condition and over-wintering survival were derived from equations available in the literature for kittiwakes (Oro & Furness 2002) and puffins (Erikstad et al. 2009). However, the kittiwake study was undertaken on a population in Shetland experiencing variable and in some years low food abundance. The puffin study was based on a population in northern Norway, where trophic interactions are different and puffins are markedly larger than those in UK populations. Thus, both populations may have differed in terms of adult body mass and relationships between condition and survival from populations in the Forth/Tay region, or the UK as a whole. Published mass/survival relationships do not exist for razorbill or guillemot, so for these species Searle et al. (2014, 2018) used estimates for puffin taken from Erikstad et al. (2009). However, as well as being from a different oceanographic region, mass/survival relationships in guillemots and razorbills may differ from puffins.

In keeping with the objective to undertake assessments of displacement and barrier effects, the goal of this project was to collate and analyse existing empirical data on body mass and survival of kittiwakes, puffins, guillemots and razorbills breeding on the Isle of May National Nature Reserve, part of the Forth Islands Special Protection Area. These data have been collected by CEH since the 1970s on the Isle of May National Nature Reserve, a Key Site in the Seabird Monitoring Programme. Our approach involved fitting a range of models to mass and survival data for each species to quantify the effect of mass on survival rates.

2 Data

This section describes the data collection methods and processing to produce the final data set for analyses; the analyses are then described in Section 3.

2.1 Data collection methods

All data were collected on the Isle of May National Nature Reserve, where CEH has been undertaking a long-term study of seabirds since the 1970s.

2.1.1 Kittiwake

Since the 1980s, adult kittiwakes have been captured at the nest using a nylon noose attached to the end of an 8 m telescopic pole from pre-laying to late chick-rearing (with most captures occurring between early incubation and mid chick-rearing). The date was recorded and birds were ringed with a numbered hard metal ring, or the ring number recorded in cases where a captured bird was already ringed. Each bird was weighed to the nearest 1g, and in a proportion of cases standard wing chord and the combined head and bill length were also taken.

At the outset of the project, we considered this the most appropriate data set for quantifying the relationship between body mass and survival because the sample size of body mass data was large particularly during the period 1997-2018. Also, some birds regurgitate during handling, and from 1997 each regurgitate was collected and subsequently weighed back at the lab to ± 0.1 g using a digital balance. Thus, focussing on the period from 1997 allowed us the option to exclude regurgitates from the estimate of body mass in such cases to obtain a more accurate estimate of mass.

However, detailed inspection of the data set revealed two important issues which presented problems for investigating mass/survival relationships. Firstly, none of the birds had been sexed using molecular techniques and relatively few had been measured to enable sexing on morphological criteria. Thus, overall the proportion of birds of known sex was very low (2.5%). This was a potentially significant issue because kittiwakes are sexually size dimorphic (males larger and heavier than females; Jodice et al. 2000). Therefore any modelled effect of mass on survival ignoring sex would necessarily imply differential survival probabilities between the sexes. Secondly, the recapture technique used meant that only birds within 8 m of the catcher were available for recapture and even birds moving only a few metres to a new site were inaccessible. Thus recapture probability was very low resulting in many birds only being captured once. Consequently, preliminary analyses of this data set produced unrealistically low estimates of adult survival rates (c. 70% in contrast to values of around 85% that had previously been estimated for Isle of May kittiwakes; Frederiksen et al. 2004b). Based on these findings the capture/recapture data set for kittiwakes was considered to be unreliable for determining mass/survival relationships in the Isle of May kittiwake breeding population.

Effort was therefore focussed on an alternative data set based on intensive mark-resighting observations. For this data set birds were again caught with an 8 m pole but in addition to a hard metal numbered ring were also given a unique three colour ring combination. Kittiwakes were first marked in this way on the Isle of May in 1986. In each subsequent year, additional birds have been marked to maintain a marked population of 100-200 individuals. From 1987 onwards, multiple visual checks of breeding sub-colonies where the colour-ringed birds were located have been made from before laying until the end of the season, to find birds that have returned to the colony. This observational method produces a high resighting probability (see Section 4) because of the high fidelity to the local breeding area, meaning that if an individual was not observed for several years the likelihood of it having died was very high. This data set has previously been used to provide survival estimates of the Isle of May kittiwake population (Frederiksen et al. 2004b). In this data set, 63% of birds were weighed at least once, typically when they were initially colour-ringed, and for 41% of these birds mass data were subsequently available on one or more additional occasions. Furthermore, many of the individuals in this data set were sexed from courtship feeding (males feed females) and mating behaviour, morphologically or molecularly, resulting in a much higher proportion of individuals of known sex (61%) in this data set. We therefore used this capture/resighting data set for analyses involving kittiwakes and model results from these data constitute the main outputs for this species.

2.1.2 Puffin

Over the period 1973-1985, CEH undertook an intensive mark-recapture study of puffins. Birds were caught directly in burrows or in mist nets placed in the breeding areas. In a high proportion of captures, a body mass was taken, resulting in 49% of individuals having at least one mass measurement. These data on marking, morphometrics and subsequent recaptures were recorded on ringing sheets and had been used in various peer-reviewed publications (e.g. Harris et al. 2013), but had not been transferred to a digital system. A preliminary assessment of the paper records indicated that recapture probability was comparatively high for a data set of this type, thus potentially making it better suited for analysis than more recent capture/recapture data collected from puffins on the Isle of May where recapture effort has been markedly lower, or CEH's intensive mark-resighting data set where the number of individuals with mass data is low. A digitisation exercise in Excel was therefore undertaken to enter and check the paper records. Only adult birds were used in the analysis and these were defined as individuals that had been caught in a burrow with an egg or chick, were carrying fish when caught in mist nets or had at least two bill grooves (Harris & Wanless 2011; Harris 2014). Puffins and other auks show slight sexual size dimorphism, with males being on average 5-10% heavier than females (Wagner 1999; Harris & Wanless 2011). Although the sex of birds in this data set was not known, a separate data set of 161 birds with known sex existed and was used along with the main data set to allow sex classification methods to be used.

2.1.3 Guillemot

From 1982 up to the present, an intensive mark-resighting study of guillemots has been undertaken on the Isle of May. Birds have been captured at the breeding ledges using a noose or crook attached to the end of a 3 - 7 pole or mist netted on the breeding ledges outside the breeding season, and fitted with three colour rings (in a unique combination) and a BTO metal ring. Birds were caught during three main periods: prior to breeding (March/April), during mid chick-rearing (June/July) and in the early autumn (October) when they return to the colony after completing the moult of their flight feathers. Daily observations of colour-ringed individuals have been undertaken throughout the breeding season in each year, a markedly higher resighting intensity compared to kittiwakes. Each year subsequent to 1982, a few additional birds have been colour-ringed to maintain a marked population of 150-400 individuals. As with kittiwakes, resighting probability is very high (see Section 4) enabling robust survival estimates to be made (Crespin et al. 2006). The majority of birds were weighed when they were colour-ringed and wing chord length and head and bill length were taken in a subset of birds. Thus, overall 63% of birds had at least one mass measurement and of these between 22% and 63% have each morphometric measurement. A small proportion of birds (12% of those with initial masses) were recaptured in subsequent years and additional mass and morphometric measurements obtained. Because birds were observed daily throughout the season, the percentage of visually sexed birds was very high due to multiple records of mating behaviour and post-fledging site attendance by females after the male had taken the chick to sea. More recently, feather samples have been taken at capture allowing birds to be sexed molecularly. Overall, the percentage of known sex individuals was very high (93%).

2.1.4 Razorbill

Since 1982, a sample of individuals have been captured using similar methods to guillemots in early incubation (3%) and in mid chick-rearing (all other data). Birds were intensively resighted in subsequent years, using a similar protocol to guillemots, from which survival estimates can be estimated. As with guillemots, many individuals were weighed at ringing (44%), and a high proportion are of known sex (72%) from visual observations of copulations and post-fledging attendance and molecular sexing from feathers.

2.2 Data available for models

The key relationship of interest in this project was between body mass at the end of the breeding season and over-wintering survival. However, the mass data available were collected throughout the breeding season rather than at the end. Therefore, for data inspection and modelling, the date when the data were collected (day of year variable) was adjusted by subtracting the appropriate species- and year-specific median laying date, available from CEH's long-term monitoring programme. These derived variables are called 'Day' throughout this report.

Data were then included if they lay between Day 0 (i.e. the median laying date) and the median fledging date (Day 0 plus the average length of incubation and chick-rearing, which varied between species - see next section). Catches outside this core period were removed because it is likely that birds may be undergoing a complex pattern of body mass change associated with a range of key life history decisions. Prior to laying, individuals will initially be seeking to attain sufficient condition for breeding, but the two sexes may then show marked divergence in body mass change. In guillemots and razorbills, females spend much time away from the colony while forming the egg while males focus on holding the nesting territory (Wanless & Harris 1986). In kittiwakes, males courtship feed females, likely to be associated with the greater energetic needs of the female in preparation for laying (Newman et al. 1998). In autumn, individual mass in auks is likely to depend on strategies for laying down fat during and immediately after feather moult (Harris et al. 2000). Crucially, these mass changes are not understood in detail because of the lack of empirical data, but it was sufficiently likely that they did not accord well with the predicted changes depicted in Fig 1a, so were removed.

We took the approach of using median laying date as the zero value for Day in each year because in the vast majority of cases we did not have laying dates associated with mass data at the individual level. The consequence of using population-level phenological data is that there will be some inaccuracy associated with 'Day' because there is a spread of laying around the median laying date, and because a proportion of individuals relay if they fail on their first attempt. Individual laying date data from CEH's long-term monitoring programme shows the following spread of dates for 90% of the population (mean ± S.D. across years): kittiwake: 17.75 ± 4.75 days; puffin: 21.67 ± 5.63; guillemot: 20.56 ± 3.10; razorbill: 23.64 ± 5.10. The proportion of individuals that relay has been estimated for two species (mean ± S.D. across years: guillemot: 8.44 ± 1.94%; razorbill 6.81 ± 3:42%): This spread of laying would also have affected which mass data were retained in the analysis. Some birds that were captured after Day 1 will not yet have laid and thus, should ideally have been excluded from the analysis. Similarly, some individuals captured before Day 1 will have laid but will have been excluded. The potential consequences of these misclassifications are hard to predict but will undoubtedly have introduced noise into the system. Typically, uncertainty of this kind typically leads to a flatter relationship (in this case between mass and Day), but will depend on whether mass trajectories prior to laying differ from those after laying.

We conducted an initial analysis to remove obvious outliers from the mass measurements. These were defined as records with unrealistically large or small mass which were almost certainly observational errors reading the balance, writing down the value or transcribing onto data sheets (see species accounts for specific criteria used to identify outliers for each species).

2.2.1 Kittiwake

On the basis of exploratory plots (Fig 2), we decided to remove from the initial data set all mass observations taken when Day was less than 0 (i.e. prior to the median laying date for that year) or greater than 70 (based on average incubation and chick-rearing durations of 25 and 45 days, respectively). We also removed five cases where mass was recorded as zero (caused by typographic errors where a zero was inserted where no mass was available). This resulted in the removal of 15.7% of body masses leaving 5782 observations. Because some birds regurgitated and some did not, we included the mass of the regurgitate if present to remove the impact of this effect.

We adopted the same outlier removal procedure for the subset of resighted birds which resulted in the removal of 10.8% of mass measurements leaving 1065 mass measurements.

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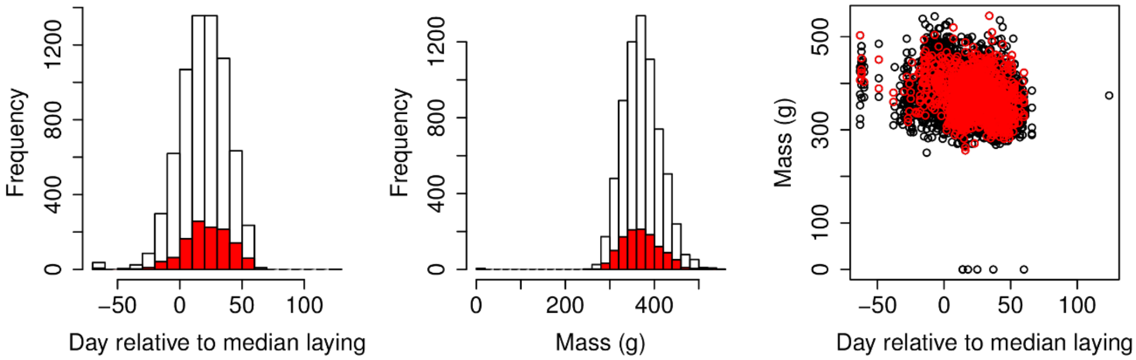


Figure 2: a) frequency distribution of Day relative to median laying date; b) frequency distribution of body mass; c) relationship between Day and body mass in kittiwakes. Red corresponds to the subset of birds that were colour ringed for resighting.

2.2.2 Puffin

On the basis of the exploratory plots (Fig 3), we removed mass observations taken when Day was less than 0 i.e. before the year-specific median laying date but retained all data thereafter. As with kittiwakes, these observations prior to Day 0 are likely to be pre-laying catches that will show a different relationship between mass and Day, and puffins are also likely to have had a different capture probability in this period. This resulted in the removal of 33.0% of body masses leaving 2384 observations (Fig 2). Although this represented a substantial proportion of the data, the retained sample size was still large enough for us to conduct a robust analysis.

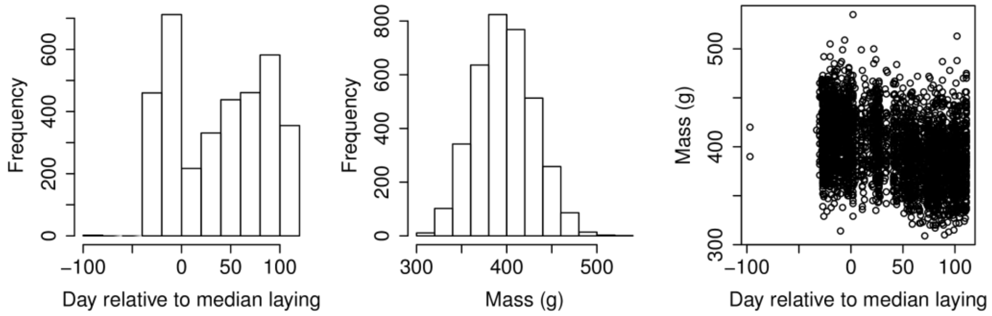


Figure 3: a) frequency distribution of Day relative to median laying date; b) frequency distribution of body mass; c) relationship between Day and body mass in puffins.

2.2.3 Guillemot

On the basis of the exploratory plots (Fig 4), we removed guillemot mass observations taken when Day was less than 0 or greater than 60 (based on incubation and chick-rearing durations of 35 and 25 days, respectively). There were three clusters for Day matching the three capture periods (see Section 2.1.3). The first cluster refers to birds caught prior to the start of the laying period in the colony and the third cluster comprises birds caught in the autumn when they are netted at the colony are likely to have different capture probabilities and are known to have different mass trajectories from those handled during the breeding season (Harris et al. 2000). This resulted in the removal of 40.6% of body masses leaving 394 observations. As with puffins, although this represented a substantial proportion of the data, the retained sample size was still large enough for us to conduct a robust analysis.

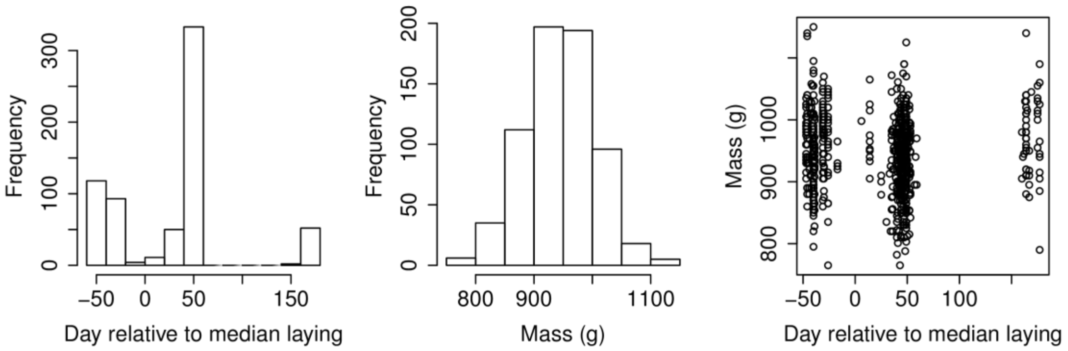


Figure 4: a) frequency distribution of Day relative to median laying date; b) frequency distribution of body mass; c) relationship between Day and body mass in guillemots.

2.2.4 Razorbill

On the basis of exploratory plots (Fig 5), we removed three mass records before Day 10. Although these fell within the period from laying to fledging, they were marked outliers relative to the main observation period and could have had strong leverage on the results. This resulted in the removal of 3% of body masses leaving 97 observations.

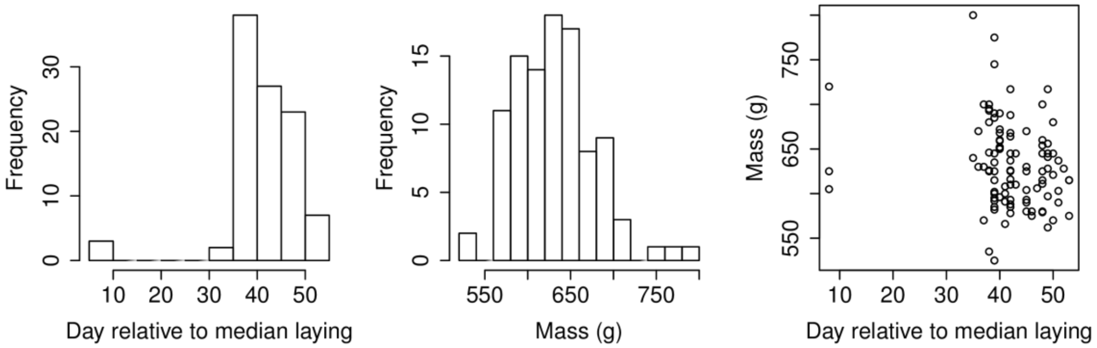


Figure 5: a) frequency distribution of Day relative to median laying date; b) frequency distribution of body mass; c) relationship between Day and body mass in razorbills.

2.2.5 Summary of retained mass data

The summary of retained data is presented in Table 1.

Species	Study years	Number of birds	Number of combinations of bird and year	Number of masses
Kittiwake *(initial)*	1997-2018	2982	4517	5775
Kittiwake *(final)*	1997-2018	498	824	1065
Puffin	1973-1985	2043	2268	2384
Guillemot	1982-2018	341	393	394
Razorbill	1982-2018	93	97	97

Table 1: Study years, number of birds, number of combinations of birds and year (“bird-years”) and measurements in each species in the retained mass data. The number of masses is higher than the number of bird-years because some birds were weighed more than once in a season. The initial data set for kittiwakes was the mark/recapture data set that produced unreliable survival estimates (see Section 2.1.1). The final data set was the mark/resighting data set which was used in the main analysis for this species.

3 Statistical methods

Our modelling strategy consisted of two stages.

Stage 1 comprised an initial analysis of the variation in measurements of body mass (and other morphometric variables) for each species using the ASReml package for fitting linear mixed models (see Section 3.1). The purpose of this stage was to establish how these variables should be modelled in the computationally more challenging models of annual observation histories (from which mass specific survival probabilities are to be estimated). For kittiwakes, this initial assessment was performed only using the first (mark/recapture) data set.

Stage 2 comprised a simultaneous analysis of data on body mass, a morphometric variable, and the capture history of each individually marked bird subsequent to the year of first capture as a breeding bird. This was informed by the results of stage 1 for each species. Estimation was performed using the Markov chain Monte Carlo (MCMC) package OpenBugs due to the large number of missing mass and covariate information (see Section 3.2).

To interpret the results of the MCMC procedure we computed survival probabilities by averaging over uncertainty in parameter estimates and taking quantiles as appropriate to produce credible intervals (the Bayesian equivalent of confidence intervals) and assess the impact of annual variation.

3.1 Stage 1: Exploratory Analysis of Body mass and Morphometric Variables

We fitted a linear mixed model to the masses for each species using Day as fixed effect and starting with categorical variables for Year, Bird and the Year by Bird interaction (Year:Bird) as random effects. We then considered dropping terms if the model failed to converge, if any variance components were estimated at zero, if a likelihood ratio test failed to give a significant result, and in some cases if the term did not greatly change the estimated residual variance. Terms were considered in order of Year:Bird, followed by whichever term has the smallest ratio of variance component to its standard error.

With the random effects established, we examined adding in additional complexity to the relationship between mass and Day. We considered two changes: adding a quadratic Day term (Day^2), and allowing the effect of Day to vary from year to year (Day:Year). These additions were assessed through the change in the residual variance, and through constructing an ANOVA table for the additional effects.

During this stage, we also attempted to identify the best morphometric variable to include in the model for mass, both to fill gaps in the mass data and to reduce the variation inherent in body mass measurements by exploiting correlations that may be present. This was done by including each of a number of candidate morphometric covariates in turn and determining which variable most improved the root mean square (RMS) of the prediction errors, and was available for most of the data set. Although this was not exactly how the covariates were are used in Stage 2, it seemed the most appropriate way to make this decision without incurring the time penalty of multiple MCMC runs.

Sex of the bird was not used for this part of the analysis due to the limited completeness of observations.

3.2 Stage 2: Joint Modelling of Mass, a Morphometric Variable and Survival

3.2.1 Model assumptions

In Stage 2, we modelled the mass data, a morphometric variable, and the survival data simultaneously. Broadly, having established a model for the variation of the mass and a chosen morphometric variable, we assumed between year and between bird components of mass (eliminating daily variability and sex differences present in the raw observed masses) have a logit-linear relationship, together with potentially other covariates, to the probability of survival of a bird from one winter to the next, with the bird having then some probability of being observed if still alive.

For the starting point for our survival modelling we therefore considered the standard assumptions of Cormack-Jolly-Seber models, except that survival probabilities were allowed to vary between individuals. The assumptions made were:

1. Captured birds were assumed to be a representative sample of the population of interest;
2. Capture and ringing were assumed to be accurately conducted and recorded with no ring loss, data errors etc;
3. The survival outcomes of individual birds were assumed to be independent, conditional on their probability of survival, and the capture and recapture of birds being independent events over years and between birds;
4. The parameters determining the effects of covariates in the survival model were assumed to be constant over the study period.

It is well known that there are inconsistencies in morphometric measurements of the same bird made by different individuals. However, the identity of the person taking the measurements used in our analyses was not always recorded meaning that we could not explicitly allow for observer identity. However, in practice this effect was likely to be reasonably small since for each species only a few, highly experienced people made the majority of measurements. In addition, changes in observers typically occur between, not within, years, so observer effects are likely to be captured by effects of year.

Within each year, we assume that the date of each mass measurement relative to the median laying time is the relevant time variable that determines the change of body masses over the course of the breeding season, with the specific relationship being based on the results from Stage 1.

For determining the probability of overwinter survival, the winter North Atlantic Oscillation index (hereafter “NAO”) was included as an index of largescale climatic conditions. It affects the demography of top predators and abundance of fish, such that warm/windy years (positive values) result in lower fish abundance and reduced demographic rates on average (Ottersen et al. 2001).The underlying relationships were assumed to apply to all adult birds, whether or not they were breeding during any particular year.

Previous studies (Frederiksen et al. 2004a; Crespin et al. 2006) demonstrated that there is senescence in Isle of May kittiwakes and guillemots, and therefore the time since a bird is first observed breeding (or initial capture if such observations were unavailable) was taken as a pseudo-age which can impact survival.

All mortality was assumed to take place during the winter, away from the colony. Although the approximate timing of death is known from ring recoveries such records are rare and in addition recovery probabilities may vary for unknown reasons. Hence, we treated these deaths as unobserved to reduce the complexity of the model.

During our modelling, we found (contrary to assumption 3) evidence of trap dependence – that is, birds caught one year were more likely to be observed again the next. Therefore, in our full modelling approach we included a term in the recapture/resighting probability to compensate for trap dependence.

3.2.2 Modelling approach

The fitted models consisted of two components. The first component was a joint model for the mass and morphometric (size) data, which included amongst the terms to be estimated the unknown (latent) mass of each bird at the end of each relevant breeding season. The second component was a model for the survival data using as covariate the latent values of mass at the end of the breeding season calculated in the model for mass. In the following, we give the full model for both components. Based on the findings from the mixed model exploratory analysis (Section 4.1), we could determine or omit some aspects of the full model for mass (see Table 2).

For mass and size, instead of using the latter as a covariate in the model for mass, we developed separate models, one for size and the other for mass. Each contained a categorical random effect for Bird, the values of which were considered to be correlated.

Specifically, we considered these variables to be a sum of an effect due to the sex of the bird $\alpha_{M\text{sex}}\mathrm{I}(\text{Sex}_i = M)$, a bird-specific effect (X_i and X'_i for mass and size of bird *i* respectively) and, for the mass only, both a year-specific effect Y_j and a linear effect

$k\alpha_{\mathrm{day,j}}$ from the day k the mass observation was taken. The models of mass and size both also included a residual observation level variability term $\epsilon^{M}{}_{ijk}$ and $\epsilon^{S}{}_{ijk}$. We allowed a correlation ρ to be present between the bird effects for size and mass, assuming their joint distribution multivariate normal (denoted by *MVN* below). The year, Bird and observation effects were assumed to be normally distributed (denoted *N* below). For simplicity of calculation, we recoded Day to produce k by deducting an estimate of the length of the breeding season, so that $k = 0$ corresponded to the end of the breeding period. Values for the four species were: 83 days for puffins, 70 days for kittiwakes, and 55 days for guillemots and razorbills.

Therefore, for the observed mass M_{ijk} and size S_{ijk} of the *i*-th bird on the *j*-th year measured on the k-th day, we have:

$$M_{ijk} = \mu_M + \alpha_{M\mathrm{sex}}(\mathrm{I}(\mathrm{Sex}_i = M) - 0.5) + X_i + Y_j + k\alpha_{\mathrm{Day,j}} + \epsilon^{M}{}_{ijk},$$
$$S_{ijk} = \mu_S + \alpha_{S\mathrm{sex}}(\mathrm{I}(\mathrm{Sex}_i = M) - 0.5) + X'_i + \epsilon^{S}{}_{ijk};,$$

where

$$Y_j \sim N(0, \sigma_Y^2),\ \epsilon^{M}{}_{ijk} \sim N(0, \sigma_M^2),\ \epsilon^{S}{}_{ijk} \sim N(0, \sigma_S^2);\text{and}$$
$$(X_i, X_i') \sim MVN\left((0,0), \begin{bmatrix} \sigma_X^2 & \rho\sigma_X\sigma_{X'} \\ \rho\sigma_X\sigma_{X'} & \sigma_{X'}^2 \end{bmatrix}\right).$$

For the survival part of the model, we considered there was a latent pattern of true presences/absences P_{ij} of birds that have some probability to being resighted/recaptured leading to the pattern of observed presences/absences O_{ij}. Following the year in which a bird first appeared as part of the breeding population, the latent pattern of true presences/absences was controlled by the probability of survival from one year to the next. We considered these survival probabilities to be an inverse logit of a linear expression involving the winter NAO for each year (N_j, plus its lag 1 variant N_{j-1}), as well as a quadratic effect in the pseudo-age A_{ij} of the bird that year (defined as the number of years since first appearing as a breeding adult in the data set; Frederiksen et al. 2004b), together with annual (*Y*) and bird specific (*X*) mass effects imputed from the mass part of the model. To compensate for the unexpectedly high number of transients (birds that appear once but never again) in the capture-recapture puffin and (mark-recapture) kittiwake data sets, we included an additional effect for $A_{ij} = 0$.

We used the pseudo-age in our models because actual age of most adult birds was lacking.

Thus, we modelled the probability of survival of bird *i* from year *j* to year *j*+1 as:

$$logit\left(Prob\left(P_{ij+1} = 1 \middle| P_{ij} = 1\right)\right) = \mu_P + \beta_X X_i + \beta_Y Y_j + \beta_{NAO} N_j + \beta_{NAOd} N_{j-1} + \beta_A A_{ij} + \beta_{A2} A_{ij}^2 + \beta_{A0} I\left(A_{ij} = 0\right) + \epsilon^P{}_j.$$

Observational probability meanwhile was taken to be the sum, on the logit scale, of an effect due to pseudo-age, a random year factor, an effect allowing for any trend that might have taken place in capture effort/efficiency and an effect allowing for any trap dependence based on being observed in the previous year.

Thus, our model of the observation probability is given by:

$$logit\left(Prob\left(O_{ij} = 1 \middle| P_{ij} = 1\right)\right) = \mu_O + \gamma_O I\left(O_{ij-1} = 1\right) + \gamma_A A_{ij} + \gamma_T j + \epsilon_j^O,$$

$$\epsilon_j^P \sim N(0, \sigma_P^2), \qquad \epsilon_j^O \sim N(0, \sigma_O^2),$$

Depending on the species, we removed some components of the full models given above to simplify the model, as justified by the results from the mixed model exploratory analysis shown in the results section, from prior work on each species, or practical difficulty in achieving convergence. The full findings from the mixed model analysis are given in Section 4.1, which are summarised in Table 2.

	Puffins	Kittiwakes	Guillemots	Razorbills
Year mass effect (Y_j, σ_Y^2)	Included	Included	Omitted	Omitted
Observation mass effect (σ_m^2)	Included	Included	Included	Set to fixed ratio of σ_X^2
Within year mass trend($\alpha_{\mathrm{day,\,j}}$)	Constant across years	Year-specific	Constant across years	Constant across years
Morphometric variable chosen ($\mathrm{S_{ijk}}$)	Bill depth	Head and bill length	Wing length	Wing length
First year survival effect (β_{A0})	Included	Omitted	Omitted	Omitted
Trend in capture effort (γ_T)	Omitted	Included	Omitted	Omitted

Table 2: Individual choices made for mixed model analysis for each species. Cells show whether specific terms were included in the estimation, omitted from the model or handled by holding to a fixed ratio of a different value. In addition we list whether the within year mass trend was allowed to vary from year to year (year-specific) or held constant across years, and indicate the choice of morphometric variable.

We adopted a data augmented Bayesian MCMC approach to parameter estimation. Fitting of the models was done in OpenBUGS. In some cases, to encourage convergence, we chose starting values at either 0 or plausible values based on our exploratory analysis. We produced three independent chains of 10,000 iterations for each species.

Due to the complexity of the model, using unrelated uninformative priors for each parameter in the model would have caused extreme values on initiation of variables in the MCMC model runs, leading to poor convergence and potentially unrealistic results. Hence, we adopted a weakly informative approach to choosing priors that gave a wide, but plausible, range of values. Hence with suitable parameters, we applied normal priors to $\mu_{\mathrm{M}}, \mu_{\mathrm{S}}, \alpha_{\mathrm{day,j}}, \alpha_{Msex}, \alpha_{Ssex}, \mu_P, \beta_X, \beta_Y, \beta_{NAO}, \beta_{NAOd}, \beta_A, \beta_{A2}, \beta_{Ao}, \mu_O, \gamma_O, \gamma_T$ and γ_A and uniform priors were applied to $\sigma_Y, \sigma_M, \sigma_S, \sigma_X, \sigma_{X'}, \rho, \sigma_P$ and σ_O.

3.2.3 Summarising results

To summarise the results for each species, we needed to handle several sources of uncertainty. Firstly, the results of the MCMC runs were a series of draws from the joint posterior distribution, exhibiting the posterior support and uncertainty in parameter estimates once the information in the data had been used. Secondly, the models included random effects corresponding to changing survival patterns from year to year. Due to the effect of the logit link, these had a non-linear effect on the survival probabilities. Thus, when model parameters combined to give high estimates of survival, the apparent impact of any covariate on the probability scale was considerably less than when model parameters combined to give estimates of survival probability near 0.5, when this impact would be at a maximum.

To resolve these issues we used some averaging to generate predictions. Firstly, we divided factors affecting survival probabilities into bird level factors and year level factors. The former included effects from body mass and pseudo-age, whereas the latter included effects from NAO, the random effect of year, and the effect of yearly variation in body mass. Because the effect on survival used only the sum of these year-level factors, we chose to aggregate these year effects into a single year quality term, which we could mimic by randomly generating values from appropriate normal distributions (using the posterior mean estimated variances and coefficients). This allowed us to produce an assessment of ‘good’, ‘bad’, and ‘normal’ years defined as the 10th, 50th and 90th percentile of these combined year effects. Defining this quantity as a year ‘quality’ level Q, our survival probability equation reduces to:

$$logit\left(Prob\left(P_{ij+1} = 1 \middle| P_{ij} = 1\right)\right) = \mu_P + \beta_A A_{ij} + \beta_{A2} A_{ij}^2 + \beta_X X_i + Q_j.$$

Since the distribution of ages amongst the birds in any population is based on many demographic characteristics that we did not include in our models, and we cannot assume that the populations we studied are representative in this respect, it was necessary to fix a value for the bird’s age A_{ij} to calculate survival probability. We chose a grid of years to provide illustrative values – an uneven grid is used because the quadratic term $\beta_{A2} A_{ij}^2$ implies survival can be high for several years before dropping off quickly.

We took the mean value over the MCMC posterior draws to obtain an estimate of survival probabilities. Credible intervals were obtained by taking quantiles from the distribution of β_X, the mass-survival coefficient.

Note that such credible intervals only show the uncertainty in β_X. Uncertainty is present in the estimates of the other factors, but these factors are dwarfed by the large variability in the baseline survival probability from year to year which our approach has removed by conditioning on their joint effect. Therefore, we have suppressed these other factors to show results for the mass-survival relationship more clearly.

Finally, since we assumed the regression coefficient for survival probability on body mass is the same for both sexes in all four species, it makes sense to present common graphs of survival probability against mass. These graphs are appropriate for males by adding one half of the estimated mean difference between sexes in body mass to the horizontal axis labels, and for females by subtracting one half of the estimated mean difference between sexes in body mass to the horizontal axis labels.

4 Model results

4.1 Stage 1: Exploratory Analysis of Body mass and Morphometric Variables

We fitted a hierarchical series of linear mixed models, assessing the removal of terms for their significance in a likelihood ratio test and the increase in residual variance. Table 3 shows the results of this procedure. For kittiwakes, this was done using only the first (mark-recapture) data set.

Species	Random model	Pval (from LRT with next model)	Residual variance
Kittiwakes	**Year + Bird + Year:Bird**	**< 0.001**	**723**
	Year + Bird	< 0.001	788
	Bird	< 0.001	863
	(Null)	-	1510
Puffins	Year + Bird + Year:Bird	Boundary	334
	Year + Bird	**< 0.001**	**334**
	Bird	< 0.001	339
	(Null)		930
Guillemots	Year + Bird + Year:Bird	Boundary	1755
	Year + Bird	0.132	1755
	Bird	**< 0.001**	**1786**
	(Null)		3399
Razorbills	Year + Bird + Year:Bird	Failed	-
	Year + Bird	0.326	1131
	Bird	**0.306**	**1293**
	(Null)		2183

Table 3: Evidence supporting selection of random effects model for mass. Bold text shows optimal models.

The key conclusions from this assessment that were carried forward into subsequent analyses were:

- Kittiwakes: We should include main effects for Bird and Year. Including the Bird:Year interaction also appeared desirable. However, the data set was large with many missing combinations of Bird and Year making its inclusion computationally too challenging.
- Puffins: The main effects model Year + Bird seemed to be a reasonable random effects model. The Year effects were very small in terms of the change to the residual variance, however, so we expect it to have little effect on survival probability.
- Guillemots: Only ~50 birds were weighed more than once, but there was reasonable evidence for a Bird effect. The Year effect was estimated as very small, making little difference to the residual variance and no statistical evidence for inclusion, so was omitted.
- Razorbills: Including at least one random effect seemed to reduce the residual variance but these cannot be estimated well as there is effectively no replication within birds. Therefore, we decided we needed to include a bird effect, but doing so required transfering information about the ratio of variances from another species. Puffins were used because of the relative completeness of the mass data set.

Table 4 shows the results of adding more complexity to the fixed effect of Day on mass. We considered a quadratic term, as well as allowing the effect of day to vary between years.

Species	Fixed terms	Pval (vs day only)	Residual variance
Kittiwakes	Day + Day ^2	< 0.001	718
	Day + Day:Year	**< 0.001**	**660**
	Day	-	723
Puffins	Day + Day ^2	< 0.001	332
	Day + Day:Year	0.002	329
	Day		**334**
Guillemots	Day + Day ^2	0.139	1812
	Day + Day:Year	0.336	1834
	Day	**-**	**1786**
Razorbills	Day + Day ^2	0.142	2156
	Day + Day:Year	0.468	2166
	Day		**2183**

Table 4: Evidence supporting selection of how Day should be included in the model for mass. Bold text shows optimal models.

Key conclusions regarding whether to include more complex effects of Day in the model for mass were:

- Day^2 was statistically significant for Kittiwakes and Puffins, but in both cases the effect was small with little impact on residual variance (c. 1% reduction). We therefore decided not to use Day^2 in any model.
- Day:Year was statistically significant for Kittiwakes and Puffins, but was only consequential in terms of drop in residual variance for Kittiwakes. Hence Day:Year was included only for Kittiwakes.

Finally, Table 5 evaluates adding in each of the available morphometric covariates to the model selected.

Species	Covariate added	Percentage of covariate values present if mass was measured	RMS Prediction error
Kittiwakes	None	100	15.8
	Wing	90.1	14.3
	Head and Bill	**89.2**	**12.5**
	Tarsus	11.1	15.8
Puffins	None	100	14.1
	Wing	95.1	13.5
	Bill length	31.9	12.9
	Bill depth	**31.3**	**12.8**
Guillemots	None	100	28.7
	Wing	**94.2**	**27.5**
	Head and Bill	23.4	15.1
Razorbills	None	100	23.2
	Wing	**94.8**	**20.4**
	Head and Bill	9.3	-

Table 5: Evidence supporting selection of a morphometric covariate to be used in the model of mass for each species in Stage 2. Bold text shows covariate selected

There were very few cases of a morphometric covariate being measured with better coverage than mass. For most species less than 2% of records had a covariate measurement and no mass. The only exception was kittiwakes for which in about 10% of cases there was a wing measurement but no associated mass. Overall, we drew the following conclusions for the selection of morphometric variable:

- Kittiwakes: Including the head and bill covariate had the largest effect on predictive ability and good coverage, so this was selected for inclusion in Stage 2.

- Puffins: None of the covariates led to a substantial improvement in predictive performance. Bill depth was the best and is known to have good correlation with sex so was selected for use in Stage 2.
- Guillemots: Neither covariate was ideal. Head and bill seemed best as it had a large effect but was only measured in the last few years of the data set. We therefore selected Wing. The likely benefit of this over no covariate was mainly for consistency of model construction with other species.
- Razorbills: Only Wing was commonly measured, and though not a very big effect seemed to have enough benefit to merit inclusion in stage 2.

4.2 Stage 2: Joint Modelling of Mass, a Morphometric Variable and Survival

The central goal of this project was to estimate mass-survival relationships, and so we present and discuss the results from the models of survival in this report. First, we present graphically the estimated relationships between survival and modelled end-of-breeding-season body mass controlling for other effects, then we present estimates of all terms in the model of survival. The linked models for mass and the selected morphometric variable, which are required to obtain the modelled values for end-of-breeding season body mass required by the model of survival, are considered subsidiary and so results from these models are summarised in Appendix 1.

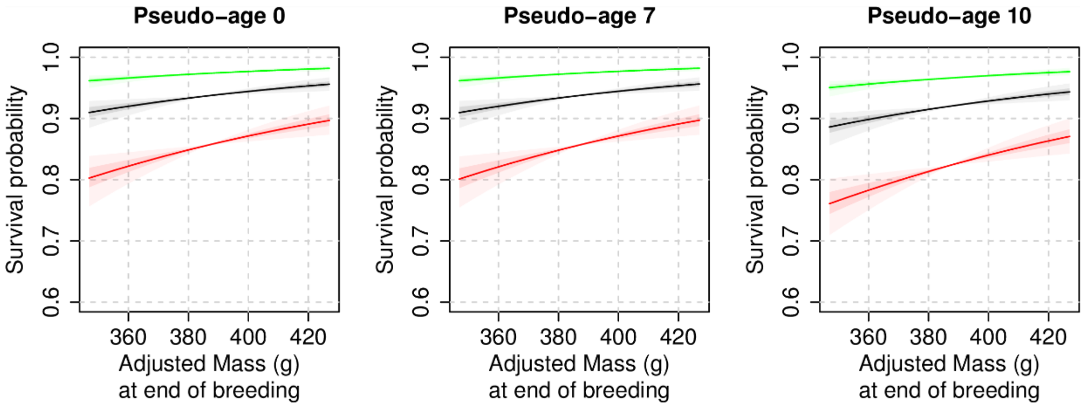
As explained in section 3.2.3, the estimated relationships between body mass and survival derived from the MCMC modelling are shown in Fig. 6, which shows the estimated probability of survival for each species as a function of body mass for stated values of year quality (including NAO) and pseudo-age. Since the models contained a single regression coefficient for survival on mass applicable to both males and females, we have provided a single survival relationship for each combination of year quality and pseudo-age, using the adjusted mass (the body mass, deducting or adding half the difference in mass between male and female birds, as shown in Table 6). The X-axis on each graph encompasses a range of ± 2 standard deviations from the mean adjusted body mass.

Our estimates showed an effect of senescence in some cases and strong variability in survival probability from year to year. Hence, the estimated body mass-survival relationships are shown for a selection of pseudo-ages and year qualities, as described in section 3.2.3.

Only puffins (Fig 6a) showed a strong and unambiguous positive relationship between survival and mass, this being most evident on the probability scale for older birds during years of low quality i.e. depressed overwinter survival. For kittiwakes (Fig 6b) and guillemots (Fig 6c), the posterior mean gave modest effects for mass on survival, but these effects were small relative to uncertainty and even the 50% credible interval included no effect. For razorbills (Fig 6d), the posterior mean gave a large negative effect of mass on survival i.e. the opposite direction to the expected. However, the credible interval in this was extremely wide due to the small sample size and so biologically meaningful positive effects of body mass on survival received non-negligible support from the data.

The pseudo-ages in these plots may be considered in the context of each species' life expectancies. This may be calculated from the MCMC model, albeit acknowledging that as Table 6 indicates, the senescence effect has substantial uncertainties. This is especially true for puffins, where the life expectancy is high relative to the length of this data set (12 years in this case, compared to 22 years for kittiwakes and over 30 years for guillemots and razorbills). Taking the posterior means, assuming 'normal' year quality, a bird with a pseudo-age 0 had an estimated life expectancy of 11.0 years for puffins, 7.6 years for kittiwakes (5.2 on the recapture data set), 14.0 years for guillemots, and 13.5 years for razorbills. Following on from this, for each gram of body mass at the end of the breeding season, puffins were estimated to gain 0.067 years of life expectancy, guillemots 0.014, kittiwakes 0.015 years and razorbills were estimated to lose 0.045 years.

a) Puffin



b) Kittiwake

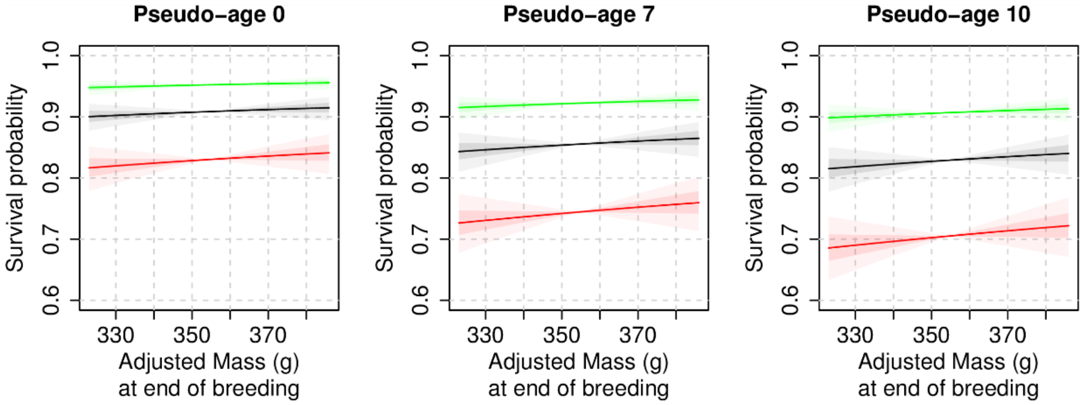
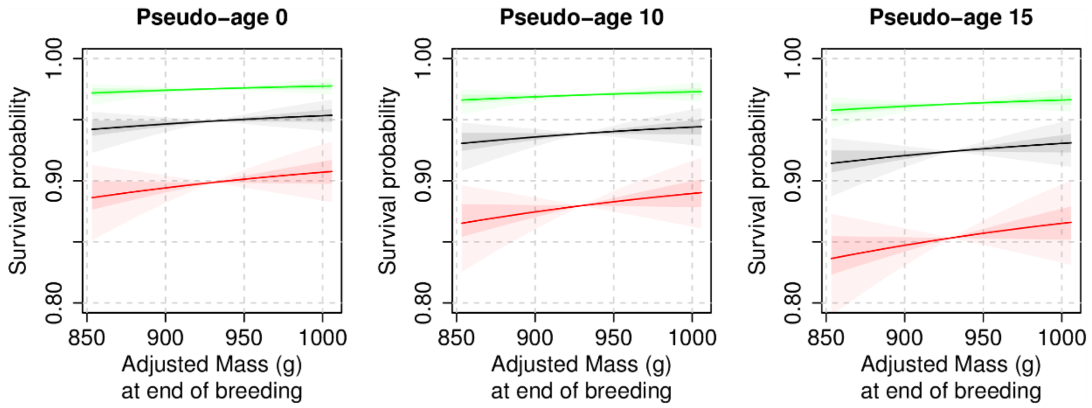


Figure 6: Predicted survival probabilities for puffins, kittiwakes, guillemots and razorbills from the Isle of May in relation to sex-adjusted mass at the end of the breeding season. Each subplot gives the results for birds of a particular pseudo-age, defined as years since the bird was first captured or sighted as a breeding bird. The colours, from red to green, give results for varying levels of aggregate year quality Q, with red being the worst and green being the best for survival. The lines give the posterior mean survival, while the darker and lighter shaded areas give 50% and 90% credible intervals respectively: a) Puffin survival probability at pseudo-ages 0, 7 and 10, vs adjusted mass (the effect of transient birds β_{A0} is omitted); b) Kittiwake survival probability at pseudo-age 0, 7 and 10, vs adjusted mass.

c) Guillemot



d) Razorbill

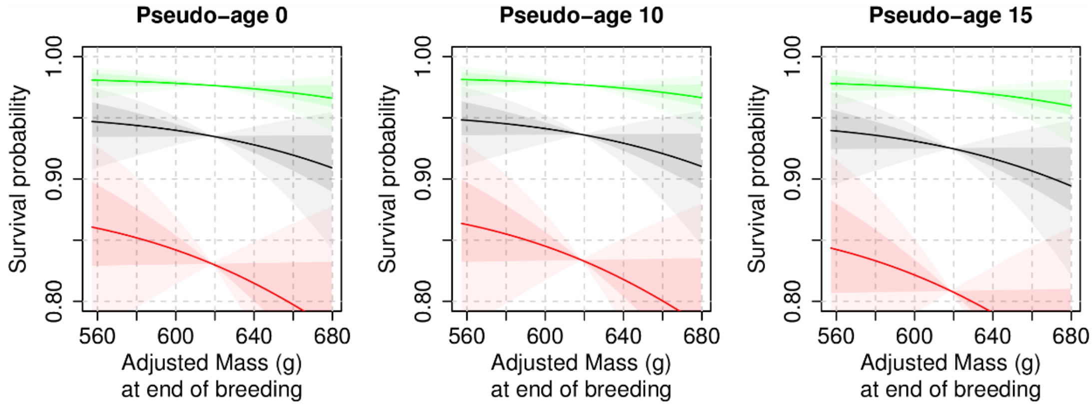


Figure 6 (cont.: c) Guillemot survival probability at pseudo-ages 0, 10 and 15, vs mass adjusted for sex differences; d) Razorbill survival probability at pseudo-ages 0, 10 and 15, vs adjusted mass.

Recalling that the survival probabilities in our model can be given in simplified form as

$$logit\left(Prob\left(P_{ij+1} = 1 \middle| P_{ij} = 1\right)\right) = \mu_P + \beta_A A_{ij} + \beta_{A2} A_{ij}^2 + \beta_X X_i + Q_j$$

Table 6 then gives coefficient estimates, SDs and credible intervals for all of the components of this simplified model.

			50% Credible Interval		90% Credible Interval	
	Mean	SD	25.00%	75.00%	5.00%	95.00%
Puffins						
Female mean mass ($\mu_{\mathrm{M}} - \alpha_{\mathrm{Msex}}/2$)	374.4	2.7	372.6	376.2	369.7	378.7
Male mean mass ($\mu_{\mathrm{M}} + \alpha_{\mathrm{Msex}}/2$)	399.6	3.7	397.2	402.2	393.0	405.3
Body mass effect (β_X)	0.0099	0.0040	0.0071	0.0123	0.0037	0.0168
Intercept (μ_P)	2.786	0.428	2.484	3.026	2.093	3.708
Pseudo-age effect (β_A)	0.0365	0.1807	-0.0576	0.1618	-0.2323	0.3348
Pseudo-age^2 effect (β_{A2})	-0.0058	0.0177	-0.0167	0.0038	-0.0358	0.0202
Kittiwakes (resighted)						
Female mean mass ($\mu_{\mathrm{M}} - \alpha_{\mathrm{Msex}}/2$)	332.9	5.5	329.2	336.6	323.5	341.8
Male mean mass ($\mu_{\mathrm{M}} + \alpha_{\mathrm{Msex}}/2$)	376.1	5.5	372.4	379.8	367.0	385.2
Body mass effect (β_X)	0.0028	0.0047	-0.0004	0.0060	-0.0050	0.0104
Intercept (μ_P)	2.294	0.143	2.195	2.393	2.062	2.519
Pseudo-age effect (β_A)	-0.0799	0.0295	-0.1005	-0.0590	-0.1291	-0.0323
Pseudo-age^2 effect (β_{A2})	0.0008	0.0020	-0.0006	0.0022	-0.0025	0.0042
Guillemots						
Female mean mass ($\mu_{\mathrm{M}} - \alpha_{\mathrm{Msex}}/2$)	923.3	5.5	919.7	927.0	914.4	932.5
Male mean mass ($\mu_{\mathrm{M}} + \alpha_{\mathrm{Msex}}/2$)	935.9	5.6	932.2	939.7	926.6	945.2
Body mass effect (β_X)	0.0015	0.0024	-0.0002	0.0029	-0.0022	0.0057
Intercept (μ_P)	2.920	0.139	2.827	3.011	2.702	3.156
Pseudo-age effect (β_A)	-0.0020	0.0171	-0.0135	0.0101	-0.0306	0.0267
Pseudo-age^2 effect (β_{A2})	-0.0017	0.0007	-0.0022	-0.0013	-0.0028	-0.0006
Razorbills						
Female mean mass ($\mu_{\mathrm{M}} - \alpha_{\mathrm{Msex}}/2$)	614.5	10.4	607.5	621.3	597.4	631.9
Male mean mass ($\mu_{\mathrm{M}} + \alpha_{\mathrm{Msex}}/2$)	622.4	10.2	615.5	629.2	605.9	639.4
Body mass effect (β_X)	-0.0048	0.0069	-0.0095	0.0002	-0.0162	0.0062
Intercept (μ_P)	2.682	0.254	2.516	2.844	2.281	3.106
Pseudo-age effect (β_A)	0.0257	0.0418	-0.0049	0.0556	-0.0418	0.0949
Pseudo-age^2 effect (β_{A2})	-0.0024	0.0020	-0.0038	-0.0009	-0.0057	0.0010

Table 6: selected coefficient estimates from the survival analysis. Masses in g, regression coefficient (Body mass effect) g^{-1}.

In terms of Q, the year quality, the standard deviation of this quantity from year to year was estimated as 0.73 for puffins, 0.55 for kittiwakes, 0.59 for guillemots and 0.84 for razorbills.

Q includes, for puffins and kittiwakes, the regression coefficient of year-specific random effects for colony-level mean mass. However, our estimates of these coefficients were small, whereas the relatively small number of years compared to the number of birds, means the posterior standard deviations in these estimates were much larger than the corresponding standard deviations for the regression coefficients of bird-specific mass.

As Table 7 suggests, we cannot definitively say what the impact of the colony-level yearly variations in mass was on subsequent survival. However, it appears to be a relatively small component of year-to-year variation in survival.

Q also includes the effect of NAO but the effects were small relative to estimation error and did not in any case make up a large proportion of this variability. The estimates are given in the appendix.

			50% Credible Interval		90% Credible Interval	
	Mean	SD	25.00%	75.00%	5.00%	95.00%
Puffins						
Yearly mass/survival effect (β_Y)	-0.0080	0.0318	-0.0318	0.0133	-0.0578	0.0467
Yearly variability in mass (σ_Y)	5.4	2.3	3.9	6.4	2.7	9.7
Sd(Q)	0.73					
Kittiwakes						
Yearly mass/survival effect (β_Y)	0.0058	0.0110	-0.0013	0.0129	-0.0123	0.0240
Yearly variability in mass (σ_Y)	17.2	4.5	14.1	19.9	10.6	25.2
Sd(Q)	0.55					

Table 7: estimated survival effect (regression coefficient) of year-specific random effect for mass, in comparison to yearly variability in mass and quality.

One additional factor to note is that for kittiwakes, observation level mass variability (σ_M) was larger relative to body mass variability (σ_X) than for puffins and guillemots. For puffins and guillemots this was 0.92 and 1.15 times the body mass variability respectively, whereas for kittiwakes this was 1.79 times σ_X . Kittiwakes also showed a higher degree of yearly mass variation (σ_Y) than puffins: 1.09 times the size of body mass variation, as compared to 0.27.

Full results of additional parameters as estimated from the model are given in Appendix 1. Of note, assuming a bird is present and was captured the previous year, we estimated recapture probabilities as approximately 19% for puffins, and resighting probabilities as 92% for kittiwakes, 99% for guillemots and 97% for razorbills. During the breeding season, puffins decreased in mass by 0.25 g per day, while kittiwakes, guillemots and razorbills lost 0.42g, 0.43g and 1.17g per day respectively.

5 Discussion

5.1 Mass/survival relationships

The main objective of this project was to quantify the relationship between the mass of breeding adult kittiwakes, puffins, guillemots and razorbills at the end of one breeding season and survival probability until the start of the following breeding season. To our knowledge, the analyses presented here are the most comprehensive of their kind for these four seabird species in terms of the size of data sets used with respect to numbers of birds and years, and complexity of modelling undertaken. All models of mass allowed for a sex effect, contained a random effect for year and were linked to a model for bird size, ensuring that bird-specific variation in mass was estimated as precisely as possible. Additionally, all models of survival contained terms for pseudo-age alongside additional terms to remove the pseudo-replication inherent in variation between years, firstly by allowing for explainable variation due to variation in mean annual mass and NAO (none was found) and secondly by including random effects to allow for additional unexplained variation in survival between years. Due to their complexity and prevalence of missing data, notably birds being of unknown sex and lack of end of season mass measurements, the models were fitted using MCMC methods using OpenBugs.

We found strong evidence of a positive relationship between body mass at the end of the breeding season and subsequent overwinter survival in puffins (logit-scale regression coefficient β_X estimated mean 0.0099 g^{-1}, SD 0.0040 g^{-1}), based on a mark/recapture data set from the late 1970s and early 1980s. This compares with a regression coefficient β_X of breeding birds of 0.040 g^{-1} (95% CI 0.011 to 0.069g^{-1}) previously estimated for a population of puffins breeding on Hornøya, Northern Norway (Erikstad et al. 2009). However, comparison with our results is complicated by the fact the stated effects in the Norwegian study were based on standardised masses (dividing the mass by the standard deviation to fix the variability of body mass at 1); after adjustment for this fact their estimate of the effect of mass on survival was greater than ours. One potential reason for this difference in the estimated relationship between body mass and survival is the different foraging conditions experienced in winter. We would predict that mass-survival relationships would be stronger when winter conditions are more severe. Current winter distributions of Isle of May and Hornøya puffins do not overlap, with birds from the Isle of May mainly distributed in the North Sea and in waters off the Faroes and Ireland, while the Hornøya puffins winter in the Barents and Norwegian Seas (Fayet et al. 2017). It is possible that winter conditions are more severe for the latter population associated with the higher latitude and shortened day-length. Evidence that foraging effort and Daily Energy Expenditure is higher in puffins from Norwegian colonies than those from UK colonies supports this assertion (Fayet et al. 2017). However, the larger size of Norwegian puffins (Harris & Wanless 2011) may serve to counteract this effect.

In contrast to puffins, we found little evidence of a relationship between mass and survival in kittiwakes. (logit-scale regression coefficient β_X estimated mean 0.00218 g^{-1}, SD 0.0047 g^{-1}). Although the precisions of estimates for kittiwakes and puffins are similar, the much smaller estimate of the posterior mean value of β_X means that even the most central (e.g. 50%) credible intervals contain 0. This lack of evidence for a relationship in kittiwakes is in marked contrast to findings by Oro & Furness (2002) showing a positive relationship between mass and survival in kittiwakes breeding in Shetland (0.038 g^{-1}, 95% CI 0.036 to 0.040g^{-1} However, their estimate was derived from modelling the effect on survival of annual mean population mass of kittiwakes breeding on Foula. Thus, rather than comparing their estimate to our between-bird regression coefficient β_X it would be more appropriate to compare their estimate to the equivalent term β_Y in our analysis (mean 0.0058 g^{-1}, SD 0.011 g^{-1}). However, the discrepancy in mean values between studies remains, and the small value of the SD (c. 0.001) implied by their confidence interval is surprising. Whilst their use of food availability and predator levels as covariates may explain some of the remaining difference in estimated effects size these seem unlikely to account for the differences between studies. One possibility is that, as with puffins, winter conditions may differ between the two populations. However, recent geolocator data indicate that there is considerable overlap in winter distribution between Shetland and Isle of May kittiwakes (Frederiksen et al. 2012; Bogdanova et al. 2017), so this explanation appears unlikely unless wintering distributions of the two populations have changed.

For guillemots (mean 0.0015 g^{-1}, SD 0.0024 g^{-1}) and razorbills (mean -0.0048 g^{-1}, SD 0.0069 g^{-1}) the posterior means of the estimated logit-scale regression coefficients β_X were both less than the corresponding measure of error (posterior standard deviation). Hence as for kittiwakes, neither analysis yielded statistically secure information about the direction of any relationship between body mass and survival, this lack of information being most apparent for razorbills due to the small sample sizes.

The lack of statistical evidence for a relationship in kittiwakes, guillemots and razorbills might be taken as suggesting that sub-lethal effects of Offshore Renewable Developments acting on adult body condition may not have downstream effects on survival. However, examination of the posterior distribution of parameters from the MCMC shows that these body mass-survival relationships cannot be estimated sufficiently precisely from the available data to rule out potentially important positive relationships – this is exhibited for example by the credible intervals in Fig 5, which cover a range of possible slopes. Further, these results are from one colony only, and the apparent difference between Isle of May and Shetland kittiwakes (this study vs Oro & Furness 2002) suggests that relationships are not necessarily consistent within a species in space and/or time. Also, these effects may still be apparent in other demographic data such as productivity and juvenile survival, so these findings should not be interpreted to mean that sub-lethal effects have no demographic consequences.

Our analysis demonstrated that there is some inherent ambiguity about survival and mass, in terms of what mass changes we are considering to have an impact on survival. Body masses can differ between birds, but also from year to year, and each bird may exhibit individual patterns of mass changes. Yearly changes and their effects on survival are much more difficult to quantify because there are far fewer years than birds, and it is rare to see multiple measurements of the same birds over multiple years. Furthermore, non-breeding is a feature of the biology of the species considered here (Aebischer 1986; Reed et al. 2015). Breeding adults may be heavier on average than individuals that are taking a sabbatical year from breeding. As a result, there may be effects of body mass on survival that are missed by catching breeding adults at colonies. Hence, when considering survival relationships to sub-lethal effects of wind farms mediated via changes in body mass, the application of mass survival relationships to the total population needs to be made with care.

In the small number of cases where we had multiple measurements of mass from birds in the same year, we saw large differences in mass that could not be attributed solely to trends in body mass throughout the breeding season. This means the variability between observations σ_M^2 is large relative to the year and bird level effects (especially in the case of kittiwakes, potentially because they carry food for their young in their stomachs), and because this day to day variability in the measured mass is unlikely to be connected to survival this makes identifying the survival effect of mass difficult. Our MCMC procedure is an attempt to avoid the loss or weakening of estimated mass survival effects due to this high variability. However, due to the small number of repeat weighings, it was difficult to disentangle bird and observational variability from each other, especially for razorbills and guillemots. This may account for some of the difficulty in identifying a survival-mass effect for these birds.

We attempted to separate out pseudo-age and mass characteristics from annual environmental conditions, Q. Our hope was that the pseudo-age and mass effects would be more generalisable among colonies, whereas the overall quality of environmental conditions would vary between studies even more widely than over our observation periods. We attempted to explain Q through variables like the NAO, but our estimates of these effects were small and uncertain, leaving the majority of this variability unexplained. This means that there is potentially a substantial role for other covariates such as severe weather events or prey distribution to explain changes in survival between years (Reiertsen et al. 2014; Mesquita et al. 2015).

It is conceivable that the mass survival relationship is different between sexes and between different years, in ways that are more complex than the mean adjustment/additive logit-linear effect we have modelled here. However, given the difficulty of estimating even the simple effects we considered, attempting to fit models containing additional complexities currently seems unfeasible.

5.2 Implications for ORD assessments

Our priority was to examine the evidence for a positive relationship between mass and survival, whereby individuals with higher masses would have a higher probability of survival than individuals with lower masses. This demographic process has been assumed to be present in UK seabird populations and is considered critically important in quantifying the impact of sub-lethal effects of ORDs such as displacement and barrier effects.

We found strong evidence for a positive relationship in puffins, but not in kittiwakes, guillemots or razorbills. The lack of statistical support in the majority of species considered might be taken as suggesting that our previous estimates of the sub-lethal effects of ORDs acting on adult survival via body condition in these species may have been overly pessimistic (Searle et al 2014; 2018). However, despite having access to extensive data sets both in terms of individuals and years and advanced modelling methods, the ranges of values supported by the data exemplified by the credible intervals indicated that we were unable to estimate mass/survival relationships precisely enough to be confident that these effects are biologically negligible.

Additional potential reasons for caution are that some effects may be masked by the exclusion from the analyses of adult birds that are not breeding. Fundamental uncertainties associated with the capture and sighting of birds and variation in mass and survival are present in this analysis are a feature of all studies of this kind. However, given the large data sets combined with more advanced analysis, we consider these mass-survival estimates to be a marked improvement on previous estimates - at least within comparable environments.

There may be additional opportunities to analyse the relationship between body mass and survival in other regions of the UK for species identified as being particularly at risk from ORDs. Although the number of studies of survival of UK seabirds is limited (Horswill et al. 2015), some may include a proportion of individuals where body mass has been taken, so analyses similar to this may be possible. However, it is likely that all such studies will suffer from the same data deficiencies that we observed. Thus, there would be considerable benefit in targeted data collection to increase the number of mass measurements per individual bird, and to obtain more data at the end of the breeding season. Such targeted work should ensure if possible that birds are of known sex, by sampling e.g. feathers for molecular analysis, and it would also be very valuable if they are of known age, to account for age effects on survival. A further refinement would be to measure individual laying date, to avoid the noise introduced by using median laying dates. However, it should be noted that filling some of these data gaps is very challenging. In particular, obtaining body mass data at the end of the breeding season is very difficult in many cases because adult birds are hard to catch and large chicks are particularly susceptible to disturbance.

Finally, it is important to note that any relationship between body mass and survival arising from natural variation among individuals may not necessarily translate into a similar relationship between body mass that has been imposed on birds by a disturbance effect (e.g. displacement from an ORD) and survival. Furthermore, sub-lethal effects of ORDs may also be apparent in other demographic rates, such as productivity and immature survival. A future research priority is therefore to quantify sub-lethal effects of ORDs on all key demographic rates in order for a comprehensive assessment of population-level impacts to be made.

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8 Appendix 1: Additional estimates from MCMC

Table of additional estimated parameters from the MCMC. “na” indicates an entry is not part of the model for a particular species. Masses are in grams, with mass effects on probability per gram.

			50% Credible Interval		90% Credible Interval	
	Mean	SD	25.00%	75.00%	5.00%	95.00%
Puffins						
Mass-survival parameters						
Body mass effect (β_X)	0.0099	0.0040	0.0071	0.0123	0.0037	0.0168
Year mass effect (β_Y)	-0.0080	0.0318	-0.0304	0.0133	-0.0578	0.0468
Other survival parameters						
Intercept (μ_P)	2.79	0.43	2.48	3.03	2.09	3.71
Sd annual variation (σ_P)	0.71	0.35	0.47	0.91	0.21	1.36
NAO effect (β_{NAO})	-0.1384	0.2481	-0.2896	0.0398	-0.5871	0.2241
NAO previous year effect (β_{NAOd})	0.0191	0.2146	-0.1083	0.1643	-0.3684	0.3432
Pseudo-age effect (β_A)	0.0365	0.1807	-0.0576	0.1618	-0.2323	0.3348
Pseudo-age^2 effect (β_{A2})	-0.0058	0.0177	-0.0167	0.0038	-0.0358	0.0202
First year effect (β_{A0})	-1.49	0.45	-1.76	-1.18	-2.29	-0.74
Mass model parameters						
Female mean mass ($\mu_M - \alpha_{Msex}/2$)	374.4	2.7	372.6	376.2	369.7	378.7
Male mean mass ($\mu_M + \alpha_{Msex}/2$)	399.6	3.7	397.2	402.2	393.0	405.3
Sd bird to bird variation (σ_X)	20.0	1.4	19.1	21.0	17.5	22.2
Sd annual variation (σ_Y)	5.4	2.3	3.9	6.4	2.7	9.7
Sd residual variation (σ_M)	18.4	0.7	17.9	18.8	17.3	19.5
Change in mass per day (α_{Day})	-0.26	0.02	-0.27	-0.25	-0.29	-0.23
Annual variation in change in mass	na	na	na	na	na	na
Observation probability parameters						
Intercept (μ_O)	-1.55	0.10	-1.62	-1.48	-1.72	-1.39
Effect of being observed last year (γ_O)	0.12	0.04	0.10	0.15	0.06	0.19
Pseudo-age effect (γ_A)	0.032	0.013	0.023	0.042	0.010	0.054
Year trend (γ_T)	na	na	na	na	na	na
Sd annual variation (σ_O)	0.33	0.10	0.26	0.39	0.20	0.51
Kittiwakes (resighted)						
Mass-survival parameters						

Body mass effect (β_X)	0.0028	0.0047	-0.0004	0.0060	-0.0050	0.0104
Year mass effect (β_Y)	0.0058	0.0110	-0.0013	0.0129	-0.0123	0.0240
Other survival parameters						
Intercept (μ_P)	2.29	0.14	2.20	2.39	2.06	2.52
Sd annual variation (σ_P)	0.54	0.12	0.46	0.61	0.37	0.75
NAO effect (β_{NAO})	-0.0620	0.0995	-0.1244	0.0027	-0.2235	0.0996
NAO previous year effect (β_{NAOd})	0.0076	0.0982	-0.0576	0.0722	-0.1506	0.1659
Pseudo-age effect (β_A)	-0.0799	0.0295	-0.1005	-0.0590	-0.1291	-0.0323
Pseudo-age^2 effect (β_{A2})	0.0008	0.0020	-0.0006	0.0022	-0.0025	0.0042
First year effect (β_{A0})	na	na	na	na	na	na
Mass model parameters						
Female mean mass ($\mu_{\mathrm{M}} - \alpha_{\mathrm{Msex}}/2$)	332.9	5.5	329.2	336.6	323.5	341.8
Male mean mass ($\mu_{\mathrm{M}} + \alpha_{\mathrm{Msex}}/2$)	376.1	5.5	372.4	379.8	367.0	385.2
Sd bird to bird variation (σ_X)	15.7	1.4	14.8	16.7	13.5	18.1
Sd annual variation (σ_Y)	17.2	4.5	14.1	19.9	10.6	25.2
Sd residual variation (σ_M)	28.2	0.8	27.6	28.7	26.9	29.5
Change in mass per day (α_{Day})	-0.42	0.13	-0.51	-0.33	-0.64	-0.20
Annual variation in change in mass	0.44	0.12	0.36	0.51	0.28	0.65
Observation probability parameters						
Intercept (μ_O)	-0.02	0.25	-0.18	0.15	-0.44	0.40
Effect of being observed last year (γ_O)	2.48	0.14	2.38	2.57	2.24	2.71
Pseudo-age effect (γ_A)	-0.052	0.021	-0.067	-0.038	-0.086	-0.017
Year trend (γ_T)	0.017	0.012	0.009	0.025	-0.003	0.038
Sd annual variation (σ_O)	0.38	0.10	0.31	0.45	0.23	0.56
Guillemots						
Mass-survival parameters						
Body mass effect (β_X)	0.0015	0.0024	-0.0002	0.0029	-0.0022	0.0057
Year mass effect (β_Y)	na	na	na	na	na	na
Other survival parameters						
Intercept (μ_P)	2.92	0.14	2.83	3.01	2.70	3.16
Sd annual variation (σ_P)	0.59	0.10	0.52	0.64	0.45	0.76
NAO effect (β_{NAO})	0.0093	0.0981	-0.0592	0.0788	-0.1521	0.1706
NAO previous year effect (β_{NAOd})	0.0157	0.0946	-0.0475	0.0794	-0.1378	0.1669
Pseudo-age effect (β_A)	-0.0020	0.0171	-0.0135	0.0101	-0.0306	0.0267
Pseudo-age^2 effect (β_{A2})	-0.0017	0.0007	-0.0022	-0.0013	-0.0028	-0.0006
First year effect (β_{A0})	na	na	na	na	na	na
Mass model parameters						

Female mean mass ($\mu_{\mathrm{M}} - \alpha_{\mathrm{Msex}}/2$)	923.3	5.5	919.7	927.0	914.4	932.5
Male mean mass ($\mu_{\mathrm{M}} + \alpha_{\mathrm{Msex}}/2$)	935.9	5.6	932.2	939.7	926.6	945.2
Sd bird to bird variation (σ_X)	38.2	5.3	34.6	42.0	28.9	46.4
Sd annual variation (σ_Y)	na	na	na	na	na	na
Sd residual variation (σ_M)	43.9	4.0	41.1	46.7	37.4	50.5
Change in mass per day (α_{Day})	-0.43	0.36	-0.67	-0.18	-1.02	0.16
Annual variation in change in mass	na	na	na	na	na	na
Observation probability parameters						
Intercept (μ_O)	0.98	0.20	0.84	1.12	0.64	1.32
Effect of being observed last year (γ_O)	3.51	0.16	3.40	3.62	3.25	3.76
Pseudo-age effect (γ_A)	-0.062	0.012	-0.070	-0.053	-0.081	-0.041
Year trend (γ_T)	na	na	na	na	na	na
Sd annual variation (σ_O)	0.29	0.10	0.21	0.35	0.13	0.47
Razorbills						
Mass-survival parameters						
Body mass effect (β_X)	-0.0048	0.0069	-0.0095	0.0002	-0.0162	0.0062
Year mass effect (β_Y)	na	na	na	na	na	na
Other survival parameters						
Intercept (μ_P)	2.68	0.25	2.52	2.84	2.28	3.11
Sd annual variation (σ_P)	0.80	0.19	0.67	0.91	0.52	1.14
NAO effect (β_{NAO})	-0.0775	0.1557	-0.1751	0.0243	-0.3429	0.1706
NAO previous year effect (β_{NAOd})	-0.2201	0.1430	-0.3138	-0.1261	-0.4547	0.0173
Pseudo-age effect (β_A)	0.0257	0.0418	-0.0049	0.0556	-0.0418	0.0949
Pseudo-age^2 effect (β_{A2})	-0.0024	0.0020	-0.0038	-0.0009	-0.0057	0.0010
First year effect (β_{A0})	na	na	na	na	na	na
Mass model parameters						
Female mean mass ($\mu_{\mathrm{M}} - \alpha_{\mathrm{Msex}}/2$)	614.5	10.4	607.5	621.3	597.4	631.9
Male mean mass ($\mu_{\mathrm{M}} + \alpha_{\mathrm{Msex}}/2$)	622.4	10.2	615.5	629.2	605.9	639.4
Sd bird to bird variation (σ_X)	30.6	2.3	29.0	32.0	27.1	34.6
Sd annual variation (σ_Y)	na	na	na	na	na	na
Sd residual variation (σ_M)	33.8	2.5	32.0	35.4	29.9	38.2
Change in mass per day (α_{Day})	-1.17	0.70	-1.63	-0.71	-2.31	-0.01
Annual variation in change in mass	na	na	na	na	na	na
Observation probability parameters						
Intercept (μ_O)	1.00	0.32	0.80	1.22	0.46	1.50
Effect of being observed last year (γ_O)	2.63	0.23	2.47	2.78	2.25	3.02
Pseudo-age effect (γ_A)	-0.111	0.021	-0.126	-0.096	-0.146	-0.077
Year trend (γ_T)	na	na	na	na	na	na
Sd annual variation (σ_O)	0.50	0.17	0.38	0.61	0.22	0.80