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# Changes in Survival with Age in Three Populations of a Long-lived Seabird, the Atlantic Puffin *Fratercula arctica*

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BIO-3950 Master's thesis in Biology, May 2021

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# ACKNOWLEDGEMENTS

# ABSTRACT

Actuarial senescence is the irreversible decline of survival with increasing age. This phenomenon varies widely between taxa and species along the slow-fast continuum. However, inter-populational senescence differences have been less investigated, especially in the avian order. Here, I compared senescence rate between three contrasting populations of the Atlantic puffin (*Fratercula arctica*), and between sex within colonies. To assess this, 31 years (1990-2020) of capture-mark-recapture data from together 2101 individuals from Isle of May, Røst and Hornøya were used. Most of the individuals were marked as breeding adults with unknown absolute age, and time elapsed since first capture (TFC) was used as a proxy for age. Productivity data were used as proxy for environmental conditions experienced in the breeding season to understand variation in senescence rates between populations. I found differences in senescence between the colonies, but not between the sexes. Productivity had different effect on senescence between the colonies suggesting different cost of reproduction under variable environment in the breeding season. Finally, resighting rate decreased with age, potentially having a biological relevance if it reflects reduced breeding probability with age. The colony with the lowest reproduction over the study span also had the lowest rate of senescence, indicating that puffins might be able to buffer poor reproduction with lower rates of senescence.

*Keywords:* Atlantic Puffin, *Fratercula arctica*, Actuarial senescence, Age-specific survival, Life-history, Capture-Mark-Recapture

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# 1. INTRODUCTION

As an individual ages, its chances of surviving and/or reproducing may decline, a phenomenon known as senescence (see Nussey et al. 2013 for a review). There is now widespread evidence for the occurrence of senescence in wild populations. Three major theories have been proposed to explain the evolution of senescence (Monaghan et al. 2018). Medawar (1952) hypothesized that senescence occurs due to accumulation of deleterious mutations, whereas Williams (1957) suggested it is caused by antagonistic pleiotropy, i.e. selection of favourable traits in early life that have deleterious effects in later life. Kirkwood (1977) proposed a theory linking senescence to early life trade-offs, known as the disposable soma theory. These three theories are not mutually exclusive, but fundamental to all of them is that the strength of natural selection declines with increasing age (Hamilton 1966; Kirkwood & Rose 1991). The occurrence of senescence has been assumed to start at the age at first reproduction (Williams 1957; Hamilton 1966), however, several studies did not find support for this, reporting onset of senescence occurring several years after maturation in some species (Péron et al. 2010; Gaillard & Lemaître 2017).

Decline in survival with age (i.e. actuarial senescence) (Robert et al. 2015; Gaillard et al. 2017) has been documented in a wide range of taxa, especially in birds and mammals, but also in invertebrates (Nussey et al. 2013). The pattern of senescence, both the onset and strength, varies between species across the slow–fast life-history continuum (Jones et al. 2014; Colchero et al. 2019), where species at the fast end have earlier onset and rate of senescence compared to those at the slow end. However, inter- and intra-populational variation in senescence has rarely been investigated (Loison et al. 1999; Bleu et al. 2015; Holand et al. 2016; Cayuela et al. 2020). Life history predicts that there are trade-offs between reproduction and survival (Stearns 1989), but the strength of this trade-off varies along the slow–fast continuum (Hamel et al. 2010). Generation time – the average age of mothers when they give birth (Leslie 1966) – is the best predictor of a species position on this continuum (Gaillard et al. 2005) and underlies trade-offs between survival and reproduction (Giaimo & Traulsen 2019). This fundamental trade-off plays a critical role in organisms' pattern of ageing and Hamilton (1966) predicted that high rates of fertility should be associated with higher rates of senescence.

Populations of the same species may be exposed to different environmental conditions, potentially affecting both their overall survival and age-specific survival differently (Cayuela et al. 2020). According to Williams (1957), higher mortality driven by environmental conditions will lead to more rapid senescence. Populations experiencing different causes and levels of mortality should therefore experience different onsets and rates of senescence (Monaghan et al. 2008; Holand et al. 2016). This has been confirmed in studies comparing the mortality and aging of captive individuals to wild individuals, among others in stalked-legged flies *Telostylinus angusticollis* (Kawasaki et al. 2008) and in ruminants (Lemaître et al. 2013), showing that individuals undergo a more rapid senescence in the wild. Different environmental conditions that vary in the wild affect mortality and senescence, for example food, predation, and weather (Monaghan et al. 2008) and some studies linked early life environmental impact on senescence (e.g. Reed et al. 2008). There is reason to believe that environment not only impact survival, but also reproduction. Cost of reproduction might for example be apparent only under harsh environmental conditions (Reznick 1985). On the other hand, favourable environmental conditions (e.g. abundant food sources, stable weather etc.) might increase cost of reproduction due to increased allocation to reproduction under favourable environmental conditions (Culina et al. 2019). Since costs are likely to vary depending on the environment, one may expect differences in senescence rates due to different environmental impact (Reed et al. 2008).

Intrinsic differences within a population such as sex, behaviour and individual quality have also different effects on the onset and rate of senescence (Pardo et al. 2013a; Patrick et al. 2015; Froy et al. 2017; Tompkins & Anderson 2019). Williams (1957) predicted that where there is a difference between the sexes, the sex with the higher mortality rate should have a steeper rate of senescence. This difference in mortality may arise due to differences in reproductive allocation, often linked to mating systems. Higher rates of actuarial senescence tend to be more male-biased in polygynous species, whereas little or no difference between the sexes is expected in monogamous species (Clutton-Brock & Isvaran 2007).

Studies of senescence have traditionally been biased towards mammals and birds (Nussey et al. 2013). There is now evidence of senescence in different avian orders including seabirds, but senescence studies in seabirds are limited due to several factors. First, estimating age of birds, based on anatomical markers (e.g. teeth, Christensen-Dalsgaard et al. 2010) is not possible

(Nisbet 2001, but see De Paoli-Iseppi et al. 2019). Hence, marking individuals as chicks is essential to accurately determine age. However, as seabirds disperse for several years after fledging and may experience high juvenile and immature mortality, in addition to natal dispersal, even large scale marking of chicks typically results in very low number of recaptures or resightings of breeding adults – contrasting to for example ungulates. Consequently, data on seabird survival are often restricted to adults of unknown age, with time elapsed since first capture (TFC) being the best proxy for age (e.g. Crespin et al. 2006). Second, due to the high longevity of most seabirds, long time series are crucial to document age-dependent changes in survival rates. Since sample size will always be lowest for the oldest age classes, large samples are needed to reach sufficient precision. Most seabirds are, however, characterised by high breeding philopatry (e.g. Coulson 2016), which helps securing high resighting rates and make them extra suitable for individual-based long-term studies.

Modelling survival in a capture-mark-recapture (CMR) framework (Lebreton et al. 1992) makes it possible to estimate survival without bias despite incomplete annual recapture or resighting (i.e. recapture/resighting probability < 1). Although age has been shown to be an important demographic component (e.g. Pardo et al. 2013b) it is not always accounted for when modelling survival and recapture in birds. Recapture rates might change with age and, thus, ignoring age in the recapture model might potentially bias survival estimates. Several studies have discussed the biological relevance of recapture rates in birds (Harris et al. 1997; Erikstad et al. 2009; Bouwhuis et al. 2012), with the possibility that it may reflect breeding probabilities. For example, Reed et al. (2008) found that older common guillemots *Uria aalge* tended to skip breeding more often than younger individuals. Breeding rate is likely to be affected by age due to reproductive senescence (i.e. decline in reproduction with increasing age) and hence lead to changed recapture/resighting probability.

Many seabirds are characterized by high adult survival rates (annual apparent survival ~ 0.9), a key demographic parameter in their life history. The population growth rate of long-lived species is most sensitive to variation in adult survival (Sæther & Bakke 2000) and seabirds avoid jeopardizing survival by foregoing reproduction to maximize their life-time reproductive output (Weimerskirch 2002). A typical example is the Atlantic puffin *Fratercula arctica* (hereafter puffin), a medium sized auk (Alcidae) breeding in colonies spread across the northern parts of the North Atlantic. The species has its strongholds in colonies in Iceland, Norway,

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Great Britain, and the Faroes. Numbers breeding at colonies in the Norwegian Sea, including Iceland and the Faroes have declined substantially, and the conservation status of the species is currently classed as 'vulnerable' (IUCN, 2019). Puffins are monogamous (Anker-Nilssen et al. 2008) and both the male and female share parental duties, albeit in unequal proportions (Creelman & Storey 1991; Anker-Nilssen et al. in manuscript). Former studies have reported no significantly effect of sex on survival in puffins (Harris et al. 1997; Harris et al. 2005; Erikstad et al. 2009) and there are few morphological differences between the sexes except that on average, the male is slightly larger (Barret et al. 1985). Adult survival of puffins in the northeast Atlantic has been linked to different environmental factors (Harris et al. 2005; Sandvik et al. 2005; Grosbois et al. 2009; Gimenez et al. 2012). However, age-specific survival has only been documented for one colony, the Isle of May (Harris et al. 1997). Although no large differences in survival rates between colonies in the northeast Atlantic have been documented (Harris et al. 2005), populations of puffins have been shown to differ in terms of several other aspects of their biology, including productivity, diet, non-breeding conditions, wintering areas and, ultimately, population trends (Barrett et al. 1987; Harris et al. 2005; Harris & Wanless 2011; Fayet et al. 2017; Reiertsen et al. in review). To what extent such differences may also affect senescence has not been investigated but may prove to have important consequences for populations and their future conservation. As the puffin is one of the most numerous North-Atlantic seabird species and is affected by many of the same environmental variables as other seabirds, it is a well-suited model species.

I used 31 years of capture-mark-recapture data for adult puffins of unknown age, using time elapsed since first capture (TFC) as a proxy for age, to investigate if three puffin colonies in the northeast Atlantic; Isle of May (North Sea), Røst (Norwegian Sea) and Hornøya (Barents Sea), show actuarial senescence and, if they do, whether it differed between colonies. While the Isle of May- and Hornøya populations have had high and relatively stable breeding success over the study period, the Røst population experienced more failed seasons (chick fledging success < 0.10 in 17 years) than seasons with moderate (0.10-0.70) or high (> 0.70) success (Cury et al. 2011; Harris & Wanless 2011; Barrett 2015; all data series updated for this study). This contrast allowed for comparison of population effects and levels of senescence. Harris et al. (1997) found evidence of actuarial senescence in puffins on the Isle of May indicating reduced survival for individuals estimated to be older than 20 years. Here I looked for similar trends at the two Norwegian colonies. In addition, I investigated differences in senescence rates between males

and females. Since the colonies experienced different rates of productivity and environmental conditions, I expected to find inter-population differences in actuarial senescence (Cayuela et al. 2020). I predicted that (1) Senescence will negatively affect generation time, i.e. colonies with the highest rate of senescence having the shortest generation time; (2) If skipping or giving up a breeding attempt increases the chances of survival to the next breeding season, birds at colonies with high productivity should have a higher rate of senescence; (3) There should be little or no sexual difference in actuarial senescence, given the morphological similarities between the sexes, the absence of evidence for a sex-effect on survival and the species' monogamous breeding system.

# 2. MATERIAL AND METHODS

## 2.1 Study colonies

Data on puffin survival and productivity were collected at 3 island colonies: Isle of May (56° 11' N, 2° 34' W) off the North Sea coast of southeast Scotland in the North Sea, and two Norwegian colonies Hernyken (67° 26' N, 11° 52' E, hereafter Røst) in the Røst archipelago in the Norwegian Sea and Hornøya (70° 27' N, 31° 9' E) on the southern coast of the Barents Sea (Fig. 1). These colonies differ with respect to environmental conditions such as the diet and climatic conditions encountered in and between the breeding season. Ultimately, they differ in breeding success and population size and trends (Table 1).
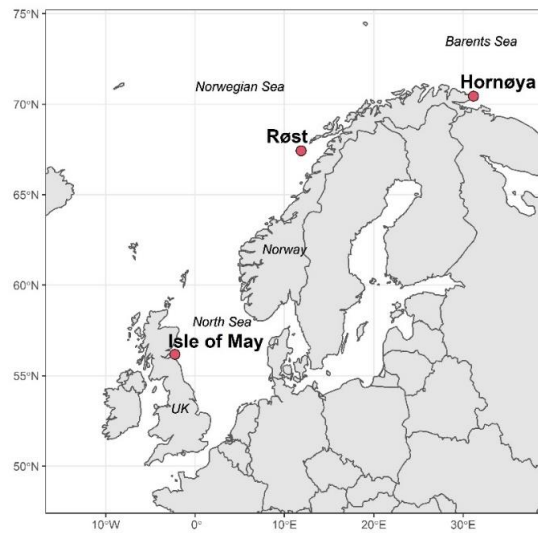


**Fig. 1:** Geographic location of the study colonies.

**Table 1**. Summary of main differences between the three colonies during the study period (1990-2020). See methods for further information on productivity. Population estimates are for year 2013 (Røst, Hornøya) and 2017 (Isle of May), adult survival rates are for year 1990-2001.

| Colony | Main wintering area[d,e] | Main prey in breeding season[f,g] | Median (range) productivity[f,g] | Mean ± SE adult survival[h] | Population size (pairs) and trend |
|---|---|---|---|---|---|
| Isle of May | North Sea | Sandeel, sprat | 0.67 (0.30-0.84) | 0.935 ± 0.007 | 39,000[a] (increase 1990-2003, decrease 2003-2009, thereafter ±stable) |
| Røst | Icelandic waters | Herring, gadoids | 0.09 (0.00-0.96) | 0.935 ± 0.013 | 418,000[b] (long-term decrease, except 2003-2007) |
| Hornøya | Barents Sea | Sandeel, capelin, gadoids | 0.77 (0.13-0.93) | 0.935 ± 0.016 | 8,300[c] (increase 1990-2003, thereafter ±stable) |

a) Harris & Wanless 2011 updated; b) T. Anker-Nilssen (SEAPOP data base) applying method of Anker-Nilssen & Røstad (1993) upscaled to the entire Røst archipelago as shown by Anker-Nilssen & Øyan (1995); c) Estimated as reported by Fauchald et al. 2015 (NINA Report 1151); d) Fayet et al. 2017; e) Reiertsen et al. (in review); f) Barrett (2015) updated ; g) Anker-Nilssen  Aarvak (2006) updated; h) Harris et al. 2005.

## 2.2 Survival and productivity data

This study uses capture-mark-recapture data from 31 years (1990-2020) collected as parts of long-term population monitoring of puffins on the Isle of May (n=605 individuals), Røst (n=569) and Hornøya (n=927). In all colonies breeding puffins were captured either on burrow (Isle of May, Hornøya), with traps (Hornøya) or with mist nets (Røst), and each marked with a numbered metal ring and either a unique combination of colour rings or, for the Norwegian colonies from 1997 and onwards, an individually coded colour-ring. Marked individuals were then visually searched for in the following breeding seasons. In most seasons, additional breeders were captured and marked to maintain sufficient sample size (See Appendix A for M-array of CMR data for each colony).

Information about sex was available for all individuals from Røst and for 43% of the individuals from Isle of May, but none for Hornøya. Individuals from Røst were either sexed based on molecular DNA by blood (n=317) (see Anker-Nilssen et al. 2017 for more detailed description), or by using a colony specific discriminant function based on head + bill length and bill depth at gonys (n=252) that was tested to classify correct sex for 86.8% of the individuals (Anker-Nilssen & Brøseth 1998). The individuals from Isle of May were sexed either by using a colony specific bill discriminant function confirmed by observations of mating or in later years by DNA samples.

Puffins have a single-egg clutch and measures of productivity were obtained at the population level for each colony by monitoring a sample of study burrows. Productivity was measured in terms of successful fledging. The definition of a successful fledging was, however, slightly different between the colonies. On the Isle of May productivity was measured as 'Chicks fledged per egg laid', on Røst as 'Chicks fledged per egg hatched' and at Hornøya as 'Large chicks (~20 days old) alive at the end of the field season per egg laid'.

## 2.3 Unknown age

Time elapsed since first captured as an adult (TFC) was used as a proxy for age, because the majority of the puffins were marked as adults and their true age was unknown for all except 55 individuals marked as chicks (29 on the Isle of May, 12 on Røst and 14 on Hornøya), corresponding to only 2.6% of the total sample. Most puffins start breeding at an age of 6 (4-8) years (Harris & Wanless 2011), hence this can be considered as the minimum age for all

individuals. As the birds did not enter the study at the same age, the drawback of the TFC method will be possible bias and increased uncertainty in our estimates (Péron et al. 2010). This approach should, however, still be sufficient to detect senescence in a population, as shown for common guillemots *Uria aalge* (Crespin et al. 2006). In an initial analysis, the use of TFC as a reasonable proxy for age in detecting senescence when the data are left truncated and the true age of individuals differ when entering the study were examined, as done by Crespin et al. (2006). Capture histories of 1000 individuals entering the study at different ages were generated with a senescence effect of 0.05. Then the initial capture histories of these was masked so the true age was unknown, and the analysis was run. The simulated estimate of senescence was close to the senescence effect (-0.055, 95% CI: -0.066, -0.044), indicating that the TFC-method will be sufficient to detect senescence.

**2.4 Environmental variables**

The variation in environmental conditions experienced by birds from the different colonies were accounted for by including two variables in the survival model, winter North Atlantic Oscillation (wNAO) and colony-specific productivity. wNAO is a climatic index measuring pressure differences between Iceland and Portugal, also known to affect weather conditions in the north Atlantic during the winter, mainly included to adjust for potential noise in the data. As winter conditions have shown to affect puffin survival (Sandvik et al. 2005; Reiertsen et al. in review), we used the station-based December-February North Atlantic Oscillation Index (Hurrell et al. 2020), since the colonies show no overlap in wintering areas during these months (Fayet et al. 2017). Colony specific productivity was used as a proxy for environmental conditions encountered in the breeding season with the justification that favourable environmental conditions increase the chances of successful reproduction, and unfavourable environmental conditions decrease success. Data on productivity were not available for three years on Hornøya (1991, 1994, 1999). As the modelling requires annual data for all covariates, the mean value of breeding success at this colony was used as a proxy for the missing years. In addition, productivity in three other years on Hornøya (2011, 2012, 2014) was most likely reduced by substantial predation from feral American mink (*Neovision vison*). We therefore also tested the model with mean values from other years for those additional three years, but this did not significantly change our results (see Table A4, Appendix B).

## 2.5 Age-specific survival analysis

The capture histories of the birds were analysed within a capture-mark-recapture (CMR) framework (Lebreton et al. 1992). As the recapture probability (hereafter resighting rate) was always less than one, birds not resighted in a given year were not necessarily dead. Although this model cannot distinguish death and permanent dispersal, once a bird has bred it rarely moves more than a few meters from its original breeding site (Ashcroft 1979; Harris & Wanless 2011). All analyses were done in R (version 4.0.3; R Core Team 2020). To estimate how age effects apparent adult survival (hereafter survival), the resighting histories for all colonies were modelled in RMark (Laake 2013), an R interface of the program MARK (White & Burnham 1999). As estimation of survival ($\phi$) depends on resighting probability (p), a Cormack-Jolly-Seber (CJS) model approach was used. A Gompertz mortality model was used to model the effect of senescence (Gaillard et al. 2004), where survival decreases with age, from equation:

$$\phi(a_i) = \exp(\alpha * \exp(\beta * a_i))$$

where $\phi(a_i)$ is the age-specific survival at age $a_i$, $\exp(\alpha)$ is baseline survival (i.e. initial survival experienced by individuals at the age of first reproduction, $a_i = 0$) and $\beta > 0$ is the rate of senescence. Hence, this model assumes senescence to start at the age of first reproduction. To use this in the context of CMR modelling, the model was rewritten, following Gaillard et al. (2004):

$$\log(-\log(\phi(a_i))) = \log(-\alpha) + \beta * a_i$$

where $\phi(a_i)$ is the age-specific survival. To implement this model in MARK, a complementary log-log-link was used, and age was included as a continuous linear effect. This is a well-used method for modelling senescence (but see Gaillard et al. 2017 for limitations of this approach).

## 2.6 Model selection

First, all three colonies were modelled separately in a simple model only including age as a categorical variable to investigate the general age-specific survival in each colony. Further, to investigate differences in senescence between the colonies, all colonies were modelled in a joint model, with age, wNAO and productivity as covariates. Different interactions between colony-age, and colony-age-productivity were tested as age and productivity impacts on survival were expected to be colony specific. In addition, for Isle of May and Røst, age- and sex specific

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survival was modelled to investigate differences in sex-specific senescence within the colonies. Each colony was therefore modelled separately with age and sex as additive or interaction effects. From all models including age a model selection was done based on the Akaike information criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002). Of models within Δ2AICc of the best model, the most parsimonious was chosen. When modelling resighting rates, differences between years and colonies were expected based on previous studies of these populations (Harris et al. 2005; Grosbois et al. 2009). Further examination of age effect on resighting rate was done, with the expectation that it would decrease with increasing age (e.g. Harris et al. 1997; Reed et al. 2008; Crespin et al. 2006; Bouwhuis et al. 2012), as this might be a result of reproductive senescence if the most experienced birds tend to skip breeding and stay away from the colony more often than younger birds. Different models for p with age, colony and time were tested and the best one was used in all candidate survival models. In addition to model resighting rate within a CMR framework, a colony-specific inspection of the capture history was done to closer investigate if resighting rate changes with age and if it was in accordance with the CMR model. In this approach, a binomial generalized linear mixed model (GLMM) with the R package *lme4* (Bates et al. 2015) was used. Individual (ID) and time (year) were included as random effects, to account for possible heterogeneity between the individuals and annual variation in resighting rates.

## 2.7 Generation time

Among species, senescence patterns (onset and rate) are highly related to their position along the slow-fast continuum, which in turn is best measured by generation time (GT). Hence, GT was estimated for each colony, by calculating a Leslie matrix (Leslie 1945) including adult survival, fecundity, and juvenile survival. Adult survival was based on the best model (see results), assuming senescence starts after average age at first reproduction (i.e. 6 years). Fecundity was based on mean annual productivity for each colony for adults 6 years or older. As little empirical data exist for juvenile survival in puffins, some assumptions had to be made to construct the matrix. Juvenile survival was assumed to be slightly lower than adult survival and set to 0.8 and increasing towards age at first reproduction. The survival rate from fledging to the next year was sat to 0.5, although Sandvik et al. (2008) found some cohorts having higher chances of survival. The R package *demogR* was used to do an eigenanalysis on the Leslie

matrix obtaining elasticities to calculate the GT following Bienvenu & Legendre (2015) as the inverse of the sum of the elasticities (e) for fecundity:

$$GT = \frac{1}{\Sigma_i \, e_\lambda(f_i)}$$

## 2.8 Goodness of fit

Prior to the analyses, a goodness of fit test was conducted using the RELEASE program implemented in MARK to examine if the data fitted the assumptions of a CJS model. The goodness of fit of the data for each colony was tested separately, and two general tests were conducted. The first (TEST 2 in RELEASE) tested for the assumption that survival and resighting are independent of specific sampling occasions (i.e. trap dependence). This was violated in all populations ($p < 0.001$), indicating a trap happiness in all colonies (i.e. that individuals seen in year $t$, have a higher probability to be seen in year $t+1$ than an individual not seen in year $t$). This was accounted for by incorporating trap dependence in the resighting model as suggested by Pradel (1993). The second test (TEST 3 in RELEASE) checked if survival and resighting were independent of prior capture histories, which was not violated for Isle of May ($\chi^2_{53} = 46.22$, $p = 0.734$) and Røst ($\chi^2_{43} = 37.94$, $p = 0.690$), but significant for Hornøya ($\chi^2_{40} = 58.92$, $p = 0.027$). This might be caused by transition, i.e. that individuals captured are never seen again because they transit to a different state by changing their behaviour or whereabouts and should ideally be accounted for. However, this was impractical as all colonies were included in the same model.

# 3. RESULTS

## 3.1 Colony-specific actuarial senescence

Puffins in all three colonies showed actuarial senescence as survival decreased when age (time since first capture, TFC) increased, as illustrated by the outputs of the general age-specific models (Fig. 2). The best supported model with all colonies together indicated an effect of age, colony, and productivity on survival, with an interaction between the three covariates. The model with an age-colony interaction was considerably better than the model without such interaction (Table 2), indicating that senescence rate differed between the colonies. The baseline mortality differed between colonies (intercept estimates (95% CI) on a cloglog scale at median colony-specific productivity: Isle of May: 2.86 (2.69, 3.03); Røst: 2.33 (2.14, 2.52); Hornøya: 2.61 (2.46, 2.77), back transformed to real survival estimates (95% CI): Isle of May: 0.944 (0.934, 0.953); Røst: 0.907 (0.888, 0.922); Hornøya: 0.929 (0.918, 0.939) (Fig. 3). Survival probability decreased with age (slope estimates (95 % CI) on a cloglog scale at median colony-specific productivity: Isle of May: -0.054 (-0.074, -0.033); Røst: -0.015 ( -0.036, 0.007); Hornøya: -0.107 (-0.127, -0.086)) (Fig. 3), in accordance with the general model of colonies modelled separately (Fig 2). Productivity was included in all the best supported models, but it had a strong negative effect on age-specific survival on Røst, i.e. acting to increase senescence, in contrast to a positive effect on Isle of May and Hornøya (Appendix B, Table A5). wNAO did not have a clear effect on senescence in any of the populations.

**Table 2:** Model selection table showing the best survival (ɸ) and recapture (p) models. A = Age as a linear effect, Col = Colony, fs = productivity, nao = winter North Atlantic Oscillation, time = year, k = number of estimated parameters.

| Model (ɸ) | Model (p) | k | ΔAICc | Weight | Deviance |
|---|---|---|---|---|---|
| A + col + fs + A*col + col*fs + A*fs + A*fs*col | t + A + Col | 46 | 0.00 | 0.726 | 19648.91 |
| A + col + fs + nao + A*col + col*fs + A*fs + A*fs*col | t + A + Col | 47 | 2.01 | 0.266 | 19648.90 |
| A + col + fs + A*col + col*fs | t + A + Col | 43 | 10.23 | 0 | 19665.19 |
| A + col + fs + nao + A*col + col*fs | t + A + Col | 44 | 12.22 | 0 | 19665.16 |
| A + col + fs + nao + A*col + col*fs + col*nao | t + A + Col | 46 | 12.76 | 0 | 19661.67 |
| A + col + A*col | t + A + Col | 40 | 74.09 | 0 | 19735.08 |
| A + col + fs | t + A + Col | 39 | 90.39 | 0 | 19753.39 |
| A + col + fs + nao | t + A + Col | 40 | 92.31 | 0 | 19753.30 |
| A + col | t + A + Col | 38 | 101.47 | 0 | 19766.48 |
| A + col + nao | t + A + Col | 39 | 103.40 | 0 | 19766.41 |
| A | t + A+ Col | 36 | 153.57 | 0 | 19822.60 |
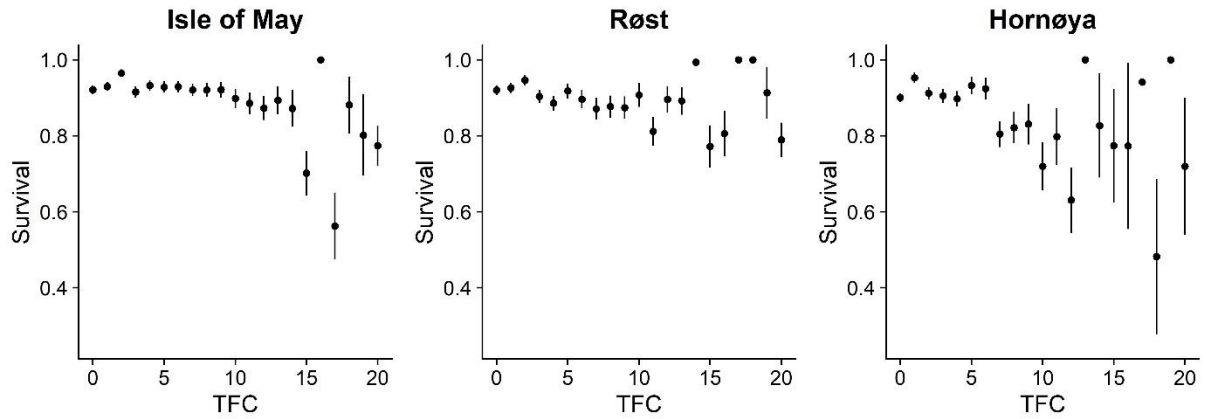
**Fig 2.** General age-specific survival of adult Atlantic puffin in each study colony. Colonies modelled separately with age (TFC) as a categorical factor, i.e. $\phi(A)P(t+A)$. Black circles are the point estimates for each age and error bars indicate ± 1 SE.
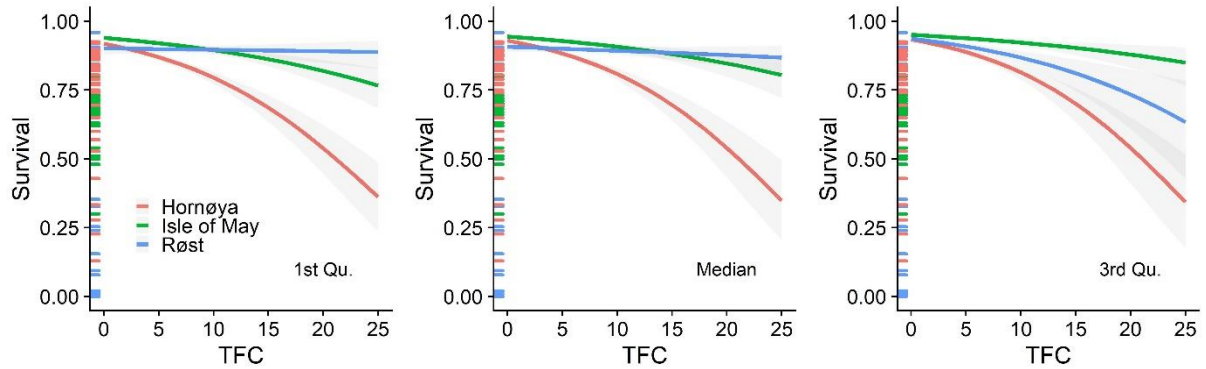


**Fig. 3:** Predicted age-specific survival for adult Atlantic puffin in the study colonies at different colony-specific levels of observed fledging success (1st Quartile, median, 3rd Quartile) during the study period (Isle of May: 1st Qu.: 0.64, Median: 0.69, 3rd Qu.: 0.73, Røst: 1st Qu.: 0.00, Median: 0.09, 3rd Qu 0.66, Hornøya: 1st Qu.: 0.61, Median: 0.77, 3rd Qu.: 0.84). Grey shading represents 95% confidence interval. Rug bars on y axis indicate colony-specific productivity during the study period (1990-2019).

## 3.2 Sex-specific actuarial senescence

The sex ratio of the individuals on Isle of May was equal ($n_{female} = 132$, $n_{male} = 130$), whereas it was skewed towards females on Røst ($n_{female} = 337$, $n_{male} = 232$). There was, however, no significant difference in actuarial senescence between males and females at either colony (Fig. 4), with a simple model with only age being within $\Delta 2AICc$ of the models including sex (Table 3). In both colonies, the simplest model including only sex as an additive effect was marginally better than the model with a sex-age interaction.

**Table 3**: Model selection table for sex specific senescence for Isle of May and Røst.

| Colony | Model (φ) | Model (p) | k | ΔAICc | Weight | Deviance |
|---|---|---|---|---|---|---|
| Isle of May | Age | t + age + sex | 34 | 0.00 | 0.53 | 2503.107 |
| | Age + sex | t + age + sex | 35 | 1.09 | 0.30 | 2502.146 |
| | Age*sex | t + age + sex | 36 | 2.43 | 0.16 | 2501.427 |
| Røst | Age + sex | t + age + sex | 36 | 0.00 | 0.48 | 5419.143 |
| | Age | t + age + sex | 35 | 1.06 | 0.28 | 5422.250 |
| | Age*sex | t + age + sex | 37 | 1.43 | 0.24 | 5418.536 |
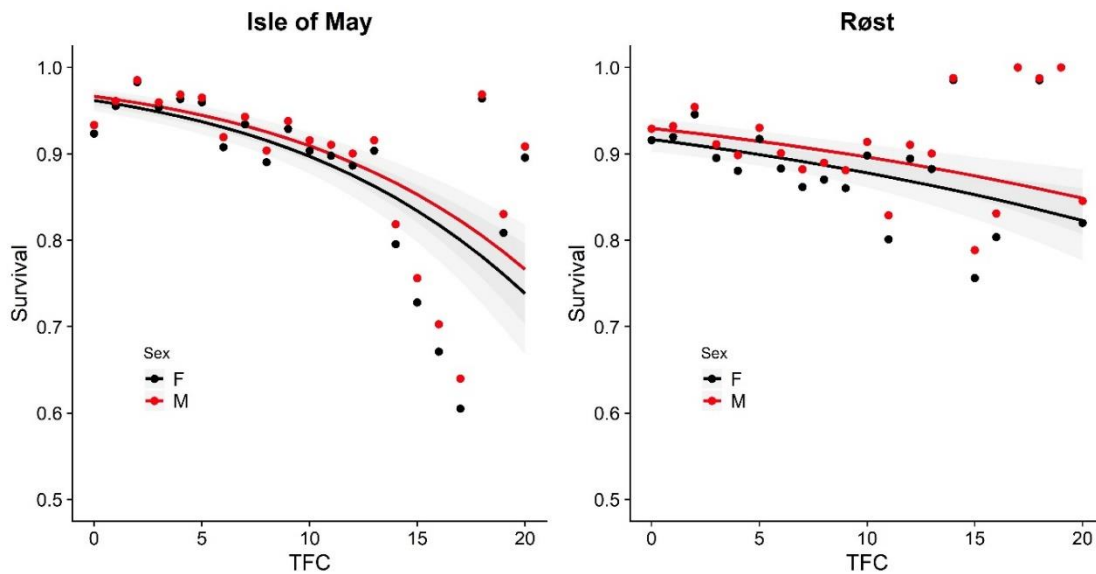


**Fig 4:** Predicted age- and sex-specific survival for adult Atlantic puffin on Isle of May ($n_{female} = 132$, $n_{male} = 130$) and Røst ($n_{female} = 337$, $n_{male} = 232$). Each plot was generated from the colony-specific model with age and sex as additive effects. Points are survival estimates for each age class and lines represent survival as a linear effect of age. Shaded area represents 95% confidence intervals.

### 3.3 Resighting rate

The resighting rate varied with colony, year, and age, with the best model including all three covariates. Age had a negative effect on resighting rate (logit scale -0.05, 95CI: -0.07, -0.04). Excluding age in the resighting model severely underestimated survival, especially for the Hornøya population, which also was the colony with the highest inter-annual variation in resighting rate. A further colony-specific inspection of capture histories to investigate how resighting rate changed with age (Fig. 5) was in accordance with findings of the joint model.
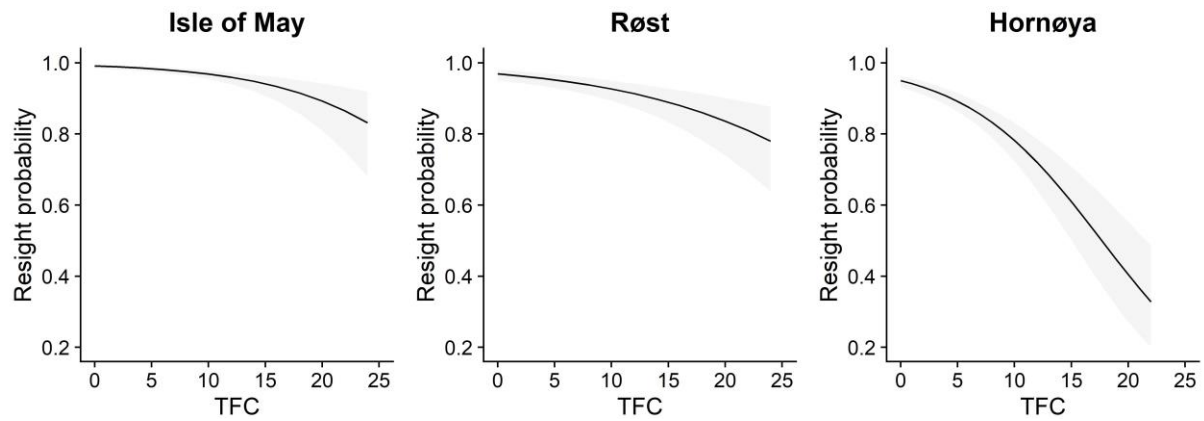
**Fig. 5:** Predicted resighting probability as a function of age (TFC) for adult Atlantic puffin in the different colonies. Gray shading represents 95% confidence interval.

## 3.4 Generation time

The generation time was calculated for each colony, using the age-specific survival estimates for adult survival at median productivity, productivity rates and approximated survival estimates for immatures. The generation time for Isle of May was estimated to be 12.4 years, Røst 16.3 years and Hornøya 10.6 years.

# 4. DISCUSSION

This study estimates rates of actuarial senescence for adult puffins in three colonies in different seas spread across a latitudinal gradient of the northeast Atlantic Ocean. The study populations differed in terms of their population status, productivity, and non-breeding distribution. As predicted, the degree of actuarial senescence differed between the colonies, but not between males and females. Resighting rate decreased with age in all colonies, suggesting that the likelihood of skipping breeding increased with age.

The baseline survival rate differed between the three populations and all showed actuarial senescence, which may well be the rule rather than the exception for most animal species (Nussey et al. 2013; Gaillard & Lemaître 2020). Our results are in accordance with earlier findings of senescence in puffins at the Isle of May (Harris et al. 1997), although derived using a slightly different approach. The mean annual adult survival rates have been reported to be very similar for the colonies investigated (Harris et al. 2005), hence the substantial differences in senescence was somewhat surprising. Williams (1957) predicted that higher extrinsic mortality should lead to higher rates of senescence. As mean adult survival rates do not account for age, differences in senescence can still be apparent. Moreover, if the baseline survival represents the degree of extrinsic mortality in a colony, one should expect a steeper senescence at Røst which had the lowest baseline survival. Although the mean adult survival rate was similar in all colonies (Harris et al. 2005), there were differences in the inter-annual variation of the annual adult survival, indicating differences in variability in survival rates between the colonies, Hornøya being the most variable. This might explain why differences in senescence is found despite small differences in the mean adult survival rate. The environmental variable wNAO was a general index aimed to adjust for noise potentially affecting the senescence estimates, due to the environmental conditions puffins experience during the winter. Puffins from the different colonies disperse to different wintering areas, with no overlap (Fayet et al. 2017; Reiertsen et al. in review). As no evidence for an effect of wNAO was found, it is not discussed any further. However, effect of environment experiences in the non-breeding season might be an important factor explaining senescence differences between the colonies, through both direct and indirect effects. This is beyond the scope of this paper but is an important question for further understanding of the demography for this species. Overall, the contrasting

differences senescence rates between the colonies are in accordance with the predictions, although surprisingly high at Hornøya. Few studies have compared senescence among populations of the same species (but see Loison et al. 1999 and Blur et al. 2015 for ungulates, Cayuela et al. 2020 for amphibians). Holand et al. (2016) found evidence of spatial variation in actuarial senescence rates in a house sparrow (*Passer domesticus*) metapopulation, but found no link to environmental differences between the populations investigated.

Some studies investigating inter-populational differences in adult survival and reproduction rates in seabirds (e.g. Weimerskirch et al. 2002; Frederiksen et al. 2005; Nevoux et al. 2010) report trade-offs between reproduction and survival. In accordance with life history theory (e.g. Stearns 1989) and the disposable soma theory (Kirkwood 1977) the rate of senescence should be higher on Isle of May and Hornøya, where puffins in contrast to Røst had a much higher and stable breeding success over the study period which covered approximately two generation times in all colonies. There was no data to distinguish between the relative contribution of reproductive effort and environmental conditions to the variation in breeding success in puffins. As long-lived seabirds are known to avoid jeopardizing their survival over reproduction (Weimerskirch et al. 2002), environmental conditions were expected to be the most important factor. The effect of productivity, here used as a proxy for environmental conditions in the breeding season, differed between the colonies. Isle of May and Hornøya showed increased senescence under poor environmental condition, while the opposite was true for Røst. In terms of energy invested per chick, it might seem that reproduction was more costly at Røst, given the steep decline in survival at higher productivity, but not in terms of energy spent per breeding attempt, with higher survival at low productivity and poor environmental conditions. This indicates an important adaptation for puffins at Røst, to some extent being able to buffer the low productivity with lower rates of senescence. Experimental studies of reproductive allocation in puffins show that they are prudent parents, able to adjust their investment based on both own and their chick's condition (e.g. Erikstad et al. 1997, 2009). The more able puffins are to limit their allocation of energy to reproduction when environmental conditions are too poor for breeding success, the higher are likely their chances of post-breeding survival. Such a flexible strategy can be a large advantage when breeding in a highly stochastic environment (Erikstad et al. 1998). This might be true for Røst, experiencing more variable environment, based on the large variability in breeding success the last decades (Anker-Nilssen & Aarvak 2006). Without combined reproduction and survival data at the individual level, one cannot

quantify the fitness-related trade-offs between survival and reproduction, but the different effect of productivity on senescence between the colonies could suggest different life-history strategies have developed at the different colonies. Other studies have found reproductive effort to accelerate actuarial senescence (Boonekamp 2020), which might be the case for our colonies as well. It can be argued that productivity is an ambiguous proxy for environmental conditions in the breeding season because it might also correlate with reproductive effort. Hence, high reproductive success might be caused by good environmental conditions but may also be costly for the individual if it leads to increased allocation of resources towards reproduction (e.g. Hadley et al. 2007). In this analysis, productivity was measured on the population level, which makes it likely to reflect the general breeding conditions experienced in the breeding season, rather than the cost of reproduction on the individual level.

At the two colonies where birds were sexed there was no significant difference in actuarial senescence between males and females, as predicted for a monogamous species like the puffin (Clutton-Brock & Isvaran 2007). As earlier findings do not provide evidence for sex-specific survival for puffins (Harris et al. 1997; Harris et al. 2005; Erikstad et al. 2009), no sex specific senescence as shown here is in accordance with Williams (1957) predictions. Interestingly, although not statistically significant, females showed consistently a slightly lower rate of survival at both colonies, indicating a systematically higher mortality in females. Anker-Nilssen et al. (in manuscript) show that colony attendance (in terms of sitting on the colony surface) on Røst is higher for males than females, whereas females provide food for the chick more often than males. Combined with the obvious difference in egg production, such differences in breeding effort and allocation could result in a corresponding difference in both survival and senescence between the sexes.

The finding that resighting rate decreases with age is biologically interesting if this is because old birds more frequently skip breeding events or abandon the offspring and leave the colony early on, i.e. reflecting an increased reproductive senescence. The pattern that the resighting rate decreases with age is also found in studies of other species (e.g. Crespin et al. 2006, Reed et al. 2008, Bouwhuis et al. 2012). This highlights the importance of including age in resighting/recapture rate estimation to avoid underestimating survival if individuals start skipping breeding seasons more often when they get older. However, other studies have found

opposite patterns, for instance terminal reproductive improvement in an albatross population, without any decrease in recapture probability (Pardo et al. 2013b).

The results need to be interpreted with some caution, as several assumptions were made, and different sources of bias were present. First, the major limitation of this study is that the exact age of individuals is unknown as almost all were marked as adults. As most puffins start breeding at around 6 (4-8) years (Harris & Wanless 2011), this is the minimum age of all individuals in the study. The generation time varied between colonies, possibly suggesting TFC differed between the colonies. It is still likely that the results reflect an actual senescence in each colony, but differences in TFC would tend to shift the onset of senescence. Harris et al. (1997) used 10 years as an average initial age for puffins entering their study. This might well be a good average estimate for individuals in this study too. As some puffins were marked (with metal rings) before the onset of this study, there was substantial heterogeneity in age at colour ringing. This violates the model assumption that all individuals are of same age when entering the model. Nevertheless, Crespin et al. (2006) also found TFC to be a reliable method for investigating senescence for another auk species on the Isle of May, the common guillemot. Although the breeding behaviour of puffins is more cryptic, possibly acting to widening the age span of individuals when entering the study and thereby underestimate the confidence interval of the estimates, the TFC simulations indicated this approach was also a valid proxy for assessing senescence in puffins.

Another source of bias might be individual heterogeneity. Individuals vary in quality (Hamel et al. 2018) and age-specific differences in individual quality might affect the results. For example, older age classes might have a higher proportion of high-quality individuals, due to selective disappearance of the lower quality individuals. Such differences could mask senescence (Gaillard et al. 2017; Gimenez et al. 2018) and several studies have emphasized the importance of accounting for heterogeneity in CMR-studies studies (e.g. Cam et al. 2002; Péron et al. 2010; Fay et al. 2018). Although I had no measurements of individual quality (e.g. body mass or reproductive success) except sex for two colonies, senescence was still detected in all three study populations despite no adjustments for individual heterogeneity.

Understanding the age structure is an important aspect of ecology and conservation of populations. The impact of senescence might be critical in populations experiencing years of

breeding failures, accelerating population decline and slowing down population recovery. Several years of no recruitment should shift the age structure in the colony towards older individuals, negatively affecting annual estimates of survival. The Røst colony has experienced virtually total breeding failures annually since 2006, meaning that any given individual today (Year 2021) will be at least 15 years old, with the average age in the population being significantly higher. If individuals on Røst had the same rate of senescence as the individuals at Hornøya, the population should already have experienced an accelerating rate of decrease, which is not the case (T. Anker-Nilssen, unpublished data).

# 5. CONCLUSION

This study is among the few exploring inter-population differences in actuarial senescence, and, to my knowledge, the first documenting this in seabirds. I show that different populations of a species simultaneously experienced large differences in rates of senescence. Understanding why life-history traits vary among populations and species is a central goal of evolutionary theory, and these findings provide valuable insight for further investigations on seabirds. The results show that generalizing across colonies should be done with caution, as different processes can have different effects on different populations. To accurately model the performance of seabird populations, and populations in general, we need more information on what influences the demographic processes in populations, such as senescence.

I have only used data from three colonies, making it hard to draw robust conclusions on the causes of differences in senescence within this species. In the future, stronger focus on comparative studies with larger number of colonies and species is important to obtain better evidence of the key mechanisms that produce intra-specific patterns in survival and senescence. Senescence is undoubtedly something that occurs in most wild populations. We need now to better understand the ecological and evolutionary mechanisms causing variations in senescence rates, and their consequences for population dynamics. My findings indicated that the high incidence of breeding failure in the Røst colony, was partly counteracted by a lower rate of senescence. Similarly, analysing causes of winter mortality may help us understanding why senescence rates were so much higher in the Hornøya population. Seabirds are threatened all over the world (Dias et al. 2019), highlighting the urgent need for increased understanding about the processes affecting them. As some populations, like Røst in our study, might experience higher incident of breeding failures impacting recruitment to the population, changes in senescence rates could be important in assessing population status and future trends.

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# APPENDIX

## APPENDIX A

**Table A1:** CMR data set from Isle of May presented as M-array. N = Number of individuals present each year (first capture or resighted). The other columns show the number of individuals resighted for the first time after they were resighted or first captured in a given year.

| Year | N | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | 2020 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1990 | 72 | 59 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1991 | 151 |  | 143 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1992 | 172 |  |  | 166 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1993 | 188 |  |  |  | 181 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1994 | 189 |  |  |  |  | 170 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1995 | 179 |  |  |  |  |  | 165 | 3 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1996 | 192 |  |  |  |  |  |  | 176 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1997 | 192 |  |  |  |  |  |  |  | 166 | 9 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1998 | 178 |  |  |  |  |  |  |  |  | 159 | 4 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1999 | 188 |  |  |  |  |  |  |  |  |  | 165 | 6 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2000 | 178 |  |  |  |  |  |  |  |  |  |  | 161 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2001 | 181 |  |  |  |  |  |  |  |  |  |  |  | 148 | 11 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2002 | 172 |  |  |  |  |  |  |  |  |  |  |  |  | 142 | 5 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2003 | 197 |  |  |  |  |  |  |  |  |  |  |  |  |  | 176 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2004 | 214 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 167 | 11 | 5 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2005 | 201 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 165 | 12 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2006 | 197 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 113 | 11 | 5 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2007 | 145 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 86 | 6 | 6 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 2008 | 135 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 112 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2009 | 130 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 116 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2010 | 177 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 156 | 7 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2011 | 176 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 158 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2012 | 168 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 143 | 3 | 5 | 0 | 0 | 0 | 0 | 0 |
| 2013 | 168 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 138 | 10 | 1 | 0 | 0 | 0 | 0 |
| 2014 | 144 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 128 | 6 | 1 | 0 | 0 | 0 |
| 2015 | 146 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 104 | 4 | 0 | 0 | 0 |
| 2016 | 130 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 115 | 5 | 1 | 0 |
| 2017 | 124 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 118 | 1 | 1 |
| 2018 | 134 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 113 | 5 |
| 2019 | 122 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 99 |

**Table A2:** CMR data set from Røst presented as M-array. For details, see Table 1A.

| Year | N | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | 2020 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1990 | 72 | 59 | 8 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1991 | 166 |  | 150 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1992 | 178 |  |  | 156 | 11 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1993 | 159 |  |  |  | 135 | 8 | 5 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1994 | 158 |  |  |  |  | 120 | 10 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1995 | 131 |  |  |  |  |  | 100 | 9 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1996 | 142 |  |  |  |  |  |  | 111 | 8 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1997 | 132 |  |  |  |  |  |  |  | 89 | 13 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1998 | 140 |  |  |  |  |  |  |  |  | 111 | 10 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1999 | 170 |  |  |  |  |  |  |  |  |  | 134 | 10 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2000 | 168 |  |  |  |  |  |  |  |  |  |  | 117 | 15 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2001 | 155 |  |  |  |  |  |  |  |  |  |  |  | 130 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2002 | 170 |  |  |  |  |  |  |  |  |  |  |  |  | 138 | 10 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2003 | 151 |  |  |  |  |  |  |  |  |  |  |  |  |  | 131 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2004 | 171 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 133 | 18 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2005 | 148 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 131 | 0 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2006 | 168 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 57 | 56 | 7 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2007 | 57 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 38 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2008 | 99 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 78 | 11 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 2009 | 94 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 82 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 2010 | 94 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 73 | 10 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2011 | 81 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 67 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2012 | 78 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 52 | 13 | 2 | 0 | 0 | 1 | 0 | 0 |
| 2013 | 85 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 70 | 4 | 0 | 1 | 1 | 0 | 0 |
| 2014 | 126 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 101 | 5 | 0 | 0 | 1 | 0 |
| 2015 | 125 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 103 | 5 | 1 | 0 | 3 |
| 2016 | 120 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 111 | 2 | 0 | 0 |
| 2017 | 128 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 113 | 6 | 1 |
| 2018 | 129 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 100 | 8 |
| 2019 | 112 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 91 |

**Table A3:** CMR data set from Hornøya presented as M-array. For details, see Table 1A.

| Year | N | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | 2020 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1990 | 35 | 3 | 19 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1991 | 235 | | 173 | 7 | 2 | 6 | 6 | 0 | 4 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1992 | 204 | | | 128 | 23 | 7 | 3 | 4 | 5 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1993 | 141 | | | | 97 | 16 | 2 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1994 | 339 | | | | | 263 | 21 | 4 | 3 | 3 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1995 | 308 | | | | | | 236 | 24 | 6 | 0 | 5 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1996 | 270 | | | | | | | 199 | 20 | 11 | 1 | 4 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1997 | 232 | | | | | | | | 183 | 9 | 2 | 5 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1998 | 278 | | | | | | | | | 183 | 16 | 9 | 1 | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1999 | 212 | | | | | | | | | | 153 | 13 | 6 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2000 | 179 | | | | | | | | | | | 121 | 18 | 4 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2001 | 159 | | | | | | | | | | | | 97 | 7 | 5 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2002 | 128 | | | | | | | | | | | | | 89 | 3 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2003 | 114 | | | | | | | | | | | | | | 55 | 4 | 1 | 1 | 1 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2004 | 107 | | | | | | | | | | | | | | | 41 | 16 | 14 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2005 | 93 | | | | | | | | | | | | | | | | 64 | 3 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2006 | 104 | | | | | | | | | | | | | | | | | 70 | 9 | 3 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2007 | 89 | | | | | | | | | | | | | | | | | | 61 | 9 | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2008 | 75 | | | | | | | | | | | | | | | | | | | 56 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 2009 | 98 | | | | | | | | | | | | | | | | | | | | 78 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2010 | 101 | | | | | | | | | | | | | | | | | | | | | 62 | 8 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| 2011 | 69 | | | | | | | | | | | | | | | | | | | | | | 47 | 6 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2012 | 93 | | | | | | | | | | | | | | | | | | | | | | | 62 | 12 | 0 | 0 | 0 | 0 | 1 | 0 |
| 2013 | 81 | | | | | | | | | | | | | | | | | | | | | | | | 34 | 12 | 1 | 0 | 0 | 0 | 0 |
| 2014 | 100 | | | | | | | | | | | | | | | | | | | | | | | | | 59 | 4 | 2 | 1 | 2 | 0 |
| 2015 | 102 | | | | | | | | | | | | | | | | | | | | | | | | | | 90 | 2 | 1 | 1 | 0 |
| 2016 | 121 | | | | | | | | | | | | | | | | | | | | | | | | | | | 96 | 12 | 2 | 0 |
| 2017 | 134 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 98 | 11 | 1 |
| 2018 | 140 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 76 | 8 |
| 2019 | 104 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 58 |

# APPENDIX B

Model tables and estimates

**Table A4.** Cloglog survival estimates from the best model (A + col + fs + A:col + col:fs + A:fs + A:fs:col) where three years (2011, 2012, 2014) of productivity negatively influences by predation was substituted with mean values of productivity over the study period (1990-2019).

| Parameter | Estimate | SE | LCL | UCL |
|---|---|---|---|---|
| Phi:(Intercept) | 2.265 | 0.110 | 2.048 | 2.481 |
| Phi:Age | -0.005 | 0.013 | -0.030 | 0.020 |
| Phi:colonyIOM | -1.000 | 0.444 | -1.870 | -0.129 |
| Phi:colonyHornøya | 0.103 | 0.412 | -0.704 | 0.910 |
| Phi:fs | 0.708 | 0.241 | 0.235 | 1.181 |
| Phi:Age:colonyIOM | -0.139 | 0.043 | -0.223 | -0.056 |
| Phi:Age:colonyHornøya | -0.107 | 0.062 | -0.229 | 0.015 |
| Phi:colonyIOM:fs | 1.676 | 0.719 | 0.267 | 3.084 |
| Phi:colonyHornøya:fs | -0.456 | 0.579 | -1.592 | 0.679 |
| Phi:Age:fs | -0.111 | 0.032 | -0.173 | -0.049 |
| Phi:Age:colonyIOM:fs | 0.247 | 0.075 | 0.101 | 0.394 |
| Phi:Age:colonyHornøya:fs | 0.126 | 0.089 | -0.049 | 0.298 |

**Table A5.** Cloglog survival estimates from the best model (A + col + fs + A:col + col:fs + A:fs + A:fs:col).

| Parameter | Estimate | SE | LCL | UCL |
|---|---|---|---|---|
| Phi:(Intercept) | 2.267 | 0.110 | 2.051 | 2.482 |
| Phi:Age | -0.005 | 0.013 | -0.030 | 0.019 |
| Phi:colonyIOM | -1.005 | 0.444 | -1.875 | -0.134 |
| Phi:colonyHornøya | -0.385 | 0.258 | -0.891 | 0.121 |
| Phi:fs | 0.706 | 0.251 | 0.233 | 1.179 |
| Phi:Age:colonyIOM | -0.138 | 0.043 | -0.222 | -0.055 |
| Phi:Age:colonyHornøya | -0.065 | 0.032 | -0.129 | -0.001 |
| Phi:colonyIOM:fs | 1.683 | 0.718 | 0.275 | 3.092 |
| Phi:colonyHornøya:fs | 0.244 | 0.410 | -0.559 | 1.047 |
| Phi:Age:fs | -0.110 | 0.031 | -0.172 | -0.048 |
| Phi:Age:colonyIOM:fs | 0.245 | 0.075 | 0.099 | 0.391 |
| Phi:Age:colonyHornøya:fs | 0.063 | 0.054 | -0.043 | 0.170 |