

# WILDLIFE BIOLOGY

## Research Article

### Variation in food availability affects the population age structure of Atlantic puffins *Fratercula arctica* in the Faroe Islands

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Across their entire Atlantic breeding range, Atlantic puffins *Fratercula arctica* have experienced decreases in food availability, often leading to population declines. The species is one of the most numerous seabirds in Føroyar (the Faroe Islands, in English) but has faced apparent, unquantified population declines. To better understand the underlying processes of this decline in Føroyar, we studied the change in the average, estimated age of puffins (i.e. the population age structure) harvested over a 20-year period (1989–2008). We assessed how the population age structure changed over time and in relation to food availability indices (i.e. phytoplankton primary production, juvenile fish). We showed that the average age of the birds in the population increased over time during the studied period, as the contribution of younger age classes declined, and cohort sizes decreased. Further, we showed that population age structure was significantly affected by food availability in the hatch year and the years preceding the hatch year, but only one of the relationships with food availability in the harvest year was significant. Our study thus suggests that reduced reproductive success driven by variability in foraging conditions is an important factor in the Atlantic puffin population decline in Føroyar.

Keywords: Faroe Shelf, juvenile fish index, primary production index, seabird

#### Introduction

Seabirds form an integral part of marine ecosystems (Signa et al. 2021), not only connecting nutrient flow between marine and terrestrial systems (Duda et al. 2020) but also linking marine habitats on a global scale (Pacyna et al. 2019, Signa et al. 2021). Their dependency on marine resources means that seabirds are exceptionally susceptible to environmental changes in their marine food webs and can thus be valuable as ecosystem sentinels (Furness and Camphuysen 1997), providing information on past, present and even future changes in their environment (Hazen et al. 2019, Olsen et al. 2025). However, this sensitivity also means that, in the context of the ongoing climate



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change and anthropogenic pressures, seabirds are globally threatened (Dias et al. 2019). Indeed, a large proportion of seabird species is reported to experience population declines (Croxall et al. 2012, Dias et al. 2019).

Population dynamics in seabirds are shaped mainly by a combination of adult survival and recruitment rate (i.e. the number of offspring returning as (prospecting) breeders; Sandvik et al. 2012). Adult survival generally fluctuates the least over time (Durham et al. 2024) as parents balance their own survival against their lifetime reproductive output (i.e. the total number of offspring surviving to breeding age; Erikstad et al. 1998). In contrast, breeding productivity (i.e. the number of fledglings per breeding pair per year) is more variable and reactive to external factors, including food availability (Crespin et al. 2006, Sandvik et al. 2012). During years with reduced prey quality or abundance, fewer juveniles may be produced and survive (Durant et al. 2005), affecting the age structure of the population in future years. Examining the age structure of seabird populations in relation to food availability thus provides vital insights into the role of prey abundance on population dynamics.

The Atlantic puffin *Fratercula arctica* (hereafter puffin) is a charismatic seabird from the Alcidae family, drawing many tourists to the breeding colonies all over the world (Huijbens and Einarsson 2018, Howard 2024). As a piscivorous, diving species it occupies a high position in the marine food web (Lowther et al. 2020) and may be considered a sentinel of the ecosystem at its higher trophic level (Thibault et al. 2019, Velarde et al. 2019). Puffins are long-lived and slow to mature, first attempting to breed between 3 and 6 years of age (Lowther et al. 2020). Puffin populations have been rapidly declining across most of their European range (BirdLife International 2021), and the species is currently classified as 'Vulnerable' globally and 'Endangered' in Europe (BirdLife International 2018).

Changes in food abundance are recognised as an important cause of puffin population declines (Barrett and Rikardsen 1992, Frederiksen et al. 2013, Fayet et al. 2021), though the effects may be complex, multifaceted and differ between geographically distinct populations (Layton-Matthews et al. 2023). Food shortages have been shown to reduce breeding success (population-wide: the proportion of fledged chicks; pair-based: whether the chick fledged or not) in several colonies (Barrett and Rikardsen 1992, Guillemette et al. 2018, Fayet et al. 2021), including the extraordinarily long series of poor breeding success on Røst (Lofoten Islands, north Norway), where virtually complete breeding failures were observed for 18 consecutive years (Cury et al. 2011). Furthermore, food shortages were linked to a decline in egg volume in northeastern populations (Barrett et al. 2012; but not in northwestern populations, Lefort et al. 2021), and to lower survival rates outside of the breeding period (Breton and Diamond 2014). Conversely, populations seem quite resistant to changes in prey composition (Eilertsen et al. 2008), though chick body mass growth may be lowered in response to changes in the quality and ratio of the preferred prey species in the diet (Baillie and Jones 2004, Wanless et al.

2005). Additionally, while delayed food peak abundance does not necessarily affect breeding success (Regehr and Rodway 1999), climate change may affect the timing of prey abundance and puffin reproduction in opposite ways, such that puffins may breed later while their prey emerges earlier in the season (Staudinger et al. 2019). Such changes might lead to a mismatch of peak food abundance and peak chick nutrient demands (Durant et al. 2005) in the most affected areas and may become more pronounced at higher latitudes in the future (Frederiksen et al. 2013).

Located in the subpolar Atlantic, Føroyar (the Faroe Islands, in English) is one of the most productive marine regions in the world (ICES 2008, Larsen et al. 2008, Eliassen 2017), accommodating large seabird colonies (Bakken et al. 2006). As established two decades ago, Føroyar is home to approximately 1.7 million breeding pairs of various seabird species (Bakken et al. 2006, BirdLife International 2026), including puffins with an estimated 550 000 breeding pairs over approximately 100 colonies (Jensen et al. 2005, Hammer et al. 2014). Puffins are a significant element of the local socio-economic system, as they attract considerable tourism interest as well as being subject of a long-standing seabird hunting tradition. Historically, seabirds represented one of the few reliable resources available to communities inhabiting these otherwise inhospitable islands (Jensen 2010).

Populations of many seabirds in Føroyar, including puffins, are rapidly declining ([https://www.jenskjeld.info/UK\\_side/indexuk.htm](https://www.jenskjeld.info/UK_side/indexuk.htm), accessed 21 February 2025). Local prey availability has been shown to affect foraging costs and breeding success in puffins (Durant et al. 2003, Cury et al. 2011, Fayet et al. 2021), potentially driving the current decline of the species (Layton-Matthews et al. 2023). However, since the relationship between food abundance and seabird demography is complex, there is an urgent need to understand the underlying processes of the ongoing declines.

Here, we analysed the population age structure of Atlantic puffins harvested on Nólsoy, Føroyar (62°00'33"N, 6°40'7"W; Fig. 1a) over time and in relation to local food availability indices (i.e. phytoplankton primary production, juvenile fish) to understand how local prey abundance may shape population dynamics. We predicted that several years of low to zero breeding success on Nólsoy (pers. obs., J-KJ), would be mirrored in the changes in population age structure within the harvest data. Namely, we expected that the proportion of younger puffins decreased, expressed both as a lower percentage of 'sub-adult' (i.e. before breeding age) puffins in the sample per year, and by an overall decline in cohort sizes over the study period (see Methods for descriptions of the measures). As puffin population dynamics are related to local environmental conditions affecting both parental breeding effort (i.e. the total amount of energy parents spend on breeding behaviours; Fayet et al. 2021) and recruitment rates (Crespin et al. 2006), breeding success in years with high food availability is higher as parents have to expend less energy on foraging and prey quality is better (Fayet et al. 2021). Therefore, we predicted that puffin population age structure in a given hatch year is related to food availability in the same

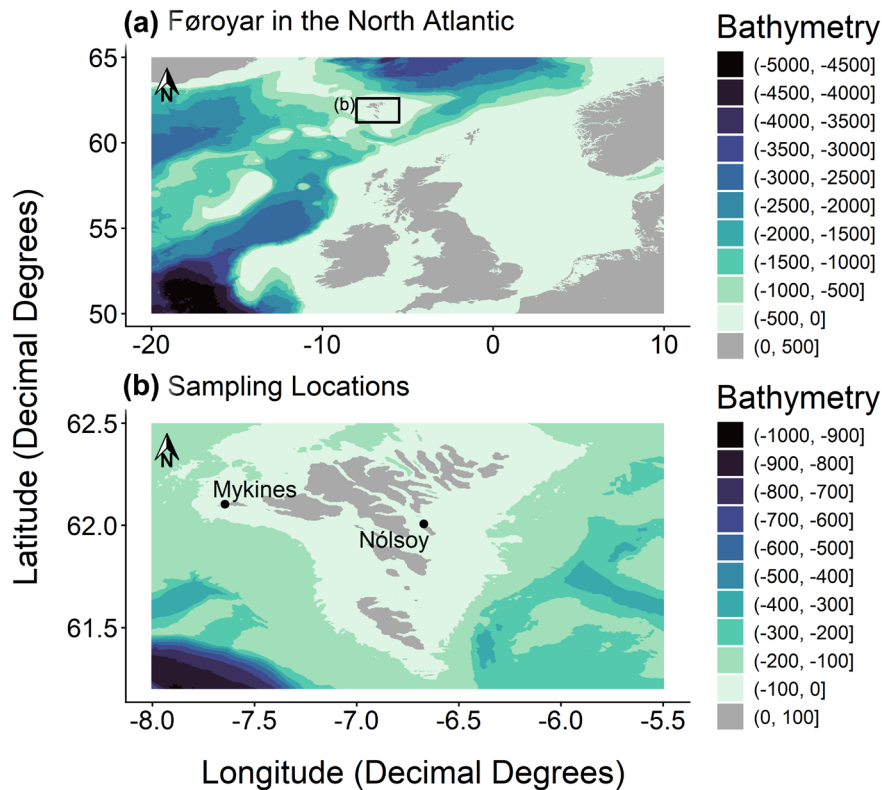


Figure 1. Location of the study sites (black dots). Background: bathymetry with the Faroe Shelf in light green in (b). Note the differences in scale between (a) and (b). Map created using `marmap` and `ggplot2` (Wickham 2016, Pante et al. 2023) in R ([www.r-project.org](http://www.r-project.org)).

year and the preceding years, with cohorts from more productive years being larger than cohorts from relatively poor years. As recruitment rates vary with environmental conditions (Crespin et al. 2006), we expected that puffin age structure in a given sample year is also related to food availability in the same year and the preceding years.

The samples used in this study were obtained from local hunters, through their regular and legal (Fuglaveiðulóginn 1984) harvesting activities during the study period. As such, puffins were not specifically harvested for our study. Puffins were taken from birds circling over the colony which are, according to the hunters, assumed to mainly include sub-adults, although there is evidence that adults that have forgone breeding or have failed join in the circling behaviour (Jensen 2010). Therefore, we believe the birds included in the study can be used as a proxy for the local population dynamic, and we predict that the sample contains relatively more young birds in productive years compared to relatively poor years when relatively more birds of breeding age may be included (Jensen 2010).

## Material and methods

### Sample collection

Hunters are expected to target puffins flying in circles over the colony, as these are assumed by the hunters to be young,

prospecting birds differentiated from breeding adults which generally adopt a straighter flightpath to and from the ocean to provision the chick (Jensen 2010). Specifically, hunters avoid catching adults carrying fish, as this is a clear sign of them being breeders, or with a wet rictal rosette indicating a return from provisioning a chick and having held fish recently (Jensen 2010). Harvesting breeding birds has been understood to severely affect population size negatively (Jensen and Olsen 2020). Due to observed, but not quantified, population declines in puffins across Føroyar, the annual harvest was reduced or suspended from 2009 until 2021 as fewer birds could be caught, although each community was setting its own limits. In 2021 the local community on Nólsoy considered the population to have recovered enough to sustain limited harvesting again and wanted to continue with the harvesting tradition (Table 1).

For a period of 20 years, between 1989 and 2008, J-KJ inspected 5472 randomly selected puffins harvested on the islands of Nólsoy from 1989 to 2006, and on Mykines from 2007 and 2008, when no puffins could be obtained on Nólsoy, Føroyar (Table 1; Fig. 1b). The local population on Nólsoy was estimated to be 35 000–50 000 breeding pairs in the 1990s (Stempniewicz and Jensen 2007). The population on Mykines was estimated at 60 000 breeding pairs in 2012 (Hansen et al. 2013). Puffins were harvested by local landowners for several days each year during the late breeding period (Jensen 2010, Jensen and Olsen 2020), officially

Table 1. Estimated harvest numbers and annual sample sizes of Atlantic puffins *Fratercula arctica* on Nólsoy, Føroyar, based on personal communication/reports from local landowners/hunters. Because of observed declines in the local puffin harvest numbers, the annual harvest was reduced or suspended in recent years. At the local governmental meeting (Grannastævna) on Nólsoy in 2021 it was agreed that a maximum of 350 puffins could be harvested. However, in 2023 there was a disagreement about the validity of the 2021 Grannastævna and the agreed upon maximum harvest. A new meeting was held in 2024 with a new maximum harvest of 50 puffins per catching location (8) per hunting day (9–28 July, except Sundays), which is hardly ever met due to adverse weather conditions and puffin numbers that are too low. NA – no data.

Year	Estimated harvest	Sample size
1989	NA	259
1990	NA	120
1991	NA	119
1992	NA	161
1993	NA	201
1994	NA	296
1995	NA	402
1996	8188	350
1997	6976	446
1998	8277	450
1999	13 324	439
2000	12 758	424
2001	10 992	390
2002	5874	379
2003	1798	200
2004	5050	296
2005	1851	193
2006	1596	198
2007	207	0 (9 from Mykines)
2008	335	0 (140 from Mykines)
2009	264	0
2010	0	0
2011	0	0
2012	537	0
2013	0	0
2014	0	0
2015	0	0
2016	0	0
2017	0	0
2018	0	0
2019	0	0
2020	0	0
2021	350	0
2022	350	0
2023	1865	0
2024	801	0
2025	153	0

starting on 2 July and ending on 8 August. However, the end date was not always adhered to, with the latest harvested puffins in our data set collected on 15 August. Upon the hunters returning to the village, J-KJ acquired an arbitrary number of puffins (range: 9–450, median: 277.5; Table 1), making sure to keep the selection process as unbiased as possible. The harvested puffins were placed on the ground in a big pile prior to processing by the hunters. Then, J-KJ collected a sample from one such pile per hunting day by closing his eyes when selecting birds. The estimated number of harvested

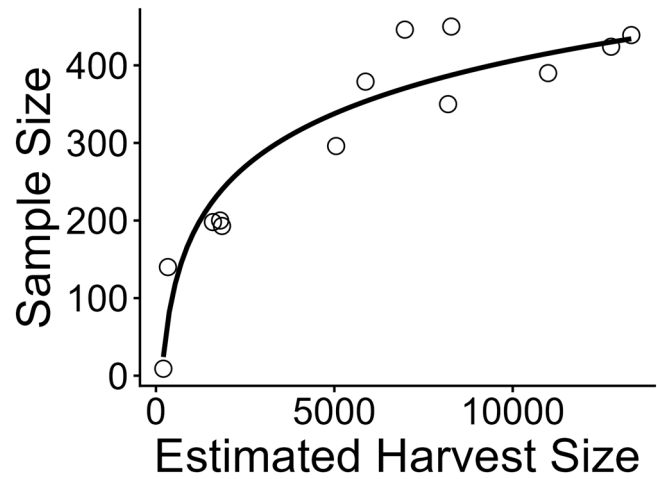


Figure 2. Annual sample size in relation to the estimated harvest size of Atlantic puffins *Fratercula arctica* on Nólsoy, Føroyar between 1996 and 2008. The black line shows a natural logarithmic relationship between the annual sample size and the estimated harvest size (F1, 11 = 101,  $p < 0.001$ ,  $R^2_{adj} = 0.89$ ). See also Table 1.

puffins between 1996 and 2008 ranged from 207 (2007) to 13 324 (1999) (Table 1) but similar counts do not exist for the period between 1989 and 1995. The annual sample size is partially related to the estimated harvest size (Fig. 2), as we limited the sample size to a maximum of 100 per year and 30 per hunting day. All samples were stored in a freezer until processing.

### Ageing methods

For each sampled puffin, J-KJ scored the number of grooves in the bill ( $n = 5\ 466$ , omitting individuals with damaged beaks) following Harris (1981). Ageing puffins by the number of grooves in the bill is a known method first described by Petersen (1976) and further defined by Harris (1981, 2014). It relies on the assumption that a bird with a certain number of grooves is most likely to be a certain age. This method was developed by scoring bill grooves of known-age puffins in the British Isles (Harris 1981) and thus assumes that the relationship between bill grooves and age is similar in other colonies. It allows for individual ageing of each specimen, so that other measurements can be related to age, but in doing so does introduce observer bias. While the scoring of bill grooves itself is already somewhat subjective (e.g. when is a groove a full groove compared to half a groove?), determining which age it corresponds to is also up to the observer. However, an experienced observer may be able to accurately estimate age by looking at the overall shape and appearance of the bill. The Faroese puffin colonies included in this study were not individually marked and observed throughout and before the study period, and age thus had to be estimated, assuming that the relationship between bill grooves and age was compatible with Harris (1981, 2014). To account for potential observer bias, we aged each individual following Harris (1981, 2014) but also calculated the likely age composition within each sample year by determining the proportion of each age by bill

grooves. All ages are expressed as calendar years (CY), where an individual is 1CY between hatch and 31 December of the same year, turns 2CY on 1 January of the following year, 3CY on the next 1 January, etc.

1. Individual ageing: the age of each individual was scored based on the number of grooves and the shape of the bill (Harris 1981) by one observer (J-KJ), assigning ages between 2nd and 4th calendar year (i.e. 2–4CY), or older (i.e. > 4CY). During this process, J-KJ primarily considered the number of grooves to age birds, assigning the age most often associated with a certain number of grooves (e.g. Harris (1981) found that of the 57 birds with 1.5 grooves, 51 were aged 4CY) using bill shape as an additional criterion when uncertain (younger birds have more triangularly-shaped bills than older birds; Harris 1981).
2. Proportional ageing: as the grooves may not be a conclusive estimate for age (Harris 2014), we also estimated the age structure per year using the proportions (Supporting information) calculated from Harris (2014). For this, we calculated the proportion of each age class assigned to groove scores in Harris (2014) (e.g. of the 68 birds with a groove score of 1.5, 55 were 4CY (80.9%), while 9 were 3CY (13.2%) and 4 were 5CY (5.9%)) and used those to estimate the sizes of the age classes per year (e.g. in 1989 73 birds had a groove score of 1.5, thus we estimated that 13.2% would be 3CY (9.6), 80.9% would be 4CY (59) and 5.9% would be 5CY (4.3)). We then summed the estimated sizes of each age class by groove score per year to estimate the total size of each age class. A complete example for 1989 can be found in the Supporting information.

For each study year, we back-calculated hatch year for ages between 2CY and 4CY to determine yearly cohort size. Because neither method is fully accurate, all statistical analyses were repeated for both age determination approaches, to provide the most complete report.

### Statistical analyses

All statistical methods were carried out in R ver. 4.4.2 ([www.r-project.org](http://www.r-project.org)). First, we assessed the difference in ageing methods between individual-based age assignments and proportional age determination, using a two-way ANOVA with interaction effect (*anova*, package 'stats') ([www.r-project.org](http://www.r-project.org)). We included both the determination method and total number of assigned ages (2–4CY, > 4CY) to test whether each class was assigned more or less often depending on determination method. We then used a Tukey HSD post hoc test (*TukeyHSD*, package 'stats') ([www.r-project.org](http://www.r-project.org)) to determine the scale of the differences found using the ANOVA.

In further analyses we approached the population age composition from two angles:

1. Share of the annual sample size: for every study year, we calculated the share of each age class in the annual sample size to determine population age composition within each sample year. When assessing whether the population age composition was changing (i.e. whether the total share of

- > 4CY birds increased over time, or with food availability) we combined all age classes  $\leq$  4CY and compared them to > 4CY. We used this measure to understand how sample year conditions affected population age composition.
2. Cumulative cohort size: we summed the annual shares (see 1) for all 'complete' hatch year cohorts – meaning all cohorts that could have been assigned a hatch year in the study period, resulting in values of cumulative cohort size that may be higher than 1 if a particular cohort was excessively present in the three years hatch year could be determined (i.e. hatch year cohorts could only be assigned to individuals  $\leq$  4CY). As the study ended in 2008, the 2007 and 2008 cohorts were not 'complete' (i.e. did not include up to 4CY individuals), and were thus removed from cohort-focused analyses. Similarly, the 1986 and 1987 cohorts were removed, as they did not include 3CY and 4CY individuals. A detailed example for the 1988 cohort can be found in the Supporting information. We used this measure to understand how hatch year conditions affected population age composition.

To determine how the cumulative cohort size changed over the study period and in relation to food availability, we used Gaussian generalised additive models (GAM; *gam*, package 'mgcv') (Wood 2011) with a thin plate regression spline as smooth term (*s* within the *gam* formula) (Wood 2003) fitted using the restricted maximum likelihood (REML) method (Wood 2017). We tested for changes in the share of the annual sample size by fitting a quasibinomial generalised additive mixed-effects model (GAMM; *gamm*, package 'mgcv') (Wood 2004) with logistic link to the share of the annual sample size of  $\leq$  4CY and > 4CY individuals (i.e. two age classes summing to one per year). We did not expect linear relationships between either measure of population age composition and the predictors (Goyert et al. 2018, Olsen et al. 2025), and we did not set out to interpret the slope of the model aside from whether it was positive or negative. Therefore, we opted for GAM(M)s over linear models, as GAM(M)s can describe any kind of relationship, including linear ones.

We tested for changes in cumulative cohort size over time by fitting a GAM to cumulative cohort size with hatch year as a smooth term. We tested for changes in the share of the annual sample size by fitting a GAMM, with study year as the smooth term by age class ( $\leq$  4CY and > 4CY).

As proxies for annual food availability on the Faroe Shelf (Fig. 1b) we used two environmental variables: the primary production index (PPI) of marine phytoplankton (available from 1990) (Gaard et al. 1998) and the mean length of juvenile fish expressed as the 0-group length index (0-GI; available from 1974) (Jacobsen et al. 2019). Although these indices are correlated (Pearson's correlation coefficient;  $r=0.74$ ,  $p < 0.001$  for hatch years,  $r=0.68$ ,  $p < 0.001$  for study years; *rcorr*, package 'Hmisc') (Harrell Jr 2024) each captures a different aspect of the ecosystem and thus both were included in the study to highlight complementary facets of food availability. The 0-GI was calculated with a PCA fitted to the length of the four most abundant fish species: cod

*Gadus morhua*, haddock *Melanogrammus aeglefinus*, Norway pout *Trisopterus esmarkii* and sandeel *Ammodytes marinus* (Jacobsen et al. 2019). These data are freely available from the Havstovan website (PPI: <https://www.hav.fo/livid-i-havinum/plantuplankton/#ljjos>; 0-GI: [https://www.hav.fo/utgavur/tidarrodur/#veida\\_av\\_fiskastovnum](https://www.hav.fo/utgavur/tidarrodur/#veida_av_fiskastovnum); accessed 14 April 2025).

Although PPI is an indirect measure of food availability for puffins, it can be linked to seabird breeding success (Ramírez et al. 2017) and population size (Laidre et al. 2008). The connection between 0-GI and seabirds has also been long established (Cairns 1988, Furness and Tasker 2000). Low fish abundance is often linked to lower breeding success (Guillemette et al. 2018, Fayet et al. 2021). In Føroyar, puffins primarily forage on sandeels, followed by Norway pout (Falk et al. 1992, Gaard et al. 2002), normally feeding 0-group sandeel to their chick but switching to 0-group Norway pout or capelin *Mallotus villosus* in poor years (Gaard et al. 2002). To account for carry-over effects of food availability in preceding years on puffin survival, fitness or breeding output, we calculated a 3-year rolling average of both PPI and 0-GI (*rollapply*, package 'zoo', with *align* = 'right' to include only preceding values and *partial* = TRUE to ignore missing values) (Zeileis and Grothendieck 2005), as this spans one 'complete' cohort period.

To determine the relationship between food availability and cumulative cohort size, we fitted a GAM to cumulative

cohort size with either PPI or 0-GI in the predicted hatch year or the corresponding 3-year rolling average as smooth terms. To determine the relationship between food availability and age class share of the annual sample size, we fitted a GAMM to the share of the annual sample size of  $\leq 4$ CY and  $> 4$ CY individuals with either PPI or 0-GI in the sample year or the corresponding 3-year rolling average as smooth terms by age class. As PPI and 0-GI are correlated we did not include both PPI and 0-GI in any models. Furthermore, as the 3-year rolling averages include the focal year and a time element, they are dependent on both year and the annual value of the included environmental variable (e.g. in year 4 the rolling average includes the annual value of years 2, 3 and 4). Therefore, to avoid collinearity, we did not include year in the food availability analyses and only compared models with the annual value of PPI or 0-GI and the corresponding 3-year rolling average. We did not include both the annual value and the 3-year rolling average in the same model.

Ultimately, we created 20 univariate models with one response variable (i.e. cumulative cohort size or share of the annual sample) and one predictor (i.e. year (hatch year or sample year), or annual values of PPI or 0-GI, or 3-year rolling average values of PPI or 0-GI; Table 2). We retained all models, despite potentially non-significant relationships, as non-significant results still provide useful information and are often underrepresented in ecology (Koricheva, 2003; Parker and Yang, 2023). The statistical layering structure (i.e.

Table 2. Summary of generalised additive (mixed) models (GAM/GAMM) assessing changes in age-composition of Atlantic puffins *Fratercula arctica* over time and in response to food availability. Population age composition was measured as cumulative cohort size explaining variation in the hatch year, and as share of the annual sample size explaining variation in the sample year. Ages were determined for each individual or as a proportion of the annual sample. Both of these are aggregated under 'Age Method'. PPI=primary production index, 0-GI=0-group length index of juvenile fish. Food availability parameters were assessed as annual value (data aggregation=none) or as a 3-year rolling average (data aggregation=3-year). Thus, there are 4 model combinations, each representing different combinations of ageing methods, i.e. 1–5 represent cumulative and individual, 6–10 cumulative and proportional, 11–15 share of annual sample and individual and 16–20 share of annual sample and proportional. See methods for further details and the Supporting Information for model structures. Edf=array of estimated degrees of freedom for the model terms. The p-value was estimated using the F-statistic and significant ( $p < 0.05$ ) values are bolded.

Model	Age method		Predictor variable	Data aggregation	edf	F	p-value	
1	Cumulative cohort size	Individual	Hatch year	None	5.63	13.7	< <b>0.001</b>	
2			PPI hatch year	None	1	4.51	<b>0.043</b>	
3				3-year	1	1.37	0.252	
4			0-GI hatch year	None	1	3.40	0.074	
5				3-year	1	0.35	0.559	
6	Proportional		hatch year	None	8.04	22.1	< <b>0.001</b>	
7			PPI hatch year	None	2.59	3.12	< <b>0.001</b>	
8				3-year	1.37	9.71	< <b>0.001</b>	
9			0-GI hatch year	None	1.78	13.9	< <b>0.001</b>	
10				3-year	1	6.36	<b>0.015</b>	
11	Share of annual sample	Individual	Sample year	None	4.24	10.6	< <b>0.001</b>	
12			PPI sample year	None	1	0.55	0.462	
13				3-year	1	3.79	0.060	
14			0-GI sample year	None	1	3.86	0.057	
15				3-year	1	6.92	<b>0.012</b>	
16		Proportional		Sample year	None	3.58	10.4	< <b>0.001</b>
17				PPI sample year	None	1	0.15	0.706
18					3-year	1	3.06	0.089
19				0-GI sample year	None	1	2.53	0.120
20					3-year	1	8.67	<b>0.006</b>

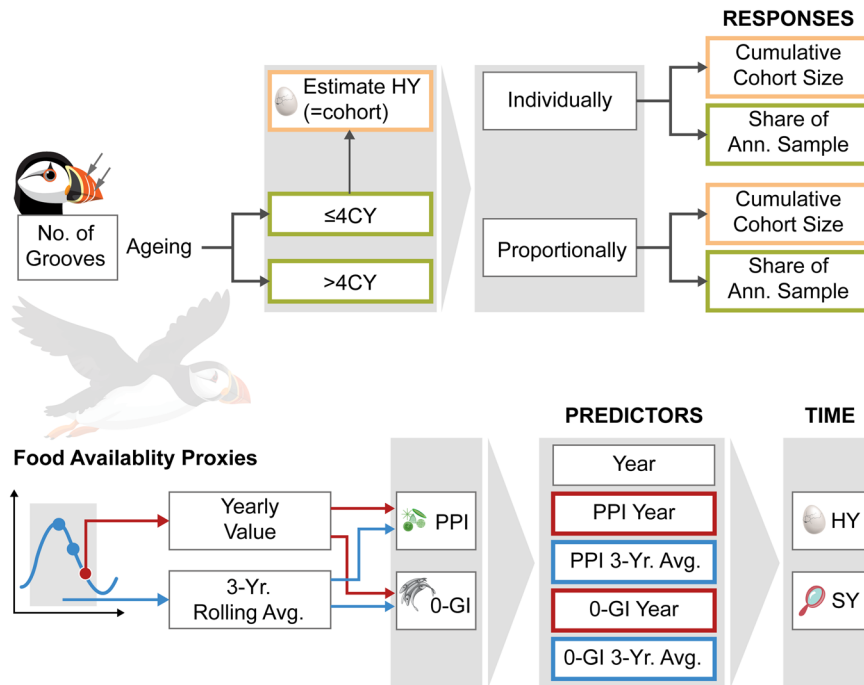


Figure 3. Graphic illustration of the pairwise model response and predictor variables. From top to bottom, left to right, the figure illustrates the ageing methods using bill grooves, separating aged individuals into  $> 4$  calendar year (CY) and  $\leq 4$  CY groups (green boxes). For  $\leq 4$  CY individuals hatch year (HY) was estimated, thus assigning a cohort (orange boxes). These methods were done either individually (i.e. for each individual separately) or proportionally (i.e. based on the proportion of birds with [X] grooves being [Y] years old in Harris 2014); see Methods and the Supporting information for further details. As response variables, we thus had cumulative cohort size (i.e. the sum of the relative size of each cohort in the sample year) and the share of the annual sample size (i.e. the ratio between  $\leq 4$  CY and  $> 4$  CY in each sample year) for both the individual and proportional ageing methods (a total of four responses). As predictors, we used the annual value (red arrows and boxes) or three-year rolling average (blue arrows and boxes) of two food availability proxies (primary production index – PPI; 0-group index – 0-GI) and focal year. These predictors were obtained for both HY and sample year (SY), resulting in ten response variables. Models included combinations of one response and one predictor variable, with cumulative cohort size models including HY predictors and share of the annual sample models including SY predictors. See also Table 2 for a list of all models.

population age composition measure, ageing method and predictor variables) is summarised in Table 2 and Fig. 3.

For each GAM/GAMM, we extracted the smooth estimates, 95% confidence intervals (CI), and the derivatives of the estimated smooths using the ‘gratia’ package (functions *smooth\_estimates*, *add\_confint*, *derivatives*, respectively) (Simpson 2024). Then, we determined the significant change points, or areas with significant increasing or decreasing relationships following Simpson (2014), by testing whether the pointwise 95% CI of the estimates of the first derivative of the splines contained zero (no significant change) or not (significant change).

The R code for the models can be found in the Supporting information.

## Results

We found a significant difference between both ageing methods (two-way ANOVA,  $F_{3, 128} = 7.62$ ,  $p < 0.001$ ; Fig. 4). On average, individually ageing resulted in a significantly smaller portion of birds assigned age 3CY (Tukey HSD,  $d = -51.2$ ,

$p = 0.04$ ) and a significantly larger portion of birds assigned age  $> 4$  CY ( $d = 53.0$ ,  $p = 0.01$ ) compared to proportional ageing (Fig. 4). The contribution of age classes 2CY and 4CY did not differ significantly between both ageing methods (Fig. 4).

Our results differed between ageing methods (Table 2), but, as our study population is unmarked, we cannot determine which method provides more accurate results. Therefore, we presented results from both methods to provide the most transparent report.

### Changes over time

We found that cumulative cohort sizes changed significantly over time for both individually aged (Model 1) and proportionally aged puffins (Model 6; Table 2; Fig. 5), with a final decrease starting with cohorts hatched after 2000 (individual ageing, Fig. 5a) and after 2002 (proportional ageing, Fig. 5b). In addition, we found significant changes in the share of the annual sample size of  $\leq 4$  CY and  $> 4$  CY birds for both individually aged (Model 11) and proportionally aged puffins (Model 16; Table 2; Fig. 6), with a final decrease in  $\leq 4$  CY starting in 2002 for both ageing methods (Fig. 6a–d).

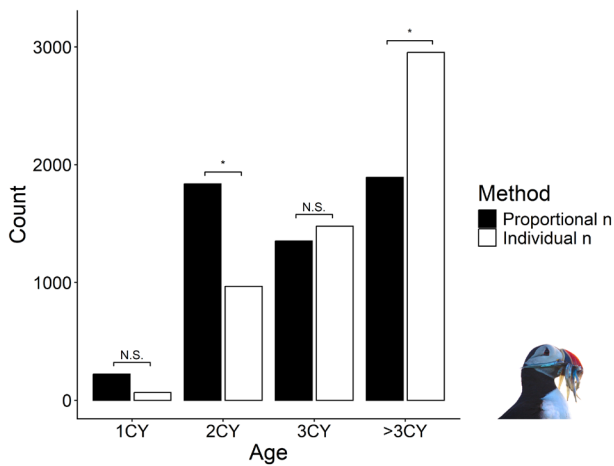


Figure 4. Age class assignments of Atlantic puffins *Fratercula arctica* harvested between 1989 and 2008 on Nólsoy and Mykines, Føroyar, based on bill grooves (Harris 1981, 2014). Ages in calendar years (CY) were assigned to individual birds (white) or by multiplying the groove scores by the proportions calculated from Harris (2014) (black). See Methods and the Supporting information for details. Significant differences (Tukey HSD,  $p < 0.05$ ) between ageing methods are marked with an \*, while non-significant differences are marked with N.S.

### Changes in cumulative cohort size

Individually aged cumulative cohort sizes varied significantly with hatch year PPI (Model 2), showing a generally positive relationship (Table 2; Fig. 7a), but did not with the 3-year rolling average (Model 3; Table 2; Fig. 7c). Proportionally aged cumulative cohort size was significantly related to hatch year PPI (Model 7) and 3-year rolling average PPI (Model 8; Table 2; Fig. 7b, d).

Individually determined cumulative cohort size was not significantly correlated with either measure of hatch year 0-GI (Models 4, 5; Table 2). Proportionally determined cumulative cohort size varied significantly with hatch year 0-GI (Model 9) and 3-year rolling average 0-GI (Model 10), generally showing positive relationships (Fig. 8).

### Changes in share of the annual sample size

None of the GAMMs showed significant relationships between age class share of the annual sample size and either measure of PPI (Models 12, 13, 17, 18; Table 2), or sample year 0-GI (Models 14, 19). However, both individually (Model 15) and proportionally determined (Model 20) age class shares of the annual sample were significantly, linearly ( $\text{edf} = 1$ ) related to 3-year rolling average 0-GI in the sample year (Table 2; Fig. 9).

## Discussion

Our results show that the average age of the population increased in the last years of the study: cohort sizes started decreasing between 2000 and 2002 (Fig. 5) while the share of  $< 4\text{CY}$  individuals in the harvested samples decreased from

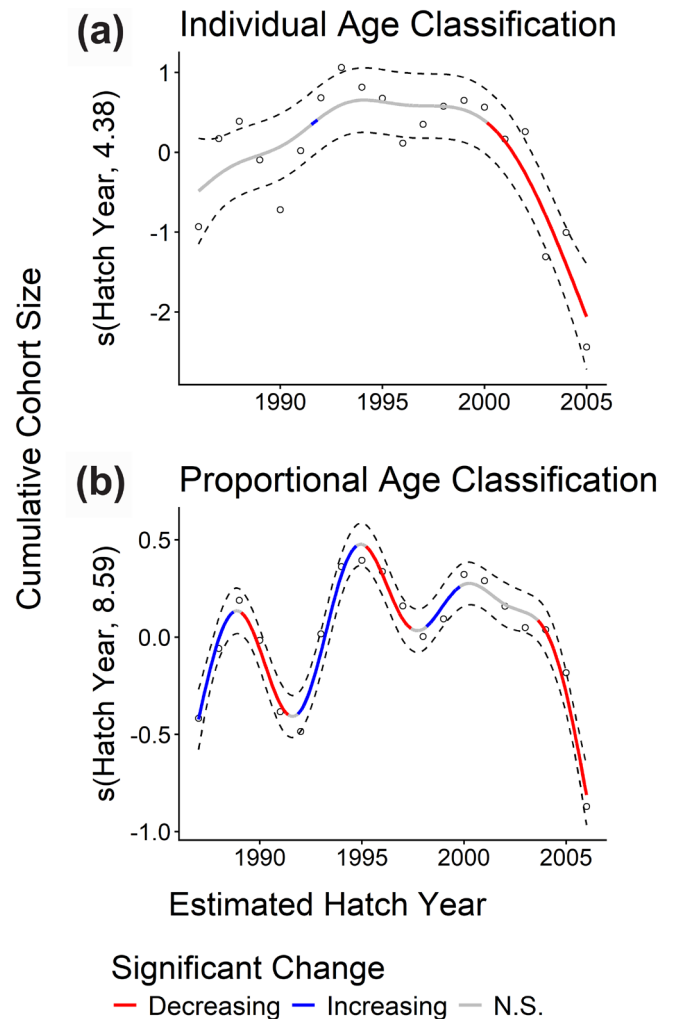


Figure 5. GAM results of changes in cumulative cohort sizes of Atlantic puffins *Fratercula arctica* over time, harvested on Nólsoy and Mykines, Føroyar, between 1989 and 2008. The solid line shows the GAM fit  $\pm$  95% CI (dashed line), with grey sections showing non-significant changes, blue sections showing significant increases and red sections showing significant decreases (see Methods for significance testing; Simpson 2014, 2024).

2002 (Fig. 6). Cohort size was generally positively correlated with food availability in the hatch year and in the preceding years, though this was predominantly apparent in the proportionally aged cohort sizes (Fig. 7, 8; Table 2). Conversely, the share of  $\leq 4\text{CY}$  and  $> 4\text{CY}$  birds in the annual sample size only significantly changed with the 3-year rolling average 0-GI in the sample year (Fig. 9; Table 2). Combined, these results suggest that low food availability affecting parental input (e.g. consistently low prior to the breeding season, or low during the breeding season) drives the changes in population age composition by reducing cohort sizes. Food availability during pre-breeding (i.e. the years prior to the sample year, or the sample year itself) affected population age composition less than food availability prior to and during the hatch year, suggesting that juvenile (i.e. in the first year of life) and sub-adult survival were less, though still, important.

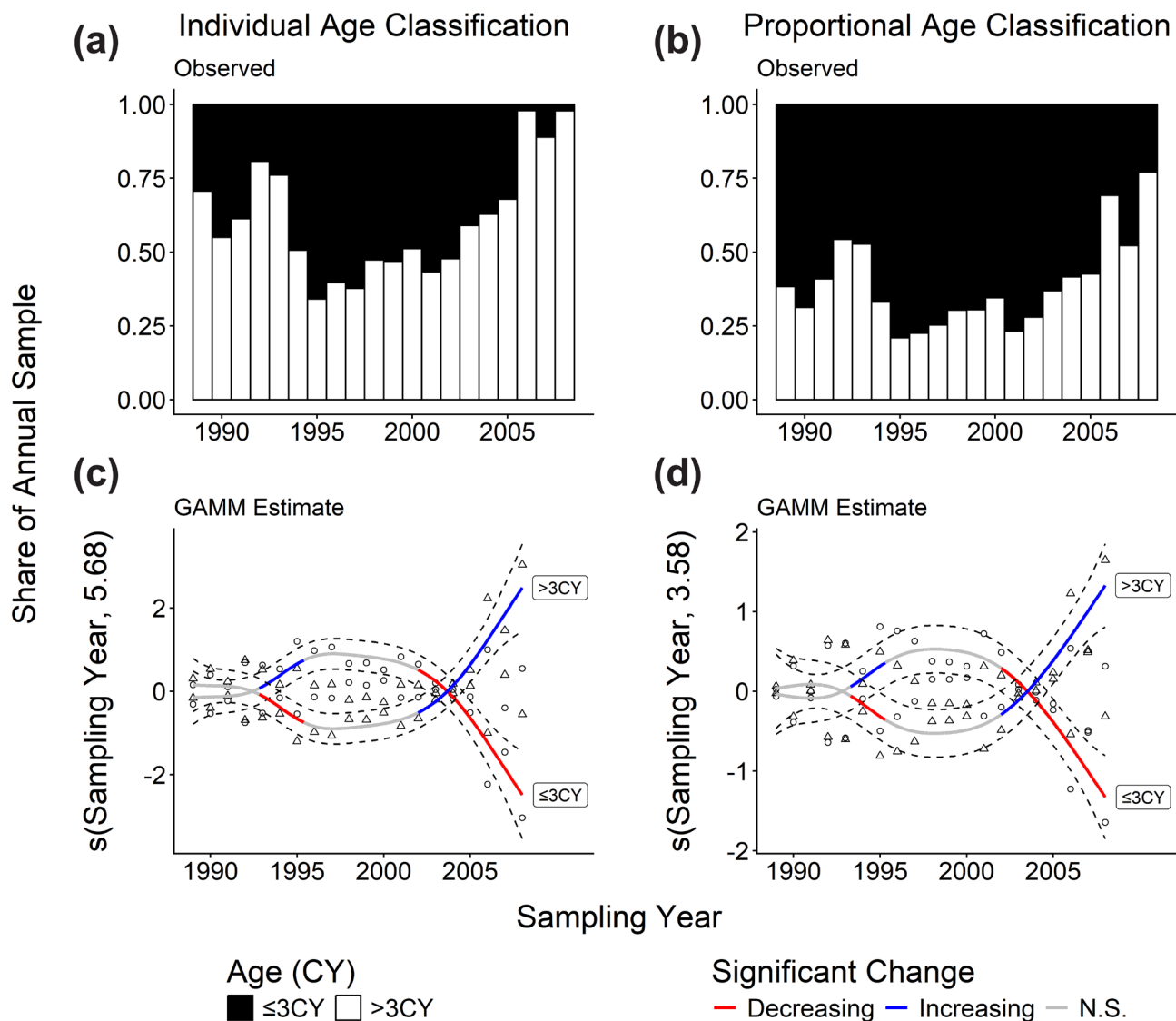


Figure 6. Share of the annual sample size of Atlantic puffins *Fratercula arctica* aged  $\leq 4$ CY and  $> 4$ CY, harvested on Nólsoy and Mykines, Føroyar, between 1989 and 2008. Puffins were aged individually (a, c) or proportionally (b, d). (a) and (b) show the observed share of the annual sample size of each age group ( $\leq 4$ CY = black,  $> 4$ CY = white). (c) and (d) show the GAMM estimates: the solid lines (labelled per age group) show the GAMM estimate  $\pm$  95% CI (dashed line), with grey sections showing non-significant changes, blue sections showing significant increases and red sections showing significant decreases (see Methods for significance testing; Simpson 2014, 2024). The open symbols show the GAMM smooth estimates over a range of covariate values ( $n=200$ ) for  $\leq 4$ CY (circles) and  $> 4$ CY (triangles).

The observed changes in the population age structure (Fig. 5, 6) show that the population is aging, as cumulative cohort sizes are declining (Fig. 5) and the share of  $< 4$ CY birds is decreasing (Fig. 6). As natal philopatry in puffins tends to be high (Sandvik et al. 2008), though variable (Breton et al. 2006), the changes in population age structure strongly suggest that recruitment rates were declining over the study period. Our study thus highlights an important signal of a declining population of a long-lived seabird. An aging population may be a precursor to population collapse as senescence speeds up the loss of adults (Landsem et al. 2023).

The positive relationship between the food availability proxies (i.e. PPI, 0-GI) in the hatch year and cumulative

cohort size (Fig. 7, 8) indicates that reproductive output is limited by food availability. Indeed, local prey availability has been shown to affect parental foraging costs and in turn breeding success (Durant et al. 2003, Fayet et al. 2021). Additionally, while a change in preferred prey availability can be mitigated when suitable alternatives are available (Baillie and Jones 2004), reduced prey quality fed to chicks may lead to breeding failure (Wanless et al. 2005).

The significant, positive relationship between the 3-year rolling average of both PPI and 0-GI of the years preceding and including the hatch year (Fig. 7, 8) suggests that parental quality or effort may play a significant role in shaping population-wide breeding success. Poor foraging conditions

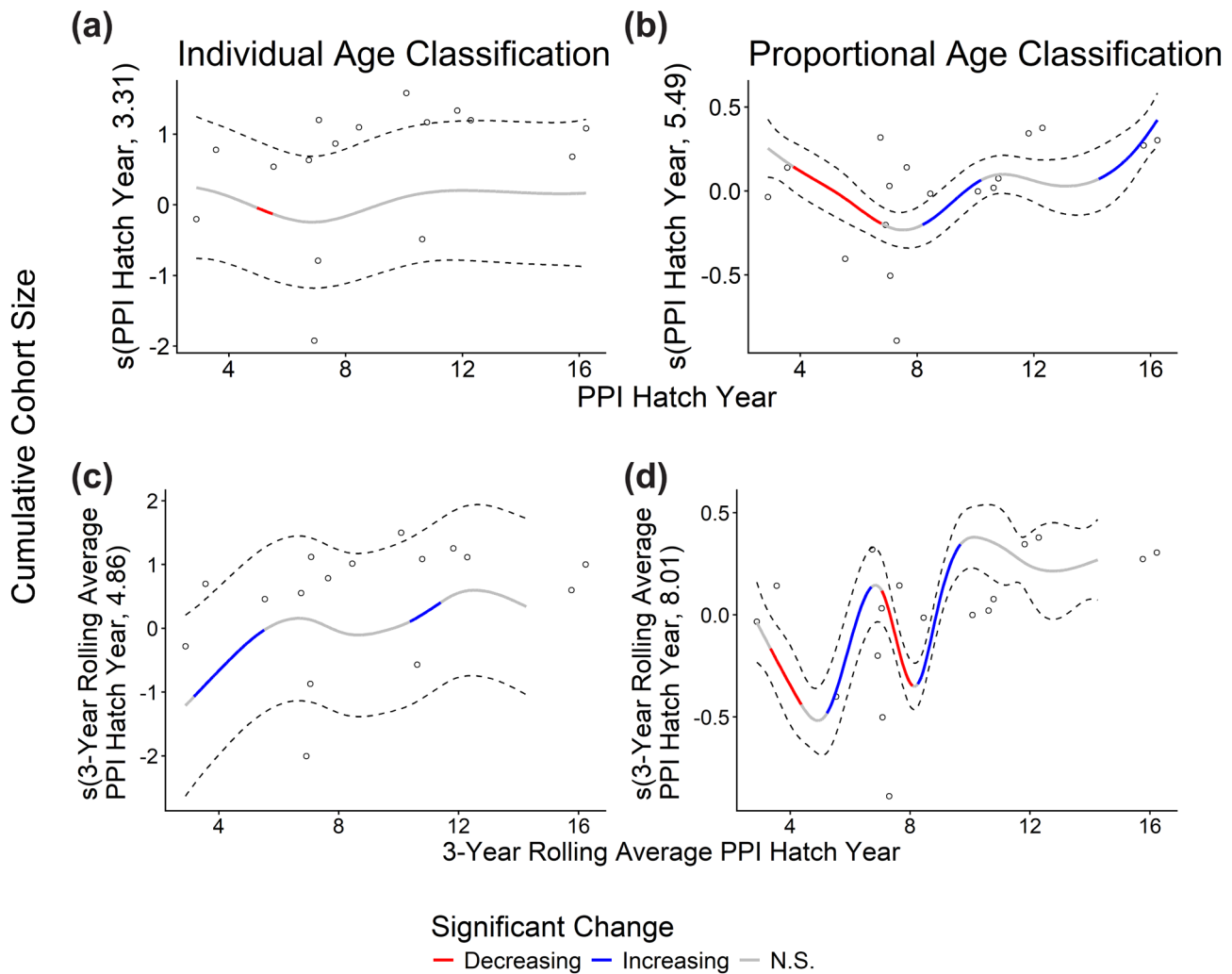


Figure 7. GAMM results assessing changes in cumulative cohort sizes of Atlantic puffins *Fratercula arctica* in response to changes in the primary production index (PPI), harvested on Nólsoy and Mykines, Føroyar, between 1989 and 2008. (a) and (c) show the results for individually aged birds; (b) and (d) show the results for the proportionally aged birds. (a) and (b) show the relationship between cumulative cohort size and hatch year PPI; (c) and (d) show the relationship between cumulative cohort size and 3-year rolling average PPI prior to the hatch year. The solid line shows the GAM estimate  $\pm$  95% CI (dashed line), with grey sections showing non-significant changes, blue sections showing significant increases and red sections showing significant decreases (see Methods for significance testing; Simpson 2014, 2024).

can lead to reduced parental fitness at the end of the breeding season (Spitsbergen; Harding et al. 2008) and may affect reproduction within the same year (Alaska; Kitaysky et al. 2010), including carry-over effects of persistent extreme weather events (North Pacific Ocean; Glencross et al. 2021). Razorbill *Alca torda* productivity (i.e. the number of fledged chicks) has been shown to be negatively correlated with lagged spring-time sea-surface temperature (Celtic Sea; Lauria et al. 2012), but the same study showed no correlation with puffin productivity. Furthermore, the 11-year rolling mean of annual sea-surface temperature was significantly related to puffin production (Iceland; Hansen et al. 2021). Sea-surface temperature is not a direct measure of local food availability, even though it is significantly correlated with marine productivity (Lauria et al. 2012). Our study, assessing the effects

of consistently low food availability in the years before the focal study year on population age structure, provides key information to our understanding of the mechanisms with which adverse environmental conditions may lead to reduced breeding success and, ultimately, population declines.

We found fewer relationships between sample year food availability proxies and puffin age class share of the annual sample size (Models 12–15, 17–20; Table 2), except for linear relationships with the 3-year rolling average 0-GI (Models 15, 20; Table 2; Fig. 9). While sub-adult puffins have relatively high survival rates (Sandvik et al. 2008) especially after the first year (Durham et al. 2024), this suggests that longer-term processes affecting food availability during the pre-breeding years may affect sub-adult survival (Fay et al. 2015), reducing return rates in a similar way as

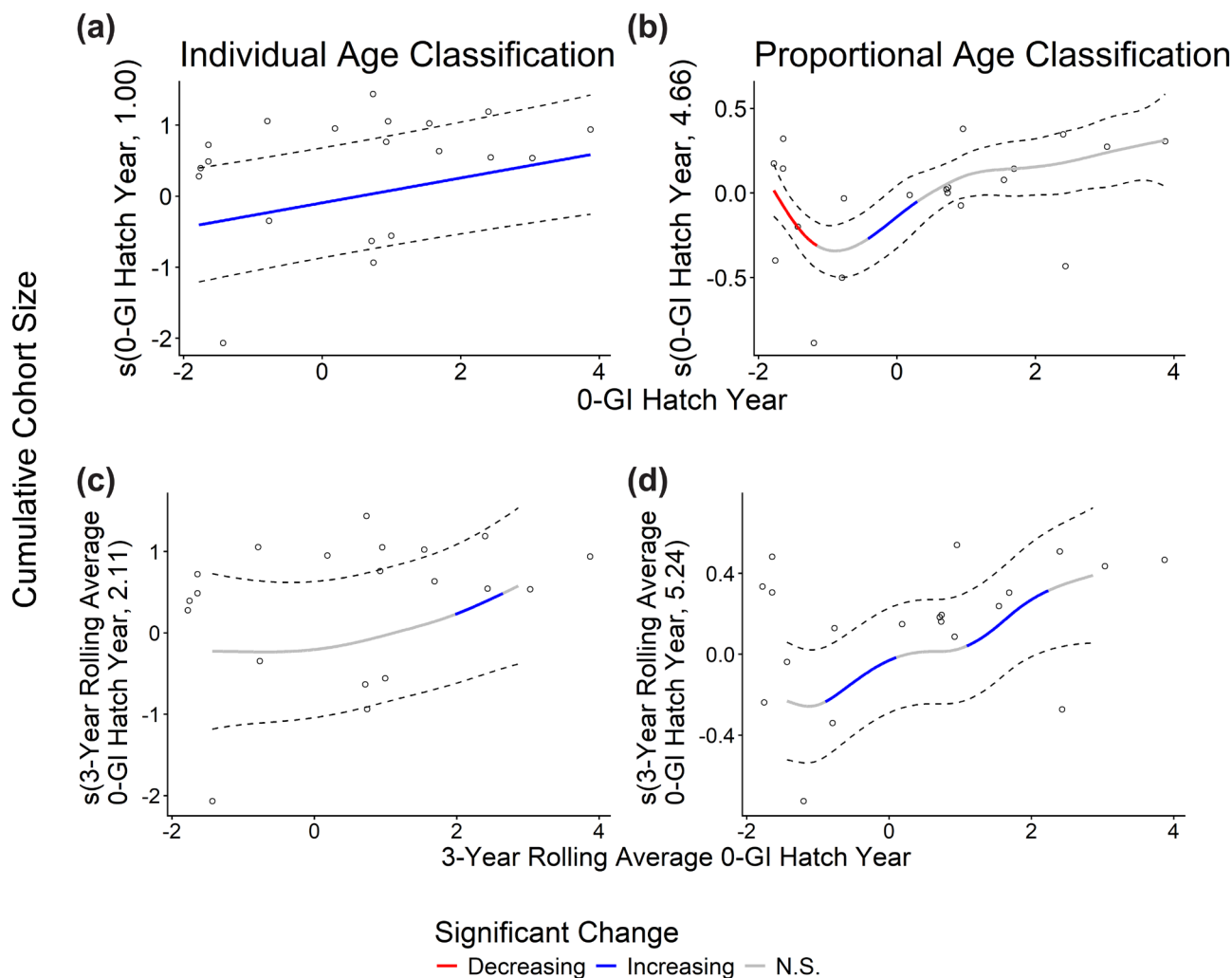


Figure 8. GAMM results assessing changes in proportionally determined cumulative cohort sizes of Atlantic puffins *Fratercula arctica* in response to changes in the juvenile fish 0-Group Index (0-GI), harvested on Nólsoy and Mykines, Føroyar, between 1989 and 2008. (a) Shows the relationship between cumulative cohort size and hatch year 0-GI; (b) shows the relationship between cumulative cohort size and 3-year rolling average 0-GI prior to the hatch year. The solid line shows the GAM estimate  $\pm$  95% CI (dashed line), with grey sections showing non-significant changes and blue sections showing significant increases (see Methods for significance testing; Simpson 2014, 2024).

in closely related seabird, the common guillemot *Uria aalge* (Crespin et al. 2006).

Our study provides a unique insight into long-term puffin population age composition changes in relation to food availability. The ageing of the puffins was done based on bill characteristics, and is thus inherently uncertain (Harris 1981, 2014). Indeed, we found that both ageing methods (individual or proportional) yielded different results (Fig. 4) which led to differences in the significance of the relationships we found with year food availability in hatch years. The Isle of May population used as a basis for the proportional ageing method was increasing at 11% per year (Harris and Wanless 2011), while the population in Føroyar was ostensibly declining. Therefore, the ratio of age classes by the number of grooves may differ between the populations, suggesting a slight advantage for the individual ageing method

which incorporates assessments of bill shape and size, as well. However, the proportionally aged cumulative cohort peaks (Fig. 5b) suggest production peaks closely mirroring the seabird productivity peaks demonstrated in Olsen et al. (2025). Without individually marking puffins at the Faroese colonies and monitoring the changes in bill morphology with age, we cannot determine which method is more correct.

While we could include direct measurements of food availability through 0-GI, our measurements of breeding success are indirect. Furthermore, while the selection of harvested individuals for the study was done randomly, the puffin harvest should be biased towards younger birds, as breeding birds (identified by their carrying fish and their straighter flightpath to and from the nest compared to non-breeding birds) were avoided (Jensen 2010, Jensen and Olsen 2020). As such, our study may overestimate the contribution

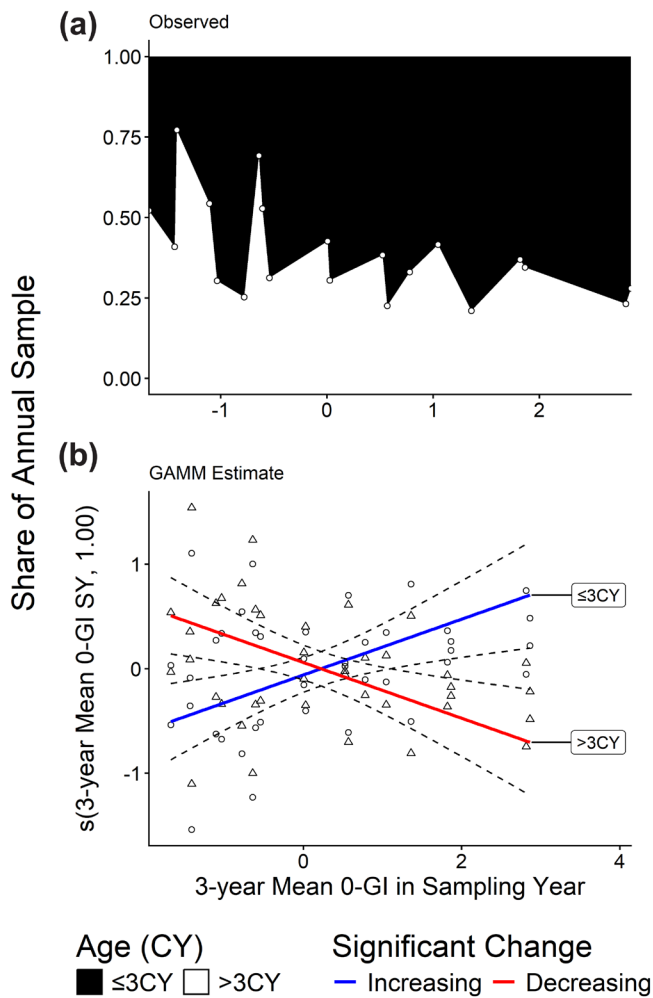


Figure 9. Changes in Atlantic puffin (*Fratercula arctica*) age class share of the annual sample size in relation to the 3-year rolling average 0-GI. (a) and (c) show the results for individually aged birds; (b) and (d) show the results for the proportionally aged birds. (a) and (b) show the observed share of  $\leq 4$ CY (black) and  $> 4$ CY (white) puffins in the sample with the dots showing each observation. (c) and (d) show the GAMM results, with the solid lines showing the estimate  $\pm$  95% CI (dashed line). The blue line represents a significant increase in  $\leq 4$ CY (circles) and the red line a significant decrease in  $>4$ CY (triangles) (see Methods for significance testing; Simpson, 2014, 2024).

of younger birds to the overall population. However, the changes in cumulative cohort sizes and age class (i.e.  $\leq 4$ CY and  $> 4$ CY) contribution will still be represented by our data. Additionally, in poor years, adults of breeding age may forego breeding or may have failed early in the season and join the younger birds in their circulating flight behaviour (Jensen 2010). Thus, poor breeding seasons may have a double negative effect on the puffin population, meaning low fledging rates and relatively higher adult mortality (Stempniewicz and Jensen 2007, Jensen 2010).

Our study is important to understand how large-scale mechanisms (e.g. food abundance; Olsen et al. 2025) may affect local puffin demography. This is especially so, given the

fact that since 1900 a decline in the number of breeding individuals and a shrinking of the colony area have been observed on Nólsoy (Jensen 2010; pers., comm. J-KJ), suggesting potential over-exploitation or disturbance of the local breeding population. In the later 20th century harvest was less intensive than in the early 20th century, partly due to lowered harvest efforts. In 1908, the highest known number of ca 35 000 birds killed by fowlers was recorded (Stempniewicz and Jensen 2007), more than double the highest number estimated during our study period (Table 1), and 20 to 230 times higher than in 2021–2022 (350), 2023 (1865), 2024 (801) and 2025 (153) (pers. comm., R. Hansen).

At the last local government meeting on Nólsoy it was decided that in each of the eight catching spots in the designated area, only up to 50 puffins can be harvested daily during the catching period (9–28 July, except Sundays) while the rest of the island is off-limits (Joensen 2024). This would be a potential total harvest of 6800 birds in 2025. It is highly unlikely that this many puffins are harvested each year, as adverse weather conditions often hinder successful harvesting in one to all locations (e.g. the actual harvest total was 153 in 2025; Table 1). Although our study did not evaluate the direct effects of puffin harvesting on the local demography, we are convinced that the harvest of a globally threatened species should be restricted (BirdLife International 2018).

In conclusion, we showed that food availability (i.e. PPI and 0-GI) before and during hatch years significantly affected puffin cohort size, while sample year food availability proxies had less of an effect on population age composition of the harvested sample. The study period includes fluctuations in PPI on the Faroe Shelf (Gaard et al. 1998), which has been shown to affect breeding parameters of seabirds (Gaard et al. 2002, Ramírez et al. 2017). The steep decline in puffin populations starting in the early 2000s was likely caused by low food availability (TemaNord 2008, Frederiksen 2010, Olsen et al. 2025). Our study provides insights into the mechanism underlying the process that causes low food availability to lead to population declines. We suggest that low recruitment rates driven by low breeding success in poor years due to reduced parental investment or low sub-adult survival may be driving factors of the puffin population decline observed in Føroyar. The annual harvest of the puffins is compounding the negative effects of environmental change (Jensen and Olsen 2020), especially as in poor years adults of breeding age may be targeted by the hunters when they forego breeding or failed early, while they are specifically excluded in richer years as they are carrying food for their chick (Jensen 2010).

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**Permits** – All studied specimens were legally hunted – see Løgtingslóg Um Fuglaveiðu, Sum Seinast Broytt Við Løgtingslóg no. 70 Frá 22 Maí 2023, Pub. L. no. 27 (1984), <https://logir.fo/Logtingslog/27-fra-09-09-1954-um-fuglaveidu-vm-sum-seinast-broytt-vid-logtingslog-nr-34-fra>.

### Author contributions

**Anne N. M. A Ausems:** Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Methodology (lead); Project administration (lead); Validation (lead); Visualization (lead); Writing – original draft (lead). **Dariusz Jakubas:** Conceptualization (supporting); Supervision (equal); Writing – review and editing (lead). **Jens-Kjeld Jensen:** Data curation (lead); Investigation (lead); Resources (lead); Writing – review and editing (supporting). **Katarzyna Wojczulanis-Jakubas:** Conceptualization (supporting); Supervision (equal); Writing – review and editing (lead).

### Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01546>.

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v9s4mw79g> (Ausems et al. 2026).

### Supporting information

The Supporting information associated with this article is available with the online version.

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