

## RESEARCH ARTICLE

# Sources of variation in estimating breeding success of migratory birds from autumn counts

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**Abstract**

1. Understanding drivers of change in population sizes requires estimation of demographic rates such as survival and productivity. In migratory geese, productivity or breeding success is typically assessed at the autumn staging and wintering grounds by observing the number of young versus adults in flocks of geese—also called age counts. Such age counts are, however, likely to be affected by a number of factors as we are compelled to sample from an open population, in which the temporal and spatial age composition can vary due to differential migration, mortality and flocking behaviour.
2. In this study we seek to provide guidance for the design of age counts, by identifying which factors need to be taken into account when collecting data. Identification of these factors will facilitate a more targeted data collection and enable better conservation and management recommendations. We use the long-term age count dataset for the Svalbard population of the pink-footed goose and focus on the following factors: May thaw days on Svalbard, region of sampling, flock size, time and cumulative harvest, calculated as the amount of shot individuals up to each observation of juveniles.
3. We find that the temporal trend in goose productivity based on raw data will be affected by variation in how (which flock sizes), where (which region) and when (which Julian day) the data have been collected.
4. The sources of variation in observations of goose productivity confound inference at the population level. Thus, if the goal is to follow changes in annual productivity, pooled totals of age counts are only useful if data are collected following a random design. We recommend adjusting for these effects using a demographic population model, particularly for hunted species where age counts are conducted during the hunting season and where annual population assessment work is used to recommend an optimal harvest strategy and allocation of hunting quotas. These considerations not only apply to geese, but more generally to migratory birds where breeding and non-breeding segments or age groups partially segregate in time and space in autumn.

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## KEYWORDS

age counts, breeding success, flock size, harvest, migration, mortality, pink-footed goose

## 1 | INTRODUCTION

Population size is regulated through basic demographic rates such as survival and productivity. Understanding drivers of change in these demographic parameters is critical for informing long-term conservation and management of wildlife populations (Nagy et al., 2012). This applies to declining species (Beekman et al., 2019; Wood et al., 2016), as well as for increasing species (Johnson, Zimmerman, et al., 2020; Madsen et al., 2017). These analyses and related conservation and management recommendations rest, however, on the assumption that the methods for collection of the demographic parameters yield representative estimates, something which is not necessarily the case.

In birds, the method for assessing productivity, or breeding success, at the individual pair level, is mostly recorded as the number of young fledging from the nest. At the population level, the breeding success can be expressed as the proportion of young in the population (Boyd, 2007; Wood et al., 2016). In case of short-lived species with a limited geographical distribution, it may be relatively easy to obtain a representative sample. In widespread populations with complex social or migratory systems, it becomes much more challenging because of spatio-temporal segregation of breeding and non-breeding segments of a population or young versus older age classes (Clausen et al., 2013; Milton, 2003).

In geese and other social migratory birds, young stay with their parents in family groups from the time of hatching and throughout the autumn and winter (Black & Owen, 1989; Scott, 1984; Weegman et al., 2016). Ideally, breeding success is assessed at the end of the breeding season by observing the number of fledged young in post-breeding flocks. However, at that time, breeders and non-breeders may be spatially segregated, and it is difficult to achieve a representative sample. Particularly for widespread Arctic breeding geese, this is both expensive and time-consuming. Therefore, an alternative gauge of productivity is the field recording of the proportion of juveniles in flocks of geese, so-called age counts, at the autumn staging and wintering grounds, when geese and swans are concentrated in large flocks (Madsen, Cracknell, et al., 1999; Rees, 2010).

Such age counts have been performed for many European goose and swan populations for several decades, providing long-term time series of their breeding success (Beekman et al., 2019; Brides et al., 2021; Madsen, Cracknell, et al., 1999). Assessing productivity at the staging and wintering grounds are, however, likely to be affected by a number of factors, as we are compelled to sample from an open population, in which the age composition can vary over space and time (Abraham et al., 2012; Madsen, Cracknell, et al., 1999). Such factors may include:

### 1.1 | Differential migration

Reed et al. (2003) found that non-breeding greater snow geese *Chen caerulescens atlantica* initiate autumn migration before breeding geese. In support of these findings, Gundersen et al. (2017) found that non-breeding pink-footed geese *Anser brachyrhynchus* arrived earlier at the autumn staging areas than family groups. The same is the case for swans, where Rees et al. (1997) found that the early migrants of Whooper Swan *Cygnus cygnus* wintering in Britain and Ireland was non-breeders or failed breeders. This temporal dynamic should result in a gradual increase in proportion of juveniles as families arrive at the staging and wintering areas.

### 1.2 | Differential mortality

Looking at proportion of juveniles over the entire autumn and winter period, Lambeck (1990) found a gradually decline of the proportion of brent goose *Branta b. bernicla* juveniles from early autumn to midwinter in four areas along the Dutch Wadden Sea. This is most likely because young geese suffer a higher post-breeding mortality compared to older geese (Francis et al., 1992; Owen & Black, 1989). Hence, the proportion of juveniles is likely to increase at the staging areas during the first period of autumn migration, due to differential migration, but later in the season this increase is expected to attenuate due to differential mortality. The differential mortality is likely to be particularly prominent in populations that are hunted in autumn because young geese are more vulnerable to hunting compared to older geese (Clausen et al., 2017; Fox, 2003; Madsen, 2010). Furthermore, this may be most prominent in the northernmost autumn staging areas due to extended stopover times by families and the fact that young geese will be inexperienced with shooting (Clausen et al., 2017).

### 1.3 | Flocking behaviour

In autumn, it is often observed that goose families are overrepresented in small flocks (Gupte et al., 2019; Madsen, 2010), which may be an attempt to avoid food competition in the larger flocks. Non-breeding geese, on the other hand, typically gather in larger flocks, possibly to access enhanced group-living benefits such as increased anti-predator vigilance (Roberts, 1996). As a result, the proportion of juveniles declines with flock size. Gupte et al. (2019) also showed that through the autumn season the proportion of families in flocks increased, and the proportion of independent juveniles increased with flock size. Thus, the proportion of juveniles is likely to be higher in

small flocks than in larger flocks, but as time progresses this effect is expected to attenuate. Furthermore, Prettitt and MacInnes (1980) showed a continuous breakup and reuniting of families under intensive shooting, resulting in an increase of over 20% in the proportion of unattached juveniles in midwinter. Moreover, Bartelt (1987) found a reduced cohesiveness within families that suffered losses. Hence, in areas with hunting, in addition to the direct effect from hunting in terms of killing, it is expected that juveniles are more likely to get separated from their families. Consequently, independent juveniles as well as families are more likely to seek safety in larger flocks, resulting in a less negative effect of flock size in areas with hunting. The spatio-temporal distribution of observations as well as the selection of flock sizes for age counts are therefore likely to influence the assessment of the proportion of juveniles. For the existing time series of breeding success in goose populations, these effects have not been systematically evaluated. In the Svalbard breeding population of the pink-footed goose, age counts have been performed annually since 1980 (Madsen, 1982). Over time, the geese have changed migratory strategy in response to land use changes, hunting regimes and climate change (Clausen, Madsen, Cottaar, et al., 2018; Madsen et al., 2015; Therkildsen & Madsen, 2000; Tombre et al., 2008). The changes in migratory strategies have meant that the age counts have had to adapt to the whereabouts of the population. As the population has increased from c. 30,000 in the 1980s to c. 80,000 in 2020 and spread over wider areas in the autumn (Heldbjerg et al., 2020; Madsen, Kuijken, et al., 1999), it has become increasingly challenging to maintain a representative sampling design. Furthermore, in 2020 an integrated population model (IPM) was developed to predict impacts of harvest on population development (Johnson, Zimmerman, et al., 2020). The modelling has raised questions over whether age counts can provide reliable annual estimates of breeding success in the population, as the analysis suggested a 23% negative bias in the observed age count data compared to estimates provided by the IPM.

Using the long-term dataset for pink-footed geese, the aim of this study was to investigate which factors might have an effect on the annual estimates of productivity, based on field collection of productivity data. Specifically, we wanted to investigate the effects of sampling in time and space, flock size and possible hunting influences. This will allow us to identify which factors need to be considered when collecting data on breeding success in the population and, more widely, to provide guidance for the design of age counts in migratory birds. In the long term this will ensure that conservation and management of migratory birds rely on the best possible information.

## 2 | MATERIALS AND METHODS

### 2.1 | Study population

The Svalbard population of the pink-footed goose breeds on Svalbard and migrates to wintering grounds in Denmark, the Netherlands and Belgium. Autumn and spring staging areas are in Norway and more

recently in Sweden and western Finland (Heldbjerg et al., 2020; Madsen, Kuijken, et al., 1999). On Svalbard, egg laying occurs from May 20 to June 14 (Madsen et al., 2007) and the overall breeding success in the population is related to the onset of spring. Hence, the earlier the thaw, the more young are produced (Jensen et al., 2014). The geese depart from the breeding grounds during September. Traditionally, they would fly nonstop to staging areas in western Jutland, Denmark, possibly with a short stopover on highland lakes in Norway (Madsen, Kuijken, et al., 1999). In Denmark, they only stayed for about 1 month before departing to the wintering grounds in Friesland, the Netherlands, and Flanders, Belgium. Beginning in the late 1990s, geese started to make an autumn stopover in the lowlands of Trøndelag, Norway, arriving in mid-September and staying until snowfall, which is usually in late October (Jensen et al., 2016). Since the mid-2000s large flocks of geese have extended their autumn stay in Denmark, and now stay throughout the winter (Madsen et al., 2015). As a result of the extended stay in Denmark, the numbers staging and wintering in the Netherlands and Belgium have declined (Madsen et al., 2015). In recent years, the majority of the population has remained in Denmark throughout the winter, fostered by an increasing area of maize, which is their main food resource during autumn and early winter (Clausen, Madsen, Nolet, et al., 2018). They have likewise started to arrive earlier in Belgium, apparently skipping the Netherlands (Clausen, Madsen, Cottaar, et al., 2018). Most recently, flocks of pink-footed geese have started to occur in the southern part of Sweden during autumn (Heldbjerg et al., 2020).

The pink-footed goose is a huntable species in Norway and Denmark, whereas it is protected in the Netherlands, Belgium and Sweden. The harvest in Denmark and Norway has increased during the last decade as a result of actions taken under the international management plan to maintain a target population size via an adaptive harvest management framework (Madsen et al., 2017).

### 2.2 | Age counts

Traditionally, age counts of pink-footed goose were performed in the Netherlands during September–October when the vast majority of the population was located there, supplemented by observations in Denmark (Madsen, Kuijken, et al., 1999). However, with geese staging longer in both Denmark and Norway since the mid-2000s, age counts were organized in both countries. With the recent autumn occurrences in Belgium and Sweden, age counts have been carried out there as well. However, because birds from Sweden most likely belong to the population breeding on Novaya Zemlya in Russia, these data have not been included in our analysis (J. Madsen pers. comm.).

Age counts are made by trained observers who count the number of juvenile birds and older birds, examining each clearly visible bird in a flock using a telescope. Birds older than 1 year ('adults') are identified based on white-edged feathers along the upper margins of their flanks and striped backs, and juveniles lack stripes and have a more 'blurred' brownish plumage (Patterson & Hearn, 2006).

Juveniles moult cover feathers over the course of autumn and winter and it becomes increasingly difficult to separate juveniles from older birds in the field.

Observers are instructed to sample flocks of different sizes (Ganter & Madsen, 2001). In small flocks all birds are aged. In these cases, the sum of adults and juveniles equals the flock size. In larger flocks the proportion of juveniles varies with position in the flock (Boyd, 1953; Lambeck, 1990) and a subset of birds on imagined transect lines through the flock is examined to avoid age bias (Ganter & Madsen, 2001); in these cases, total flock size is registered in addition to the number of aged adults and juveniles.

The fieldwork in this study did not require any licences or permits.

## 2.3 | Explanatory variables

### 2.3.1 | Time and region

The spatial resolution for the current analysis was by region, defined as Norway (Trøndelag) since 2013, Denmark (northern and western Jutland) in 1995, 1996 and since 2011, the Netherlands (Friesland) since 1995 (with the exception of 2017) and Belgium (Flanders) since 2018.

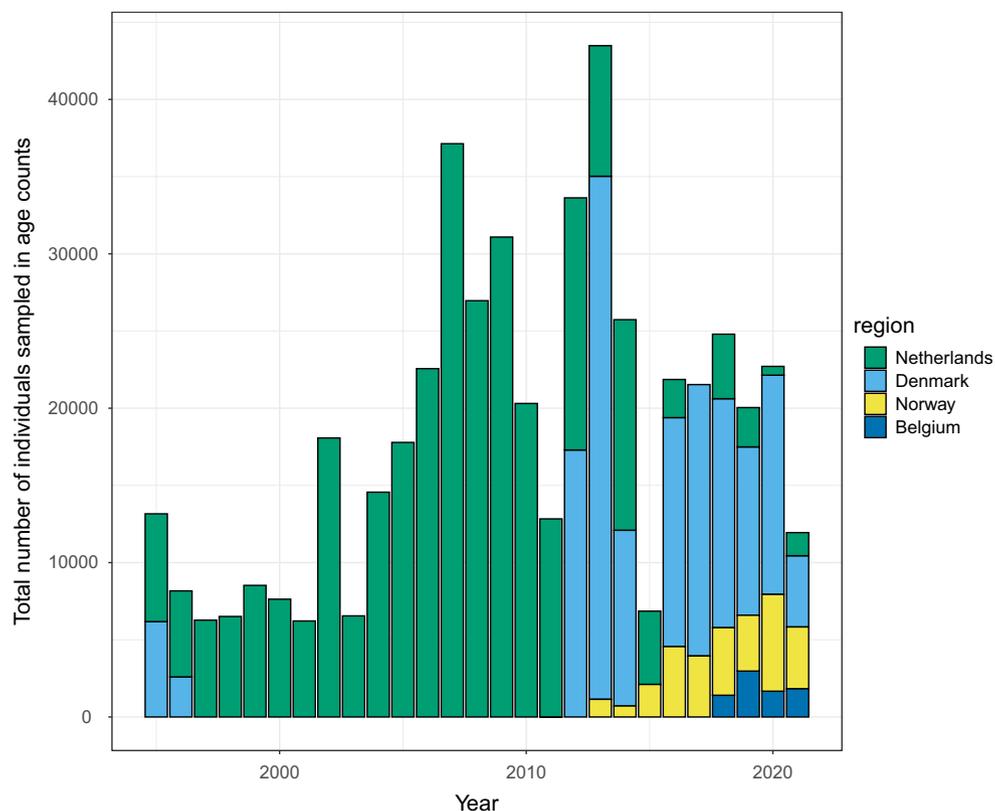
The total number of individuals sampled per year in the Netherlands decreased from a mean of 15,033 between 1995

and 2011, to a mean of 6050 between 2012 and 2021 (Figure 1; Table S1). The change in sampling effort in the Netherlands corresponds roughly to the time when sampling was started or intensified in the other countries, particularly in Denmark, where few or no birds were sampled before 2011, but which increased to a mean of 15,502 individuals sampled between 2012 and 2021. The numbers sampled in Norway ranged from 713 to 6271 individuals per year and in Belgium between 1407 and 2973 individuals per year (Figure 1).

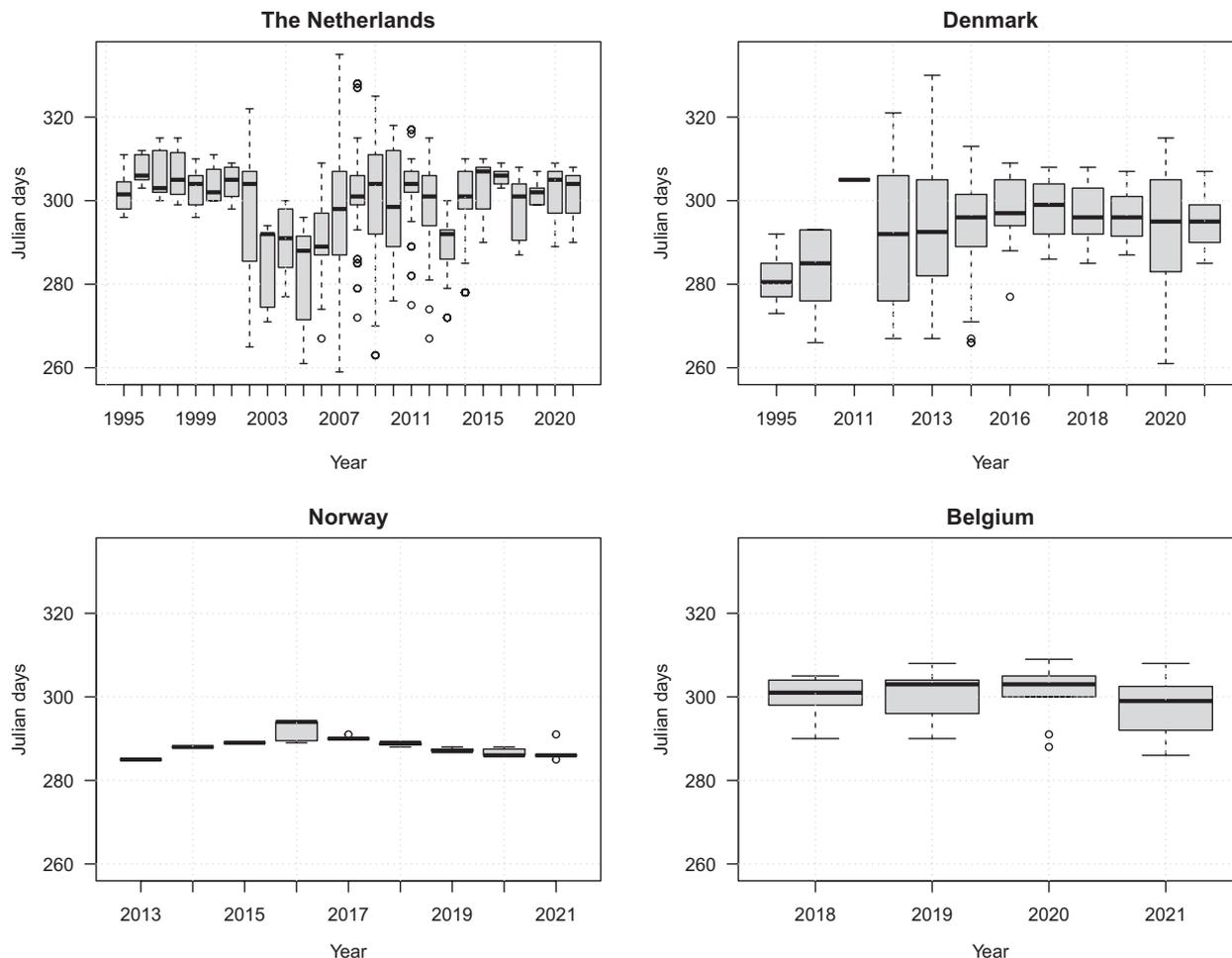
Age counts were mainly performed during 12 October and 4 November since 2011; however, age counts with flock size records spanned from 16 September to 1 December in the Netherlands and 17 September to 26 November in Denmark (Figure 2). In Belgium and Norway, data were collected in a narrower window from 13 October to 4 November and 12–20 October respectively. Due to unbalanced collection of age counts in Denmark and the Netherlands versus Belgium and Norway, as well as the difference in quantity of observations between the regions, the effect of time was only investigated for Denmark and the Netherlands. In the analysis time was investigated using Julian days, that is, the ordinal date.

### 2.3.2 | Flock size

Overall, group (hereafter ‘flock’) size ranged from 1 to 15,000 individuals. However, two flock sizes (of 15,000) were far higher than



**FIGURE 1** Total number of individuals of pink-footed goose sampled in age counts per year in the four regions; the Netherlands, Denmark, Norway and Belgium from 1995 to 2021.



**FIGURE 2** Temporal variation in Julian days for age counts from the four regions. Provided are median values (bold horizontal line), the interquartile distances (the box), the extreme values (whiskers) and the outliers (circles).

the next highest flock sizes of 9300. To avoid influential outliers, these two observations were discarded in the analysis. The resulting mean flock size was 950 individuals ( $\pm 1171$  SD,  $n_{\text{observations}} = 1598$ ) between 1995 and 2021. Across years, a significant negative trend in flock size through time was observed (Figure S1). As flock size information is missing from Denmark in 2015, this year is not included in the analysis. Region-specific flock size information is provided in Table S1.

### 2.3.3 | Hunting

The pink-footed goose has an open hunting season in Denmark (1 September to 31 December on land; for marine environments outside the high-water line until 31 January; since 2014/2015 the hunting season has been open in both environments until 31 January, with the exception of 2015/2016) and in Norway (10 August to 23 December; Svalbard 20 August to 31 October). In both countries, reporting of harvest is mandatory and has been compiled since 1941 by the Danish Bag Statistics and since 1992 by Statistics Norway. Prior to 2016, Danish hunters only reported their hunting bag by group (e.g. geese), but through the Danish Wing Survey, operating

since 1982, species-specific estimates were obtained using the relative species distribution. Furthermore, wings submitted to the wing survey include date of harvest, and therefore give a measure of the temporal distribution of the bag. Annual wing sample sizes during 1990–2021 varied between 12 and 959, with an average of 272 wings received per year (Table S1).

As it has only been possible to derive the temporal distribution of harvest for Denmark, the effect of hunting was only investigated for this region. The effect of hunting was investigated using the derived variable cumulative harvest, calculated as the number of shot individuals up to each age count date. The cumulative harvest per year ranged from 660 to 3717 (Figure S2; Table S1). Furthermore, due to a significant positive correlation between cumulative harvest and Julian days ( $r = 0.77, n = 700, p < 0.001$ ), only one variable (Julian days or cumulative harvest) was used at a time and only in the analysis for Denmark.

### 2.3.4 | Thaw days

To the observational effects of flock size, time, region and hunting, we also included the population-level effect of spring temperatures

Model	Model number	df	AIC	dAIC	AIC weight	Theta
Thaw days + region + region × flock	5	10	12,801.71	0.0	0.51	25.59
<b>Thaw days + region + flock</b>	<b>4</b>	<b>7</b>	<b>12,801.78</b>	<b>0.1</b>	<b>0.49</b>	<b>25.53</b>
Thaw days + region	3	6	12,819.52	17.8	<0.001	25.07
Thaw days + flock	2	4	12,874.15	72.4	<0.001	23.77
Thaw days	1	3	12,900.16	98.4	<0.001	23.14
Intercept	0	2	13,081.55	279.8	<0.001	19.89

**TABLE 1** Akaike's information criterion (AIC) and theta (overdispersion) values of the candidate models of the relationship between explanatory variables and the proportion of juveniles expressed by a beta-binomial distribution of the absolute number of juveniles observed in the flock. The models use data from 1995 to 2021 from all four regions (Norway, Denmark, the Netherlands and Belgium). Models marked in bold represent the best model based on the likelihood ratio test.

on the breeding grounds. The advancement of spring melt, measured as the number of days in May on Svalbard with average daily mean temperature above 0°C. (thaw days), is a strong indicator of the breeding success, and is included as an index for the overall population productivity (Jensen et al., 2014). Thaw days are derived from the Norwegian Centre for Climate Services (<https://seklima.met.no/observations/>), and available from all years from the two weather stations Ny-Ålesund and Svalbard Airport in Longyearbyen. Temperature data from these two stations show a strong correlation with snow cover on the breeding grounds for the population. A full description of the methods can be found in Jensen et al. (2014). Between 1995 and 2021 the average number of thaw days from the two stations ranged from 0 days (1998) to 27 days (2018) with a mean of 10 ( $\pm 7$ ,  $n = 27$ ). Between 1990 and 2021, there was a positive and significant trend in thaw days through time (Figure S3).

## 2.4 | Statistical analysis

The ability of different covariates to explain variation in the proportion of juveniles was assessed using maximum likelihood estimation. We used a generalized linear model with a logit-link function using a beta-binomial error distribution for the proportion of juveniles. The beta-binomial error distribution was used to account for overdispersion in the counts arising from other sources than the assessed covariates (i.e. from observer experience, hunting in Norway, derogation and other uncontrolled factors; Bolker, 2008). To test the effect of covariates on the proportion of juveniles ( $p_i$ ), we used a model of the form:

$$\text{logit}(p_i) = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \beta_4 D_i + \beta_5 F_i + \beta_6 C_i + e_i. \quad (1)$$

where  $\beta$  is a regression coefficient,  $X_1, X_2, X_3 = 0$  if region is Denmark,  $X_1 = 1$  if region is Belgium or 0 otherwise,  $X_2 = 1$  if region is the Netherlands or 0 otherwise,  $X_3 = 1$  if region is Norway or 0 otherwise,  $D$  is thaw days,  $F$  is flock size and  $C$  is either Julian days or cumulative harvest, but not both due to the presence of collinearity between the two variables. The residuals are beta-binomial distributed as:

$$e_i \sim \text{binomial}(\text{beta}(\hat{p}_i, \theta), n_i),$$

where  $\hat{p}_i$  is the model expectation,  $\theta$  is the overdispersion parameter and  $n_i$  is sample size.

In addition to the main effects, the two-way interaction between region and flock size, as well as between Julian days and flock size was analysed. A quadratic effect of Julian days, allowing the slope to change over time, was also examined.

The presence of collinearity between explanatory variables was tested using Pearson's correlation coefficient. We used values of  $r > 0.7$  as indicative of collinearity (Dormann et al., 2013). In cases of collinearity between the variables, only one variable was analysed at a time (Table S2). Furthermore, to reduce multicollinearity and because the model contains quadratic as well as interaction terms, our explanatory variables; thaw days, flock size, Julian days and cumulative harvest were standardized by subtracting the mean and dividing by the standard deviation (Kutner et al., 2004). Thus, the regression intercepts represented mean values and coefficients represented the change in the proportion of juveniles with one standard deviation change in the covariate. We assessed relative model utility using Akaike's information criterion (AIC; Burnham & Anderson, 2002). The model with the smallest AIC value was selected as providing the best description of the data. Model weights were also obtained based on the AIC values, reflecting the relative weight of evidence in favour of the respective models from among all the candidate models. Furthermore, a likelihood ratio test was used to compare pairwise nested models. The null hypothesis is that the simple model is the best model. If the null hypothesis is rejected, then the more complex model is a significant improvement over the simple one. All analyses were performed using the R statistical program, version 4.2.1 (RC Team, 2022), including the following packages dplyr (Wickham et al., 2022), padr (Thoen, 2021), lubridate (Grolemund & Wickham, 2011), ggplot2 (Wickham, 2016), plyr (Wickham, 2011), GGally (Schloerke et al., 2021), bbmle (Bolker & Team, 2022) and emdbook (Bolker, 2020).

## 3 | RESULTS

### 3.1 | Overall population productivity model

Given the set of candidate models using data from 1995 to 2021 and from all four regions (Table 1, model 0–5), the model using thaw days, region, flock size and the interaction between flock size and region (model 5) had the lowest AIC value and highest

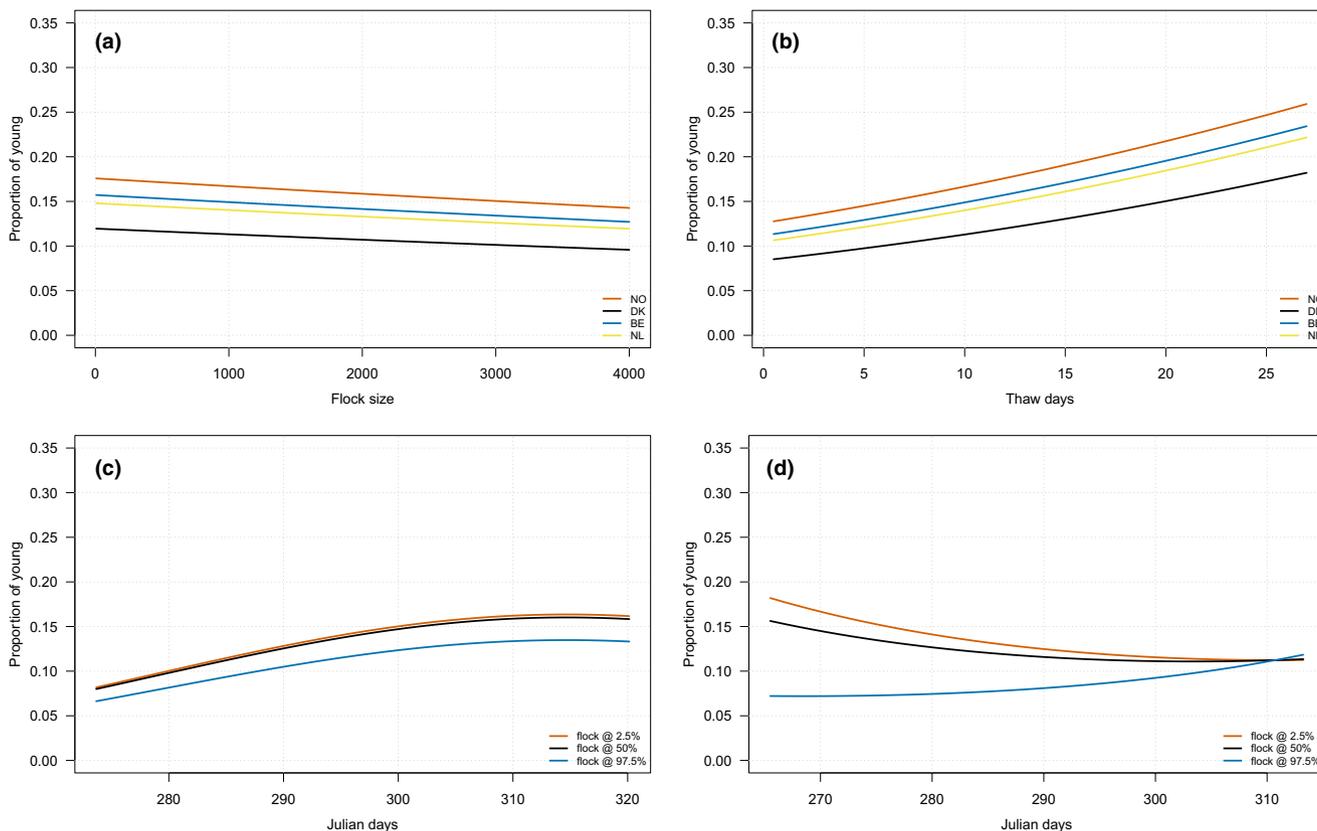
model weight (dAIC: 0.0, weight: 0.51; Table 1), compared to the second-best model (model 4), which excluded the interaction between flock size and region (dAIC: 0.1, weight: 0.49; Table 1). The likelihood ratio test, however, did not support the inclusion of the interaction term ( $p = 0.109$ ), and results for model 4 are presented (Table 4). Model 4 shows a positive relationship with thaw days, and a negative relationship with flock size. Thus, the proportion of juveniles is highest in small flocks and following an early thaw on Svalbard (Figure 3a,b). Furthermore, using coefficients from model 4 and setting the covariates at their standardized means, the lowest mean estimate of proportion of juveniles was expected for Denmark (0.114) followed by the Netherlands (0.141), Belgium (0.150) and Norway (0.168).

### 3.2 | Regional productivity models

The effect of Julian days was only investigated for the Netherlands and Denmark, which had the longest period of intra-year observations. Furthermore, the effect of cumulative harvest was only investigated for Denmark, which was the only region with data concerning the temporal distribution of harvest.

#### 3.2.1 | The Netherlands

Given the set of candidate models using data from the Netherlands (Table 2; model 0–6), model 4, using thaw days, flock size and including Julian days as a quadratic term, had the lowest AIC value and highest model weight (dAIC: 0.0, weight: 0.52; Table 2), compared to the second-best model (model 6), which included the interaction between Julian days and flock size (dAIC: 0.1, weight: 0.48; Table 2). The likelihood ratio test supported the exclusion of the interaction term ( $p = 0.171$ ), and results from model 4 are provided (Table 4). As for the overall model, proportion of juveniles showed a positive relationship with thaw days and a negative relationship with flock size. Additionally, there was a positive relationship with Julian days, hence later in the season the proportion of juveniles increased. However, as indicated by the negative quadratic term, the relationship changed and was described by a concave parabolic curve. Using the standardized mean values of thaw days and flock size as well as the 2.5%, 50% and 97.5% quantile range of Julian days, the proportion of juveniles increased from 0.0763 in the beginning of the period (Julian day 274) to 0.1458 (Julian day 303), thereafter the rate of increase decreased towards the end of the period, resulting in a proportion of juveniles of 0.152 on Julian day 320 (Figure 3c).



**FIGURE 3** Predicted proportion of juveniles at the 95% quantile range of (a) flock sizes, (b) thaw days (model 4) and Julian days using data from (c) the Netherlands (model 4NL), and (d) Denmark (model 6DK). Other variables were kept at their standardized mean values. For (a) and (b) the predictions are shown per region, and for (c) and (d) the predictions are shown for the 2.5%, 50% and 97.5% quantile of flock sizes.

Model	Model number	df	AIC	dAIC	AIC weight	Theta
<b>Thaw days + flock + Julian + Julian<sup>2</sup></b>	<b>4</b>	<b>6</b>	<b>6573.96</b>	<b>0.0</b>	<b>0.52</b>	<b>33.23</b>
Thaw days + flock + Julian + Julian <sup>2</sup> + Julian × flock	6	7	6574.08	0.1	0.48	33.34
Thaw days + flock + Julian	3	5	6598.50	24.5	<0.001	32.26
Thaw days + flock + Julian + Julian × flock	5	6	6600.40	26.4	<0.001	32.28
Thaw days + flock	2	4	6677.24	103.3	<0.001	28.93
Thaw days	1	3	6678.39	104.4	<0.001	28.67
Intercept	0	2	6748.25	174.3	<0.001	25.60

**TABLE 2** Akaike's information criterion (AIC) and theta (overdispersion) values of the candidate models of the relationship between explanatory variables and the proportion of juveniles expressed by a beta-binomial distribution of the absolute number of juveniles observed in the flock. The models use data from 1995 to 2021 from the Netherlands. Models marked in bold represent the best model based on the likelihood ratio test.

Model	Model number	df	AIC	dAIC	AIC weight	Theta
<b>Thaw days + flock + Julian + Julian<sup>2</sup> + Julian × flock</b>	<b>6</b>	<b>7</b>	<b>5148.21</b>	<b>0.0</b>	<b>0.813</b>	<b>22.11</b>
Thaw days + flock + Julian + Julian × flock	5	6	5151.20	3.0	0.182	21.91
Thaw days + flock + Julian + Julian <sup>2</sup>	4	6	5158.82	10.6	0.004	21.64
Thaw days + flock + Julian	3	5	5162.23	14.1	<0.001	21.40
Thaw days + flock + cumulative harvest + cumulative harvest × flock size	8	6	5163.19	15.0	<0.001	21.59
Thaw days + flock + cumulative harvest	7	5	5164.25	16.0	<0.001	21.49
Thaw days + flock	2	4	5166.18	18.0	<0.001	21.20
Thaw days	1	3	5179.93	31.7	<0.001	20.58
intercept	0	2	5262.51	114.3	<0.001	17.22

**TABLE 3** Akaike's information criterion (AIC) and theta (overdispersion) values of the candidate models of the relationship between explanatory variables and the proportion of juveniles expressed by a beta-binomial distribution of the absolute number of juveniles observed in the flock. The models use data from 1995 to 2021 from Denmark. Models marked in bold represent the best model based on the likelihood ratio test.

Model	4	4NL	6DK	7DK
Intercept	-2.056*	-1.804*	-2.082*	-2.024*
Denmark	0*			
Belgium	0.318*			
The Netherlands	0.246*			
Norway	0.452*			
Thaw days	0.224*	0.212*	0.227*	0.219*
Flock size	-0.073*	-0.067*	-0.113*	-0.105*
Julian days		0.179*	-0.046	
Julian days <sup>2</sup>		-0.067*	0.043*	
Cumulative harvest				0.052*
Flock size × Julian days			0.085*	

**TABLE 4** Regression coefficients for model 4, 4NL, 6DK and 7DK.

Note: Model 4 uses data from all regions (Table 1), model 4NL uses data from the Netherlands (Table 2) and model 6DK and 7DK uses data from Denmark (Table 3).

\*Significant at 5% level.

### 3.2.2 | Denmark

Given the set of candidate models using data from Denmark (Table 3; model 0–8), model 6, using thaw days, flock size and including Julian days as a quadratic term, as well as the interaction between Julian days and flock size, had the lowest AIC value and highest model

weight (dAIC: 0.0, weight: 0.8130; Table 3), compared to the second-best model (model 5) which did not include the quadratic term (dAIC: 3.0, weight: 0.182; Table 3). The likelihood ratio test supported the inclusion of the quadratic term ( $p < 0.001$ ), and results for model 6 are provided (Table 4). Based on results from model 6, the proportion of juveniles showed a positive relationship with thaw days and a

negative relationship with flock size. Additionally, there was a negative relationship with Julian days, hence later in the season the proportion of juveniles declined. However, as indicated by the positive quadratic term, the relationship was described by a convex parabolic curve. Thus, using the standardized mean values of thaw days and flock size as well as the 2.5%, 50% and 97.5% quantile range of Julian days, the proportion of juveniles decreased during the first half of the period from 0.1466 (Julian day 266) to 0.113 (Julian day 293), and thereafter the decrease attenuated for the second half of the period (0.116 on Julian day 313; [Figure 3d](#)). Furthermore, the interaction between Julian days and flock size was significant, meaning that the effect of flock size was dependent on Julian days. Thus, in the beginning of the period a higher proportion of juveniles was observed in small flocks compared to large flocks, whereas in the end of the period there was no difference in proportion of juveniles in small versus large flocks ([Figure 3d](#)). Using the standardized mean values of thaw days and the 2.5% and 97.5% quantile of Julian days and flock size, the proportion of juveniles was 0.185 in small flocks (99) and 0.074 in large flocks (4205) in the beginning of the period (Julian day 266), whereas in the end of the period (Julian day 313) the proportion of juveniles was 0.115 in small flocks (99) and 0.121 in large flocks (4205; [Figure 3d](#)). Moreover, there was a slight increase in the proportion of juveniles in larger flocks towards the end of the observational period, whereas we saw a continuous decline for smaller flocks, which attenuated towards the end of the period.

Surprisingly, a significant positive relationship ( $p < 0.05$ ) was found between the proportion of juveniles and the cumulative harvest, thus the higher the cumulative harvest the higher proportion of juveniles. The models including cumulative harvest did, however, not get any support in the model selection ([Table 3](#); model 7 and 8). The likelihood ratio test did, however, support the inclusion of cumulative harvest compared to the simpler model only using flock size and thaw days (model 7 and 2; [Table 3](#)).

## 4 | DISCUSSION

An analysis of potential sources of bias in the monitoring program for the Svalbard population of pink-footed goose suggested a 23% negative bias in the observed age count data compared to estimates provided by an IPM (Johnson, Zimmerman, et al., 2020). In this study we have identified several factors which can contribute to the explanation of this bias; namely region, flock size and seasonal timing. We found that all factors had an effect on estimates of proportion of juveniles, and therefore need to be carefully considered in the design of monitoring programs and assessment of data.

### 4.1 | Region

Among the four regions included in this study, the lowest estimate of proportion of juveniles was observed in Denmark, followed by

the Netherlands, Belgium and highest in Norway. This fits partly with our hypothesis that regions closer to breeding grounds, such as Norway, were expected to have a higher proportion of juveniles compared to regions further away from the breeding grounds. Conversely, Denmark, the second closest region to the breeding grounds, held the lowest estimate of proportion of juveniles. There may be at least two reasons for this. First, there is a longer migration route to Denmark than to Norway, which gives rise to higher natural mortality, and thereby a lower proportion of juveniles in Denmark compared to Norway. Second, hunting is practiced in Denmark and Norway during the observation period. Thus, birds staging in Denmark and Norway are to a greater extent exposed to harvest compared to birds staging in the Netherlands and Belgium, where hunting on pink-footed goose is prohibited. If harvest is responsible for the regional difference, it implies that not all birds stop in Denmark and/or Norway; if they do, only for a short time. Otherwise, there would have been a cumulative effect throughout the migratory flyway. Both data on the seasonal phenology in numbers, as well as resightings of neck-banded individuals in the regions, lend support to the conclusion that not all birds stop in Denmark and/or Norway (Clausen, Madsen, Cottaar, et al., 2018; Kuijken et al., 2005; Madsen et al., 2015).

The implication is that data from different regions cannot be pooled to increase sample size, unless the effect of region is taken into account in the modelling framework. This is particularly relevant for migratory waterbirds, such as pink-footed geese, which have changed their spatial distribution during the period when age counts have been conducted, have a highly dynamic winter migration strategy and where new areas have been added for monitoring.

### 4.2 | Flock size

As observed by other studies (Gupte et al., 2019; Madsen, 2010; Rees et al., 1997), a negative and significant relationship between proportion of juveniles and flock size was found. It is therefore important to either randomly sample varying flock sizes or use flock sizes in a modelling framework to account for potential heterogeneity. Moreover, we found that in recent years observations have generally focused on smaller flock sizes, compared to large flocks in the early observational period. This potentially confounds comparisons across years. However, part of the explanation may be that the flock dynamics have changed. In the 1990s the geese gathered in few large flocks in Friesland, in the Netherlands and in western Denmark, whereas more recently, the geese have started to spread out in smaller flocks over a much larger area. This change of flocking behaviour may be in response to food availability, such as maize that has increased in extent (Madsen et al., 2015). Hunting may likewise have an effect on flock size, however, this effect might go two ways: either flock size decreases due to continuous breakup under intensive shooting, or flock size may increase as birds seek safety in larger flocks.

### 4.3 | Time

In migratory geese, differential migration of non-breeding geese and families has been documented for greater snow geese and pink-footed geese (Gundersen et al., 2017; Reed et al., 2003). The increase in proportion of juveniles observed in the Netherlands through the first part of the autumn period can likely be explained by a later influx of family groups. The observed increase attenuates in the last part of the autumn, and this may partly be a result of higher juvenile natural mortality compared to adults, as well as increasing difficulties distinguishing juveniles from adults.

In Denmark a gradual seasonal decline in the proportion of juveniles was observed for most flock sizes. A likely explanation is the negative effect from hunting activities in Denmark, given that juveniles are more vulnerable to hunting than adults. For large flock sizes, however, a slight increase in the proportion of juveniles was observed, particularly at the end of the autumn observational period. This can be an indirect effect in areas with intense shooting, where juveniles are more likely to get separated from their parents and, as a result, seek safety in larger flocks. Thus, even though a later seasonal influx of families in Denmark is likely, harvest might mask this. Towards the end of the observation period the rate of decline in proportion of juveniles was levelling off in most flock sizes in Denmark. It is possible that at this point the differential hunting vulnerability of juveniles has decreased, which will lead to a stabilization in the proportion of juveniles. This is supported by a similar seasonal levelling off in the decrease in proportion of juveniles observed in the hunting bag of pink-footed geese (Heldbjerg et al., 2020). Here it was argued that the gradual decline in juvenile proportions in the hunting bag could either be explained by the comparatively higher hunting mortality of juvenile birds, leading to a reduction in the juvenile segment of the population as the season progresses, or that juveniles increasingly learn to avoid hunting.

In addition to the direct effect of time on the proportion of juveniles, time also seems to influence the effect of flock size. In the two regional models for Denmark and the Netherlands, respectively, the effect of flock size was strongest in the beginning of the autumn period, whereas towards the end of the period the proportion of juveniles was independent of the flock size. This corresponds with findings by Gupte et al. (2019) who showed that through the season the proportion of families in larger flocks increased, and the proportion of independent juveniles increased with flock size. Furthermore, as the interaction between Julian days and flock size was significant in the regional model for Denmark and not for the Netherlands, this could indicate that the interaction effect is stronger in areas with disturbance from hunting, resulting in breaking up of families and juveniles seeking safety in larger flock.

Finally, we saw that the sample size of observations shifted from the Netherlands in the early years to particularly Denmark in recent years. This confounds comparisons across years because the regions have different mean levels of observed proportion of juveniles.

### 4.4 | Cumulative harvest

The cumulative harvest variable was developed to analyse the possible effect of the disproportionate harvest of young birds on the proportion of juveniles. This variable, however, did not get any support in the model selection. One possible explanation might be the method for developing this variable. First, it is assumed that the temporal wing submissions resemble the true temporal distribution of hunting within a given year. Second, harvest is confounded with time/Julian days, and thereby the two variables are hard to tease apart. Third, it may be a matter of confounding cause and effect; that is, does the amount of harvest drive the proportion of juveniles or does the proportion of juveniles drive the amount of harvest? The significant positive relationship found between the proportion of juveniles and the cumulative harvest in this analysis supports the latter. This is furthermore supported by Clausen et al. (2017), who stated that the recently observed increase in harvest rate appears to be primarily driven by an increased hunting mortality of young birds. Although it is implicit that hunting will affect the proportion of juveniles due to their higher vulnerability, further investigations are needed to confirm the negative effect hunting is expected to have on the proportion of juveniles.

### 4.5 | Age ratio assessment recommendations

Based on these findings it is clear that investigation of the temporal trend in proportion of juveniles based on raw data will be affected by variation in how (which flock sizes), where (which region) and when (which Julian day) the data have been collected. And, particularly for hunted species, the proportion of juveniles is likely to be affected by the differential vulnerability of juveniles. Only using a random sampling design will it be possible to make reliable inference about the proportion of juveniles at the population level using only raw data, and it will still be subject to effects of the timing of age counts. Alternatively, an integrated population modelling framework can be used to adjust for these effects and thereby estimate the overall breeding success for the population. This is the case for the Svalbard population of pink-footed, where an IPM has been implemented in the annual population assessment work used to recommend an optimal harvest strategy (Johnson, Jensen, et al., 2020). This is the case as well for the Northwest European population of Bewick's swan, where an IPM was developed to study the population dynamics and underlying vital rates to help inform management and conservation decisions (Nuijten et al., 2020). Both the IPM for pink-footed goose and the model for Bewick's swan found a discrepancy between the model estimates and the productivity parameters recorded in autumn/winter. IPMs can to some extent help with temporal-spatial mismatches of demographic data (Zipkin & Saunders, 2018); for example, by taking advantage of other sources of information to estimate the proportion of juveniles. IPMs can also be used to estimate the proportion of young prior to any hunting, which is needed to produce optimal

harvest management recommendations. As the age counts are typically carried out in the middle of the hunting season, however, this requires that the amount of harvest before the time of age count is known (or can be estimated), which is the case in pink-footed geese. Thus, fully accounting for spatial and temporal heterogeneity in demographic processes remains challenging (Michielsens et al., 2008). It therefore continues to be important to carefully consider sampling protocols as well as accounting for relevant covariates when predicting population dynamics and the impact of management actions. It should be noted, however, that IPMs cannot remove inherent biases within a dataset, such as imperfect detection (Kery & Schaub, 2012), unless ancillary data, such as double observers to estimate detection probability, are included in the model.

In conclusion, our research suggests that many factors can influence the proportion of young birds in individual samples above and beyond demographic stochasticity. Even if important factors are accounted for using logistic regression, the data may still be over-dispersed relative to the binomial distribution, which is typically assumed for these kinds of data. Thus, simply pooling samples of young and adult birds are not expected to provide reliable measures of productivity unless samples are collected randomly on spatial, temporal and organizational (e.g. flock size and hunting) scales, which is rarely if ever feasible. In the absence of a random sampling design, the best that might be done is to account for changes in the nature of the sample by using a logistic regression model to predict the proportion of young for a standardized set of values for the temporal, spatial and organization covariates. This potentially could provide a useful index of productivity, but the magnitude of this index relative to the true proportion of young in the population will remain unknown. Moreover, in the absence of other demographic data, the utility of such an index is limited (Caughley, 1974). Finally, we remind readers that although logistic regression is a powerful tool for analysing samples of young and adult birds, it is subject to many of the same constraints and assumptions of simple linear regression (Stoltzfus, 2011). All of these considerations not only apply to geese, but more generally to migratory birds where breeding and non-breeding segments or age groups partially segregate in their temporal and spatial occurrence along the autumn flyways.

#### AUTHOR CONTRIBUTIONS

Gitte Høj Jensen, Jesper Madsen and Fred A. Johnson conceived the ideas, designed the methodology and led the writing of the manuscript; Jesper Madsen collected the data; Gitte Høj Jensen and Fred A. Johnson analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

#### PEER REVIEW

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#### DATA AVAILABILITY STATEMENT

Data available from Zenodo Data Repository <https://doi.org/10.5281/zenodo.7223565> (Jensen et al., 2022).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Temporal variation in mean flock sizes scanned for age counts across the four regions; the Netherlands, Denmark, Norway, and Belgium from 1995 to 2021.

**Figure S2.** Temporal variation in the cumulative harvest in Denmark from 1995 to 2021, during the period 18 September–26 November.

**Figure S3.** Temporal variation in the number of thaw days in May on Svalbard from 1990 to 2021.

**Table S1.** Descriptive statistics for the response and explanatory variables in the four regions (Norway, Denmark, the Netherlands and Belgium).

**Table S2.** Pearson correlations matrix for explanatory variables used in (a) the overall productivity model, (b) the productivity model using data from the Netherlands and (c) the productivity model using data from Denmark.

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