



FEATURE ARTICLE

Spatial variation in vital rates and population growth of thick-billed murre in the Atlantic Arctic

Morten Frederiksen^{1,*}, Sébastien Descamps², Kyle H. Elliott³, Anthony J. Gaston⁴, Nicholas P. Huffeldt^{1,5}, Yann Kolbeinsson⁶, Jannie Fries Linnebjerg¹, Erlend Lorentzen², Flemming R. Merkel^{1,5}, Hallvard Strøm², Thorkell Lindberg Þórarinnsson⁶

¹Department of Bioscience, Aarhus University, 4000 Roskilde, Denmark

²Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway

³Canada Research Chair in Arctic Ecology, Department of Natural Resource Sciences, McGill University, Montreal, QC H9X 3V9, Canada

⁴Environment and Climate Change Canada, Ottawa, ON K1A 0H3, Canada

⁵Greenland Institute of Natural Resources, 3900 Nuuk, Greenland

⁶Northeast Iceland Nature Research Centre, 640 Húsavík, Iceland

ABSTRACT: Understanding spatiotemporal variation in vital rates and population growth rates is a central aim of population ecology, and is critical to conservation of migratory species where different populations may spend the non-breeding season in sometimes widely separated areas. However, estimating those parameters and identifying the underlying drivers of variation for species migrating to remote areas is challenging. The thick-billed murre *Uria lomvia* is a colonial seabird with a pan-Arctic distribution. Previous studies have documented large-scale spatial variation in population growth in the species' Atlantic range, with eastern populations declining and western populations being stable, and suggested that this variation was linked to conditions in the wintering areas. We analyse variation in breeding success and adult survival from colonies throughout the Atlantic range, construct region-specific stochastic population models, and compare model predictions to observed colony growth rates. Breeding success was uniformly high in Greenland and Iceland, lower and more variable in Spitsbergen, Bjørnøya and Hudson Bay, and low at Jan Mayen. Adult survival was average or high in all colonies during the 2010s. Observed colony growth rates were lower than modelled growth rates for most populations. This suggests that pre-breeding survival or breeding propensity must have been lower than assumed in many of these populations. Low pre-breeding survival could be linked to poor feeding conditions in fall and winter, possibly influenced by large-scale oceanographic variation. Our results support the idea that seabird populations not



A pair of thick-billed murre *Uria lomvia* attending their single chick on a cliff ledge in Iceland.

Photo: Yann Kolbeinsson

subject to breeder mortality due to anthropogenic causes are regulated mainly through variation in pre-breeding survival.

KEY WORDS: Demography · Adult survival · Pre-breeding survival · Breeding success · Colony growth rates · Seabird · *Uria lomvia* · Brünnich's guillemot

*Corresponding author: mfr@bios.au.dk

1. INTRODUCTION

Most animal species show extensive spatial variation in vital rates, most importantly survival and reproductive output, and rate of population change or growth (Bjørnstad et al. 1999, Frederiksen et al. 2005). Such variation occurs on scales ranging from very local (Tavecchia et al. 2008, Sanz-Aguilar et al. 2009) to global (Irons et al. 2008, Suryan et al. 2009). For some species, interannual variability in vital rates or population growth is synchronised over relatively large spatial scales (Liebhold et al. 2004), while others show extensive spatial variation with little or no synchrony (Cayuela et al. 2020, Descamps et al. 2020). However, the underlying causes of spatial variation in population trends are often unclear.

Several mechanisms have been proposed to explain spatial variation in vital rates. Underlying large-scale gradients in primary productivity may affect vital rates and life history variation across several trophic levels, e.g. between ocean basins (Suryan et al. 2009). Large-scale interannual climatic variation, often summarised in derived indices such as the Southern Oscillation Index, has in some cases been shown to synchronise demographic variation over large scales (Jenouvrier et al. 2009). However, observed patterns of spatial demographic variation are often difficult to reconcile with such large-scale paradigms (Ringsby et al. 2002, Pironon et al. 2017, Tjørnløv et al. 2020) and are more reflective of relatively local-scale variation in e.g. habitat suitability (Ens et al. 1992), predation pressure (Ekroos et al. 2012), or anthropogenic impacts (Lee et al. 2016). For migratory species, conditions on the wintering grounds may have a strong impact on survival and thus lead to differences and similarities (e.g. synchrony) among populations (Gaston 2003, Reneerens et al. 2020).

A good understanding of spatial variation in vital rates, and the environmental factors driving this variation, is particularly important for species of conservation or management concern (Johnson et al. 2010). For such species, successful management relies on understanding current vital rates and the possibilities of modifying them (Norris 2004). If population trends, vital rates or the factors affecting them show substantial spatial variation, managers need to be aware of this and target their actions appropriately. Spatial scale is particularly important for trans-boundary management efforts, as population change driven by large-scale processes may not be responsive to local management efforts (Dallimer & Strange 2015, Harrison et al. 2018).

For seabirds, there are 2 main hypotheses regarding population regulation. Ashmole (1963, see also Birt et al. 1987, Elliott et al. 2009) suggested that seabird colony size is regulated by prey availability during the breeding season because birds deplete prey resources near the colony and travel distance thus increases with colony size, which sets a limit to reproduction. On the other hand, Lack (1966) suggested that prey availability during the non-breeding season is more likely to regulate population size because of the generally lower productivity and thus availability of prey at this time of year. We suggest that variation in vital rates and population growth between seabird populations wintering in different areas would support Lack's view.

The thick-billed murre (or Brünnich's guillemot) *Uria lomvia* is an abundant colonial seabird with a pan-Arctic distribution (Gaston & Hipfner 2020). Thick-billed murres are long-lived, and pairs produce a maximum of 1 chick annually, which leaves the colony when less than half grown accompanied by the male parent (Gaston & Jones 1998). Males provide post-fledging parental care for several weeks (Elliott et al. 2017). Many murre populations in the Atlantic Arctic are declining rapidly, particularly those in Svalbard, Iceland and a large part of Greenland, which mainly overwinter off southwest Greenland and around Iceland (Frederiksen et al. 2016). At the same time, populations breeding in Canada and northwest Greenland, and wintering off the Atlantic coast of Canada, seem to be stable (reviewed in Frederiksen et al. 2016). Potential drivers of the observed declines include climate-driven deterioration of winter food supply (Descamps et al. 2013, Fluhr et al. 2017), mercury pollution (Albert et al. 2021), and direct anthropogenic mortality due to hunting and oil pollution (Frederiksen et al. 2019). However, the relative role of these and other drivers, and the causes of the observed large-scale variation in population trends, remain poorly understood. Populations across the Canadian Arctic fluctuated synchronously in the late 20th century, presumably because populations were regulated via mechanisms, possibly harvest, on their common wintering grounds (Gaston 2003).

Until recently, information on vital rates of thick-billed murres was limited to a few long-term studies, e.g. at Coats Island in Hudson Bay (Gaston et al. 1994) and Bjørnøya in Svalbard (Fluhr et al. 2017). However, recent expansions of monitoring efforts in Greenland, Iceland and Norway (Jan Mayen and Spitsbergen) have provided a much broader picture of demographic variation. Here, we collate and analyse the recent (mainly since 2010) available data on

adult survival and reproductive output from colonies throughout the Atlantic range of the species. We estimate means and temporal variation for each colony, and use the results to construct demographic projection models for each regional population. Finally, we compare the projected growth rates to observed regional population trends and discuss potential demographic and ecological mechanisms behind the observed spatial variation in demography and population trends.

2. MATERIALS AND METHODS

2.1. Study sites and regions

Breeding success and population size were monitored at 12 colonies in Canada, Greenland, Iceland and Norway (Jan Mayen, Spitsbergen and Bjørnøya), and adult survival was monitored at 6 of these colonies (Table 1, Fig. 1; see Section 2.4, 2nd paragraph, for Iceland). Most time series started after 2005 (Table 1), but monitoring of at least 1 parameter was initiated at Coats Island, Canada in 1990 and at Bjørnøya, Svalbard in 1986. Based on biogeographic and ecological differences in breeding and wintering areas, as well as data availability, we grouped the study sites into 6 regions: Canada, Greenland, Iceland, Jan Mayen, Spitsbergen and Bjørnøya.

2.2. Colony growth

The mean growth rate of each study colony during the 2010s was estimated based on available plot, transect or complete counts of murre present in the colony (Table 1). For each colony separately, counts were regressed against year (for Bjørnøya with an additive effect of plot to allow for missing plot counts in some years), with a log link function and quasi-Poisson errors. The regression coefficients were back-transformed to the real scale for comparison with modelled growth rates.

Table 1. Thick-billed murre study colonies in the 6 regions, with overview of data collection for estimation of breeding success and adult survival. For breeding success, N: annual number of egg-laying pairs followed. For adult survival, N_{marked} : total number of individuals marked; N_{eff} (effective sample size): N_{marked} plus the cumulated number of individuals resighted or recaptured, not including the last year of the study. Sources for population size: Gaston et al. (1993), for Canada; F. R. Merkel (unpubl.) for Greenland; Garðarsson et al. (2019) for Iceland; Anker-Nilssen et al. (2015) for Jan Mayen; Strøm et al (2008) for Spitsbergen and Bjørnøya

Region Colony	Latitude	Longitude	Colony size Estimate Year (pairs)	Breeding success		Method	Adult survival		
				Years	N (mean and range)		Years	$N_{\text{marked}}/N_{\text{eff}}$	
Canada									
Coats	62.58° N	82.75° W	30 000	1990–2019	100 (39–141)	Observations	1990–2019	2012, 2014	288/1882
Greenland									
Kippaku	73.72° N	56.63° W	14 500	2011–2017	2013	Time lapse	2009–2018		142/401
Apparsuit	73.79° N	56.65° W	35 400	2016–2017		Time lapse			
Ritenbenk	69.80° N	51.21° W	800	2011–2017		Time lapse	2013–2020		105/219
Iceland									
Grimsey	66.57° N	18.02° W	4000	2017–2019		Time lapse			
Heilavíkurbjarg	66.46° N	22.57° W	183 700	2018–2019		Time lapse			
Látrabjarg	65.50° N	24.53° W	118 000	2017–2019		Time lapse			
Skoruvíkurbjarg	66.38° N	14.87° W	2500	2016–2019		Time lapse			
Jan Mayen									
Jan Mayen	70.92° N	8.72° W	>110 000	2012–2019		Observations	2011–2019		158/585
Spitsbergen									
Diabasodden	78.37° N	16.13° E	830	2011–2017		Observations	2005–2019		454/1663
Ossian Sars	78.93° N	12.45° E	950	2011–2019		Observations	2009–2019		204/906
Bjørnøya									
Bjørnøya	74.35° N	19.10° E	95 000	2005–2019		Observations	1986–2019	1987, 1994	357/1545

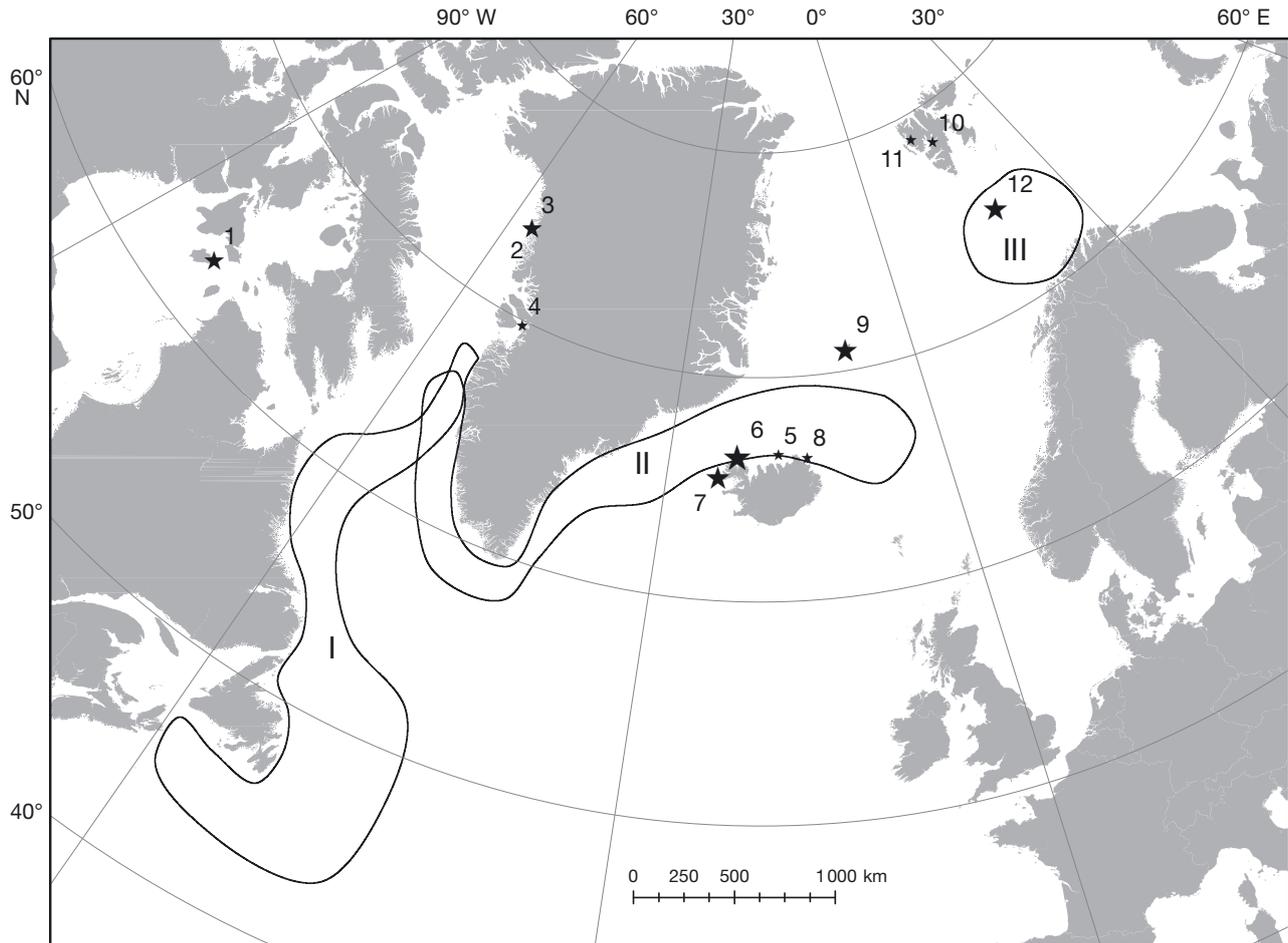


Fig. 1. Study area and thick-billed murre colonies (1–12, with size of ★ indicating colony size, see Table 1) included in this study. 1: Coats, 2: Kippaku, 3: Apparsuit, 4: Ritenbenk, 5: Grímsey, 6: Hælavíkurbjarg, 7: Látrabjarg, 8: Skoruvíkurbjarg, 9: Jan Mayen, 10: Diabasodden, 11: Ossian Sarsfjellet, 12: Bjørnøya. Polygons: generalised wintering areas (I–III) based on Frederiksen et al. (2016) and SEATRACK (<https://seapop.no/en/seatrack/>, accessed 15 June 2021). Murres from Canada and north-west Greenland use wintering area I, those from Iceland, Jan Mayen and West Spitsbergen use II, while those from Bjørnøya use III and the eastern part of II

2.3. Breeding success

Breeding success, i.e. the proportion of eggs laid that resulted in a ‘fledged’ chick, was estimated using either traditional methods where observers recorded the fate of each egg in dedicated plots (Walsh et al. 1995) at Coats, Jan Mayen, Spitsbergen and Bjørnøya, or time-lapse photography following Merkel et al. (2016) in Greenland and Iceland. At Kippaku, Greenland, 2 time-lapse plots were used. Observers usually arrived at study colonies during early to mid-incubation and sometimes left before all chicks had departed, and some early egg losses or late chick losses may therefore have been missed. Time-lapse photography was not affected by this limitation, as monitoring of nest sites was initiated before egg laying

and extended until all birds had left the plots. See Table 1 for details.

Stochastic matrix models (see Section 2.5) require unbiased (i.e. unaffected by sampling error) estimates of between-year variation in demographic parameters. We used a variance components approach (Link & Nichols 1994, Gould & Nichols 1998) to estimate process variance (i.e. between-year variation corrected for sampling error) for each decade, assuming zero covariance between years or colonies: $Var_{process} = Var_{between-year} - \frac{1}{n} \sum_{i=1}^n Var_i$, where i indicates the n annual estimated means, and Var_i is affected only by sampling error. When several colonies were monitored in 1 region (Greenland, Iceland and Spitsbergen), we also included between-colony variation in process variance.

2.4. Adult survival

Breeding thick-billed murres were captured using a noose on an extendable (4–8 m) fishing rod, and marked with individually coded engraved plastic or metal rings, or individual colour ring combinations, in dedicated observation plots in Canada (Coats), Greenland (Kippaku), Jan Mayen, Spitsbergen (2 colonies) and Bjørnøya (Table 1). Resightings were carried out during incubation and/or chick rearing by experienced observers from hides or fixed vantage points (up to 50 m from plots), using binoculars or telescopes with zoom oculars. Annual encounter histories were compiled from the marking and resighting data.

No colour-ringing data were available for Iceland. Instead we used capture-recapture data from breeding murres tagged with light loggers at 3 colonies (Látrabjarg, Grímsey and Langanes (incl. Skoruvíkurbjarg)) (Linnebjerg et al. 2018, www.seapop.no/en/seatrack/). Birds released without loggers were removed from the sample (i.e. treated as losses on capture), and entered as new individuals if they were tagged again in subsequent years. In this way, estimated recapture probabilities only refer to birds carrying loggers. Birds tagged on ledges that were subsequently deserted by breeding murres were not included (40 of 145 murres tagged in 2013–19 were excluded). Data from the 3 colonies were pooled, because numbers released were low and recapture effort was similar between colonies.

Capture-recapture/resighting data were analysed using live encounter models in MARK 9.0 (White & Burnham 1999). Goodness of fit to the standard Cormack-Jolly-Seber model (Lebreton et al. 1992) was tested in U-CARE 2.3.4 (Choquet et al. 2009). In all cases, the directional test for trap-dependence was highly significant, indicating trap-happiness, i.e. animals observed in the previous year were more likely to be observed in the current year than those not observed. Trap-happiness likely reflects some breeding sites being more visible or accessible than others due to cliff topography, in combination with extremely high site fidelity (Harris et al. 1996) and between-individual variation in behaviour and thus observability. To account for this, we used multi-state models with a dummy state for unobserved birds, with survival constrained to be the same for observed and unobserved birds (Gimenez et al. 2003). In these models, nominal resighting probabilities are fixed to respectively 1 and 0, and real resighting probabilities are estimated as transition probabilities between the 2 states (high and low observability). Resighting probabilities of the 2 states were constrained to vary in parallel over time

(additive model, Pradel 1993). Goodness of fit of the model with additive trap-dependence was tested using the median \hat{c} -hat procedure in MARK, and a variance inflation factor was applied if necessary.

We fitted models where survival was constrained to be either constant over time, varying from year to year, or varying among decades (1980s, 1990s, 2000s, 2010s). The decadal model was designed to allow comparison of recent mean survival between time series of widely differing lengths (Table 1). All models had year-to-year variation in resighting probability, with an additive effect of trap-dependence. We used the variance components approach in MARK to estimate mean survival, standard error of the mean, and process variance (i.e. between-year variation corrected for sampling error) for each decade with available data, based on the model with year-to-year variation in survival. Process variance was estimated for the entire time series. The last estimate of survival in a time series is not separately identifiable in fully time-dependent models and was for this reason not included in the variance components procedure. In Spitsbergen, 2 time series of adult survival were available, and we combined the estimated means from the 2 colonies assuming independence (i.e. zero sampling covariance) as for breeding success (Section 2.2).

2.5. Population model

We constructed stochastic matrix projection models with a pre-breeding census (Caswell 2001) for each region in R 3.6.2 (R Core Team 2019). The models were parameterised using region-specific means and process variances of breeding success and adult survival for the 2010s. In the absence of region-specific empirical estimates, values of other demographic parameters were set to be the same in all regions and taken from the literature (Wiese et al. 2004, Harris et al. 2007) or assumed; see Table 2. Two scenarios were run for non-observed parameters, 1 basic (optimistic) and 1 more pessimistic, i.e. with lower parameter values (Table 2). The model was run for 10 years using 10 000 stochastic simulations. Model simulations accounted for both sampling error, i.e. uncertainty of mean values of demographic variables, and environmental stochasticity, i.e. process variance. In each simulation, mean values of breeding success and adult survival were drawn from a beta distribution with the overall region-specific mean and standard error of the mean. Year-specific values of these parameters were then drawn from a beta distribution with the simulation-specific mean

Table 2. Parameters of the stochastic projection model. Apart from thick-billed murre adult survival and breeding success, parameter values used were the same in all regions. Values of demographic parameters were assumed when no empirical information was available

Parameter	Mean (basic/pessimistic)	Process variance (assumed)	Source
First-year survival	0.56/0.50	0.01	Harris et al. (2007)
Second-year survival	0.79/0.75	0.0025	Harris et al. (2007)
Third-year survival	0.90/0.85	0.0025	Assumed
Fourth-year survival	0.92/0.90	0.0025	Assumed
Adult survival (fifth year and older)	See Fig. 3	See Fig. 3	Present study
Proportion breeding, 3 yr old	0.025/0	0	Wiese et al. (2004)
Proportion breeding, 4 yr old	0.367/0	0	Wiese et al. (2004)
Proportion breeding, 5 yr old	0.700/0.50	0	Wiese et al. (2004)
Proportion breeding, 6 yr and older	0.985/0.90	0	Wiese et al. (2004)
Breeding success	See Fig. 2	See Fig. 2	Present study
Sex ratio	0.5	0	Assumed

and a standard error derived from the estimated process variance. For pre-breeding survival, values were drawn from beta distributions with a mean taken from the literature and an assumed process variance (Table 2). Values of age-specific proportions of breeders and sex ratio were deterministic in the model (Table 2). Simulations were initialised with a stable age distribution based on the overall region-specific mean parameter values, derived using the R package *popbio* (Stubben & Milligan 2007). Stochastic annual growth rate was calculated for each simulation as $\sqrt[10]{N_{end} / N_{start}}$, where N is the total population summed over all age classes.

3. RESULTS

3.1. Breeding success

Mean breeding success during the 2010s varied between regions, from 0.40 to 0.78 chicks pair⁻¹ (Fig. 2). No complete breeding failures were observed in 70 colony-years (nor in 22 seasons prior to 2010 at Coats, Canada, or in 5 seasons prior to 2010 at Bjørnøya), and annual estimates varied from 0.16 to 0.92 chicks pair⁻¹ (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m672p001_supp.pdf). Breeding success during the 2010s was highest, most stable (lowest process variance) and most precisely estimated (lowest standard error of the mean) in Greenland and Iceland, lowest at Jan Mayen, and most variable in Canada (Fig. 2).

3.2. Adult survival

Results of goodness-of-fit tests are shown in Table S1 in the Supplement. The directional z-test for

trap-happiness was highly significant in all colonies ($-9.6 < z < -2.4$, $6 \times 10^{-22} < p < 0.015$), whereas the median c-hat test of the model with additive trap-dependence showed little sign of remaining lack of fit (c-hat < 1.25 in all cases). The best model for describing adult survival probability varied among colonies (Table 3). In some colonies, there was substantial between-year (Coats) and between-decade (Bjørnøya) variation, whereas survival in other colonies was much more stable (Fig. S2 in the Supplement). The lowest annual estimate (0.58) occurred at Bjørnøya in 2007/08, and the lowest decadal mean (0.82) at Bjørnøya during the 2000s.

Mean adult annual survival probability during the 2010s was fairly similar among regions, varying from 0.93 at Bjørnøya to 0.88 at Spitsbergen (Fig. 3). Between-year variation was highest in Iceland and lowest at Spitsbergen.

3.3. Population growth

The mean projected annual population growth rate varied among regions (Fig. 4), being lowest (0.976) at Jan Mayen and highest (1.036) in Iceland. In the more pessimistic scenario with lower values of pre-breeding survival and breeding propensity, mean projected growth rates ranged from 0.958 (Jan Mayen) to 1.008 (Iceland). Projected growth rates were most variable in Iceland (Fig. 4), where process variation and standard error of the mean were highest for adult survival.

In 10 of the 12 study colonies, the observed annual growth rate was <1, i.e. colonies declined in size over the 2010s (Fig. S3 in the Supplement). Observed growth rates ranged from 0.86 at Jan Mayen to 1.02 at Kippaku (Greenland). In most cases, observed growth rates were lower than pro-

Fig. 2. Estimates of mean breeding success (chicks fledged per egg-laying pair) of thick-billed mures during the 2010s (top panel), standard error of the mean (middle panel), and process variance (between-year variation excluding sampling error; lower panel) in the 6 regions. Greenland, Iceland and Spitsbergen represented by respectively 3, 4 and 2 study colonies; Canada represented by 1 colony (Coats)

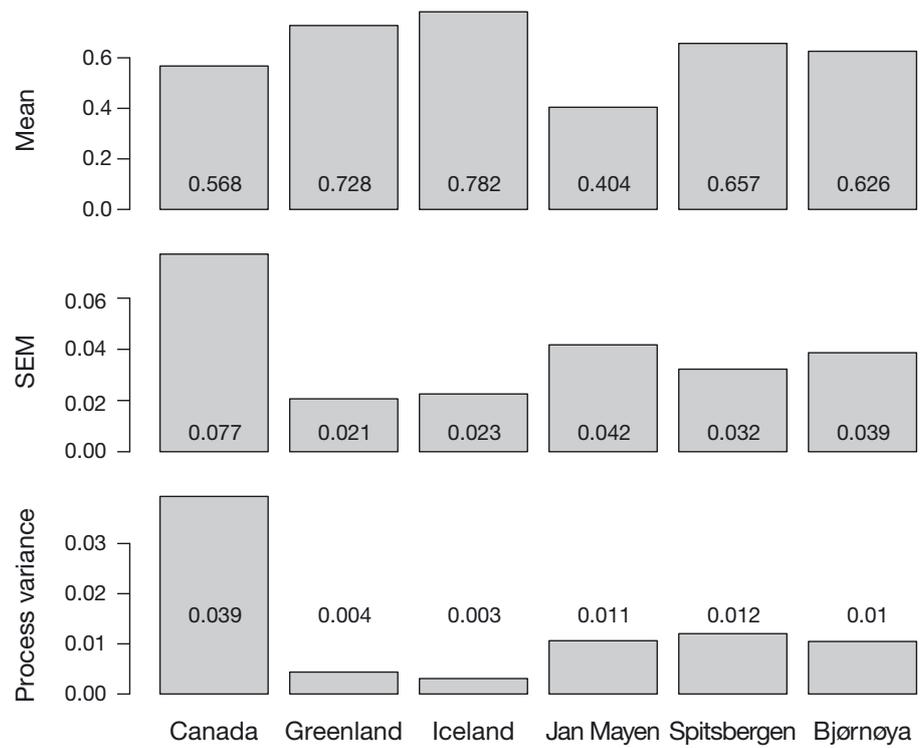
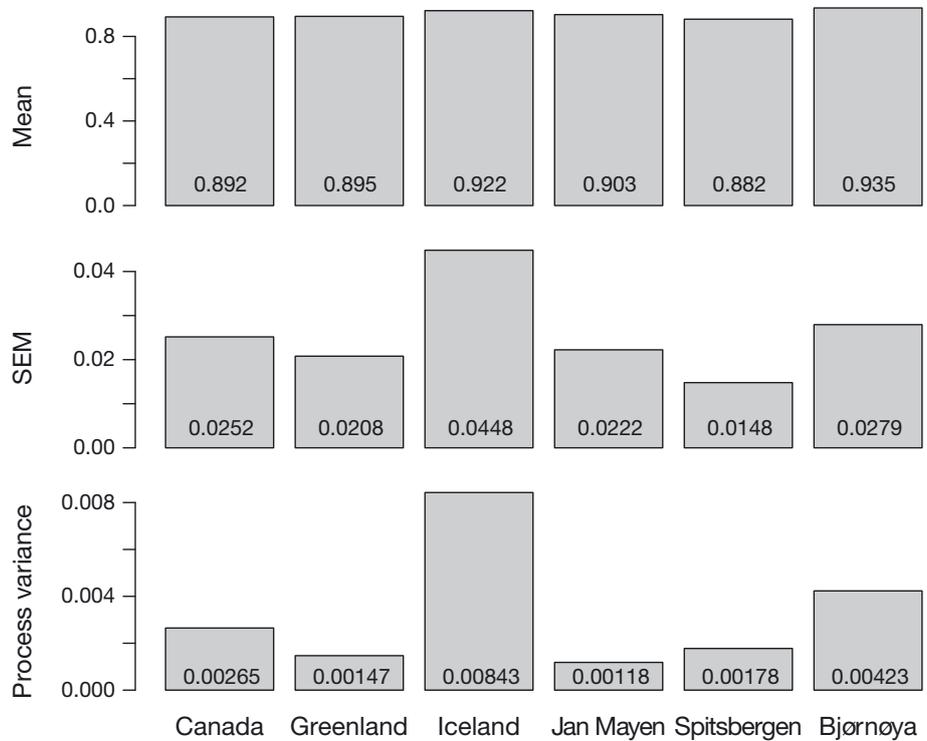


Fig. 3. Estimates of mean adult annual survival probability of thick-billed mures during the 2010s (top panel), standard error of the mean (middle panel), and process variance (between-year variation excluding sampling error; lower panel) in the 6 regions. Iceland and Spitsbergen represented by respectively 3 and 2 study colonies; Canada and Greenland represented by 1 colony each (respectively Coats and Kippaku)



jected growth rates from the basic scenario, based on regional estimates of adult survival and breeding success (Fig. 5). Observed growth rates showed strong local variation in some cases, e.g. between

1.02 at Kippaku and 0.93 at Apparsuit, 2 colonies located <10 km apart. Observed growth rates also differed substantially among colonies in Iceland, but less so in Spitsbergen.

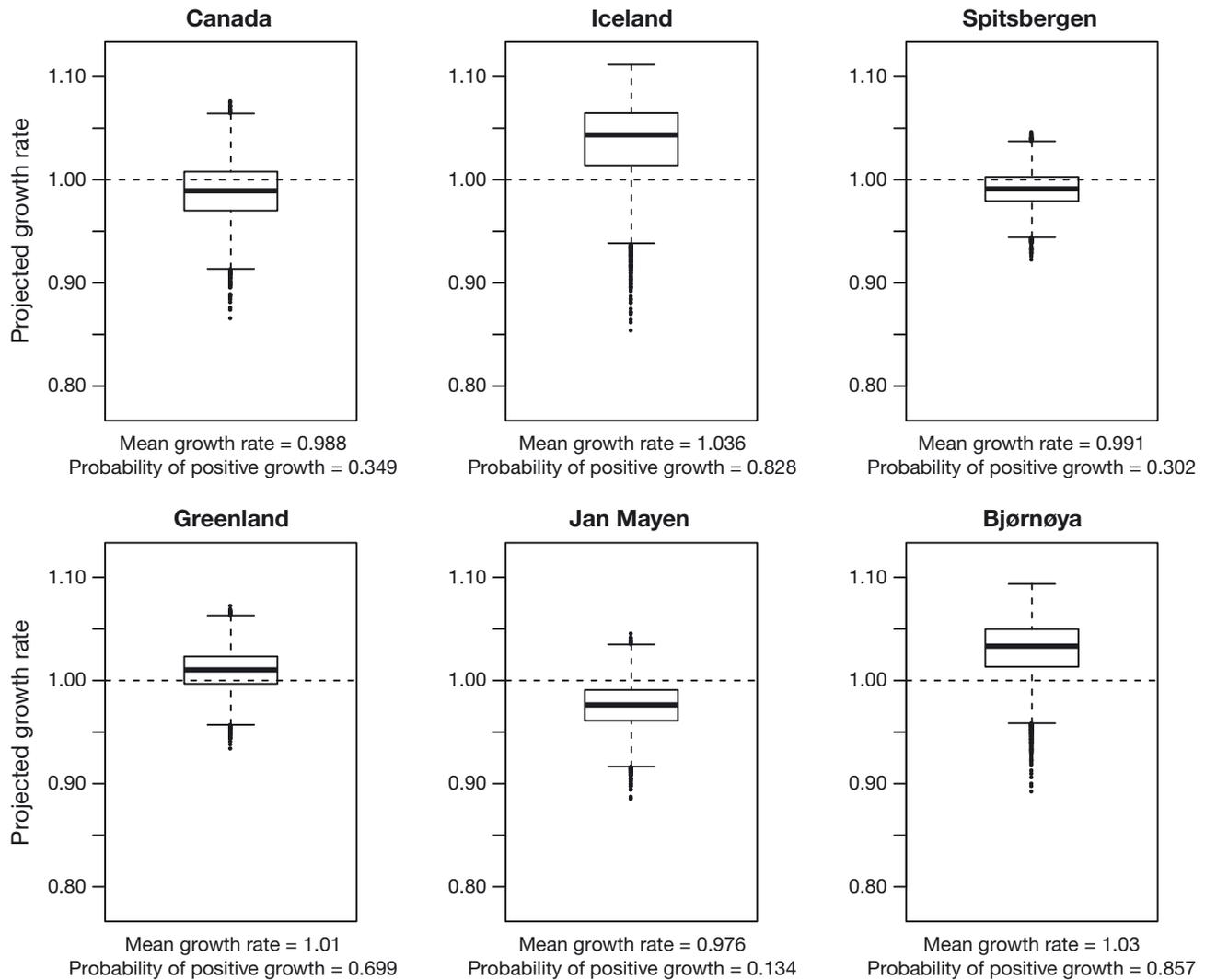


Fig. 4. Estimated stochastic population growth rate of thick-billed murres in the 6 regions under the basic scenario. Box plots: distribution of the 10 000 simulations; horizontal dashed line: growth rate of 1, i.e. a stable population; box limits: lower to upper quartile; bold line: median; whiskers: 1.5× the interquartile range; dots: outliers. Models for Greenland, Iceland and Spitsbergen based on demographic data from respectively 3, 4 and 2 study colonies; Canada represented by 1 colony (Coats)

Table 3. The 3 survival models fitted to each thick-billed murre resighting data set. ΔQAIC_c : quasi-Akaike's information criterion corrected for small sample size and overdispersion, relative to the 'best' model among the three. Dashes: for Iceland and Jan Mayen, data were only available for 1 decade (2010s). Rightmost column: amount of between-year variation explained by decadal model, derived using analysis of deviance (Skalski et al. 1993)

Colony	Survival model ΔQAIC_c			% Variation explained by decadal model
	Constant	Decadal	Yearly	
Canada/Coats	31.0	30.2	0	5.9
Greenland/Kippaku	0	2	8.3	1.1
Iceland	0	–	1.9	–
Jan Mayen	0	–	3.3	–
Spitsbergen/Diabasodden	8.2	0	7.6	40.4
Spitsbergen/Ossian Sarsfjellet	2.7	4.8	0	0.0
Bjørnøya	68.8	0	8.5	61.5

4. DISCUSSION

We have collated and analysed the most extensive data set to date on spatiotemporal variation in demography of thick-billed murres. While adult survival showed only minor regional variation, breeding success was more variable. Observed colony growth rates were also variable, and in most cases lower than expected, given our estimates of breeding success and survival. Overall, the observed values of survival and breeding success are in accordance with previously published studies (Gaston et al. 1994, Sandvik et al.

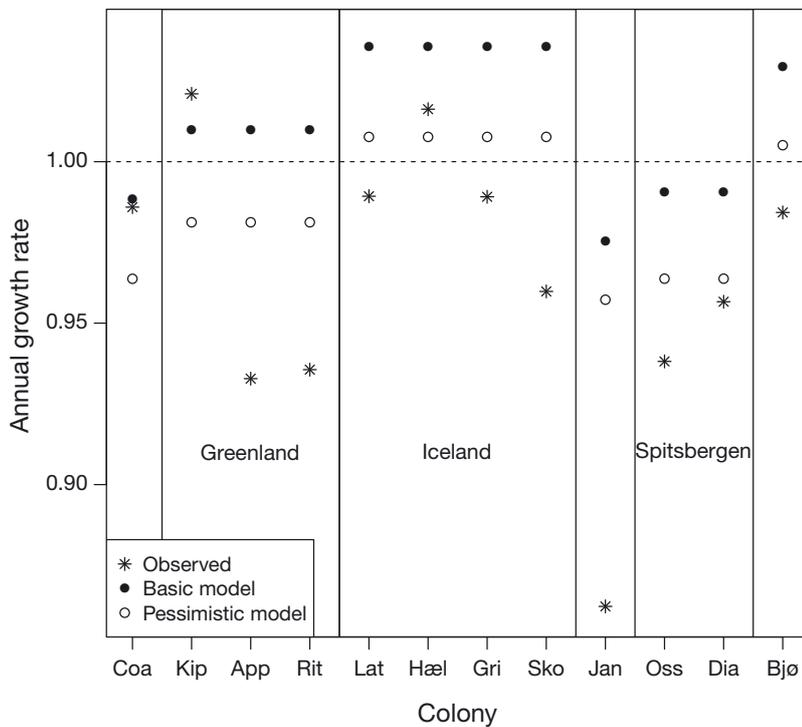


Fig. 5. Comparison of observed and modelled growth rates of thick-billed murre study colonies for the 2010s. Colonies ordered from west to east, with codes based on first 3 letters of colony names (Table 1). Modelled growth rates refer to the 6 regions, while observed growth rates refer to the 12 study colonies. Dashed horizontal line: growth rate of 1, i.e. a stable population

2005). Mean breeding success in our Atlantic study colonies was generally higher than in Alaska, where complete breeding failures are sometimes observed and long-term colony means range from 0.25 to 0.65 chicks fledged per nest site (Dragoo et al. 2019). Estimated breeding success in Greenland and Iceland was very high, but similar values were recorded at Prince Leopold Island in the Canadian high Arctic in the 1970s (Gaston & Nettleship 1981), and in other older studies in Arctic Canada and Greenland (summarised in Gaston et al. 1994). The high variance in breeding success at Coats was due to predation by polar bears *Ursus maritimus* and parasitism by mosquitoes (Gaston & Elliott 2013). In years when a polar bear fed in the colony, all eggs and chicks in large areas of the colony, including several study plots, were destroyed. In years when mosquito activity was intense, many pairs in particular parts of the colony did not reproduce. Mean breeding success was very low at Jan Mayen. The reasons for this are unclear, but may be related to the topography of the study plots, which only allows small groups of murres to nest together. These small groups may be more vulnerable to the combination of investigator disturbance and predation by glaucous gulls *Larus hyperboreus* (Gilchrist & Gaston 1997).

Mean adult survival showed relatively little variation among colonies (Fig. 3), and in most colonies, variation over longer (decadal) time scales was modest (Table 3, Fig. S2). The main exception was Bjørnøya, where our results indicate a major improvement in survival after 2010, following the very low values recorded in the 2000s (Fig. S2). Fluhr et al. (2017) showed that murre survival at Bjørnøya up to 2011 was correlated with fluctuation in the Subpolar Gyre. We have not updated this analysis with the longer time series, partly because of the recent scientific debate over the choice of Subpolar Gyre index (Foukal & Lozier 2017, Koul et al. 2020). However, several of the candidate indices show a switch of sign after 2010 (Koul et al. 2020, their Fig. 3), which would be consistent with the improved survival of Bjørnøya murres.

The projected growth rates from our regional population models were in most cases higher than the observed growth rates, at least for the basic scenario with optimistic values of non-observed vital rates (Fig. 5). This implies that our estimates of breeding success (Fig. 2) or adult survival (Fig. 3) are biased high, that our assumed values of other demographic variables (Table 2) are too optimistic, or that positive between-year covariance among vital rates (which we did not take into account in our model) reduced population growth rates (Fieberg & Ellner 2001, Doak et al. 2005). Breeding success may be biased high in observational studies because not all breeding attempts can be followed from egg-laying until departure. On the other hand, investigator disturbance may cause a negative bias (Cairns 1980). Bias in estimates of breeding success or adult survival could also occur if the study plots are unrepresentative of the colonies. Intra-colony variation in demographic performance has previously been demonstrated in murres as well as in other seabird species (Gaston & Nettleship 1981, Harris 1987, Descamps et al. 2009), and if high-quality areas are overrepresented in study plots, this could lead to a positive bias in parameter estimates. Positive bias in total fertility (the product of breeding propensity and breeding success) could also occur if breeding propensity declines and mainly high-quality birds remain in the colony, while low-quality birds

(with potentially lower survival probability) abstain from breeding (Lescroël et al. 2009). On the other hand, colour-ringing usually takes place in peripheral parts of colonies, which could be predominantly occupied by lower-quality birds (Coulson 1968). Positive covariance between survival of different age classes is likely, because they are affected by the same environmental conditions through most of the year. However, we have no empirical information to quantify covariance.

On the larger scale, it is striking that only 2 colonies in the western part of the range (Coats Island in Canada and Kippaku in Greenland) had observed growth rates close to or above those expected under the basic scenario, whereas all colonies in Iceland, Jan Mayen, Spitsbergen and Bjørnøya declined faster than expected under this scenario (Fig. 5). Earlier studies showed positive growth of murre colonies in the Canadian Arctic (incl. Coats) during 1976–2000 (Gaston 2002), and pre-breeding survival at Coats appeared to be very high during this period (Gaston et al. 1994). This strongly suggests that either pre-breeding survival (from ‘fledging’ to recruitment) or breeding propensity (age-specific proportions of breeders) was lower for eastern murre populations. These eastern populations, most of which are declining, overwinter mainly off Southwest Greenland and around Iceland, whereas the more stable western populations winter off Labrador and Newfoundland (Frederiksen et al. 2016). In the case of Jan Mayen, the observed colony growth rate (0.862) was lower than mean estimated adult survival (0.903), implying that little or no recruitment of new breeders has taken place during the 2010s. Previous work has suggested that failing recruitment is one of the main drivers of the observed synchronised decline in Spitsbergen murre colonies (Descamps et al. 2013), possibly linked to fluctuations of the Subpolar Gyre, the main multiannual pattern of oceanographic variation in the wintering area of Spitsbergen murre (Hátún et al. 2005). There is no direct evidence of the timing of or mechanisms behind increased mortality before the age of recruitment, but one period of elevated vulnerability to e.g. low prey availability could be during and after the transition from paternal post-‘fledging’ care to independence in autumn (approx. 37 d after leaving the colony, Elliott et al. 2017). Major mortality events (wrecks) of murre are occasionally reported in Southwest Greenland and Iceland, and the available evidence suggests that the cause of mortality is starvation (Nielsen & Einarsson 2004, F. R. Merkel unpubl. data). In Greenland, approx. 50% of individuals affected by wrecks in 2003,

2014 and 2018 were first-winter birds and 75% were females, whereas most murre recorded during a wreck in Iceland in 2001/02 were adults with a surplus of males (Nielsen & Einarsson 2004, F. R. Merkel unpubl. data). However, there is so far no direct evidence linking such wrecks to declines in specific colonies or populations.

Variation in recruitment to the breeding population or in breeding propensity of established breeders could be an important driver of population growth rate, and thus contribute to the mismatch between observed and modelled colony growth rates (Jenouvrier et al. 2005). Breeding propensity could be linked to variation in prey availability during spring. Results from Spitsbergen indeed suggest that poor environmental conditions (i.e. low sea-ice extent) around the colonies in the spring were associated with lower population size (Descamps & Ramirez 2021). The proposed mechanism was that poor conditions affected food availability (and notably polar cod *Boreogadus saida* abundance) in the spring negatively, resulting in a lower breeding propensity of murre. This is similar to the pattern observed for common eiders *Somateria mollissima* feeding on blue mussels *Mytilus* spp. by Jean-Gagnon et al. (2018). Increased disturbance by predators like polar bears, possibly linked to climate change, could also affect breeding propensity negatively.

Previous work has shown that while legal harvest of murre in Canada and Greenland has a measurable impact on population growth in all breeding areas, this impact is insufficient to explain the rapid declines observed in the eastern populations (Frederiksen et al. 2019). Our results support this and show that these declines cannot be explained by low adult survival or breeding success (unless our estimates are strongly biased high), implying that the demographic mechanism responsible is either low pre-breeding survival or low breeding propensity (or a combination of the two). Post-fledging survival has been shown to be independent of body condition at fledging in common murre (Harris et al. 2007), most likely due to extended paternal care, and conditions around independence (approx. mid-September, Elliott et al. 2017) are presumably critical for survival. Pre-breeding survival and breeding propensity are most likely primarily affected by feeding conditions during the non-breeding season, which again is likely to be mainly driven by oceanographic variability (Descamps et al. 2013). This leaves wildlife management agencies with few options for reversing the observed declines, other than reducing or eliminating any anthropogenic mortality due to hunting, oil

spills or bycatch in fishing gear, and minimising human disturbance of breeding colonies. Although we found that both adult survival and breeding success were generally high (except breeding success at Jan Mayen), further improvements in these demographic parameters will partly offset the declines due to low pre-breeding survival or breeding propensity.

Overall, the consistent discrepancy between observed and modelled growth rates in populations breeding east of Greenland (Fig. 5) suggests that large-scale variation in population growth rate in Atlantic thick-billed murres is strongly related to post-breeding and/or wintering areas, as proposed by Frederiksen et al. (2016). Populations wintering off Newfoundland and Labrador may have higher pre-breeding survival than those wintering around Iceland and off Southwest Greenland and are thus able to maintain a higher population growth rate. The 2 main wintering areas are influenced by different oceanographic patterns. Biological productivity and species distributions in the Iceland-Greenland wintering area is strongly influenced by the balance between the warm Irminger Current and the cold East Greenland Current, which again is related to the strength of the Subpolar Gyre (Hátún et al. 2016, Post et al. 2021). The Newfoundland-Labrador Shelf ecosystem is mainly influenced by the cold Labrador Current, particularly in winter (Han et al. 2008). Contrasting population trends between murres breeding in the eastern and western Atlantic, probably related to large-scale atmospheric variation, have been noted previously by Irons et al. (2008). Fluctuations in large-scale ocean currents may thus have profound impacts on spatial variation in population trends of widely distributed marine predators. Our finding that among-region differences in growth rate of thick-billed murre colonies seem to be mainly driven by conditions in the non-breeding areas also supports Lack's (1966, see also Cairns 1992) hypothesis that seabird population size is largely regulated by food availability during the non-breeding season. However, prey availability during the breeding season may still be the main factor limiting the size of individual seabird colonies (Ashmole 1963).

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