



Population status and trend of the threatened ivory gull *Pagophila eburnea* in Svalbard

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ABSTRACT: The ivory gull *Pagophila eburnea* is a high-Arctic seabird associated with sea ice throughout the year. It breeds at high latitudes, mostly in the Atlantic sector of the Arctic. It is rare (<11 500 breeding pairs globally) and remains one of the most poorly known seabirds in the world. Although Svalbard (Norway) supports breeding populations of international significance, the population trend in the region was unknown prior to this study. We conducted annual surveys of known breeding sites from 2006 to 2019 to estimate the size of the ivory gull population in Svalbard and to assess the population trend. We visited 117 colonies, 60 of which were new discoveries during this study. All breeding sites were situated in cliffs, and no ground-breeding ivory gulls were found. Based on the most complete survey in 2019, we estimated the Svalbard breeding population to be between 1500 and 2000 breeding pairs. We recorded an overall 40% decline in the number of breeding ivory gulls, but the trends varied significantly among colonies. The inter-annual fluctuations in the number of breeding pairs were not synchronous among colonies, which can be explained by the movements of adult breeding birds between colonies. The current decline in the Svalbard ivory gull population could be related to the ongoing decline in sea ice extent and quality in the Barents Sea. It may also be driven by ecological changes along the migration routes or at the wintering grounds, as hypothesized for the Canadian breeding population.

KEY WORDS: *Pagophila eburnea* · Endangered species · Climate warming · Sea ice · Seabirds · Svalbard

1. INTRODUCTION

Arctic biodiversity is under pressure from climate change and other anthropogenic stressors on a level never seen before (CAFF 2013). The Arctic is warming at 3 times the rate of the global average and the summer sea ice extent is currently declining by 13% per decade (Meredith et al. 2019). This has important consequences for Arctic biota, including marine birds and mammals that use the highly productive marginal ice zone throughout their life cycle (Post et al. 2013). The ivory gull *Pagophila eburnea* is a rare, high-Arctic, colonial seabird that is associated with sea ice all year round (Gill et al. 2016). Despite an early discov-

ery by Jonas Poole on Spitsbergen in 1609 (Purchas 1625), it remains one of the most enigmatic seabird species alive today (Mallory et al. 2008). The ivory gull has a patchy circumpolar breeding distribution across northern Canada, Greenland, Norway (Svalbard) and Russia and its global population is estimated at 6325–11 500 breeding pairs. Most (approx. 86% of the global population) occur in colonies in Arctic Russia (Gilchrist et al. 2008). The ivory gull feeds on ice-associated fauna, primarily small fish and macro-zooplankton, and on remains of marine mammals killed by polar bears *Ursus maritimus* (Mallory et al. 2008). Ivory gulls migrate between high-Arctic breeding grounds and the more southerly wintering areas

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along the sea ice edge and rarely move far from sea ice (Gilg et al. 2010).

The ivory gull is declining in parts of its range, likely due to its year-round affinity to sea ice that is disappearing at an alarming rate. The Canadian population of ivory gulls has declined by 70% since the 1980s (Gilchrist & Mallory 2005, Gaston et al. 2012). The Greenland population appears to be declining in the south of its breeding range, while in northern Greenland the trends are unclear (Gilg et al. 2009). In the Russian Arctic, however, surveys conducted in 2006–2008 and incidental observations from colonies in subsequent years suggest stable populations in some regularly visited colonies, with no signs of an overall decline. Nevertheless, more recent observations in the 2010s revealed multiple events of colony abandonment or breeding failure (Gavrilo & Martynova 2017). In Svalbard, the population status and trend could not be assessed until now due to scarce and fragmented data and a lack of population surveys (Strøm 2013).

The growing concern in the circumpolar Arctic for the population status of the ivory gull led to the development of an international circumpolar Conservation Strategy and Action Plan presented by the Arctic Council that highlights the need for new population surveys in the 4 Arctic nations in which the species breeds (Gilchrist et al. 2008). This is also supported by the IUCN and the OSPAR Commission, who consider the ivory gull to be 'Near Threatened' and 'threatened and/or declining', respectively, and emphasize that further surveys are required to clarify the global population status (BirdLife International 2018). In general, the population size of the ivory gull is difficult to assess because breeding colonies are not consistently occupied each year (e.g. Volkov & DeKorte 1996) and because some sites are likely still unknown. The shifts in breeding sites and irregular numbers of attending birds between years requires regular (annual) and widespread surveys to determine changes in the size and distribution of the breeding population and to understand the population dynamic of the species (Gilchrist & Mallory 2005).

The main aims of our study were to (1) complete a comprehensive census of the ivory gull population in Svalbard using data from aerial surveys combined with analyses of aerial images and a literature review to identify all potential breeding sites, (2) assess the ongoing population trend using 10 yr of monitoring data from a subset of colonies, and (3) assess the synchrony of inter-annual fluctuations in the number of breeding pairs among monitored colonies (i.e. the correlation of temporal fluctuations in colony sizes

between localities). Examining synchrony in population fluctuations can help identify the scale at which environmental factors operate in driving the dynamics of the population and can have important management or conservation applications. The risk of extinction is positively related to synchrony between colonies or sub-populations (Heino et al. 1997, Palmqvist & Lundberg 1998, Engen et al. 2002) because populations with synchronous dynamics are more susceptible to drastic declines.

2. MATERIALS AND METHODS

2.1. Population census

We conducted a literature review of all published sources relating to ivory gull breeding sites in Svalbard and we contacted ornithologists, tourist cruise guides, and scientists who had reported colonies of ivory gull and asked for additional information to identify historical colonies. We searched for place names including words like 'ivory' or 'ismåse' (the Norwegian name for ivory gull) in the place name database for Norwegian polar areas (<https://place.names.npolar.no>). Unpublished records of breeding colonies were extracted from the Norwegian Polar Institute's (NPI) Fauna Database and Seabird Colony Database for Svalbard (Bakken 2000). We also used high-resolution vertical aerial photos to search for potential breeding sites based on topography combined with signs of vegetation, which often becomes very distinguishable when utilizing the near-infrared band of the photos (see e.g. Schwaller et al. 2013 who used the same concept based on satellite images).

We surveyed known colony sites and searched for new colonies by helicopter, ship or on foot from 2006 to 2019. From 2009 onwards, we only used a helicopter. Not all colonies were visited each year due to weather or logistical constraints, except for 2019 when the survey effort was increased as part of an international, coordinated population survey of ivory gulls in the 4 Arctic nations supporting the global population, initiated by the Circumpolar Seabird Group (CBird) of the Arctic Council's Conservation of Arctic Flora and Fauna (CAFF) Working Group.

All surveys were conducted between 08:00 and 20:00 h UTC during the incubation and early chick-rearing stages in the last week of June and the first 2 wk of July. The weather during the surveys was in general sunny or had light cloud cover in all years. However, because of their remoteness, we could not avoid that some colonies were surveyed under less

optimal conditions (fog or low cloud cover). We surveyed the colonies by flying ca. 250–350 m from cliff faces at 70–80 km h⁻¹ in a Eurocopter AS365 Dauphin (2007–2015), Airbus AS332 Super Puma (2016–2019) or Eurocopter AS350 B2 Ecureuil (2006 and occasionally in later years). The survey crew consisted of 1 navigator/data manager and 2 observers, one of whom photo-documented the colonies. The 2 observers were usually placed on the same side of the helicopter with the windows facing the colony and used handheld binoculars. Gulls were easily spotted. As the helicopter approached, most remained on their nests, white against the usually dark rock, while some flew off the cliff and circled over the colony, bright against the blue sky. When approaching the colony, the helicopter reduced speed and a window or door was opened to facilitate photography and the documentation of the colony site and the birds present. The counting unit in the field was an adult bird, based on a direct count from the helicopter or counted on photographs taken during the survey. We considered the number of nesting birds to be representative for the number of pairs because usually only 1 parent attends the nest at any time and there is no evidence that non-breeding birds attend the colony during brooding and chick-feeding (Mallory et al. 2008, H. Strøm unpubl. data). At some sites, colonies were spatially divided into sub-colonies: groups of birds breeding approx. 100 m to several kilometers apart (e.g. in high and long cliff walls). We treated 2 or more sub-colonies as 1 colony if they were situated <ca. 2 km apart and breeding in the same topographic/geological feature, e.g. a mountain side.

2.2. Population trend and synchrony in inter-annual fluctuations

To assess the population trend of Svalbard ivory gulls, we considered a subset of 31 colonies scattered over the archipelago and visited annually from 2009 to 2019 (see Fig. 1). We ran linear mixed models with a Poisson error distribution and a log-link function (Bolker et al. 2009, Zuur et al. 2009) using the glmer function from package lme4 (Bates et al. 2015) in R version 3.5.1 (R Development Core Team 2016). Colony identity was defined as a random factor to take the non-independence from repeated sampling into account. We only tested for a linear trend because preliminary analyses indicated that considering a non-linear (e.g. quadratic or cubic) trend did not improve the fit of the models. We compared dif-

ferent models using an information-theoretic approach based on the quasi Akaike's information criterion (QAIC) (Burnham 2002). Using QAIC allowed us to adjust the likelihood of the models for the overdispersion observed in our data, i.e. $\hat{c} = 7.2$ calculated as the ratio of the sum of the squared Pearson residuals to the residual degrees of freedom from the most general model (Harrison 2014). These models were used to test whether there was a significant trend in the population and whether this trend was similar among colonies. Analysis of model residuals (with the acf function of R) indicated very limited temporal auto-correlation, suggesting that density dependence was likely not a key factor driving the colony dynamics.

We then quantified the synchrony among monitored colonies in their inter-annual fluctuations. We used the same subset of 31 colonies visited annually in the period 2009–2019. We calculated the mean cross-correlation and associated bootstrap confidence intervals using the mSynch function from the ncf package (Bjørnstad 2009) in R version 3.5.1. A cross-correlation coefficient between 2 time series measures the synchrony in these time series; the mean cross-correlation is calculated as the mean of all cross-correlation coefficients between every pair of colonies and represents the average region-wide synchrony (in our case, the average synchrony among all 31 ivory gull colonies). The method is described in detail in Bjørnstad et al. (1999). All colony time series were standardized (i.e. to achieve a mean of 0 and standard deviation of 1) before the synchrony analysis. We then tested if colonies closer to each other were characterized by a higher synchrony (i.e. a higher proportion of shared inter-annual fluctuations in numbers). To do this, we used a spline correlogram (Bjørnstad et al. 1999) that describes the relationship between geographic distance between colonies and their synchrony (function spline.correlog from package ncf).

3. RESULTS

3.1. Breeding sites and habitat

The literature review revealed 65 breeding sites that we considered reliable (Table S1 in the Supplement at www.int-res.com/articles/suppl/n043p435_supp.pdf). The majority (77%) were described as being situated in cliffs and 11 (17%) were on the ground. The breeding habitat of 4 sites was not specified. Only 25 (39%) of the 65 sites had been visited

more than once since they were discovered (range: 2–7 visits). We found 57 of the 65 breeding sites during our surveys (Table S1), but only 18 were occupied when visited by us in 2006–2019. Some colonies were taken over by other species (black-legged kittiwake *Rissa tridactyla*, possibly also northern fulmar *Fulmarus glacialis* in western parts of Spitsbergen)

and some sites had been affected by erosion and were likely no longer suitable as breeding sites.

Our 2006–2019 surveys also revealed 60 previously unknown breeding sites (Table 1). These were found in nunatak areas in south Spitsbergen (N = 9), central Spitsbergen (N = 11), northeast Spitsbergen (N = 21), and Nordaustlandet (N = 10; Fig. 1). In addition, 4

Table 1. Ivory gull colonies in Svalbard occupied for 1 or more years since 2006 (see also Fig. 1). NPI: Norwegian Polar Institute. Regions: A: Spitsbergen South; B: Central Spitsbergen; C: Spitsbergen Northwest; D: Spitsbergen Northeast; E: Nordaustlandet; F: Kong Karls Land; G: Barentsøya

| Colony no. | Region | Colony name | Latitude (°N) | Longitude (°E) | No. of pairs in 2019 | First described by |
|------------|--------|--------------------|---------------|----------------|----------------------|--|
| 1 | A | Mefonntoppene | 76.86 | 16.47 | 13 | Winsnes (1959) |
| 2 | | Cholmfjellet | 77.15 | 16.54 | 28 | Present study |
| 3 | | Grimfjellet | 77.16 | 16.60 | 51 | Norderhaug (1972) |
| 4 | | Bendefjellet | 77.21 | 16.55 | 12 | Birkenmajer & Skreslett 1963 |
| 5 | | Ostra Bramatoppen | 77.30 | 15.89 | 22 | Present study |
| 6 | | Waweltoppen | 77.31 | 15.90 | 3 | Present study |
| 7 | | Waly Hetmanskiefj. | 77.33 | 16.13 | 31 | Present study |
| 8 | | Vindegga | 77.47 | 17.28 | 0 | Present study |
| 9 | | Ronden | 77.57 | 16.71 | 0 | Present study |
| 10 | | Rondekammen | 77.63 | 16.81 | 16 | Present study |
| 11 | | Dynamittoppen | 77.72 | 16.82 | 16 | Present study |
| 12 | | Scheelefjellet | 77.75 | 16.94 | 5 | Present study |
| 13 | B | Tverregga | 77.80 | 17.31 | 0 | Present study |
| 14 | | Brodtkorbfjellet | 77.84 | 17.30 | 7 | Present study |
| 15 | | Bjarmeskolten | 78.02 | 18.03 | 13 | Present study |
| 16 | | Lardyfjellet | 78.05 | 17.97 | 54 | Hakala (1975) |
| 17 | | Agardhfjellet | 78.09 | 18.88 | 0 | Present study |
| 18 | | Væringen | 78.12 | 18.79 | 50 | Flipse & de Roever (1964), Larsen (1965) |
| 19 | | Buckfallet | 78.18 | 18.71 | 0 | Present study |
| 20 | | Domen | 78.21 | 18.84 | 0 | Present study |
| 21 | | Kroghfjellet | 78.30 | 18.79 | 0 | Present study |
| 22 | | Panofskyfjellet | 78.32 | 18.52 | 11 | Present study |
| 23 | | Hilgardfjellet | 78.37 | 18.27 | 11 | Present study |
| 24 | | Bairdfjellet | 78.39 | 18.25 | 10 | Present study |
| 25 | | Pöschefjellet | 78.39 | 18.24 | 0 | Present study |
| 26 | C | Skansebogen | 79.56 | 14.62 | 0 | Present study |
| 27 | | Finnkammen | 79.60 | 14.56 | 0 | Present study |
| 28 | | Svenskesteinen | 79.62 | 14.51 | 0 | Present study |
| 29 | | Krumtappen | 79.64 | 14.69 | 1 | Present study |
| 30 | D | Sandfordfjella | 78.56 | 18.80 | 29 | Present study |
| 31 | | Wilhelmberget | 78.57 | 18.43 | 40 | Present study |
| 32 | | Amadeusberget | 78.67 | 19.13 | 21 | Present study |
| 33 | | Gardebreen | 78.71 | 19.24 | 43 | Present study |
| 34 | | Ekkoknausane | 78.72 | 17.39 | 20 | NPI Seabird Colony Database ^a |
| 35 | | Bumerangkammen | 78.74 | 17.26 | 8 | Present study |
| 36 | | Vasilevfjellet | 78.75 | 20.53 | 0 | Present study |
| 37 | | Hellwaldfjellet | 78.76 | 20.79 | 0 | Present study |
| 38 | | Hellerusthamaren | 78.76 | 17.32 | 42 | Present study |
| 39 | | Storebrørne | 78.79 | 20.77 | 0 | Present study |
| 40 | | Steinhausarfjellet | 78.80 | 20.73 | 0 | Present study |
| 41 | | Arielhamaren | 78.81 | 17.01 | 40 | Present study |
| 42 | | Oberonhammaren | 78.83 | 17.25 | 94 | Present study |
| 43 | | Pachtusovfjellet | 78.84 | 18.54 | 4 | Present study |
| 44 | | Rundemannen | 78.93 | 19.71 | 0 | Present study |
| 45 | | Galileotoppen | 79.03 | 17.30 | 35 | Present study |

Table continued on next page

Table 1 (continued)

| Colony no. | Region | Colony name | Latitude (°N) | Longitude (°E) | No. of pairs in 2019 | First described by |
|------------|--------|---------------------|---------------|----------------|----------------------|--|
| 46 | | Valettkausen | 79.11 | 17.70 | 5 | Present study |
| 47 | | Irvinefjellet | 79.12 | 17.07 | 24 | Present study |
| 48 | | Granittryggen | 79.14 | 17.75 | 15 | Frazer (1924) |
| 49 | | Åsgardsreia N | 79.45 | 16.94 | 0 | Present study |
| 50 | | Åsgardsreia S | 79.54 | 16.97 | 5 | Present study |
| 51 | | Sørfjellet | 79.75 | 16.92 | 3 | Present study |
| 52 | | Ivorytoppen | 79.77 | 16.79 | 8 | Present study |
| 53 | | Rosenfjella | 79.78 | 16.75 | 0 | Glen (1935) |
| 54 | E | Svartknausane | 79.42 | 21.80 | 71 | NPI Seabird Colony Database ^a |
| 55 | | Palanderdalen | 79.57 | 20.54 | 1 | Dalgety (1932) |
| 56 | | Flykollen | 79.86 | 22.45 | 18 | Present study |
| 57 | | Stegjuvet | 80.00 | 22.67 | 9 | Present study |
| 58 | | Weaselbukta | 80.02 | 19.01 | 0 | Present study |
| 59 | | Tvillingstakken | 80.08 | 23.65 | 2 | Present study |
| 60 | | Ismåsetoppen | 80.12 | 21.14 | 11 | Norderhaug (1968) |
| 61 | | Wrighttoppen | 80.27 | 23.20 | 9 | Present study |
| 62 | | Krasil'ščikovtoppen | 80.41 | 19.86 | 1 | Present study |
| 63 | | Snøtoppen | 80.42 | 19.60 | 3 | Winsnes (1959) |
| 64 | | Håvatnet | 80.43 | 19.83 | 3 | Present study |
| 65 | | Tumen | 80.44 | 23.25 | 8 | Present study |
| 66 | | Laponiafjellet | 80.47 | 19.71 | 11 | Present study |
| 67 | | Trollnykjen | 80.70 | 21.01 | 0 | NPI Seabird Colony Database ^a |
| 68 | | Høgberget | 80.72 | 20.94 | 95 | NPI Seabird Colony Database ^a |
| 69 | | Tryggve Granfjellet | 80.74 | 20.56 | 0 | Present study |
| 70 | F | Flathøgda | 78.70 | 26.79 | 0 | NPI Seabird Colony Database ^a |
| 71 | | Kjølen | 78.79 | 26.60 | 3 | NPI Seabird Colony Database ^a |
| 72 | | Dunérfjellet | 78.79 | 26.56 | 14 | NPI Seabird Colony Database ^a |
| 73 | | Sjögrenfjellet | 78.85 | 27.97 | 7 | Kolthoff (1901) |
| 74 | | Utsynet | 78.87 | 28.31 | 0 | Present study |
| 75 | G | Freemanbreen | 78.38 | 21.45 | 43 | Present study |
| 76 | | Sigden | 78.40 | 21.60 | 6 | Present study |
| 77 | | Hübnerbreen | 78.41 | 21.68 | 13 | Present study |
| 78 | | Auga | 78.51 | 21.76 | 1 | Present study |
| Total | | | | | 1119 | |

^aSee Bakken (2000)

breeding sites were found in NW Spitsbergen, 1 in Kong Karls Land, and 4 on Barentsøya (Table 1, Fig. 1). All breeding sites were on steep cliffs, 2 of which were in canyons.

Of the 78 breeding sites found occupied during 2006–2019 (60 new and 18 previously known; Table 1), the distance between the sites and the nearest seashore varied from <1 km (8 sites) to 31.5 km (mean \pm SD: 8.5 \pm 6.2 km), with 64% (50) of the colonies situated >5 km inland. The colony in Pachtusovfjellet (colony no. 43) in NE Spitsbergen is the most remote breeding site, and the birds travel >30 km to reach the sea (34.5 km is the furthest possible distance from the coast in Svalbard, except for the inner part of the ice cap Austfonna on Nordaustlandet). The altitude of the sites ranged from 82 to

1248 m above sea level (mean \pm SD: 521 \pm 248.4 m) and the average distance between breeding sites was 8.0 km (\pm 8.7 SD). The mean distance between the breeding sites and the nearest tidewater glacier front (i.e. a key foraging habitat for ivory gulls when sea ice is scarce; Lydersen et al. 2014, H. Strøm unpubl. data) was 14.8 km (\pm 10.4 SD).

3.2. Colony and population size

Colony sizes ranged from 1 to 165 breeding pairs in 2006–2019 (mean: 16 \pm 3.11 breeding pairs per colony, n = 78 breeding sites). Between-year variation was large. This was exemplified by Ismåsetoppen (colony no. 60), where the number of pairs varied

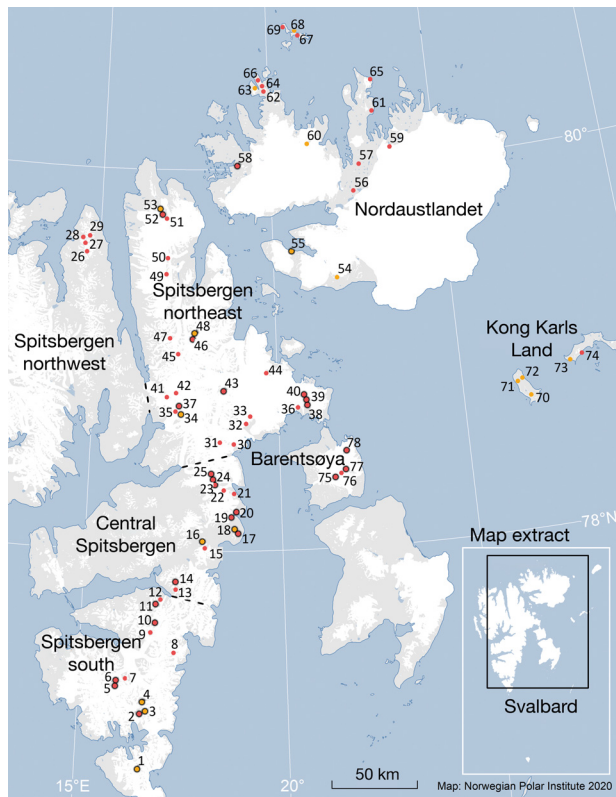


Fig. 1. Ivory gull breeding colonies in Svalbard occupied 1 or more years in 2006–2019. Red dots: new colonies (found since 2006); yellow dots: colonies known before 2006; dots within black circles: colonies monitored annually 2009–2019. See Table 1 for colony ID numbers

from 2 pairs in 2009 and 65 in 2010, to 103–132 in 2011–2012 and back to 6 pairs in 2013. Breeding sites may also be unused for 1 or more years before they again become occupied. Of the 78 breeding sites occupied between 2006 and 2019, 33 (42%) were occupied in all years visited by us, whereas 45 (58%) were empty in 1 or more years. The most complete survey was conducted in 2019 (all known sites visited), with a minimum of 1191 breeding pairs in 55 occupied colonies.

3.3. Population trend and synchrony in colony size fluctuations

The ivory gull population in the 31 colonies visited annually declined by >40% in 2009–2019 (Fig. 2, Table 2). Indeed, a model including a linear trend was much more strongly supported than a model assuming a constant population size (Table 2; slope estimate: -0.38 ± 0.14 SE). Though the overall population has been clearly declining, the trends varied

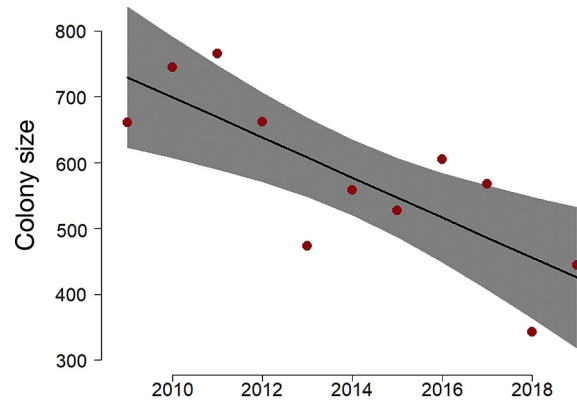


Fig. 2. Trend in the ivory gull population breeding on Svalbard. Red symbols: total number of pairs in a given year in a subset of 31 colonies monitored annually; line: regression line; shaded area: the associated 95% CI. The regression line is from a linear model ($t = -3.80$, $p = 0.004$)

significantly among colonies (and were even positive for some colonies), which was indicated by the better fit of a model with random slopes (Table 2). The subset of 31 colonies supported on average 577 breeding pairs (± 129 SD) in 2009–2019, which amounts to 30–40% of the estimated breeding population in Svalbard.

The inter-annual fluctuations in the number of breeding pairs were not synchronous (i.e. not parallel) among colonies, as indicated by the low and non-significant cross-correlation coefficient (cross-correlation coefficient: 0.037, 95% CI: -0.024 to 0.129 ; see Fig. A1 in the Appendix). This synchrony was slightly higher among colonies located closer to each other, but the effect of the distance between colonies on their synchrony was not significant (i.e. the confidence interval around the spline correlogram overlaps with the zero-correlation reference line that corresponds to the Svalbard-wide correlation; Fig. 3).

4. DISCUSSION

This study is the first to present the population size and trend of ivory gulls in Svalbard based on systematic annual surveys and the first study to present regional trend information based on annual monitoring of a large number of colonies.

4.1. Population status

A systematic search for new breeding colonies resulted in 60 new sites. Most were found far inland in

Table 2. Models considered to test for a linear trend in the Svalbard ivory gull population. n: number of parameters in each model; QAIC: quasi Akaike's information criterion (AIC), the AIC adjusted for overdispersion; Δ QAIC: difference in AIC units between a given model and the model with the lowest QAIC

| Response variable | Fixed effect | Random structure | Biological interpretation | n | QAIC | Δ QAIC |
|-------------------|--------------------|------------------|--------------------------------------|---|--------|---------------|
| Colony counts | 1 (intercept only) | (1 Colony) | No trend | 2 | 711.83 | 141.16 |
| Colony counts | 1+Year | (1 Colony) | Same linear trend for all colonies | 3 | 689.32 | 118.65 |
| Colony counts | 1+Year | (1+Year Colony) | Variable linear trend among colonies | 4 | 570.67 | 0.00 |

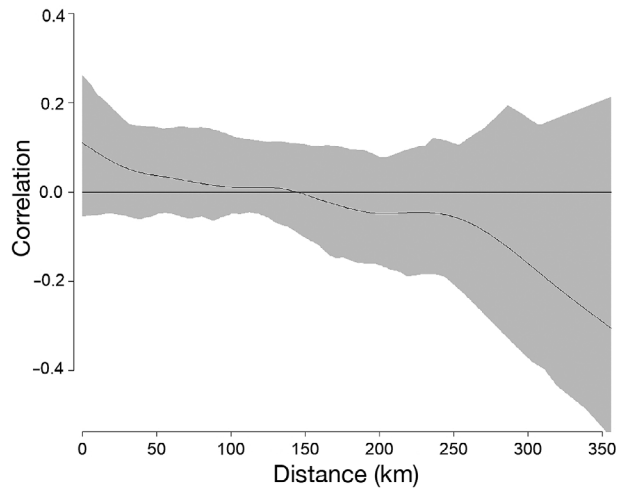


Fig. 3. Relationship between synchrony in colony size fluctuations (i.e. proportion of inter-annual fluctuations shared among colonies) and distance between colonies. Line: spline correlogram; shaded area: the associated 95% bootstrap confidence intervals. Correlation coefficients have been centered around the mean region-wide correlation (i.e. the zero-correlation line)

nunatak areas whose remoteness may explain why so many colonies have remained undiscovered. The inland areas in Svalbard are rarely visited by scientists or tourists. As ivory gull colonies in Svalbard are usually small (<165 pairs) and occupied by birds from May to September (H. Strøm unpubl. data), i.e. outside the winter tourist and snowmobile season, they are difficult to find without dedicated surveys.

Of the 57 previously known breeding sites, only 18 were occupied during the survey years. It is unclear why <30% of the previously known colonies were occupied; however, some colonies were apparently taken over by other species (black-legged kittiwake and northern fulmar) and some sites had been affected by erosion and are likely no longer suitable as breeding sites. No ground-breeding ivory gulls were found during the survey years despite records of relatively large colonies in the early 1900s (e.g. Ahlmann & Malmberg 1931) and records of small colonies (1–20 pairs) on Nordaust-

landet from the 1950s up to the 1990s (e.g. Norderhaug 1968, Bangjord 1999). Based on the literature, ground colonies appear to have been more common in Svalbard in previous years, but probably less frequent than, for example, Canada (Gilchrist & Mallory 2005) or Russia (>99% of the known colonies are on the ground; Gavrilov 2011). One reason may be that Svalbard lacks the huge, low-lying islands found in the Canadian and Russian Arctic, and, where the ivory gull does breed in east Svalbard, the coastal plains are relatively narrow. Many of the ground colonies in Canada and Russia are situated inland, apparently as a response to predation by Arctic foxes *Vulpes lagopus* and polar bears (Mallory et al. 2008). Since polar bears are common throughout Svalbard, cliff breeding may be a response to predation pressures in general.

Based on the most complete survey (2019) and given an incomplete detection of colonies, we estimated the Svalbard breeding population to be 1500–2000 breeding pairs. This figure is 3–4 times higher than previous estimates. For example, Gilchrist et al. (2008) suggested that, based on literature reviews, the population in the mid-2000s was 350–500 pairs. Our estimate should, however, be considered as a minimum, because failed breeders that may have left the colony at the time of the survey are not included. We currently do not know how big this source of error is. It is difficult to assess the proportion of still-unknown colonies, but it is likely that there are more colonies to discover. However, as the ivory gull colonies in Svalbard are relatively small (mean: 16 breeding pairs per colony), colonies discovered in the future are likely to contribute relatively little to the overall population estimate.

4.2. Population trend and synchrony among colonies

We found a population decline of >40% over a 10 yr period (2009–2019) in a subset of 31 ivory gull colonies in Svalbard. As the subset of monitored

colonies accounts for 30–40% of the estimated population in Svalbard and covers the species' range in the archipelago, it is reasonable to assume this trend is representative for the entire Svalbard population. Although the overall population decline is clear, the trends varied significantly among colonies. The inter-annual fluctuations in the number of breeding pairs were not parallel among the colonies. Although the synchrony was slightly higher among colonies located closer to each other, this was not significant. A 40% reduction over 10 yr is alarming for such an apparently small population, but is in accordance with findings in Canada over the last 20 yr. The Canadian population has declined by 70% since the 1980s at colonies that were known before 2002 (Gilchrist & Mallory 2005, Gaston et al. 2012). Our findings are also supported by the decline in the number of ivory gulls observed during spring migration in the settlement of Longyearbyen on the west side of Spitsbergen (Bangjord 1999). In the 1990s, ivory gulls were numerous here during spring, with >60 birds ringed in a single year (1995; Bangjord 1997), whereas during the 2000s, the number of observed birds has gradually declined and the ivory gull is now a rare visitor (Bangjord 1999, G. Bangjord unpubl. data). Although we cannot exclude the possibility that the decline in the number of observed ivory gulls in Longyearbyen is caused by other factors, such as changes in regional migration routes or sea ice cover in nearby fjords, it may nevertheless be related to a declining breeding population.

The long-term population trend for Svalbard is difficult to assess because historical data are scarce. Birkenmajer (1969) summarized declines at Svalbard colonies in the mid-20th century: at Storøya, from 100–150 pairs in 1887 to 11 pairs in 1930; at Wahlenbergfjorden (Ismåsefjellet), from 100 pairs in 1924 to <40 pairs in 1958; at Palanderbukta (Palanderdalen), from about 30 pairs in 1930, 1931 to 0 pairs in 1958; at Bodleybukta E (Winsnesbreen), from 12 pairs in 1957 to 0 pairs in 1958. One small increase was recorded at the Polakkfjellet colony, where 1 pair in 1958 increased to 6 pairs in 1966 (Birkenmajer 1969). Because of the inter-annual fluctuations in the number of breeding pairs and the fact that the sites were only visited twice, it is not possible to draw robust conclusions from such historic data, except that ground colonies may have been more common in Svalbard in the past (see Section 4.1).

The current decline in the Svalbard ivory gull population could be related to changes in sea ice

extent or quality (e.g. proportion of multiyear ice). Indeed, sea ice cover in the Barents Sea has declined substantially over the last 30 yr, with an increase in the ice-free period of >20 wk from 1979 to 2013 (Laidre et al. 2015). This change has already affected the marine food web, with negative impacts on several fish species, including polar cod *Boreogadus saida* (Descamps et al. 2017), an important prey for ivory gulls (Lucia et al. 2017, H. Strøm unpubl. data). Whereas changes in the sea ice extent on a regional scale east of Svalbard are less well documented, studies of seasonal sea ice cover in fjords on the west coast of Spitsbergen confirm a decline parallel to that in the Barents Sea (Muckenhuber et al. 2016, Pavlova et al. 2019, Dahlke et al. 2020).

While a large-scale sea ice decline may be associated with the overall population decline in Svalbard (through changes in food webs), variation in population trends among the colonies also suggest that local or regional factors have affected colony dynamics. However, with a highly mobile species like the ivory gull, the relatively short distances between colonies (mean: 8.6 km) and from the colonies to the sea (mean: 8.5 km), and the fact that birds from colonies situated as far as 120 km apart have overlapping feeding areas (Lydersen et al. 2014, H. Strøm unpubl. satellite tracking data), local environmental factors are an unlikely explanation for the variation in colony dynamics. Rather, this variation in inter-annual fluctuations may be driven by movements of breeders between colonies. Indeed, simulations indicate that even if the population is linearly declining, a movement of only 1% of the breeders between colonies from one year to the next may create a lack of synchrony in inter-annual fluctuations among colonies (see the Appendix).

The decline in the Svalbard ivory gull population may also have been driven by changes in environmental conditions outside Svalbard and the Barents Sea. The decline in the Canadian breeding population has been hypothesized to have resulted mainly from ecological changes on the wintering grounds, pollution and excessive hunting (Gilchrist & Mallory 2005), but also changes in the habitat (mainly the sea ice) in northern Canada during the summer and migration period (Gilg et al. 2009). As ivory gulls from Svalbard, Canada, and Greenland share the same wintering area in the Labrador Sea and Davis Strait (Gilg et al. 2010, Spencer et al. 2014), it is likely that the Svalbard population is also influenced by these same factors on the wintering grounds and during migration.

Acknowledgements. Funding for this study was provided by the Norwegian Ministry for Climate and the Environment through the Joint Norwegian-Russian Commission on Environmental Protection, the Norwegian Polar Institute (NPI), the Norwegian seabird monitoring program SEAPOP (www.seapop.no, grant no. 192141), and the Svalbard Environmental Protection Fund. We thank Georg Bangjord, Morten Bergan, Krzysztof Birkenmajer, Synnøve Elvevold, Per Espen Fjeld, Eirik Grønningssæter, Odd Harald Hansen, Reidar Hindrum, Palle Ude Jepsen, Jacobus de Korte, Thor Larsen, Fridtjof Mehlum, Are Mobæk, Viggo Ree and Andrei Volkov for contributing information about breeding sites of ivory gulls in Svalbard. Thanks to Sigurd Bangjord, Bjørn Frantzen, Hálfán Helgi Helgason, Audun Igesund, Kjell Isaksen, Morten Kersbergen, Odd Kindberg, Rupert Krapp, Hanne Margrethe Ingebrigtsen and Cecilie Miljeteig for taking part in the aerial surveys or the ground-based field work on Svenskøya and Barentsøya. We are indebted to Lufttransport and their professional and very dedicated pilots and Torgeir Mørk and Ine-Therese Pedersen at the Weather Service at Longyearbyen Airport for invaluable support while conducting the surveys. Thanks to Jon Aars and the NPI polar bear program for the good collaboration, and to the NPI logistical department in Longyearbyen for the good support. Thanks to Rob Barrett for proofreading the manuscript and improving the English and to 3 anonymous referees for helping improve the manuscript.

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Appendix. Simulations of movements of breeders between breeding colonies

In order to simulate the colony trajectories when some individuals move between colonies, we considered 31 colonies (with the same initial size as the 31 ivory gull colonies included in the trend analyses; see Sections 2 and 3) and a linear decline of 5% every year in each colony. Basically, each colony declines by 5% from time t to $t + 1$. At $t + 1$, some individuals move to another colony before the breeding season with a probability p . We ran simulations over 10 time steps (2009–2018), assuming that there is no distance threshold above which individuals cannot move from 1 colony to another (i.e. an individual can move

to any colony). Initial sizes for these 31 simulated colonies were the ivory gull colony sizes observed in 2009.

Results indicate that even just a 1% probability to move between colonies (i.e. on average 1 individual out of 100 will move to another colony before breeding) leads to colonies that do not fluctuate synchronously (average synchrony with $p = 0.01$: $r = 0.07$, 95% CI: -0.001 to 0.22), despite a total population size declining by 5% every year. Increasing the probability p to 5% leads to an even lower synchrony among colonies ($r = 0.02$, 95% CI: -0.02 to 0.09). Results are illustrated in Fig. A1.

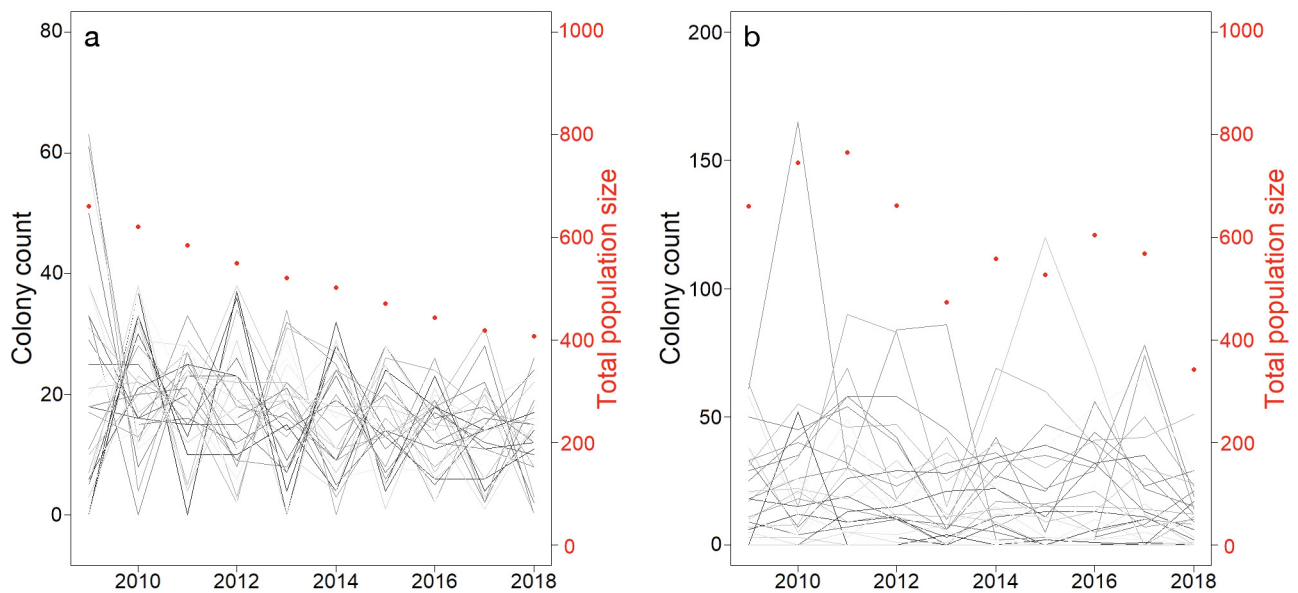


Fig. A1. Inter-annual variations in colony size. (a) Simulated trajectories ($n = 31$ colonies), assuming an annual decline of 5% in each colony and a 5% probability to move between colonies. (b) Observed trajectories of 31 ivory gull colonies monitored annually 2009–2019 in Svalbard

Editorial responsibility: Rory Wilson,
Swansea, UK

Submitted: June 20, 2020; Accepted: October 8, 2020
Proofs received from author(s): December 8, 2020