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Why is the last Thick-billed Murre *Uria lomvia* colony in central West Greenland heading for extinction?

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Summary

Ritenbenk/Innaq in Disko Bay is the only remaining Thick-billed Murre colony in central West Greenland. It has declined by 72% since 1980 and now (2012) holds c.1,100 breeding pairs. In 2005–2006 and 2011–2012, a number of studies were carried out in this colony to improve our understanding of the population decline and its causes. Hunting has previously been identified as a problem for the colony, but local breeding conditions have never been studied and the non-breeding distribution was known only from ringing. Our studies showed that breeding success was moderate to good in the Ritenbenk colony and apparently not limited by food availability. The impact of gull predation was more uncertain, but seemed limited in our study plot. In contrast, estimates of maximum sustainable harvest levels showed that hunting, including illegal activities, was and still is too high and probably can explain much of the population decline. It is puzzling though, that the steepest population decline was observed within the most recent decade when the harvest level was markedly reduced. This may indicate that something else besides hunting mortality affects the colony. The winter distribution of the Ritenbenk birds includes areas in the central North Atlantic, such as the waters around South Greenland, where conditions have been identified as potentially deteriorating due to pronounced oceanographic changes. The potential impact on the Ritenbenk colony, as well as other colonies in the North Atlantic, needs to be studied further.

Introduction

The Thick-billed Murre *Uria lomvia* has a circumpolar Arctic distribution and is considered a species of conservation concern according to the CAFF (Conservation of Arctic Flora and Fauna) working group under the Arctic Council (CAFF 1996), due to direct or indirect anthropogenic influence, such as hunting, tourism, oil pollution and bycatch (e.g. Bakken and Falk 1998, Chardine and Mendenhall 1998, Denlinger and Wohl 2001, Wiese *et al.* 2004). In Greenland and most other Arctic areas, the potential risks from these activities are currently increasing due to more shipping, more tourism and intensified exploration for oil, gas and minerals (Huntington 2007, PAME 2009). In addition, climate change is recognized as rapidly increasing in the Arctic (Solomon *et al.* 2007, Post *et al.* 2009) and it has been documented that large temperature shifts have the potential to affect murres negatively, presumably through changes of the underlying food webs (Irons *et al.* 2008).

In Greenland, the Thick-billed Murre population has undergone a large decline over the past century. The decline was first reported on a national scale by Kampp *et al.* (1994), who documented a population decline of 30–50% over a period of 50–60 years with the most severe developments (80–90% decline) in western Greenland south of Upernavik, including the extinction of several colonies. The reason for this decline was primarily believed to be excessive hunting (Kampp *et al.* 1994), and from the late 1980s several information campaigns and hunting regulations were introduced in Greenland, targeting sustainable harvest issues and the sensitive life history of murres. However, recent colony surveys indicate that this has had little effect – several colonies have continued a steep decline (Merkel *et al.* 2014). The Ritenbenk colony in Disko Bay is one of these. It has declined from around 5,500 attending individuals in 1980 to 1,560 individuals in 2012. From a conservation point of view, Ritenbenk is important as it represents the last remaining Thick-billed Murre colony in central West Greenland (see *Study area*).

A number of studies were carried out in this colony in 2005–2006 and 2011–2012, with the purpose of improving our understanding of the population decline and its underlying causes. We aimed at studying attendance patterns, foraging effort, chick growth and breeding success to explore whether the decline could be related to low reproduction. We also wanted to estimate sustainable harvest levels and identify non-breeding staging areas that potentially could be critical to the health of the colony. Combined with previous ringing activities and surveys of this colony, these studies make Ritenbenk the best studied declining murre colony in Greenland, and thus our best chance of understanding the mechanisms behind the population decline. This paper compiles the results of the above studies and discusses their implications with reference to other available information from this colony/area (Table 1).

Methods

Study area

The Ritenbenk colony is located in the inner part of Disko Bay in central West Greenland (69°48′N, 51°13′W). With the nearest colonies situated 400 km to the north and 500 km to the south, it is the only remaining Thick-billed Murre colony in central West Greenland. The region used to hold four other small murre colonies with up to 250 individuals per colony in the 1940s, but these colonies were abandoned in the 1970s (Kampp *et al.* 1994). Besides the Thick-billed Murres, the Ritenbenk colony presently includes around 30 individuals of Razorbill *Alca torda*, around 50 individuals of Black Guillemot *Cepphus grylle*, 1,800–4,200 pairs of Black-legged Kittiwake *Rissa tridactyla*, 250–550 pairs of Iceland Gull *Larus glaucoides*, 50–100 pairs of Glaucous Gull *Larus hyperboreus* and 30–90 pairs of Great Cormorant *Phalacrocorax carbo* (2006–2011; DCE and GINR 2012).

Population size and colony attendance

Population change in the Ritenbenk colony is here described for the period 1980–2012, based on total counts of birds present made in 1980, 1984, 1994, 1998, 2006, 2011 and 2012. In 2006, 2011

Table 1. Overview of available data for the Thick-billed Murre colony Ritenbenk/Innaq in Disko Bay

Parameter	Study period	Method	Source
Colony size	1980–2012 (7 counts)	Direct or photo counts	This paper, Kampp (1994)
Colony attendance	1998, 2005–06, 2011–12	Time-lapse camera	This paper, Mosbech *et al.* (2009)
Feeding frequency & diet	2006, 2011	Direct observations	This paper, Mosbech *et al.* (2009)
Time budgets	2006, 2011–12	Time-depth recorders	This paper
Chick growth	2011–12	Chick weighing	This paper
Breeding success	2011–12	Time-lapse camera	This paper
Non-breeding distribution	2011–12	Geo-locator tags	This paper
Post-breeding migration	2005–06	Satellite telemetry	Mosbech *et al.* (2009)
Survival, hunting mortality	1946–2006	Ringing recoveries	Lyngs (2003), Mosbech *et al.* (2009)
Harvest statistics	1993–2011	Hunters' reports	Greenland Government

and 2012, counts were made from photos, while the other estimates were derived from direct counts on site using a telescope. All counts, except 1980 (4 August) and 1994 (26 June), were made in the period 6–19 July, corresponding to the first half of the chick rearing period. This is within the recommend monitoring period for cliff-nesting auks (Lloyd 1975, Hatch and Hatch 1989). Estimates were based on a single count (in some cases the best of two counts, based on observation conditions or photo quality), however from 1998 onwards estimates were corrected for potential bias caused by diurnal and day-to-day variation in colony attendance. This information was collected by means of direct counts (1998) or photo-counts from time-lapse photos from one, two or three study plots (one photo/count per hour over a period of 6–13 days; in 1998 only 24 hours). For additional details about the murre counts and the photo technique, see Mosbech *et al.* (2009) and Huffeldt and Merkel (2013). Mean annual colony growth rate (1980–2012) was estimated using ordinary and piecewise linear regression of log-transformed count data using the 'lm' function in R (R Core Team 2013). When converting the number of attending murres into a number of breeding pairs, we used a K-factor of 0.73 (Evans 1987, Kampp 1990).

Food provisioning and activity budgets

Direct observations of feeding rates of 21 breeding pairs were carried out in one study plot in 2006 as continuous observation in blocks of 8–16 hours, spread over the period 12–17 July. Observation time added up to approximately 60 hours in total and covered the full diurnal cycle. In 2011, chick feedings were recorded during two full 24-hour observation periods on 10 and 13 July, partly within the same study plot and covering 20 breeding pairs. Some food items were visually identified. When calculating feeding rates, both feedings recorded as "food seen" and as "likely feeding" (behavioural cues) were included.

Activity budgets were studied in 2006 and 2011–2012 using time-depth recorders (TDRs). Chick-rearing murres were caught on the nest site with an 8 m noose pole, and TDRs, attached with two cable ties and silicone glue to metal tarsus bands, were deployed on the leg. In 2005–2006 TDRs from StarOddi (DST Micro data loggers, 25 mm long cylinder, diameter 8 mm, weight 3.3 g) were used, whereas in 2011–2012 TDRs from Lotek Marine Technology (LAT2500 and LAT1500, 35 mm long cylinder, diameter 8 mm, weight 3.6 g) were used. A sampling rate of 10 seconds was used in 2006, 16 seconds in 2011 and four seconds in 2012. Six TDRs were deployed in 2006 and five were successfully retrieved the same year. In 2011, 16 TDRs were deployed, of which two were retrieved in 2011 and seven in 2012. In 2012, two of the three loggers deployed were retrieved.

To estimate activity budgets, four types of behaviour (colony, foraging, flight and rest at-sea) were identified by interpretation of the TDR data following Linnebjerg *et al.* (2014). Foraging was defined as dives greater than 3 m (to eliminate noise from display and comfort behaviour at the sea surface) including post-dive recovery time $\leq$ 260 s (following Gentry and Kooyman 1986).

Chick body condition and breeding success

The body condition of chicks was measured on two occasions, 14 July 2011 and 15 July 2012. Wing length and body mass were measured for 35 and 32 chicks, respectively; two chicks from 2012 were subsequently excluded because of likely recording errors. Chick age was estimated from wing length following Gaston & Nettleship (1981: 176), and hatch date back-calculated. Non-linear growth curves (reparameterised von Bertalanffy curves), with an exponential approach to an asymptotic fledging mass, were fitted to wing length and body mass data. Estimated parameters were mean hatching mass (mass at a wing length of 23 mm), fledging mass (mass at a wing length of 90 mm), and exponential growth rate. A nested set of models were fitted, where fledging mass and growth rate were allowed to be either identical or different for the two years, whereas hatching mass was assumed to be the same in both years. Growth curves were fitted using the 'nls' function in R (R Core Team 2013).

Breeding success in 2011 and 2012 was determined using time-lapse photography with one-hour intervals during incubation and chick rearing. The method is similar to the traditional method where productivity is measured by means of repeated direct observations during the breeding season, as described in Gaston and Nettleship (1981) or in Walsh *et al.* (1995), but in this case derived from photos. A potential breeding site was defined as an active breeding site if occupied by a sitting adult on every photo over a period of at least three days (72 occasions), following the definition used by Lorentzen *et al.* (2012), The date of egg laying was defined as the first day when a sitting adult constantly occupied such an active breeding site. Chick fledging or breeding failure was determined by inspecting relevant photos when the adult birds no longer consistently attended the breeding site. In 2011, we did not cover the first three weeks of the incubation period, which meant that only fledging success could be accurately calculated, while the measured breeding success represents a maximum estimate. In contrast, breeding success was accurately measured in 2012, but due to missing time-lapse photos during the last three weeks of the incubation period and the first week of the chick period, breeding success could not be separated into hatching and fledging success.

Non-breeding distribution

Information on spatial distribution during the non-breeding season was collected by means of light-based geolocating archival tags. In 2011, 10 Lotek LAT2500 geolocators were deployed, seven of which were retrieved in 2012. We used daily positions (noon) obtained by means of the on-board template fit algorithm (Ekstrom 2004). During periods of almost continuous daylight, geographical positions cannot be accurately estimated, and we thus discarded all positions before 15 August 2011 and after 17 April 2012. Furthermore, around the times of the equinox, estimates of latitude are unreliable, and for this reason we excluded the periods 13 September–16 October 2011 and 26 February–30 March 2012. Besides this consistent period-based filtering, a small number of clearly erroneous positions were removed (approximately 2% of the positions remaining after the period-based filtering). To illustrate the spatial distribution during the non-breeding season, we pooled locations across individuals on a monthly basis and calculated kernel densities using the package adehabitatHR V.0.4.10 (Calenge 2006) in R (R Core Team 2013). We used least squares cross-validation to estimate the smoothing parameter and mapped 50% and 95% kernel density contours.

Estimation of survival

We estimated adult survival based on 297 adult murres ringed in the colony in 1984 (Kampp 1991), 19 of which were recovered as shot between 1984 and 1997. Survival was estimated using the models described by Brownie *et al.* (1985) and the software package MARK (White and Burnham 1999). These models estimate annual probability of survival as well as the probability that a bird is shot, retrieved by the hunter, and the ring number reported to the ringing scheme (recovery probability). Due to the sparse data, we only fitted two models. Both estimated a constant (mean) annual survival; one model had a constant recovery probability over the entire period, while the other allowed a change in recovery probability in 1989, when hunting legislation in Greenland changed.

Modelling impact of harvest on population growth

To identify the demographic mechanism responsible for the population decline in Ritenbenk and to estimate the maximum sustainable harvest levels for the colony, we constructed a matrix population model using the software package ULM (Legendre and Clobert 1995). The model included five age classes and a pre-breeding census, using basic demographic parameter values from the literature. These included: fecundity = 0.68 chicks/pair, sex ratio = 0.5, first-year survival = 0.56, second-year survival = 0.79, adult survival = 0.9 and age of first breeding = 5 years (Gaston and Hipfner 2000, Harris *et al.* 2007). We then adjusted fecundity and adult survival to mimic the observed population growth rate. To estimate the potential impact of harvest on population development we used the approach described by Dillingham and Fletcher (2008), which allows estimation of the maximum sustainable harvest (or other additional mortality) of a population when data are sparse. 'Potential biological removal' (PBR) is estimated as $PBR = 0.5 \cdot R_{max} \cdot N_{min} \cdot f$, where R_{max} is the maximum annual growth rate (under ideal conditions), N_{min} is a conservative estimate of total population size, and f is a 'recovery factor' between 0.1 and 1, chosen to reflect the conservation status and concern of the population. Here, we use a range of f-values for illustration and in order to compare PBR with reported harvest levels from the Greenland hunting statistics (Ministry of Fishery, Hunting and Agriculture, Greenland Government).

Results

Population size development

Based on total counts, the number of attending murres in the Ritenbenk colony decreased from 5,500 individuals in 1980 to 1,560 in 2012, which is an overall decline of 72%. Based on linear regression this corresponds to an annual decline of 3.6% ($R^2 = 0.95$, 95% CL = 2.7% –4.5%) over a period of 32 years (Fig. 1). The data, however, indicate a more rapid decline at the end of the period. A piecewise regression shows a significant break point between 1998 and 2006 ($F_{2,3} = 13.2$, $P = 0.03$), with a decline rate of 2.5% p.a. until 1998 and a steeper decline of 7.0% p.a. after 1998.

Food provisioning and activity budgets

Among 143 feedings recorded in 2006, the food was identified as "fish sp." (n = 63), capelin *Mallotus villosus* (n = 55), sea scorpion *Myoxocephalus scorpius* (n =5), polar cod *Boreogadus saida* (n =1), sandeel *Ammodytes* sp. (n = 1) or as unknown (n = 18). In 2011, only a small proportion (19%) of the fish (n = 70) brought to the chicks were identified to species, but among these all but one (polar cod) were identified as capelin. In 2006, the average feeding rate was 2.7 meals/chick/day (range: 0–6), with peak activity occurring during the morning hours (05h00–09h00). In 2011, it was slightly higher with 3.2 meals/chick/day (range: 1–6) and peak activity around midnight.

Activity budgets based on analyses of the TDR data (Fig. 2) showed that the time spent foraging varied between 2006 (16.7% or 10.9% without recovery time) and 2011–2012

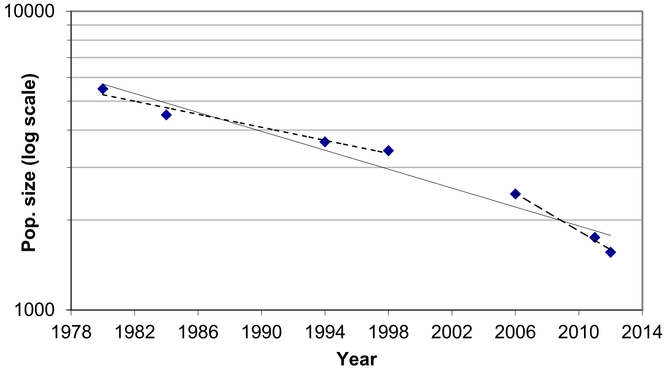

Figure 1. Population development (on a log scaled Y-axis) in the Ritenbenk Thick-billed Murre colony, 1980–2012, with a fitted linear regression curve for the entire period (unbroken line) and with the alternative regression fit resulting from a piecewise linear regression analysis (broken lines, see text).

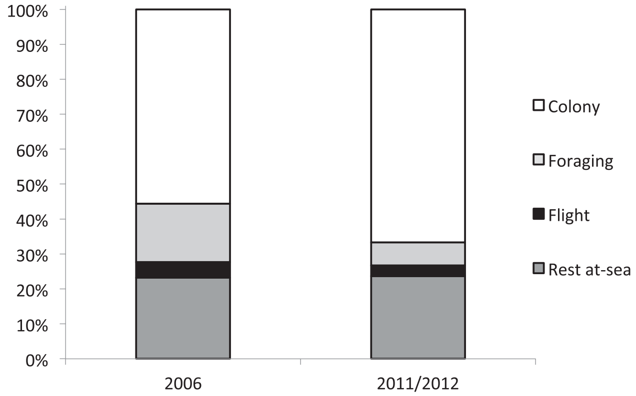

Figure 2. Daily activity budgets of Thick-billed Murres breeding at Ritenbenk, West Greenland, in 2006 ($n = 5$) and combined for 2011 ($n = 9$) and 2012 ($n = 2$). Foraging includes post-dive recovery time ≤ 260 s (following Gentry and Kooyman 1986).

(6.6% or 4.9% without recovery time). This was associated with deeper dives in 2006 (60% time below 20 m versus 30% time below 20 m in 2011–2012; Fig. 3) and less time spent in the colony in 2006 (55.6% of total time versus 66.7% in 2011–2012). The amount of time spent flying was also larger in 2006 (4.5%) compared to 2011–2012 (3.0%), while resting at sea was almost equal between the two study periods (23.2% in 2006 versus 23.7% in 2011–2012). The average flight duration in 2006 was 0.43 ± 0.34 SD hours per round trip (maximum flight time in one trip = 1.8 hours), and 0.28 ± 0.26 SD hours per round trip in 2011–2012 (maximum flight in one trip = 2.3 hours). Assuming an average flight speed of 70 km/h (Croll *et al.* 1991, Benvenuti *et al.* 1998), and direct flight to and from the colony, the average foraging range was 15 km in 2006 and 9.8 km in 2011–2012. On one occasion in 2006 (July 21), a foraging area was identified from a small boat by following the track of incoming murres, returning to the colony from feeding trips. This led to the identification of a foraging area about 20 km west of the colony. This supports the estimated time budgets, suggesting relatively short feeding trips.

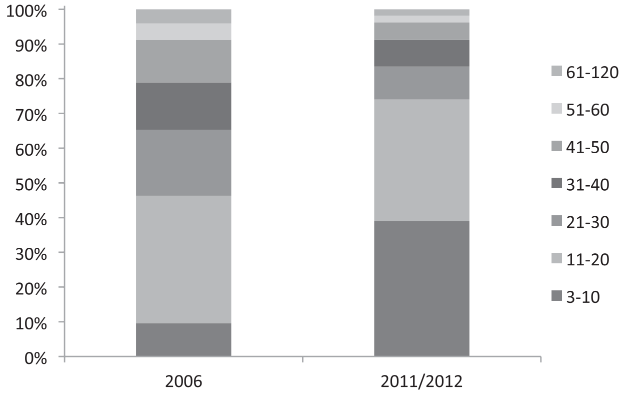

Figure 3. The relative time spend at different depth intervals (meters) for Thick-billed Murres in 2006 ($n = 5$), 2011 ($n = 9$) and 2012 ($n = 2$) breeding at Ritenbenk, West Greenland. The average dive depth in 2006 was 26.5 m ± 16.7 SD (max depth = 96 m) and in 2011-2012 (pooled) 17.3 m ± 15.0 SD (max depth = 119.5 m).

Chick body condition and breeding success

Based on chick wing length, the mean estimated hatch date was 4 July in 2011 and 30 June in 2012. The difference of 3.84 days (SE 0.90) was highly significant ($t_{63} = 4.3$, $P = 0.00007$). The most appropriate model to describe the chick growth data had different growth rates for the two years, but identical fledging mass; this model explained 79% of the total variation in body mass. The difference in growth rate was significant ($F_{1,61} = 8.4$, $P = 0.0053$), and given this there was no evidence for a difference in fledging mass ($F_{1,60} = 0.02$, $P = 0.89$). Estimated mean hatching mass (at a wing length of 23 mm) was 64.9 g (SE 15.1), and estimated mean fledging mass (at a wing length of 90 mm) was 278.4 g (SE 14.5). It was clear that growth conditions differed between the two years, with faster mass growth for young chicks in 2011 (Figure 4). However, because no large chicks (wing length > 60 mm) were encountered in 2011, it was difficult to determine whether final fledging mass was different.

Fledging success within the photo-plot was 63–70% in 2011 (26 fledged of 37–41 hatched). The interval represents uncertainty about four breeding sites, for which it could not be determined whether breeding failure occurred before or after hatching. Of 11 definite breeding failures occurring during chick-rearing, time-lapse photos indicated that glaucous gulls took at least four chicks, while three chicks were observed lying dead at the breeding site. A maximum estimate of overall breeding success was calculated as 59% (26 of 44 known active sites), but since only the last week or so of the incubation period was covered by the time-lapse photos, the true breeding success was most likely lower than this. In contrast, breeding success was fairly high in 2012, estimated at 74% (40 fledged of 54 eggs laid). Among the 14 breeding failures, three pairs failed during early incubation, six pairs failed during the period with no photos available (10 June–9 July, egg or chick) and five chicks went missing during early brooding. In 2012 the mean date of egg laying was 1 June and mean fledging date was 27 July. Assuming an incubation period of 33 days (Gaston and Hipfner 2000), the chicks fledged at a mean age of 22 days in 2012. In 2011, the chicks fledged on average two days later, on 29 July.

Non-breeding distribution

Of the seven Lotek geolocators retrieved in 2012, six contained data from a full year and one only until 26 February. During the period August–October the birds gradually left West Greenland waters (Disko Bay and the adjacent shelf area), and by November, six of seven birds were

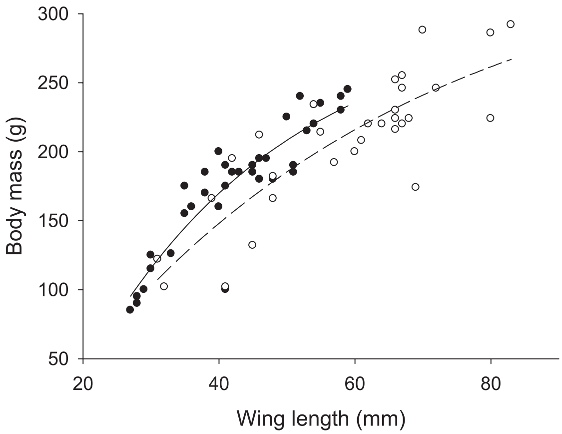

Figure 4. Wing length and body mass, with fitted growth curves, of chicks measured at Ritenbenk in 2011 (solid symbols, solid line) and 2012 (open symbols, dashed line).

distributed in coastal and offshore waters off Labrador and Newfoundland (Fig. 5). From January most birds moved to offshore areas in the central Davis Strait, Grand Banks or further east into the deeper parts of the north-west Atlantic. One bird moved as far east as Iceland before returning to south-west Greenland in April. The seventh bird spent all winter (October–February) in the central Davis Strait. By mid-April, five of six birds were back in the central or northern part of south-west Greenland and only one bird still remained in the north-west Atlantic.

Adult survival

The model with different recovery probabilities in two periods (1984–1989 and 1990 onwards) was better supported by the data ($\Delta AIC_c = -0.98$). Under this model, annual adult survival probability was estimated as 0.885, with a low precision (95% confidence limits: 0.586-0.976).

Modelling impact of harvest on population growth

With the basic parameter values from the literature (see Methods) the theoretical population was projected to be approximately stable (0.7% annual increase). In order to mimic the observed decline for the entire period (3.6%/year), fecundity had to be reduced to 0.34 chicks/pair, which is less than the lowest mean value recorded for this species (Gaston and Hipfner 2000), or adult survival had to be reduced to 0.855. For the recent period where the annual observed decline was 7.0%/year, the corresponding values were 0.14 chicks/pair or adult survival of 0.820.

R_{max} was estimated by substituting optimal values of demographic parameters in the matrix model. With fecundity set to 0.8 chicks/pair and adult survival probability to 0.94, values which are probably close to optimal (Gaston and Hipfner 2000), the projected annual growth rate would be 5.7%. Total population size is unknown, but the stable age structure of the matrix model

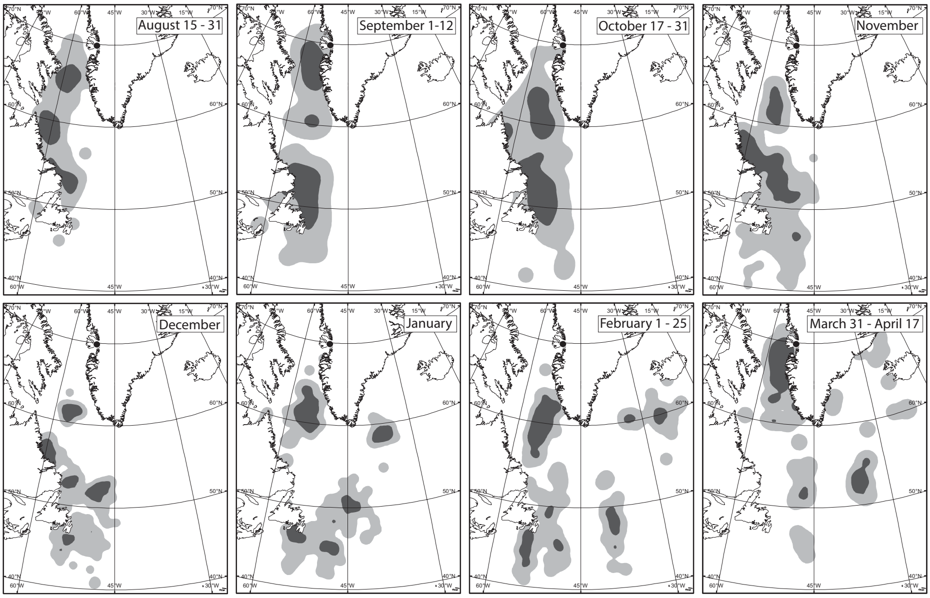

Figure 5. Monthly 50% (dark grey) and 95% (light grey) kernel density contours of positions from seven geolocating archival tags deployed in 2011 and retrieved in 2012. Note that some months are only partial due to the filtering of the positions (see Methods). The Ritenbenk colony is indicated with a black dot.

provides a conversion factor between breeding pairs and total population size. This factor was 3.18 for the basic values of the demographic parameters (see Methods). Total population size can thus be estimated as approximately 3.18 · 3400 · 0.73 = 7,900 individuals in 1998 (before harvest regulation change) and 3.18 · 1560 · 0.73 = 3,600 individuals in 2012 (most recent survey). The recovery factor *f* should be set to reflect the conservation concern: 0.1 for threatened species, 0.3 for 'Near Threatened' and 0.5 for 'Least Concern' species (Dillingham and Fletcher 2008). For these three values of *f*, PBR can thus be estimated as respectively 22, 67 and 112 birds per year in 1998 and 10, 31 and 52 birds in 2012. From 1993 to 2001, the annual number of murres reported shot (illegally) in the district of Ilulissat and Qeqertarsuaq in June and July was 61–398 (mean = 226), see Figure 6. Since 2002, the annual number has declined to 0–23 murres (mean = 8).

Discussion

Colony size

The Ritenbenk murre colony has been declining at least since the 1980s and after 1998 by as much as 7.0% p.a. The breeding population is now down to approximately 1,100 breeding pairs and probably faces extinction in the near future unless effective management initiatives are implemented immediately. A similar-sized colony existed in southern Upernavik in 1989, Apparsuit, but gradually disappeared over a period of 12 years (DCE and GINR 2012). At least during the final year with observed colony attendance, the birds were no longer breeding (F. Merkel unpubl. data). Reduced individual fitness at low population size or density can result in a critical population threshold below which the population declines to extinction, a phenomenon known as the Allee effect (Courchamp *et al.* 2008, Schippers *et al.* 2011). This may already be a concern for the Ritenbenk colony. One component of the Allee effect may be reduced anti-predator defence efficiency as demonstrated by Gilchrist (1999), who found that a declining Thick-billed Murre colony experienced higher gull predation rates as low breeding densities left more room for gulls to forage extensively on foot on the ledges. The impact of gull predation has not been studied at the Ritenbenk colony, but given the large decline in breeding numbers and the fact that the overall extent of the breeding area did not shrink correspondingly, it is likely that some

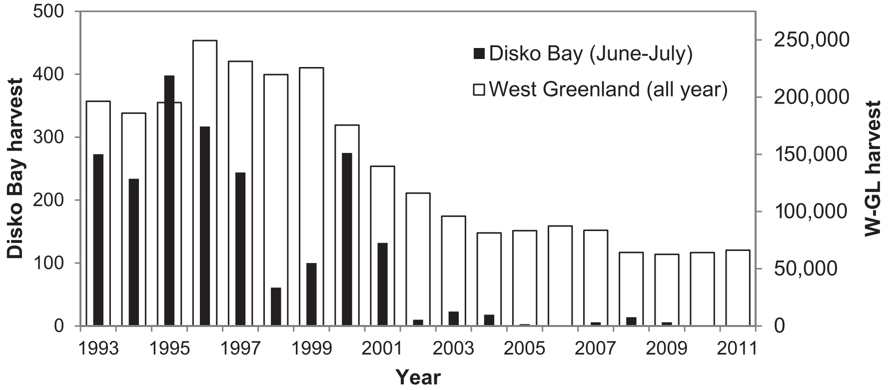

Figure 6. Reported harvest (no. of individuals) of Thick-billed Murres in the Disko Bay area (district of Ilulissat and Qeqertarsuaq) in June and July 1993-2011 and throughout the year in all of West Greenland. In 2001 the hunting season was shortened from 1 September–31 May to 1 September–15 February in most of north-west Greenland (Disko Bay included) and in south-west Greenland from 15 October–15 March to 15 October–15 February. In 2008 the hunting season was extended to 28/29 February in all of West Greenland. Source: Ministry of Fishery, Hunting and Agriculture, Greenland Government.

breeding areas are experiencing higher gull predation. Due to the isolation of the Ritenbenk colony, recolonization from neighbouring colonies (which are declining or stable) seems rather unlikely (Schippers *et al.* 2011).

Foraging and breeding conditions

It is expected that seabirds will adjust their behaviour in response to changes in the environment, e.g. availability of prey, and activity budgets are therefore likely to reflect resource availability (Cairns 1987, Uttley *et al.* 1994). Activity budgets published for Thick-billed Murres indicate that the proportion of time allocated for foraging (without recovery time) is in the range of 13–17% of the total activity budget (Falk *et al.* 2002, summary in Tremblay *et al.* 2003). Thus, the time the murres spent foraging without recovery time at Ritenbenk (2005–2006: 10.9%, 2011–2012: 4.9%) was at the lower end of the range of other localities. Overall, the limited time spent foraging and the close proximity of the feeding areas to the colony suggest that foraging conditions at Ritenbenk were rather good in 2005–2006 and particularly in 2011–2012. Our observations indicate that the main prey species delivered to the chicks was capelin. This is probably what we should expect as capelin is known as a key prey species for both seabirds and marine mammals over a wide range in West Greenland (Hedeholm 2010), and has previously been reported as an important prey source in Thick-billed Murre colonies in South Greenland and the Atlantic region of Canada (Birkhead and Nettleship 1987, Kampp and Falk 1994, K. Woo unpubl. in Gaston and Hipfner 2000).

The fact that the faster chick growth in 2011 was associated with lower breeding success than in 2012, suggests that breeding success was not limited by food availability. The reason for the observed difference in breeding success (2011: max. 59%, 2012: 74%) is not known, but time-lapse photos indicate that predation from Glaucous Gulls could be a factor. In any case, the observed breeding success at Ritenbenk is within the range reported from other colonies in the western North Atlantic (48–79%, summarized in Gaston and Hipfner 2000), and therefore probably not of significant importance for the observed population decline, at least if we assume that the 2011–2012 situation is representative of the normal breeding conditions in the Disko Bay area. There is no guarantee that this is the case, and large inter-annual fluctuations in breeding success among auk species do occur (e.g. Durant *et al.* 2003). However, no severe breeding failures, similar to those reported for some seabird species from other countries in the eastern North Atlantic (Frederiksen 2010), have been observed during previous work in the Ritenbenk colony or in other colonies in Greenland, and support our assumption that breeding success has been moderate to high throughout the decline phase.

Non-breeding distribution

Among birds ringed at Ritenbenk in the period 1946–2005 (mainly 1946–1963) and recovered in winter (November-March), more than half of the adults (58%) and immatures (70%) were recovered in south-west Greenland and the rest in Canada (Lyngs 2003, Mosbech *et al.* 2009). The current geolocator study, as well as recent satellite telemetry (Mosbech *et al.* 2009), confirm that breeding birds from Ritenbenk use both Canadian and Greenlandic coastal waters during the non-breeding season. Due to the small sample size it is difficult to know if the geolocator study gives a good representation of the winter areas used, and inter-annual variation in the winter distribution may also occur (McFarlane Tranquilla *et al.* 2014), but the study shows that murres from Ritenbenk to some extent also use areas far offshore in the Davis Strait and north-west Atlantic during winter, not only coastal areas.

Birds from several large breeding colonies in north-west Greenland (the Qaanaaq area) and high-arctic Canada primarily or exclusively winter in Canadian waters (Lyngs 2003, Boertmann and Mosbech 2011, Gaston *et al.* 2011, McFarlane Tranquilla *et al.* 2013), and these colonies appear to be stable or slightly increasing in numbers (Gaston *et al.* 2012, Merkel *et al.* 2014).

Thus, there seems to be little reason to suspect excessive winter mortality for the Ritenbenk birds if/when wintering on the Canadian shelf. However, recent studies indicate that winter mortality might be elevated in waters south and south-east of Greenland. From this part of the North Atlantic, Descamps *et al.* (2013) reported a strong correlation between major changes in oceanographic conditions (the Subpolar Gyre, Hátun *et al.* 2005) and severe population declines in Thick-billed Murre colonies in Svalbard, which to some extent share the same wintering area (Steen *et al.* 2013). Descamps *et al.* (2013) suggested a causal pathway through low juvenile winter survival and thus low recruitment to the breeding area, and a similar effect on the Ritenbenk colony cannot be ruled out as a contributing factor for the population decline.

Demographic mechanisms of the decline

The baseline matrix model indicated that a population with demographic rates taken from the literature, and no net emigration, would be stable or slightly increasing. In order to mimic the observed mean decline of 3.6%/year, mean fecundity at Ritenbenk would have had to be as low as 0.34 chicks/pair over several decades, which seems highly unrealistic. For the period after 1998, sustained near-complete breeding failures would have been necessary to cause the observed decline of 7.0%/year. While the estimated annual adult survival (0.89) for 1984–1997 also was higher than that required to obtain the observed decline, and indeed similar to other estimates for this species; e.g. 0.9 in Arctic Canada (Gaston and Hipfner 2000) and 0.916 in northern Norway (Sandvik *et al.* 2005), the confidence interval was very wide. Population growth rate was very sensitive to variation in adult survival, and reduced immature and/or adult survival is thus probably the most important mechanism for the observed population decline (although in recent years not necessarily caused primarily by hunting). This is strongly supported by the fact that a large proportion (80%) of all adult birds recovered in Greenland (ringed at/near Ritenbenk, including c.2,200 birds ringed between 1946 and 1963) has been recovered (shot) locally in the Disko Bay region during the summer months, implying a major mortality factor for breeders (Kampp 1991, Lyngs 2003, Mosbech *et al.* 2009). The reported local harvest level up to 2001 (Figure 6) was also well above the PBR and thus unsustainable, in particular as the autumn and winter harvest in Greenland and Canada as well as the potential summer harvest from nearby communities should be added. The reported June–July harvest in Disko Bay since 2002 was much reduced (0–23 murres annually), but probably still unsustainable as the recommended PBR is now down to approximately 10 birds per year (highest concern level) including autumn and winter harvest in Greenland and Canada. Moreover, the summer hunt is illegal (see Fig. 6), and the numbers voluntarily reported by the hunters are most likely underestimates. However, the apparently reduced harvest levels since 2002 are in contrast to the accelerating decline rate at Ritenbenk, beginning at some point between 1998 and 2006, and may indicate that additional sources of mortality besides hunting are affecting the Ritenbenk population, such as a climate-related winter mortality of juveniles as suggested for the Svalbard breeding population (Descamps *et al.* 2013). Lack of recruitment to the breeding population may also be an increasing problem, if the colony has become less attractive to prospecting pre-breeders due to the low density. An increasing incidence of non-breeding among adults could also contribute to the decline, although widespread non-breeding rarely if ever has been reported for alcids (Harris and Wanless 1995).

Conclusions and recommendations

It seems indisputable that unsustainable harvest has played a major role in the population decline of the Ritenbenk colony, at least up until 2001 when reported harvest levels were markedly reduced. With an estimated sustainable harvest level as low as 10 birds/year for the Ritenbenk colony, the current harvest is probably still too high. Considering that several other murre colonies in Greenland are experiencing similar steep declines (Merkel *et al.* 2014), that breeding populations in Iceland and Svalbard, which contribute to the winter population in south-west

Greenland (Lyngs 2003, Steen *et al.* 2013), are also declining (Frederiksen 2010, Descamps *et al.* 2013), and that Thick-billed Murres have a very low reproductive capacity, a total hunting ban in Greenland should be considered as a realistic alternative to the current management regime. In addition, the illegal spring and summer hunting in the Disko Bay area should be terminated.

It should be noted, though, that the steepest population decline in the Ritenbenk colony has been observed within the most recent decade when general harvest levels have been seriously reduced, which may suggest that other factors besides hunting mortality are contributing to the Ritenbenk decline, such as the potential deterioration of the marine environment in parts of the North Atlantic (Descamps *et al.* 2013). We recommend looking into the diet and body condition of the murres wintering in Southwest Greenland to compare the current situation with previous sampled material (e.g. Falk and Durinck 1993).

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