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Wintering-site fidelity of Brünnich's Guillemot *Uria lomvia* breeding in Greenland colonies

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Abstract

The behaviour of individual animals to return to a previously used location is referred to as site fidelity and is driven by predictable resource distributions in time and space. Understanding site fidelity in seabirds under global change is important as changes in environmental conditions may vary spatially. This study investigated site fidelity to wintering areas (wintering-site fidelity) of Brünnich's Guillemots *Uria lomvia* in three West Greenland breeding colonies (Kippaku, Sermilinnguaq, Kitsissut Avalliit) using light-based geolocation data collected over 9 years (2008-2012, 2019-2022). Considering the ocean-scale distribution and long migration of the species, we found that Brünnich's Guillemots from these colonies showed wintering-site fidelity. Mean inter-track distance (MID), as a measure of site fidelity, was 3.5 times greater among birds than among years for the same bird (log scale coefficient = -1.25, 95% confidence limits -1.42 – -1.069), suggesting wintering-site fidelity at an individual level. Kippaku and Sermilinnguaq Guillemots had within-individual MIDs of less than 200 km, while among-individual MIDs remained below 700 km. Based on empirical data, Kitsissut Avalliit had a within-individual MID of less than 258 km and an among-individual MID of 724 km. While wintering-site fidelity did not differ between colonies, Kippaku birds showed larger variation in space-use when compared to Sermilinnguaq birds. Wintering-site fidelity did not differ? between sexes. This work highlights that Brünnich’s Guillemots are site faithful to specific areas of the North Atlantic Ocean during their wintering period. The protection of these wintering areas is important for the continued conservation of the species, particularly for declining colonies.

Eqikkaaneq

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Keywords Thick-billed Murre, non-breeding ecology, individual consistency, conservation

Introduction

Seabirds are one of the most threatened groups of vertebrates, with almost half of all species experiencing population declines due to hunting, oil spills, bycatch, and shifts in prey distributions, amongst other known threats (Dias *et al.* 2019). Many seabird species are known for their long-distance migrations and ocean-scale distribution during their wintering period (Carey *et al.* 2014; Alerstam *et al.* 2019). Understanding the spatial use of seabird populations and linking breeding populations to wintering habitats is important for conservation efforts, not least because many seabirds use several jurisdictions during their annual cycle (Frederiksen *et al.* 2016; van Bemmelen *et al.* 2017; Léandri-Breton *et al.* 2021; Strøm *et al.* 2021). By identifying important non-breeding areas, it is possible to get a better ecological understanding of the demography and population trajectories of seabirds (Fauchald *et al.* 2019, Bråthen *et al.* 2021). SEATRACK is an example of a project investigating the space use of seabirds. The project aims to map the non-breeding distribution and abundance of 16 colony-nesting seabird species encircling the North Atlantic (https://www.seatrack.net). One aspect of space use is site fidelity, which describes an animal's behaviour of repeatedly returning to previously used locations, and is impacted by spatial and temporal predictability of patchily distributed resources (Switzer 1993). But a strong site fidelity can limit an individual's ability to relocate if habitat conditions deteriorate (Merkel *et al.* 2022). For seabirds, habitat loss and deterioration of key wintering area could have population-level consequences if individuals cannot readily shift to alternative sites (Tranquilla *et al.* 2010). Knowledge of seabirds' site fidelity to wintering areas (referred to as wintering-site fidelity) is therefore important for understanding their resilience to changes in environmental conditions in these areas. Understanding site fidelity in species, populations, colonies, and individuals is important, as groups with stronger fidelity may be more vulnerable to rapid environmental changes. Knowledge of site fidelity and the location of preferred wintering areas will thus be important for the future management and conservation of seabirds.

Brünnich's Guillemot *Uria lomvia* (hereafter 'Guillemot') is one of the most abundant marine birds in the Northern Hemisphere (Paleczny 2015), wintering predominantly in low Arctic ice-free waters (McFarlane Tranquilla *et al.* 2013; Gaston and Hipfner 2020). Chicks leave the nest before they have completed growing full flight feathers, whereafter the male parent continues to provision the chick for six to eight weeks (Sealy 1973; Nettleship 1985; Elliott *et al.* 2017). This causes a difference in migration behaviour between the sexes, as males leave the colony earlier and migrate slower (accompanying their fledgling), whereas females leave later and migrate faster (Frederiksen *et al.* 2016). While large population declines have already been seen in Greenland since the 1930's, caused by human-induced mortality factors such as hunting and oiling, these factors can only explain part of the more recent decline (Merkel *et al.* 2014; Frederiksen *et al.* 2019). Gaining a greater understanding of Guillemot wintering-site fidelity could help reveal current drivers behind recent population declines and inform conservation measures such as the placement of marine protected areas.

While the Guillemot, and closely related species, exhibit consistent wintering strategies (Merkel *et al.* 2021a; Merkel *et al.* 2021b), there is currently a gap in knowledge concerning the degree and variation of wintering-site fidelity. Specifically, it is not known to what extent the same individuals consistently use the same oceanic wintering locations year after year, or if this differs between colonies or sexes. The aim of this study was to investigate the wintering-site fidelity of Guillemots breeding in three West Greenland colonies, based on data collected over 9 years (2008-2012, 2019-2022). This was done using light-based geolocation to track individuals. We investigate whether individual birds show wintering-site fidelity, and whether wintering-site fidelity differs between colonies and sexes.

Materials and methods

Data and study system

Tracking data used in this study was collected prior to the initiation of the SEATRACK project and during its implementation. Breeding adult Guillemots at three Greenland colonies (Kippaku: 73 °43'N, 56 °39'W; Sermilinnguaq: 65 °25'N, 52 °53'W; and Kitsissut Avalliit: 60 °47'N, 48 °30'W) were equipped with a Global Location Sensor (GLS) attached to a plastic leg ring. Birds were captured at their nest during one breeding season, ringed, and outfitted with a GLS logger of the model BAS mk9 or Biotrack/Lotek mk3006. Instrumented individuals were then recaptured 1−4 years later to recover the GLS. Birds were held for as short as possible (handling time < 10 min), and although no systematic study of device effect has been carried out, initial data suggested no impact of tags on body condition within or between breeding seasons (Frederiksen *et al.* 2014). Birds were sexed using DNA extracted from feathers collected during capture.

Tracking data from November to February were included in analysis, as this is when Guillemots are most stationary at their wintering location (Frederiksen *et al.* 2016; Gaston and Hipfner 2020). The Kippaku colony had data from the wintering periods of 2008 to 2012 and from 2019 to 2022, Sermilinnguaq from the wintering periods of 2019 to 2022, and Kitsissut Avalliit from the wintering periods of 2009 to 2012. Position data were obtained for 77 Guillemots, 51 of which were tracked for more than one year, resulting in 149 bird-years of data (Table 1). A total of 33,957 positions across bird-years were obtained, in which there were 372 data gaps, with a gap classified as a day with no positions. All individuals had fewer than 30 gaps, except for one individual from the Kippaku colony which had 104 gaps. Gap days were excluded from the dataset prior to calculating the mean inter-track distances used in the analysis (see Inter-track distance). Individual-level data on number of tracks and number of gaps are provided in Appendix A.1

The raw light data collected by the GLS were processed following routines developed within the SEATRACK program (Fauchald *et al.* 2019; Bråthen *et al.,* 2021). Briefly, two positions per day were estimated from the ambient light levels recorded by the geolocators. Longitudes were calculated from the estimated timing of noon and midnight, while latitudes were based on the estimated length of day and night, using a threshold method (Lisovski *et al.* 2020). The procedure is described in detail in Bråthen *et al.* (2021) and is reliable except during the equinoxes and continuous night/day periods.

Table 1 Tracking data of Brünnich’s Guillemots *Uria lomvia*, by colony. Gaps are defined as days with zero GLS positions.

	Kippaku	Sermilinnguaq	Kitsissut Avalliit	Total
Individuals	52	21	4	77
Individuals tracked >1 years	31	16	4	51
Tracks	96	44	9	149
Positions	21,745	10,198	2014	33,957
Gaps	300	31	41	372

Inter-track distance

Inter-track distance was calculated as a measure for wintering-site fidelity, following the approach of van Bemmelen *et al*. (2017), with comparisons between individuals restricted to birds from the same colony. Daily inter-track distance was calculated using the distance between Guillemot positions recorded within the same time window but in different years. For each day in the wintering period, a reference position was compared to positions from other years that occurred within a 7-day window around the day with the reference position. We calculated daily inter-track distance as described by van Bemmelen *et al*. (2017), using the three functions *rdist.earth2*, *nearest* and *track.consistency.near* provided by the author (van Bemmelen, pers. comm.; Appendix A.2). The function *rdist.earth2* was first used to calculate the great-circle distance (the shortest distance between two points on the surface of a sphere) between two positions. Next, we used the function *nearest* to find the nearest position in the comparison track for the reference position, within a specified time window. Lastly, the function *track.consistency.near* was used to organise the comparison of tracks, either for the same bird in different years or for different birds in different years (see Appendix A.2 for further description of the functions). The output was a daily inter-track distance for each day in the wintering period for every track-comparison. A comparison thus included either tracks from the same bird in different years or from different birds from the same colony, also in different years. Longer time windows can account for variations in migration timing, while shorter windows provide more precise estimates of daily inter-track distance. Analysis showed that the choice of time window did not significantly affect results, as they remained qualitatively and quantitatively similar across 7-day, 10-day, and 30-day windows (see Appendix A.3). The conclusion remained the same while the parameter estimates differed slightly. We selected a 7-day time window to maximise precision of inter-track distances while still accounting for minor differences in the timing of migration. Subsequently, daily inter-track distance values were averaged for each track-comparison, resulting in a seasonal inter-track distance, referred to as mean inter-track distance (MID). This was done to circumvent temporal autocorrelation, as positions on subsequent days were non-independent.

Statistics

We used linear models using the lm function from the *stats* package ((R Core Team 2025). We applied a log transformation to the MID values to reduce skewness and stabilize variances, which improved the normality and homoscedasticity of model residuals, thereby meeting analysis assumptions of the linear models used. Due to the low number of birds tracked from Kitsissut Avalliit, we did not include this colony in the statistical analysis but provide simple empirical statistics for comparison. In some cases, both mates of a breeding pair were tracked in the same years, but since paired Guillemots are not known to show coordinated migration (Huffeldt *et al.* 2024), we did not take pair identity into account. In all linear models, colony was included as a fixed effect to account for colony-specific differences.

Firstly, we tested whether wintering-site fidelity differed between individuals by comparing MID within and among individuals. The response variable was the log-transformed MIDs distances. Fixed effects included comparison type (i.e. same bird in different years, or different birds in different years) and colony. Secondly, we tested whether wintering-site fidelity differed between sexes by comparing within-individual MID. Fixed effects included colony and sex.

We used the maximum likelihood (ML) method for model selection (Luke 2017). Akaike's Information Criterion (AIC) was then used to evaluate support among competing models, and the model with the lowest AIC was identified as the one receiving the most support from our data. When top models differed <2 in AIC, the simplest model was selected (Burnham and Anderson 2004). All plots and analysis were done running R v. 4.5.1 (R Core Team 2025) and estimates are provided with 95% confidence limits (CL). The *performance* package (Lüdecke *et al*. 2021) was used to assess model performance using the function *check_model*, with outputs from the best supported models provided in Appendix A.4.

Results

The spatial distribution of positions used in the calculation of daily inter-track distance, divided by colony affiliation and sex, are shown in Figure 1. Position data at the individual level are provided in Appendix A.5.

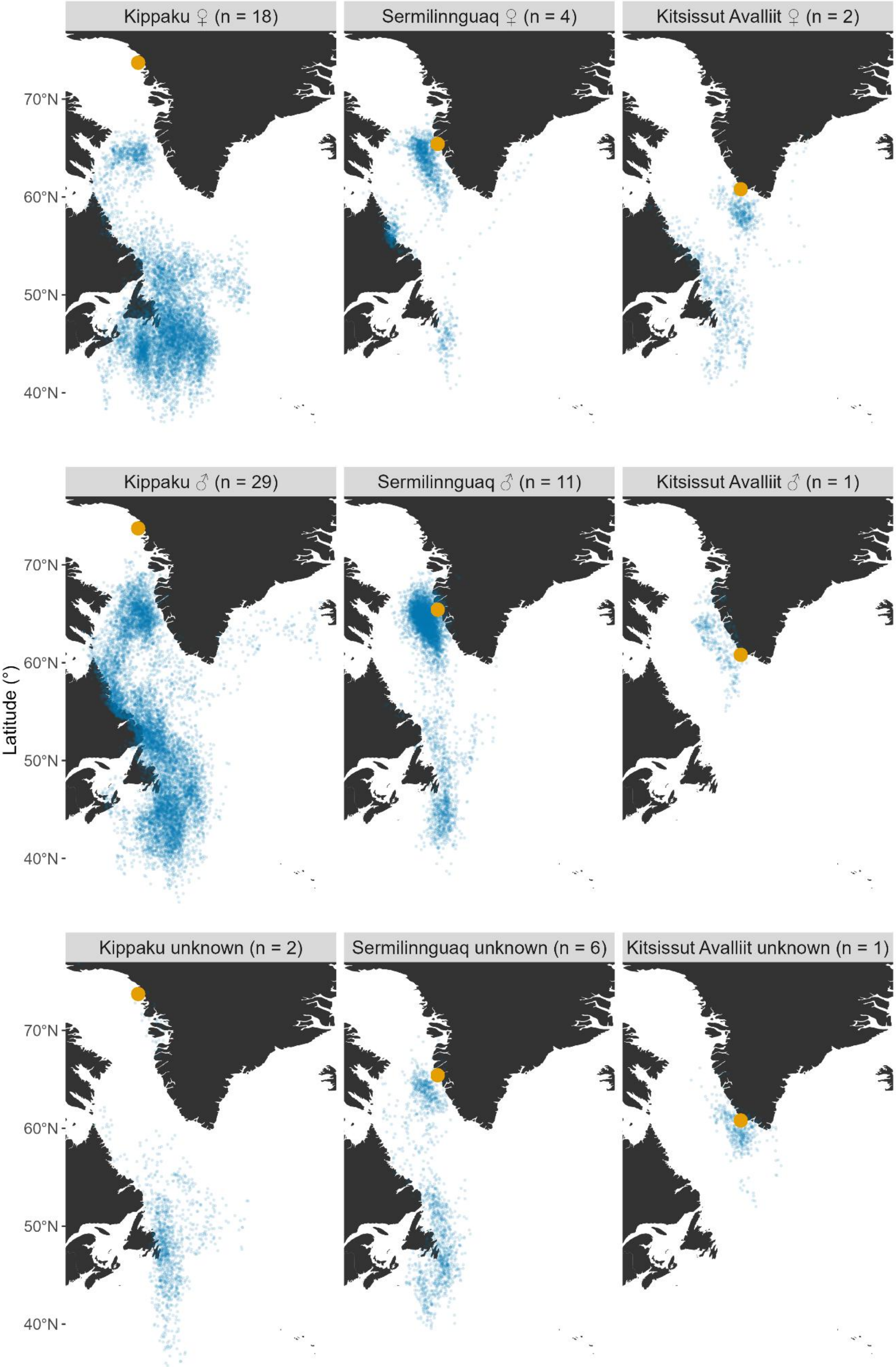
Kippaku ♀ (n = 18)
Sermilinnguaq ♀ (n = 4)
Kitsissut Avalliit ♀ (n = 2)
Kippaku ♂ (n = 29)
Sermilinnguaq ♂ (n = 11)
Kitsissut Avalliit ♂ (n = 1)
Kippaku unknown (n = 2)
Sermilinnguaq unknown (n = 6)
Kitsissut Avalliit unknown (n = 1)
70°N
60°N
50°N
40°N
Latitude (°)
60°W
50°W
40°W
30°W
Longitude (°)

Figure 1 The spatial distribution of Brünnich's Guillemots *Uria lomvia* included in the study is shown by their recorded positions throughout the wintering period (November to February). Each plot represents a specific combination of colony affiliation and sex. Breeding colony locations are indicated by orange filled circles and bird positions are indicated with blue dots.

The best supported and simplest model included additive effects of comparison type and colony (Table 2), with both effects being significant (Table 3, Fig. 2). MID was 3.5 times greater among Guillemots than within (log scale coefficient = -1.25, 95% CL -1.42 – -1.069), indicating that individuals were likely to return to similar wintering areas year after year and thus display wintering-site fidelity. There was no statistical support for an interaction between comparison type and colony, indicating that the relative difference between within-individual MID and among-individual MID was the same across colonies. The observed difference in MID between colonies therefore indicate a difference in wintering space-use, not site fidelity. For Kippaku Guillemots MID was 1.8 times greater compared to Sermilinnguaq Guillemots (Figs. 2 and 3). Guillemots from the Kippaku colony had a predicted MID of 642 km among birds and 185 km within birds. For Sermilinnguaq Guillemots, the respective predicted MIDs were 341 km among birds and 98 km within birds. Kitsissut Avalliit Guillemots had an empirical MID of 724 km among birds and 258 km within birds.

Table 2 Summary of linear model selection results showing AIC, ΔAIC (difference between each model's AIC and the lowest AIC in the set) and R^2 for models comparing within- and among-individual mean inter-track distance. Comparison type and colony as fixed effects with the best supported model marked in bold.

Model	AIC	ΔAIC	R^2
log(Distance) ~ 1	11112.1	517.9	0
log(Distance) ~ colony	10783.1	188.9	0.073
log(Distance) ~ comparison type + colony	10595.4	1.2	0.11
log(Distance) ~ comparison type * colony	10594.2	0	0.11

Table 3 Estimated fixed effects for the linear model including additive effects of comparison type and colony (Table 2). Kippaku as the reference value for colony, and among-bird as the reference value for comparison type.

Fixed effects	Estimate (log km)	Confidence interval 2.5%	Confidence interval 97.5%	Std. Error	t value	p value
Intercept	6.466	6.439	6.492	0.0135	479.13	
Sermilinnguaq	-0.634	-0.703	-0.564	0.0355	-17.87	<0.001
Within-bird	-1.245	-1.42	-1.069	0.0894	-13.92	<0.001

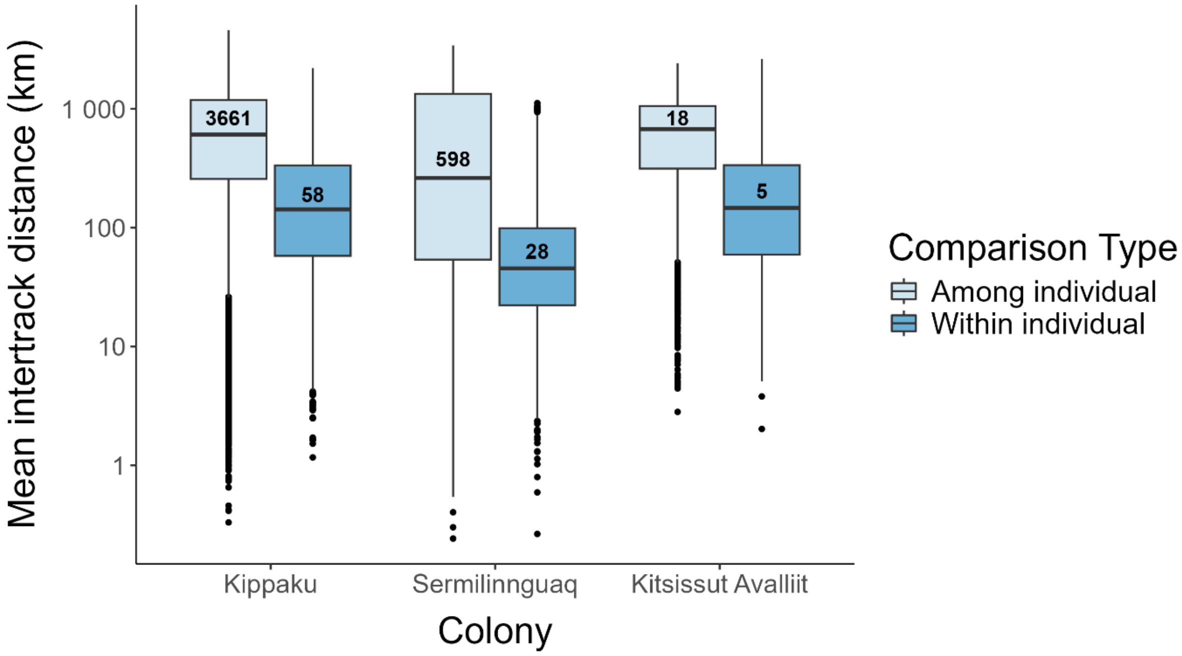

Figure 2 Mean inter-track distance (km) across colonies (n shown in figure). Among-individual comparisons refer to distances calculated between two different individuals across different years, whereas within-individual comparisons refer to distances calculated for the same individual across different years. The y-axis is shown on a logarithmic scale.

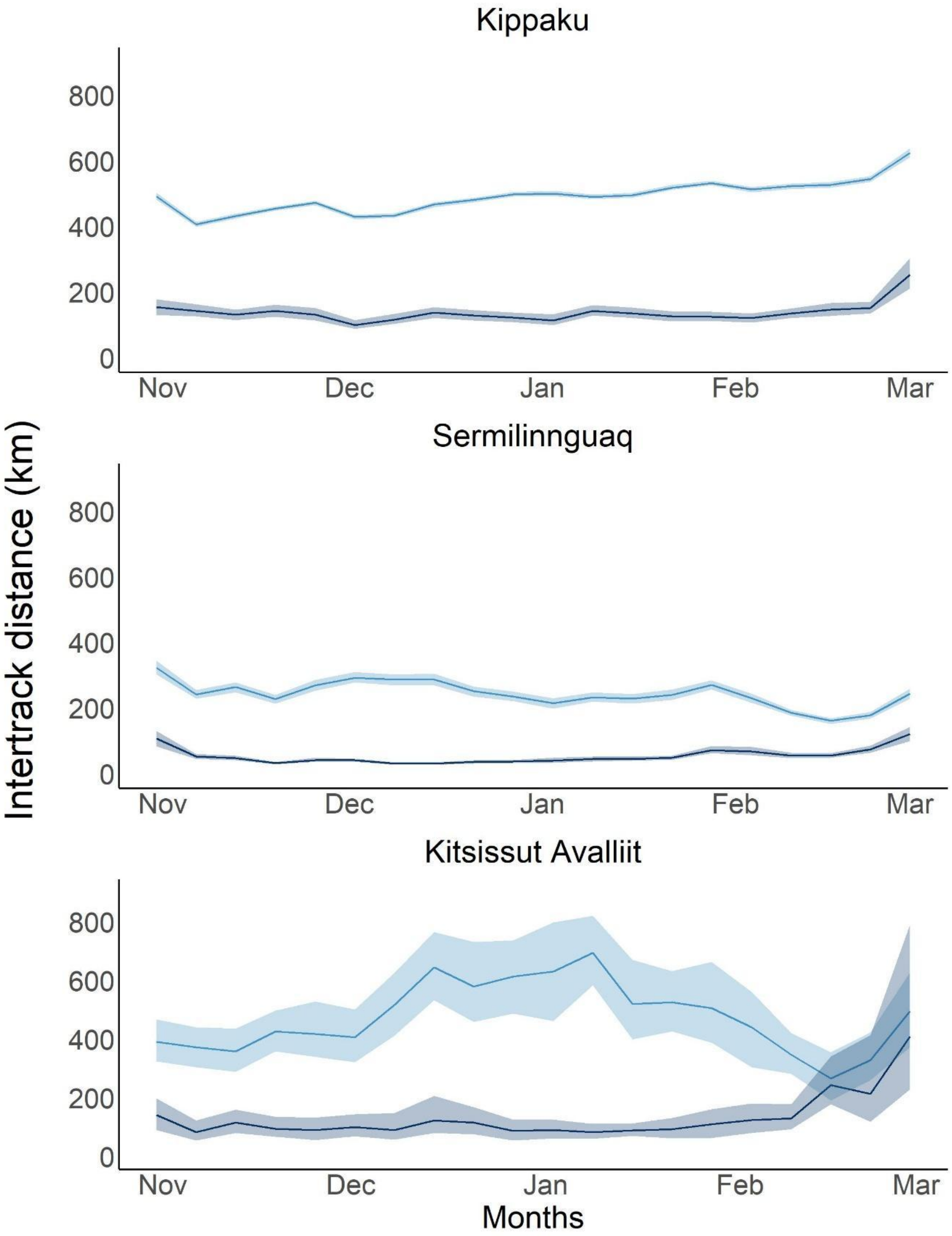

Figure 3 Inter-track distance (km) for the different colonies throughout the wintering period (November to February), with among-individual comparisons in light blue and within-individual comparisons in dark blue. The values represent weekly means, and the 95% confidence intervals were calculated using bootstrapping with 250 resamples.

The simpler model without sex as an explanatory term had a delta AIC within 2 of the model including sex, and so we selected the simpler model (Table 4). Furthermore, as was also seen in the model including comparison type (Table 3), colony affiliation in these models also proved a significant factor in within-individual MID (Table 5). Within-individual MID was 2.5 times higher for Kippaku Guillemots compared to Sermilinnguaq Guillemots (Fig. 2 and 3).

Table 4 Summary of linear model selection results showing, AIC, ΔAIC (difference between each model's AIC and the lowest AIC in the set) and R^2 for models explaining variation in within-individual mean inter-track distance. Sex and colony as fixed effects with the best supported model marked in bold.

Model	AIC	ΔAIC	R^2
log(Distance) ~ 1	193.4	42.4	0
log(Distance) ~ colony * sex	152.5	1.5	0.400
log(Distance) ~ colony	151.7	0.7	0.391
log(Distance) ~ colony + sex	151.003	0	0.397

Table 5 Estimated fixed effects for the linear model including colony (Table 4) with Kippaku as the reference value for colony.

Fixed effects	Estimate (log km)	Confidence interval 2.5%	Confidence interval 97.5%	Std. Error	t value	p value
log(Distance) ~ colony						
Intercept	5.328	5.187	5.474	0.0736	72.443	
Sermilinnguaq	-0.937	-1.187	-0.686	0.126	-7.436	<0.001

Discussion

Wintering-site fidelity was higher in individual than population

We found that individual Guillemots are more likely to return to similar wintering areas from year to year than expected by chance. Considering the ocean-scale distribution and long migration of the species, birds from these West Greenland colonies preferred to winter in the same areas year after year. But the true spatial differences remain uncertain (see Caveats) as positions obtained using light-based geolocation are associated with a mean error of ~185 km (Phillips *et al.* 2004). A high wintering-site fidelity has also been found in another alcid, the Black Guillemot *Cepphus grylle* (Bråthen *et al.* 2026), and in other transoceanic migratory seabird species; the Black-legged Kittiwake *Rissa tridactyla* (Léandri-Breton *et al.* 2021) and Lesser Black-backed Gull *Larus fuscus* (Brown *et al.* 2021). Multiple behavioural strategies could explain the high site fidelity found within individuals. The "win-stay, lose-shift" strategy suggests that if an individual succeeds in a particular area, it is more likely to remain there (Switzer 1993). On the other hand, the "always-stay" strategy involves a strong commitment to a specific area regardless of challenges or setbacks (Switzer 1993). The "always-stay" strategy seems the most likely explanation for the high wintering-site fidelity found in Guillemots. This is supported by Merkel *et al.* (2021a), who introduced the concept of *individual migration strategy fidelity* (IMSF) - when within-individual variation in space use during the non-breeding period is lower than that observed across the population as a whole. In their study, Guillemot and Common Guillemot *Uria aalge* exhibited IMSF during the wintering period, which aligns with our findings. Individuals of both Guillemot species and almost all colonies showed fidelity to geographical sites and not to specific habitats, which was best explained by site familiarity rather than habitat specialization (Merkel *et al.* 2021a). In the context of rapidly changing environments, species displaying IMSF driven by site familiarity may not be able to adjust their migration strategies sufficiently fast as favourable habitats shift locations. Furthermore, consistent use of specific wintering areas across years could cause seabirds to face prolonged exposure to the same conditions, including pollutants like heavy metals, PFAS, and oil spills (Montevecchi *et al.* 2012; Albert *et al.* 2021; Léandri-Breton *et al.* 2024).

It is worth noting that our data were obtained from colonies that mainly or in part use apparently favourable wintering areas (Frederiksen *et al.* 2016). Frederiksen *et al*. (2016) found a strong correspondence between breeding population status and wintering area, where western stable breeding populations (West Greenland, Canada) wintered mainly off the Atlantic coast of Canada, while declining eastern breeding populations (Svalbard, Iceland) wintered mainly in waters off southwest Greenland and around Iceland. This same pattern was also found in a study of the Svalbard breeding population by Descamps *et al.* (2025) where increasing colonies in northeast Svalbard wintered in the northern Barents Sea, while decreasing colonies in western and southern Svalbard wintered between Iceland and Canada. It has been suggested that low pre-breeding survival could be linked to poor feeding conditions in wintering areas used by declining populations (Frederiksen *et al.* 2021). Comparing wintering-site fidelity from declining populations from Svalbard and Iceland could be of interest in further studies, as declining populations may have a lower wintering-site fidelity due to less predictable or low-quality prey available in wintering areas. Knowledge on wintering behaviour including distribution, site fidelity and space-use, is of great importance for the future management and conservation of the Guillemot.

Wintering space-use differ between colonies

While wintering-site fidelity remained consistent across colonies, Kippaku Guillemots had a higher space-use compared to Sermilinnguaq Guillemots. This suggests that although individuals show similar wintering-site fidelity regardless of colony affiliation, the extent of the area they use is larger for birds from Kippaku. Kitsissut Avalliit Guillemots may have a space-use similar to birds from Kippaku, although there were not enough individuals tracked to make this conclusion with certainty. While little is known about colony-specific wintering space-use in Guillemots, Merkel *et al.* (2021a) also found that within-individual variation in space-use during the wintering period differed between colonies, while McFarlane Tranquilla *et al.* (2013) found considerable inter-colony variation in which ocean areas were used during winter. For our findings, one possible explanation for the observed difference in wintering space-use between colonies could be that Guillemots breeding in the Sermilinnguaq colony generally have a shorter migration route to their wintering area than Guillemots breeding in Kippaku. Previous studies on Guillemots have found that differences between breeding colonies can be caused by distance to, and foraging conditions in, nearby feeding areas (Birkhead and Nettleship, 1981; Falk *et al.* 2002; Harding *et al.* 2013). However, a study by Bråthen *et al*. (2026) found that while migration distance differed between colonies, wintering space-use did not. Our findings support the importance of assessing individual breeding populations within a species, as populations with strong migratory connectivity wintering in small areas are more vulnerable to site specific threats e.g. a spatially restricted oil spill.

Wintering-site fidelity does not differ between sexes

We found no indication that wintering-site fidelity differed between male and female Guillemots. This aligns with previous studies on Guillemots (Merkel *et al*. 2021a) and Black Guillemots (Bråthen *et al.* 2026), which also reported no sex-based differences. Similarly, in another pelagic, long distance migratory seabird, the Black-legged Kittiwake, sex-related differences in site-fidelity were not observed. Because our chosen time window (November to February) excludes the fall migration period, when sex-specific differences would be expected due to males swim-migrating with their chicks (Frederiksen *et al.* 2016), any difference between sexes would be differences in winter-site fidelity, not moult or migration fidelity.

Caveats

Positions obtained using light-based geolocation are associated with a mean error of around 185 km (Phillips *et al.* 2004), although the overall error of geolocators decreases as the number of days positions are pooled over increases (Bennett *et al.* 2025). Individual estimated distances between positions are affected by this error, and the selection of the smallest position-to-position distance over a 7-day time window will lead to a negative bias in daily inter-track distance. However, this bias will affect all among-group comparisons equally, and our conclusions should thus be robust to position error. The mean inter-track distances displayed in Figs. 2 and 3 are likely biased low. Nevertheless, the true spatial difference between years within and among individuals remains uncertain.

Conclusion

In conclusion, Guillemots showed remarkable consistency in their use of wintering locations among years. Individuals were more likely to return to similar wintering areas than expected by chance, which suggests that individuals use memory to return to familiar and profitable locations year after year. Consistent use of key foraging locations is likely associated with foraging success, which is a strong driver of overwintering survival. Wintering-site fidelity did not vary among colonies, but space-use did, suggesting that space-use may be influenced by learned behaviour or genetic inheritance within breeding populations. Wintering-site fidelity did not differ between sexes, indicating that the known differences in migratory behaviour between males and females do not carry over into the wintering period. Prioritising the protection of consistently used wintering areas in the North Atlantic is important for the continued conservation of these three West Greenland colonies.

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Data Availability

A data availability statement will be provided soon.

References

Albert, C., Bråthen, V. S., Descamps, S., Anker-Nilssen, T., Cherenkov, A., Christensen-Dalsgaard, S., Danielsen, J., Erikstad, K. E., Gavrilo, M., Hanssen, S. A., Helgason, H. H., Jónsson, J. E., Kolbeinsson, Y., Krasnov, Y., Langset, M., Lorentzen, E., Olsen, B., Reiertsen, T. K., Strom, Systad, G. H., Tertitski, G., Thompson, P. M., Thórarinsson, T. L., Bustamante, P., Moe, B. & Fort, J. 2021. Inter-annual variation in winter distribution affects individual seabird contamination with mercury. *Marine Ecology Progress Series*, 676: 243-254. https://doi.org/10.3354/meps13793

Alerstam, T., Backman, J., Gronroos, J., Olofsson, P., & Strandberg, R. 2019. Hypotheses and tracking results about the longest migration: The case of the arctic tern. *Ecology and Evolution*, 9: 9511-9531. https://doi.org/10.1002/ece3.5459

Amélineau, F., Merkel, B., Tarroux, A., Descamps, S., Anker-Nilssen, T., Bjornstad, O., Bråthen, V. S., Chastel, O., Christensen-Dalsgaard, S., Danielsen, J., Daunt, F., Dehnhard, N., Ekker, M., Erikstad, K. E., Ezhov, A., Fauchald, P., Gavrilo, M., Hallgrimsson, G. T., Hansen, E. S., Harris, M. P., Helberg, M., Helgason, H. H., Johansen, M. K., Jónsson, J. E., Kolbeinsson, Y., Krasnov, Y., Langset, M., Lorentsen, S. H., Lorentzen, E., Melnikov, M. V., Moe, B., Newell, M. A., Olsen, B., Reiertsen, T., Systad, G. H., Thompson, P., Thorarinsson, T. L., Tolmacheva, E., Wanless, S., Wojczulanis-Jakubas, K., Åström, J. & Strom, H. 2021. Six pelagic seabird species of the North Atlantic engage in a fly-and-forage strategy during their migratory movements. *Marine Ecology Progress Series*, 676: 127-144. https://doi.org/10.3354/meps13872

Bennett, S., Phillips, R. A. & Green, J. A. 2025. Quantifying the effect of time on geolocations accuracy in seabirds. *Marine Ornithology*, 53: 331-335. https://doi.org/10.5038/2074-1235.53.2.1654

Birkhead, T. R., & Nettleship, D. N. 1981. Reproductive Biology of Thick-Billed Murres (*Uria lomvia*): An Inter-Colony Comparison. *The Auk*, 98:258–269. http://www.jstor.org/stable/4086064

Brown, J. M., van Loon, E. E., Bouten, W., Camphuysen, K. C. J., Lens, L., Müller, W., Thaxter, C. B. & Shamoun-Baranes, J. 2020. Long-distance migrants vary migratory behaviour as much as short-distance migrants: An individual-level comparison from a seabird species with diverse migration strategies. *The Journal of Animal Ecology*. 90:1058-1070. https://doi.org/10.1111/1365-2656.13431

Bråthen, V.S., Moe, B., Amélineau, F., Ekker, M., Fauchald, P.,Helgason, H.H., Johansen, M. K., Merkel, B., Tarroux, A., Åström, J. & Strøm, H. 2021. An automated procedure (v2.0) to obtain positions from light-level geolocators in large-scale tracking of seabirds. A method description for the SEATRACK project. *NINA Report* 1893*. Norwegian Institute for Nature Research.* ISBN: 978-82-426-4666-8

Bråthen, V. S., Dehnhard, N., Fayet, A. L., Christensen-Dalsgaard, S., Lorentsen, S.-H., & Anker-Nilssen, T. 2026. Divergent migratory strategies of black guillemots from two colonies in the Norwegian Sea. *Mar Biol* 173: 22. https://doi.org/10.1007/s00227-025-04757-7

Burnham, K. P., & Anderson, D. R. 2004. Multimodel inference - understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33: 261-304. https://doi.org/10.1177/0049124104268644

Carey, M. J., Phillips, R. A., Silk, J. R. D., & Shaffer, S. A. 2014. Trans-equatorial migration of Short-tailed Shearwaters revealed by geolocators. *Emu-Austral Ornithology*, 114: 352-359. https://doi.org/10.1071/mu13115

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Yates, O., Phillips, R. A., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. 2019. Threats to seabirds: A global assessment. *Biological Conservation*, 237: 525-537. https://doi.org/10.1016/j.biocon.2019.06.033

Descamps, S., Merkel, B. & Strøm, H. 2025. Local variations in population trends and migration strategies of Brünnich's guillemots on Svalbard. *Marine Ecology Progress Series,* 765:101-114. https://doi.org/10.3354/meps14893

Elliott, K. H., Linnebjerg, J. F., Burke, C., Gaston, A. J., Mosbech, A., Frederiksen, M. & Merkel, F. 2017. Variation in growth drives the duration of parental care: a test of Ydenberg's model. *American Naturalist*, 189: 526-538. https://doi.org/10.1086/691097

Fauchald, P., Tarroux, A., Bråthen, V., Descamps, S., Ekker, M., Helgason, H., Merkel, B., Moe, B., Åstrøm, J., & Strøm, H. 2019. Arctic-breeding seabirds' hotspots in space and time - A methodological framework for year-round modelling of environmental niche and abundance using light-logger data. *NINA Report* 1657: 85. *Norwegian Institute for Nature Research.* ISBN: 978-82-426-3401-6

Falk, K., Benvenuti, S., Dall'Antonia, L., Gilchrist, G., & Kampp, K. 2002. Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an inter-colony comparison. *Marine Ecology Progress Series*, 231:293–302. http://www.jstor.org/stable/24865143

Frederiksen, M., Descamps, S., Elliott, K. H., Gaston, A. J., Huffeldt, N. P., Kolbeinsson, Y., Linnebjerg, J. F., Lorentzen, E., Merkel, F. R., Strom, H., & Thorarinsson, T. L. 2021. Spatial variation in vital rates and population growth of thick-billed murres in the Atlantic Arctic. *Marine Ecology Progress Series*, 672: 1-13. https://doi.org/10.3354/meps13823

Frederiksen, M., Descamps, S., Erikstad, K. E., Gaston, A. J., Gilchrist, H. G., Grémillet, D., Johansen, K. L., Kolbeinsson, Y., Linnebjerg, J. F., Mallory, M. L., Tranquilla, L. A. M., Merkel, F. R., Montevecchi, W. A., Mosbech, A., Reiertsen, T. K., Robertson, G. J., Steen, H., Strom, H., & Thórarinsson, T. L. 2016. Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: Conservation implications. *Biological Conservation*, 200: 26-35. https://doi.org/10.1016/j.biocon.2016.05.011

Frederiksen, M., Falk, K., Huffeldt, N. P., Johansen, K., Labansen, A. L., Linnebjerg, J. F., Merkel, F., & Mosbech, A. 2014. Seabird baseline studies in Baffin Bay, 2008-2013. Colony-based fieldwork at Kippaku and Apparsuit, NW Greenland. Roskilde, Denmark: Aarhus University, DCE – Danish Centre for Environment and Energy. Scientific Report No. 110. ISBN: 978-87-7156-087-9

Frederiksen, M., Linnebjerg, J. F., Merkel, F. R., Wilhelm, S. I., & Robertson, G. J. 2019. Quantifying the relative impact of hunting and oiling on Brunnich's guillemots in the North-west Atlantic*. Polar Research*, 38: 3378. https://doi.org/10.33265/polar.v38.3378

Gaston, A. J., & Hipfner, J. M. 2020. Thick-billed Murre (*Uria lomvia*). In S. M. Billerman (Ed.), *Birds of the World (version 1.0 ed.)*. Cornell Lab of Ornithology. https://doi.org/https://doi.org/10.2173/bow.thbmur.01

Harding, A., Paredes, R., Suryan, R., Roby, D., Irons, D., Orben, R., Renner, H., Young, R., Barger, C., Dorresteijn, I. & Kitaysky, A. 2013. Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography, 94: 178-191. https://doi.org/10.1016/j.dsr2.2013.03.013.

Huffeldt, N. P., Ballesteros, M., Helm, B., Linnebjerg, J. F., Merkel, F. R., Mosbech, A., & Frederiksen, M. 2024. Thick-billed Murres in breeding pairs migrate and overwinter far apart but in similar photic environments. *Journal of Ornithology*, 165: 881-888. https://doi.org/10.1007/s10336-024-02176-x

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., et al. 2020. Light-level geolocator analyses: A user's guide. Journal of Animal Ecology, 89:221-236. https://10.1111/1365-2656.13036.

Léandri-Breton, D. J., Jouanneau, W., Legagneux, P., Tarroux, A., Moe, B., Angelier, F., Blévin, P., Brathen, V. S., Fauchald, P., Gabrielsen, G. W., Herzke, D., Nikiforov, V. A., Elliott, K. H., & Chastel, O. 2024. Winter Tracking Data Suggest that Migratory Seabirds Transport Per- and Polyfluoroalkyl Substances to Their Arctic Nesting Site. *Environmental Science & Technology*, 58: 12909-12920. https://doi.org/10.1021/acs.est.4c02661

Léandri-Breton, D. J., Tarroux, A., Elliott, K. H., Legagneux, P., Angelier, F., Blévin, P., Bråthen, V. S., Fauchald, P., Goutte, A., Jouanneau, W., Tartu, S., Moe, B., & Chastel, O. 2021. Long-term tracking of an Arctic-breeding seabird indicates high fidelity to pelagic wintering areas. *Marine Ecology Progress Series*, 676: 205-218. https://doi.org/10.3354/meps13798

Luke, S. G. (2017). Evaluating significance in linear mixed-effects models in R. *Behavior Research Methods*, 49:1494-1502. https://doi.org/10.3758/s13428-016-0809-y

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. 2021. An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, 6, 3139:60. https://doi.org/https://doi.org/10.21105/joss.03139

Merkel, B., Descamps, S., Yoccoz, N. G., Grémillet, D., Daunt, F., Erikstad, K. E., Ezhov, A., Harris, M. P., Gavrilo, M., Lorentsen, S. H., Reiertsen, T. K., Steen, H., Systad, G. H., Pórarinsson, P. L., Wanless, S., & Strom, H. 2021a. Individual migration strategy fidelity but no habitat specialization in two congeneric seabirds. *Journal of Biogeography*, 48: 263-275. https://doi.org/10.1111/jbi.13883

Merkel, B., Descamps, S., Yoccoz, N. G., Grémillet, D., Fauchald, P., Danielsen, J., Daunt, F., Erikstad, K. E., Ezhov, A. V., Harris, M. P., Gavrilo, M., Lorentsen, S. H., Reiertsen, T. K., Systad, G. H., Thórarinsson, T. L., Wanless, S., & Strom, H. 2021b. Strong migratory connectivity across meta-populations of sympatric North Atlantic seabirds. *Marine Ecology Progress Series*, 676: 173-188. https://doi.org/10.3354/meps13580

Merkel, F., Labansen, A. L., Boertmann, D., Mosbech, A., Egevang, C., Falk, K., Linnebjerg, J. F., Frederiksen, M., & Kampp, K. 2014. Declining trends in the majority of Greenland's thick-billed murre (*Uria lomvia*) colonies 1981-2011. *Polar Biology*, 37: 1061-1071. https://doi.org/10.1007/s00300-014-1500-3

Merkle, J., Abrahms, B., Armstrong, J., Sawyer, H., Costa, D. & Chalfoun, A. 2022. Site fidelity as a maladaptive behavior in the Anthropocene. *Frontiers in Ecology and the Environment*, 20: 187-194. https://doi.org/10.1002/fee.2456

Montevecchi, W. A., Hedd, A., Tranquilla, L. M., Fifield, D. A., Burke, C. M., Regular, P. M., Davoren, G. K., Garthe, S., Robertson, G. J., & Phillips, R. A. 2012. Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. *Biological Conservation*, 156: 62-71. https://doi.org/10.1016/j.biocon.2011.12.001

Nettleship, D. N., Birkhead, T. R., & Bédard, J. 1985. The Atlantic Alcidae: the evolution, distribution, and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas. *Academic Press*.

Paleczny M., Hammill E., Karpouzi V. & Pauly D. 2015. Population Trend of the World's Monitored Seabirds, 1950-2010. *PLoS ONE* 10: e0129342. https://doi.org/10.1371/journal.pone.0129342

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. & Briggs, D. R. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series,* 266: 265-272. https://doi.org/10.3354/meps266265

R Core Team. 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Sealy, S. G. 1973. Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. *Ornis Scandinavica*, 4:113-121. https://doi.org/10.2307/3676112

Strøm, H., Descamps, S., Ekker, M., Fauchald, P., & Moe, B. 2021. Tracking the movements of North Atlantic seabirds: steps towards a better understanding of population dynamics and marine ecosystem conservation. *Marine Ecology Progress Series*, 676: 97-116. https://doi.org/10.3354/meps13801

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, 7: 533-555. https://doi.org/10.1007/BF01237820

Tranquilla, L. M., Hedd, A., Burke, C., Montevecchi, W. A., Regular, P. M., Robertson, G. J., Stapleton, L. A., Wilhelm, S. I., Fifield, D. A., & Buren, A. D. 2010. High Arctic sea ice conditions influence marine birds wintering in Low Arctic regions. *Estuarine Coastal and Shelf Science*, 89: 97-106. https://doi.org/10.1016/j.ecss.2010.06.003

McFarlane Tranquilla, M. L. A., Montevecchi, W. A., Hedd, A., Fifield, D. A., Burke, C. M., Smith, P. A., Regular, P. M., Robertson, G. J., Gaston, A. J. & Phillips, R. A. 2013. Multiple-colony winter habitat use by murres Uria spp. in the Northwest Atlantic Ocean: implications for marine risk assessment. *Marine Ecology Progress Series*, 472:287-303. https://doi-org.ez.statsbiblioteket.dk/10.3354/meps10053

van Bemmelen, R., Moe, B., Hanssen, S. A., Schmidt, N. M., Hansen, J., Lang, J., Sittler, B., Bollache, L., Tulp, I., Klaassen, R., & Gilg, O. 2017. Flexibility in otherwise consistent non-breeding movements of a long-distance migratory seabird, the long-tailed skua. *Marine Ecology Progress Series*, 578: 197-211. https://doi.org/10.3354/meps12010

Supplementary Materials

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