



Contribution to the Theme Section 'Non-breeding distribution and movements of North Atlantic seabirds'

# Transpolar and bi-directional migration strategies of black-legged kittiwakes *Rissa tridactyla* from a colony in Novaya Zemlya, Barents Sea, Russia

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**ABSTRACT:** Atlantic black-legged kittiwakes *Rissa tridactyla tridactyla* breeding in the Barents Sea have long been considered to winter in the North Atlantic region. Here, we present the first evidence of bi-directional and transpolar migrations of kittiwakes breeding in the south-eastern Barents Sea. Using geolocators, we revealed previously unknown migration patterns of kittiwakes that breed at Yuzhny (Southern) Island of the Novaya Zemlya Archipelago. Of 27 studied individuals, 21 migrated to the North Atlantic, while 6 (22%) wintered in the North Pacific. Two birds repeated an eastward migration over 3 subsequent years, and 3 kittiwakes did so over 2 years. We hypothesize that such bi-directional migration strategies can reflect the history of the kittiwakes' colonization of the eastern Barents Sea, where North Pacific birds may have colonized Novaya Zemlya from the east and maintained their traditional wintering grounds in the Pacific. However, we also expect that the exchange of Atlantic and Pacific (*Rissa t. pollicaris*) kittiwakes will increase as the sea ice barrier shrinks in the following decades, potentially having a great impact on these 2 subspecies.

**KEY WORDS:** Black-legged kittiwakes · Migration strategies · Geocator · Transpolar migration · Wintering grounds · Novaya Zemlya · Pacific Ocean · Atlantic Ocean

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## 1. INTRODUCTION

Most arctic seabirds are migratory multi-areal animals seasonally commuting between breeding, staging and wintering quarters, where they face varying conditions in terms of weather events, food availability, hunting pressure and/or environmental pollution (Newton 2010). To interpret the population variability, to assess risk exposure and to predict further population changes in response to natural and human-

induced impacts, detailed knowledge of the birds' seasonal distribution and migratory connectivity, i.e. dependence on different areas during the life cycle, is of primary importance (Webster & Marra 2005).

Although arctic bird migration has long been subject to special research interest (e.g. Vaughan 1992, Egevang et al. 2010 for terns, Gilg et al. 2013 for skuas, Davis et al. 2016 for gulls), detailed documentation of migration patterns of some arctic seabirds is still lacking. Possible reasons include the con-

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straints of traditional methodological approaches, such as ringing, namely low retrieval percentage and rare encounter of ringed birds in the open sea. At the same time, spatiotemporal patterns of seabird migration strategies are important to know, as they provide crucial information about the species' life histories.

Studies of seabirds' seasonal movements have recently seen significant advances through the development and introduction of remote tracking tools — especially light geolocators (Wilson et al. 1992, Burger & Shaffer 2008, Bridge et al. 2011). The availability of geolocators has made it possible to generate large-scale datasets concerning location of wintering areas, routes and timing of migration (e.g. for arctic seabird species: Egevang et al. 2010, Davis et al. 2016, Gilg et al. 2016a, Frederiksen et al. 2016) plus individual and interannual variabilities of migration patterns (Orben et al. 2015a,b, 2018, Merkel et al. 2020). The potential of such studies for providing missing data is especially promising for arctic seabirds, since the inaccessibility of their habitats throughout the entire annual cycle has led to significant gaps in basic knowledge of their marine life, including patterns of their at-sea distribution and migration. Studies addressing this problem are also relevant because of the rapid and significant climate changes currently occurring in the Arctic (Meredith et al. 2019). This includes a dramatic decline in the extent of sea ice that is considered a barrier for the transpolar migration of seabirds (Clairbaux et al. 2019) and a key ecological factor shaping their life traits and affecting their distribution at sea (e.g. Hunt 1991, Stirling 1997). There are, however, still uncertainties considering the understanding of the non-breeding distribution, ecology and migration of otherwise well-studied species. One of the most abundant species is the black-legged kittiwake *Rissa tridactyla* (hereafter referred to as kittiwake) (Frederiksen et al. 2012). Knowledge of migration strategies of kittiwake populations in different parts of the Arctic can provide important insights into past and current environmental changes and patterns of the birds' adaptation to them.

The kittiwake has a circumpolar distribution in the northern hemisphere and breeds all around the Arctic

Ocean (Fig. 1). The species is typically split into 2 subspecies: the Atlantic kittiwake *Rissa t. tridactyla* and the Pacific kittiwake *Rissa t. pollicaris*, with corresponding North Atlantic and North Pacific wintering grounds (Cramp & Simmons 1983, Yudin & Firsova 2002). In the northernmost part of the Atlantic, the kittiwake breeds along all the coasts of the Eurasian Arctic seas, with largest numbers occurring in the Barents Sea (Johansen et al. 2020). In particular, kittiwakes breed along the coast of northern Norway and northern Kola Peninsula, Russia, as well as on all large islands and archipelagos, including Novaya Zemlya in the eastern Barents Sea (Bakken 2000). The Barents Sea kittiwakes belong to the Atlantic subspecies *R. t. tridactyla* and are traditionally believed to winter in the North Atlantic (Krasnov & Nikolaeva 2016). The first documentation of wintering areas of the kittiwakes breeding in the Russian part of the Barents Sea came from traditional ringing, with all birds but one being recovered in the North Atlantic or as vagrants inland (Dementiev 1955, Nikolaeva et al. 1997, Krasnov & Nikolaeva 2016). Extensive telemetry studies with the use of geolocators in the North Atlantic show that kittiwakes breeding in Northern Norway, Murman Coast and Svalbard usually attend their colonies from mid-spring (spring = March to May) to late summer (summer = June to



Fig. 1. Kittiwake circumpolar breeding distribution. Background map with breeding colonies (red dots) are taken from the Johansen et al. (2020), subspecies ranges are depicted after Yudin & Firsova (1988) as dashed lines, reoccurring flaw polynyas are shown as dark blue areas; they are averaged for the period 1996 to 2015 (from Solovveyev et al. 2017)

August). After the breeding season, most individuals migrate southwards in autumn (September to November) and reside in the North Sea or west of the mid-Atlantic ridge in the North Atlantic through the winter (December to February, Frederiksen et al. 2012). However, a few individuals were also shown to reside in the Barents Sea through the winter.

From previous tracking studies, kittiwakes can be classified as nomadic migrants that utilize several staging areas during the non-breeding season (e.g. González-Solís et al. 2011). However, until now, little was known about the migration and wintering areas of the kittiwakes breeding in archipelagos of the northeastern and eastern Barents Sea (Krasnov & Nikolaeva 1998). In particular, almost no data from large kittiwake colonies on Novaya Zemlya in the eastern Barents Sea were available, and the distribution at sea and possible migration routes and wintering grounds of birds from these colonies were speculative (Krasnov & Nikolaeva 2016), as no geolocators had been deployed on Novaya Zemlya. According to the few data previously obtained on the Novaya Zemlya archipelago (A. V. Ezhov unpubl. data, Kandalaksha State Reserve unpubl. data), the first appearance of kittiwakes in the colonies of the archipelago occurs at the end of April. At this time, birds concentrate in coastal waters, where they feed and visit nesting sites. The beginning of mass reproduction of kittiwakes in colonies on Novaya Zemlya was noted in the first 10 d of June. Mass abandonment of nests was observed in the first 10 d of September. However, not all birds left the nesting area immediately; some of them stayed in the coastal water area until the first 10 d of October. During the rest of the year, the birds were outside the archipelago and its coastal waters (Krasnov & Nikolaeva 1998, A. V. Ezhov unpubl. data).

Geolocator studies on the Novaya Zemlya archipelago were predicted to maybe show an eastward winter migration of some of these kittiwakes, based on results from previous ringing studies. Of 427 rings deployed on kittiwakes in western Novaya Zemlya in 1934–1949, only 5 were recovered, namely one on the coast of the northwestern Pacific (Kamchatka Peninsula) and 4 others inland in northern Asia (Dementiev 1955). These scarce data suggested that kittiwakes from the eastern and northern Barents Sea migrated eastwards and northeastwards (Dementiev 1955), whereas in later reviews this assumption was largely overlooked (Yudin & Firsova 1988, 2002, Dufour et al. 2020). Considering this lack of data on adult kittiwakes breeding in the eastern Barents Sea, the aim of our study was to reveal their wintering grounds and migration routes by analyzing spatial

data derived from geolocators. We discuss implications of our findings and further research in the context of the species' evolutionary history, systematics, conservation and management.

## 2. MATERIALS AND METHODS

### 2.1. Study species and field procedures

Geolocators (1.9 g, mk4083, Biotrack) were deployed on individuals at a colony of ~5000 breeding pairs on Yuzhny (Southern) Island, located near Karskie Vorota Strait, southern Novaya Zemlya Archipelago, in the southeastern Barents Sea (70.59° N, 55.02° E) between 2015 and 2018. In late June or early July of each year, adult kittiwakes were captured on the nest using a noose pole, and geolocators were attached by mounting on a plastic leg ring. Birds were captured during the nesting period (incubation or early chick brooding), but breeding was not confirmed for all individuals because in some years, eggs had not been laid by the time of capture. Loggers were retrieved in the following breeding season. From 2016 to 2019, 38 out of 89 deployed loggers were retrieved, and data were successfully downloaded from 37 of these. However, 3 loggers had stopped logging in February, before the first arrival at the colony. In total, we obtained geolocation data from 28 individual kittiwakes (with some individuals being tracked in more than 1 year). In total, data from 28 kittiwakes resulted in 50 tracked years, where 1 tracked year was defined as the time between one breeding season and the next, thereby representing a full non-breeding season.

### 2.2. Estimating positions

Geolocators used in the present study recorded light in arbitrary units from 0 (dark) to 64 (sun above the horizon) in 5 min intervals. To estimate positions from geolocator data, we followed the procedures described in Bråthen et al. (2021). In short, a threshold method was applied for identifying the time of sunset and sunrise (twilight events) from when the light-levels crossed a threshold value that separates daytime from nighttime, using the `twilightCalc` function from the `GeoLight` package (Lisovski & Hahn 2012). After removing unlikely twilight events that did not follow a probable diurnal pattern, positions were estimated from the length of a day or night (latitude) and the time of noon or midnight (longitude), yielding 2 posi-

tions each day. For estimating latitudes, it is necessary to assign a sun elevation angle that yields realistic latitudes. These were estimated from inspecting a series of latitude versus time plots and maps for each track, where latitudes were calculated from a range of sun angles (for examples and further details, see Hanssen et al. 2016 and Bråthen et al. 2021).

The uncertainty of positions estimated from light-level data is considered to be high (e.g.  $\pm 185$  km, Phillips et al. 2004). We therefore applied a set of filters (travel speed, bird distribution, distance + angle, and local regression filtering) to remove unrealistic positions (for further explanation or references, see Bråthen et al. 2021 and Table S1 in the Supplement at [www.int-res.com/articles/suppl/m676p189\\_supp.pdf](http://www.int-res.com/articles/suppl/m676p189_supp.pdf)). The retained positions were double-smoothed to compensate the influence of the birds' movement on the timing of twilight events.

Positions cannot be estimated from light-levels recorded during continuous daylight (midnight sun) or continuous darkness (polar night). To obtain positions as close to polar night or midnight sun as possible, we chose a low threshold of 1 from October to February, to enable timing of twilights during poor light conditions in winter. From March to September, we used a high threshold instead, to enable timing of twilights when light-levels above 1 can be recorded during nighttime. Using different thresholds, we also applied different sun elevation angles:  $-1$  from March to September and  $-3.32$  from October to February. Using a threshold of 1 yielded 9.5% more positions from October to February compared to using a threshold of 50, while a threshold of 50 yielded 12.1% more positions from March to September than using a threshold of 1.

Latitudes are imprecise in periods close to the spring and autumn equinox when day length is similar across the globe. These periods get shorter, the closer the geolocator is to the poles, as the daylength changes dramatically during spring and autumn at higher latitudes. In the present study, we define latitudes recorded from 27 February to 29 March in spring and 13 September to 15 October in autumn as influenced by the equinox. Positions obtained within these periods were excluded from plots.

### 2.3. Analyses of migration and timing

Individuals were classified as either wintering in the North Atlantic, in the Barents Sea or in the North Pacific based on where they resided during the darkest month of the year, in December. To analyze the

distance each individual moved away from the colony during the non-breeding season, we calculated the shortest distance over sea between the colony and median monthly positions for each individual and each year, using the `gridDistance` function in the `raster` package (Hijmans & van Etten 2020).

To analyze the timing of migration and colony attendance, we defined the start of the spring or autumn migration as the time when the birds crossed  $66^\circ$  N (northwards or southwards, respectively), either through the Bering Strait or between Greenland and the Norwegian coast. The first arrival to the colony was defined as the date of a bird's first assumptive visit to the colony ('assumptive' because we cannot be sure whether the bird visited the colony itself or was in an area near the colony), although many of them returned to the open sea soon after and would not start their nesting activity until sometime later. Departure from the colony was defined as the date of the last assumptive presence in the colony. Whenever the midnight sun prevented timing of the first arrival or departure from the colony with use of positional data (positions were not achievable from  $\sim 10$  May to  $\sim 1$  August), we used saltwater immersion data to estimate the dates of arrival and departure.

Geolocators record immersion in saltwater or lack thereof every 3 s; these recordings are then summed into 10 min intervals, and the results are presented as values between 0 (the logger was dry during the whole interval) to 200 (the logger was immersed in saltwater during the whole interval). We first calculated the median time when the logger was immersed in saltwater each day and ran a 5 d running mean with the `runmean` function from the `caTools` package (Tuszynski 2021). Since most 5 d values showed that a logger was in contact with saltwater during most of the day in the non-breeding season, and the immersion time declined considerably close to the breeding season, we extracted the first and last date when the 5 d percentage of immersion time was below 50% as the dates of the first and last visit to the colony, respectively; however, we only looked at the time period after the individual had returned to the Barents or Kara Seas in spring and before it crossed  $66^\circ$  N southwards in autumn, respectively.

### 2.4. Analysis of foraging

Feeding effort can reflect an increased effort to compensate for a high recent or present energy demand or reduced feeding efficiency, when individuals have to spend more time foraging to catch



enough food. From immersion data, we analyzed the daily time spent foraging by calculating the time the geolocator was partly (5–95% of the time) immersed in saltwater. This method has been confirmed for kittiwakes, using GPS data as comparison in Christensen-Dalsgaard et al. (2017).

## 2.5. Statistical analyses

We tested for differences in non-breeding strategies using the median distance from the colony in December, the average daily time spent foraging from one breeding season to the next, the timing of crossing 66°N in spring and autumn and of the first arrival and departure to the breeding colony as dependent variables in separate linear mixed-effects models (LMMs), with the Atlantic, Barents or Pacific classification as a fixed effect factor. Individuals and years were used as random effects. LMMs were fitted with a restricted maximum likelihood (REML) for normally distributed data (lmer function, lme4 package, Bates et al. 2015). Models with and without the fixed effect were then refitted with maximum likelihood (ML) and compared to obtain statistical significance. Summary statistics with p-values were obtained with Satterthwaite's degrees of freedom (lmerTest package, Kuznetsova et al. 2017).

For visualizing relationships between time spent foraging and day of the year for the different non-breeding strategies we used a generalized additive model (GAM, gam function, mgcv package, Wood 2011) for making predictive lines and confidence intervals and plotted these using the geom\_smooth function (ggplot2 package, Wickham 2016).

Maps showing sea ice extent were created using polar stereographic projection. Monthly median limits of the ice extent were downloaded from the National Snow and Ice Data Center (dataset ID: 'G02135', Fetterer et al. 2017), and sea ice concentrations were provided by the National Oceanic and Atmospheric Administration/Earth System Research Laboratories' Physical Sciences Laboratory (Boulder, Colorado, USA, <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>, Reynolds et al. 2007). Mean polynya (open water area) extent averaged for the period of 1996 to 2015 was taken from Solovyev et al. (2017) (shown in Fig. 1). All analyses and figures were made using R version 4.0.3 (R Core Team 2020).

## 3. RESULTS

### 3.1. Migration strategies

Kittiwakes tracked from Yuzhny Island displayed 3 distinct strategies in the darkest part of the non-breeding season: of 28 successfully tracked individuals, 16 individuals migrated to the North Atlantic, 6 stayed in the Barents Sea and 6 migrated to the North Pacific (Table 1). Among the 19 individuals tracked over 2 or 3 non-breeding seasons, only one individual switched its strategy the following year, from the Barents Sea to the North Atlantic (Table 1, Fig. 2). These strategies also showed distinct differences in the average ( $\pm$ SE) distance individuals had traveled between leaving their breeding colony and December (Table 2, Fig. 3):  $317.6 \pm 56.5$  km for birds overwintering in the Barents Sea,  $4137.7 \pm 210.6$  km for the North Atlantic birds and  $6650.5 \pm 327.8$  km for the North Pacific birds. In 6 cases, both parents from a nest were tracked (based on both individuals having been seen sitting on the same nest); one of these pairs exhibited contrasting non-breeding strategies (with one partner migrating to the Atlantic [PS21239] and the other to the Pacific Ocean [PS21231], see Fig. S1 for individual maps), while in the remaining pairs, both partners resided in the North Atlantic during the non-breeding season.

Within each oceanic region, individuals were dispersed over large areas, but individuals tracked over multiple years show a general preference for returning to the same areas each winter (Fig. 2). In the Atlantic, kittiwakes spent winters off southwestern Greenland, western Iceland, in the North Sea and in the central North Atlantic. Individuals that resided in the Barents Sea aggregated close to the ice edge near the south of Novaya Zemlya. In the Pacific region, kittiwakes spent the winter in the central and

Table 1. Overview of the number of tracks per year and in total for kittiwakes from different non-breeding locations (as of December) and the number of individuals tracked for one or more non-breeding (N-B) season. Barents Sea/North Atlantic: 1 individual was located in the Barents Sea one year and in the North Atlantic the following year

Non-breeding location in (December)	Year				No. of tracks	N-B season			No. of inds.
	2015	2016	2017	2018		1	2	3	
North Atlantic	1	14	13	3	31	3	9	3	15
Barents Sea	0	1	5	4	10	3	3	0	6
North Pacific	1	3	4	3	11	3	1	2	6
Barents Sea/North Atlantic	0	0	0	0	0	0	1	0	1
Total	2	18	22	10	52	9	14	5	28

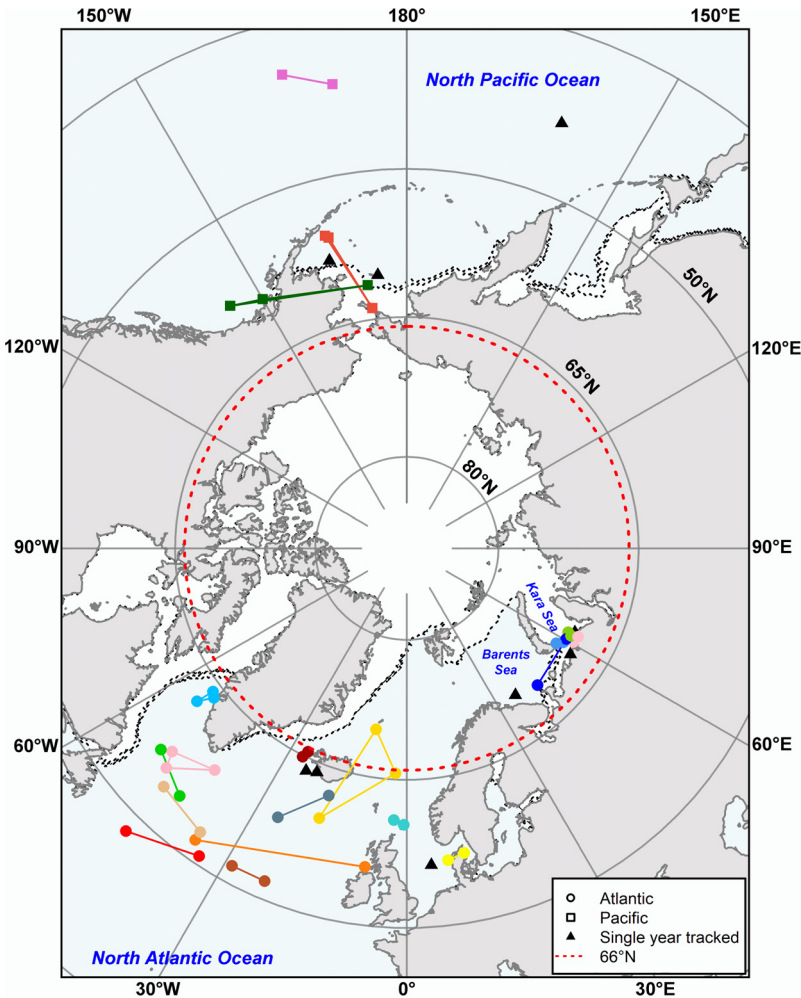


Fig. 2. Plotted median December positions. If an individual was tracked over several non-breeding seasons, median positions are uniquely colored for that individual. All individuals tracked for only 1 non-breeding season are plotted as black triangles. Lines connect positions of individuals tracked over multiple non-breeding seasons. Monthly sea ice extent (white area delineated by black dashed lines) is plotted as yearly medians (2016–2019)

western parts of the Bering Sea, in the Gulf of Alaska, as well as in offshore areas of the North Pacific, where they ranged as far south as ~30°N, but spent most of their time in latitudes close to 40°N.

3.2. Timing of migration

Kittiwakes departed from the colony in late August or early September. Their non-breeding strategy did not differ in their timing of departure, but Atlantic-wintering birds left the arctic region later than and returned to the Barents Sea earlier than Pacific-wintering birds (Table 3), staging in the Barents Sea before and after crossing 66°N. In contrast to this, North Pacific kittiwakes migrated eastwards straight away along the ice edge and spent most of September and October in the Chukchi Sea immediately north of the Bering Strait (Fig. 4).

In autumn, the North Pacific kittiwakes crossed 66°N in mid-October and spread out across the North Pacific. The majority of the Atlantic-wintering birds left the arctic region later than those migrating to the Pacific side—on average 38 d later, towards the end of November (Tables 2 & 3). Birds residing in the Barents Sea did not cross 66°N by December, but 2 individuals undertook short trips out

Table 2. Results from comparing each linear mixed model to a model without a fixed effect factor. n: number of tracks represented in each model;  $\Delta\log\text{Lik}$ ,  $\Delta\text{AIC}$ : difference in log likelihood or Akaike Information Criterion, respectively, between the null and the multilevel model

Model	Null model	n	$\Delta\log\text{Lik}$	$\Delta\text{AIC}$	$\chi^2$	df	p
Distance~N-B.Strategy + (1 Year) + (1 BirdID)	Distance~1 + (1 Year) + (1 BirdID)	51	-18.95	33.9	37.9	2	<0.001
Foraging~N-B.Strategy + (1 Year) + (1 BirdID)	Foraging~1 + (1 Year) + (1 BirdID)	52	-1	-4	0.6	2	0.748
Arrival~N-B.Strategy + (1 Year) + (1 BirdID)	Arrival~1 + (1 Year) + (1 BirdID)	50	-18.5	33	37.1	2	<0.001
Departure~N-B.Strategy + (1 Year) + (1 BirdID)	Departure~1 + (1 Year) + (1 BirdID)	52	-1.6	-0.7	3.3	2	0.194
Spring66°N~N-B.Strategy + (1 Year) + (1 BirdID)	Spring66°N~1 + (1 Year) + (1 BirdID)	41	-6.1	10.2	12.2	1	<0.001
Autumn66°N~N-B.Strategy + (1 Year) + (1 BirdID)	Autumn66°N~1 + (1 Year) + (1 BirdID)	42	-11.4	20.7	22.8	1	<0.001

of the Barents Sea, usually towards Iceland, before and after December. We did not classify this as a migration event, as they did not settle anywhere before their return.

In spring, the Pacific-wintering kittiwakes concentrated in the eastern Bering Sea in March and April and started their migration over the Arctic Ocean a few days apart in late April (Fig. 4, Table 3). Their first possible visit to the colony occurred on average 10 d later. The fastest individual made the trip in 4–5 d, covering a minimum distance of 4500 km. Two of the Pacific-wintering birds remained off the western coasts of the Barents Sea and a third moved as far south as the North Sea after first passing the colony in spring (PS21255, see Fig. S1 for individual map).

In contrast, the return of Atlantic-wintering kittiwakes in the Barents occurred over a longer time period, from January to early April. However, timing of their first possible visit to the colony in April was more concentrated and coincided with the first visits of the kittiwakes that stayed in the Barents Sea through the non-breeding season, on average 28 or 29 d earlier compared to the Pacific-wintering kittiwakes (Tables 2 & 3).

### 3.3. Quantification of foraging

We found no evidence that either of the non-breeding strategies required more time foraging per year (Table 2, Fig. 5). All tracked kittiwakes were foraging for less than 5 h per day on average ( $277 \pm 142.6$  [SD] min for the North Atlantic;  $284 \pm 147$  min for the Barents Sea;  $280 \pm 147.8$  min for the North Pacific). However, the temporal fluctuations in foraging differed throughout the year. The least time spent foraging was in July while breeding, when all groups foraged  $\sim 3.5$  h a day, followed by the most time spent foraging in September, right after the end of the breeding season, reaching a daily average maximum of  $\sim 6$  h or more. Kittiwakes residing in the North Atlantic or in the Barents Sea during the non-breeding season reached their daily average maximum of foraging time as they aggregated in the northern part of the Barents Sea (7 Sep,  $5.9 \pm 0.1$  h [SE] and 12 Sep,  $5.9 \pm 0.1$  h, respectively), while the North Pacific migrants reached the daily average maximum about 3 wk later, after their arrival to the Chukchi Sea (1 Oct,  $6.3 \pm 0.1$  h). The time spent foraging remained below the annual average through most of the non-breeding period for North Pacific and North Atlantic migrants, while it stabilized at the level of the annual average for the Barents Sea resi-

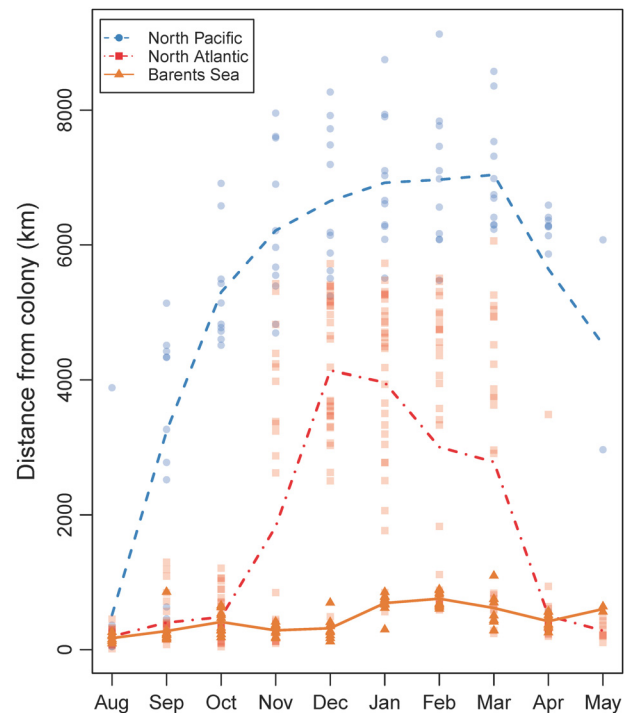


Fig. 3. Monthly median distance to the colony over sea for all birds, classified by whether individuals resided in the North Atlantic, Barents Sea or the North Pacific in December. Points: individual median distances in each month; lines: the average distance for each classification

dents. However, foraging time increased for all groups before onset of breeding, in which North Atlantic migrants show the most pronounced increase (difference from 1 Jan to date of maximum foraging time before breeding: North Atlantic = 2.6 h, max. 5.7 h on 17 May; Barents Sea = 0.7 h, max. 5.7 h on 2 May; North Pacific = 1.4 h, max. 5.5 h on 25 May).

## 4. DISCUSSION

Our data on the migration routes and wintering grounds of adult kittiwakes breeding in the southeastern Barents Sea revealed a bi-directional migration and amphiboreal wintering grounds for birds from the same colony. Almost 20% of the tracked birds breeding on the southernmost tip of Novaya Zemlya moved to the Pacific wintering grounds, where they overlapped with Pacific breeding birds and remained in the productive upwelling areas north of the North Pacific Polar Front ( $>35^\circ\text{N}$ ) (McKnight et al. 2011, Orben et al. 2015a,b). The rest of the tracked birds shared their wintering range with other Atlantic-breeding populations (Bogdanova et al. 2011, Frederiksen et al. 2012). Besides having



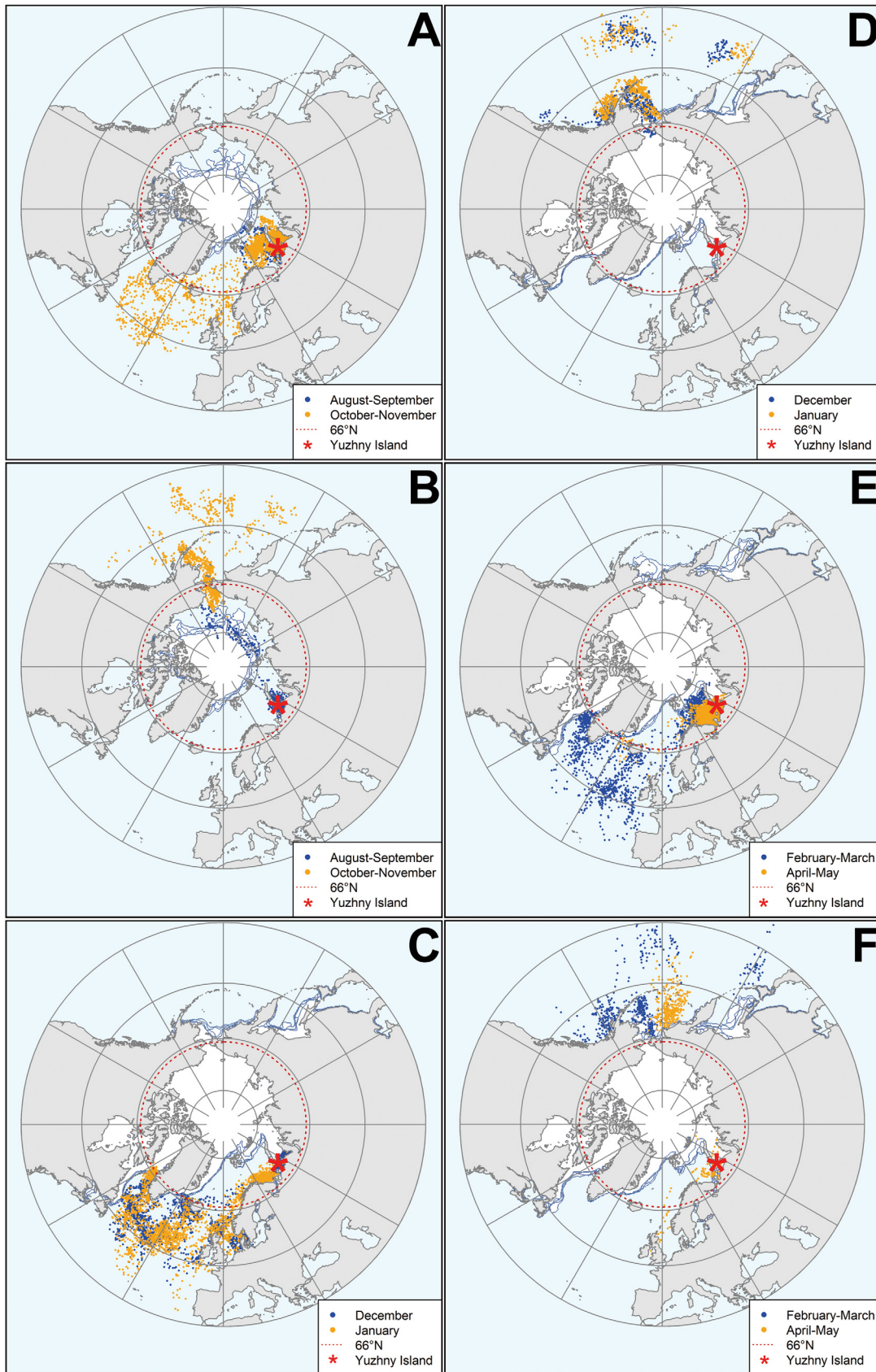


Fig. 4. Daily positions of kittiwakes plotted and colored by period of the year: (A–B) August to November, (C–D) December to January, and (E–F) February to May. The shown positions are of kittiwakes that winter in (A, C, E) the North Atlantic (B, D, F) the North Pacific. Red asterisk: colony. The sea ice extent (white area delineated by blue lines) is plotted as yearly medians of January (2016–2019), April (2016–2019) and September (2015–2018). Positions during the equinox periods are excluded from the plots



Table 3. Timing of spring migration events (crossing 66° N towards the north), first colony arrival, colony departure and autumn migration events (crossing 66° N towards the south) for kittiwakes breeding on Yuzhny Island. Data: mean dates with SD (in d) in parentheses, grouped by their non-breeding location (as of December). The timing of the spring and autumn migration for individuals staying in the Barents Sea is not defined, as they do not cross latitude 66° N, and stay in the Barents Sea region, and thus there are no criteria for definition of the exact timing of their migration

Non-breeding location (December)	Spring migration	Colony arrival	Colony departure	Autumn migration
North Atlantic	26 Feb (33.1)	7 Apr (10.8)	22 Aug (6.1)	21 Nov (13.5)
Barents Sea	–	7 Apr (14.0)	26 Aug (9.1)	–
North Pacific	23 Apr (10.2)	4 May (9.2)	24 Aug (9.2)	16 Oct (15.5)

wintering grounds spread thousands of kilometers apart, differences in timing and seasonal spatio-temporal structure along the migration routes were observed as the kittiwakes migrated in the 2 directions. Once on the wintering grounds, both wintering sub-populations demonstrated wintering site fidelity, consistent with data available for both the Pacific and Atlantic breeding kittiwakes (Orben et al. 2015a,b, Léandri-Breton et al. 2021 in this Theme Section).

To our knowledge, such eastward migration to the Pacific has never been previously recorded among the numerous tracked populations of Atlantic kittiwakes breeding in the Northeast Atlantic, including Franz-Josef Land and the Kola Peninsula in the eastern Barents Sea (Frederiksen et al. 2012, <http://seatrack.seapop.no/map/>). However, this finding confirms migration of Atlantic kittiwakes to Pacific wintering grounds, which had previously been conjectured from a single ring recovery (Dementiev 1955). All recoveries from traditionally ringed kittiwakes breeding in the Russian part of the Barents Sea (including Novaya Zemlya) have previously demonstrated that the Barents Sea breeding kittiwakes winter in the North Atlantic (Dementiev 1955, Nikolaeva et al. 1997, Krasnov & Nikolaeva 2016), with one exception. This single exception was a 2nd year kittiwake ringed as a nestling in August 1948 in Bezmyannaya Bay, western Novaya Zemlya, and recovered in June of the following year in western Kamchatka (Dementiev 1955; note that there is an error in the year of recovery in Dementiev 1951). Analyzing the other 4 recoveries of birds ringed in Bezmyannaya Bay that occurred inland but en route to the Pacific, Dementiev (1955) suggested a possible Pacific connectivity of kittiwake populations from the eastern and northeastern Barents Sea, i.e. Novaya Zemlya and Franz-Josef Land, with eastern wintering grounds in the Bering Sea. Our data corroborate this assumption for the South Novaya Zemlya local population, while kittiwakes from Franz-Josef Land have so far only been recorded in the North Atlantic (<http://seatrack.seapop.no/map/>).

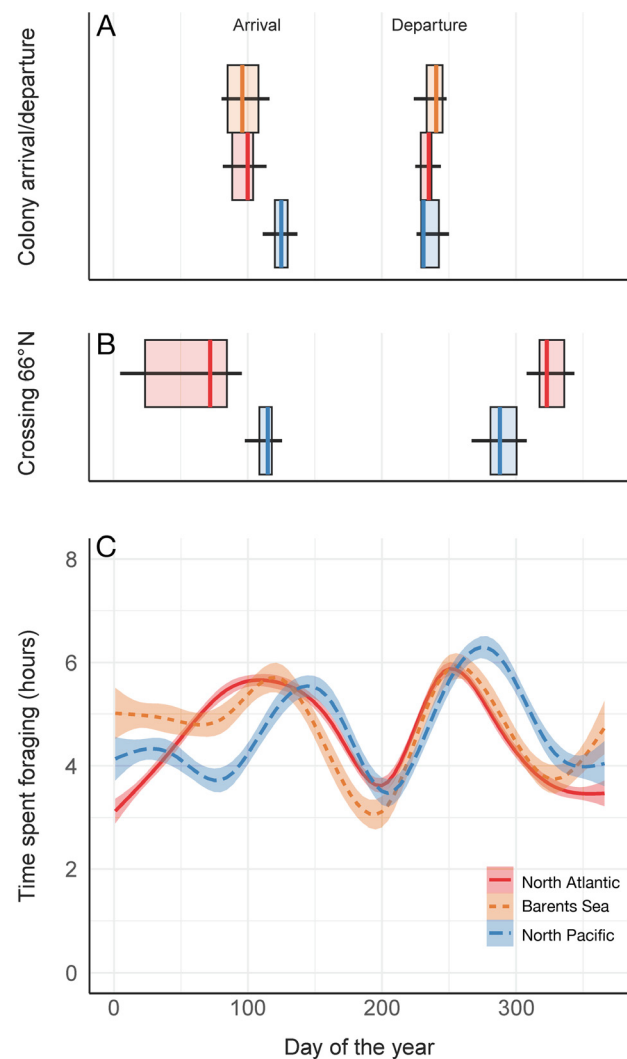


Fig. 5. (A) Median timing of arrival and departure from the breeding colony and (B) timing of migration events in spring and autumn (crossing 66° N either southwards or northwards, respectively) plotted with a box representing the 50% CI, whiskers show the 90% CI. (C) Time spent foraging each day of the year, averaged for birds with different wintering locations (North Atlantic = red, Barents Sea = orange, North Pacific = blue) plotted with color shaded areas representing 95% CI

#### 4.1. The influence of current environmental conditions on foraging and migration

An avian migration system is a comprehensive phenomenon demonstrating both stable patterns persisting throughout millennia and flexible strategies that adapt to changing environments in the course of several generations (Newton 2007, Pulido 2007). The key factors determining kittiwake winter distribution are food availability, thermoregulatory costs and possibly day length (Fort et al. 2009). Both of the wintering areas in the Atlantic and Pacific provide trophic conditions that are favourable for kittiwakes, and our findings show that birds with both of these wintering strategies spend equal average time foraging per day. However, all wintering strategies differed in their temporal foraging effort (Fig. 5).

The time spent foraging in autumn can be explained by the difference in the timing of the birds' arrival to the wintering sites. The kittiwakes wintering in the North Atlantic and in the Barents Sea fed extensively in the northern Barents Sea area immediately after breeding (Fig. 5). However, the Pacific-wintering kittiwakes refrained from staying in the Barents Sea through their autumn moult, despite particularly rich food abundance at this time, as their foraging effort peaked almost 3 weeks later compared to the other 2 populations. Instead, they migrated east in early autumn towards Pacific staging areas that are similarly productive (Zheng et al. 2020).

For kittiwakes that spent the winters in the Barents Sea, their wintering area coincided with areas of the highest concentrations of capelin in winter (Krasnov & Ezhov 2020). We suppose these kittiwakes target capelin or other high energy food during winter, rather than migrating southwards to areas with more daylight, which most kittiwakes seem to prefer (Frederiksen et al. 2012). They do, however, spend more time foraging from late December to mid-February compared to the Pacific and North Atlantic migrants (Fig. 5), which can be interpreted as a need to increase foraging effort during the polar night to compensate for poor light conditions or low temperatures.

While birds wintering in the Barents Sea maintained a relatively stable feeding schedule through winter and spring, birds returning from the wintering areas in the North Atlantic or the North Pacific increased their foraging intensity significantly in spring, most likely to accumulate resources necessary to start breeding. The North Atlantic wintering kittiwakes spent less time feeding through December and January than birds using either of the other 2 wintering strategies but increased their effort greatly in Febru-

ary and March (about the time when they arrive in the Barents Sea again) and reached a similar level of foraging effort in April–July (while breeding) as kittiwakes wintering in the North Pacific or Barents Sea. Whereas the North Atlantic birds mainly relied on the nutrient rich waters in the Barents Sea in spring, the North Pacific group already increased their feeding intensity when they aggregated in the Bering Sea in the weeks before they crossed the Arctic Basin (Fig. 4E,F) and maintained a high feeding intensity until right after arrival to their breeding grounds.

To cross the Arctic Basin, the North Pacific wintering kittiwakes passed the Siberian Shelf seas which are covered with pack ice most of the year (Frolov et al. 2009), except for the polynyas in the Laptev and East Siberian Seas (Fig. 1). While kittiwakes are not an ice-dependent species, they are capable of foraging in relatively dense ice (Mehlum 1989) and are regularly observed as far north as the North Pole (Rutilevskiy & Uspenskiy 1957, Vuilleumier 1996). Our results show that the Pacific-wintering kittiwakes spent considerable time in the Siberian Shelf seas, between departure from the colony and the Kara Sea and crossing the Bering Strait in autumn (over 50 d later on average, Table 3). During that time, they probably foraged in both open pelagic waters and along the ice edge, as the extent of the sea ice is close to its annual minimum — conditions in which they find productive foraging areas (Hatch et al. 2020 and references therein). In April, the kittiwakes face much more extensive and dense sea ice with poor foraging conditions along the Siberian shelf and cross the Arctic Basin in a much shorter time, spending on average only 10 d between passing northwards through the Bering Strait and their first potential visit to their colony (Table 3). The differences between the Atlantic- and Pacific-wintering kittiwakes in terms of migration phenology and connectivity between staging and wintering areas could be interpreted as the influence of ancestral migration routes on the movement strategies of birds using the different wintering grounds (see van Bemmelen et al. 2019).

#### 4.2. Bilateral migrations of seabirds in the Northern Hemisphere

Partial migration of northeastern Atlantic populations to the Pacific wintering grounds is not unique for kittiwakes. Bi-directional migration routes to disparate Atlantic and Pacific wintering grounds have been recently described for other arctic seabirds, i.e. the ivory gull *Pagophila eburnea* and Sabine's gull

*Xema sabini*, after the introduction or discovery of telemetry and intrinsic markers (Gilg et al. 2010, Davis et al. 2016). The majority of the populations that breed in the High Arctic in northeastern Greenland, Svalbard and Franz-Josef Land winter in the Labrador Sea and Davis Strait, while some birds migrate eastwards to the North Pacific (Gilg et al. 2010). Despite the bi-directional migration connectivity, ivory gulls and kittiwakes have different population structures and differing migration strategies. The ivory gull is a High Arctic species with an Atlantic breeding range (Mallory et al. 2020) and a panmictic global population (Yannic et al. 2016). In autumn it generally follows the marginal ice zone (Gilg et al. 2016b) either westwards or eastwards (Gilg et al. 2010). In contrast, the Holarctic population of kittiwakes is split into 2 distinct subspecies, *Rissa tridactyla tridactyla* and *R. tridactyla pollicaris*, with separate wintering grounds in the Atlantic and Pacific, respectively. Based on our findings, individual Atlantic-breeding kittiwakes demonstrated disparate primary winter destinations; however, all birds showed consistent migration connectivity with either the Atlantic or Pacific wintering grounds.

#### 4.3. History and origin of bi-directional migrations of the Novaya Zemlya kittiwakes

The 2 currently recognized subspecies of kittiwakes were initially described based on their morphometry and appearance (Bent 1921, Dementiev 1951, Yudin & Firsova 1988, Chardine 2002), and their differentiation has subsequently been confirmed genetically (Sauve et al. 2019). Extensive studies of both subspecies have revealed striking differences in their life histories, prompting some researchers to consider them as 2 species (Hatch et al. 2020 and references therein). The divide between the 2 subspecies in the Nearctic is well established due to a considerable geographical gap between populations in the High Arctic areas of North America (Hatch et al. 2020). In the Palearctic, however, kittiwakes have a continuous breeding distribution across arctic Eurasia. The morphology, movements and genetics of kittiwakes of the Asian populations remain largely unknown (Yudin & Firsova 1988, 2002).

Genetic studies suggest that the Atlantic and Pacific kittiwakes diverged 640 000 to 280 000 yr ago, coinciding with the Middle Pleistocene, when the Atlantic and Pacific Oceans must have been isolated by the Bering Land Bridge and large ice sheets during the cold periods (Sauve et al. 2019). During

the last cold epoch, the Last Glaciation Maximum (LGM), much of the current eastern Atlantic breeding range of the kittiwakes was covered by glaciers or sea ice until ~10 000 yr BP (e.g. Hughes et al. 2016, Patton et al. 2017). Analysis of genetic markers suggests recolonization of the northeastern Atlantic from 2 different Atlantic refugia (Sauve et al. 2019). However, the same study also found a common Pacific haplotype in a single kittiwake from a Greenland breeding colony, which suggests that Pacific birds were capable of migrating to the Atlantic in the past.

Based on past ring recoveries from Atlantic birds far east of Novaya Zemlya, findings of common Pacific haplotypes in an Atlantic kittiwake, and the distinct differences in migratory phenology between Pacific- and Atlantic-wintering kittiwakes, we hypothesize that kittiwakes could have colonized the Eurasian arctic as far as Novaya Zemlya also from the Pacific refugium after the LGM. A study of genetic structures in populations of thick-billed murre *Uria lomvia* shows that the Chukchi Sea could represent a place for a second contact (after the LGM) in this marine species and thus provide the opportunity for gene exchange between the Pacific and Atlantic populations (Tigano et al. 2015). Likewise, breeding areas from the Chukchi Sea and across the Eurasian arctic could potentially provide a second contact between the Pacific *R. t. pollicaris* and the Atlantic *R. t. tridactyla*, which started to explore new available pelagic areas beyond the Bering Strait following sea ice retreat and formation of productive waters on the East Siberian shelf, recolonizing coasts of the eastern Palearctic. Kittiwakes could have settled in the Laptev Sea in the early to mid-Holocene (8000–11 000 yr BP), when the climate was warmer than today (Bauch et al. 2001), and the oceanographic conditions were less favourable for sea ice formation (Thibodeau et al. 2018), or later, around 7000 yr BP, when conditions similar to those of today were established along the migration route of kittiwakes in the western Laptev Sea (Klyuvitkina & Polyakova 2019). In the eastern Laptev Sea, environmental conditions similar to today were established by 3800 yr BP only (Mueller-Lupp et al. 2004), which could be the latest possible time that kittiwakes from the Pacific expanded their range to the Barents Sea. An indirect proof of our hypothesis of recolonization of the Arctic from the Pacific is the finding of a common Pacific haplotype in a single kittiwake from a Greenland breeding colony (Sauve et al. 2019).

At the same time, kittiwakes from the Atlantic refugia could have dispersed eastwards beyond the Barents Sea, following the Atlantic waters that penetrated into the Arctic Ocean along the continental shelf

break and entered the Laptev Sea from the north. Similar dispersal of the thick-billed murres *Uria lomvia* resulted in colonization of the New Siberian Islands from an Atlantic refugium and further admixture of Atlantic and Pacific murres in the Chukchi Sea, as indicated by the genetic structure of the populations (Tigano et al. 2015). Counter-dispersal of the kittiwakes in the Arctic Ocean could have resulted in admixture of Atlantic and Pacific kittiwakes and formation of a transitional breeding zone as suggested by Yudin & Firsova (1988), with kittiwakes migrating into the Siberian Arctic either from the west or from the east and maintaining their traditional wintering areas in the Atlantic and Pacific oceans, respectively.

For most Palearctic migratory birds, there is a distinct migratory divide at 100°E along the Taymyr Peninsula in Russia, which forms the most northerly continental barrier to east-west migration (Rogacheva 1987, Irwin & Irwin 2005) and lies roughly halfway between suitable wintering marine habitats in the Atlantic and Pacific regions (Davis et al. 2016). Our findings shift the westernmost boundary of the kittiwake migration divide westwards to southern Novaya Zemlya, extending the zone of a second contact between the Atlantic and the Pacific kittiwakes proposed by Yudin & Firsova (1988).

Alternatively or complementary to our hypothesis, kittiwakes from the southern Novaya Zemlya colonies may also have started to explore eastwards migration routes in response to the reduced ice barrier in the Central Arctic, or will do so in the near future as the barrier will continue to melt in the next decades (IPCC 2014). The reduced ice barrier has already been related to an intensified faunal exchange across ocean basins in the last decades (McKeon et al. 2016), and a recent study on the migration ecology and energetic costs of Arctic-breeding seabird species revealed that several Arctic-breeding species, including kittiwakes, could benefit from starting to migrate to the North Pacific as the sea ice decreases in the Arctic Ocean (Clairbaux et al. 2019).

While a melting ice barrier will make conditions more suitable for crossing the Arctic Basin from both the Pacific and the Atlantic regions, favorable conditions to migrate to and from the Pacific possibly also existed before the current ice melt. The fact that kittiwakes already have a continuous breeding range across the Siberian seas, along with having access to systems of recurring flaw polynyas across the Siberian Arctic even under severe ice conditions (Kupetsky 1958, 1961, Spiridonov et al. 2011, our Fig. 1), supports the hypothesis that a second contact could have established well before the current sea ice melt.

#### 4.4. Implications and future studies

To test our hypothesis, tracking studies in the Arctic from the eastern Barents Sea (Novaya Zemlya) towards the Chukchi Sea are required, along with genetic screening of the kittiwake populations. The heterogeneity in their movements that we discovered has numerous implications for the interpretation of the evolutionary history and life history traits of this abundant but threatened seabird species, as well as for its conservation and management (Webster & Marra 2005, Faaborg et al. 2010). The striking differences in the life history traits between the Atlantic and Pacific kittiwakes (Hatch et al. 2020 and references therein) also create a necessity to conduct further tracking studies of kittiwakes in the Barents Sea and eastwards. Such studies can potentially lead to better understanding of the global processes in the changing Arctic, such as the influence of sea ice extent in the Arctic Ocean on the living organisms there. In particular, transpolar migration may be a response to the ongoing climatic changes and a continued reduction in sea ice extent (Clairbaux et al. 2019).

This is the first time kittiwakes have been tracked from Novaya Zemlya. We argue that the observed migratory divide and the trans-polar migration may be rooted in the history of the kittiwakes' colonization of the Arctic. As such, our tracking study will serve as baseline for future research assessing potential changes in migration strategies due to global climate change.

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