Articles

Post-breeding movements of northeast Atlantic ivory gull *Pagophila eburnea* populations

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The post-breeding movements of three northeast Atlantic populations (north Greenland, Svalbard and Franz Josef Land) of the ivory gull *Pagophila eburnea*, a threatened high-Arctic sea-ice specialist, were studied between July and December 2007 using 31 satellite transmitters. After leaving their breeding grounds, all birds first dispersed eastward in August–September, to an area extending from the Fram Strait to the northwestern Laptev Sea (off Severnaya Zemlya). Most returned along the same flyway in October–November, hence describing a loop migration before moving south, off east Greenland. Wintering grounds were reached in December, in southeast Greenland and along the Labrador Sea ice-edge, where Canadian birds also overwinter. One to two birds from each population however continued eastwards towards a third wintering area in the Bering Strait region, hence demonstrating a bi-directional migration pattern for the populations and elucidating the origin of the birds found in the north Pacific during winter time. Overall, all birds breeding in the northeast Atlantic region used the same flyways, had similar rates of travel, and showed a peak in migratory activity in November. Though the total length of the main flyway, to the Labrador Sea, is only and at most 7500 km on a straight line, the mean total distance travelled by Greenland birds between July and December was 50 000 km when estimated from hourly rates of travel. Our study presents the first comprehensive and complete picture for the post-breeding movements of the different ivory gull populations breeding in the northeast Atlantic.

Although usually difficult to obtain, information on post-breeding movements is particularly helpful to understand some of the many facets of the biology of migratory birds. For example, post-breeding movements must allow the individuals to reach the most cost-effective feeding areas to recover from the physiologically demanding breeding cycle. Also, for conservation issues, the spatial and temporal monitoring of post-breeding movements may reveal key areas used by the species or, in the long-term, how a species will adapt to changes in its habitat.

The ivory gull *Pagophila eburnea* is one of the most poorly known seabird species in the world (Mallory et al. 2008). However, it is also currently one of the most threatened, with biomagnification of contaminants (Braune et al. 2007, Miljeteig et al. 2009) and the ongoing and forecasted further reduction of its main habitat, the sea-ice (Holland et al. 2006, Gascard 2008, Kerr 2009, Perovich and Richter-Menge 2009), as the major identified threats. In Canada for example, the ivory gull population has already declined dramatically by 80–85% during the last 20 years (Krajick 2003, Gilchrist and Mallory 2005, Robertson et al. 2007). Although the status of the species on its other breeding grounds (Greenland, Svalbard/Norway and Russia) is still unsatisfactorily assessed, it is likely that at least some of the other populations are also declining (Gilchrist et al. 2008, Gilg et al. 2009).

However, before being able to implement a circumpolar conservation strategy (Gilchrist et al. 2008), several unknown aspects of the species' life history have to be unravelled. For example, our knowledge of their feeding grounds, migratory flyways and wintering grounds is fragmentary, being mainly based on incidental observations, in only parts of their distribution range and in limited periods of their annual cycle. An accurate and unbiased assessment of the year-round distribution and movements of the ivory gull is critically needed before starting to discuss the reasons of past changes, and to predict the future fate of the species. This was the main aim of our circumpolar satellite tracking initiative, from which the results are presented in this paper for the post-breeding period.

Material and methods

The ivory gull, the only species of the genus *Pagophila* (literally 'the one who likes the ice'), breeds in the Canadian Arctic Archipelago, in Greenland, in Svalbard and in the western Russian Arctic Islands (Mallory et al. 2008). It is one of few sympagic (ice-associated) bird species found in the northern hemisphere, feeding mostly by hovering and contact dipping in open leads in ice-filled waters (Divoky 1976), or scavenging on marine mammal remains (Mallory et al. 2008). The birds monitored in this study were from populations breeding in the northeast Atlantic region, i.e. north Greenland, Svalbard and Franz Josef Land (northwestern Russian Arctic).

A total of 31 birds were fitted with satellite transmitters on four sites (Table 1). All birds were adults with developed brood patches. Most were trapped on their nest sites, except for one bird from Hayes Island (Russia), trapped near the Krenkel polar station, and for the seven birds trapped at Station Nord (Greenland; captured near the kitchen and the doghouses, two km from the breeding colony that was still covered by snow at the beginning of July 2007). Birds were trapped using a noose on a pole (Svalbard), a noose on a cord (Russia), or with flap nets (Greenland and one bird from Russia).

Satellite tracking

We used three different types of Argos-compatible bird tracking PTTs (Platform terminal transmitters) designed and commercialized by North Star Science and Technology LLC and Microwave Telemetry Inc. Twenty gram battery-powered PTTs were used in all study sites and 12 g solar-powered PTTs were also used in Greenland (Table 1). All transmitters were attached on the birds as a backpack using ca 55 cm of Teflon ribbon and silver rings to build the harness. The harness mass was 3 g for the Greenland birds (4 silver rings) and 3.2 g for the others (3 silver rings and one Y-shaped silver cross). On average, the PTT and harness masses represented 3.0% ($\pm$0.2 SD) and 3.9% ($\pm$0.3 SD) of bird body mass for solar-powered and battery-powered PTTs, respectively.

The eight solar-powered PTTs used on Greenland birds only worked in daylight. However, because they had no duty cycle program, i.e. pre-defined transmitting periods, they were continuously transmitting when the solar radiation was sufficient. A solar PTT tested during the winter 2006–2007 near the geographic North Pole (onboard the polar schooner 'Tara') proved to work reliably even at very low temperatures, provided that the solar angle was positive. All battery-powered PTTs had duty cycles, sending signals every second day during the assumed breeding period (i.e. for 60 days after activation for the Svalbard and Russian birds, and for 95 to 113 days for the Greenland birds), and every 7.7 (Greenland) or 9 days (Svalbard and Russia) afterwards. The battery life expectancy of these PTTs being 400–500 h, our duty cycles were estimated to provide bird locations for 14–16 months but given the harsh conditions prevailing in the high Arctic, this was only a theoretical maximum. During the study period from 3 July to 31 December (i.e. 180 days), the 31 transmitters provided data for an average of 139 days (minimum: 17 days, maximum 180 days, Table 1).

PTTs were located using the Argos positioning system (CLS 2008) that provided positions in seven precision classes. The location errors of the classes called LC3, LC2, LC1 and LC0 follow a normal distribution with a standard deviation of <150, <300, <1000 and >1000 m respectively. There is no accuracy estimate associated with the remaining classes (i.e. LCA, LCB and LCZ) but Hays et al. (2001) and Vincent et al. (2002) reported that LCA locations have an accuracy similar to that of LC1 locations. In contrast, LC0, LCB and LCZ are less accurate, the latter often being totally unreliable (never used in this study). In the results presented below, we only used LC1, LC2 and LC3, except to select the 'best daily locations' and the 'best weekly positions' for which we also included a limited number of LCA, LCB and LC0 locations (here, 'best' means the most accurate available position for the given time period). To determine the 'best daily' and the 'best weekly positions', we selected successive locations of 0.5–2.5 and 5–9 days apart, respectively. By doing so, we avoided artefacts that can arise by comparing locations collected over short periods, even with high accuracy LC (Hays et al. 2001). We used the online 'Satellite Tracking and Analysis Tool' to store and manage Greenland data

Table 1. Study sites and satellite tracking metadata.

Study sites	Location	No. of birds tagged	Tagging period	PTT used	Mean body mass in g (SD)	Mean duration of monitoring in days (SD)
North Greenland						
Station Nord	81°37.5′N/16°40.5′W	4	July 4–5	12g solar[1]	529 (17)	154 (41)
		3	July 3–5	20g battery[1]	605 (22)	176 (7)
Henrik Krøyer Holme	81°38.6′N/13°45′W	4	July 12–14	12g solar[1]	485 (33)	165 (14)
		2	July 13	20g battery[1]	554 (26)	164 (10)
Svalbard						
Svenskøya	78°34′N/57°35′E	10	July 6–11	20g battery[2]	594 (39)	110 (54)
Russia – Franz Josef Land						
Hayes Island	81°34′N/57°35′E	8	July 31–Aug 4	20g battery[2]	623 (58)	133 (20)
TOTAL/MEANS		31			577 (60)	139 (42)

[1]North Star Science and Technology LLC.
[2]Microwave Telemetry Inc.

(Coyne and Godley 2005). Norwegian and Russian data are stored in the Norwegian Polar Institute database in Tromsø.

Data analysis

We used orthodromic distances (i.e. the shortest way between two points on the globe's surface) to calculate distances moved by the birds and related rates of travel, but loxodromic angles to calculate dispersal vectors, as advised by European ringing centres (Gudmundsson and Alerstam 1998, Speek et al. 2008). Indeed, orthodromic angles can be very misleading at high latitudes to present the flyways used by birds moving long distances along the same latitudes, as in the present study (formulas in Imboden and Imboden 1972).

Weekly dispersal vectors were calculated for each population and for every month using all available pairs of successive 'best weekly positions'. Each vector presents the mean dispersal speed and direction of a given population and for a given month, based on weekly measurements from different individuals. Contrary to the 'rate of travel' (below), the 'dispersal vector' (i.e. the length of the vector) is a weekly mean for all individuals of a given population and will hence remain small, regardless of the birds' rates of travel, if the birds move randomly in all possible directions. We used circular statistics (Zar 1999) to investigate these dispersal vectors.

The distance travelled and time elapsed between two successive Argos location was used to calculate what we refer as the 'rate of travel' (sensu James et al. 2005). This is very different from the 'flight speed' because within the time period used in the calculation, the bird can either fly, walk, feed, rest, or alternate between moving and non-moving activity phases. Estimating rates of travel from Argos positions remains challenging because, by assuming a linear displacement between two successive locations (which is rarely true, except for very small time periods, Desholm 2003), calculations of rates of travel are subject to large variation depending upon the time scale used. On the other hand, using too small time scales (e.g. typically less than 10 min) introduces another bias because each Argos position is calculated using several signals (the 'Doppler effect') over a time period of ca 5–15 min (CLS 2008). To overcome the latter difficulty, we removed all 'rates of travel' estimated for time periods shorter than 0.1 h.

Seasonal changes in movement patterns were investigated using rates of travel calculated on hourly (0.5–3.0 h), daily (0.5–2.5 days) and weekly (5–9 days) time scales (only the weekly time scale was investigated for Norwegian and Russian birds due to small sample sizes).

Finally, we used LC1, LC2 and LC3 Argos locations to estimate the total distance travelled by the Greenland birds over the 6 month period. The bias arising from closely spaced successive primary locations, within the error limits of the Argos locations, potentially produces false movements and was reduced by filtering primary distances less than 2 km. Two alternate calculations were also performed. The first was a simple assessment of the orthodromic distance according to the main flyway used by the birds during the six month study. The second used the rates of travel calculated for every month (above) to assess the total distance travelled according to three different time scales: hourly, daily or weekly estimates.

Daily sea-ice maps used in some figures and discussion of results were provided by Dr Georg Heygster and Heidrun Wiebe, Univ. of Bremen (archives available at <www.seaice.de>).

Results

Altogether, the 31 birds produced 25 314 locations between 4 July and 31 December 2007: 16 424 from Greenland birds, 4237 from Norwegian birds and 4653 from Russian birds. Forty percent of these locations had high accuracy (5% LC3, 11% LC2 and 24% LC1), six percent were LCA locations, and the remaining 54% were LCB, LC0 and LCZ.

Monthly distributions

We used the 'best daily locations' collected for each bird to determine the geographical range used by the three populations for each month (Fig. 1). This included 1453 locations (864 for Greenland, 288 for Norway, 301 for Russia), 91.4% being LC1, LC2 or LC3, 4.1% LCA, and 4.5% LC0 or LCB.

In July, Greenland and Svalbard birds remained within 600 and 400 km of their colonies, respectively (only one location of a Russian bird in July). With the exception of one non-breeding Greenland bird that went to the north of Svalbard immediately after its release, birds from the Greenland and Svalbard populations did not mix in July. All birds remained between ca 76°N and 82°N during this period. Greenland birds mainly moved to the northeast of Station Nord (where there was dense sea-ice) or to the east of Henrik Krøyer Holme (scattered sea-ice in the 'north east water' polynya). Svalbard birds remained in the eastern and northeastern part of the archipelago, i.e. where the nearest sea-ice could be found, with the exception of one bird that moved to the south into a region of open water, where it apparently fed along glacier fronts.

In August, Svalbard birds used a similar area as in July, just extending it slightly to the northeast as the ice-edge retreated to the north. The fact that several birds remained along the coast (including on glacier fronts) instead of using their typical sea-ice habitat is probably best explained by the fact that the nearest ice-edge was ca 250 km from their breeding sites in mid August. The two outliers to the south, over open water (Fig. 1), are the same Svalbard individual as in July. Russian birds remained within 400 km of their colony in August, mainly to the northeast in relatively dense ice (up to 84.16°N), or within shorter distances of the colony within the Franz Josef Land archipelago. Again, Greenland birds used the largest area during this month, overlapping both with Svalbard and Russian birds. This is explained by the fact that the birds that were marked on Henrik Krøyer Holme (Greenland) had their nest predated on by polar bears on 10–15 July and left the colony a few days later. Hence, at the end of August, some of these birds were already more than 1100 km from their colony.
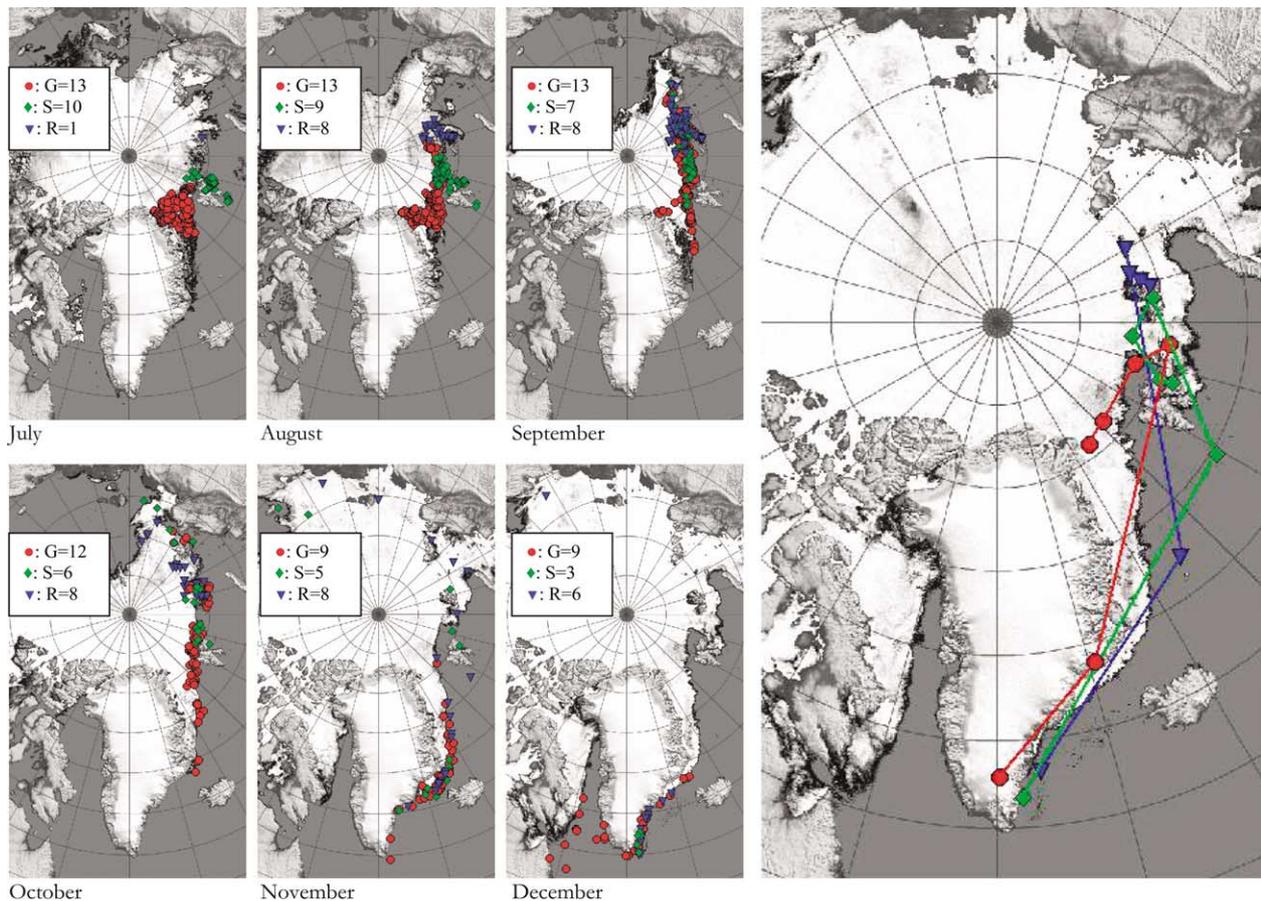
Figure 1. Monthly distribution of 31 ivory gulls monitored in July–December 2007. Only the 'best daily positions' are given (i.e. at most, one location per bird and per day). The origin and numbers of monitored birds are given in the legend boxes (G for Greenland, S for Svalbard and R for Russia/Franz Josef Land). The median extent of sea-ice is also presented in each panel (limits for the 15th day of each month). Note that the few data points found in the southern Labrador Sea in December for Greenland birds are from the end of the month, i.e. when sea-ice extended further south than seen on the map. In the large panel on the right, we plotted the six monthly barycentre positions (linked in chronological order; starting with the July dots near the breeding sites) calculated for each population (same symbols as in small panels) by averaging all daily positions presented in the other panels (each bird is given the same weight in this calculation, regardless of the number of 'best daily positions' available; the four birds that migrated to the Pacific Ocean were removed from the calculations). The bimodal distribution of data points for Svalbard and Russian birds explains the outlying position of their barycentre in November.

With the exception of two birds that remained in Greenland until 2 September, all birds had left their breeding grounds in Greenland and Svalbard by September. In Russia, however, several birds remained near the colony until the end of the month (below). By the end of September, birds from the three populations had mixed and used the same areas. Most of the ivory gulls had moved eastwards, with some Greenland birds reaching Severnaya Zemlya at 105°E, i.e. 2000 km from their breeding grounds. Concurrently, some of the Greenland birds already started to move south along the coast of east Greenland (southernmost location in September: 75.3°N).

This bi-directional pattern was maintained in October when some birds continued to move eastwards until they were stopped by the easternmost extent of sea-ice (at about 128°E), while others (three Greenland birds) continued to move south, one reaching 68.5°N by the end of the month. The fact that birds from all three populations were present in the Franz Josef Land archipelago in October is also worth mentioning. Some of the Russian birds that stayed there in

September were late breeders (Strøm et al. in press) but their presence in October is probably due to favourable feeding conditions rather than because of the proximity of their breeding grounds (Discussion).

November was a very active month for the gulls, having to cope with a rapid rebuild of the sea-ice and a total disappearance of the sun, especially in Russian waters (i.e. in the northeastern part of their range). Most of the birds returned westward along the same ice edge they had followed after leaving their colonies, and then moved southward along the east Greenland ice edge. The first birds to reach the southeastern-most tip of Greenland (60–62°N) on 30 November were two individuals from Greenland. Several birds travelled more than 1000 km along this flyway within 7–9 days (below). However, four out of the 22 birds that were monitored in November continued to move eastwards towards the northern Pacific (not all locations included within the area displayed on Fig. 1). One Svalbard bird passed Wrangel Island (71°30′N/179°30′E) on 12 November and arrived in

the Bering Strait on 22 November. Two Russian birds were located along the Siberian coast at 158°E and 169°E on 25 November and 3 December, respectively. One Greenland bird (solar-powered transmitter) was also located south of St Lawrence Island at 173°W/62°N at the very end of the year and in early 2008.

In December, with the exception of four birds that had moved to the Pacific, all birds continued to move southward along the east coast of Greenland and were found south of ca 68°N. But while the first Svalbard and Russian birds had only reached the southernmost tip of Greenland by the end of this month, three of the Greenland birds crossed the Labrador Sea on 1, 4 and 12 December and reached their main supposed wintering grounds along the Labrador Sea and Davis Strait ice-edges. To reach this area, some crossed offshore directly from Cape Farewell (the southernmost tip of Greenland) while others first moved northwards along the west coast of Greenland before turning west, hence the latter birds had a shorter distance to fly over offshore open waters. In both cases, it was the first time since we started the satellite tracking (ca 5 months earlier) that these birds left their typical sea-ice habitat to fly over long stretches of open water.

Overall, most birds displayed similar post-breeding movements, but Greenland birds had the longest distances to travel in order to reach Russian waters. They also seemed to be slightly ahead of the two other populations, being the first to really move south and leave Russian waters in October, the first to reach south Greenland in November, and the first to cross the northern Labrador Sea towards its ice-edge off the Canadian coast in December.

Dispersal vectors

Distribution maps presented in Fig. 1 depict the overall post-breeding migration route, but do not provide detailed information on the monthly changes in migration speed and direction. Dispersal vectors were hence calculated (Fig. 2) to fill this gap. The results can be summarized in five major patterns. First, all populations showed limited (≤ 15 km day^{-1}) dispersal in July–September. Second, the direction of this dispersal was only significantly ($p < 0.05$) directed to the east in September for the Greenland and the Svalbard populations, the Russian birds being more sedentary. Third, all populations significantly ($p < 0.05$) moved towards the southwest in October–November, but movements were still limited in October (ca 10–30 km day^{-1}) compared to the highest values recorded in November (ca 40–55 km day^{-1}). Fourth, the Russian population had hardly begun to disperse southwestward in October compared to the two others (i.e. ≈ 10 vs 20–30 km day^{-1}), but took in this delay in November when it outscored the others with a record value of ca 55 km day^{-1}. Fifth, the Greenland population was moving more actively in December than the two other populations, and in a more westerly direction. This is best explained by the fact that only Greenland birds started to cross the northern Labrador Sea towards the Canadian ice-edge during this month (Fig. 1).

Seasonal changes in movement patterns

Seasonal changes in rates of travel were further investigated at three different time scales (i.e. hourly, daily and weekly, Fig. 3a). Results revealed four spatial use patterns during the six month period. In summer, movements showed a relatively chaotic organisation. Rates of travel were similar in September and October, but the difference between daily and weekly rates was limited, suggesting that daily and weekly movements were more unidirectional in early autumn than in summer. This latter pattern was also found in November, except for the hourly rate of travel, which was by far higher during this month. In December, the pattern was nearly opposite, with hourly and daily movements more or less unidirectional compared to weekly movements.

To better illustrate these different patterns in special use, we schematically produced four theoretical bird movements (Fig. 3b) using the values presented above. December presents the most incongruous pattern, with daily travel legs strikingly different from the overall weekly movements; both in speed and direction (Discussion).

Overall, the weekly rates of travel were similar between populations (Fig. 3c), with only minor differences best explained by the geographic origin and dispersal phenology (Fig. 1, 2).

Total distance travelled

Summing up all distances between successive Argos data, the estimated distance travelled by Greenlandic ivory gulls in July–December 2007 ranged from 5000 to 12 000 km for all but the bird which wintered in the northern Pacific region (> 17500 km).

On a straight line, the 'Atlantic' flyway is at least 4000 km if the birds do not move beyond Svalbard (to the east) and south Greenland (to the west). Moving further east in autumn adds an extra 1500 (return trip to Franz Josef Land) to 2500 km (to Severnaya Zemlya), moving further west in winter to the Labrador Sea an additional 1000 km. The entire route is about 600 km shorter for Svalbard birds and 1300 km shorter for Russian birds.

The rates of travel presented in Fig. 3a can also be used to assess the total distance travelled by ivory gulls during this period. Estimates are > 50000 km on average for Greenland birds if we consider all small scale (hourly) movements and 15 000 km if we consider daily rates of travel. Considering weekly rates of travel, distances are ca 7000 km for Greenland birds and 5500 km for Svalbard and Russian birds. Though these figures are much higher than that assessed with the two previous methods, they present a more comprehensive figure of the true distances (mean for the population) travelled by ivory gulls during the six months of this study.

Discussion

This paper presents the first comprehensive study of ivory gull movements and the first satellite tracking program launched for birds at such northern latitudes. It is also one
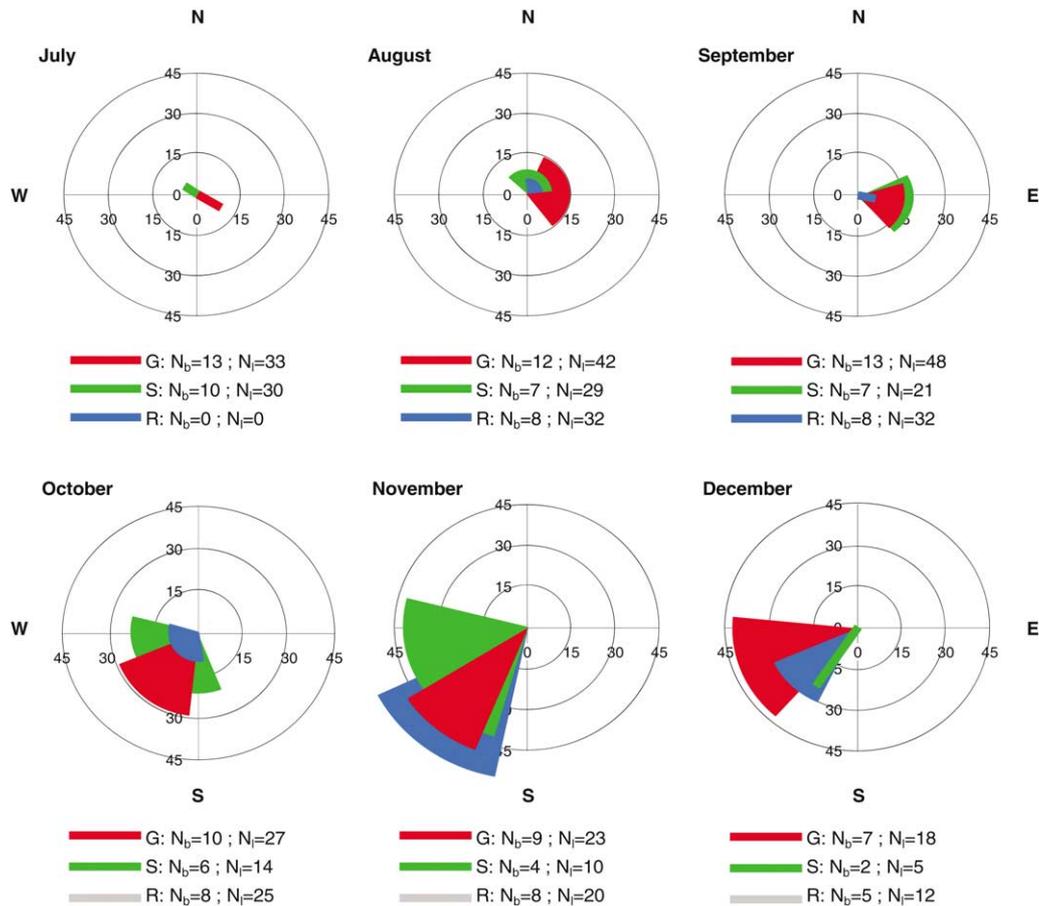
Figure 2. Mean weekly dispersal vectors (in km day^{-1}) and directions (loxodromic angles; Material and methods) for three populations of ivory gulls based on 31 birds monitored in July–December 2007. The number of monitored birds (N_b) and the number of useful data pairs (N_l) are given for each population: G for Greenland, S for Svalbard and R for Russia/Franz Josef Land. The 95% confidence interval of the vectors' angles are given graphically when significant and unless the primary data (vectors between two successive 'best weekly position') had a bimodal circular distribution (Zar 1999).

of the few studies that has monitored more than 30 birds of the same species in a single year, hence producing enough data (more than 25 000 Argos locations available in our case) to study movement patterns of a species at the population level and in such great spatial and temporal details. Although the harsh climate prevailing in the high Arctic, especially in winter, can limit such studies using relatively fragile and miniaturized electronic devices, the region also offers unique advantages for satellite tracking compared to more southern latitudes: the polar orbit of Argos satellites greatly increases the number of possible daily locations and the continuous daylight in summer allows solar-powered PTTs to produce a great number of high quality locations 24 h a day. However, it is mandatory to use a combination of solar- and battery-powered PTTs in order to collect enough data over such a long period north of the Arctic Circle.

Post-breeding movements

Our study can be summarized by its five major results. First, ivory gulls from all populations remained along the northernmost ice-edges available in the northeast Atlantic

(for 2–3 months) after they left their colonies, and first dispersed eastwards before heading south (Fig. 1), hence following a loop-like flyway (except for four birds continuing eastward).

Second, the most active migration was in November (Fig. 2) when birds had to cope with two major changes in their high-Arctic environment: the arrival of the polar night and the rapid rebuild of compact sea-ice in Russian waters (Fig. 1).

Third, the first birds only arrived on their wintering grounds (Bering Sea, southeast Greenland, Davis Strait/ Labrador Sea) in December, and there was an apparent delay between Greenland (arriving first), Svalbard (arriving second) and Russian birds (Fig. 1). Also, four of the 22 birds monitored in November–December moved towards the north Pacific wintering area. Although the sample size is small, the likelihood for a bird to winter in the Pacific could therefore be negatively related to the distance from its breeding site (11% of Greenland, 20% of Svalbard and 25% of Franz Josef Land birds moved to the Pacific). If this is a general pattern, then most of the birds wintering in the Pacific may originate from the largest Russian colonies, i.e. from the Kara Sea islands and Severnaya Zemlya (Volkov and Korte 1996, Gavrilo 2009).
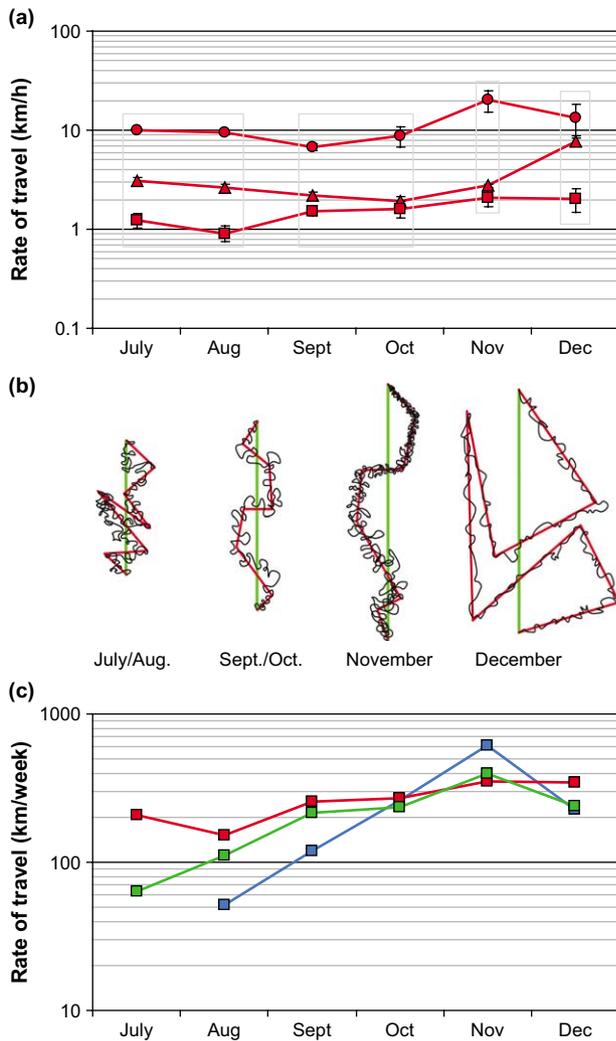
Figure 3. Seasonal changes in the movements patterns of ivory gulls assessed at hourly (circles), daily (triangle) and weekly (square) time scales: (a) rates of travel estimated for 13 Greenland birds (error bars present the S.E. and the four light boxes refer to the four main patterns presented in Fig. 3b); (b) schematic representation of the four main movement patterns using the values from Fig. 3a (the scale is the same for all panels with weekly legs in light grey, daily legs in dark grey and smoothed hourly legs in black); (c) weekly rates of travel estimated for all birds (white squares for 13 Greenland birds; grey squares for 10 Norwegian birds and black squares for 8 Russian birds).

Fourth, rates of travel estimated for Greenland birds varied from less than 2 km h^{-1} (on a weekly time scale) to 20–40 km h^{-1} (on an hourly time scale). Instantaneous flight speeds measured with an optical range finder of Ross's gull *Rhodostethia rosea* and Sabine's gull *Xema sabini* in Siberia were ca 48 km h^{-1} and 50 km h^{-1} respectively (Hedenström 1998). On average, the birds we monitored moved much faster (i.e. 10–15 km h^{-1} faster) during active migration in November than in the other months, and changes in rates of travel at different time scales suggest seasonal changes in spatial use patterns (Fig. 3). The December panel in Fig. 3b appears as the most surprising pattern, but it is a logical result of birds that move from east Greenland to the Labrador ice-edge following the

Greenland coastline, i.e. having to change their headings on a daily basis (respectively southwest, west near Cape Farewell, northwest towards Nuuk, and finally west over open waters) while the straight line for this leg (on a weekly basis) crosses the icecap and is much shorter.

Lastly, the true distance travelled by ivory gulls between July and December appears to be close to 50 000 km (on average) for most Greenland birds, and even more for the four individuals that moved to the Pacific Ocean.

The northern Barents–Kara Seas post-breeding staging areas

Why do ivory gulls fly eastward after breeding, and why do most return in late autumn on a loop-like flyway while a few continue to the Bering Strait on what can be considered an intercontinental flyway? To answer this question probably calls for a mix of environmental (e.g. food availability, light and ice conditions), behavioural, historical and maybe even genetic clues (Alerstam et al. 2007, Mueller and Fagan 2008). From a simple geographic point of view, the sea-ice available along the northeast coast of Greenland would appear to be more profitable to use after the breeding season as it is already on the way to the main and closest wintering grounds (i.e. southeast Greenland and Labrador Sea, Fig. 4). The Greenland Sea is, however, a region of relatively low productivity in summer (Gradinger et al. 1999), one possible explanation for the eastward dispersion of ivory gulls. This trophic assumption is further supported by levels and changes in nitrogen concentrations (i.e. a proxy for primary productivity) found in polar seas (Colony and Timokhov 2001). In summer, the highest concentrations (ca 4 µmol l^{-1} NO$_3$) are found in the Arctic Ocean between north Greenland and the Severnaya Zemlya Archipelago (i.e. just north of most ivory gull colonies and exactly where birds disperse after breeding, Fig. 1). However, the primary producers need light to develop, and can only make use of it towards the end of the summer, when the compact sea-ice disintegrates and the extent of leads increases (Bluhm and Gradinger 2008). At that time of year (summer), the southern part of the Greenland Sea, the east Siberian and Chukchi Seas, and the Bering Strait region (three areas where ivory gulls do not occur in significant numbers in summer and early autumn) have much less nitrogen (0–2 µmol l^{-1} NO$_3$). This overall situation changes dramatically, however, during winter in the Greenland Sea and the Bering Strait (used by ivory gulls in late autumn and winter) when NO$_3$ concentrations reach 3–4 µmol l^{-1}, while the waters in the Beaufort Gyre in the Canadian basin (where only a few ivory gulls are seen regardless of season) remain oligotrophic all year round (0–2 µmol l^{-1} NO$_3$). This productivity pattern matches surprisingly well with the seasonal distribution of ivory gulls described in this paper (Fig. 1) and have already been proposed to discuss the diversity and density of marine mammals in the different Arctic regions (Bluhm and Gradinger 2008). The only mismatch between ivory gulls (absent) and nitrogen concentrations (high) is for the Barents, Kara and Laptev Seas in winter, but one should remember that sea-ice only occurs at high latitudes in these regions in winter (i.e. above the Polar Circle with limited, if
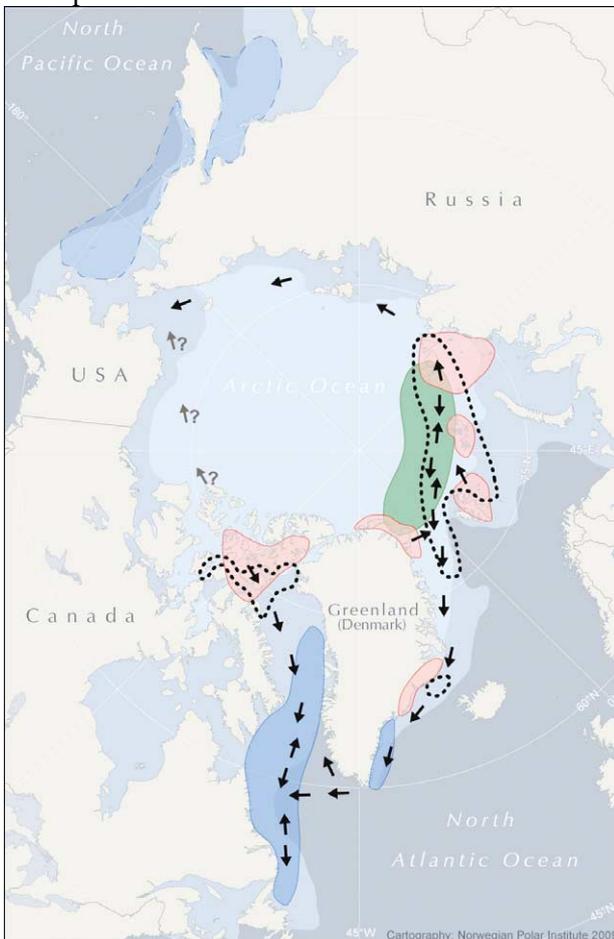
Figure 4. Post-breeding movements (arrows) of the ivory gull from its breeding areas (pink areas) to its wintering grounds (blue areas; variable during the winter and between years according to the extension of the sea-ice), synthesized from published sources and the present study. Despite their large extent, the Bering and Okhotsk Seas wintering areas (roughly delimited with a broken line after Artyukhin 2006, Mallory et al. 2008) are probably only hosting a small fraction of the world population. The three dotted areas present the post-breeding staging areas. Black arrows present the confirmed dispersal and migration routes. Grey arrows with question marks refers to another possible but yet unconfirmed minor flyway to the Bering Strait. The area of highest summer concentration of nitrogen in the region is also given by the green area between North Greenland and Severnaya Zemlya (Discussion). Background map presents the average sea-ice extents in September (light blue) and March (grey blue) between 1979–2007 (data from the National Snow and Ice Data Center, Boulder, Colorado; http://nsidc.org/).

any, sunlight for part of the winter, preventing phytoplankton development), compared to the three main wintering grounds presented in Fig. 4 (all below the Polar Circle, hence having some sunlight every day).

Whatever the true reasons driving this eastward post-breeding dispersal, they concern all birds, regardless of their origin (Greenland, Svalbard and Franz Josef Land). For the birds that have reached the easternmost part of this loop flyway, i.e. Severnaya Zemlya, the remaining distance to the Bering Strait is only 3000 km (compared to >5000 km to

the Labrador Sea). Hence, some might be attracted by this shorter flyway, despite the fact that most of it is still ice free in November–December. According to our results, the origin of birds overshooting their eastern dispersal route to the Bering Strait looks relatively random, or might at best be a function of the distance between the breeding areas and this wintering area. This assumption could be investigated in the future by monitoring a few of the birds breeding in Severnaya Zemlya (north of the Taymyr Peninsula), an area that has already been presented as a migratory divide between the eastern and western flyways for several other Arctic birds (Rogacheva 1987, Alerstam et al. 2007).

Seasonal distribution and flyways

Ivory gull breeding range and status is now relatively well known in the four countries where it breeds (Volkov and Korte 1996, Gilchrist and Mallory 2005, Robertson et al. 2007, Gilchrist et al. 2008, Gavrilo 2009, Gilg et al. 2009, Boertmann et al. 2010, Strøm and Gavrilo in press) and two main wintering grounds, the north Pacific (Bering Sea and Sea of Okhotsk) and the northwest Atlantic (Davis Strait and Labrador Sea), are commonly suggested to host most of the world population (Orr and Parsons 1982, Mallory et al. 2008). However, because ivory gulls can be seen in virtually any ice covered region between July and December, from Newfoundland (50°N) to the geographical North Pole (Collett and Nansen 1900, Buinitsky 1946, Portenko 1946, Uspenski 1956, Vuilleumier 1996, Gavrilo 2007, 2008, Mallory et al. 2008, unpubl. results from 'TARA Arctic' transpolar drift, courtesy from Captain Hervé Bourmeau), the respective wintering areas and main flyways used by birds of different origins were nearly unknown and only speculatively based on very few ring recoveries (i.e. one bird ringed in Labrador found in central east Greenland in spring: Salomonsen 1971, Lyngs 2003; one bird from Franz Josef Land found in Labrador and another one in the Bering Sea: Tomkovich 1990, Bakken and Tertitski 2000; and several birds from Canadian colonies found in Labrador: Stenhouse et al. 2004). By answering several long-lasting questions, our results clarify this situation: 1) they strongly confirm the reality of a bi-directional transpolar migration, towards the two main wintering areas described above, and involving all three northeast Atlantic populations; 2) they provide evidence for a new wintering ground in southeast Greenland (the less prospected area of this country; Boertmann 1994) and document regular but nearly unnoticed (Boertmann 1994, Durinck and Falk 1996, Merkel et al. 2002) coastal migration along the coast of southwest Greenland in December; 3) they suggest that birds seen in late August and September along the northeast Greenland ice-edge (Hjort 1976, Joiris et al. 1997, Gilg et al. 2005, Byrkjedal and Madsen 2008) are only dispersing birds, the peak migration (higher rates of travel and more constant directions) occurring later in the season (October–November), at a time when days are short and systematic bird surveys very occasional (but see Bensch and Hjort 1990, Garðarsson 1999); and finally 4) they do not support the existence of significant wintering areas along the coast of northeast

Greenland or in the Barents Sea (Del Hoyo et al. 1996, Gilchrist et al. 2008), although a few immature and adult birds can be seen along the ice edge in the northern Barents Sea all year round (Bakken and Tertitski 2000), nor the use of a shorter flyway over north or continental Greenland during post-breeding movements (as suggested for spring migration by Lyngs 2003).

The monthly distribution of the northeast Atlantic populations presented in Fig. 1 also allows some inference for the Canadian population. Indeed, none of the birds we monitored reached the 'north water Polynya' (the northern extension of the Baffin Bay between northwest Greenland and northeast Canada) and the nearby Lancaster Sound, an area known to host large numbers of ivory gulls (groups of up to several hundred individuals) in late summer and early autumn (Renaud and McLaren 1982, Brown and Mactavish 1988, Chardine et al. 2004, Karnovsky et al. 2009, Jean-François Therrien pers. comm.). Hence, our results strongly suggest, at least for adults, that the ivory gulls using this area mainly originate from the Canadian colonies (most within a few hundred km) and at best also from a limited number of birds from currently unknown colonies in northwest Greenland (see Gilg et al. 2009 for location of historical colonies). This assumption is also supported by the concurrent declining trend in recorded numbers from these post-breeding staging areas (Chardine et al. 2004) and from the Canadian breeding sites (Mallory et al. 2003, Gilchrist and Mallory 2005), but not for the Greenland population (Gilg et al. 2009). Later in the season, when the ice rebuilds in the Baffin Sea, this Canadian population moves south to the Labrador Sea where, based on our present results, we can now confirm that it mixes with Greenland, Svalbard and Russian birds. This pattern is probably valid for most Canadian birds, as suggested by the recovery on Seymour Island (the largest and westernmost Canadian colony) of two birds ringed in winter in Labrador (MacDonald and Cooper 1979, Renaud and McLaren 1982) and by the recovery in the Labrador and in west Greenland of several birds ringed on Seymour Island (Lyngs 2003, Stenhouse et al. 2004).

Along the 'eastern flyway' (i.e. between the Barents Sea and the north Pacific), previous knowledge can be summarized as follows. Numerous observations at sea during late summer and autumn indicate that ivory gulls are widely distributed in ice-covered waters off the breeding grounds in the northern Barents Sea (to mid-November) and the Kara Sea (to late September), east of the Taimyr Peninsula towards the Bering Strait (early September to November) and in the Bering Sea and Sea of Okhotsk (from October: Portenko 1946, Butyev 1959, Konyukhov et al. 1998, Bakken and Tertitski 2000, Yudin and Firsova 2002, Gavrilo 2009). The only pronounced eastward autumn movements of ivory gulls in Russia are known from the south coast of Wrangel Island where large numbers were first reported by Portenko (1973). Here, the migration occurs from mid September to early November, although it may not be observed in some years and varies greatly depending on local sea-ice conditions (Stishov 1995). Overall, this pattern fits well with our results (discussion about the origin of these birds above).

Based on the literature and our results, we are now able to draw a comprehensive map of the different areas and post-breeding flyways used by ivory gulls from the different populations (Fig. 4). Note that there is a small post-breeding area in southeast Greenland that has not yet been discussed in this paper. It probably only concerns a small number of birds (recent records are all less than 100), but it is indicated on this map because it relates to the small isolated and southernmost population breeding on the nearby nunataks (Degerbøl 1937, Glahder 1995, Gilg et al. 2005, Boertmann et al. 2009, Gilg et al. 2009). The Barents Sea and northeast Greenland wintering areas, reported in some previous studies (COSEWIC 2006), are no longer included in our map as we found no recent evidence to support them.

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