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FEATURE ARTICLE

Seasonal variations in migration strategy of a long-distance Arctic-breeding seabird

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ABSTRACT: Long-distance migratory seabirds need to adjust their migration strategy according to internal (breeding, molting) and external factors (seasonality, resource availability). Time-minimizing strategies are common during spring migration to arrive at the optimal time to breed. We studied the annual movements and migration strategy of the long-tailed jaeger *Stercorarius longicaudus*, a small arctic-nesting seabird. First, we documented year-round movements (routes, wintering sites) of male and female jaegers breeding in the Canadian Arctic. We then compared their migration strategies between seasons (phenology, stopover use, travel distance, speed) to determine whether they adopt a time-minimizing strategy in spring. Over 6 yr, we collected 43 tracks from geolocators deployed on Bylot and Igloodik Islands. Jaegers departed the breeding site over a 5 wk period and traveled on average 32375 km (round trip) before returning to breed, one of the longest documented migrations on Earth. Birds used a major stopover area east of the Grand Banks of Newfoundland in spring and fall, and wintered in high marine productivity areas of the South Atlantic. Unexpectedly, the spring migration was 40 % longer and 32 % slower than in fall, and birds increased their time spent on water (foraging and/or resting) by 61 %. A time-minimizing strategy in fall may help to reach the wintering site rapidly and start molting early. In spring, a fly-and-forage strategy seems to be adopted to increase foraging effort, probably for the accumulation of body reserves before breeding and in anticipation of unfavorable conditions that may prevail at arrival on their arctic breeding site.



Long-tailed jaeger *Stercorarius longicaudus* equipped with a geocator to monitor its year-round movements and migration strategy between the Canadian Arctic and the southern Atlantic.

Photo: Yannick Seyer

KEY WORDS: Non-breeding movement · Geolocators · Global Location Sensor · GLS · Tracking · Satellite transmitters · Benguela Current · *Stercorarius longicaudus* · Long-tailed jaeger

1. INTRODUCTION

Migratory seabirds can travel long distances across the planet, connecting distant ecosystems and exposing themselves to a diversity of environmental conditions and resources along the way. Migration path and phenology, and wintering area used, can have a

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strong impact on key demographic traits such as survival or reproduction if individuals are not at the right place at the right time (Norris et al. 2004, Newton 2008, Klaassen et al. 2014, Senner et al. 2019). Because of seasonal and annual variations in resource availability, seabirds should adjust their migration strategy (e.g. timing of migration, travel speed, use of stopover and wintering areas) to maximize their fitness. In addition, intrinsic factors such as body condition and reproductive or molting state can also influence the migration strategy (Newton 2008, 2011, Alerstam 2011).

Migratory birds can face different environmental conditions and selection pressures during their pre-breeding (spring) and post-breeding (fall) migration (Newton 2008, Horton et al. 2016), which can lead to seasonal variation in optimal migration strategy (Nilsson et al. 2013, Zhao et al. 2017, Schmaljohann 2018). For instance, competition for breeding territories and high reproductive success in early breeders can favor birds arriving early and in good body condition on their breeding grounds (Rowe et al. 1994, Kokko 1999, Verhulst & Nilsson 2008). Under these conditions, individuals are expected to complete their spring migration as fast as possible, given constraints on flying speed and energy acquisition rate. Such a time-minimization strategy is commonly thought to play a major role during the pre-breeding migration (Hedenström & Alerstam 1997, Zhao et al. 2017) and may explain why spring migration is faster than fall migration in many long-distance migrants (Nilsson et al. 2013, Schmaljohann 2018). This may be especially important in species breeding at high latitudes where the summer is brief (Reséndiz-Infante & Gauthier 2020).

Seasonal variation in environmental conditions such as weather pattern or food availability on the wintering and stopover sites can also have a strong effect on migratory behavior, and the benefits of a fast spring migration can be counterbalanced by various costs (Schmaljohann 2018, Deng et al. 2019). For instance, unfavorable wind and limited resources at stopovers when individuals need to build up body reserves can reduce the pace of the spring migration (Petrie & Wilcox 2003, Kölzsch et al. 2016, Deng et al. 2019). Moreover, individuals nesting in highly seasonal environments, such as the Arctic, could suffer from unfavorable weather or food shortage if they arrive on their breeding grounds too early and in poor body condition (Bêty et al. 2004, Nuijten et al. 2014, Jean-Gagnon et al. 2018). In contrast, a high abundance of energy-rich food during late summer on the breeding grounds may allow prolonged non-

stop flights in fall in some species, shortening the post-breeding migration (Bustnes et al. 2013, Alves et al. 2016, Kölzsch et al. 2016). The timing of the post-breeding molt is another factor that can influence the timing and speed of the fall migration (Jahn et al. 2013, Kulaszewicz & Jakubas 2015, Kiat & Izhaki 2016). Overall, the optimal migration strategies can vary between taxa (Schmaljohann 2018), and between populations of the same species (Klaassen et al. 2012, Bustnes et al. 2013) depending on environmental conditions and selection pressures faced by individuals during their entire annual cycle.

The long-tailed jaeger *Stercorarius longicaudus* (hereafter jaeger) represents a good study model to investigate seasonal variations in migratory behavior. It is a relatively small seabird that achieves one of the longest documented migrations on Earth, from its High Arctic breeding sites to its subtropical wintering areas in the southern hemisphere (Gilg et al. 2013, van Bemmelen et al. 2017). Jaegers are pelagic for most of the year, but they switch to the terrestrial environment to breed. Their breeding season is constrained by the short arctic summer and food abundance that often decreases as the summer progresses (Gauthier et al. 2011, Fauteux et al. 2015). They consume exclusively terrestrial prey during the summer, and they rely on lemming populations to breed successfully in most parts of their range (Maher 1970, Furness 1987, Therrien et al. 2014). Once they acquire a territory, individuals can return and use the same site yearly (Maher 1970, Seyer et al. 2020). However, food accessibility can be highly unpredictable when approaching the arctic breeding ground and on arrival due to the timing of ice cover at sea and snowmelt on land, as well as cyclic population fluctuations in lemmings.

In this study, we document for the first time the year-round movements of long-tailed jaegers breeding in the Canadian Arctic by tracking more than 45 males and females. We first describe their fall and spring oceanic migratory routes and identify their main stopover and wintering sites. We then compare the marine productivity, a proxy of food availability, at the different wintering and stopover sites used by jaegers. We also analyze their migration strategy in fall and spring in terms of phenology, stopover location, travel distance, travel speed, and time spent in flight vs. on the water to determine if jaegers have a more rapid spring migration as found in many bird species. Due to the constraints imposed by the short arctic summer on their breeding grounds, we expected jaegers to adopt a time-minimizing migration strategy in spring.

2. MATERIALS AND METHODS

2.1. Study site and field methods

The field work was conducted during the long-tailed jaeger breeding season (mid-June to early August) in 2008 and from 2014 to 2019 at Bylot Island (73° 08' N, 80° 00' W), and from 2016 to 2019 at Igloodik Island (69° 39' N, 81° 54' W). Both sites are located in Nunavut in the Canadian High Arctic. Nests of long-tailed jaegers are spaced out on the tundra, and systematic nest searches were carried out annually in late June and early July to find breeding pairs. Territorial pairs were identified by their alarm calls, and nests were found by spotting incubating birds returning to their nest. Some nests were also found opportunistically during other field activities on the outskirts of the main study area. All nests were georeferenced when found and monitored until hatching or failure. Because jaegers are faithful to their nesting site (Seyer et al. 2020), we also made systematic searches where marked jaegers previously nested.

We captured most jaegers at their nest using a bownet trap, but also sometimes in the nest vicinity using a noose carpet, a netgun, or a bal-chatri trap baited with a lemming. All captured birds were marked with metal and plastic numbered bands for individual identification and sexed by DNA analysis using feather pulp, except for a few birds in 2008 (see Seyer et al. 2019 for more details).

From 2014 to 2018, we equipped birds with a geolocator (light-level loggers; Intigeo-C65, Migrate Technology) attached to the plastic band with a cable tie through 2 small holes (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m677p001_supp/). Geolocators measured 14 × 8 × 6 mm and weighed 1 g, representing about 0.7% (geolocator with the band) of the body mass (female: 318 g, male: 286 g; Seyer et al. 2019). They were equipped with both light and wet-immersion sensors. We deployed 65 geolocators on Bylot Island (2014–2016: $n = 20 \text{ yr}^{-1}$, 2018: $n = 5$) and 5 on Igloodik Island in 2016 between 20 June and 10 July (Table S1 in Supplement 2). We attempted to recover geolocators from 2015 to 2019 between 19 June and 10 July (i.e. during the incubation). Considerable effort was made to recapture breeding birds on their nest and non-breeding birds in their previous nesting territory using the capture methods previously described.

In 2008, we deployed 10 satellite transmitters (PTT-100, Microwave Telemetry) on adults (8 females, 2 unknown) from 1 to 12 July on Bylot Island (Table S1).

The devices weighed 10 g, representing about 3% of the body mass following the recommendation of Phillips et al. (2003). Transmitters were attached with a backpack harness made of Teflon ribbons (Fig. S2; Steenhof et al. 2006). All protocols were approved by the Animal Care Committee of Université Laval following the guidelines of the Canadian Council on Animal Care.

2.2. Analyses of geolocator data

Geolocators sampled light intensity each minute and recorded its maximum value every 5 min. A wet-immersion sensor measured conductivity every 30 s and was programmed to record a wet count only for immersion in saltwater (value >63 on an arbitrary scale from 0–127; Fox 2013). Wet counts were summed, and the values were saved every 4 h.

Before deployment, we performed a calibration in an open field in southern Québec (46° 44' N, 71° 28' W), and during the deployed period, we performed a Hill-Ekstrom calibration during the longest stable position (i.e. the wintering period; Lisovski et al. 2012). Twilight events were identified using the threshold method (Ekstrom 2004, Lisovski & Hahn 2012) with the 'TwGeos' package (Lisovski et al. 2016) in R (other packages mentioned below are also in R). We set the threshold value to 1.15 lux to avoid noise in the night-time light levels. To determine the geographic locations, we analyzed light-level data using a Bayesian approach with the 'SGAT' package (Wotherspoon et al. 2013). We simulated a total of 11 700 samples. We provided the model with (1) raw location estimates calculated with the threshold method, (2) a spatial mask where inland positions were less likely than at-sea positions, and (3) a movement model defining probable flight speed. We assumed a mean travel speed of 14 km h⁻¹ with a maximum at 61 km h⁻¹ (Spear & Ainley 1997, Sittler et al. 2011). More details about the geolocator data analysis are provided in Supplement 3.

Saltwater immersion data were used to estimate the maximum time spent in flight daily throughout the non-breeding period. Each wet count recorded was associated with a contact with saltwater. However, wet signals could not be assigned to a specific activity, as jaegers may be on the water to forage or to rest. In contrast, considering that jaegers are highly pelagic and seldom rest on land outside the breeding season (Wiley & Lee 2020), each dry period (no wet count) was associated with flight (Mejías et al. 2017, Schacter & Jones 2018, Studholme et al.

2019). Accordingly, a higher number of immersions was associated with less time spent in flight. At sea, some stercorariids use kleptoparasitism, with about 20% of the chases being successful (Furness 1987). The extent to which the small long-tailed jaeger relies on kleptoparasitism to feed is unclear, but it appears less important than in other members of the Stercorariidae (Furness 1987, Wiley & Lee 2020). Thus, we assumed that kleptoparasitism represented a negligible portion of the time spent flying.

Because jaegers become entirely terrestrial during breeding, we used a changepoint analysis (Killick & Eckley 2014) to identify the start and end of migration based on a sudden change in the daily number of immersions when the birds switch between marine and terrestrial lifestyles (Fauchald et al. 2019). To identify fall and spring migration stopovers, we looked at stationary periods estimated by the 'ChangeLight' function in the 'GeoLight' package (Lisovski & Hahn 2012) with a minimum duration of 3 d. Finally, to define the wintering period, we used a 3-step approach based on the 'Migratory Analytical Time Change Easy Detection' method (Chen et al. 2016, Doko et al. 2016). More details about the estimation of the start and end of these periods are provided in Supplement 3.

We calculated the total distance for each migration step by summing the distance between successive locations using the great-circle distance ('distVincentyEllipsoid' function in the 'Geosphere' package; Hijmans 2019). Because geolocators are inaccurate in 24 h daylight regions, we estimated the distance traveled between the arctic breeding site and the first location estimated by the geolocator (or vice versa) based on the path recorded by satellite transmitters (see Section 3).

To estimate the duration of migration, we calculated the difference between departure (or arrival) date from the breeding site and arrival (or departure) on the wintering site, excluding the stopover duration. To estimate the duration of the stopover and the wintering periods, we calculated the difference between the arrival and departure dates at each site. Finally, to estimate the travel speed for each migration leg, we divided the distance traveled by its duration using only portions of the tracks recorded by the geolocators (i.e. excluding the segments in the Arctic where no positions were available).

We estimated the individual home range (75% utilization) and core area size (50% utilization) during the wintering and stopover periods using the kernel utilization distribution method with the 'kernelUD' function of the package 'adehabitatHR' (Calenge

2006). We used the bivariate normal kernel method and the least-square cross-validation algorithm to find the best smoothing parameter value (h , Table S2 in Supplement 3) controlling for the amount of variation in each component of the estimate (Worton 1989). We repeated the same methods for the home range and core area sizes at the population level or to compare males vs. females. To delimit the main wintering sites, we used the 50% minimum convex polygon for each site observed, considering separately all the locations recorded at each site.

2.3. Analysis of satellite transmitter data

Satellite transmitters were programmed to transmit a signal continuously during 6 h at 4 d intervals. We received the locations via the Argos system (Collecte Localisation Satellites 2016), and each location was assigned to a class (0, 1, 2, 3, A, B, Z) depending on its estimated precision. The estimated accuracy of the location classes 0, 1, 2, and 3 followed a normal distribution with a standard deviation of >1500, <1500, <500, and <250 m, respectively, and classes A and B had no accuracy estimation. Locations of class Z failed and were excluded, and in the case of multiple records with the same time label, we retained the most accurate one. All remaining locations were filtered using a speed-distance-angle filter ('argosfilter' package; Freitas et al. 2008, Freitas 2012). We specified a speed threshold of 67 km h^{-1} , corresponding to the predicted mean + 1 SD ground flight speed of jaegers and skuas with tailwinds (Spear & Ainley 1997), a value slightly higher than the maximum flight speed recorded by Sittler et al. (2011). We used the default settings for distances and angles, removing locations requiring turning angles of 165° and 155° if the track leading to them was longer than 2.5 and 5.0 km, respectively (Freitas et al. 2008). Our 3-step filter retained $88 \pm 3\%$ (SD) of the original locations among individuals.

To avoid non-independence of spatial data because of the multiple recorded locations for each period of transmission, we averaged to a single mean daily location. We considered that a bird had started its migration when its movement at sea was directional without turning back for a 6 h recording period or when it reached a distance $\geq 150 \text{ km}$ away from Bylot Island. Departure date was defined as the median between the previous recorded date and the first one recorded on migration. We applied the same method to estimate the arrival date on the fall stopover area off Newfoundland.

2.4. Marine productivity

We used marine productivity as a proxy of food availability at the main wintering and stopover sites used by jaegers. We used the MODIS-Aqua Level-3 chlorophyll *a* (chl *a*) data at 9 km resolution (NASA OB DAAC 2018), which is a good proxy of marine productivity (Ware & Thomson 2005). We calculated the mean annual concentration of chl *a* from 2002 to 2020 within each wintering site and the mean over 32 d in spring (23 April to 24 May) and in fall (29 August to 29 September) for stopover sites used by jaegers.

2.5. Statistical analyses

We assessed the influence of the period of the annual cycle on the total distance traveled with a linear mixed-effect model (LMM) based on a restricted maximum likelihood approach in the package ‘nlme’ (Pinheiro et al. 2018). We used bird IDs as a random factor for all LMMs because some individuals were monitored more than once. However, we applied linear models (LMs) when we had ≤ 2 individuals monitored twice to avoid overfitting and because the random effect explained a negligible portion of the variance. We used LMs to assess if sex affected the total distance traveled annually (from the breeding to the wintering site and back to the breeding site), and the size of the individual core wintering area. We also used LMs to compare the chl *a* concentration between the different wintering sites or between fall and spring stopovers.

We used LMMs to assess sex differences in departure date from the breeding site and to compare departure date from the breeding site and arrival date at the stopover between tracking devices (geolocators vs. satellite transmitters). We used LMMs or LMs to test the influence of sex or wintering site on the duration of stopover and wintering periods, arrival and departure dates from the wintering site, and arrival date at the breeding site. Finally, we used an LMM to test if the combined duration of migration and stopover changed between fall and spring migrations.

We assessed the influence of the period of the annual cycle on travel speed during migration and at stopovers and on the daily number of immersions (proxy of the time spent in flight vs. resting or foraging at sea) with LMMs. We tested the influence of sex, wintering site used, departure date from the breeding or wintering site, and type of tracking de-

vice on fall and spring migration travel speed with LMs or LMMs. Finally, we tested if the daily number of immersions varied according to travel speed and between fall and spring migrations using an LMM. For all LMMs, we calculated the marginal R^2 (for fixed effects) and the conditional R^2 (for fixed and random effects) based on Nakagawa & Schielzeth (2013). All analyses were done using the software R (R Core Team 2020) and we used a significance value (α) of 0.05. Means are presented \pm SD throughout.

3. RESULTS

We retrieved 42 geolocators (Bylot Island: $n = 40$; Igloolik Island: $n = 2$) 1–5 yr after deployment, giving an overall recovery rate of 60% (Table S1). We collected 43 tracks from 34 different individuals (19 females and 15 males), including 23 complete 2-way migrations (5 devices yielded no or little information).

We received positions of birds marked with satellite transmitters from 42–95 d after their deployment (Table S1). None of the 10 individuals marked in 2008 with transmitters were ever seen again in the following breeding seasons up to 2019.

3.1. Migratory path and distance

Long-tailed jaegers departing the eastern Canadian Arctic traveled through Baffin Bay and Davis Strait to the North Atlantic and then crossed the ocean to the western African coast (Fig. 1; Animation S1 at www.int-res.com/articles/suppl/m677p001_supp/). In the austral regions, most birds continued through the eastern part of the Atlantic Ocean. During both migrations, most individuals (fall: 88%, $n = 43$; spring: 83%, $n = 23$) had one major stopover located east of the Grand Banks of Newfoundland (Fig. 2), while the others did not use any stopover. The fall stopover area of the population was more spatially restricted (60% smaller) than the spring one. Stopover sites were generally similar for males and females, although their core area overlapped more in fall (60–65% depending of sex) than in spring (33–39%; Fig. S4 in Supplement 4).

The total distance traveled annually by jaegers estimated from geolocators averaged $61\,344 \pm 9\,101$ km (range = 43 227–76 021 km; $n = 23$). If we exclude the stopovers and the wintering period, they traveled on average $32\,375 \pm 6\,546$ km during migrations (range = 20 437–44 743 km; $n = 23$). The distance traveled during the spring migration, exclud-

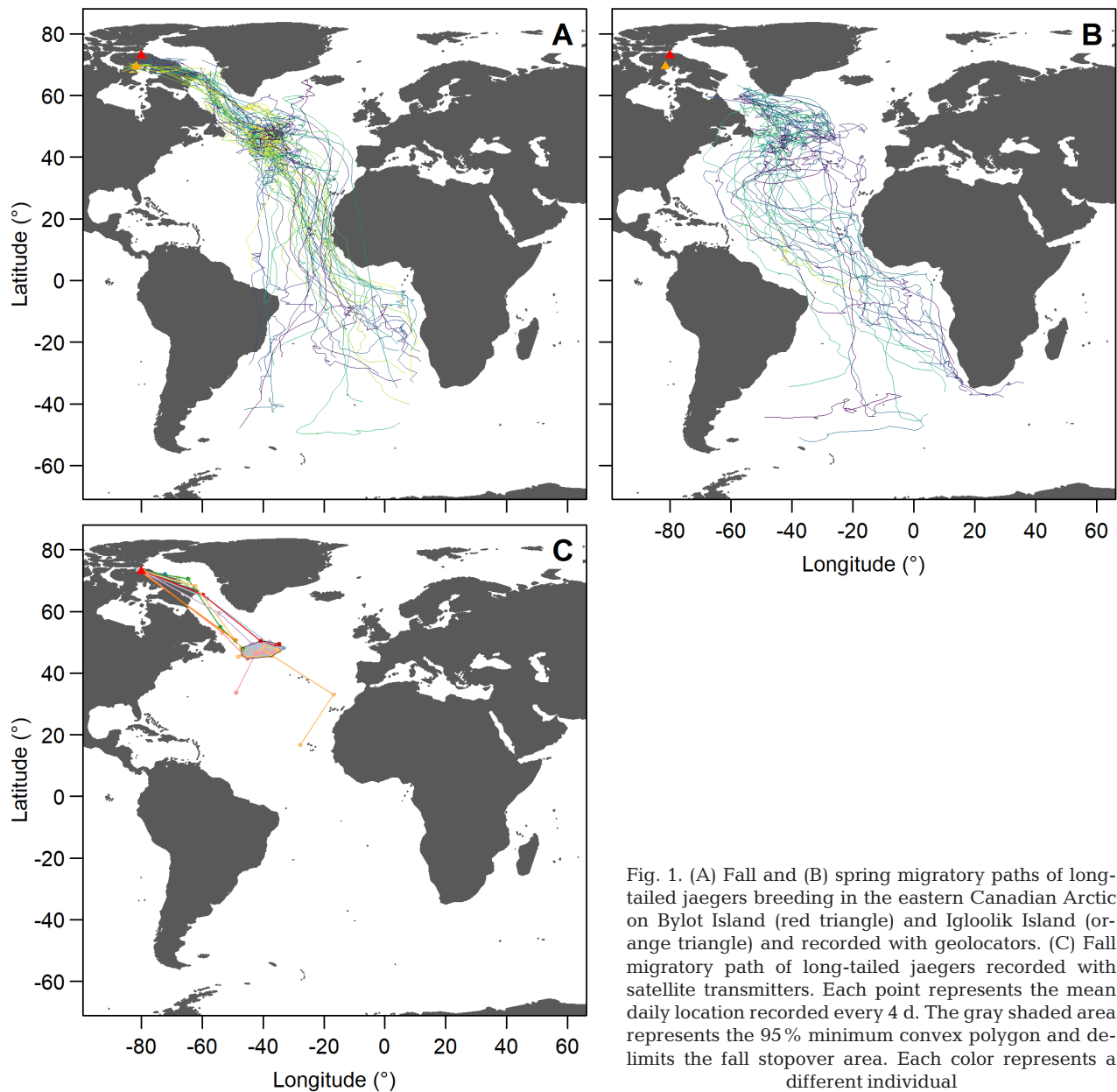


Fig. 1. (A) Fall and (B) spring migratory paths of long-tailed jaegers breeding in the eastern Canadian Arctic on Bylot Island (red triangle) and Igloolik Island (orange triangle) and recorded with geolocators. (C) Fall migratory path of long-tailed jaegers recorded with satellite transmitters. Each point represents the mean daily location recorded every 4 d. The gray shaded area represents the 95 % minimum convex polygon and delimits the fall stopover area. Each color represents a different individual

ing the stopover, was significantly longer by about 20% compared to the fall (Table 1; Table S4 in Supplement 5) and the total distance traveled annually during migration did not differ between males ($32\,505 \pm 6482$ km) and females ($32\,256 \pm 6890$ km).

3.2. Wintering period

Based on individual core area used, we were able to delimit 6 different wintering sites, all of which were associated with major oceanic currents, 4 in the

eastern Atlantic (i.e. Canary, Guinea, Benguela, and Agulhas Currents) and 2 in the western Atlantic (i.e. North Equatorial and Brazil Currents; see Figs. 2 & 3; Fig. S5 in Supplement 4). The Benguela Current was the most heavily used site (68% of the individuals; $n = 40$), whereas other sites were used by about 3–15% of the individuals. Males and females used the same wintering sites (Fig. 2). The mean size of individual core areas tended to be higher for females ($290\,414 \pm 111\,619$ km²; $n = 14$) than for males ($223\,285 \pm 107\,774$ km²; $n = 12$), but we found no significant difference (Table S4).

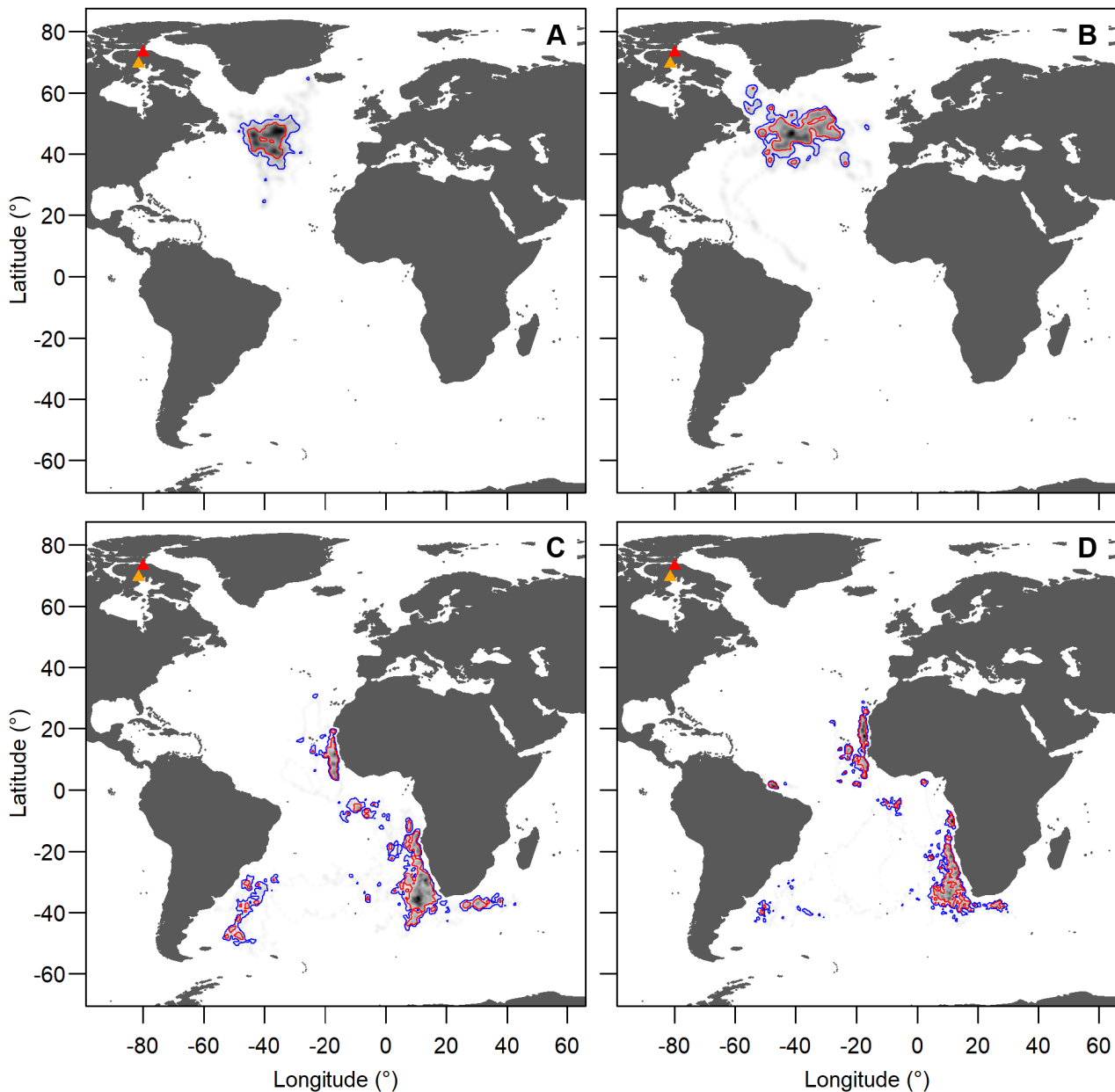


Fig. 2. (A) Fall and (B) spring stopover sites, and winter distributions of (C) female and (D) male long-tailed jaegers breeding in the eastern Canadian Arctic on Bylot Island (red triangle) and Igloolik Island (orange triangle) and recorded with geolocators. Blue lines enclose the 75% area and red lines enclose the 50% core area used. Gray shading represents the intensity of the kernel utilization distribution based on all locations recorded during the period; darker colors represent a higher utilization

Among the individuals with a complete wintering period, 18 used only 1 site for the whole period: 10 in the Benguela Current, 4 in the Canary Current, 3 in the Brazil Current, and 1 in the Guinea Current. If we also consider incomplete wintering periods, individuals used on average 1.3 different sites during the winter (range: 1–2; $n = 40$). Individuals from the same pair did not systematically use the same wintering sites (Table S3 in Supplement 4).

3.3. Marine productivity

The second most heavily used wintering sites (Canary Current) had the highest mean annual chl *a* concentration ($1.14 \pm 0.22 \text{ mg m}^{-3}$; Fig. 3; Fig. S6 in Supplement 6) and was significantly higher than other wintering sites (Guinea: 0.19 ± 0.03 , Benguela: 0.23 ± 0.02 , Agulhas: 0.30 ± 0.03 , North Equatorial: 0.31 ± 0.09 , Brazil: $0.36 \pm 0.04 \text{ mg m}^{-3}$; Table S5 in

Table 1. Movement characteristics (mean \pm SD) for different periods of the annual cycle of long-tailed jaegers breeding in the eastern Canadian Arctic and recorded with geolocators. Sample sizes (n) for the duration and the distance only include individuals tracked for the whole period, whereas those for travel speed and the number of daily immersions include incomplete tracks. Fall and spring migration periods exclude the stopover periods

Period	n ^a	Distance (km)	Duration (d)	n ^b	Travel speed (km d ⁻¹)	No of daily immersions
Fall migration	40	14730 \pm 3053	42.7 \pm 16.0	43	385 \pm 90	1055 \pm 269
Fall stopover	37 ^c	3682 \pm 2341	19.7 \pm 12.8	37	190 \pm 33	1112 \pm 209
Wintering	26	20487 \pm 4574	144.8 \pm 34.4	40	149 \pm 27	2005 \pm 267
Spring migration	23	17705 \pm 4610	63.6 \pm 21.1	26	263 \pm 60	1702 \pm 303
Spring stopover	19 ^c	5597 \pm 3873	26.8 \pm 16.0	19	199 \pm 46	1872 \pm 332

^aSample size for distance and duration; ^bSample size for travel speed and daily number of immersions in saltwater; ^cIndividuals with no fall or spring stopover were excluded

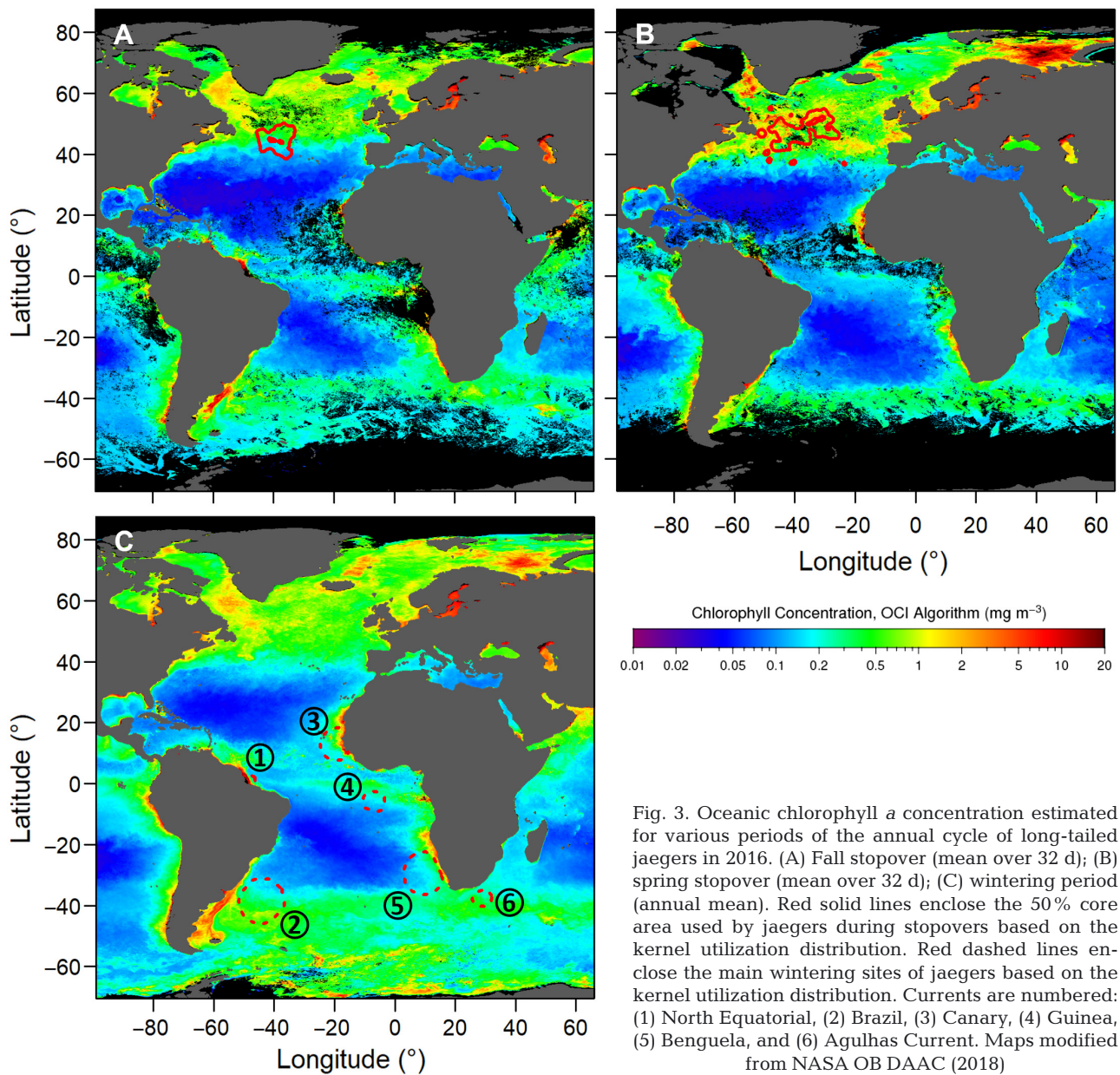


Fig. 3. Oceanic chlorophyll a concentration estimated for various periods of the annual cycle of long-tailed jaegers in 2016. (A) Fall stopover (mean over 32 d); (B) spring stopover (mean over 32 d); (C) wintering period (annual mean). Red solid lines enclose the 50% core area used by jaegers during stopovers based on the kernel utilization distribution. Red dashed lines enclose the main wintering sites of jaegers based on the kernel utilization distribution. Currents are numbered: (1) North Equatorial, (2) Brazil, (3) Canary, (4) Guinea, (5) Benguela, and (6) Agulhas Current. Maps modified from NASA OB DAAC (2018)

Supplement 5). However, the Benguela and Agulhas Currents presented the lowest coefficients of variation through time, 8.6 and 9.8%, respectively, compared to 19.5% for the Canary Current (Fig. S6). The mean 32 d chl *a* concentration was 3.8 times higher on the spring stopover than on the fall stopover (Fig. S6, Table S5) but showed a similar coefficient of variation (18%).

3.4. Migration phenology

Jaegers marked with geolocators left Bylot Island over a 5 wk period (12 August \pm 9 d, range: 23 July to 27 August; $n = 41$; Fig. S7 in Supplement 7), and the 2 individuals from Igloolik Island left on 8 and 21 August. Departure dates did not differ between sexes (Table S6 in Supplement 5). Individuals marked with satellite transmitters had similar departure dates (17 August \pm 4 d, range: 12 to 25 August; $n = 9$; Table S6). Jaegers arrived within 14 ± 5 d at the North Atlantic stopover site and at the same time for geolocators (26 August \pm 10 d, range: 29 July to 8 September, $n = 38$) and satellite transmitters (24 August \pm 4 d, range: 16 to 28 August, $n = 7$; Table S6). Jaegers stayed there about 20 ± 13 d (Table 1), but individuals wintering at the most distant sites (Benguela and Agulhas Currents) spent less time on the fall stopover than individuals wintering at the closest one (Canary Current; Table S6).

Individuals arrived on their wintering site on 10 October \pm 17 d (range: 1 September to 21 November; $n = 40$) and departed on 6 March \pm 32 d (range: 14 January to 13 May; $n = 26$). We found no difference in the arrival date to the different wintering sites, but the departure date from the northernmost wintering site (Canary) was 47 d later than for other sites and the duration of the wintering period was 32% longer (Table S6). We found no sex difference in the arrival and departure dates, nor in the duration of the wintering period (Table S6).

Jaegers arrived at the North Atlantic stopover site around 23 April \pm 17 d (range: 20 March to 19 May; $n = 19$) and spent about 27 ± 16 d there (Table 1). Jaegers wintering at the southernmost site spent more time on the stopover than birds from the northernmost site. Females also spent more time than males (30 ± 18 vs. 15 ± 15 d) at the spring stopover, contrary to the fall period (12 ± 14 vs. 22 ± 12 d, respectively; Table S6). Arrival at the breeding site occurred over a 2.5 wk period (average: 3 June \pm 4 d, range: 26 May to 13 June; $n = 23$), a shorter span than for the departure date. Arrival date did not differ

between sexes or wintering sites (Table S6). Arrival date of individuals of the same pair was on average 5 ± 2.6 d apart (Table S3). The total time spent in migration and at the stopover was shorter in fall (60 ± 16 d) than in spring (86 ± 31 d; Table S6).

3.5. Travel speed and immersions

The average daily travel speed differed between periods, ranging from 149 km d^{-1} during the wintering period to 385 km d^{-1} during the fall migration (Table 1; Table S4). Fall migration was on average 46% faster than spring migration (Table 1). When birds were using stopover areas, their daily travel speeds were similar in spring and fall but 27–33% higher than in winter (Table 1). Both sexes traveled at the same speed in fall and spring (Table S4). Average fall migration travel speed was similar for birds heading to different wintering sites, but birds wintering in the Guinea Current traveled at a slightly lower speed in spring compared to birds originating from other sites (Table S4). During spring, migration speed increased with the departure date from the wintering site, but not in fall (Fig. 4; Table S4). Travel speed of birds tracked with satellite transmitters during the first part of the fall migration ($428 \pm 155 \text{ km d}^{-1}$; $n = 7$) was similar to birds tracked with geolocators ($385 \pm 90 \text{ km d}^{-1}$; $n = 43$; Table S4).

The average daily number of immersions in salt-water was 61% higher during the spring migration than during the fall migration (Table 1; Table S4). In spring, the daily number of immersions after the stopover was 12% higher than before the stopover (1857 ± 344 vs. 1658 ± 309 immersions per day) and equal to the stopover period (1872 ± 332 ; Table S4). The daily number of immersions also decreased as individual travel speed increased, and this relationship was steeper in spring than in fall (Fig. 5; Table S4). The immersions were also 7–90% higher during the wintering period than in other periods (Table 1; Table S4).

4. DISCUSSION

We documented for the first time the annual movements and migration phenology of the Canadian population of long-tailed jaegers, long-distance migrants breeding in the Arctic. We confirmed the presence of a major stopover in the North Atlantic and found that their main wintering sites are located in the austral region of the Atlantic Ocean, predominantly off

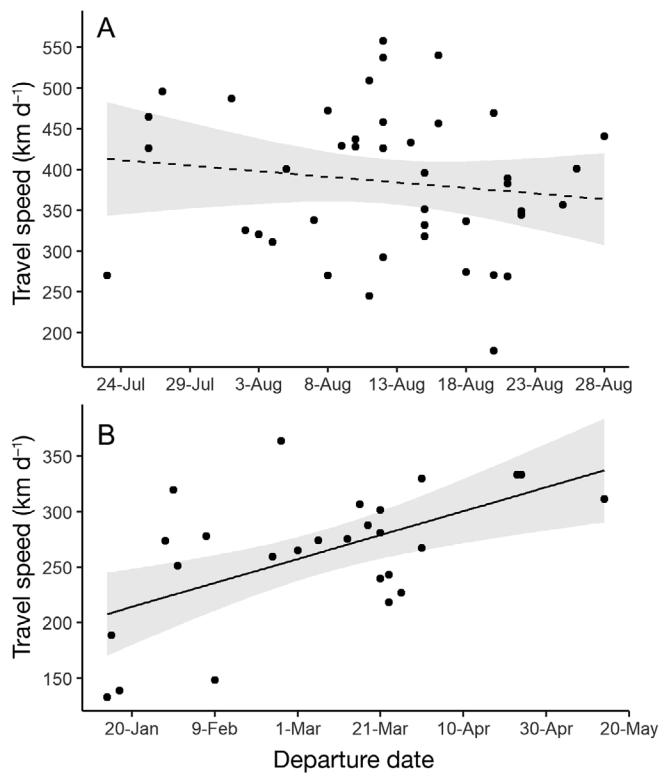


Fig. 4. Relationship between travel speed during migration and departure date (A) from the breeding site and (B) from the wintering site in long-tailed jaegers. Each point represents the mean travel speed during fall or spring migration for 1 individual. Solid line represents a significant relationship and dashed line a non-significant one (gray shading is the 95% confidence interval)

the African coast. Contrary to most migratory bird species, and especially species breeding in the Arctic where the reproductive season is very short, jaegers traveled faster during the fall migration than during the spring migration and did not adopt a time-minimizing strategy during the spring migration.

4.1. Migratory path

The migration of long-tailed jaegers roughly followed a figure-eight pattern, turning clockwise in the North Atlantic and somewhat counter-clockwise in the South Atlantic. This pattern is displayed by several other trans-equatorial migrating seabirds (González-Solís et al. 2007, Egevang et al. 2010, Hedd et al. 2012). Jaegers breeding in the Eurasian Arctic displayed a similar migratory route across the Atlantic Ocean to those breeding in the Canadian Arctic and also showed a similar wider migratory path in spring compared to the fall (Gilg et al. 2013,

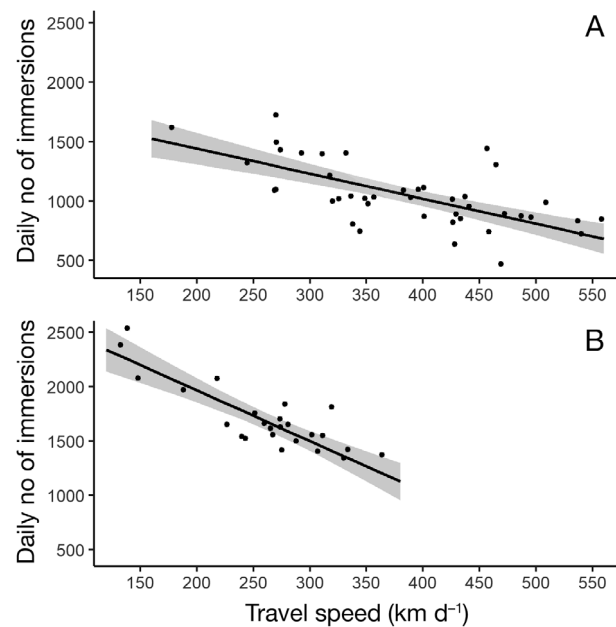


Fig. 5. Relationship between the daily number of immersions in saltwater and travel speed during (A) fall and (B) spring migrations of long-tailed jaegers. Each point represents the mean number of immersions during fall or spring migration for one individual. Solid line represents a significant relationship (gray shading is the 95% confidence interval)

van Bemmelen et al. 2017). These paths do not follow the shortest distance between the breeding and wintering sites but they follow the dominant winds in the Atlantic (González-Solís et al. 2007, Felicísimo et al. 2008, Egevang et al. 2010). Therefore, these paths probably represent an energy-optimization strategy to benefit from tailwinds (Alerstam 2011).

Long-tailed jaegers breeding in the eastern Canadian Arctic used the same stopover area in the North Atlantic during both spring and fall migrations. Located east of the Grand Banks of Newfoundland, this area was used for 3 to 4 wk by most individuals. It is associated with the subpolar front between the Grand Banks and the Charlie-Gibbs fracture zone. It is recognized as a hotspot for seabirds because of its important productivity and predictability, especially in spring as also shown by our results (Boertmann 2011, Scales et al. 2014, Davies et al. 2021). Many seabirds use this area either as a stopover (e.g. Cory's shearwater *Calonectris borealis*, Arctic tern *Sterna paradisaea*, European and Greenlandic long-tailed jaegers) or as a wintering site (e.g. great skua *Stercorarius skua*, sooty shearwater *Ardenna grisea*, Cory's shearwater; Egevang et al. 2010, Dias et al. 2011, Hedd et al. 2012, Magnúsdóttir et al. 2012, Gilg et al. 2013, van Bemmelen et al. 2017, Davies et al. 2021).

This area should therefore be considered as a major refueling stop for the migrating long-tailed jaegers and reinforces the need to protect it to ensure the sustainability of many seabird populations (Davies et al. 2021).

4.2. Wintering period

We identified 6 main wintering sites used by long-tailed jaegers breeding in eastern Canada. These sites were predominantly located in the south Atlantic Ocean and most jaegers wintered, at least partly, in the Benguela Current. European and eastern Greenlandic populations are also concentrated along the west African coast in winter, from the Guinea to the Benguela Current, with the latter site being the most heavily used site (Gilg et al. 2013, van Bemmelten et al. 2017). Overall, these results indicate a weak migratory connectivity in long-tailed jaegers, as individuals originating from the same breeding site can spread over several distant wintering sites and are mixed with birds originating from different breeding populations. Weak migratory connectivity makes it more difficult to target particular areas to protect specific populations that could be in trouble (Webster et al. 2002).

Jaegers wintered in areas of high marine productivity; thus, presumably in predictable and food-rich areas. All of their wintering sites, especially the 2 most heavily used, the Benguela and Canary Currents, are influenced by strong upwellings leading to high productivity. The Benguela Current is one of the most important and stable upwelling regions in the world, providing high productivity year-round (Chavez & Messié 2009). It is a known wintering area for many seabird species (e.g. Cory's shearwaters, Sabine's gull *Xema sabini*; Dias et al. 2011, Stenhouse et al. 2012, Davis et al. 2016), and is also an important migratory passage (e.g. Arctic tern; Egevang et al. 2010) and breeding (e.g. cape gannet *Morus capensis*; Crawford 2007) area for other species. Its consistent productivity between years probably makes this area more attractive for jaegers than other sites. Despite a high marine productivity, the Canary Current is influenced by strong seasonality (Chavez & Messié 2009) and displays important inter-annual variability.

Gilg et al. (2013) suggested that by concentrating their activity at sites heavily used by other seabirds, jaegers may incur additional benefits due to their occasional kleptoparasitic habit, but this hypothesis remains to be validated. Moreover, it is possible

that long-tailed jaegers benefit from fishing vessels, which also concentrate in upwelling and high productivity areas, by feeding on fishing discards from ships (Wiley & Lee 2020). However, this may pose a risk for their survival due to bird bycatch associated with fisheries (Dias et al. 2019).

4.3. Travel speed and phenology

Migratory birds often travel faster in spring than in fall, which allows them to arrive early on the breeding site before competitors and at the optimal time for breeding (Kokko 1999, Alerstam 2011, Nilsson et al. 2013, Schmaljohann 2018). However, our results showed the opposite in long-tailed jaegers, with the fall migration being the faster one, as previously found by Gilg et al. (2013). Jaegers may use this strategy to arrive rapidly at their wintering site and start molting their flight feathers as soon as possible. Although information on molting pattern is limited in this species (Wiley & Lee 2020), van Bemmelten et al. (2018) showed that molt only starts after completion of the fall migration, once birds have reached their wintering site. This pattern is common in long-distance migrants (Alerstam 1990, Kjellén 1994, Newton 2011), including seabirds (Voelker 1997, Lee et al. 2020). As molting can reduce flight efficiency, birds rarely molt flight feathers during long-distance migrations and especially in fall when feathers are old and worn (Newton 2011).

Jaegers traveled a greater distance and spent much more time traveling and on stopovers in spring than in fall. This pattern differs from other seabirds that follow similar migratory paths. For instance, Arctic terns migrate 1.5 times faster in spring than in fall while covering similar distances (Egevang et al. 2010, Hromádková et al. 2020). The slower travel speed in spring and the higher number of daily immersions (more time in contact with saltwater) compared to fall provide evidence that jaegers adopt some sort of fly-and-forage migration strategy in spring (Strandberg & Alerstam 2007). This is especially true after the spring stopover when jaegers increased their number of immersions compared to before the stopover, suggesting a reduction of time spent in flight and an increase in foraging and/or resting on the water. It is unlikely that the fly-and-forage strategy is due to a lower food availability considering the higher marine productivity found at the stopover site in spring compared to fall (Fig. S6; NASA OB DAAC 2018). Jaegers may use a fly-and-forage strategy to increase their feeding effort during the spring migration and the

stopover in anticipation of unfavorable conditions that may prevail upon arrival at the breeding site. Extensive sea-ice cover restricts access to open water in spring in the Arctic. Thus, feeding opportunities are likely limited to a few polynyas or the mouth of thawing rivers in the Baffin Bay and Foxe Basin regions in spring (Hunt 1991, Barber & Massom 2007). On land, lemming density varies considerably between years (Fauteux et al. 2015), and the presence of snow cover in spring greatly reduces their accessibility to avian predators (Therrien et al. 2015). Therefore, the high unpredictability of arctic marine and terrestrial food resources in spring may favor increased feeding at sea during the stopover and the last portion of their migration. This would allow birds to arrive in good body condition and invest in reproduction shortly after arrival while minimizing the risk of starvation (de Korte 1985, Lamarre et al. 2017, Jean-Gagnon et al. 2018). Our results thus support the idea that migratory seabirds that depend on terrestrial prey on their arctic breeding grounds may reduce travel speed in spring to prevent adverse effects on their fitness (Béty et al. 2004, Nuijten et al. 2014, Deng et al. 2019).

In spring, the spread of arrival dates at the breeding site was almost halved compared to the spread of departure dates in late summer (2.5 vs. 5 wk), a pattern typical of what we would expect for most species. In spring, the timing of arrival can be critical because laying date is an important determinant of breeding success, especially in the Arctic due to the shortness of the breeding season (Béty et al. 2004, Reséndiz-Infante & Gauthier 2020). A concentrated arrival period may appear contradictory with their slow travel speed during spring migration. However, jaegers may adjust their arrival date by changing their travel speed near the end of the migration in response to local environmental conditions. Unfortunately, we could not verify this hypothesis due to the lack of positions at high latitudes in spring with the 24 h daylight. In the fall, departure dates may be less critical and depend on weather conditions or food availability on the breeding grounds (Newton 2008).

4.4. Sex variability

Our results suggest no or few sex differences in the phenology, migratory movements, and wintering site. Parental roles in avian reproduction often contribute to sex differences in the migration phenology, with males typically arriving earlier in spring to defend a good territory (Alerstam 2011, Newton 2011, De Felipe et al. 2019). Size dimorphism could also ex-

plain differences in the migratory distance (Müller et al. 2015). The absence of sex-specific differences in jaegers is thus not surprising, as males and females have rather similar roles and investment in reproduction (Furness 1987), and size dimorphism is small (Seyer et al. 2019). The few pairs that we tracked did not migrate together and used different wintering sites most of the time. Thus, pair reunification could also be an additional factor behind the smaller variance in arrival dates during spring compared to the departure dates in late summer. A synchronous arrival should facilitate pair reunification on the breeding territory. Indeed, a long interval between the arrival of pair members may increase the chances that the first arriving bird decides to form a new pair bond to avoid losing a breeding opportunity (Choudhury 1995, González-Solís et al. 1999).

4.5. Negative impact of satellite transmitters

The signal of all individuals marked with satellite transmitters was lost within a few weeks after the start of the fall migration, as also reported by Sittler et al. (2011) on the same species. Despite important field efforts to monitor jaegers for >10 yr at the breeding site, none of the 10 marked individuals was ever resighted, unlike individuals marked with geolocators (minimum return rate of 74 %, n = 70). This strongly suggests that satellite transmitters installed as backpack harnesses had a negative impact on the survival of long-tailed jaegers, as reported in other seabirds (great skuas, Thaxter et al. 2016; herring gulls *Larus argentatus*, Anderson et al. 2020). Thaxter et al. (2016) suggested that a reduction in flight agility and foraging efficiency could have affected the kleptoparasitic behavior of skuas. It is also possible that the device and/or the harness affected flight performance during their long migration, created friction on the skin, or compromised insulation due to feather wear, thus increasing mortality due to exhaustion (Thaxter et al. 2016). If plumage gets damp, pelagic seabirds do not have the possibility to rest on land to dry, which may rapidly lead to death due to chilling. Even though satellite transmitters respected the 3% of body mass rule (Phillips et al. 2003), this additional weight may also have affected survival through an increase in energy expenditure during their long migration. However, transmitters apparently had a minimal effect on travel speed and migration phenology since these parameters were similar to those of individuals tracked with geolocators during early migration. Nonetheless, for future research on long-tailed jaegers, we strongly

recommend the use of small and light devices such as geolocators to avoid the problems reported here and by Sittler et al. (2011).

5. CONCLUSIONS

We reported for the first time migratory movements of long-tailed jaegers breeding in the Canadian Arctic. Only a few arctic seabirds are long-distance trans-equatorial migrants like long-tailed jaegers (Egevang et al. 2010, Stenhouse et al. 2012, Davis et al. 2016, Hromádková et al. 2020). Although several of these species share similar migratory paths and stopover areas (Davies et al. 2021), the optimal migration strategies appear species specific. Contrary to most other species, the fall migration of arctic-nesting jaegers was 46% faster and more direct than the spring migration. A time-minimizing strategy in fall may be partly favored by the need to molt as soon as possible after the completion of the migration. In spring, a fly-and-forage strategy could be the best strategy, as higher foraging effort during migration may allow birds to arrive in the Arctic in good body condition, hence in a better position to face unpredictable and adverse environmental conditions.

Documenting travel paths of long-distance migrating seabirds allows the identification of key areas for the conservation of these species, such as the eastern end of the Grand Banks of Newfoundland or the Benguela Current in the case of long-tailed jaegers. This provides baseline information to evaluate how threats such as climate warming or increased fishing activity may potentially affect these distant areas and ultimately the seabirds using them. Furthermore, integrating events and constraints faced during the entire annual cycle can increase our ability to explain variations in migration strategies used by seabirds or demographic trends observed at their breeding site due to carry-over effects. Ultimately, this will improve our ability to take proper conservation actions when needed.

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