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Research article

Multi-colony tracking of two pelagic seabirds with contrasting flight capability illustrates how windscapes shape migratory movements at an ocean-basin scale

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Migration is a common trait among many animals allowing the exploitation of spatiotemporally variable resources. It often implies high energetic costs to cover large distances, for example between breeding and wintering grounds. For flying or swimming animals, the adequate use of winds and currents can help reduce the associated energetic costs. Migratory seabirds are good models because they dwell in habitats characterized by strong winds while undertaking very long migrations. We tested the hypothesis that seabirds migrate through areas with favourable winds. To that end, we



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used the SEATRACK dataset, a multi-colony geolocator tracking dataset, for two North Atlantic seabirds with contrasting flight capabilities, the black-legged kittiwake *Rissa tridactyla* and the Atlantic puffin *Fratercula arctica*, and wind data from the ERA5 climate reanalysis model. Both species had on average positive wind support during migration. Their main migratory routes were similar and followed seasonally prevailing winds. The general migratory movement had a loop-shape at the scale of the North Atlantic, with an autumn route (southward) along the east coast of Greenland, and a spring route (northward) closer to the British Isles. While migrating, both species had higher wind support in spring than in autumn. Kittiwakes migrated farther and benefited from higher wind support than puffins on average. The variation in wind conditions encountered while migrating was linked to the geographical location of the colonies. Generally, northernmost colonies had a better wind support in autumn while the southernmost colonies had a better wind support in spring, with some exceptions. Our study helps understanding how the physical environment shapes animal migration, which is crucial to further predict how migrants will be impacted by ongoing environmental changes.

Keywords: animal movement, bird flight, *Fratercula arctica*, migration, *Rissa tridactyla*, wind

Introduction

Wind is involved in numerous biological processes, in particular with regards to the movements and dispersal of individual organisms, and can therefore act as a strong driver of species distribution (Chapman et al. 2010), genetic diversity (Kling and Ackerly 2021), and evolution (Di Musciano et al. 2020). Wind patterns can for instance explain the biodiversity of passively dispersed species, with prevailing winds influencing community composition over vast areas (Muñoz et al. 2004, Chapman et al. 2015, Epele et al. 2021, Kling and Ackerly 2021). While micro-organisms, plants (seeds and pollen), and some wingless arthropods can only drift passively while being transported by wind, flying animals can adjust their behaviour to wind conditions and optimize their use of the airflow to reduce their movement costs (Liechti 2006, Chapman et al. 2011). Wind conditions can affect the movement behaviour of flying birds at various spatiotemporal scales, from short foraging trips (Tarrowx et al. 2016, Hedrick et al. 2018, Collins et al. 2020) to long migrations (Sjöberg et al. 2021). Seabirds are well-known to take advantage of wind for movement, especially since their marine habitats are often characterised by strong winds (Felicísimo et al. 2008, Weimerskirch et al. 2012, Hromádková et al. 2020). Seabirds are thus particularly well suited to study the effects of wind conditions on flight behaviour, and in particular the extent to which the use of wind conditions encountered along migratory routes is optimised (Alerstam 2011).

Given the high energetic costs of flying, optimizing flight behaviour according to wind conditions may be critical for long-distance migrants (Newton 2010). Models simulating migrations show that routes with favourable winds effectively reduce travel time even when they are not the shortest ones (Kranstauber et al. 2015), and a large number of tracking studies now suggest that many long-distance migrants favour longer routes, but with better wind assistance (Shaffer et al. 2006, Egevang et al. 2010, Shamoun-Baranes et al. 2017, Vansteelant et al. 2017, Hromádková et al. 2020). These routes with favourable wind conditions are shared by multiple species and represent major migratory flyways (Newton 2010, Shamoun-Baranes et al. 2017).

The wind predictability (temporal variability in wind conditions) is an important aspect because it allows addressing questions about how migratory birds adjust to wind conditions at larger temporal scales (Kranstauber et al. 2015). At global scale, wind patterns are relatively predictable and reflect the general atmospheric circulation (Ahrens 2014). In the Northern Hemisphere, prevailing winds blow north eastwards at latitudes between 30° and 60° (westerlies), and southwards at higher latitudes. For example, in the North Atlantic westerlies flow from North America to northern Europe, while around Greenland winds blow predominantly from the north (Fig. 1). In other areas such as the Barents and Norwegian Seas, winds are more variable and blow from various directions throughout the year (Fig. 1). Consequently, wind conditions encountered during migration for seabirds from various colonies in the North Atlantic are expected to be contrasting. For example, some well-known wintering grounds such as the Grand Banks, the Greenland Sea, or the North Sea, are shared by seabirds from different colonies (Frederiksen et al. 2012, 2016, Fort et al. 2013, Fayet et al. 2017, Merkel et al. 2021) which are expected to have different migratory routes and likely encounter distinct wind conditions during migration between their breeding and wintering grounds. Such differences in encountered wind conditions during the non-breeding season could have carry-over effects on subsequent breeding attempts or influence adult survival, and ultimately impact population dynamics (Bogdanova et al. 2017, Desprez et al. 2018, Reiertsen et al. 2021).

Many studies have modelled the energetic costs of flight under varying wind conditions and at fine spatiotemporal scale based on biologging data. It was found that flying with headwinds not only decreases the ground speed, but also increases the flight duration and the associated energetic expenditure (Weimerskirch et al. 2000, Amélineau et al. 2014). Selecting routes with favourable wind conditions might thus not only reduce the duration of migration, but also the energetic costs of flight (Shamoun-Baranes et al. 2017). For flapping flight, energetic costs were also higher with stronger headwinds (Elliott et al. 2014). How migrant birds respond to wind conditions will therefore also depend on their flight mode (e.g. flapping, glide-flapping or soaring),

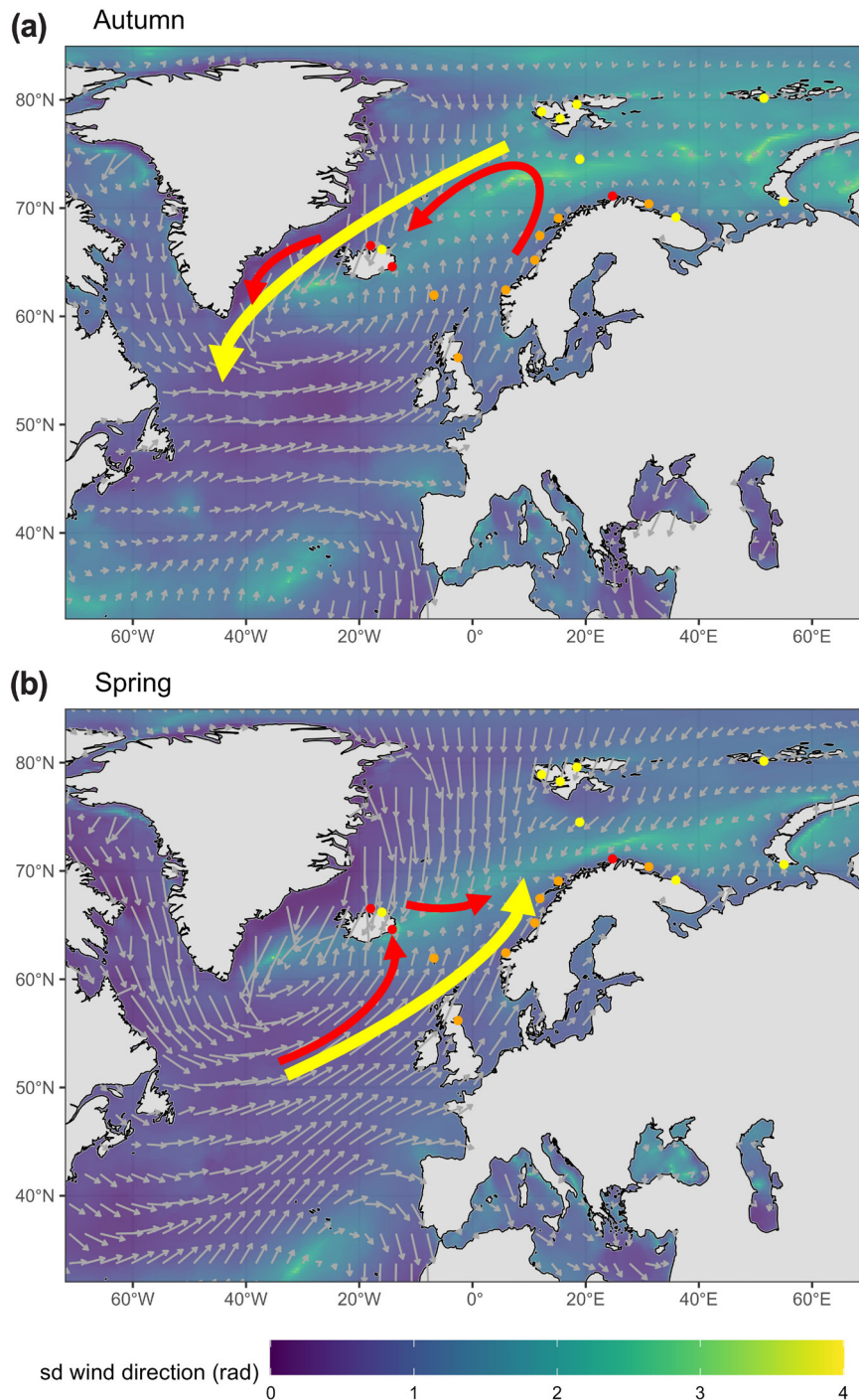


Figure 1. Wind patterns and main migratory movements in the North Atlantic during autumn (a) and spring (b). Main migratory movements of kittiwakes (yellow arrows) and puffins (red arrows) are based on the migratory segments presented in Fig. 2. Grey arrows represent wind direction and speed. Background colour represent the SD in wind direction (rad), with a dark colour representing a low variability in wind direction and a light colour a high variability in wind direction. Dots represent colonies with kittiwakes (yellow), puffins (red) and both species (orange). Mean wind direction and speed were calculated from the monthly means of the ERA5 dataset for the study period (2014–2020); autumn includes August to November (outbound migration) and spring December to April (inbound migration).

their body mass, aspect ratio (wing length divided by wing width) and wing loading (body mass divided by the area of the wing) (Bowlin and Wikelski 2008, Horton et al. 2018). Migrants can further adjust their behaviour to wind

conditions by waiting for optimal wind conditions to engage in migration (Gill et al. 2009), selecting an altitude with favourable winds (Mateos-Rodríguez and Liechti 2012), or, when possible, landing and waiting when winds are

unfavourable (Shamoun-Baranes et al. 2017, Geisler et al. 2022). Furthermore, if the prevailing winds are stable throughout the year, wind conditions along a given route are likely to be more favourable during either the outbound or the inbound migration. Having more favourable winds during the inbound migration might ensure higher fitness, allowing earlier arrival at the colony which is generally associated with higher breeding success (Kokko 1999, Verhulst and Nilsson 2008) or reducing energy expenditure, hence leading to a better body condition at the start of the breeding season, and subsequently a higher reproductive output (Drake et al. 2014, de Zwaan et al. 2022).

Understanding how much the physical environment influences movement is one of the key questions in marine vertebrate ecology (Hays et al. 2016) and is important for our understanding of how animals migrate (Bowlin et al. 2010). The overall goal of this study was to investigate the relationships between wind conditions and seabird migratory movements at the scale of the North Atlantic Ocean. Our study utilizes a long-term, multi-colony and multi-species tracking dataset developed under the SEATRACK project (Strøm et al. 2021). We selected as study models two pelagic seabirds that are long-range migrants but with different flight capacity, the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) and the Atlantic puffin *Fratercula arctica* (hereafter puffin). Both species use flapping (as opposed to glide-flapping or soaring) flight, but differ in morphology (wing area, wingspan, general body shape), wing loading, and flight speed (Pennycuik 1987). While kittiwakes are surface feeders, puffins are wing-propelled divers. Puffin wings are shorter and their wing loading higher, resulting in very high flight costs (Elliott et al. 2013). Despite the high flight costs, seabirds with a higher wing loading can fly with higher wind speeds (Nourani et al. 2023), and have a lower increase in airspeed when headwinds increase (Spear and Ainley 1997a). Thus, it seems that a higher wing loading confers a higher tolerance to unfavourable wind conditions and reduces the benefits of wind support. We therefore expected that wind conditions might affect the migratory flight behaviours of puffins and kittiwakes differently.

Our main hypothesis was that kittiwakes and puffins take advantage of favourable wind conditions when they migrate. We predicted that both kittiwakes and puffins would prefer routes that provide wind support during their migration bouts and have on average a positive wind support at the species level. We expected windscapes to differ between birds of different colonies, depending on where they were located relative to prevailing winds and key wintering areas, with larger differences for colonies situated further away from each other. We also expected differences between seasons, as prevailing wind patterns in the subpolar North Atlantic region remain relatively similar throughout the year, formed by the polar easterlies and the northern extreme of the westerlies, while birds migrate in opposite directions during autumn and spring. Finally, we predicted that puffins could face less favourable wind conditions than kittiwakes on average, linked to their higher wing loading.

To test our hypothesis, we compared migratory routes of kittiwakes and puffins with wind patterns in the North Atlantic extracted from global climate models produced by the European Centre for Medium-Range Weather Forecasts (ERA5; Hersbach et al. 2020). First, we mapped and described the general migratory and wind patterns (obj. 1) as well as the average wind support encountered by migrating seabirds (obj. 2) at the scale of the North Atlantic Ocean. Then, using a cluster analysis, we investigated the similarities in encountered windscapes between colonies (obj. 3). Finally, we investigated the differences in wind support among species and seasons (autumn/outbound and spring/inbound migration) (obj. 4).

Material and methods

Bird tracking data

We used data collected by the SEATRACK project between 2014 and 2020. In total, 794 kittiwakes and 425 puffins from 18 colonies (Supporting information) were equipped with geolocators attached on a ring, and recaptured in following breeding seasons. Models of geolocators were c65, c65_super, f100 and w65 produced by Migrate Technology, mk18 produced by BAS, and mk4083 and mk4093 from Biotrack (Supporting information). All of these models recorded light and saltwater immersion data. Details on the logger types, number of deployments per colony and frequency of data acquisition are presented in the Supporting information. The median number of annual tracks per individual (a track being defined as data recorded between two successive breeding seasons) was two (range 1–6 tracks per individual, Supporting information).

Positions were estimated from raw light data based on an automatic processing fully described in Bråthen et al. (2021). This method estimates positions based on a threshold method (Lisovski et al. 2020) and filters inaccurate locations based on speed, angle and position. An error of 200–250 km is expected for these latitudes (Halpin et al. 2021). As latitude is inaccurate during equinoxes (Lisovski et al. 2020), periods between 8 September–20 October and 20 February–3 April were removed. Gaps were also present in the data when tracked individuals were north of the Arctic Circle in the winter or summer due to polar night or midnight sun. Missing locations were interpolated based on the informed random movement algorithm (IRMA), fully described in Fauchald et al. (2019) and based on an algorithm that was originally developed by Technitis et al. (2015). Six kittiwakes breeding in Kara Gate (Novaya Zemlya) and migrating to the Pacific (Ezhov et al. 2021) were excluded from the current study, which is focused on the North Atlantic. For each track, we selected only one location per day (midnight) to compute the daily movement vectors. As kittiwakes and puffins fly mostly during the day, we decided to keep only positions at night; we then extracted the wind conditions at the midpoint between two successive nightly positions to get an accurate estimate of winds encountered during the day.

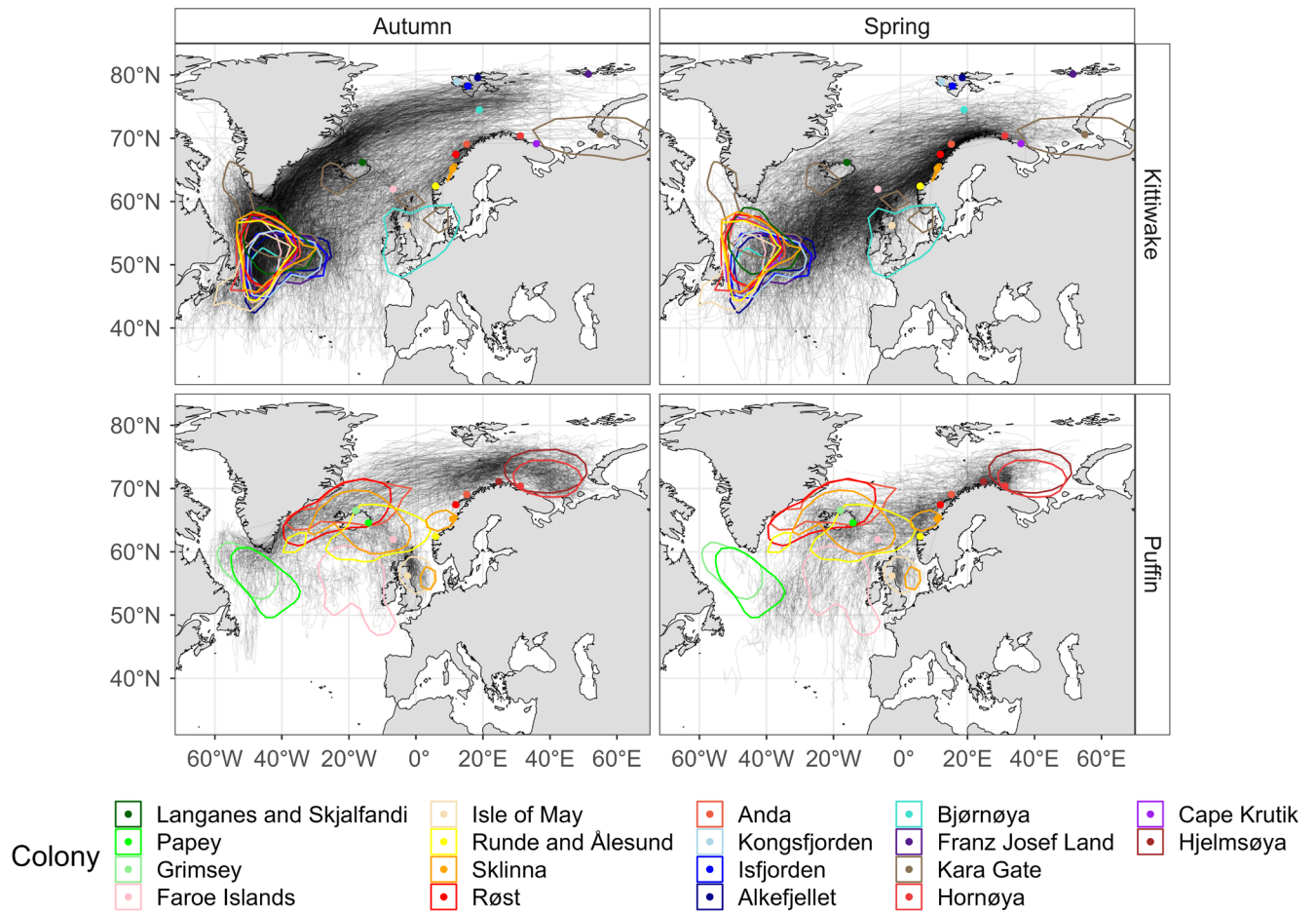


Figure 2. Maps showing all migratory segments (black lines) in autumn (left) and spring (right) for kittiwakes (top row) and puffins (bottom row), together with winter distribution of each breeding population plotted as colony coloured 50% kernel utilisation distribution.

Only periods when birds were migrating (hereafter migratory segments) were included in the analyses (Fig. 2). First, we excluded the breeding season based on saltwater immersion data, for each colony, species and year (Fauchald et al. 2019), as well as December and January for puffins as there were no clear migratory movements on average during these months. We then followed the method of Amélineau et al. (2021) to identify migratory segments and exclude stationary periods during the remaining months for each track. Based on the excluded periods, seasons were defined as follows for each species: autumn contained data from August to November for kittiwakes, and from July to November for puffins; spring contained data from December to April for kittiwakes, and from February to May for puffins. For each migratory segment, we calculated the detour by dividing the total length of the migratory segment (cumulative sum of the distances between successive locations) by the shortest distance between the departure and arrival locations. For each individual, the overall migratory distance was calculated as the cumulative distance between the centroids of successive stationary periods (the first and last stationary periods being the breeding season at the colony) and represents the whole non-breeding season. Distances were calculated as great circle

distances using the function *distGeo* from the ‘geosphere’ package (Hijmans 2021). For each colony and species, the winter distribution (Fig. 2) was calculated as the 50% utilisation distribution kernel calculated on the December positions with the ‘adehabitatHR’ package (Calenge 2006), using a smoothing factor (h) of 200km, a grid with 50×50 km cells and a Lambert azimuthal equal area coordinate system.

Wet/dry sensors of the geolocators were used to calculate the proportion of time spent wet per 24 h, which gives an approximation of the proportion of time spent on the water and in the air.

Wind data

We used wind from the ERA5 model (Hersbach et al. 2020), a reanalysis model from the European Centre for medium-range weather forecast (ECMWF). Data were obtained from the climate data store (<https://cds.climate.copernicus.eu/>). Wind data of the ERA5 model are available at 10 m (surface winds), 100 m, and higher altitudes. We chose winds at 10 m as previous studies found a median flight altitude of 16 m (range 0–81 m) for kittiwakes (Borkenhagen et al. 2018), and < 10 m for puffins (Johnston et al. 2014). We extracted

the hourly u (east) and v (north) components of surface wind (10 m height) on a 0.25° grid over the study area. We then calculated the daily mean u and v wind components. To get wind conditions encountered along the track, we calculated the midpoint between two successive locations, and extracted the daily mean wind at this midpoint. We then defined the wind support as the wind vector component in the direction of the track, and the cross-wind as the wind vector component perpendicular to the track (Fig. 3) (Safi et al. 2013), assuming a complete compensation.

To calculate expected wind conditions, we used monthly average u and v components of surface wind (10 m) available from the ERA5 model for the study period (2014–2020, 0.25° resolution). For each month, we calculated the monthly SD of the wind direction (index of the variability of the wind direction) with the *sd.circular* function of the ‘circular’ package in R (www.r-project.org, Agostinelli and Lund 2022) and the monthly averaged wind speed (scalar mean) for the whole study period, and extracted these values at each position.

Cluster analysis

A K-means cluster analysis (Hartigan and Wong 1979) was performed to investigate similarities between colonies in wind conditions and seabird behaviour during migration (Supporting information). For each species and season, variables included in the cluster analysis encompassed daily wind conditions encountered (wind support, cross wind, wind speed), bird behaviour (mean proportion wet per 24 h, detour)

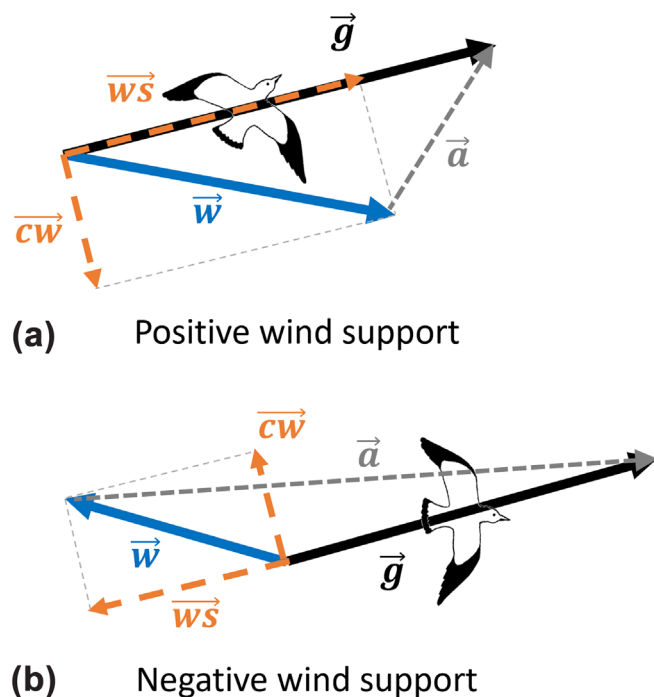


Figure 3. Calculation of the wind support in a case of positive wind support (a) and negative wind support (b). \vec{g} : ground speed, \vec{a} : airspeed, \vec{w} : wind speed, \vec{ws} : wind support, \vec{cw} : crosswind.

and average wind conditions based on interannual monthly wind during the study period 2014–2020 (SD of wind direction and scalar average wind speed at each location). Variables were aggregated by calculating, for each season and species, the median value per migratory segment (except for detour where we already had one value per segment), track, year and colony. Each variable was then normalized. The function *fviz_nbclust* of the R package ‘factoextra’ (www.r-project.org, Kassambara and Mundt 2020) was used to detect the optimal number of clusters.

Statistical analyses

All analyses were performed in R ver. 4.1.2 (www.r-project.org).

We investigated the variation in wind support between seasons and species. We worked at the scale of an annual track, with one median value per track and per season. We fitted linear mixed-effects models with the *lmer* function of the ‘lme4’ package (Bates et al. 2015). To take the lack of independence in our data into account (repeated measurements per individual, per colony and per year), we included a random effect of year, and a random effect of individual nested in colony (Zuur et al. 2009). We considered all combinations of covariates. We then used AIC (Akaike’s information criterion) for model selection. If the difference in AIC values between two models was < 2 , the models had equal statistical support and in case of nested models, the simplest was preferred (Burnham and Anderson 2002). We detected no pattern in the distribution of model residuals indicating that the normality and homoscedasticity assumptions were met. The ‘MuMin’ package was used to generate the marginal R^2 (variance explained by the fixed effects) and the conditional R^2 (variance explained by the fixed and random effects) (Bartoń 2022). Unless otherwise mentioned, results are presented as median and 95% confidence interval. The presented maps have a plate carrée projection.

Results

Seabird migratory routes and wind patterns in the North Atlantic (Obj. 1)

The migratory movements were generally directed toward the southwest in autumn, and the northeast in spring for both species (Fig. 2). Spring migration routes differed from autumn migration routes and the overall movement had a loop-shape, which appeared to correspond very well to the wind circulation patterns over the North Atlantic during these periods (Fig. 1). The wind circulation patterns are similar during both periods, following a generally circular and anti-clockwise pattern (Fig. 1). The prevailing winds follow the eastern coast of Greenland southwards, and the main autumn migratory movements of kittiwakes and puffins followed these winds between Greenland and Iceland. Some birds of both species from Norwegian colonies flew first to the Barents Sea before migrating south through the Greenland Sea. Between Newfoundland and mainland Europe, prevailing winds blow

towards the northeast. The main migratory movements of kittiwakes and puffins followed these prevailing winds in spring, heading further east towards the British Isles and Norway, except for puffins overwintering north of Iceland who headed east without following the prevailing winds in this area (Fig. 1, 2). Our results provide clear evidence for an anti-clockwise migration movement pattern in kittiwakes and puffins when considering both seasons and all our study colonies (Fig. 2).

Wind supports encountered by seabirds in the North Atlantic (Obj. 2)

To get a better overview of winds encountered during migration, and whether they helped or hindered the movement,

we plotted the average direction of bird movements and average wind support encountered per species and season in the North Atlantic (Fig. 4). For both species and seasons, there was large spatial variation in encountered wind support. Some fly paths had a higher wind support, mainly birds flying southwards along the east coast of Greenland in the autumn, and birds following the westerlies in the spring. In contrast, birds flying south of Iceland in the autumn had negative average wind support, and the same applied to birds flying northward between Iceland and Greenland in the spring. In the Barents Sea, the wind support was generally low and negative. Due to the regional variation in wind support, we expected differences in the windscapes experienced by birds from distinct colonies.

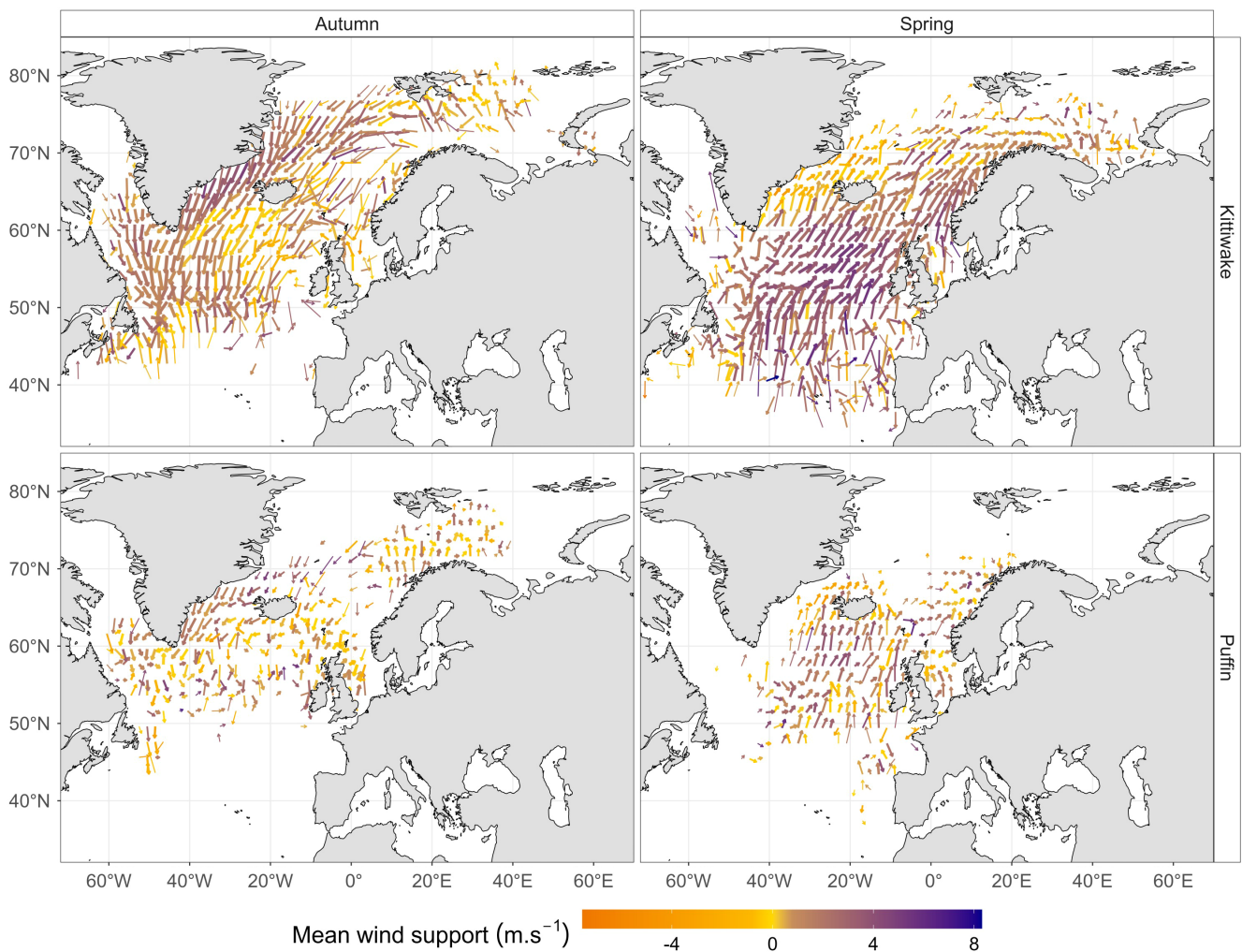


Figure 4. General bird movement patterns and associated wind support for kittiwakes in autumn (top left) and spring (top right), and puffins in autumn (bottom left) and spring (bottom right). The study area was divided into a grid ($2 \times 2^\circ$ resolution). Each vector represents the mean speed and direction of bird movement at all the bird positions within a given cell. The colour of the vector represents the average wind support encountered by all individuals located in the cell. Cells with few observations (≤ 5) were removed to avoid bias due to low sample size. We first calculated the average speed and wind support per colony, and then averaged values for all colonies. The longer an arrow, the more birds flying in the mean direction. Short arrows indicate birds at the given location moving in different directions, and the resulting direction of the average movement is only partially informative. The thickness of the arrow represents the amount of data for each cell (thin = small amount of data, thick = large amount of data).

Intra-colony variations in windscares (Obj. 3)

In autumn, kittiwake colonies could be grouped in five clusters (Fig. 5a–b, Supporting information). Our results show clear differences among these clusters in several parameters linked to wind and migratory behaviour. The wind support was in general slightly higher for kittiwakes breeding in the Barents Sea colonies (2.12 m s^{-1} [1.71–2.71] for Spitsbergen and Franz Josef Land (cluster E), and 2.07 m s^{-1} [1.77–2.49] for Anda, Hornøya and Cape Krutik (cluster C)), except for Bjørnøya and Kara Gate that had a lower wind support (1.26 m s^{-1} [–0.49 to 1.61], cluster D). The wind support was also low for birds from Isle of May, Ålesund and Sklinna (0.89 m s^{-1} [0.41–1.47], cluster A). The wind direction was highly variable for kittiwakes from Bjørnøya and Kara Gate (median SD: 59.6° [58.4–63.0], cluster D), whereas the lowest variability was found for colonies in the southwestern parts of the study area (median SD: 32.1° [28.6–37.8] for Iceland, Faroes and Røst (cluster A), median SD: 32.7° [29.2–35.5] for Isle of May, Ålesund and Sklinna (cluster B), Supporting information).

In spring, kittiwake colonies were grouped in four clusters (Fig. 5c–d, Supporting information). The wind support was higher for kittiwakes from the Norwegian west coast (5.52 m s^{-1} [5.00–6.18], cluster B), and the southwest (Iceland and North Sea: 3.95 m s^{-1} [3.42–4.46], cluster A), intermediate for the Barents Sea (excluding Bjørnøya and Kara Gate: 2.27 m s^{-1} [1.44–3.26], cluster C) and lowest

for Bjørnøya and Kara Gate (1.39 m s^{-1} [1.17–1.84], cluster D). The wind direction was most variable for kittiwakes from Bjørnøya and Kara Gate (median SD: 51.6° [47.6 – 57.3], cluster D), and less variable for the kittiwakes from the southwest (median SD: 30.4° [28.6 – 30.9], cluster A, Supporting information).

In autumn, puffins were grouped in four clusters (Fig. 5e–f, Supporting information). The wind support was lower for birds from the Isle of May and the Faroes (0.46 m s^{-1} [0.04–0.75], cluster B), intermediate for birds from Iceland (0.66 m s^{-1} [–0.08 to 1.18], cluster A) and higher for birds from the Barents Sea (0.81 m s^{-1} [0.41–1.69], cluster D) and western Norway (0.94 m s^{-1} [0.61–1.20], cluster C). Wind direction showed strong variability for birds migrating from the Norwegian colonies (median SD: 78.5° [74.5–83.1] for Runde, Sklinna, Røst and Anda (cluster C), median SD: 80.8° [75.1–84.2] for Hjelmsøya and Hornøya (cluster D)), while it was moderately variable for birds from the Isle of May and the Faroes (median SD: 53.9° [53.3–57.9], cluster B), and less variable for birds from Iceland (median SD: 38.4° [32.7–40.1], cluster A, Supporting information).

In the spring, puffins were grouped in two clusters (Fig. 5g–h, Supporting information). Puffins from Iceland experienced higher wind support (1.50 m s^{-1} [0.88–2.77], cluster A, versus 0.78 m s^{-1} [0.41–1.10] for other colonies, cluster B). The wind direction was more predictable for puffins from Iceland (median SD: 40.1° [36.7–43.5], cluster A, versus 60.2° [58.4–64.7] for other colonies, cluster B).

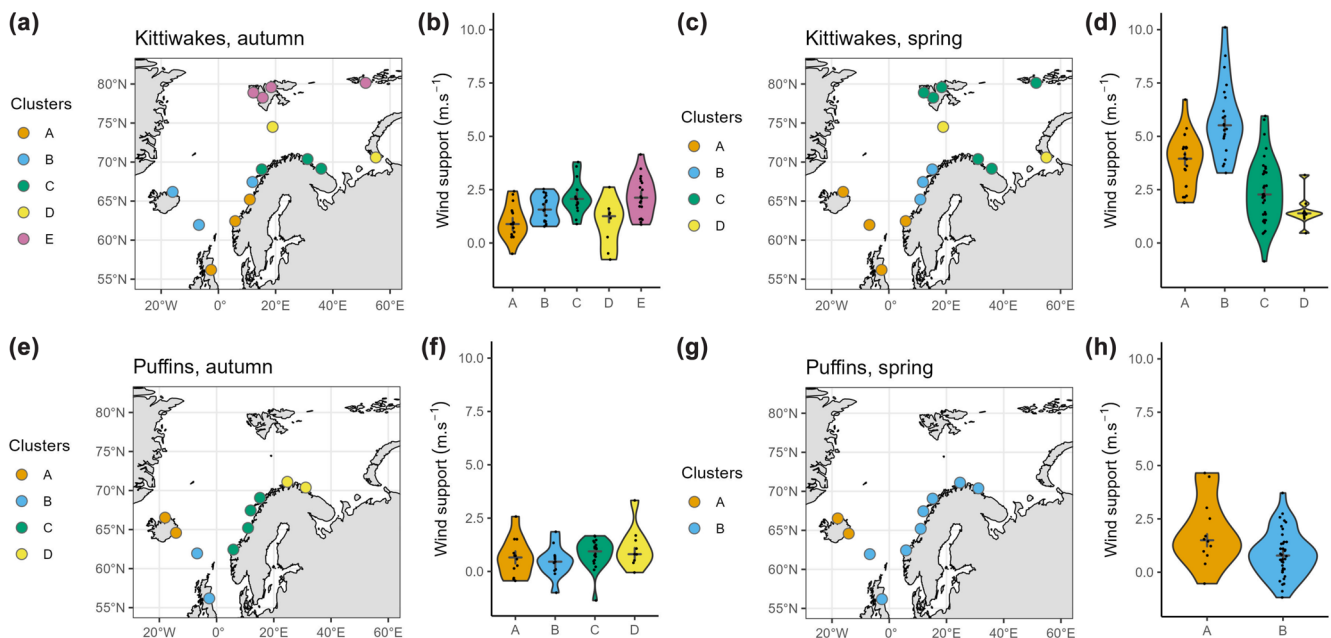


Figure 5. Result of cluster analysis to investigate similarities in windscares encountered by kittiwakes (a)–(d) and puffins (e)–(h) from different colonies during autumn and spring migrations. Cluster analysis was made with a median value per colony of wind support, cross wind and wind speed (representing encountered wind conditions), mean proportion wet and detour (representing bird behaviour), and SD of wind direction and scalar average wind speed (representing average wind conditions). (a, c, e, g) location of the colonies and associated clusters by species and season; (b, d, f, h) violin plots showing for each cluster the distribution of the annual median of wind support (m s^{-1}) per year and colony. Grey crosses represent median for each cluster. Black dots represent median values per colony and per year.

Differences in wind support between seasons and species (obj. 4)

The wind support varied between species and seasons, and the seasonal difference in wind support was not the same for both species (i.e. the best model included a species \times season interaction; Table 1a–b). Both kittiwakes and puffins experienced a positive wind support on average during both autumn and spring migrations, and the wind support of kittiwakes was 2.7 times higher than the wind support of puffins (kittiwakes: 2.66 m s^{-1} [2.54–2.78] ; puffins: 0.98 m s^{-1} [0.85–1.10]). In addition, we observed seasonal differences. The wind support of kittiwakes was twice as large in spring than in autumn (3.61 m s^{-1} [3.43–3.80] versus 1.72 m s^{-1} [1.58–1.86], Fig. 6). In comparison, puffins only had a slightly higher wind support in spring than in autumn (1.13 m s^{-1} [0.91–1.34] versus 0.84 m s^{-1} [0.69–1.00], Fig. 6).

Discussion

Our results highlight the importance of winds in shaping migratory routes in two seabird species despite their different flight capacity, suggesting that winds affect migration patterns across a wide range of species. Indeed, kittiwakes and puffins shared the same migratory pathways, following the prevailing winds in the North Atlantic. They had on average favourable wind conditions during their migratory movements, although puffins had generally lower wind support than kittiwakes. While both species experienced higher wind support during spring than autumn, there were also differences in wind support among colonies, depending on their location.

Migratory corridors reflect prevailing winds favouring migratory movements

Kittiwakes and puffins had on average a positive wind support during both autumn and spring migrations. Main migratory routes were shared by both species and corresponded to areas where prevailing winds blew in a favourable direction. The general movement had a loop-shape, with birds flying southwards along the east coast of Greenland in the autumn and flying northwards along the coasts of the British Isles and

Norway in the spring. Birds that took other routes, such as birds flying northwards between Greenland and Iceland in the spring, or birds flying southwards southeast of Iceland during the autumn, had a negative wind support. The migratory corridors identified in our study are shared not only by these two species, but by other seabird species such as little auks *Alle alle*, Brünnich's guillemots *Uria lomvia* and long-tailed skuas *Stercorarius longicaudus* (Gilg et al. 2013, Amélineau et al. 2021).

Wind corridors have also been identified in other ocean basins. Some examples are the eight-shaped loop corridors of terns (Sternidae), Cory's shearwaters *Calonectris borealis* and skuas (Stercorariidae) across the Atlantic (Felicísimo et al. 2008, Wong et al. 2021), and of sooty shearwaters *Ardeenna grisea* in the Pacific (Shaffer et al. 2006), as well as the circumpolar migration of wandering albatrosses *Diomedea exulans* following westerlies in the Southern Ocean (Weimerskirch et al. 2015).

Terrestrial birds and insects also follow most favourable wind corridors and can have a different route between autumn and spring migrations (Stefanescu et al. 2013, Chapman et al. 2015, Kranstauber et al. 2015, Åkesson et al. 2016, Vansteelant et al. 2017). In soaring terrestrial birds, migratory corridors are also dependent on the presence of updrafts and thermals, and tend to follow land topography favouring the formation of orographic updrafts and thermals (Nourani and Yamaguchi 2017). Flying with favourable winds is an efficient way to reduce both the costs of moving and the duration of migration.

Geographical variation in winds and migratory behaviour

Inter-colony variation in wind conditions encountered while migrating was linked to the geographical location of the colonies. Birds from colonies situated at higher latitudes had in general higher wind support during autumn and lower wind support during spring than birds from colonies situated at lower latitudes, according to where the colonies were located relative to the favourable prevailing winds. There were however some exceptions. Puffins from Isle of May, Hjelmsøya and Hornøya migrated in several directions from the colony during the non-breeding season (dispersive migration). This

Table 1. Summary of the statistical model explaining wind support as a function of species and season. (a) model selection, (b) parameter estimation. The model with the lowest AIC is indicated in bold. Npar: number of parameters; CI: confidence interval. The marginal R^2 (variance explained by the fixed effects) was 0.14, and the conditional R^2 (variance explained by both fixed and random effects) was 0.22

(a) Models	npar	AIC	deltaAIC
season \times species	8	23072.04	0.00
season + species	7	23142.57	70.53
Season	6	23370.18	298.14
species	6	23376.20	304.16
intercept	5	23610.68	538.64
(b) Parameters	Estimate	2.5% CI	97.5% CI
Intercept	0.54	−0.04	1.11
season_spring	0.26	−0.05	0.57
species_kittiwake	1.24	0.93	1.55
season_spring:species_kittiwake	1.64	1.26	2.01

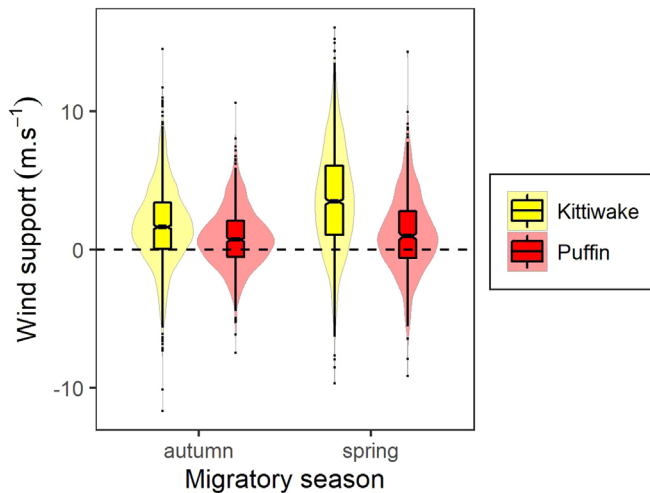


Figure 6. Wind support per species and migratory season. Boxplots show the median (thick line), the first (25%) and third (75%) quartiles (box), the lowest and highest values within 1.5 interquartile range (vertical segments) and outliers (dots). Notches represent the 95% confidence interval of the median ($1.58 \times \text{interquartile range}/\sqrt{n}$).

contrasted with other colonies where birds from a given colony followed similar migratory routes and travelled over longer distances (Amélineau et al. 2021). While this behaviour is likely linked to the availability of resources, it could also reflect more unpredictable winds around these colonies. This is especially the case in the Barents Sea, where wind was least predictable. For kittiwakes, two colonies in the Barents Sea had a different migratory behaviour: Kara Gate and Bjørnøya. Contrary to all other kittiwake colonies for which the majority of individuals migrated to the Grand Banks area, many kittiwakes from Bjørnøya and Kara Gate migrated to the North Sea, and some from Kara Gate stayed at high latitudes during the winter (Fig. 2) (Amélineau et al. 2021). Kittiwakes from these two colonies had a particularly low wind support, especially in the spring, as well as a very high variability of the direction of encountered wind. This migratory behaviour contrasts with kittiwakes from other colonies of the Barents Sea such as Spitsbergen or Franz Josef Land, that travel to the Grand Banks during the winter and encounter higher wind support and more predictable winds. Overall, migration destination will be a tradeoff between the relative profitability of the breeding and wintering grounds, and the costs of travelling between them. If in some cases birds seem to be making sub-optimal decisions in terms of travel costs, it could be because the increase in profitability at the destination offsets travel costs. Such differences in migratory distance and wind conditions encountered are likely resulting in different energetic balance, and may have further implications for subsequent timing of breeding, carry-over effects, or survival (Alerstam 2011, Weimerskirch et al. 2015, Fayet et al. 2017) but see (Dufour et al. 2021). Such differences in windscapes will be larger for colonies that are further away from each other, compared to colonies that are closer to each other.

The use of windscapes varies among species

Puffins had a lower wind support than kittiwakes during both autumn and spring migrations, suggesting that they used wind conditions differently during migration. The main differences between the two species are their foraging mode and their morphology. Puffins are divers, and their wings, used for swimming and flying, are shorter compared to kittiwakes that are surface feeders and forage from the air. As a consequence, puffins have a higher wing loading (Pennycuik 1987). Puffins could be less selective towards favourable winds due to their higher wing loading, as birds with higher wing loading have a lower increase in airspeed (and thus energetic costs) when wind speed increases or when wind direction is less favourable (Spear and Ainley 1997a). Moreover, their migratory range is different, with puffins migrating shorter distances than kittiwakes (Amélineau et al. 2021). During migratory bouts, puffins spend also less time flying daily (18% on average, versus 30% in kittiwakes) and have a lower movement rate (6.25 km h^{-1} on average, versus 12.37 km h^{-1} in kittiwakes (Amélineau et al. 2021)). The best strategy for puffins could be to use more direct routes with low wind support, which could be beneficial for shorter distance migration, while when migrating farther and faster such as the kittiwakes, it could be more advantageous to have a route with better wind support. Their different migratory strategies are linked to a different use of wind.

More generally, wing shape seems under selective pressure in migrants: migratory birds tend to have more pointed wing-tips (Lockwood et al. 1998, Sheard et al. 2020) and migratory insects tend to have higher aspect ratio than non-migrants (Le Roy et al. 2019), although this is not always the case as other selective pressures can impact wing shape, such as the need for manoeuvrability in stationary habitats (Le Roy et al. 2019), or the use of wings to swim (Elliott et al. 2013). Ultimately, wing shape will be linked to flight abilities and the use of winds (Spear and Ainley 1997b, Dehnhard et al. 2021).

A higher wind support in the spring

For both species, wind support was higher during spring than autumn. This has also been observed in other species such as Arctic terns *Sterna paradisaea* (Hromádková et al. 2020), and nocturnal terrestrial migrant birds through Europe (Kemp et al. 2010). The fact that winds were more favourable during the inbound migration can be linked to prevailing winds at the latitudes where these species migrate (Kemp et al. 2010), and to the detour that some transequatorial migrants do to follow prevailing winds (Felicísimo et al. 2008, Hromádková et al. 2020). Having more favourable winds during the inbound migration might ensure higher fitness, allowing earlier arrival at the colony which is generally associated with higher breeding success (Kokko 1999, Verhulst and Nilsson 2008) or reducing energy expenditure, hence leading to a better body condition at the start of the breeding season, and subsequently a higher reproductive output (Drake et al. 2014, de Zwaan et al. 2022). More generally,

stronger time selection during spring migration compared to the autumn has been found for migratory birds (Nilsson et al. 2013), which supports the positive influence of early arrival on fitness. How wind conditions encountered during the non-breeding season, and especially during the spring migration, impact arrival date, body condition and reproductive performances in migratory birds remains to be tested.

Can winds influence seabird species distribution?

Adult kittiwakes and puffins show a high individual repeatability in their migratory routes (Guilford et al. 2011, Léandri-Breton et al. 2021). Such a repeatability in routes support the hypothesis that individuals migrate along routes that optimize wind conditions and have been selected through time. Indeed, one could expect a high individual variability in routes if birds follow winds encountered along the way, especially in regions with high wind variability. Selection of optimized routes is possible when there is genetic inheritance of migratory routes (Berthold 1991, Liedvogel et al. 2011), or cultural inheritance with a transmission via one of the parents or other individuals (Jesmer et al. 2018, Byholm et al. 2022). Additionally, the selection of optimized migratory routes could arise through learning, if the individuals refine their routes over the course of their life, as found in sea turtles (Scott et al. 2014), black kites *Milvus migrans* (Sergio et al. 2014) and Cory's shearwaters (Campioni et al. 2020). Further investigations are needed on the individual variability in migratory routes and in encountered wind supports to deepen our understanding of the selection of migratory routes at the individual scale.

If wind shapes migratory routes, we can further question whether wind could be a factor influencing species distribution. For a given species, some areas might be difficult to exploit due to unfavourable atmospheric conditions (Krietsch et al. 2020). Moreover, if different populations face contrasting wind support, one could expect differences in terms of average individual fitness among them, and further local impacts on population dynamics (Newton 2006, Reiertsen et al. 2021). Indeed, wind has been identified as a factor explaining the global distribution of Procellariiforms and of some albatross species in the North and Central Pacific (Suryan et al. 2008, Davies et al. 2010). Wind conditions also explain the spatial segregation between male and female black-browed and grey-headed albatrosses (*Thalassarche melanophris* and *T. chrysostoma*), where males with a higher wing loading forage at higher latitudes where wind speeds are higher (Phillips et al. 2004). How wind would influence the distribution of other seabirds and flying migrants in general remains to be tested, keeping in mind that many other factors are involved in shaping a species' distribution, such as food availability, habitat, competitors or predators.

In the context of climate change, wind conditions are expected to change according to the Intergovernmental Panel on Climate Change (IPCC) predictions (Pinto and Ludwig 2020, Masson-Delmotte et al. 2021). It is therefore important to understand how migratory species will respond and

cope with these changes. While phylogenetic studies suggest that migratory behaviour can evolve relatively quickly in birds, based on the great range of migratory behaviours observed within taxa (Alerstam et al. 2003), the rapidity of ongoing changes means that plasticity would be much more important than the potential for evolution. More studies investigating the plasticity of birds in different wind conditions as well as temporal variations in wind conditions are thus needed, and will require long term tracking programs.

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Data availability statement

All the R code is publicly available on GitHub (<https://github.com/FAmelineau/SeaWinds3>). Contains modified Copernicus Climate Change Service information [2021]. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.z34tmpgm6> (Amélineau et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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