

# Time for barrier crossing: nocturnal bird migration phenology of the North Sea

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## Aims of this report

The primary aim of this report is to provide a regional overview of nocturnal bird migration phenology across the Dutch North Sea, focusing on seasonal and within-night migration timing and intensity across offshore radar locations. The study explores how ecological barriers influence spatiotemporal migration intensity patterns and provides insights for improving conservation measures such as wind turbine curtailment.

- In **Introduction**, we review the role of ecological barriers in shaping bird migration phenology and introduce the North Sea as a major barrier along the East Atlantic Flyway. We describe the known challenges and gaps in offshore migration research, as well as the recent technological advances that enabled this study.
- In **Materials and Methods**, we present the radar monitoring network, study locations, and migration seasons included in this study. We explain the radar setup, data filtering and post-processing methodology, and describe the statistical approaches used to assess migration intensity, phenology, and synchrony.
- In **Results**, we report the observed patterns in migration intensity and timing across radar locations. We highlight differences between spring and autumn, seasonal and within-night phenology, and discuss spatial correlations in migration traffic rates.
- In **Discussion and Conservation Implications**, we interpret the observed spatiotemporal patterns in the context of ecological barrier navigation and species-specific migration strategies. We explore how these insights can support dynamic, regionally tailored curtailment strategies for offshore wind farms.
- In **Supplementary Information**, we provide detailed tables and figures supporting the main text, including annual time series, pairwise distance matrices, clutter filtering criteria, and statistical test results.

## Introduction

Nocturnal bird migration over land generally occurs across a broad spatial front, with nightly peaks in migration intensity often synchronized across large spatial extents (Doren and Horton 2018, Nilsson et al. 2018, Kranstauber et al. 2023). Nevertheless, regional variation in migration timing and intensity can arise due to species-, sex- and age-specific differences in migratory behaviour (Newton 2011), as well as weather conditions (Richardson 1990) and topographic features (Harmata et al. 2000). Ecological barriers (e.g. mountains, large bodies of water, deserts) within migratory corridors can further accentuate such differences (Jiguet et al. 2019), resulting in heterogeneous regional migration patterns (Alerstam 2001).

Ecological barriers can influence bird migration timing and intensity in two ways. First, the size and shape of a barrier, along with a bird's body condition and seasonal weather patterns, can prompt varying, species-specific strategies for barrier navigation (Alerstam 2001, Deppe et al. 2015, Jiguet et al. 2019). As a result, timing and intensity can vary (seasonally) across a barrier, with different species crossing the barrier at varying locations and times and under different pressures (La Sorte and Fink 2017), reducing the synchronization of migration at regional scales. Second, barriers can cause temporary concentration of migrants near the barrier before or after crossing, as birds spend time refuelling and waiting for favourable weather conditions for departure (Buler and Moore 2011, Ćiković et al. 2021, Schekler et al. 2022, Guo et al. 2023). This can lead to a more temporally "pulsed" migration, a phenomenon observed across regions and types of ecological barriers (Biebach et al. 2000, Hirschhofer et al. 2024, Nussbaumer et al. 2024). However, refuelling time and the weather selectivity for departure vary among species (Dierschke and Delingat 2001, Packmor et al. 2020) leading to non-synchronous waves of migration, even from shared accumulation sites.

Nocturnal migrants typically depart around sunset (Alerstam 1990, Akesson et al. 2002). However, depending on distances to cover, weather conditions and possibilities for landing and refuelling, departure times can vary during the night (Sjöberg et al. 2015, 2017, Müller et al. 2016, 2018). This variation leads to within-night differences in migration timing across locations. For instance, observations by a weather radar network in NW Europe show that the nightly timing of migration is more uniform across inland locations but tends to have more pronounced peaks along coastlines (Kranstauber et al. 2023). This is likely influenced by the presence of bodies of water that landbirds cross without stopping due to no opportunities for resting or refuelling (Kranstauber et al. 2023).

As one of the ecological barriers of the East Atlantic Flyway, the North Sea occupies an area of 750000 km<sup>2</sup> between the English Channel in the southwest, the Scandinavian straits in the east and 62-degree latitude in the north (Cohen et al. 2017). Each spring and autumn, hundreds of millions of nocturnally migrating birds from over 250 species cross the North Sea, following the predominant west-east migration axis from the UK to continental Europe in spring and a northeast-southwest axis from Scandinavia and northern Netherlands to southern Europe and Africa in autumn (Lack 1959, Hüppop et al. 2006, Shamoun-Baranes and van Gasteren 2011, Bradarić et al. 2020). While the NE-SW migration axis represents the main seasonal direction of bird migration movements, birds fly following a range of directions in different seasons (Lack 1959, 1963a, b, Buurma 1995, Lensink et al. 1999). A combination of radar data and trajectory models at the western and northern Dutch coast showed that birds seen at offshore radar locations in the North Sea predominantly come from the UK (but also France, Belgium and Ireland) in spring, and NW Germany and N Netherlands (but also Norway, Sweden and Denmark) in autumn (Shamoun-Baranes and van Gasteren 2011, Bradarić et al. 2020).

The diversity in migration routes, species composition, the complex regional weather system (Cohen et al. 2017, Manola et al. 2020) and the crossing distances (Figure 1), likely contribute to considerable regional differences in both seasonal and within-night migration timing and intensity across the North Sea. For example, close to the departure areas that are perpendicular to the main migration axes (Figure 1), peaks are expected earlier in the night due to mass take-offs shortly after sunset (Kranstauber et al. 2023). Further offshore and close to arrival areas, migration intensity may remain elevated until late in the night or have one late-night arrival peak, corresponding to the time needed to cross the sea (Kranstauber et al. 2023). In spring, the predominance of westerly winds (Cohen et al. 2017) supports the W-E movement across the North Sea (Bradarić et al., 2020), leading to expectations of lower, more spread-out migration peaks than those in autumn, when weather conditions are mostly unfavourable for migration (Bradarić et al., 2020; Packmor et al., 2020; Shamoun-Baranes & van Gasteren, 2011). Furthermore, migration patterns are expected to be more similar between nearby locations.

Until recently, studying mass migration movements over the sea at regional scales has been limited by logistical and technological constraints in placing radars offshore. The knowledge we have on bird migration over the North Sea principally comes from radars positioned on land and coastal areas (Lack 1961, 1963a, b, Buurma 1987, Shamoun-Baranes and van Gasteren 2011), as well as short deployments of individual radars at sea (Hüppop et al. 2006, Fijn et al. 2015, Krijgsveld et al. 2015, Bradarić et al. 2020). A few years ago, efforts to continuously monitor bird migration offshore started, resulting in an increase in bird tracking radars deployed at different locations and distances from the coast in the Dutch North Sea (Figure 1). This distributed sensor network enables a first glimpse into potential regional differences in patterns of migratory mass movements that might result from navigating a barrier. Furthermore, recent methodological advances in tracking radar data post-processing have increased the range of possibilities for using tracking radars in ecological research (van Erp et al. 2024).

Exploring heterogeneity in migration intensity and timing across ecological barriers advances our understanding of complex migration dynamics and informs migration forecasting, critical for conservation efforts (Doren and Horton 2018, Horton et al. 2021, Lippert et al. 2022, Bradarić et al. 2024a). Since 2023, on-demand curtailments of wind turbines have been implemented in the Dutch North Sea to allow a safe passage for migratory birds during intense bird migration, minimising collision risk and potential barrier effect (Bradarić et al. 2024a). If regional differences exist, identifying them will allow regionally tailored curtailments, further improving the conservation measure's ecological and economic efficiency.

In this paper, we aim to provide an overview of migration timing over the North Sea by assessing the synchrony and similarity of nocturnal bird migration activity across different locations in this ecological barrier of the East Atlantic's flyway. We leverage the unique opportunity to compare multi-year data collected by six bird tracking radars located at various locations along the Dutch coast (Figure 1) to provide a regional overview and explore i) how seasonal and within-night migration intensity varies across locations, ii) how the duration and timing of migration compare across locations and iii) which locations show the highest level of synchrony and similarity in different seasons. The radar data used in this study (see methods) has an altitudinal detection range of approximately 300 m for small birds and captures the mode of migration intensity in both spring and autumn (Bradarić et al. 2024b). Our findings shed light on phenology and the temporal dynamics of migration across an ecological barrier, providing insight for regionally tailored conservation measures, including wind turbine curtailment. We provide concrete suggestions on how these insights can be used to adapt forecast models for wind turbine curtailment.

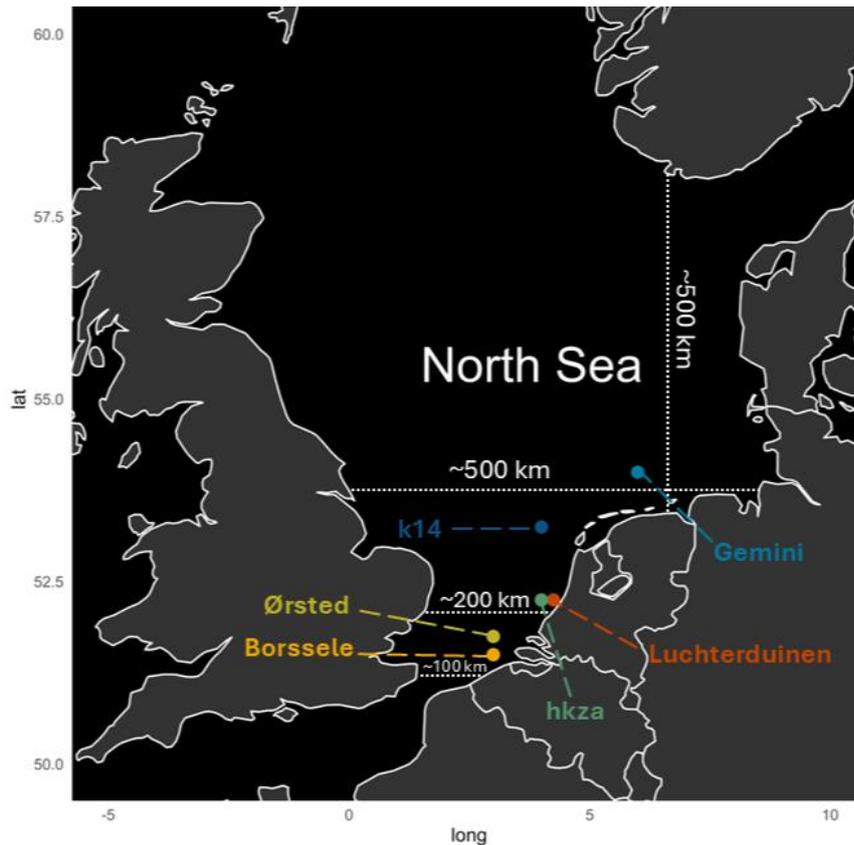
## Materials and methods

### Study location, period and radar system

The data for this study was collected in the spring (February 15 – May 31) and autumn (August 15 – November 30) migration seasons of 2022 - 2024 by tracking radars (Robin Radar 3D fix, Robin Radar Systems BV, the Hague, Netherlands) located at six different offshore locations: Gemini, k14, Luchterduinen, hkza (HKZ alpha), Ørsted and Borssele (BSA) (Figure 1). Even though some of the radars have been in operation for a longer period, we have selected years in which the most radars were operational simultaneously for comparative analysis and to limit the amount of variation between radar locations that would potentially arise from interannual differences in environmental conditions. Details on the radars' positions and data used in this study per radar are available in Table 1.

**Table 1.** Overview of radars, their positions and data used in this study, in descending order from north to south. DD (decimal degrees).

<b>Radar location</b>	<b>Lat (DD)</b>	<b>Long (DD)</b>	<b>Altitude asl (m)</b>	<b>~Straight-line distance from the closest Dutch coast (km)</b>	<b>Spring data used in the study (years)</b>	<b>Autumn data used in the study (years)</b>
<b>Gemini</b>	54.03	6.04	32.0	80.0	2022-2024	2022-2024
<b>k14</b>	53.26	3.62	32.9	85.0	2024	2023-2024
<b>Luchterduinen</b>	52.42	4.18	22.8	25.0	2022-2024	2022-2024
<b>HKZA</b>	52.31	4.04	41.0	28.0	2023-2024	2023-2024
<b>Ørsted</b>	51.78	3.03	17.0	51.0	2023-2024	2023-2024
<b>Borssele</b>	51.69	3.05	48.6	45.0	2022-2024	2022-2024



**Figure 1.** A map of the North Sea and the surrounding countries. Dots represent radar locations: Gemini (blue), k14 (dark blue), Luchterduinen (red), hkza (green), Ørsted (yellow) and Borssele (orange). Dotted white lines indicate approximate distances between different coasts around the North Sea, showing the straight-line crossing distances for migratory birds.

The radar system consists of two antennae (Furuno Marine) that rotate at 45 rpm in different planes. A vertically-rotating X-band antenna with the power of 25 kw and a beam width of 20° collects information about bird numbers and altitudes, while a horizontally-rotating S-band antenna with a power of 60 kW and a beam width of 12.5° collects information on numbers, directions and speeds of targets. Using proprietary software, the system detects moving targets and, based on echo characteristics (e.g. speed, direction, radar-cross section), distinguishes between bird and non-bird targets. All bird targets that were available in at least eight consecutive rotations in the horizontal antenna or five consecutive rotations in the vertical antenna were joined in tracks and stored in a centralized database. As tracking bird movements at sea and especially near wind parks poses technical challenges, post-processing has proven essential to improve data quality (van Erp et al. 2024). Due to the availability of speed, direction and turning angles in the horizontal antenna as well as information on clutter filters, and established post-processing steps (Bradarić et al. 2024a, van Erp et al. 2024) data from the horizontal antennae were deemed most suitable for this study. The horizontal antenna has a high detection probability for small migrants (passerines) up to 300m, which previous studies identified as altitudes where most of the nocturnal migration occurs in this region over land (Kemp et al. 2013, Hoekstra et al. 2024) and sea (Fijn et al. 2015, Bradarić et al. 2024b). Since we are interested in nocturnal migration, we only used data collected between civil sunset and sunrise.

## Radar data post-processing

While the automated Robin Radar algorithm detects and filters various types of clutter (e.g., rain, waves) based on echo characteristics before data entry, some clutter with similar echo properties to those of bird targets was still mistakenly classified as bird tracks, leading to its inclusion in the database. To discard such instances, we applied post-processing steps with which we further filtered the data based on the tracks' distance from the radar, their straightness and derived airspeed and moments during which the clutter filter activity was high (expressed as a percentage of radar image with detected clutter activity), as described in Bradarić et al. 2024a and van, Erp et al. 2024. Airspeed was calculated from radar-measured groundspeed and ERA5 100 m wind data (Hersbach et al. 2020). Since radars were positioned at different locations and heights above mean sea level within the North Sea (Table 1), resulting in different sensitivities to various types of environmental clutter, the thresholds used to define moments in which the clutter filter activity was too high to consider the data reliable were assessed and adjusted per radar (van Erp et al. 2024). Following the methodology of defining the high clutter filter activity threshold described in van Erp et al. 2024, we excluded all minutes of data in which clutter filter activity occurred in more than 21% of the radar image in Gemini, 15% in k14, 30% in Luchterduinen, 19% in hkza, 16% in Ørsted and 20% in Borssele. An additional filtering step with a combination of strict filters for straightness and track length, not described in the previous studies, was introduced to further remove the tracks which most likely originated from static clutter (e.g. turbines and multi-path effects). The filtering step was developed by visually inspecting the data and defining two categories of "bird tracks" and "turbine tracks", based on the consistent direction of their movement. A decision tree model was then run on the two categories to explore which track properties explain the two defined categories the best. Finally, based on the results of the model, all tracks that were shorter than 577.5 m and had a straightness lower than 0.95 were removed. More information on the filtering step introduced to further remove the static clutter is provided in S1.

## Migration intensity at different radar locations

Migration traffic rates (MTR, birds/km/hr) were calculated following Bradarić et al. 2024a to assess migration intensity at different radar locations. Sizes of blind zones for each radar location are listed in the supplement (S2). We provided an overview of seasonal quantiles per radar location. To examine similarities in seasonal migration intensity between locations, we compared hourly MTR distributions across different radar locations within each season using the Kruskal-Wallis test. Spearman's correlation coefficient was calculated between pairs of radar locations to assess the level of correlation in migration intensity in overlapping time periods between different radar locations in two different seasons.

## Seasonal and within-night phenology

To assess seasonal migration phenology, a generalized additive model was fit for each radar location and season using MTR as a response variable, day of year (Julian date) with a smoothing spline ( $k=7$ ) as the predictor variable and year as a random effect. To assess within-night phenology, a GAM was fit to each radar and season using MTR as a response variable, hour after sunset with a smoothing spline ( $k=5$ ) as the predictor variable and day of year as a random effect. For both GAMs, we used the quasipoisson family to restrict predictions to positive values and restricted maximum likelihood (REML) to account for the non-normal distribution of our data and decrease the chance of overfitting. Using GAMs, discrete predictions of seasonal and within-night phenology were generated per season and radar location. To evaluate spatiotemporal variation in migration phenology, we applied two non-parametric tests that addressed different aspects of the data. The Friedman test was used to assess whether there were overall differences in seasonal migration patterns

(phenology) across all radar locations. This allowed us to test for variation in the shape and timing of predicted migration intensity curves between sites. In contrast, the Wilcoxon Signed-Rank test (results in Supplement S5) was used to assess pairwise consistency in migration intensity over time between locations. This test quantified how similarly each radar location tracked migration peaks and troughs across the season, enabling a more detailed comparison of spatiotemporal alignment between site pairs.

## Results

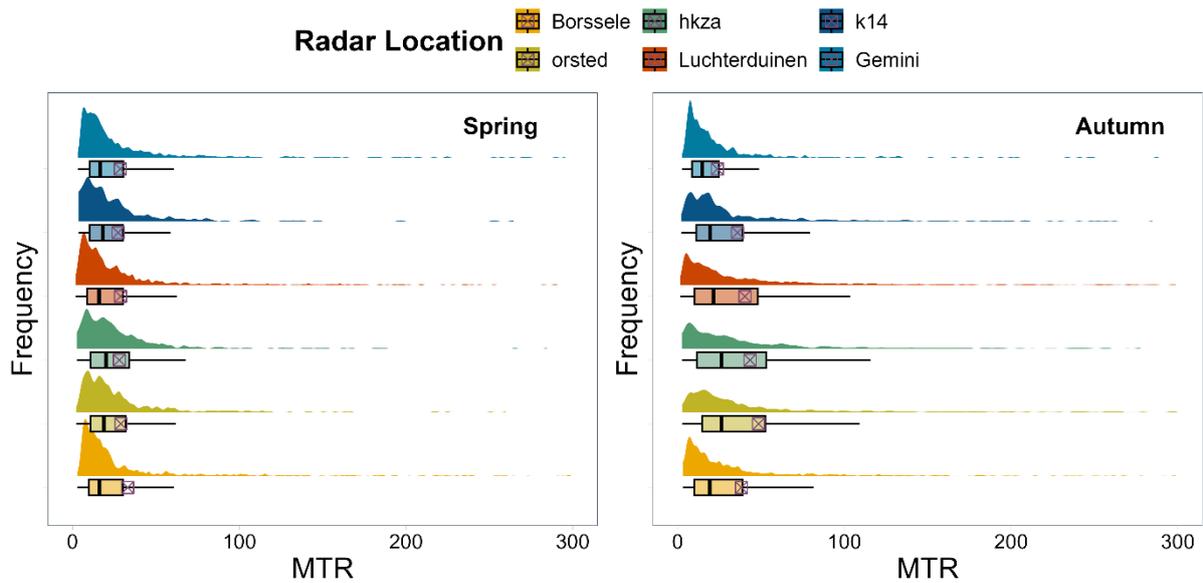
### Migration intensity at different radar locations

Migration intensity is generally lower in spring than in autumn at all radar locations except for Gemini, with the highest seasonal difference in mean MTR observed in Ørsted (Table 2). As often shown in studies of migration fluxes, our observations also reveal heavily right-skewed distributions of migration intensity in both seasons (Figure 2), highlighting the rare occurrence of intense bird migration periods.

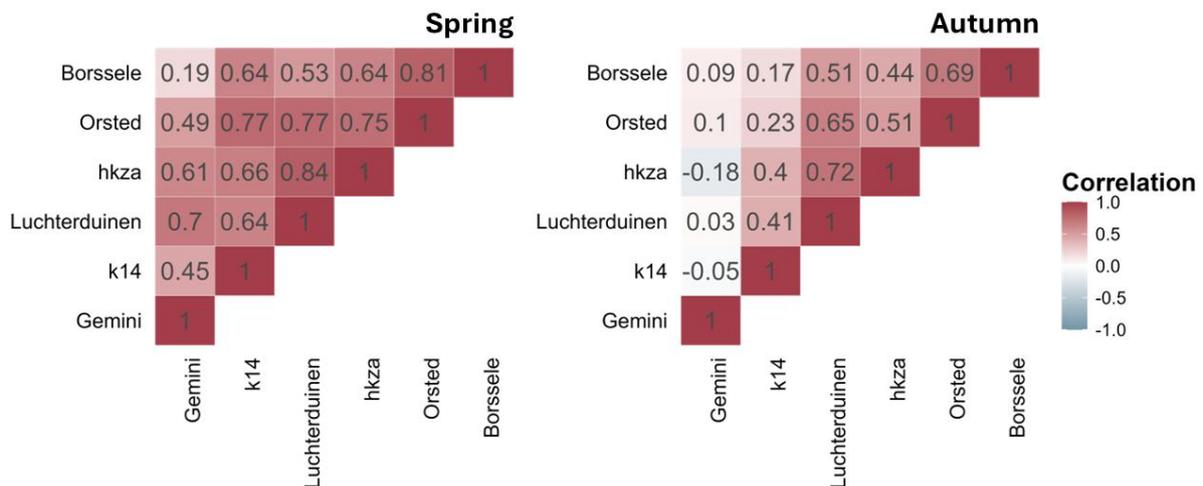
In both seasons, Ørsted has the highest mean MTR (39.5 birds/km/h in spring and 68.7 birds/km/h in autumn, Table 2), while k14 has the lowest mean MTR in spring (31.8 birds/km/h, Table 2) and Gemini in autumn (32 birds/km/h, Table 2). The highest peak migration (95<sup>th</sup> percentile) is observed in Borssele in spring (161.9 birds/km/h) and hkza in autumn (320.1 birds/km/h), while the lowest is observed at k14 in spring (86.2 birds/km/h) and Gemini in autumn (107.8 birds/km/h). Distributions of MTRs in both spring ( $H=26.4$ ,  $df=5$ ,  $p<0.001$ ) and autumn ( $H=203.11$ ,  $df=5$ ,  $p<0.001$ ) differ significantly across locations (Figure 2).

**Table 2.** Overview of migration intensity summary statistics and observation hours in spring and autumn at different radar locations, ordered descending from north to south. P90 and P95 represent the 90<sup>th</sup> and 95<sup>th</sup> quantiles of seasonal MTR, respectively.

Radar	Season	Hours (#)	Mean $\pm$ SD MTR (#/km/h)	Median MTR (#/km/h)	P90 MTR (#/km/h)	P95 MTR (#/km/h)
Gemini	Spring	1674	36.5 $\pm$ 76.9	16.5	66.5	114.2
	Autumn	1531	32.0 $\pm$ 66.6	14.9	50.6	107.8
k14	Spring	579	31.8 $\pm$ 49.9	18.2	58.9	86.2
	Autumn	1358	48.8 $\pm$ 98.5	19.8	102.0	182.6
Luchterduinen	Spring	2004	38.4 $\pm$ 91.1	16.1	69.0	140.4
	Autumn	2346	60.3 $\pm$ 107.0	22.7	140.6	279.8
hkza	Spring	922	38.2 $\pm$ 106.8	20.1	56.5	89.3
	Autumn	1251	66.0 $\pm$ 112.3	28.2	155.9	320.1
Ørsted	Spring	871	39.5 $\pm$ 79.8	19.0	68.8	111.9
	Autumn	1419	68.7 $\pm$ 109.6	28.4	178.9	298.8
Borssele	Spring	1842	38.3 $\pm$ 71.5	16.3	91.0	161.9
	Autumn	2312	55.5 $\pm$ 105.4	20.4	127.5	250.6



**Figure 2.** Hourly MTR distributions per season and radar location, complemented by boxplots where the left and right limits of the box show the interquartile range of the 1<sup>st</sup> and 3<sup>rd</sup> quartile, and the whiskers extending to the most extreme values within 1.5 interquartile range from the 1<sup>st</sup> and 3<sup>rd</sup> quartile. Vertical lines indicate seasonal medians, and purple squares with “x” indicate seasonal means. The x-axis is limited to 300 MTR for visibility purposes (the max value in spring was 1620 birds/km/h in spring, and 1025.602 in autumn).



**Figure 3.** Spearman's correlation heatmaps of hourly MTRs that were available across all radar locations in spring and autumn (n = 30 in spring and n = 115 in autumn, respectively).

In spring, mean MTRs are similar (correlation > 0.5) between most locations, with the exception of Gemini, which has lower correlations with k14 and Ørsted and almost no correlation with Borssele (Figure 3). The strongest correlation is observed between hkza and Luchterduinen (two close locations, ~16 km apart, Table S4.1), and the weakest between Borssele and Gemini (two distant locations, ~330 km apart, Table S4.1) (Figure 3). Despite the two locations being closest to each other and farthest from the coast (Figure 1, Table S4.1), there is a weak correlation between k14 and Gemini (Figure 3), whereas Ørsted and Gemini have a slightly stronger correlation (Figure 3).

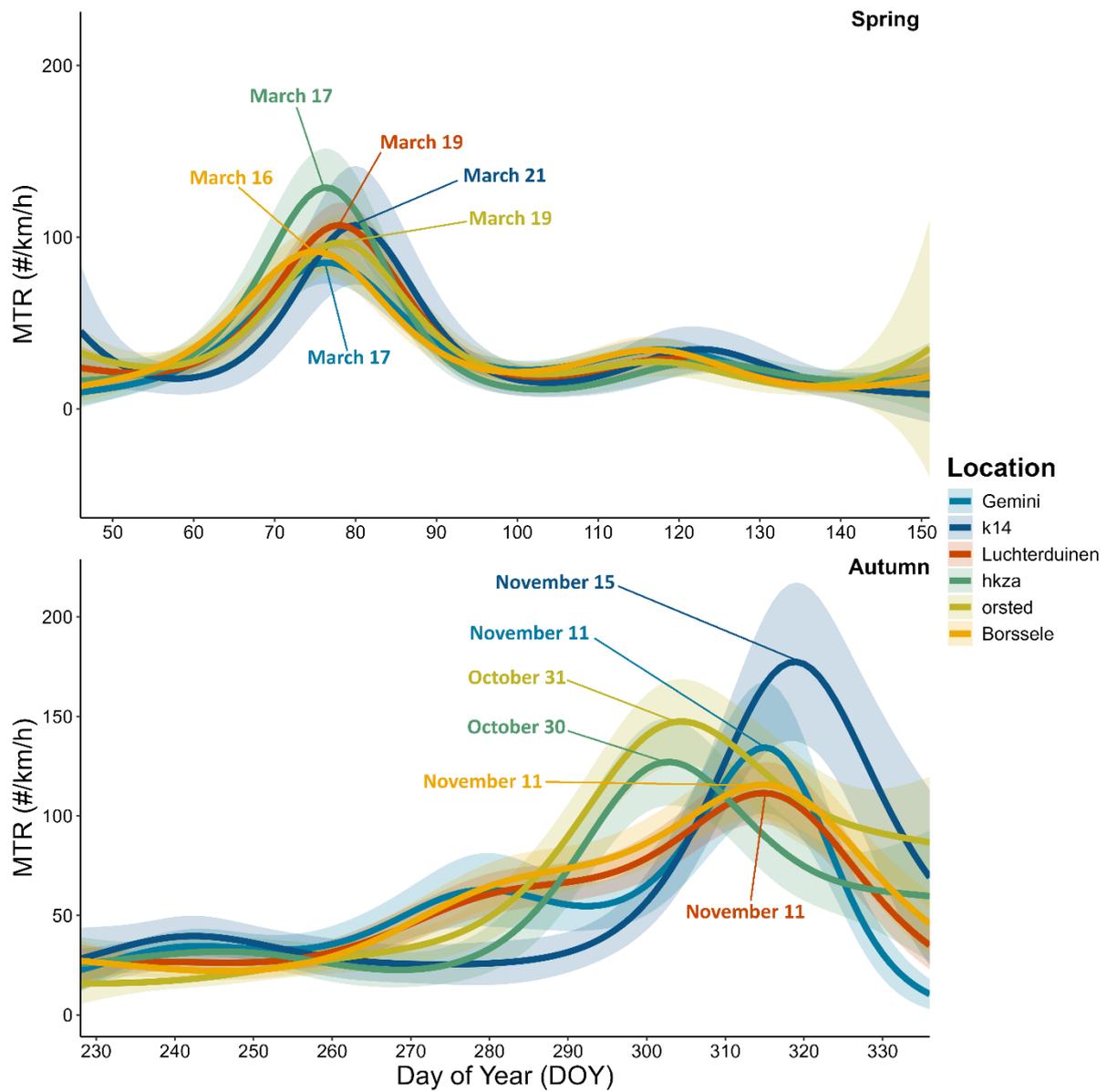
In autumn, hourly MTRs are generally less similar across locations than in spring, suggesting more diverse migration patterns (Figure 3). Hourly MTRs show the strongest positive correlation between hkza and Luchterduinen (as in spring). Gemini has the weakest overall correlation with other radars, showing no meaningful correlation, followed by k14, indicating that these two locations exhibit different MTR patterns compared to the rest of the radars, while also differing from each other.

### Seasonal and within-night phenology

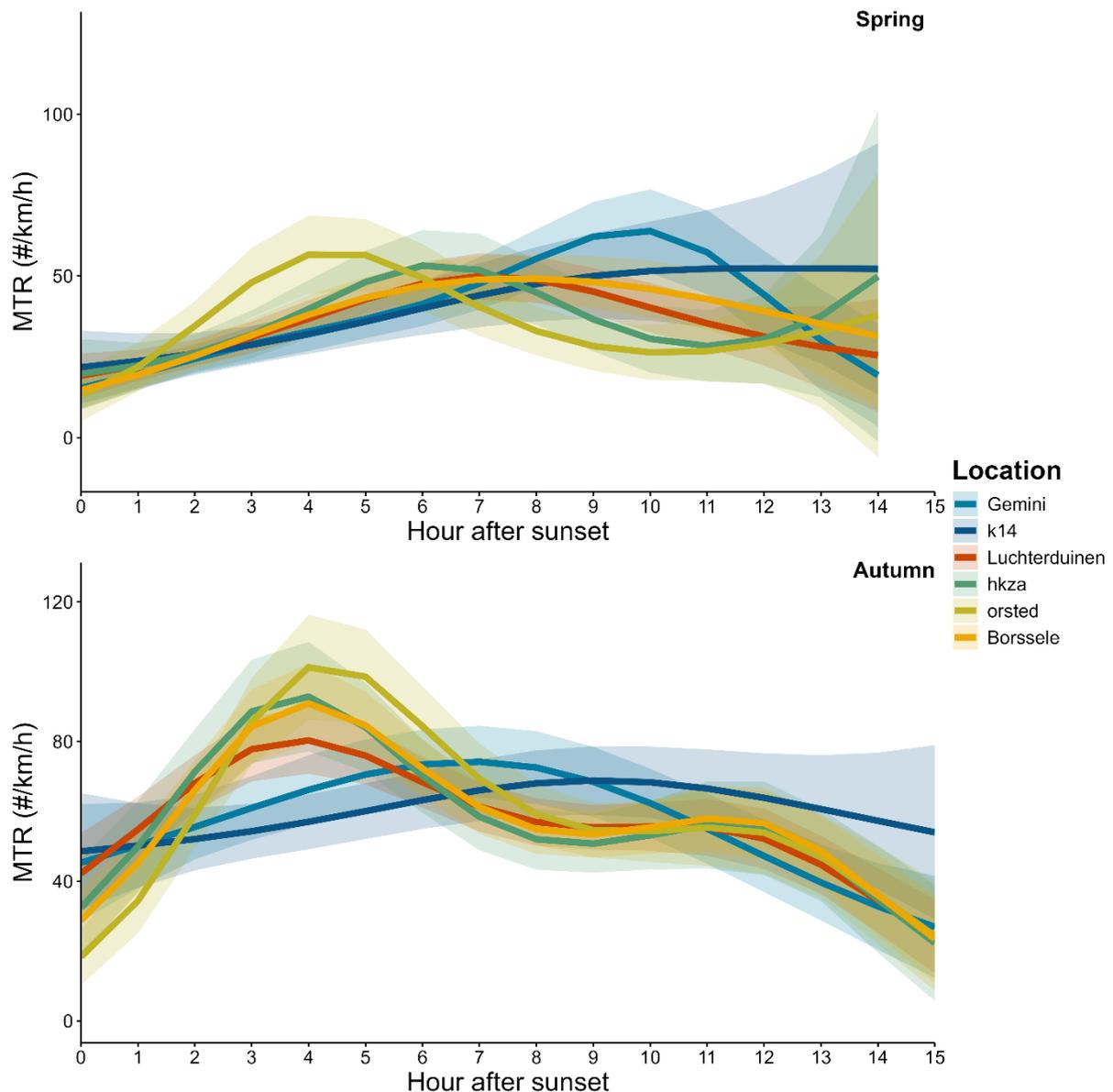
Friedman test indicated no overall differences in seasonal phenology across locations in spring ( $\chi^2=2.09$ ,  $df=5$ ,  $p=0.83$ ), and seasonal consistency in migration intensity over time is not significantly different between radar location pairs (Figure S5.1). On average, spring nocturnal bird migration peaks between March 16 and March 21 (Figure 4), with Luchterduinen and Ørsted experiencing the highest peak on March 19 (Figure 4).

In autumn, overall seasonal phenology differs significantly across radar locations ( $\chi^2=21.06$ ,  $df=5$ ,  $p=0.0007$ ), with seasonal consistency in migration intensity over time differing significantly between Luchterduinen and Ørsted and Luchterduinen and Borssele, as well as between hkza and Ørsted and hkza and k14 (Figure S5.1). Depending on the location, migration peaks occur between October 30 and November 15, a period ten days longer than in spring (Figure 4), indicating higher inter-annual variability in peak migration timing compared to spring.

Overall, within-night phenology does not differ significantly across radar locations in spring ( $\chi^2=2.92$ ,  $df=5$ ,  $p=0.71$ ) or in autumn ( $\chi^2=4.12$ ,  $df=5$ ,  $p=0.53$ ). Migration intensity over time is consistent between all locations in both seasons (Figure S5.2). In spring, one nightly peak is observed at all radar locations. However, the peak occurs at different times of night, depending on the location: peaks are earlier in the night at Ørsted and hkza, followed by Borssele and Luchterduinen and, finally, k14 and Gemini (Figure 6). In autumn, within-night phenology is more uniform than in spring across most locations (except for k14 and Gemini) and shows an early and late-night peak, with the former being of higher magnitude (Figure 6). Gemini and k14 show more homogenous migration intensity throughout the night (Figure 6).



**Figure 4.** Modelled seasonal phenology of the North Sea nocturnal migration per radar location, with shaded areas denoting 95 confidence intervals, which indicate inter-annual variation. Peak migration nights are marked for each season.



**Figure 5.** Modelled within-night phenology of nocturnal bird migration across the North Sea locations. Shaded areas denote 95 confidence intervals, which indicate variation among nights.

## Discussion

Migration intensity and timing across the Dutch North Sea show varying levels of synchrony and similarity among locations in both migration seasons and are overall more homogeneous in spring than in autumn (Figures 2 and 3; Table 2). As hypothesized and as regional studies over land have shown (Hoekstra et al. 2024), spring migration has a lower magnitude than autumn migration (Figure 2; Table 2), likely due to higher number of individuals migrating after the breeding season and high mortality of juveniles in the first winter (Dokter et al. 2018) and in this region, migration occurring more inland during autumn (Hoekstra et al. 2024). Contrary to expectations, spring does not exhibit multiple peaks of similar magnitude throughout the season; instead, it shows a clearly defined peak in mid-March, which is almost perfectly synchronized across all radar locations (Figure 4). While seasonal phenology is similar across sites, within-night spring phenology varies, with differences spanning up to six hours between some radars (Figure 5). In autumn, the pattern is reversed.

Seasonal peaks are not synchronized across locations and are spread between late October and mid-November (Figure 4), whereas within-night phenology is well-aligned, showing clear early- and late-night peaks across most radars (Figure 5). Even though our study focuses on nocturnal migration up to 300 m of altitude, we show that the relative patterns of intensity and timing are similar to those over land, observed across larger altitude spans (Dokter et al. 2018, Hoekstra et al. 2024).

Intense nocturnal migration is concentrated around a few days in mid-March (Figure 4). As winds are generally favourable in spring (Kemp et al. 2013), and mid-March peaks are recurring in different years (Figure S3.1). We expect this to be a result of the birds' endogenous circannual rhythm (Gwinner and Helm 2003) in addition to the favourable wind conditions (Bradarić et al. 2020), which migrants use to cross ecological barriers more efficiently. Earlier studies have shown that in spring, seasonal phenology seems to be the most important driver of migration intensity at one of the North Sea locations (Bradarić et al. 2024a). Our results indicate this is likely the case across the whole North Sea.

Previous research has shown that the majority of birds observed by an offshore radar close to the Dutch coast in spring likely depart from the UK coast (Bradarić et al. 2020). Therefore, variations in nightly timing likely result from birds leaving the eastern UK coast in the early hours of the night and crossing the North Sea, reaching each radar at different times (Figure 5). The timing of arrival depends on the distance between departure sites and radar locations, wind assistance en route, and the birds' airspeed. Our observations show that the closer a radar is to the UK departure coast (Figure 1; Table 1), the earlier the within-night migration peak occurs, with Gemini recording arrivals only toward the end of the night (Figure 5).

The greater heterogeneity in seasonal migration timing across radar locations in autumn (Figure 4) is likely driven by a complex interplay of factors. Contributing factors likely include the scarcity of tailwind (Kemp et al. 2013, Bradarić et al. 2020), the shape of the Dutch coastline (Figure 1), more complex offshore migration directions (Buurma 1987, Lensink et al. 2002, Shamoun-Baranes and van Gasteren 2011, Bradarić et al. 2020), and differences in migration strategies among species, but also seasonal phenology generally playing a negligible role in driving the autumn migration peaks (Bradarić et al. 2024a). These factors may explain why some radars detect seasonal peaks earlier than others. As in spring, prevailing autumn wind directions are primarily from the southwest and west (Kemp et al. 2013). Birds departing from Scandinavia, the Netherlands, and Germany and migrating predominantly southwest or west can only benefit from tailwinds during specific time windows (Bradarić et al. 2020, Manola et al. 2020) requiring them to be selective about departure timing. The shape of the coastline and, in some cases, the need for longer crossings may require a stepwise migration across the North Sea (van Dobben 1953, Lack 1959, Buurma 1995). For example, migrants departing from Norway under crosswinds may first fly to Denmark and then continue southwestward when winds become supportive, resulting in synchronized peaks at the Gemini, Luchterduinen, and Borssele as birds follow the coastline (Figure 4). Peaks in Ørsted in hKza radars may result from birds departing the Dutch Wadden Islands and flying across the sea toward the UK in a west-southwest direction. Alternatively, this pattern could reflect a direct sea crossing by birds departing from Norway and flying southwest. Despite seasonal variability in timing, autumn migration exhibits clear within-night peaks across radar locations (Figure 5). The first peak, the higher of the two, likely corresponds to sunset departures from the nearby coast, while the second, smaller peak reflects late-night arrivals from other locations, consistent with the hypothesis of stepwise migration. The Gemini and k14 radars show a single peak throughout the night, likely due to their greater distance from the nearest coastline (Figure 1).

Migration patterns observed by Gemini and k14 radars differed the most from those observed at other radar sites in both seasons. These two radars recorded the lowest mean migration intensity (Figure 2; Table 2) and exhibited the weakest correlation with all other radar sites in both spring and autumn (Figure 3). Two main factors likely contribute to this. First, Gemini and K14 are the two northernmost radar sites in the network and are located farther from the other radars, which are clustered along the western and southwestern Dutch coasts (Figure 1). Second, they are also the furthest from the coast (Table 1), which likely explains their lower recorded migration intensity. This might indicate that migration intensity tends to decrease with increasing distance from the coast. The Gemini site was the only location that recorded lower migration intensity in autumn than in spring (Figure 2; Table 2). This may indicate that birds crossing the North Sea from Scandinavia to the Netherlands in autumn tend to take more inland routes on most nights, generally bypassing the Gemini radar site (Figure 1), as previously suggested (van Dobben 1953, Lack 1959). However, considering that some of the direct autumn crossings of large numbers of migrants between southern Norway and the northern coast of the Netherlands have been recorded by the military radars (Shamoun-Baranes and van Gasteren 2011), it is possible that such nights get removed from our data due to large amounts of sea clutter. Clutter tends to be more pronounced at the locations further offshore due to generally higher sea states.

Early-season migration peaks in spring and late-season peaks in autumn suggest that the most intense migration movements across the North Sea primarily reflect the nocturnal passage of short-distance migrants in the region (Nilsson et al. 2014, Packmor et al. 2020). While peaks in late April, August, and early October, which likely correspond to movements of long- or medium-distance migrants (Nilsson et al. 2014), are observed at some radar locations, their magnitude is considerably lower (Figure 5). This suggests that long-distance migrants either fly at higher altitudes beyond the radar detection range, or follow more inland routes, thus avoiding radars used in this study.

To our knowledge, this study provides the first comprehensive overview of large-scale seasonal and within-night phenology of low-altitude nocturnal migration offshore. We demonstrate that the presence of an ecological barrier along migration routes differently affects the synchrony and similarity of migration timing and intensity across seasons, with seasonal phenology being more synchronous in spring and within-night phenology in autumn. These patterns are likely defined not only by the barrier and its shape but also by associated weather conditions and the complexity of migration directions in different seasons.

### Implications for existing conservation efforts

In addition to characterizing seasonal and within-night phenology of offshore migration in the region, our results offer valuable insight for ongoing conservation efforts aimed at reducing collision risk with offshore wind turbines for nocturnal migrants (Bradarić et al. 2024a). Rather than implementing blanket curtailments across all operational wind farms simultaneously, curtailments could be adjusted based on local spatiotemporal patterns, to minimize energy loss and enhance grid stability.

While performing curtailments on the same nights across different locations in spring seems unavoidable (Figure 3; Figure 4), our within-night phenology results suggest that curtailments could be implemented at different hours depending on location, with curtailments first being initiated at Ørsted and Hkza, followed by Luchterduinen and Borssele, and finally k14 and Gemini at the second part of the night. A similar approach could be applied in autumn, particularly at the northernmost sites, which generally exhibit distinct within-night migration patterns (Figure 5).

Although autumn migration seasonal phenology seems more heterogeneous across locations, many radars still observe peak migration intensity on the same day (Figure 4). Due to generally poorer

weather conditions for autumn (Kemp et al. 2010), radar measurements are more frequently affected by noise or unreliability (van Erp et al. 2023). Due to this and the fact that some locations have only one or two years of data, implications for conservation should be treated with care. Interannual variation, especially in autumn (Figure 4), highlights the need for longer-term datasets to derive more robust phenology curves and strengthen conservation guidance for this season. At this stage, we advise starting discussions on whether location-specific curtailment adjustments within conservation procedures and protocols based on our results are desirable or feasible. We advise that the actual adjustments be implemented only after more years of data have been collected to determine the extent to which general phenological patterns are predictable at various radar locations.

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## Supplementary information

### S1 Filtering steps

After performing the first five filtering steps (Table S1.1) on the data collected at the Gemini radar location, unusual directions towards south and south-east were observed, mainly in spring 2023 (Figure S1.1). As reported in earlier studies, the occurrence of this movement was observed throughout the year at the Gemini location, suggesting its non-biological origin (Van Erp and Shamoun-Baranes 2024). Even though tracks with these directions are prevalent throughout the year, their visibility was more pronounced in spring 2023. Little data was generally collected during this season, with only a few limited moments of intense migration, allowing the dominance of tracks with SE movement.

**Table S1.1** Filtering steps in the order in which they were performed according to van Erp et al, 2024, and Bradarić et al, 2024b, with the purpose of each filtering step on the radar data.

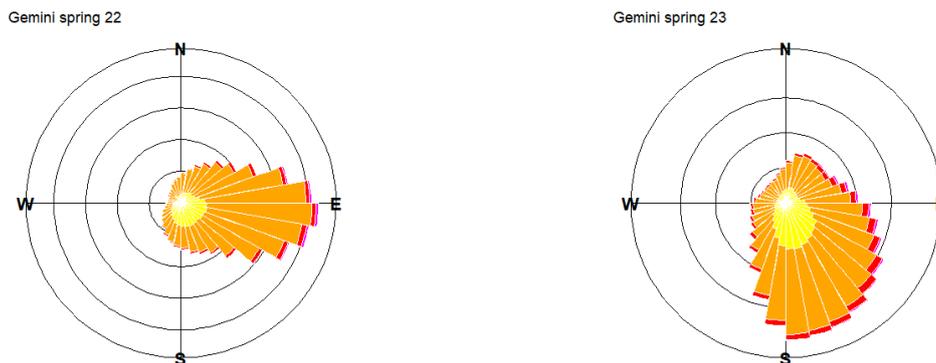
Filtering step	Purpose of the filtering step
Remove the tracks that fall into the category of those with the lowest 10% displacement over time	Removes static tracks (appear on the radar screen for a long time, but stay in place)
Remove tracks whose centroids are closer than 1000 m and further than 2000 m away from the radar	Keeps only tracks that fall into the optimal radar detection range, not considering areas close to the radar and far away from the radar that are prone to clutter activity and target loss
Remove tracks with straightness < 0.7	Migration tracks appear long and straight on the radar. This radar step makes sure that everything that is not a migratory bird gets removed
Remove tracks with airspeed < 5 m/s	Removes slow targets and insects
Remove minutes of high-clutter filter activity*	Makes sure to set unreliable moments in which radar collected a lot of clutter from the data to avoid erroneous inclusion of clutter, such as sea waves, into the analysis
Remove tracks with straight-line length < 577.5 & straightness < 0.95	Makes sure to remove relatively short and wiggly tracks that were not removed by the above criteria and are likely static clutter, discovered through visual inspection of the Gemini radar data.

\*The filtering thresholds differ per radar location, as indicated in the main text

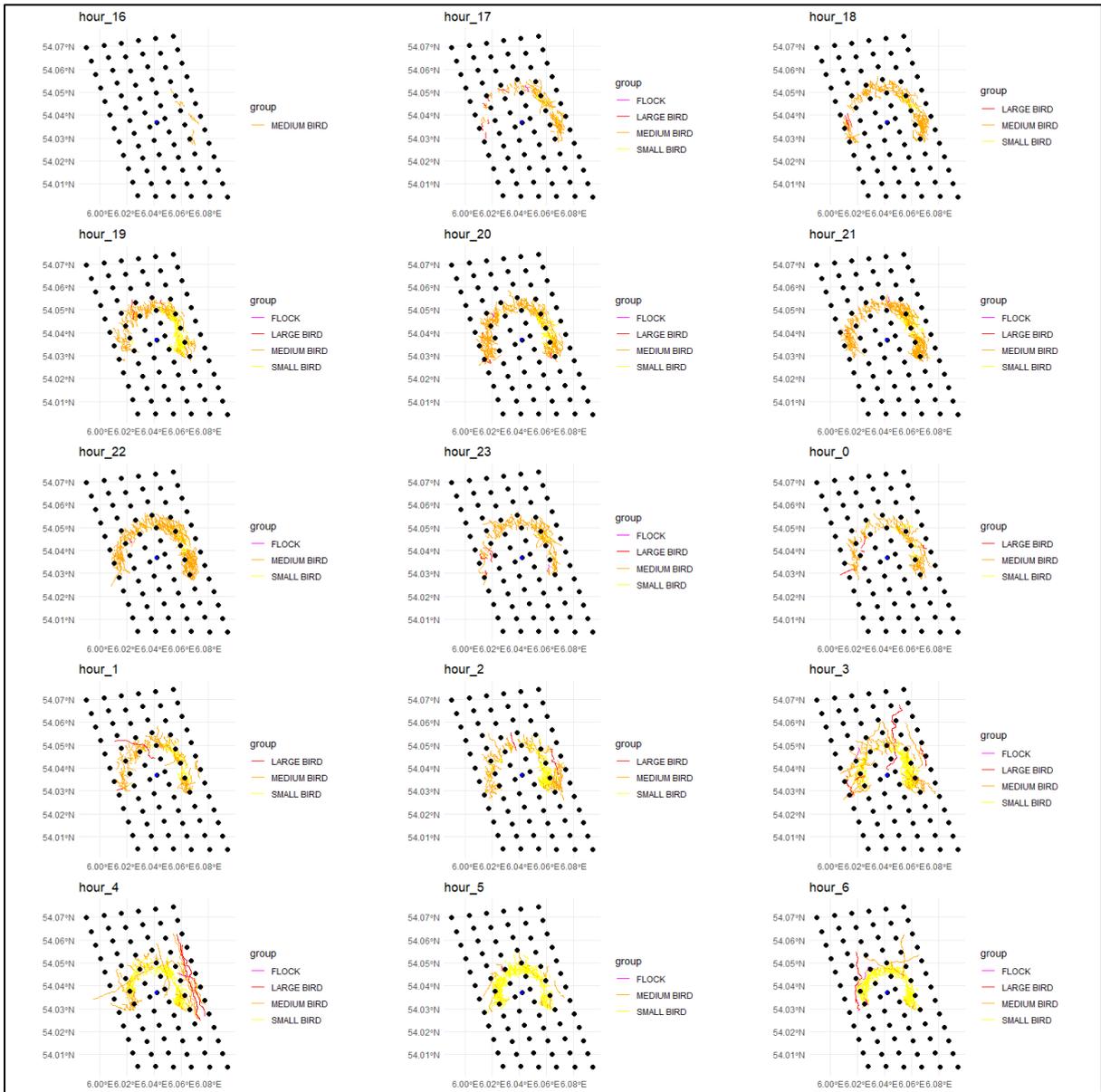
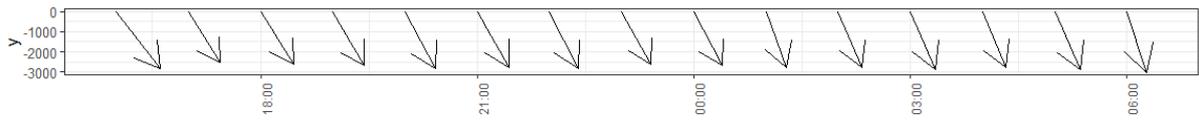
After the visual inspection, a division was made based on directions between tracks, with directions towards SE (track directions between 100 and 200 degrees) and the rest of the tracks (all the other directions). The visual difference was immediately visible when these tracks were plotted in a horizontal plane. SE tracks were visibly shorter and more wiggly (Figure S1.2) than the rest of the tracks, which were longer and straighter (Figure S1.3), generally fitting more to the appearance of migration tracks on the tracking radars. After looking into SE and other tracks at other radar locations, a similar pattern was observed.

Based on this exploration, two categories of “good tracks” and “bad tracks” were made for multi-year datasets (2022-2023) for spring and autumn migration seasons collected at Gemini, Luchterduinen and Borssele radar locations. After visual inspections of distributions of a number of track properties for both these categories, none clearly delineated the two. Therefore, using a “tree” package in R (Ripley, 2024), a decision tree model was run on the two categories to explore which track properties best explain the two defined categories. Before the model was run, due to class imbalance between good and bad tracks, data sampling was performed using the ROSE package (Lunardon et al., 2014). The sampling method balanced the number of samples in each class (“good” and “bad”) within the training set, ensuring that the model would not be biased toward the majority class.

The model was trained on the sampled training dataset using the tree() function, with the response variable type (levels: “good”, “bad”). A minimum node size of five (minsize = 5) was specified to prevent overfitting on small sample splits. The decision tree output (Figure S1.4) provided an interpretable set of rules used by the model to classify track quality. The root node and subsequent splits indicate which features best separate “good” from “bad” tracks, based on purity maximization. The first and most significant split in the tree was based on the feature rho\_diff, with a threshold of 577.491. Tracks with a rho\_diff below this value were routed down the left branch of the tree, while those above were classified as “good” regardless of other variables. Further branching of the left path showed the importance of straightness: if straightness was below 0.9538, the tree continued to consider other variables. Based on these results, all tracks that were shorter than 577.5 m while at the same time having a straightness lower than 0.95 were removed.



**Figure S1.1** Overview of track direction at the Gemini radar locations in spring seasons of 2022 and 2023.



**Figure S1.2** An example of what appears to be a migration night with most tracks having the average hourly track direction towards SE (upper panel) and their representation in the horizontal plane amongst wind turbines (lower panel). In the lower panel, tracks in the horizontal plane are visibly shorter and wigglier than those presented in Figure S1.3, which represent the real migration movement.

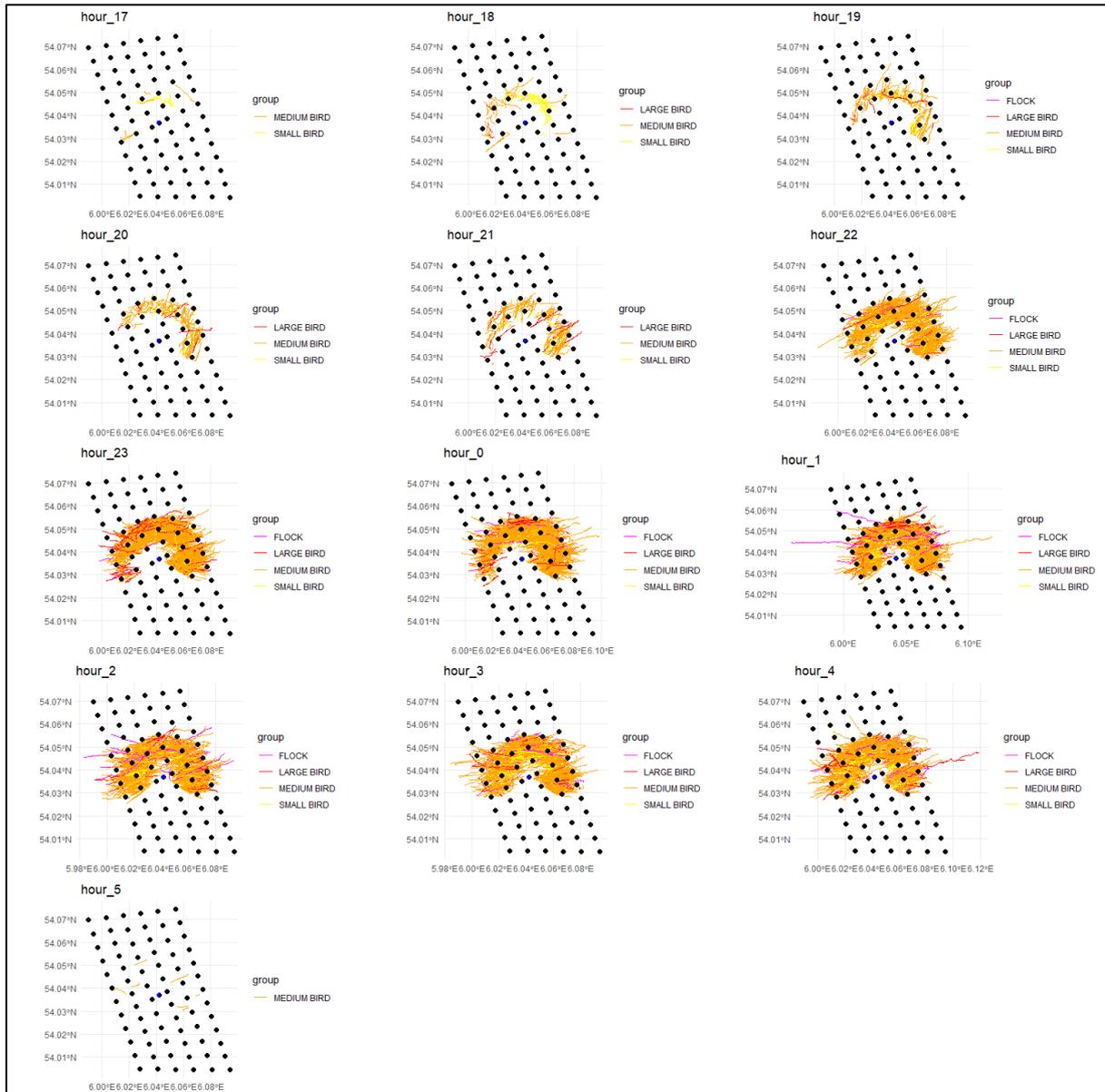
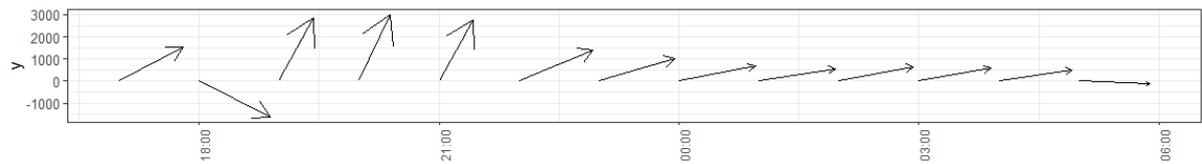


Figure S1.3 An example of a real migration night with most tracks having the average hourly track direction towards NE and E (upper panel) and their representation in the horizontal plane amongst wind turbines (lower panel). In the lower panel, tracks in the horizontal plane are visibly longer and straighter than those presented in Figure S1.2, which mainly represent clutter.

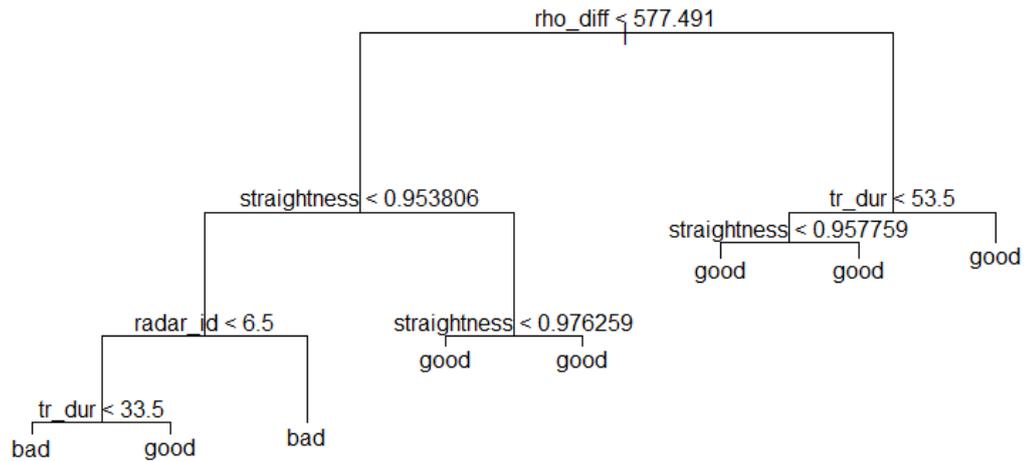


Figure S1.4 Output of the decision tree.

## S2 Blind zones per radar location

Table S2.1 Sizes of blind zones per radar location and their position within the horizontal radar azimuth, where north is indicated by 0/360°.

Radar	Blind zone within the horizontal radar azimuth (in degrees from north)	Size of the blind zone used in MTR calculations (in degrees)
<b>Gemini</b>	127-240	113
<b>k14</b>	97-197	100
<b>Luchterduinen</b>	275-346	71
<b>hkza</b>	5-116	111
<b>Ørsted</b>	100-239	139
<b>Borssele</b>	355-122	127

## S3 Annual time series of MTRs

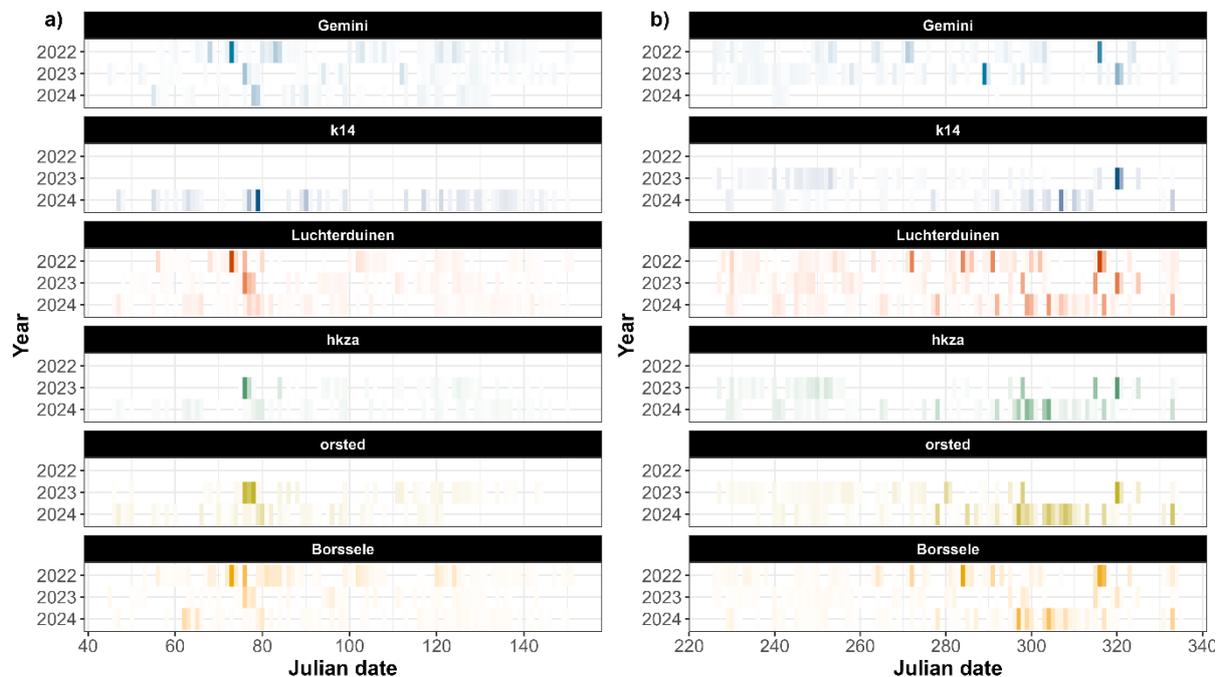


Figure S3.1. Annual time series of nightly MTRs at the radar locations, where each night is a sum of hourly MTRs.

## S4 Pairwise distances of radar locations

Table S4.1 Approximate straight-line distance (km) between pairs of radar locations. Distances were approximated using Google Earth Pro 7.3.6.10201.

	Gemini	k14	Luchterduinen	hkza	Ørsted	Borssele
Gemini	-					
k14	182	-				
Luchterduinen	218	102	-			
hkza	233	110	16	-		
Ørsted	322	170	107	91	-	
Borssele	330	180	112	96	10	-

## S5 Wilcoxon Signed-Rank test results

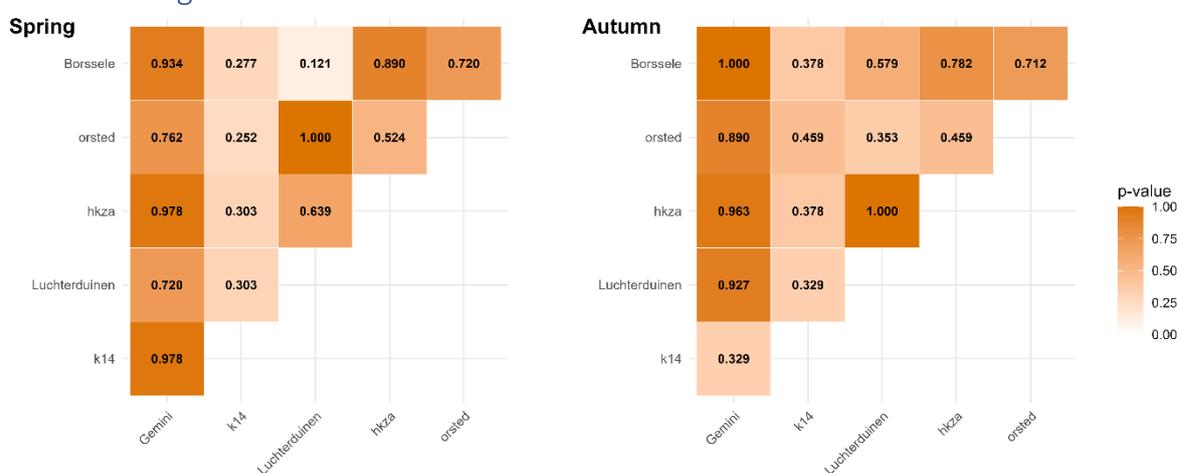


Figure S5.1. Wilcoxon signed-rank test p-values for seasonal phenology between pairs of locations across the North Sea.

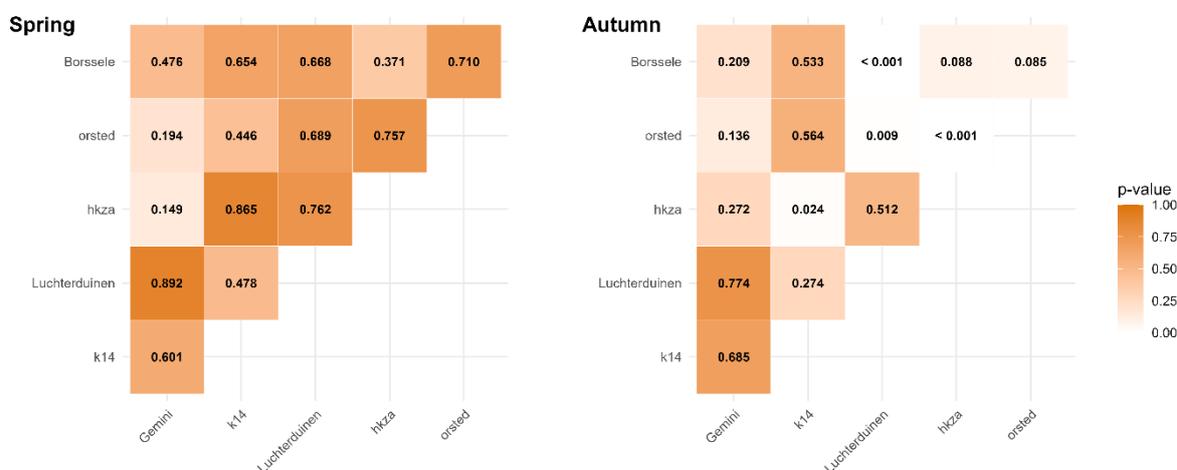


Figure S5.2 Wilcoxon signed-rank test p-values for within-night phenology between pairs of locations across the North Sea.

## References for supplement

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