



Fine-scale behavioural responses to mixing fronts are linked to variation in geographic space use in a medium ranging seabird

Ian R. Cleasby¹ · Ellie Owen² · Peter I. Miller³ · Saskia Wischniewski⁴ · Mark Bolton⁵

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Abstract

Marine predators forage in dynamic, heterogeneous environments, where resources are unevenly distributed. Consequently, predators often concentrate foraging activity in areas where oceanographic processes, such as tidal mixing fronts, enhance prey abundance and availability. Using GPS telemetry data from breeding Black-legged Kittiwakes (*Rissa tridactyla*) at two neighbouring North Sea colonies (Flamborough and Filey, NE England), foraging in areas characterised by well-defined seasonal mixing fronts, we investigated fine-scale behavioural responses of the birds to front-related covariates: distance to the nearest front, sea surface temperature (SST), and surface chlorophyll. We combined generalized hidden Markov models (gHMM) with spatial clustering of individual-level tracking data to classify the at-sea behaviour of Kittiwakes and identify distinct foraging areas. Three space-use clusters were identified at Flamborough and four at Filey, primarily differentiated by direction and distance travelled from the colony. The clearest response to front activity was observed in Kittiwakes at Flamborough in space-use cluster 3, where birds were more likely to be classified as foraging/searching within 5 km of the nearest front. Across clusters, Kittiwakes were generally more likely to forage in cooler waters with lower chlorophyll concentrations. However, behavioural responses to the environmental covariates varied across space-use clusters and were sometimes non-linear. Overall, behavioural responses were context-dependent, shaped by local environmental conditions and the extent of overlap with tidal fronts. Our findings highlight how individual variation in space use can lead to divergent foraging strategies, especially when key oceanographic features occur in specific locations.

Keywords Foraging behaviour · Individual variation · Kittiwake · Movement ecology · Stratifications

Introduction

Understanding how individual animals move and respond to their environment to secure sufficient resources for survival and reproduction is a central focus in movement ecology (Nathan et al. 2008; Hays et al. 2016; Eikelboom et al. 2020). Ultimately, the movement and distribution of animals across a landscape are the result of successive fine-scale behavioural decisions (Potts and Börger 2023). A fundamental principle of optimal foraging theory is that animals should aim to maximize the time spent in productive areas (Stephens and Krebs 1986). However, movement and habitat selection are also influenced by factors such as the heterogeneity of prey distributions (Nonaka and Holme 2007) and constraints such as territoriality or the need to periodically return to a central place, such as a breeding colony (Börger et al. 2008).

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✉ Ian R. Cleasby
ian.cleasby@rspb.org.uk

¹ RSPB Centre for Conservation Science, Etive House, Inverness IV2 3BW, UK

² National Trust for Scotland, Balnain House, 40 Huntly Street, Inverness IV3 5HR, UK

³ Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK

⁴ RSPB Centre for Conservation Science, Sandy, Bedfordshire SG19 2DL, UK

⁵ RSPB Centre for Conservation Science, Aberdeen AB10 1YP, UK

Tracking individuals in dynamic environments provides a means to assess how movement patterns, behaviour, and species distributions shift over time as environmental conditions change (Cagnacci et al. 2010), and can inform conservation planning (Guisan et al. 2013; Zurell et al. 2022). A key aspect of marine spatial management is identifying the factors that influence the distribution and behaviour of marine megafauna (Wakefield et al. 2017; Allen and Singh 2016; Lennox et al. 2019). This information plays a crucial role in various aspects of marine conservation, including supporting the identification and development of suitable Marine Protected Areas (MPAs, Davies et al. 2021; Fauchald et al. 2021), investigating the potential impacts of climate change (Hindell et al. 2020), planned infrastructure developments (Lane et al. 2020; Croll et al. 2022) or other anthropogenic activities (Cleasby et al. 2022). Consequently, understanding how animals use different marine areas or habitats, particularly where they forage, can enhance the effectiveness of existing ecological impact assessments by reducing or better quantifying uncertainty (Searle et al. 2023), and by identifying key habitats where animals engage in specific behaviours (Chivers et al. 2013; Dean et al. 2013).

Large marine predators forage in dynamic oceanographic environments where prey distributions are highly spatially heterogeneous. As a result, many predators target areas where physical processes enhance prey density or availability (Cox et al. 2018). These predators may target a variety of features that operate across different spatio-temporal scales. One class of features that have been highlighted as important across multiple species are tidal mixing fronts. Tidal mixing fronts are transition zones where seasonally stratified waters meet mixed coastal waters (Simpson and Hunter 1974; Pingree and Griffiths 1978), typically marked by strong horizontal temperature gradients (Miller 2009). These fronts are often associated with enhanced local primary production and the aggregation of prey due to the action of tidal currents and water column mixing (Murphy 1995; Hunt et al. 1999; Goetsch et al. 2023). In addition, because the location of fronts is driven by interactions between water depth and tidal velocity, they tend to be relatively consistent features across broader spatio-temporal scales (Simpson 1981; Simpson and Sharples 2012). However, the processes that drive the formation and maintenance of these fronts are considered vulnerable to the effects of climate change and the large-scale development of marine infrastructure—both of which could alter mixing in the water column and, therefore, stratification (Sharples et al. 2013; De Dominicis et al. 2017; Dominicis et al. 2018). Consequently, frontal zones are not only potentially important areas for marine protection but also represent potential zones of conflict between human activities and wildlife conservation (Scales et al. 2014).

Across multiple oceanographic regions, mixing fronts serve as crucial marine habitats for many seabird species (Bost et al. 2009; Cox et al. 2018). Numerous seabird species concentrate their habitat use in areas near fronts or regions with high levels of frontal activity (Decker and Hunt Jr 1996; Begg and Reid 1997; Cleasby et al. 2024a). In some colonies, individuals appear to direct some foraging trips toward consistent fronts, sometimes travelling substantial distances to reach them (Dean et al. 2015; Christensen-Dalsgaard et al. 2018). Additionally, key demographic parameters, such as annual reproductive success, may be linked to the timing and strength of seasonal stratification (Carroll et al. 2015) or the exact location of fronts (Inchausti et al. 2003; Hátún et al. 2017).

Beyond broader-scale evidence that seabird distributions are influenced by the location of mixing fronts, there is also evidence that seabirds adjust their fine-scale foraging behaviour within these frontal zones. For example, Northern Gannets (*Morus bassanus*) were predicted to engage in area-restricted searches (ARS) within 5 km of tidal mixing fronts (Hamer et al. 2009; Grecian et al. 2018) and modify their diving behaviour based on whether they were on the mixed or stratified side of a front (Cleasby et al. 2015) or in relation to distance from a front and/or front strength (Cox et al. 2016). Similarly, transitions between foraging and commuting behaviours in other seabird species, such as auks, Manx Shearwaters (*Puffinus puffinus*), and Red-footed Boobies (*Sula sula*), were found to be associated with sea surface temperature (SST) and surface chlorophyll concentrations (Delord et al. 2020; Kane et al. 2020; Dunn et al. 2024)—covariates commonly used as the basis for mapping ocean fronts. Additionally, birds may encounter higher abundances of prey or specific prey species near fronts (Waggitt et al. 2018; Vlietstra et al. 2005), which could influence their foraging behaviour.

Black-legged Kittiwakes (*Rissa tridactyla*) have experienced significant declines across their range in recent years (Johansen et al. 2020). The species is currently listed as vulnerable on the IUCN Red List of Threatened Species and is included on the OSPAR List of Threatened and/or Declining Species. Kittiwakes are predominantly surface feeders and may rely on bio-physical processes to drive prey to the surface, enabling birds to access them (Schneider et al. 1991; Chivers et al. 2012; Embling et al. 2012). Consequently, they are thought to use frontal zones as key foraging habitats when such features are available (Bertrand et al. 2021; Cleasby et al. 2024a). The importance of tidal fronts to Kittiwakes is highlighted by changes in the reproductive success of certain breeding colonies in relation to changes in stratification within their foraging range (Scott et al. 2006; Carroll et al. 2015). Although broad-scale habitat studies have demonstrated associations between tidal fronts

and Kittiwake habitat usage (Trevail et al. 2021; Cleasby et al. 2024a), the fine-scale behaviour of Kittiwakes and their responses to frontal activity in these regions remain less well understood, though may have important conservation implications (Ruffino et al. 2023; O'Hanlon et al. 2024). While habitat selection may favour areas near fronts, this preference is likely influenced by the accessibility and availability of such habitats (Cleasby et al. 2024a). For instance, local oceanographic conditions around breeding colonies, including proximity to well-defined fronts, may influence fine-scale foraging behaviours (e.g., Christensen-Dalgaard et al. 2018; Gilmour et al. 2018). Additionally, many aspects of animal movement exhibit significant individual variation (Shaw 2020). Even within a single colony, variation in space use and site fidelity can lead to individuals utilizing areas with differing habitat characteristics (Wakefield et al. 2015; Sanchez et al. 2018; Harris et al. 2020; Cleasby et al. 2024b; Regan et al. 2024), potentially resulting in diverse responses to oceanographic features, such as mixing fronts, both between and within breeding colonies.

In the current study, we use generalised Hidden Markov Models (gHMM) to classify GPS movement data from tracked Kittiwakes into different behavioural models to examine their fine-scale behavioural responses to front activity. We focus on two colonies tracked across multiple years, whose foraging ranges overlap with an area of consistent and well-studied frontal activity in the North Sea, the Flamborough front (Hill et al. 1993). At each tracked colony, we identify distinct areas of space use to investigate the relationship between where birds forage and their response to environmental covariates linked with frontal activity. Given the importance of frontal activity in previous habitat selection studies on Kittiwake (Trevail et al. 2021; Cleasby et al. 2024a) and other seabird species, our *a priori* expectations were that: (1) birds are more likely to switch to a searching/foraging mode of behaviour closer to fronts or in areas with greater front activity; (2) variation in space use — both between colonies and within the same colony — results in divergent responses to front activity; and (3) measures of front activity or distribution influence Kittiwake movement patterns, specifically flight speed and directional persistence.

Materials and methods

Tracking data collection

Fieldwork was conducted at two Kittiwake colonies located at Flamborough Cliffs (54.1161° N, 0.0839° W) and Filey (54.2094° N, 0.2556° W) along the North Yorkshire coast, UK. Both colonies are located within the wider Filey and

Flamborough Coast Special Protection Area (SPA) and forage in the North Sea during the breeding season, within the vicinity of a major mixing front known as the Flamborough Front (Hill et al. 1993). In this region, mixing fronts typically run parallel to the coastline, about 10 km offshore to the north of Flamborough Head. Once reaching Flamborough Head one branch of the Flamborough Front system veers eastward offshore, circling the Dogger Bank, while a southern branch heads south of Flamborough Head and extends along 54°N to the east (Hill et al. 1993; Luyten et al. 2003). Birds from Flamborough Cliffs were tracked every year from 2010 to 2015 whereas birds from Filey were tracked in the years 2013–2015. However, individual birds were only ever tracked in one year of the study. More details on colony locations, maps of local bathymetry, and sample sizes are available in the Supplementary Materials (Table S1 & Figs S1 & S2). Kittiwakes were trapped on nesting ledges at the breeding colony using a noose pole during either the late incubation or early chick-rearing stage. We temporarily attached a modified i-GotU GT-120 (Mobile Action Technology, Taipei, Taiwan) GPS logger to a bird's back or tail with Tesa tape (Tesa SE, Norderstedt, Germany). GPS loggers were set to record at 100 s intervals. The loggers deployed weighed either 17.4 ± 0.07 (SE) or 15.0 ± 0.18 , representing 4.5% or 4.2% of Kittiwake body mass respectively. However, there was no evidence that bird behaviour differed between loggers of different mass (Cleasby et al. 2020). Additionally, at the Flamborough and Filey colonies, we found little evidence of differences in foraging ranges or colony attendance patterns between birds fitted with the GPS loggers used in the current study and those equipped with lighter loggers (~2.5% of Kittiwake body mass) in a subsequent tracking study conducted in 2017 (Cleasby et al. 2020). Birds were tagged for periods of 1–9 days after which birds were recaptured and the loggers removed (for more details see: Wakefield et al. (2017). GPS data were screened for errors and only trips > 1 km from the colony and comprising more than 10 observations were classed as foraging trips using the track2KBA R package (Beal et al. 2021) in the R Environment (R Version 4.4.2, R Core Team 2024). For each identified foraging trip, we calculated the maximum distance birds reached from the colony (km) using great circle distances, trip duration (hrs), and the bearing between the distal location during each trip and the colony (for more details, see Cleasby et al. 2024c). All subsequent processing and analysis of tracking data were conducted in the R environment.

Collation of environmental data

To model the fine-scale responses of Kittiwakes to tidal front activity, we focused our modelling efforts on four

covariates: SST, surface Chlorophyll-a concentration, front strength, and distance to the nearest front. SST and Chlorophyll-a are commonly used in front detection algorithms to assess front strength and persistence (Belkin 2021). They also help identify areas of higher marine productivity (Isaksson et al. 2023) and water column features like upwellings and vertical mixing (Miller et al. 2015).

High resolution SST and Chlorophyll-a data were obtained from NEODAAS (NERC Earth Observation Data Analysis and Artificial Intelligence Service) at a resolution of 1 km² daily. SST data were based on the Multiscale Ultra-high Resolution (MUR) multisensory product and processed via NEODAAS. Chlorophyll-a data from NEODAAS were based on the CMEMS OC5 Chlorophyll product (Tilstone et al. 2021). Due to high levels of cloud cover on certain days, which resulted in missing values, we used Chlorophyll-a data averaged over weekly rather than daily intervals, with a spatial resolution of 1 km². Composite ocean front maps from AVHRR SST were created to obtain measures of thermal front gradient magnitude (front strength, °C/1.2 km) and the distance to the nearest front in 1 km cells throughout the study area (Miller 2009). Composite front maps were based on a seven-day moving window that included the day on which tracking locations were observed as well as the preceding 6 days to minimise the influence of missing data due to cloud cover. Front metrics of strength and distance were then calculated according to Miller et al. (2015). Front strength was obtained by applying a Gaussian smoothing filter ($\sigma=5$ pixels) to a map of the mean gradient magnitude values and provides a local neighbourhood average of frontal activity and is useful for identifying persistent, stable frontal features (Suberg et al. 2019). Front distance quantifies the distance from any location within the defined study area to the closest front identified using a simplified version of the front strength maps (P. I. Miller, unpubl. data). For more details see Cleasby et al. (2024a). Summary plots of each covariate across the timeframe of the study available in the Supplementary Material (Figs S3 – S8).

Variation in space use at each colony

To examine how variation in space use influenced the fine-scale behavioural responses of Kittiwakes to the environmental covariates, we grouped individuals into clusters based on the locations they visited during tracking. Firstly, individual-level Utilisation Distributions (UD) were calculated using biased random bridge approach (Benhamou and Cornelis 2010) via the adehabitatHR package (Calenge 2020, for more details on methodology see: Supplementary Material, Cleasby et al. 2019). Next, we used the Earth Mover's Distance (EMD, Rubner et al. 2000) to compare the similarity of each pair of individual-level UD

from a specific colony and generate a distance matrix for clustering purposes. EMD quantifies the similarity between UD based on the effort required to shape one UD into another (Kranstauber et al. 2017). Using EMD-based distance matrices, clustering was performed with the `hclust()` function in the R environment (R Core Team 2024) using Ward's D2 agglomeration method. The optimal number of clusters at each colony was determined through a combination of visual inspection of dendrograms and the average Silhouette method (Rousseeuw 1987). Ultimately, we identified three clusters at Flamborough and four at Filey. Once clusters were identified, we created cluster-level UD by averaging all the individual-level UD within each defined cluster to visualise space-use patterns.

Behavioural segmentation and analysis of tracking data

To identify when Kittiwakes engaged in foraging behaviour, we used a Hidden Markov Modelling (HMM) approach to classify tracking data into different behavioural states. Initially, basic HMMs that included no environmental covariates were run separately for birds in each spatial cluster identified at the Flamborough and Filey colonies, respectively, and served as null models upon which to develop more complex models. All HMMs were performed using the `momentuHMM` R package (McClintock and Michelot 2018).

In our initial HMMs, we defined three distinct behavioural modes, which we termed 'resting', 'searching/foraging', and 'transit/commuting'. This interpretation was based on step lengths and turn angles calculated between successive GPS fixes. The decision to identify three behavioural modes was based on prior experience with Kittiwake tracking data, which suggested that HMMs can usually distinguish three behavioural states in such data relatively clearly (Trevail et al. 2021; Bogdanova et al. 2022). Based on prior research findings, we constructed HMM design matrices such that step lengths were set to be shortest when resting, intermediate during searching/foraging, and longest during transit (resting < searching < transit). Likewise, turn angles were set up as transit < searching, indicating more direct flight during transit compared to searching. For resting behaviour, we placed no constraints on the estimation of turn angles. Additionally, during initial runs of our HMMs, we observed that birds rarely transitioned directly between resting and transit behaviours, so the probability of transitioning between these states was set to 0.

We ran each HMM ten times using randomly generated initial values to avoid problems associated with model convergence to local maxima (McClintock and Michelot 2018) and selected the model with the highest likelihood. For all

models, validation was performed by graphically comparing the marginal distributions from the fitted HMM with the empirical distributions.

Following model validation, we extended our initial HMM to incorporate the influence of selected environmental covariates on the probability of transitioning between different behavioural states within each identified space-use cluster. This was achieved by including environmental covariates specifying either a standard linear relationship or allowing for a non-linear relationship using B-splines with $k=4$ knots. Running models separately per cluster allowed us to identify different situations in which either a linear or non-linear relationship performed best. Additionally, we included an effect of time of day in our HMMs using a cosinor function for cyclical data to account for the assumption that resting behaviour should be more common overnight.

Although the correlations between each of the covariates considered were not particularly strong ($r < 0.4$ in all cases), we found evidence of concavity between front strength and distance to the nearest front (see also: Cleasby et al. 2024a). Specifically, front strength was generally higher near fronts and decreased with distance from them. As a result, front strength and distance to the nearest front were never included in the same model. Ultimately, models including the distance to the nearest front consistently outperformed those including front strength, as measured by AIC scores, mirroring a previous finding when modelling broader-scale habitat usage (Cleasby et al. 2024a). Therefore, we report results from models in which distance to the nearest front was included.

Table 1 Estimated mean step length and associated standard deviation for each behavioural model identified in a 3-state gHMM for birds in each space use cluster. Estimates reflect outputs of best performing models for each space-use cluster and reflect step length when each covariate was set at its mean value across observations within a particular cluster and setting the time of day as midday (12:00:00)

Space Use Cluster	Behaviour		
	Resting	Searching	Transit
Flamborough – 1	Mean = 99.32 SD = 41.42	Mean = 386.09 SD = 455.48	Mean = 1847.91 SD = 618.21
Flamborough – 2	Mean = 88.23 SD = 39.03	Mean = 432.49 SD = 515.83	Mean = 2085.84 SD = 553.49
Flamborough – 3	Mean = 98.06 SD = 48.35	Mean = 461.14 SD = 489.63	Mean = 2045.64 SD = 532.37
Filey – 1	Mean = 53.51 SD = 29.76	Mean = 229.38 SD = 219.27	Mean = 1182.06 SD = 337.95
Filey – 2	Mean = 39.87 SD = 20.13	Mean = 339.97 SD = 359.97	Mean = 1310.75 SD = 321.16
Filey – 3	Mean = 88.65 SD = 61.37	Mean = 676.45 SD = 384.95	Mean = 1547.68 SD = 329.68
Filey – 4	Mean = 63.81 SD = 42.85	Mean = 496.86 SD = 357.62	Mean = 1443.3 SD = 320.84

Standard HMMs allow covariates to influence the probability of transitioning between behavioural states but do not allow them to affect underlying movement characteristics, such as step lengths and turning angles. However, in certain circumstances, it can be beneficial to allow movement parameters to vary in response to environmental conditions (Carter et al. 2020). Therefore, we extended our HMMs into generalised HMMs (gHMM) by modelling step lengths and directional persistence in both the ‘searching/foraging’ and ‘commuting/transit’ modes in response to each of the environmental covariates considered.

Initial parameter values for gHMMs were informed by estimates from simpler HMMs to aid model convergence. Nevertheless, when modelling the effect of environmental covariates on movement parameters in gHMMs, we were restricted to examining linear effects as modelling non-linear responses resulted in models failing to converge. As when modelling behavioural transition probabilities, model performance was assessed using model AIC scores and covariates were only retained in our best model if they improved model AIC scores. In general, gHMMs that modelled step length and directional persistence in response to environmental covariates outperformed conventional HMMs, as indicated by lower AIC scores (see Tables S2 & S3 for model selection results). Consequently, all the results reported are based on the outputs of the best performing gHMM model. Once the best performing gHMM for each cluster was identified, behavioural states were assigned to each Kittiwake observation using the Viterbi algorithm within momentuHMM package (McClintock and Michelot 2018). In addition, model residuals were checked to ensure model assumptions relating to autocorrelation and normality of model residuals. Summaries of step length and directional persistence in each behavioural state are presented in Tables 1 and 2.

Results

Variation in space use

In total, we tracked 97 birds at Flamborough and 47 at Filey. At Flamborough, we grouped individuals into three clusters based on the similarity (EMD) scores of individual-level UD. A total of 22 individuals were placed in cluster 1, 41 in cluster 2, and 34 in cluster 3 (Table S4). Clusters were primarily differentiated by the directions birds travelled from the colony and the typical length of their foraging trips (Fig. 1). Kittiwakes in cluster 1 tended to travel on southerly bearings, staying relatively close to the coastline as a result (Figs. S9 & S10). In contrast, Kittiwakes from cluster 2 at Flamborough generally departed on more easterly bearings,

Table 2 Estimated directional persistence and associated 95% confidence interval for each behavioural model identified in a 3-state gHMM for birds in each space use cluster. Estimates reflect outputs of best performing models for each space-use cluster and reflect directional persistence when each covariate was set at its mean value across observation within a particular cluster and setting the time of day as midday (12:00:00)

Space Use Cluster	Behaviour		
	Resting	Searching	Transit
Flamborough – 1	0.91 (0.90–0.92)	0.34 (0.31–0.36)	0.88 (0.87–0.89)
Flamborough – 2	0.89 (0.88–0.90)	0.36 (0.34–0.38)	0.91 (0.91–0.92)
Flamborough – 3	0.82 (0.81–0.83)	0.33 (0.31–0.35)	0.91 (0.90–0.92)
Filey – 1	0.87 (0.86–0.88)	0.30 (0.26–0.33)	0.86 (0.85–0.87)
Filey – 2	0.84 (0.83–0.85)	0.31 (0.29–0.33)	0.91 (0.90–0.92)
Filey – 3	0.51 (0.48–0.53)	0.61 (0.58–0.64)	0.93 (0.92–0.94)
Filey – 4	0.55 (0.52–0.57)	0.32 (0.28–0.36)	0.93 (0.92–0.93)

while Kittiwakes from cluster 3 typically departed on south-easterly bearings, between the directions observed in clusters 1 and 2 (Fig. S10). Trip durations and foraging ranges in cluster 2 also tended to be greater than observed in the other two clusters (Figs S11 & S12).

At Filey, individuals were grouped into four space-use clusters (Cluster 1 - $n=14$ individuals; Cluster 2 - $n=18$; Cluster 3 - $n=6$; Cluster 4 - $n=9$, Table S5), with each cluster differing in the direction birds travelled from the colony (Fig. 1 & Fig. S13). Birds in Cluster 1 generally headed north-northeast, those in Cluster 2 headed east-northeast, birds in Cluster 3 primarily headed east-southeast, and those in Cluster 4 headed east (Fig. S14). Foraging trips in Cluster 1 were typically the shortest in both duration and maximum range, while trips in Cluster 2 tended to be the longest (Figs S15 & S16).

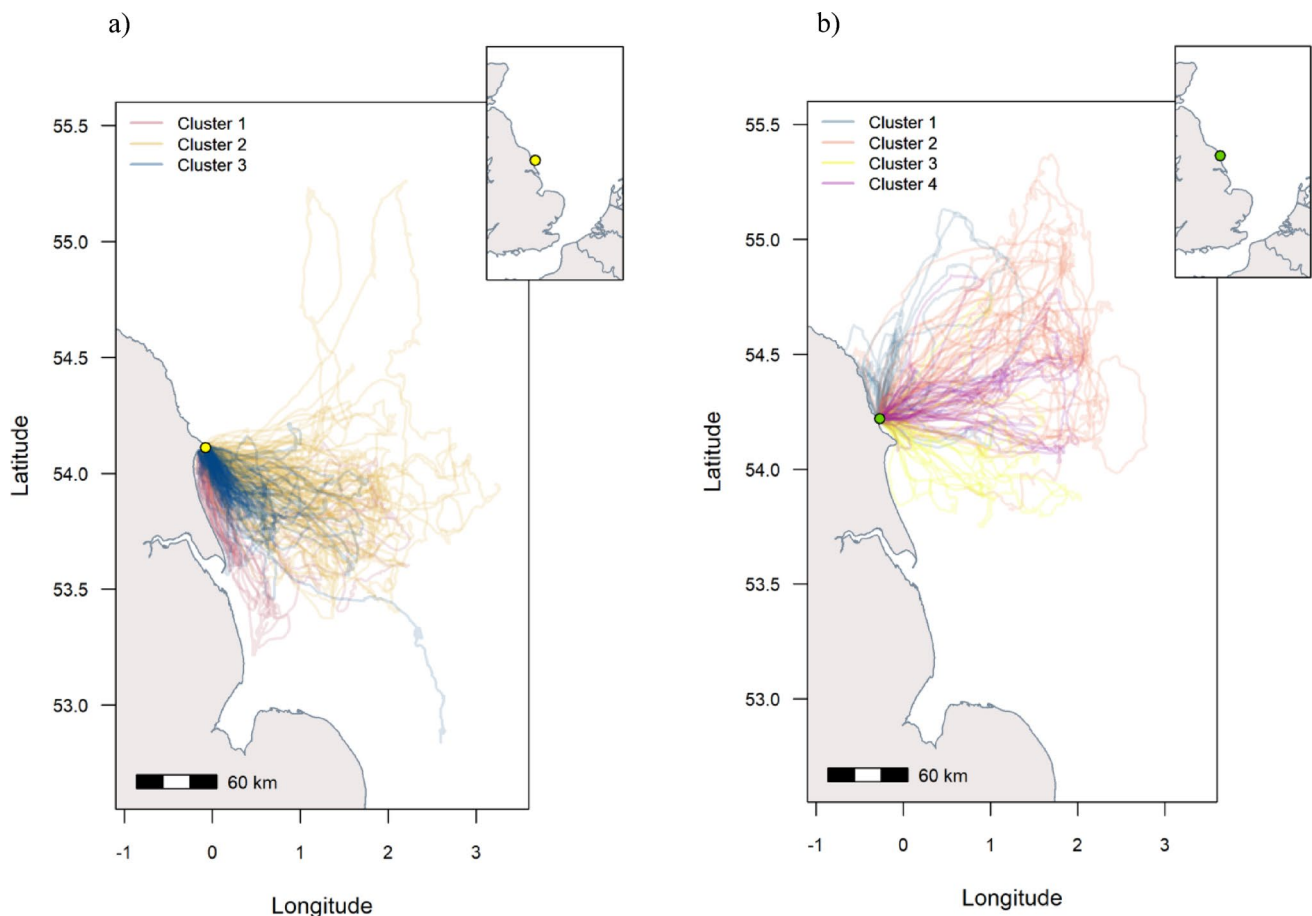


Fig. 1 Plots showing Kittiwake foraging tracks recorded at (a) Flamborough and (b) Filey. Tracks are displayed as opaque, coloured lines with line colour denoting the space-use cluster to which individual

birds were assigned. Colony location is displayed as either a yellow circle (Flamborough) or a green circle (Filey)

Movement analysis from gHMMs

Effect of environmental covariates on the probability of transitioning between behaviours

In general, the probability of transitioning between different behaviours in response to each of the environmental covariates considered varied both within and between colonies (Figs. 2, 3 and 4, see Tables S6 & S7 for model coefficients).

Chlorophyll concentration The probability of being classified as searching/foraging was negatively associated with chlorophyll concentration for Kittiwakes in Flamborough cluster 1 and Filey cluster 4. We also observed non-linear responses to chlorophyll concentration for Kittiwakes in spatial cluster 3 at Flamborough and cluster 2 at Filey (Fig. 2). For Kittiwakes in Flamborough cluster 3, the probability of being classified in the searching behavioural mode peaked at concentrations of 1.5 mg m^{-3} before declining thereafter (Figs S17 & S18). For Kittiwakes in Filey cluster 2, the probability of being classified as searching was greatest at the lowest chlorophyll concentrations, declining rapidly as chlorophyll concentration rose to a value of 0.5 mg m^{-3} before levelling off at a constant value as chlorophyll concentration increased further. Therefore, in these cases,

the likelihood of being in the searching mode was greatest at lower to intermediate values of chlorophyll concentration (Figs S19 & S20). For birds in Filey cluster 2, the probability of being classed as resting also rose at higher values of chlorophyll concentration ($> 3 \text{ mg m}^{-3}$) alongside a concomitant decrease in transit behaviour. In the remaining spatial clusters identified, there was no clear relationship between chlorophyll concentration and behavioural classification.

Sea surface temperature Regarding SST, we observed different non-linear responses across the different spatial clusters identified (Fig. 3). For Kittiwakes at Flamborough, there was a tendency for the probability of being classified as searching/foraging to be negatively associated with SST across spatial clusters 1 and 2. In contrast, a peak in the probability of searching behaviour occurred at values around $11.5\text{--}12^\circ\text{C}$ in cluster 3 at Flamborough (see also Figs S21 & S22). Similarly, at Filey birds in cluster 1 showed a peak in searching behaviour as SST approached 12°C , but there was also evidence of a second peak in searching behaviour at higher SSTs ($> 15^\circ\text{C}$) that was not observed in other spatial clusters at either colony (Figs S23 & S24). In the remaining three clusters at Filey, we did not observe a clear relationship between the probability of being classed

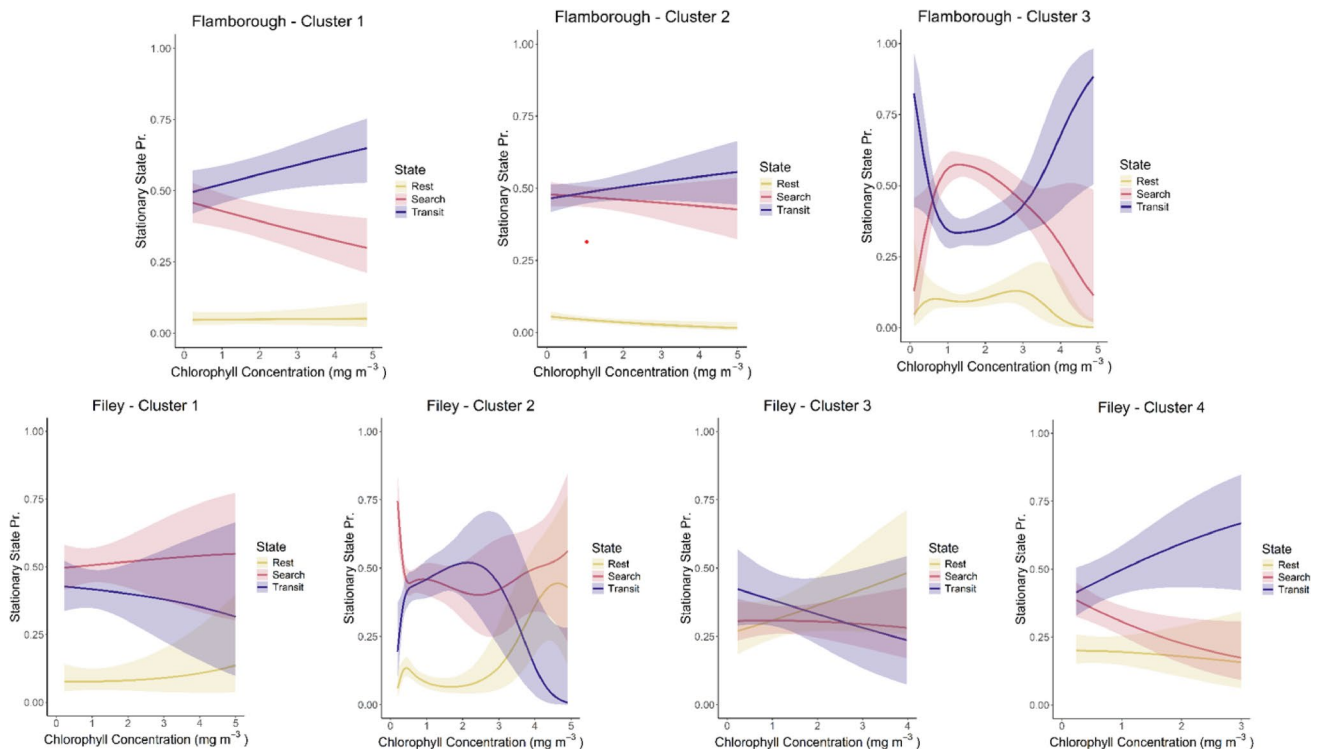


Fig. 2 Stationary state probabilities derived from gHMMs of being in each of three identified behavioural states for Kittiwakes in response to surface chlorophyll concentration. Probabilities displayed for birds from the Flamborough and Filey colonies in each identified space-use

cluster. Probabilities calculated with all other covariates held at their mean value based on the conditions observed across all tracking locations from that cluster and assuming the time of day as midday. Opaque envelopes around predicted curves represent 95% confidence intervals

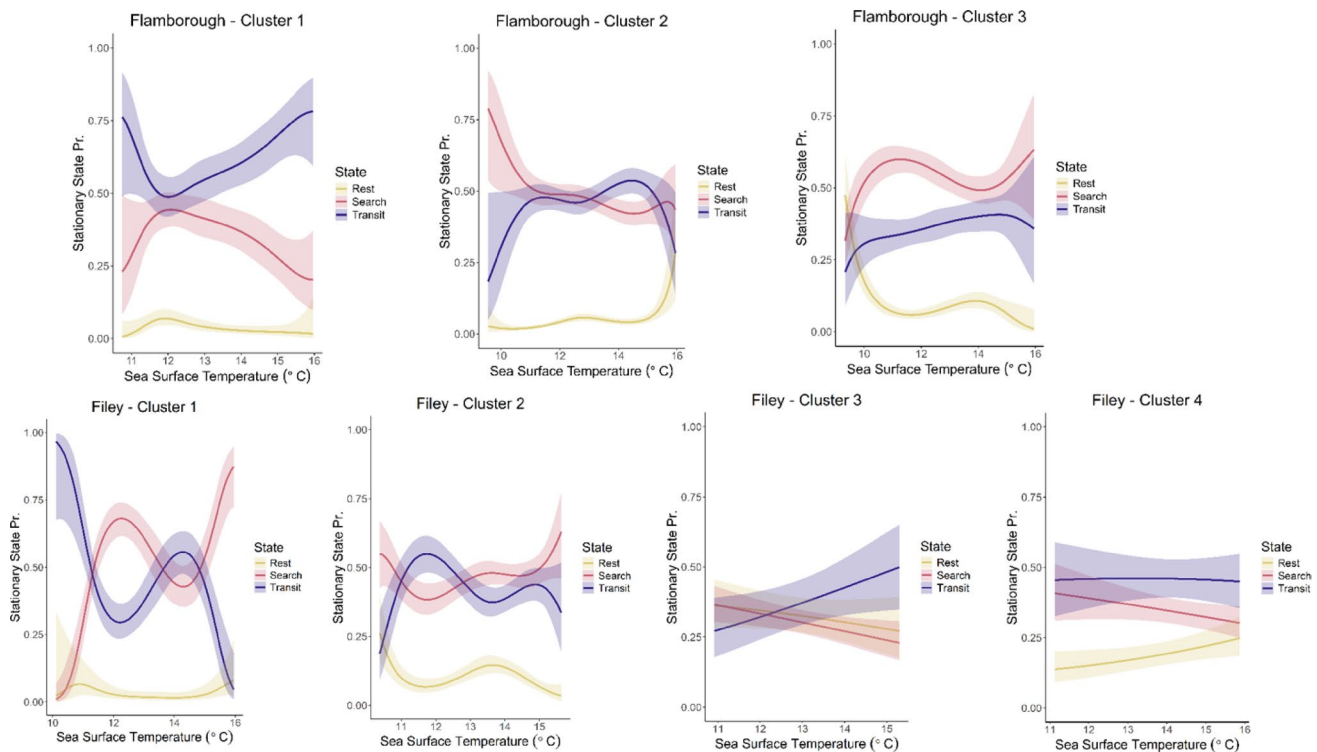


Fig. 3 Stationary state probabilities derived from gHMMs of being in each of three identified behavioural states for Kittiwakes in response to Sea Surface Temperature. Probabilities displayed each identified space-use cluster at Flamborough or Filey. Probabilities calculated

in the searching mode and SST. However, in Filey clusters 3 and 4 there was a tendency for searching behaviour to decline as SST increased. For individuals in Filey cluster 2, the clearest result we observed was a peak in the probability of being classified in the transit mode, occurring at around 11.5 °C, which was mirrored by a corresponding decrease in the probability of engaging in resting behaviour.

Distance to nearest front At Flamborough, Kittiwakes in clusters 1 and 2 showed a marked increase in the probability of being classified as searching in areas relatively far from the nearest front (> 30 km) while at the same time, the probability of engaging in transit behaviour declined (Fig. 4). However, it should be noted that birds rarely visited areas this far from the nearest front (Figs S25 & S26). In contrast, in cluster 3 at Flamborough, the probability of being classified as searching was greatest when birds were located right on the front, then declined as distance to the nearest front increased to 5 km. In addition, birds in this cluster exhibited a second peak in the likelihood of searching behaviour in areas approximately 20 km from the nearest front. At the Filey colony, birds in cluster 2 showed a non-linear response to distance to the nearest front, with the probability of being classified as foraging peaking slightly when close

with all other covariates held at their mean value based on the conditions observed across all tracking locations from that cluster and assuming the time of day as midday. Opaque envelopes around predicted curves represent 95% confidence intervals

to the nearest front (~5 km), with a second larger peak in searching activity in areas approximately 40 km from the nearest front (Fig. 4, Figs S27 & S28). Across the other spatial clusters at Filey, there was no clear association between searching behaviour and the distance to the nearest front. However, in Filey cluster 4, there was an increase in the probability of resting behaviour as distance from the nearest front increased.

Across all clusters, we observed clear diurnal patterns in behaviour, with a higher likelihood of transit and searching behaviour during the middle of the day, while resting on the water was most prevalent during the night (Figs S29 & S30).

Effect of environmental covariates on movement parameters

Overall, while the generalised Hidden Markov Models (gHMMs), which incorporated environmental covariates as predictors of movement parameters, outperformed conventional HMMs, we did not find consistent associations between covariates and movement parameters across the 7 spatial clusters examined. Instead, environmental variables showed a mix of positive, negative, and non-significant

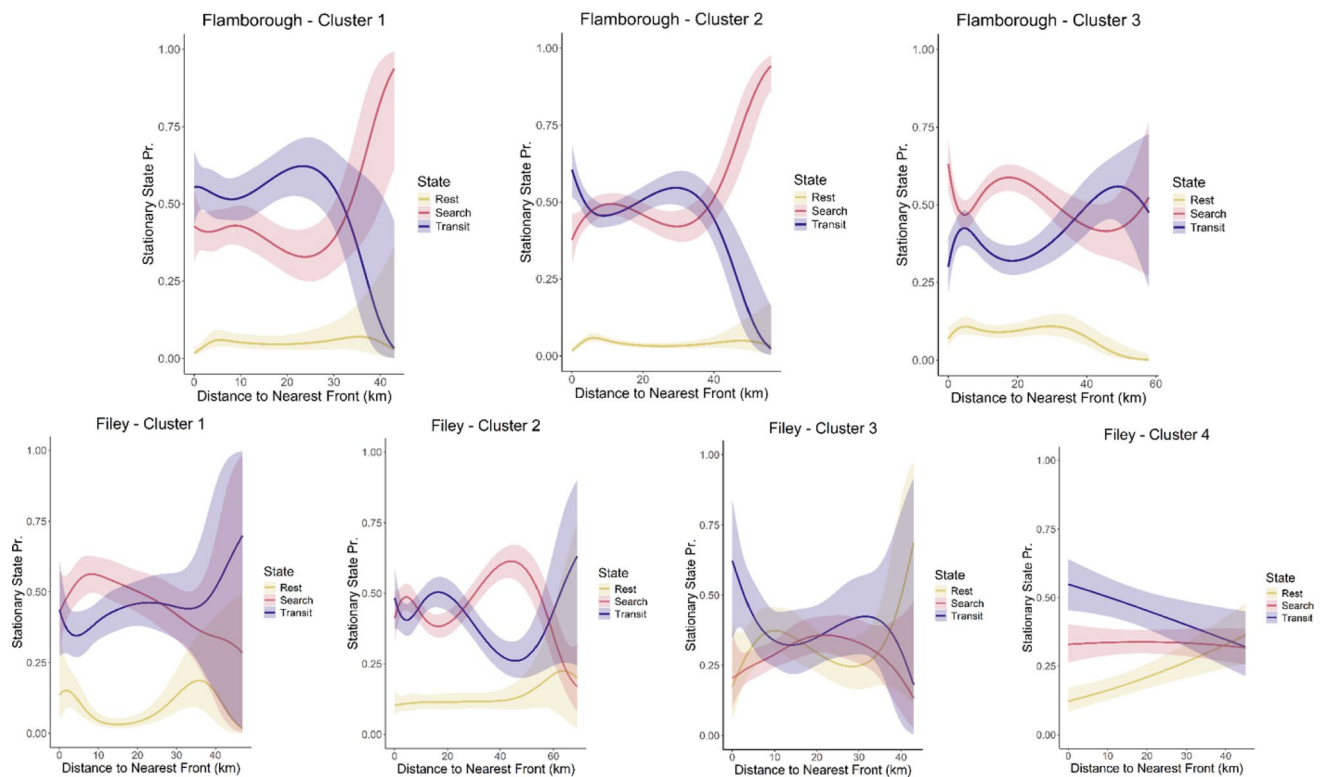


Fig. 4 Stationary state probabilities derived from gHMMs of being in each of three identified behavioural states for Kittiwakes in response to Distance to the nearest Front. Probabilities displayed each identified space-use cluster at Flamborough or Filey. Probabilities calcu-

lated with all other covariates held at their mean value based on the conditions observed across all tracking locations from that cluster and assuming the time of day as midday. Opaque envelopes around predicted curves represent 95% confidence intervals

associations with movement parameters, varying by space-use cluster (Table 3, see also: Figs S31 – S42).

Focussing on results from within a single colony, the most consistent findings were observed at Flamborough, where we found: (1) a negative association between step length and chlorophyll concentration during transit across all three space-use clusters and (2) a positive association between SST and step length during searching behaviour also across all three space-use clusters. In contrast, at Filey, we did not observe any consistent, directional responses to environmental covariates across the four space use clusters identified.

Discussion

The potential importance of mixing fronts as key foraging areas for marine predators has been highlighted in many species across diverse regions (Bailey and Thompson 2010; Scales et al. 2014; Miller et al. 2015; Cox et al. 2018). In this study, we demonstrate that breeding Black-legged Kittiwakes do indeed modify their foraging behaviour in response to environmental variables related to front activity, including the distance to the nearest front. The exact

relationships we identified between environmental covariates were influenced by the local conditions experienced by birds. Specifically, by clustering individuals based on the two-dimensional distribution of their foraging trips, we were able to identify areas where birds were likely foraging in association with fronts. At the same time, we also identified foraging areas where birds may have focused on other environmental features further from any mixing fronts. More broadly, these findings support the idea that the foraging behaviour of marine predators is influenced by local oceanographic conditions (Gilmour et al. 2018). As a result, individual behavioural plasticity and variation among individuals, even those from the same colony but utilising different foraging areas within a broader colony-level range, may lead to divergence in foraging tactics, geographic space use, and potentially individual specialisation (Carlson et al. 2021; Schwarz et al. 2021).

Table 3 Summary of results from a gHMM examining associations between environmental covariates (surface chlorophyll, SST, and distance to the nearest front) and movement parameters (step length and directional persistence) during transit and searching behaviours in Black-legged Kittiwakes. The table reports the number of Spatial clusters (N) showing positive, negative, or non-significant associations, along with the specific clusters in each category. Details on model coefficients are provided in tables S8 & S9

Environmental Covariate	Movement Parameter	Behavioural State	Positive association	Negative association	No association
Surface Chlorophyll	Step Length	Transit	N=2 Filey 1 & 3	N=5 Flamborough 1–3 Filey 2 & 4	
		Searching	N=1 Filey 4	N=1 Flamborough 3	N=5 Flamborough 1 & 2 Filey 1–3
	Directional Persistence	Transit	N=2 Filey 1 & 4	N=2 Flamborough 1 & 2	N=3 Flamborough 3 Filey 2 & 3
		Searching	N=3 Flamborough 1 & 3 Filey 4		N=4 Flamborough 2 Filey 1–3
	SST	Transit	N=3 Flamborough 2 & 3 Filey 1	N=1 Filey 4	N=3 Flamborough 1 Filey 2 & 3
		Searching	N=3 Flamborough 1–3		N=4 Filey 1–4
Distance to Nearest Front	Step Length	Transit	N=1 Flamborough 2	N=3 Flamborough 3 Filey 2 & 4	N=3 Flamborough 1 Filey 1 & 3
		Searching	N=1 Filey 3	N=1 Filey 2	N=5 Flamborough 1–3 Filey 1 & 4
	Directional Persistence	Transit	N=1 Flamborough 2	N=3 Flamborough 3 Filey 2 & 4	N=3 Flamborough 1 Filey 1 & 3
		Searching	N=1 Filey 3	N=3 Flamborough 2 & 3 Filey 2	N=3 Flamborough 1 Filey 1 & 4
	SST	Transit	N=3 Flamborough 2 & 3 Filey 1	N=1 Filey 4	N=3 Flamborough 1 Filey 2 & 3
		Searching	N=3 Flamborough 1–3		N=4 Filey 1–4

Effect of environmental covariates on the probability of transitioning between behaviours

Distance to nearest front

The spatial clusters that showed the clearest response to frontal activity were those most closely aligned with the approximate location of different parts of the Flamborough front system. Specifically, for Kittiwakes in Flamborough cluster 3, the probability of being in searching mode—which we interpret as representing foraging behaviour—was highest when birds were located near a front. This probability declined as the distance from the front increased, reaching a local minimum at 5 km, suggesting that foraging behaviour was concentrated within 5 km of the front (Fig. 4). This finding supports previous fine-scale studies

of seabird behaviour, which have shown that seabirds alter their behaviour in proximity to fronts, either by engaging in ARS within 5 km of fronts (Hamer et al. 2009) or modifying diving behaviour close to fronts (Grecian et al. 2018; Cox et al. 2016). Birds in Flamborough's space-use cluster 3 typically travelled on south-easterly bearings from the colony, suggesting use of the southerly branch of the Flamborough Front system that extends past Flamborough Head (Hill et al. 1993; Luyten et al. 2003; Miller and Christodoulou 2014; Timko et al. 2019). Supporting this, many identified searching locations in this cluster overlapped waters classified as predominantly mixed or intermittently stratified (van Leeuwen et al. 2015; Chen et al. 2022).

We also observed a second peak in foraging activity at distances approximately 20 km from the nearest front. A similar peak in Kittiwake habitat usage in areas approximately

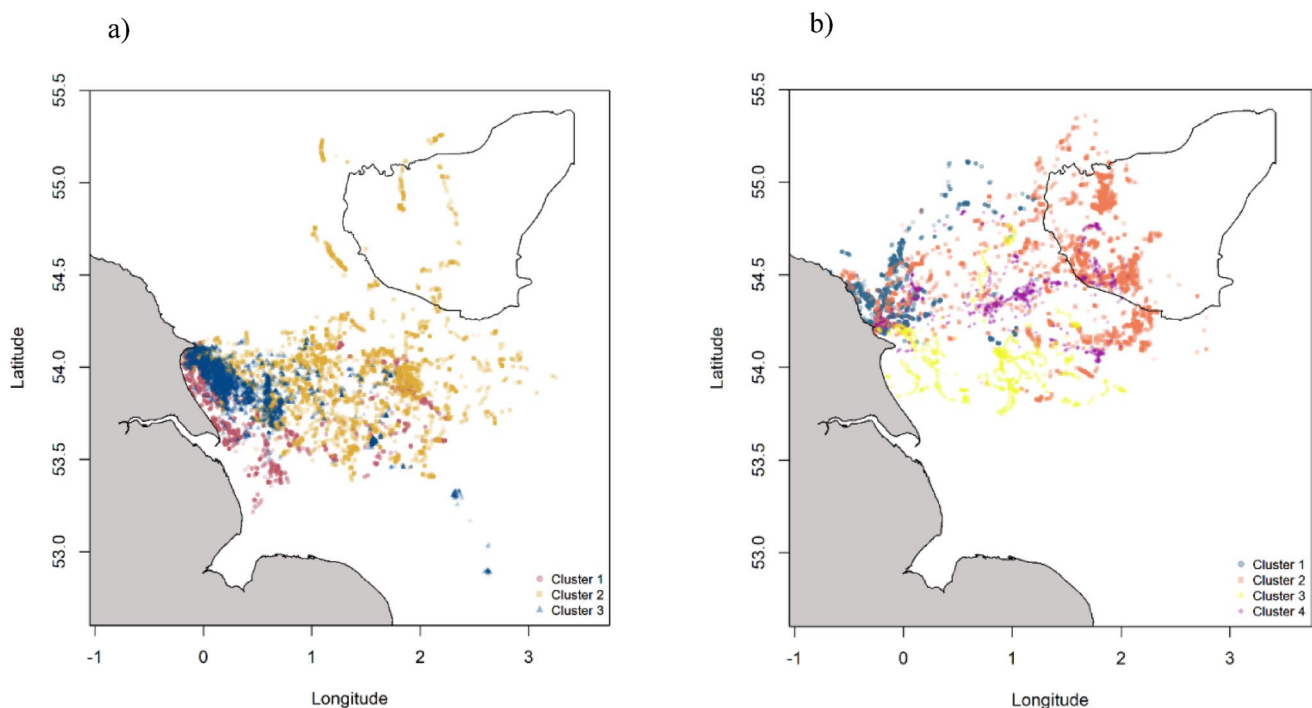


Fig. 5 Map showing the locations identified by gHMMs as searching/foraging behaviour for Kittiwakes in each identified space use cluster at Flamborough (a) and Filey (b). Points are displayed using opaque

colours to help identify areas with a greater concentration of observations. The location of the Dogger Bank is also displayed as black polygon (see also: Fig. S1)

25 km from fronts was also observed in an earlier, broader-scale habitat selection study (Cleasby et al. 2024a). On the stratified side of fronts, the spring-neap cycle may result in variability in primary productivity in areas within 15–50 km of fronts (Sharples 2008), thus birds may still be responding to the action of tidal fronts. Additionally, for birds in Flamborough cluster 3, many locations classified as searching and within 15–25 km of the nearest front in this cluster were located on the western, offshore side of the Holderness Offshore Marine Conservation Zone (MCZ), which is an area of high habitat and species diversity (DEFRA; Holderness Offshore MCZ 2019) and may represent an important Kittiwake foraging site (Fig. S43).

Birds in the space use clusters at Filey also showed some evidence of foraging close to fronts. For birds in Filey cluster 1 there was a slight peak in the likelihood of being classified as searching as opposed to transit behaviour when birds were approximately 5–10 km from the nearest front (Fig. 4). Birds in this cluster also made relatively short trips and foraged north of Flamborough Head, where the front is located about 10 km offshore, running parallel to the coast (Hill et al. 1993). For birds in Filey cluster 2, there was a small peak in the likelihood of foraging behaviour centred on a value of 2.5 km from the nearest front, before a second larger peak occurred in areas further from fronts (40 km). Given that many locations classified as searching/foraging for Kittiwake in Filey Cluster 2 were also located offshore

(Fig. 5), this may reflect their use of the shallower waters (<25 m, Fig. S44) and slopes of the Dogger Bank, which are also utilized by other marine predators (Wyles et al. 2022).

There was less evidence that Kittiwakes in the remaining space-use clusters identified responded as strongly to frontal activity. Unlike the results for space-use Cluster 3 at Flamborough, we did not observe an increased likelihood of searching near fronts for birds in space-use Clusters 1 and 2 at Flamborough. Instead, the probability of searching behaviour remained relatively constant before increasing in areas more than 40 km away from fronts. However, areas far from fronts were rarely encountered by the birds at Flamborough and typically occurred at the distal end of longer foraging trips. In the remaining space-use clusters identified at Filey (space-use clusters 3 and 4), the likelihood of switching to foraging behaviour remained relatively flat in response to distance from the nearest front. However, the number of individuals in these clusters was relatively small ($n < 10$ individuals in both cases), which may influence our ability to detect responses to environmental covariates.

Sea surface temperature

Previous studies on Kittiwakes have reported a preference for areas with cooler sea surface temperatures (SSTs) more typical of mixed waters (Robertson et al. 2014; Trevail et al. 2021; Wakefield et al. 2017; Cleasby et al. 2024a; but

see also: O'Hanlon et al. 2024). Consequently, our a priori prediction was that Kittiwake searching behaviour would be more prevalent when SST was lower. In line with expectation, birds in Flamborough cluster 2 were more likely to be classified as searching rather than commuting at the lowest SSTs encountered. Birds in Flamborough clusters 1 and 3 showed a peak in searching at SSTs between 11.5 °C and 12 °C, beyond which searching behaviour declined (Fig. 3). In addition, SST was weakly negatively associated with the likelihood of engaging in searching behaviour for birds in space use clusters 3 and 4 at Filey (Fig. 3). Together, these results broadly support the prediction that Kittiwakes are more likely to forage in cooler waters, particularly those areas where SST is 13 °C or below in the current study.

In the remaining two space use clusters identified, Filey cluster 1 and Filey cluster 2, the relationship between searching behaviour and SST showed some evidence that searching behaviour increased at higher SST values. In general, areas with higher SSTs were primarily associated with birds foraging in stratified waters to the north-east of the Filey colony, especially for birds in cluster 1, or over warmer but well-mixed waters at the Dogger Bank.

Surface chlorophyll concentration

Chlorophyll concentration is often used as an indicator of phytoplankton abundance in the water column, which forms the foundation of marine food webs upon which top marine predators ultimately rely (Suryan et al. 2012; Warwick-Evans et al. 2021). Previous studies have reported positive associations between chlorophyll concentration and Kittiwake abundance (Scott et al. 2010; Chivers et al. 2013; Robertson et al. 2014). However, research on the broader-scale habitat use by North Sea Kittiwakes has suggested that responses to surface chlorophyll concentrations are influenced by local environmental conditions. Specifically, habitat use may be directed toward areas with lower surface chlorophyll concentrations, reflecting foraging in offshore areas away from the coastline (Cleasby et al. 2024a), as observed in other seabirds (Grémillet et al. 2008).

At the behavioural scale, we found that the likelihood of foraging behaviour did not increase in response to surface chlorophyll concentration. While responses to chlorophyll concentration varied across space-use clusters, associations with foraging behaviour were either flat or negative. Within the study region, the highest surface chlorophyll levels are typically found in areas near the coastline, in waters less than 30 m deep (Amorim et al. 2024), particularly around the mouths of the Humber and Wash estuaries (Peters et al. 2005; Fig. S2). These areas were rarely visited, if at all, by Kittiwakes tracked at Flamborough and Filey during this and other tracking studies at these colonies (Cleasby et al. 2020).

This suggests that the combination of shallow coastal waters with high surface chlorophyll and potentially high turbidity does not represent a key foraging habitat for this species. Instead, for Kittiwakes tracked at Flamborough, the distribution of chlorophyll concentrations experienced during foraging showed a clear, narrowly defined peak at approximately 1.5 mg m⁻³ across all spatial clusters (Fig. 2, Fig. S17). The foraging ranges of birds in Filey space use cluster 3 overlapped with those observed at Flamborough, and a similar peak at 1.5 mg m⁻³ was also observed in the birds within this cluster (Fig. S19). Mapping chlorophyll values around this peak in the range of 1.25–1.75 mg m⁻³ reveals a band of chlorophyll located offshore, which approximately aligns with the locations of SST thermal fronts (Fig. S3). More generally, SST fronts are often co-located with chlorophyll fronts (Belkin and O'Reilly 2009; Xia et al. 2021) and seasonal stratification can lead to a reduction in surface chlorophyll biomass (van Haren et al. 1998; van de Pol et al. 2013). Given that the likelihood of being in a searching or foraging mode peaks at approximately 1.5 mg m⁻³ for birds in Flamborough cluster 3, we believe this supports the conclusion that Kittiwakes in this cluster were foraging near fronts. Although no similar response was detected in Flamborough space use clusters 1 or 2, or in Filey space-use cluster 3, the peak in chlorophyll concentrations at 1.5 mg m⁻³ across observed foraging locations may still reflect the importance of chlorophyll fronts for Kittiwakes in these other spatial clusters.

For birds in the remaining space use clusters at Filey (1, 2, and 4), we rarely observed chlorophyll values above 1 mg m⁻³ at locations where birds were classed as searching/foraging, particularly once birds were at least 10 km from the coast. Although chlorophyll concentrations in these areas were low, we were limited to investigating surface chlorophyll. However, subsurface maxima in chlorophyll concentrations have been observed in seasonally stratified North Sea waters (Weston et al. 2005) and have also been linked to increased foraging activity and abundance in several marine predators, including Kittiwakes (Skov and Durinck 2000; Scott et al. 2010, 2013; Embling et al. 2012). Recent advances in satellite mapping techniques and analytical approaches for identifying water density levels should increase the availability and extent of information on subsurface chlorophyll in the future (Yasunaka et al. 2021; Zampollo et al. 2023), which will assist future studies of seabird habitat use.

Effect of environmental covariates on movement parameters

In addition to influencing the probability of switching behaviour, we also observed that gHMMs, in which step

length and turn angle varied in response to environmental covariates, outperformed models where these relationships were held constant. This result mirrors previous findings in other marine predators (Carter et al. 2020) and underscores the importance of understanding how environmental covariates influence movement, and consequently foraging behaviour (Cox et al. 2016; Hays et al. 2016). However, across all spatial clusters, we did not observe consistent responses in movement parameters (step length and turning angle) to any of the environmental covariates considered (Table 3). In other studies, high levels of individual variation in Kittiwake step length in response to environmental covariates such as SST and front density have also been observed, emphasizing that consistent directional relationships between movement characteristics and environmental covariates may be hard to detect (O'Hanlon et al. 2024). Nevertheless, when focusing on a single colony, the most consistent findings we observed were that across all three space-use clusters at Flamborough, SST was positively associated with step length during search behaviour, while step length during transit behaviour was negatively associated with chlorophyll concentration.

Variation in space use within a colony

Our results highlight how variation in space use among individuals can lead to differences in the environmental conditions they experience, influencing their responses to marine habitats and foraging strategies. This aligns with a growing body of research on seabirds and other marine predators, linking variation in foraging behaviours to local oceanographic conditions, habitat accessibility, and behavioural plasticity (Christensen-Dalsgaard et al. 2018; Gilmour et al. 2018; McDuie et al. 2018; Carpenter-Kling et al. 2020; Kane et al. 2020; Schwarz et al. 2021). In Kittiwakes specifically, habitat selection models based on tracking data from multiple North Sea breeding colonies showed that individuals were more likely to use areas near fronts when such areas were more readily available to them (Cleasby et al. 2024a). Overall, this underscores the importance of accounting for variation in habitat availability when aiming to better understand and predict seabird distributions and behaviour (Matthiopoulos et al. 2011; Wakefield et al. 2017; Holbrook et al. 2019).

The clustering approach used in this study offers valuable insights into habitat use by examining sub-colony variation in space use among birds within a single colony (see also: Schwarz et al. 2021). This builds upon previous research that has demonstrated that individuals from the same colony do not necessarily forage in the same locations (Cleasby et al. 2015; Sanchez et al. 2018, Cleasby et al. 2019, 2024b). As such, individual site- or route-level fidelity can influence

space use within a colony, potentially driving variation in habitat use, foraging behaviour, and diet (Wakefield et al. 2015; Cleasby et al. 2024b; Regan et al. 2024).

Understanding individual site fidelity and its temporal scale is essential for interpreting how animals use predictable yet dynamic features such as fronts—especially when incorporating these features into marine spatial planning (Miller and Christodoulou 2014; Scales et al. 2014; Searle et al. 2023). In our study, the limited number of trips per individual over a short timeframe restricts our ability to assess long-term site fidelity. Therefore, we cannot conclude whether the distinct space-use clusters reflect short-term phenomena, such as recent memory of productive foraging patches (Carroll et al. 2018; Collet et al. 2025), or indicate more persistent site fidelity. Longer tracking deployments per individual will be crucial for exploring this behaviour further and investigating individual environmental niches (Carlson et al. 2021; Schwarz et al. 2021).

Conservation implications

The predictability and persistence of oceanographic features are thought to influence the movement patterns of marine predators, with habitat use often directed toward consistently productive areas (Scales et al. 2014). Tidal mixing fronts are one such feature—their location is shaped by the relatively predictable interactions of tides and bathymetry, and evidence from a variety of marine predators suggests that these fronts are significant habitat features. As a result, mixing fronts have been proposed as dynamic oceanographic features that could aid in the identification and conservation of ecologically important marine areas (Miller and Christodoulou 2014; Scales et al. 2014). In the UK, for instance, there are MPAs centred around important fronts, such as the Irish Sea Front SPA (<https://jncc.gov.uk/our-work/irish-sea-front-spa/>, accessed 1 July 2025), and mapping of such fronts has also supported MPA design in Scotland (Miller et al. 2014).

The results presented here highlight the importance of fronts for foraging seabirds, with Kittiwakes in some spatial clusters switching to a searching/foraging mode of behaviour in the vicinity of fronts. Moreover, this result builds on previous work where functional response models of habitat selection showed Kittiwakes using areas closer to fronts when they were more accessible (Cleasby et al. 2024a). Linking broader-scale studies of habitat selection with more fine-grained behavioural analysis also provides insight into animal decision making at different spatio-temporal scales. Specifically, Kittiwake may first select to use areas of habitat with certain environmental conditions before making more fine-grained decisions about where to forage within a particular area (Dunn et al. 2024).

The importance of tidal mixing fronts for Kittiwake also highlights the importance of understanding how mixing of the water column and stratification are expected to change in the future. In this context, two of the most important considerations are likely to be the twin actions of climate change and large-scale windfarm construction which may influence the strength and timing of stratification (Holt et al. 2010; Sharples et al. 2020; De Dominicis et al. 2018; Chen et al. 2022). In addition, within our study region the specific impacts of offshore development upon the Flamborough front and its importance to marine wildlife is included within various ecological assessments to which our results have relevance (Ørsted 2022; The Crown Estate 2023; Riddell and Davison-Smith 2023). Crucially, responses to distance to the nearest front varied across spatial clusters suggesting that while birds foraging in some areas, close to the approximate location of the Flamborough front, may be focusing on such features, other birds visit different areas and may therefore have been using other habitats. This variation means that MPAs designed around a particular feature such as a front should not be expected to capture all the important sites used by birds from a given colony. Similarly, impacts related to anthropogenic activity are unlikely to be felt equally across all individuals at a colony. Individuals from a population do not behave in a uniform way. Heterogeneity in space use and responses to the prevailing environment result in differences between individuals, or population subgroups. Such variation may not be apparent if focusing on population-level averages and conservation measures based on such measures may be less effective for certain individuals or population subgroups (Merrick and Koprowski 2017). Here, many of the responses observed in different spatial clusters may have been reduced in magnitude or obscured if we had taken a population-wide average of behaviour. Instead, focussing on variation in space use provided a clearer insight into how animals utilise space by accounting for individual space use and context dependency (Bastille-Rousseau and Wittemyer 2019, 2022; Winter et al. 2024).

Our study demonstrates how birds from Filey, particularly those in Filey clusters 2 and 4, utilize the Dogger Bank for foraging. This is particularly relevant given the area's significance as a site for offshore wind farm development (Jansen et al. 2022). In contrast, we rarely observed birds from Flamborough foraging at or near the Dogger Bank, except for two individuals from Flamborough cluster 2, despite its relative proximity to the Flamborough colony. Birds from Flamborough that visited the Dogger Bank also avoided the most direct route to the area, instead traveling east for several kilometres before turning north, rather than departing the colony on a north-easterly bearing. This behaviour may indicate spatial segregation between birds

from these neighbouring colonies (Wakefield et al. 2015), which are approximately 15 km apart.

Conclusions

In shelf seas, the potential importance of tidal mixing fronts as key foraging areas has long been recognised. In the current study, we highlight the significance of one such frontal system in the North Sea, the Flamborough Front, for breeding Kittiwakes. The clearest responses to fronts were observed in birds whose tracking data most aligned with the approximate geographic location of the fronts. However, similar responses to fronts were not observed for Kittiwakes in other spatial clusters. Therefore, while some individuals may frequent areas where a mixing front is a key habitat feature, other birds—sometimes from the same colony—may travel elsewhere and utilise different features.

This study focuses on fine-scale behavioural responses to distance from the front, but the results align with a previous, broader-scale study of Kittiwake habitat selection (Cleasby et al. 2024a), which also emphasised the importance of areas close to fronts. Both studies, despite being conducted across different spatial scales, suggest that responses are context-dependent and vary depending on the areas where individual Kittiwakes forage, and the extent to which this area overlaps with the location of mixing fronts. Variation in space use, coupled with the relatively predictable nature of mixing fronts—whose location is influenced by the strength of tidal currents and water depth—has the potential to drive individual-level variation in responses to fronts (Bastille-Rousseau and Wittemyer 2019). This would be particularly evident if individual Kittiwakes exhibit high site fidelity, with some individuals consistently visiting sites where mixing fronts tend to occur. From a conservation perspective, this highlights the importance of fronts and underscores the need to consider how factors such as climate change and marine development could alter water stratification patterns. A deeper understanding of the linkages between variation in geographic space-use, habitat selection, and foraging behaviour, both within and between individuals, could also enhance our understanding of how such diversity ultimately shapes population-level distributions (Carlson et al. 2021; Bastille-Rousseau and Wittemyer 2022).

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Data availability Seabird tracking data are available to view at the BirdLife Seabird Tracking database, <https://www.seabirdtracking.org/>. Tracking data used available via a data request to the RSPB.

Declarations

Conflict of interest All the authors declare that they have no conflict of interest related to this publication.

Ethical approval All seabird tracking was conducted under BTO licensed ringers with additional mist-net and special methods (attaching data logger) endorsement.

References

- Allen AM, Singh NJ (2016) Linking movement ecology with wildlife management and conservation. *Front Ecol Evol* 3:155
- Amorim FLL, Balkoni A, Sidorenko V, Wiltshire KH (2024) Analyses of sea surface chlorophyll a trends and variability from 1998 to 2020 in the German bight (North Sea). *Ocean Sci* 20:1247–1265
- Bailey H, Thompson PM (2010) Effect of oceanographic features on fine-scale foraging movements of bottlenose dolphins. *Mar Ecol Prog Ser* 418:223–233
- Bastille-Rousseau G, Wittemyer G (2019) Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. *Ecol Lett* 22:1417–1427
- Bastille-Rousseau G, Wittemyer G (2022) Simple metrics to characterize inter-individual and temporal variation in habitat selection behaviour. *J Anim Ecol* 91:1693–1706
- Beal M, Oppel S, Handley J, Pearmain EJ, Morera-Pujol V, Carneiro AP et al (2021) track2KBA: an R package for identifying important sites for biodiversity from tracking data. *Meth Ecol Evol* 12:2372–2378
- Begg GS, Reid JB (1997) Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. *ICES J Mar Sci* 54:552–565
- Belkin IM (2021) Remote sensing of ocean fronts in marine ecology and fisheries. *Remote Sens* 13:883
- Belkin IM, O'Reilly JE (2009) An algorithm for oceanic front detection in chlorophyll and SST satellite imagery. *J Mar Syst* 78:319–326
- Benhamou S, Cornélis D (2010) Incorporating movement behavior and barriers to improve kernel home range space use estimates. *J Wildl Manag* 74:1353–1360
- Bertrand P, Strøm H, Bêty J, Steen H, Kohler J, Vihtakari V et al (2021) Feeding at the front line: interannual variation in the use of glacier fronts by foraging black-legged Kittiwakes. *Mar Ecol Prog Ser* 677:197–208
- Bogdanova MI, Wischniewski S, Cleasby IR, Whyte K, Regan C, Gunn C et al (2022) Seabird GPS tracking on the Isle of May, St abb's head and Fowlsheugh in 2021 in relation to offshore wind farms in the Forth/Tay region. *Marine Scotland*, <https://marine.gov.scot/node/23278> (accessed 02/07/25)
- Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol Lett* 11:637–650
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C et al (2009) The importance of oceanographic fronts to marine birds and mammals of the Southern oceans. *J Mar Syst* 78:363–376
- Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Phil Trans R Soc Lond B Biol Sci* 365:2157–2162
- Calenge C (2020) Package 'adehabitatHR'. R package version 0.4. 18
- Carlson BS, Rotics S, Nathan R, Wikelski M, Jetz W (2021) Individual environmental niches in mobile organisms. *Nat Commun* 12:4572
- Carpenter-Kling T, Reisinger RR, Orgeret F, Connan M, Stevens KL, Ryan PG et al (2020) Foraging in a dynamic environment: response of four sympatric sub-Antarctic Albatross species to interannual environmental variability. *Ecol Evol* 10:11277–11295
- Carroll MJ, Butler A, Owen E, Ewing SR, Cole T, Green JA et al (2015) Effects of sea temperature and stratification changes on seabird breeding success. *Clim Res* 66:75–89
- Carroll G, Harcourt R, Pitcher BJ, Slip D, Jonsen I (2018) Recent prey capture experience and dynamic habitat quality mediate short-term foraging site fidelity in a seabird. *Proc Roy Soc B: Biol Sci* 285:20180788
- Carter MI, McClintock BT, Embling CB, Bennett KA, Thompson D, Russell DJ (2020) From pup to predator: generalized hidden Markov models reveal rapid development of movement strategies in a naïve long-lived vertebrate. *Oikos* 129:630–642
- Chen W, Staneva J, Grayek S, Schulz-Stellenfleth J, Greinert J (2022) The role of heat wave events in the occurrence and persistence of thermal stratification in the Southern North sea. *Nat Haz Earth Syst Sci* 22:1683–1698
- Chivers LS, Lundy MG, Colhoun K, Newton SF, Houghton JD, Reid N (2012) Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Mar Ecol Prog Ser* 456:269–277
- Chivers LS, Lundy MG, Colhoun K, Newton SF, Houghton JDR, Reid N et al (2013) Identifying optimal feeding habitat and proposed marine protected areas (pMPAs) for the black-legged Kittiwake (*Rissa tridactyla*) suggests a need for complementary management approaches. *Biol Cons* 164:73–81
- Christensen-Dalsgaard S, May R, Lorentsen SH (2018) Taking a trip to the shelf: behavioral decisions are mediated by the proximity to foraging habitats in the black-legged kittiwake. *Ecol Evol* 8:866–878
- Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick SC, Newton J et al (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar Ecol Prog Ser* 518:1–12
- Cleasby IR, Wakefield ED, Morrissey BJ, Bodey TW, Votier SC, Bearhop S, Hamer KC (2019) Using time-series similarity measures

- to compare animal movement trajectories in ecology. *Behav Ecol Sociobiol* 73:1–19
- Cleasby IR, McCluskie A, Owen E, Wischniewski S, Wilson L, Wright LJ, Bolton M (2020) An investigation of the effects of GPS tagging on the behaviour of black-legged kittiwakes *Rissa tridactyla*. Technical Report. RSPB Research Report 68. RSPB Centre for Conservation Science. ISBN: 978-1-905601-64-6 (accessed 06/10/24)
- Cleasby IR, Wilson LJ, Crawford R, Owen E, Rouxel Y, Bolton M (2022) Assessing bycatch risk from gillnet fisheries for three species of diving seabird in the UK. *Mar Ecol Prog Ser* 684:157–179
- Cleasby IR, Owen E, Miller PI, Jones RJ, Wilson LJ, Bolton M (2024a) Functional responses of a medium-ranging marine predator highlight the importance of frontal zones as foraging locations. *Mar Ecol Prog Ser* 740:175–191
- Cleasby IR, Hughes R, Morrissey BJ, Elliott S, le Bouard F, West F, Owen E (2024b) Evidence of colony- and individual-level variation in habitat usage of Atlantic Puffins (*Fratercula arctica*). *Mar Biol* 171:188
- Cleasby IR, Owen E, Butler A, Baer J, Blackburn J, Bogdanova MI et al (2024c) Assessing the importance of individual- and colony-level variation when using seabird foraging ranges as impact assessment and conservation tools. *Ibis* 166:871–895
- Collet J, Thiebault A, Bonnet-Lebrun AS, Tremblay Y, Carpenter-Kling T, Keys D et al (2025) A marine predator relies on both social cues and frequently updated memory to search for prey. *Proc R Soc Lond B Biol Sci* 292:20242327
- Cox SL, Miller PI, Embling CB, Scales KL, Bicknell AWJ, Hosegood PG et al (2016) Seabird diving behaviour reveals the functional significance of shelf-sea fronts as foraging hotspots. *Royal Soc Open Sci* 3:160317
- Cox SL, Embling CB, Hosegood PJ, Votier SC, Ingram SN (2018) Oceanographic drivers of marine mammal and seabird habitat-use across shelf-seas: a guide to key features and recommendations for future research and conservation management. *Estuar Coast Shelf Sci* 212:294–310
- Croll DA, Ellis AA, Adams J, Cook ASCP, Garthe S, Goodale MW (2022) Framework for assessing and mitigating the impacts of offshore wind energy development on marine birds. *Biol Conserv* 276:109795
- Davies TE, Carneiro AP, Tarzia M, Wakefield ED, Hennicke JC, Frederiksen M et al (2021) Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conserv Lett* 14:e12824
- De Dominicis M, Murray ROH, Wolf J (2017) Multi-scale ocean response to a large tidal stream turbine array. *Renew Energy* 114:1160–1179
- De Dominicis M, Wolf J, Murray ROH (2018) Comparative effects of climate change and tidal stream energy extraction in a shelf sea. *J Geophys Res Oce* 123:5041–5067
- Dean B, Freeman R, Kirk H, Leonard K, Phillips RA, Perrin CM et al (2013) Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *J Roy Soc Int* 10:20120570
- Dean B, Kirk H, Fayet A, Shoji A, Freeman R, Leonard K et al (2015) Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area. *Mar Ecol Prog Ser* 538:239–248
- Decker MB, Hunt GL Jr (1996) Foraging by murres (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Mar Ecol Prog Ser* 139:1–10
- DEFRA (2019) Holderness Offshore MCZ. <https://assets.publishing.service.gov.uk/media/5cefdd76ed915d7b9bf5e5a/mcz-holderness-2019.pdf>. Accessed: 26/03/2025
- Delord K, Barbraud C, Pinaud D, Letournel B, Jaugeon B, Gorguer H et al (2020) Movements of three alcid species breeding sympatrically in Saint Pierre and Miquelon, Northwestern Atlantic ocean. *J Ornithol* 161:359–371
- Dunn RE, Freeman R, Nicoll MA, Ramsden J, Trevail AM, Wood H (2024) From route to dive: multi-scale habitat selection in a foraging tropical seabird. *Mar Biol* 171:124
- Eikelboom JA, de Knegt HJ, Klaver M, van der Wal T, Prins HHT (2020) Inferring an animal's environment through biologging: quantifying the environmental influence on animal movement. *Move Ecol* 8:1–18
- Embling CB, Illian J, Armstrong E, van der Kooij J, Sharples J, Camphuysen KC, Scott BE (2012) Investigating fine-scale spatio-temporal predator–prey patterns in dynamic marine ecosystems: a functional data analysis approach. *J Appl Ecol* 49:481–492
- Fauchald P, Tarroux A, Amélineau F, Bråthen VS, Descamps S, Ekker M et al (2021) Year-round distribution of Northeast Atlantic seabird populations: applications for population management and marine spatial planning. *Mar Ecol Prog Ser* 676:255–276
- Gilmour ME, Castillo-Guerrero JA, Fleishman AB, Hernández-Vázquez S, Young HS, Shaffer SA (2018) Plasticity of foraging behaviors in response to diverse environmental conditions. *Ecosphere* 9:e02301
- Goetsch C, Gulka J, Friedland KD, Winship AJ, Clerc J, Gilbert A et al (2023) Surface and subsurface oceanographic features drive forage fish distributions and aggregations: implications for prey availability to top predators in the US Northeast shelf ecosystem. *Ecol Evol* 13:e10226
- Grecian WJ, Lane JV, Michelot T, Wade HM, Hamer KC (2018) Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *J R Soc Interface* 15:20180084
- Grémillet D, Lewis S, Drapeau L, van Der Lingen CD, Huggett JA, Coetzee JC et al (2008) Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *J Appl Ecol* 45:610–621
- Grecian WJ, Lane JV, Michelot T, Wade HM, Hamer KC (2018) Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *J Royal Soc Interface* 15(143):20180084
- Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tuloch AIT et al (2013) Predicting species distributions for conservation decisions. *Ecol Lett* 16:1424–1435
- Hamer KC, Humphreys EM, Magalhães MC, Garthe S, Hennicke J, Peters G et al (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *J Anim Ecol* 78:880–889
- Harris SM, Descamps S, Sneddon LU, Bertrand P, Chastel O, Patrick SC (2020) Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J Anim Ecol* 89:68–79
- Hátún H, Olsen B, Pacariz S (2017) The dynamics of the North Atlantic subpolar gyre introduces predictability to the breeding success of kittiwakes. *Front Mar Sci* 4:123
- Hays GC, Ferreira LC, Sequeira AM, Meekan MG, Duarte CM, Bailey H et al (2016) Key questions in marine megafauna movement ecology. *Trends Ecol Evol* 31:463–475
- Hill AE, James ID, Linden PF, Matthews JP, Prandle D, Simpson JH et al (1993) Dynamics of tidal mixing fronts in the North sea. *Phil Trans Roy Soc Lond A: Phys Eng Sci* 343:431–446
- Hindell MA, Reisinger RR, Ropert-Coudert Y, Hückstädt LA, Trathan PN, Bornemann H et al (2020) Tracking of marine predators to protect Southern Ocean ecosystems. *Nature* 580:87–92
- Holbrook JD, Olson LE, DeCesare NJ, Hebblewhite M, Squires JR, Steenweg R (2019) Functional responses in habitat selection: clarifying hypotheses and interpretations. *Ecol Appl* 29:e01852

- Holt J, Wakelin S, Lowe J, Tinker J (2010) The potential impacts of climate change on the hydrography of the Northwest European continental shelf. *Prog Oceanogr* 86:361–379
- Hunt GL, Mehlum F, Russell RW, Irons D, Decker B, Becker PH (1999) S34. 3: Physical processes, prey abundance, and the foraging ecology of seabirds. – In: Adams NJ, Slotow RH (eds) Proc. 22nd International Ornithological Congress, Durban. BirdLife South Africa, Johannesburg, pp. 2040–2056
- Inchausti P, Guinet C, Koudil M, Durbec JP, Barbaud C, Weimerskirch H et al (2003) Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the kerguelen sectors of the Southern ocean. *J Avian Biol* 34:170–176
- Isaksson N, Scott BE, Hunt GL, Benninghaus E, Declerck M, Gormley K, Williamson BJ (2025) A paradigm for understanding whole ecosystem effects of offshore wind farms in shelf seas. *ICES J Mar Sci* 82(3):194
- Jansen M, Duffy C, Green TC, Staffell I (2022) Island in the sea: the prospects and impacts of an offshore wind power hub in the North Sea. *Adv Appl Energy* 6:100090
- Johansen M, Irgens M, Strøm H, Anker-Nilssen T et al (2020) International Black-legged Kittiwake Conservation Strategy and Action Plan, Circumpolar Seabird Expert Group. Conservation of Arctic Flora and Fauna, Akureyri, Iceland. ISBN 978-9935-431-85-1
- Kane A, Pirotta E, Wischniewski S, Critchley EJ, Bennison A, Jessopp M et al (2020) Spatio-temporal patterns of foraging behaviour in a wide-ranging seabird reveal the role of primary productivity in locating prey. *Mar Ecol Prog Ser* 646:175–188
- Kranstauber B, Smolla M, Safi K (2017) Similarity in spatial utilization distributions measured by the Earth mover's distance. *Meth Ecol Evol* 8:155–160
- Lane JV, Jeavons R, Deakin Z, Sherley RB, Pollock CJ, Wanless RJ (2020) Vulnerability of Northern Gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Mar Environ Res* 162:105196
- Lennox RJ, Engler-Palma C, Kowarski K, Filous A, Whitlock R, Cooke SJ et al (2019) Optimizing marine Spatial plans with animal tracking data. *Can J Fish Aqua Sci* 76:497–450
- Luyten PJ, Jones JE, Proctor R (2003) A numerical study of the long- and short-term temperature variability and thermal circulation in the North Sea. *J Phys Oceanogr* 33:37–56
- Matthiopoulos J, Hebblewhite M, Aarts G, Fieberg J (2011) Generalized functional responses for species distributions. *Ecology* 92:583–589
- McClintock BT, Michelot T (2018) Momentuhmm: R package for generalized hidden Markov models of animal movement. *Meth Ecol Evol* 9:1518–1530
- McDuie F, Weeks SJ, Congdon BC (2018) Oceanographic drivers of near-colony seabird foraging site use in tropical marine systems. *Mar Ecol Prog Ser* 589:209–225
- Merrick MJ, Koprowski JL (2017) Should we consider individual behavior differences in applied wildlife conservation studies? *Biol Conserv* 209:34–44
- Miller P (2009) Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. *J Mar Syst* 78:327–336
- Miller PI, Christodoulou S (2014) Frequent locations of oceanic fronts as an indicator of pelagic diversity: application to marine protected areas and renewables. *Mar Policy* 45:318–329
- Miller PI, Xu W, Lonsdale P (2014) Seasonal shelf-sea front mapping using satellite ocean colour to support development of the Scottish MPA network. Scottish Natural Heritage Commissioned Report 538
- Miller PI, Scales KL, Ingram SN, Southall EJ, Sims DW (2015) Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic. *Functional Ecology* 29(8):1099–1109
- Murphy EJ (1995) Spatial structure of the Southern Ocean ecosystem: predator-prey linkages in Southern Ocean food webs. *J Anim Ecol* 84:333–347
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D et al (2008) A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci U S A* 105:19052–19059
- Nonaka E, Holme P (2007) Agent-based model approach to optimal foraging in heterogeneous landscapes: effects of patch clumpiness. *Ecograph* 30:777–788
- O'Hanlon NJ, Thaxter CB, Clewley GD, Davies JG, Humphreys EM, Miller PI et al (2024) Challenges in quantifying the responses of Black-legged Kittiwakes *Rissa tridactyla* to habitat variables and local stressors due to individual variation. *Bird Study* 71:48–64
- Ørsted (2022) Hornsea Project 4. Marine Processes Supplementary Report, May 2022
- Peters SWM, Eleveld M, Pasterkamp R, Van der Woerd H, Devolder M, Jans S et al (2005) Atlas of Chlorophyll-a concentration for the North sea based on MERIS imagery of 2003. Vrije University, Amsterdam, The Netherlands
- Pingree RD, Griffiths DK (1978) Tidal fronts on the shelf seas around the British Isles. *J Geophys Res Oceans* 83:4615–4622
- Potts JR, Börger L (2023) How to scale up from animal movement decisions to spatiotemporal patterns: an approach via step selection. *J Anim Ecol* 92:16–29
- R Core Team (2024) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Regan CE, Bogdanova MI, Newell M, Gunn C, Wanless S, Harriss MP et al (2024) Seabirds show foraging site and route fidelity but demonstrate flexibility in response to local information. *Move Ecol* 12:46
- Riddell R, Davison-Smith H (2023) 2022–2026 Flamborough Head European Marine Site Management Plan. <https://yorkshiremarinenaturepartnership.org.uk/wp-content/uploads/2023/02/22-12-19-2022-2026-FHEMS-Management-Plan-Full-Doc-FINAL.pdf>. Accessed on 26 March 2025.
- Robertson GS, Bolton M, Grecian WJ, Monaghan P (2014) Inter- and intra-year variation in foraging areas of breeding Kittiwakes (*Rissa tridactyla*). *Mar Biol* 161:1973–1986
- Rousseeuw PJ (1987) Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *J Comp Appl Math* 20:53–65
- Rubner Y, Tomasi C, Guibas LJ (2000) The earth mover's distance as a metric for image retrieval. *Int J Comp Vis* 40:99–121
- Ruffino L, Arjona Y, Clear N, Martin E (2023) Towards better understanding blacklegged kittiwake and fish prey interactions. An assessment of scientific evidence to inform future research needs in the North Sea. Report to Ørsted. JNCC Report 733, JNCC, Peterborough, ISSN 0963–8091. <https://hub.jncc.gov.uk/assets/ef7b01db-ca48-4469-b5ce-642efe0f7ed2>
- Sánchez S, Reina RD, Kato A, Ropert-Coudert Y, Cavallo C, Hays GC et al (2018) Within-colony spatial segregation leads to foraging behaviour variation in a seabird. *Mar Ecol Prog Ser* 606:215–230
- Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC (2014) On the front line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *J Appl Ecol* 51:1575–1583
- Schneider DC (1991) The role of fluid dynamics in the ecology of marine birds. *Oceanogr Mar Biol Annu Rev* 29:487–521
- Schwarz JF, Mews S, DeRango EJ, Langrock R, Piedrahita P, Páez-Rosas D et al (2021) Individuality counts: a new comprehensive approach to foraging strategies of a tropical marine predator. *Oecologia* 195:313–325
- Scott BE, Sharples J, Wanless S, Ross ON, Frederiksen M, Daunt F (2006) The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. In: Boyd IL, Wanless S, Camphuysen CH (eds) Top

- predators in marine ecosystems. Their role in monitoring and management. Conservation Biology Series No 12. Cambridge University Press, Cambridge
- Scott BE, Sharples J, Ross ON, Wang J, Pierce GJ, Camphuysen CJ (2010) Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Mar Ecol Prog Ser* 408:207–226
- Scott BE, Webb A, Palmer MR, Embling CB, Sharples J (2013) Fine scale bio-physical oceanographic characteristics predict the foraging occurrence of contrasting seabird species; Gannet (*Morus bassanus*) and storm petrel (*Hydrobates pelagicus*). *Prog Oceanography* 117:118–129
- Searle KR, O'Brien SH, Jones EL, Cook ASCP, Trinder MN, McGregor RM et al. (2023) A framework for improving treatment of uncertainty in offshore wind assessments for protected marine birds. *ICES J Mar Sci* fsad025
- Sharples J (2008) Potential impacts of the spring-neap tidal cycle on shelf sea primary production. *J Plankton Res* 30:183–197
- Sharples J, Holt J, Dye SR (2013) Impacts of climate change on shelf sea stratification. *MCCIP Sci Rev* 2013:67–70
- Sharples J, Holt J, Wakelin S (2020) Impacts of climate change on shelf sea stratification, relevant to the coastal and marine environment around the UK. *MCCIP Sci Rev* 2020:103–115
- Shaw AK (2020) Causes and consequences of individual variation in animal movement. *Mov Ecol* 8:12
- Simpson JH (1981) The shelf-sea fronts: implications of their existence and behaviour. *Philos Trans R Soc Lond A* 302:531–546
- Simpson JH, Hunter JR (1974) Fronts in the Irish Sea. *Nature* 250:404–440
- Simpson JH, Sharples J (2012) Introduction to the physical and biological oceanography of shelf seas. Cambridge University Press, Cambridge, UK
- Skov H, Durinck J (2000) Seabird distribution in relation to hydrography in the Skagerrak. *Cont Shelf Res* 20:169–187
- Stephens DW, Krebs JR (1986) Foraging theory, vol 6. Princeton University Press
- Suberg LA, Miller PI, Wynn RB (2019) On the use of satellite-derived frontal metrics in time series analyses of shelf-sea fronts, a study of the Celtic Sea. *Deep Sea Research Part I: Oceanographic Research Papers* 149:103033
- Suryan RM, Santora JA, Sydeman WJ (2012) New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Mar Ecol Prog Ser* 451:213–225
- The Crown Estate (2023) Offshore wind leasing round 4. Appendix D – Round 4 strategic compensation – Artificial nesting structure site selection. 19th December 2023, NIRAS. <https://infrastructure.planninginspectorate.gov.uk/wp-content/ipc/uploads/projects/EN010130/EN010130-000572-7.8.3%20App%20D%20NIRAS%20Site%20Selection%20ANS%20AoS.pdf>. Accessed on 26 March 2025
- Tilstone GH, Pardo S, Dall'Olmo G, Brewin RJ, Nencioli F, Dessailly D et al (2021) Performance of ocean colour chlorophyll a algorithms for Sentinel-3 OLCI, MODIS-Aqua and Suomi-VIIRS in open-ocean waters of the Atlantic. *Remote Sens Environ* 260:112444
- Timko PG, Arbic BK, Hyder P, Richman JG, Zamudio L, O'Dea E et al (2019) Assessment of shelf sea tides and tidal mixing fronts in a global ocean model. *Ocean Model* 136:66–84
- Trevel AM, Green JA, Bolton M, Daunt F, Harris SM, Miller PI et al (2021) Environmental heterogeneity promotes individual specialisation in habitat selection in a widely distributed seabird. *J Anim Ecol* 90:2875–2887
- Van De Poll WH, Kulk G, Timmermans KR, Brussaard CPD, Van Der Woerd HJ, Kehoe MJ et al (2013) Phytoplankton chlorophyll a biomass, composition, and productivity along a temperature and stratification gradient in the Northeast Atlantic ocean. *Biogeosciences* 10:4227–4240
- van Haren H, Mills DK, Wetsteyn LP (1998) Detailed observations of the phytoplankton spring bloom in the stratifying central North sea. *J Mar Res* 56:665–680
- van Leeuwen S, Tett P, Mills D, van Der Molen J (2015) Stratified and nonstratified areas in the North Sea: long-term variability and biological and policy implications. *J Geophys Res Oceans* 120:4670–4686
- Vlietstra LS, Coyle KO, Kachel NB, Hunt GL Jr (2005) Tidal front affects the size of prey used by a top marine predator, the short-tailed shearwater (*Puffinus tenuirostris*). *Fish Oceanogr* 14(s1):196–211
- Waggitt JJ, Cazenave PW, Howarth LM, Evans PG, Van der Kooij J, Hiddink JG (2018) Combined measurements of prey availability explain habitat selection in foraging seabirds. *Biol Lett* 14:20180348
- Wakefield ED, Cleasby IR, Bearhop S, Bodey TW, Davies RD, Miller PI et al (2015) Long-term individual foraging site fidelity—why some Gannets don't change their spots. *Ecology* 96:3058–3074
- Wakefield ED, Owen E, Baer J, Carroll MJ, Daunt F, Dodd SG et al (2017) Breeding density, fine-scale tracking, and large-scale modeling reveal the regional distribution of four seabird species. *Ecol Appl* 27:2074–2091
- Warwick-Evans VA, Santora J, Waggitt JJ, Trathan PN (2021) Multi-scale assessment of distribution and density of procellariiform seabirds within the Northern Antarctic Peninsula marine ecosystem. *ICES J Mar Sci* 78:1324–1339
- Weston K, Fernand L, Mills DK, Delahunty R, Brown J (2005) Primary production in the deep chlorophyll maximum of the central North Sea. *J Plank Res* 27:909–922
- Winter VA, Smith BJ, Berger DJ, Hart RB, Huang J, Manlove K (2024) Forecasting animal distribution through individual habitat selection: insights for population inference and transferable predictions. *Ecography* 2024:e07225
- Wyles HM, Boehme L, Russell DJ, Carter MI (2022) A novel approach to using seabed geomorphology as a predictor of habitat use in highly mobile marine predators: implications for ecology and conservation. *Front Mar Sci* 9:818635
- Xia L, Liu H, Lin L, Wang Y (2021) Surface chlorophyll-A fronts in the yellow and Bohai seas based on satellite data. *J Mar Sci Eng* 9:1301
- Yasunaka S, Ono T, Sasaoka K, Sato K (2021) Global distribution and variability of subsurface chlorophyll a concentration. *Ocean Sci Discuss* 2021:1–22
- Zampollo A, Cornulier T, Murray ROH, Tweddle JF, Dunning J, Scott BE (2023) The bottom mixed layer depth as an indicator of subsurface chlorophyll a distribution. *Biogeosci* 20:3593–3611
- Zurell D, König C, Malchow AK, Kapitza S, Bocedi G, Travis J et al (2022) Spatially explicit models for decision-making in animal conservation and restoration. *Ecograph* 2022

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