Functional responses of a medium-ranging marine predator highlight the importance of frontal zones as foraging locations

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ABSTRACT: The distribution of marine predators is linked to bio-physical processes that structure the spatio-temporal availability of prey species. Within shelf seas, tidal fronts are highly productive regions occurring at the interface between mixed and stratified waters. Fronts are predictable but dynamic features, with their timing and strength varying seasonally and annually. The availability of frontal habitats will also vary between animal populations depending on geographic location. Thus, understanding the associations between marine predators and frontal habitats across a range of environmental conditions will assist marine management and conservation. Here, we assessed functional responses of breeding black-legged kittiwakes *Rissa tridactyla* to environmental covariates related to tidal fronts (front strength, distance to fronts, sea surface temperature [SST] and surface chlorophyll concentration) from 10 UK colonies located throughout the North Sea. Kittiwakes showed a tendency to forage in areas of higher, but not maximal, front strength when such areas were available. Areas closer to fronts (<10 km) were selected when available, though we also observed increased usage of areas distant from fronts (30–50 km). Kittiwakes tended to forage in cooler, mixed waters, particularly as average SST rose. When average chlorophyll concentrations were low, habitat usage peaked in areas of higher chlorophyll. The results highlight the importance of frontal habitats and the dynamic, non-linear nature of seabird responses to habitat. Accounting for dynamic changes in habitat availability will play a key role in future conservation efforts, particularly as marine renewable installations and climate change may influence water stratification patterns.

KEY WORDS: Seabird · Species distribution model · Ocean fronts · Stratification · Movement ecology

1. INTRODUCTION

Shelf seas are regions of shallow water (<200 m depth) adjacent to the coastline that sit upon the continental shelf. Such seas are dynamic environments that support high levels of biodiversity and represent important areas for many marine species including seabirds (Baylis et al. 2019). However, shelf seas are also subject to multiple anthropogenic pressures, such as fishing (Grémillet et al. 2018), the development of offshore renewables (Bailey et al. 2014) and climate change (Holt et al. 2010). Therefore, a crucial part of marine spatial planning and conservation is to identify and understand the key factors influencing

seabird distributions and movement patterns (Embling et al. 2012, Wakefield et al. 2017).

Within shelf seas, a variety of habitat features influences the spatio-temporal distribution of marine megafauna and their prey (Cox et al. 2018). For example, bio-physical processes can act to generate relatively consistent areas of high productivity which attract prey species and hence top predators (Schneider 1982, Yen et al. 2006). One important biophysical process in shelf seas is the development of seasonal temperature stratification between late spring and autumn (Simpson 1981, Simpson & Sharples 2012). Increased solar irradiation heats up the surface of the water, generating a layer of warm, well-lit, but often nutrient-poor, water and a deeper, darker layer of colder, nutrient-rich water. These layers of warm surface water and colder deeper water are divided by a thin, seasonal thermocline, within which water temperature changes rapidly. Tidal mixing fronts occur at the interface between mixed and stratified waters and are typically marked by high levels of productivity that may arise from enhancement of local primary production, changes in prey behaviour, or prey transport and aggregation at frontal areas, due to the action of tidal currents (Hunt et al. 1999, Vlietstra et al. 2005, Waggitt et al. 2018).

The importance of tidal mixing fronts as key foraging locations has been identified across different oceanic regions for a wide range of seabird species, encompassing species with different foraging modes (Bost et al. 2009, Hamer et al. 2009). Many species appear to direct at least some of their foraging trips to the location of fronts, sometimes travelling substantial distances (Russell et al. 1999, Dean et al. 2015). In some studies, annual reproductive success was also associated with the timing and strength of seasonal stratification (Carroll et al. 2015) or the location of fronts (Hátún et al. 2017). As a result, tidal mixing fronts have been identified as a dynamic feature that could aid in the identification of marine protected areas (MPAs; Miller & Christodoulou 2014, Scales et al. 2014). However, as dynamic features, tidal fronts vary in strength and location across multiple temporal scales, including inter-annually, seasonally, throughout the spring—neap cycle, in response to local weather conditions (wind-induced overturning) and even throughout the course of the tidal cycle (Simpson 1981, Belkin 2021). For example, the timing and strength of stratification may be impacted by warming global temperatures (Sharples et al. 2020). Similarly, marine renewables may alter water stratification by extracting energy from the ecosystem (e.g. wind or tide power) and therefore reducing the level

of water column mixing (De Dominicis et al. 2017). On the other hand, renewable structures themselves may promote local mixing within the water column (Carpenter et al. 2016). Therefore, human impacts such as climate change and marine renewable development are likely to influence stratification patterns now and into the future, which may, in turn, alter seabird distributions.

To better understand how seabirds utilise tidal fronts, it is necessary to take into consideration how they respond to changes in the availability of this habitat feature across relevant spatio-temporal scales. Given the dynamic nature of tidal mixing fronts, there is likely to be substantial variation in how different populations and individuals use such features (Trevail et al. 2021). At the broadest scale, seabird colonies will differ in their proximity to established mixing fronts, and this will shape habitat usage (Christensen-Dalsgaard et al. 2018). Even within a colony, different individuals may forage in distinct locations with different frontal characteristics (Wakefield et al. 2015, Cleasby et al. 2019). Functional response modelling is one means to understand how species' habitat usage patterns change due to shifts in the underlying characteristics and availability of different habitats (Mysterud & Ims 1998). Such models represent an extension to existing species distribution models (Matthiopoulos et al. 2011) and are based on the idea that habitat usage is shaped by the relative availability of different habitats (Holbrook et al. 2019). Functional responses can play an important role in ecosystem management and conservation (e.g. Herfindal et al. 2009, Wakefield et al. 2017), particularly in heterogeneous and dynamic environments (Paton & Matthiopoulos 2016) such as shelf seas by allowing patterns of habitat use to shift as conditions change. Crucially, this would assist in the design of more dynamic MPAs (Game et al. 2009, Pinsky et al. 2020) and contribute to a better understanding of how anticipated anthropogenic impacts such as climate change or installation of marine renewables will change water stratification patterns and hence expected seabird distributions.

In the present study, we used long-term tracking data sets collected over multiple years (2010—2015) to understand how breeding black-legged kittiwakes *Rissa tridactyla* (hereafter 'kittiwakes') utilise dynamic tidal front habitats within the North Sea. The North Sea is a well-studied shelf sea surrounded by high densities of human populations (Emeis et al. 2015), subject to high anthropogenic impacts (Moullec et al. 2021) and characterised by multiple tidal mixing fronts (Appendix 1d in UK OESEA3 2016). The

Dogger Bank, a large sandbank, separates the North Sea into 2 broad areas to the north and south (Emeis et al. 2015). The southern North Sea is typically shallow (<50 m), and in most areas, water is mixed year round due to the influence of winds and tides. In contrast, the northern North Sea contains deeper areas (>50 m) and is subject to stratification during the summer (Pohlmann 1996), though in shallower areas, the water column may remain mixed (Pingree & Griffiths 1978). The North Sea is also home to important numbers of kittiwakes including multiple special protected areas (SPAs) designated to protect important kittiwake breeding colonies. Notably, most of the major UK kittiwake colonies on the North Sea coast are located within or close to the northern section of the North Sea. Kittiwakes have experienced large declines in recent years throughout their range (Eaton et al. 2015, Johansen et al. 2020). Currently, the species is listed as Vulnerable on The IUCN Red List of Threatened Species (BirdLife International 2024) and occurs on the OSPAR List of Threatened and/or Declining Species (OSPAR 2023).

Kittiwakes have previously been shown to forage on or around tidal mixing fronts and, as surface feeders, may require bio-physical processes such as tidal mixing fronts to drive prey aggregations to the surface (Chivers et al. 2012). For example, environmental covariates associated with kittiwake habitat selection are often descriptors of properties of the water column (such as sea surface temperature [SST] or measures of stratification) or linked to processes such as turbulent mixing, which may enhance production at lower trophic levels or make prey more accessible at the surface (Wakefield et al. 2017, Stempniewicz et al. 2021). As such, kittiwakes are thought to be vulnerable to changes in stratification patterns, with subsequent impacts upon their annual reproductive success in the North Sea (Scott et al. 2006, Carroll et al. 2015). Therefore, understanding how patterns of habitat usage change in relation to tidal front activity is a key component of spatial conservation management for the species (Scales et al. 2014, Ruffino et al. 2023), especially given the number of marine developments planned within the North Sea and the impact of climate change. However, while previous research has examined kittiwake functional responses to some aspects of tidal front behaviour (Wakefield et al. 2017), assessment of the influence of dynamic covariates such as SST and front gradient were based on average conditions during the summer months across a 5 yr period. Therefore, information on the spatio-temporal variation in such dynamic variables was lost, and such models may subsequently

struggle to capture shifts in habitat usage in response to changing habitat characteristics. Advances in both habitat selection modelling procedures and the development of new remote sensing tools with finer spatio-temporal resolutions now provide a means to address this issue (Belkin 2021).

The aims of the current study were to generate functional responses of breeding kittiwakes originating from 10 UK North Sea colonies to a suite of dynamic environmental covariates (surface chlorophyll *a* [chl *a*], front strength, distance to nearest front and SST) related to tidal front behaviour. We aimed to construct habitat selection models that can incorporate potential non-linearity in kittiwake responses to habitat variables and are conducted at a finer spatio-temporal scale than previously achieved to reflect the dynamic nature of tidal fronts and subsequent seabird responses. Given the established importance of tidal fronts to a range of marine predators, including kittiwakes, we predicted that kittiwakes will tend to select areas of habitat that are closer to fronts and characterised by higher front strength. Based on previous research, we also predicted that kittiwakes will target areas of cooler water (lower SST) and higher chlorophyll concentrations (Robertson et al. 2014, Wakefield et al. 2017, Trevail et al. 2021). Furthermore, we predicted that responses to each covariate will be non-linear, and that habitat usage will be influenced by the prevailing habitat availability.

2. MATERIALS AND METHODS

2.1. Tracking data collection

Fieldwork was conducted at 10 kittiwake colonies located along North Sea coast of Great Britain during May—July over the period 2010—2015. Colony locations ranged from Flamborough Head (54.1161° N, 0.0839° W) in the south to Fair Isle (59.5339° N, 1.6333° W) in the north (Fig. 1). This range encompasses many of the major kittiwake colonies along the UK North Sea coast. However, there are kittiwake colonies farther south (e.g. East Anglia, Kent) and farther north (Shetland Islands archipelago) that were not sampled here. More details on colony locations, colony sizes, tracking dates and sample sizes are available in Table S1 in the Supplement at www.int-res.com/articles/suppl/m740p175_supp.pdf.

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
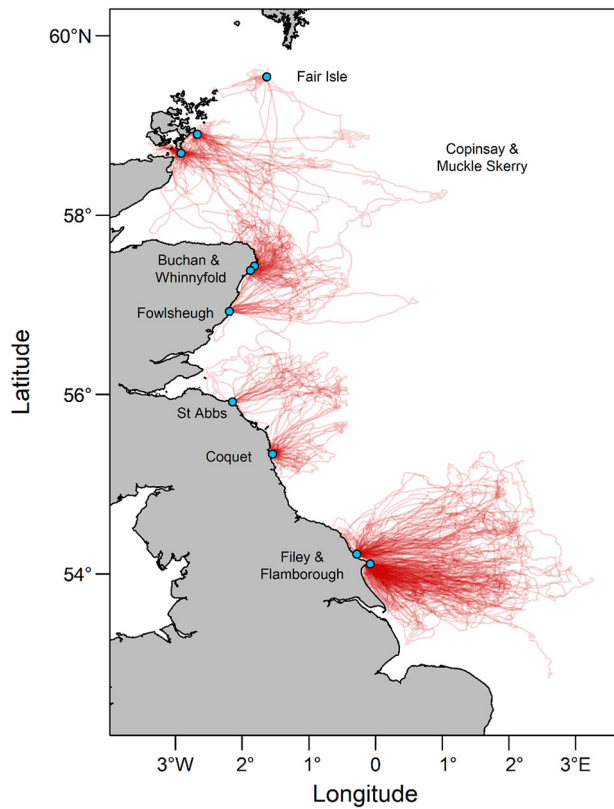
Fig. 1. Locations of tracked black-legged kittiwake colonies (blue circles) and GPS tracking observations (red lines) in the North Sea. Foraging tracks are plotted using a semi-opaque colour to highlight areas with a higher density of tracking locations. Colony names are displayed on the map; in instances when 2 colonies were located close together, colonies are labelled together with the more northerly colony listed first. More details on colony names, locations and tracking sample sizes are given in Table S1 in the Supplement

Action Technology) GPS logger to a bird's back or tail with Tesa tape. GPS loggers were set to record at 100 s intervals. The loggers deployed weighed either 17.4 ± 0.07 g (mean ± SE) or 15.0 ± 0.18 g, representing 4.5 or 4.2% of a kittiwake's body mass, respectively. Device mass exceeded 3% of body mass which, after consideration, was deemed to be acceptable since deployments were typically short in duration. We previously found little evidence of device effects on a range of trip summary metrics (including maximum foraging distance from the colony and trip duration) or change in body mass when comparing kittiwakes carrying regular (17.4 g) or lighter (15.0 g) GPS loggers across the North Sea colonies studied here (Cleasby et al. 2020, but also see Heggøy et al. 2015). In addition, we found little difference in colony attendance patterns between kittiwakes tagged dur-

ing this study in North Yorkshire and birds tagged with lighter GPS tags (8.5 g) in 2017 (Cleasby et al. 2020). Devices were deployed for periods of 1–9 d, after which birds were recaptured and the loggers removed. No individual birds were tracked in more than 1 year of the study. For more details on field data collection, see Wakefield et al. (2017).

2.2. Behavioural segmentation of tracking data

All data processing and analysis steps were conducted in the R Environment (R Version 4.2.1; R Core Team 2022). 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 R package 'track2kba' (Beal et al. 2021; for more details, see Cleasby et al. 2024). We used hidden Markov models (HMMs) to classify kittiwake tracking data into 3 distinct modes, which we termed 'resting', 'foraging' and 'transit', based on step lengths and turn angles obtained from tracking data. The choice to identify 3 foraging modes was based on prior experience with kittiwake tracking data that suggested the HMMs can usually distinguish 3 clear behaviours in such data (Trevail et al. 2021, Bogdanova et al. 2022). Similarly, based on prior findings, we set up HMM design matrices such that step lengths tended to be smallest when resting, intermediate during foraging and highest during transit (resting > foraging > transit). Likewise, turn angles were set up as transit > foraging to suggest more direct flight during transit compared to foraging. HMMs identified a putative foraging mode typified by intermediate step lengths and greater turning angles than those observed during resting or transit (see Fig. S1). In addition, we included an effect of time of day in our HMMs using a cosinor function for cyclical data to account for our assumption that resting behaviour should be more common during hours of darkness (Fig. S2). All HMMs were performed using the 'momentuHMM' R package (McClintock & Michelot 2018). Subsequently, the habitat usage models constructed (see Section 2.4) were based only on those observed locations classified as foraging.

2.3. Environmental data

We created functional response models for 4 covariates related to tidal front activity: surface chl a concentration, front strength and distance to the nearest front and SST. SST and chl a are commonly used in

front detection algorithms to derive information on front metrics such as front strength or persistence (Belkin 2021). Moreover, SST and chl *a* are often used to identify areas of higher productivity for marine species (Isaksson et al. 2023) as well as other features of water column-mixing such as localised upwellings and vertical mixing (Miller et al. 2015). Consequently, the inclusions of information on SST and chl *a* alongside frontal metrics can improve the performance of species distribution models (Miller et al. 2015).

High-resolution SST and chl *a* data were obtained via a data request to the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS). SST data were based on the Multiscale Ultrahigh Resolution (MUR) multisensory product and processed via NEODAAS. The spatio-temporal resolution of SST data was 1 km^2 at daily intervals. Chl *a* data from NEODAAS were based on the CMEMS OC5 chlorophyll product (Tilstone et al. 2021). Initially, we obtained daily chl *a* data, but this was characterised by high levels of cloud cover on certain days and therefore missing values. Instead, we used chl *a* data calculated at weekly intervals with a 1 km^2 spatial resolution. Composite ocean front maps from AVHRR SST were created to obtain measures of thermal front gradient magnitude (front strength, °C/km) and the distance to the nearest front in 1 km cells throughout the North Sea study area (Miller 2009). Composite front maps were based on a 7 d moving window that included the day on which tracking locations were observed as well as the preceding 6 d in order to minimise missing data due to cloud cover. Thus, front maps were updated daily. Time windows were structured in this way because we felt it was reasonable to assume birds could have some prior knowledge of an area but not future knowledge of conditions. 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 (σ = 5 pixels) to a map of the mean gradient magnitude values. It is designed to provide 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 via a custom simplification algorithm (P. I. Miller unpubl. data). To visualise changes in frontal activity across the spatio-temporal extent of our study, Hovmöller diagrams showing changes in front strength throughout the course of each tracking period across the years studied are presented in Fig. S3. Such plots highlight the seasonal progression on front de-

velopment and differences in frontal activity across the range of latitudes studied. Finally, for each colony, we calculated distance by sea on a 500 m grid using the 'gdistance' R package (van Etten 2012) to account for distance from the colony, which is a key movement constraint on central-place foragers.

2.4. Habitat selection models and functional responses

We used a resource selection function (RSF) approach to model kittiwake distributions using the 'amt' R package (Signer et al. 2019). RSFs compare covariates associated with locations where the animal was observed with covariates associated with randomly selected locations within a spatial domain wherein any location is assumed to be equally available to the animal. Defining the area available to an animal is therefore key to modelling inference and interpretation (Johnson 1980, Northrup et al. 2022). Here, the area deemed as available to each bird was set using a minimum convex polygon (MCP) that contained all tracking observations (both foraging and non-foraging) from a given bird, with an additional 10 km buffer around this MCP. We used such a buffer to ensure we could sample points in a radius around observed points even if they occurred close to the edge of an MCP. A value of 10 km has previously been identified as the average scale of area-restricted search for kittiwakes across a range of UK colonies, including the North Sea colonies studied here (Cleasby et al. 2020). For each observed foraging location included within our RSFs, we generated a set of n = 40 available points. Available points were chosen randomly and allowed to fall anywhere within the space deemed available to a particular individual and were given a matching timestamp to the observation point with which they were paired. Such timestamp matching was required because within the same year, even individuals tracked from the same colony may have been tracked over a different period of days. We extracted data on the environmental covariates listed above based on both spatial coordinates of observed and available points as well as the date on which they occurred. This approach allows individuals, even those from the same colony, to experience differing levels of habitat availability (De Groeve et al. 2020). We adopted this approach here because (1) individuals tracked at the same colony do not necessarily visit the same areas and hence experience different environments (Matthiopoulos 2022). However, models fitted at larger spatial scales (e.g.

colony-level home range) will tend to average across the responses of individuals that occupy regions with different habitat compositions (Paton & Matthiopoulos 2016); (2) environmental conditions change both annually and seasonally so that even birds consistently visiting the same geographic area will not experience the same habitat as the breeding season progresses or across years. Based on the definitions of spatial scale provided by Johnson (1980), our definition of availability at the individual level therefore fits within third-order selection or the selection of habitat components within an individual's foraging range. Boxplots showing the environmental conditions at available points for each individual and across each colony are displayed in Figs. S4—S47.

We fitted RSFs using logistic regression and assigned arbitrarily large weights, $w = 1000$, to available locations and a weight of $w = 1$ to all observed foraging locations. This weighting scheme helps ensure that coefficient estimates from a logistic regression will converge to the estimates given by an inhomogeneous Poisson process (IPP), a process that underpins various species distribution modelling approaches (Warton & Shepherd 2010). Rather than fit environmental covariates as linear coefficients, we allowed for non-linear responses to covariates via the use of radial basis functions (RBFs). RBFs are often used, particularly in machine learning settings, to model non-linear regression responses. An RBF is a function whose points are defined as distance (often Euclidean distance) from an origin, such that $\emptyset(x) = \emptyset(\| x \|)$, or a given point, called a centre (c), such that $\emptyset(x) = \emptyset(\| x - c \|)$. Basis functions will be radially symmetric about these centre points. In practice, RBFs are often used as a collection or set to build up functional approximations, where a function can be represented as linear combinations of the associated, centered RBFs (Adcock et al. preprint doi:10.48550/arXiv.2211.12598). Such RBFs can be viewed as a class of spline and can be interpreted as roughness-minimising splines (Hickernell & Hon 1999). Here we use a standard RBF form (Bishop 1995, see also Aldossari et al. 2022):

$$\gamma_i(\boldsymbol{x}) = \sum_j \sum_m \delta_{i,j}^{(m)} \exp\left(-\frac{1}{2} \frac{(x_j - \xi_{j,m})^2}{\sigma_{j,m}^2} \right) \quad (1)$$

where γ_i denotes the coefficients of a generalised functional response (GFR) to $\boldsymbol{x}$ environmental covariates ($x_1, x_2 \ldots x_j$); $\delta_{j,m}^2$ represents a coefficient of $\gamma_i(\boldsymbol{x})$ for the mth power of the jth covariate; $\xi_{j,m}$ is the centre of the mth basis function for the jth covariate, and $\sigma_{j,m}^2$ is a bandwidth parameter that controls the smoothness of the RBF. Here we set the centres of the RBFs

$\xi_{j,m}$ as the 5, 25, 50, 75, and 95% quantiles of the jth environmental covariate, giving a total of $m = 5$ basis functions per covariate. The bandwidth parameter $\sigma_{j,m}^2$ was then set as the largest of the differences calculated between consecutive quantiles (see Aldossari et al. 2022).

Functional responses were assessed by examining the relationship between habitat usage and habitat availability over a specified spatio-temporal extent (Matthiopoulos et al. 2011). Specifically, non-linear basis functions for the jth environmental covariate were fitted along with a 2-way interaction with the corresponding estimate of habitat availability of the jth environmental covariate. Habitat availability was summarized as the mean value of the jth environmental covariate over an individual's putatively available foraging range (defined using individual-level MCPs, see above) across the dates a given individual was tracked (Figs. S48—S51). Thus, each individual in the study experienced a unique value of habitat availability for each environmental covariate based on the unique spatio-temporal footprint of their own observed tracking data.

While we did not account for spatial autocorrelation in our study for the sake of model tractability, each model included distance from the colony as a spatial predictor, fitted using $m = 5$ RBFs, to account for the mechanistic constraints of central-place foraging on habitat accessibility. In addition, we also included a 2-way interaction between each of the $m = 5$ basis functions relating to distance from the colony and $\log_{10}$ colony size. An interaction between distance from the colony and colony size was included because colony size is often positively correlated with foraging range in seabirds (Jovani et al. 2016, Cleasby et al. 2024). Colony size estimates were taken from Mitchell et al. (2004) and further processed as described by Wakefield et al. (2017). Because our data set included multiple measures of habitat use from the same individual and multiple individuals from the same colony, we also included random intercepts for individual identity and colony identity within our models. Following Muff et al. (2020), these random intercepts were assigned a large, fixed value. Initially, we also tried to incorporate random slopes for each environmental covariate considered by allowing for random slopes in each of the $m = 5$ basis functions that described the response to that particular covariate. However, models with random slopes failed to converge, and we restricted ourselves to the random intercept-only models. To further account for the lack of independence of observations from the same individual, we used cluster-level bootstrapping to resample individuals and generate more

robust standard errors for each of the coefficients in our models (Fieberg et al. 2020).

Initially, we ran one over-arching habitat selection model that included functional responses for all of the environmental covariates examined. However, while correlations between each of these covariates were not particularly strong, we found evidence of concurvity between front strength and distance to the nearest front. Front strength tended to be higher close to fronts and declined with distance to the front (Fig. S52). Therefore, we ran 2 habitat models: one which included chlorophyll concentration, distance to the nearest front and SST as covariates and another which included chlorophyll concentration, front strength and SST. As the model which included distance to nearest front had lower Akaike's information criterion (AIC) scores, we report the results from this model when discussing results relating to chlorophyll concentration, distance to nearest front and SST. However, we still report results relating to front strength which are based on the model with the best (lowest) AIC score when this covariate was used rather than distance to the nearest front. In addition, although initial models were constructed with $m = 5$ basis functions for each environmental covariate (as described above), we used model AIC scores to evaluate if simpler models with fewer basis functions performed better (Aldossari 2023). We present results based on the model with the lowest AIC score. Results of these models are visualised using plots of relative selection strength (RSS) calculated following Avgar et al. (2017).

2.5. Model validation via used-habitat calibration plots

We validated the performance of our habitat models via used-habitat calibration (UHC) plots (Fieberg et al. 2018). By comparing model predictions to out-of-sample data, such procedures can help identify various issues with species distribution models (SDMs), including missing covariates, non-linearity and multicollinearity. Briefly, we used 10-fold cross-validation to generate different testing and training data sets from our entire data set. We then summarized the distribution of each environmental covariate across the kth test data sets using kernel density estimators. The RSFs described above were then fitted to the kth training set and stored. Both the model coefficients $\hat{\beta}$ and the model variance-covariance matrix $cov(\hat{\beta})$ were stored. Next, $n = 500$ random samples from were drawn from a multivariate normal distribution defined by $\hat{\beta}$ and $cov(\hat{\beta})$ to estimate the relative

probability of selection for the test data. The relative probability of selection was used to draw a weighted random sample of observations from the test data. For each simulation, the distribution of the environmental covariates associated with the points selected was summarized using kernel density estimators. We then compared the observed distribution of environmental covariates at used points in the test data set with a 95% simulation envelope built using the predictions from our n = 500 simulations. UHC plots are presented in Text S1, Figs. S53–S57.

3. RESULTS

3.1. Chlorophyll concentration

GFRs showed that kittiwake responses to surface chlorophyll concentration were influenced by the average chlorophyll levels across the available envi-
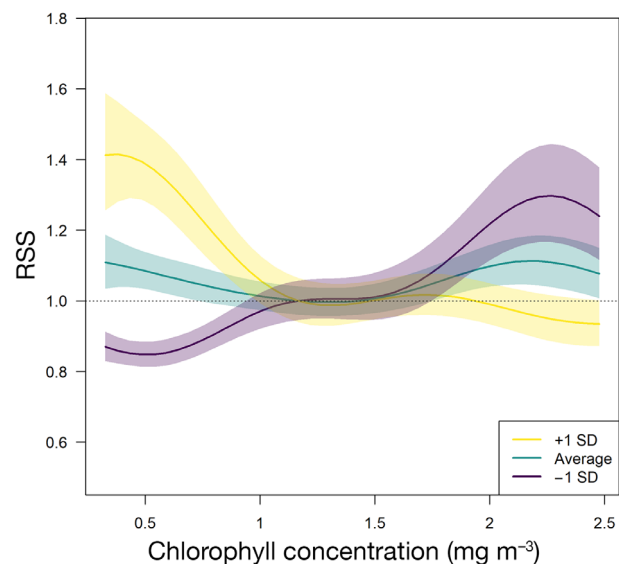

Fig. 2. Generalised functional responses of breeding black-legged kittiwakes to surface chlorophyll concentration. Relative selection strength (RSS) was calculated by comparing selection strength between a putative location (x_1) when chlorophyll concentration was set at its mean value across all available points within the current study to a vector of locations (x_2) over which chlorophyll concentration values ranged from the minimum observed to the upper 99% quantile observed. The values of all other covariates in the model were held constant at their mean values. RSS responses are shown at different levels of habitat availability to visualise the interaction between habitat availability and nonlinear basis functions. Curves show response when average chlorophyll concentration is set at the average level observed across all individual-level minimum convex polygons in the study or ±1 SD (Fig. S48). Curves based on fitted model coefficients with a corresponding 95% confidence envelope

ronment (Fig. 2). When average chlorophyll levels were low, habitat usage was greater in areas with higher chlorophyll concentrations. However, when average chlorophyll concentrations were at the highest values, the opposite occurred, and habitat use was directed towards areas with lower chlorophyll concentrations. The best fitting model for chlorophyll concentration was identified as the one in which the response to chlorophyll was modelled using RBFs with $m = 5$ centres. Coefficients for all habitat selection models including that relating to chlorophyll concentration are presented in Table S2.

3.2. Front strength

Kittiwake responses to front strength were influenced by the average level of front strength in the available environment (Fig. 3; Table S3). When average front strength values were high, we observed an increase in usage of areas with higher front strength. Under such conditions, habitat usage peaked at values of front strength of ~0.006 based on estimated RSS values before declining slightly. Therefore, usage is greatest at relatively high values of front strength but not at the most extreme values. However, RSS values were close to 1.0 and estimated with relatively high uncertainty throughout the range of front strength examined. In addition, as average front strength in the available environment decreased, responses to front strength flattened. The best fitting model for front was identified as one in
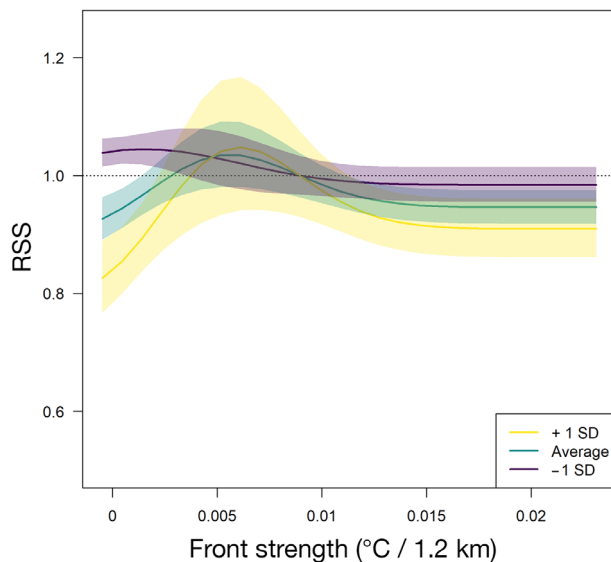
which the response to front strength was modelled using RBFs with $m = 2$ centres occurring at the 50 and 75% quantile of this covariate (Table S3).

3.3. Distance to nearest front

We observed non-linear responses between kittiwake habitat usage and the distance to the nearest front, which were also influenced by the availability of such habitat (Fig. 4). When the average distance to the nearest front was lower, habitat usage peaked in areas close to the front (<10 km) or in areas farther from fronts (>30 km). However, when the average distance to the nearest front was higher, and fronts were therefore farther away, there was no increase in the usage of areas close to a front. The best fitting model for distance to the nearest front was identified as the one in which the response to distance to front was modelled using RBFs with $m = 3$ centres occurring at the 25, 50 and 75% quantile of this covariate (Table S2).

3.4. SST

Kittiwake responses to SST were non-linear and dependent on the average SST level across the available environment (Fig. 5). In general, regardless of the prevailing availability of SST, we saw clear evidence of selection of regions with cooler SST. The estimated RSSs in this case were typically large relative to those observed for the other environmental
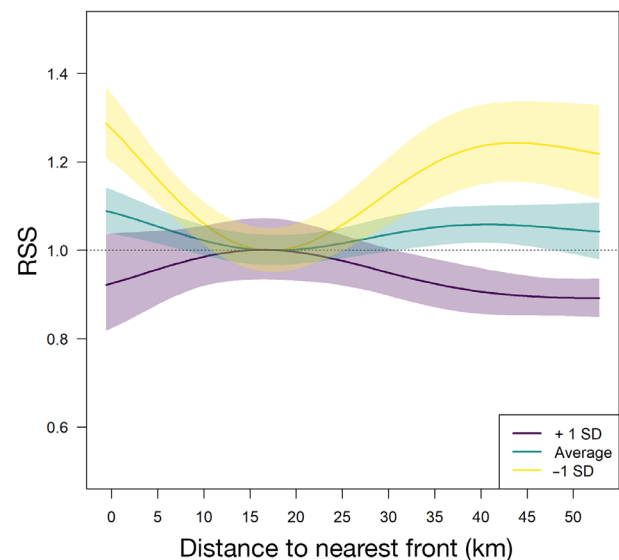

Fig. 3. As in Fig. 2, but for front strength (also see Fig. S49)

Fig. 4. As in Fig. 2, but for distance to the nearest front (also see Fig. S50)
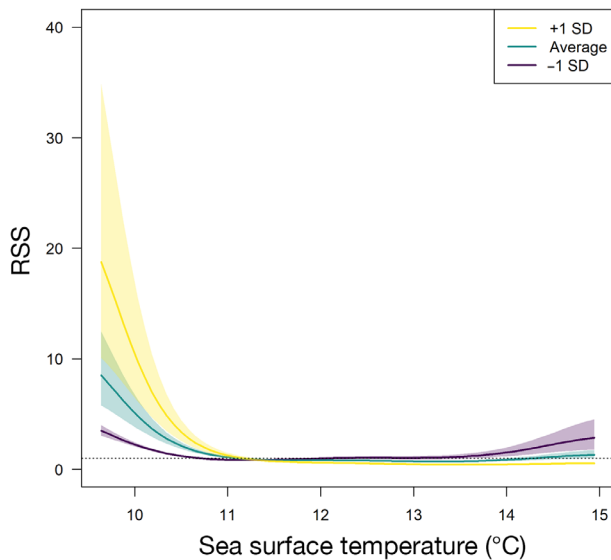
Fig. 5. As in Fig. 2, but for sea surface temperature; here, x_2 ranged from the minimum observed to the maximum observed (also see Fig. S51). A plot with a modified y-axis with a reduced upper limit is available in Fig. S58 to better visualise responses on the right-hand side of the plot

covariates we examined (Fig. S5, Table S2). Preferences for cooler water temperatures appeared slightly weaker when average SST was lower. For example, when average SST was lower, while we observed a peak in habitat usage at lower SSTs, this occurred alongside an additional smaller peak in habitat usage in areas of warmer water (SST >14°C, Fig. S58). In contrast, when average SST was high, we observed a stronger increase in habitat usage solely at lower SST values (<11.5°C, Fig. S58). The best fitting model for SST was identified as the one in which the response to SST was modelled using RBFs with $m = 5$ centres.

3.5. Distance from the colony

The best fitting model for distance from the colony was identified as that which included $m = 5$ centres and incorporated a 2-way interaction between basis functions and $\log_{10}$ colony size (Table S2). The main reason for including distance from the colony within our models was to account for the constraints that central-place foraging places on the accessibility of areas farther from the colony rather than direct interpretation of this covariate. Nevertheless, model predictions showed that usage declined with distance to the colony and that this decline was steeper for larger colonies (Fig. S59). However, we also observed a peak in usage of areas at 160–180 km from the colony,

which may have reflected birds foraging at the distal point of longer foraging trips.

4. DISCUSSION

4.1. Kittiwake functional responses to habitat

The importance of tidal mixing fronts as relatively predictable and productive habitats at which marine predators congregate has been established in a variety of species across multiple, distinct sea regions (Bost et al. 2009, Bailey & Thompson 2010, Scales et al. 2014, Miller et al. 2015). In kittiwakes specifically, several studies have previously shown associations between frontal activity and habitat use (e.g. Durazo et al. 1998, Markones 2007, Scott et al. 2010, Embling et al. 2012). Our results support these findings by demonstrating how kittiwakes foraging in the North Sea responded to environmental covariates related to tidal fronts and shifts in their spatio-temporal availability.

Kittiwakes showed a non-linear functional response to distance to the nearest front. In this case, we observed peaks in habitat usage in areas close to fronts (<10 km), along with higher levels of usage in areas farther from fronts (30–50 km) when the average distance to the nearest front was relatively low. Given the previous evidence regarding the importance of tidal fronts to marine predators (Bost et al. 2009), the use of areas closer to fronts when fronts were relatively close and therefore accessible was in line with initial predictions. The reasons behind the usage of areas farther from fronts is less clear. In some situations, birds may still be utilising tidal fronts even if they are not foraging directly at the location of a front. For example, there is variation within and between seabird species regarding how close to and on which side of a front (mixed or stratified) to forage (Schneider 1982, Durazo et al. 1998, Russell et al. 1999, Scott et al. 2010, Cleasby et al. 2015, Cox et al. 2016). Furthermore, in stratified regions farther (15–50 km) from mixing fronts, the spring–neap cycle is thought to lead to periodicity in primary production and carbon flux (Sharples 2008). Therefore, birds may still be responding to the action of tidal fronts even if they are not foraging directly at front boundaries. One way to examine the role of the spring–neap cycle would be to incorporate the relative position in the spring–neap cycle when investigating habitat selection (e.g. Cox et al. 2017). However, because the GPS deployments in the current study were typically of short duration, we were unable to sample across the entire spring–neap cycle in any year at any colony.

We also observed slight peaks in habitat usage when average levels of front strength were higher. In this case, when areas of frontal activity were more available, regions with lower front strength were less likely to be used. Kittiwake preferences for front strength peaked at a value of ~0.006 before declining slightly. For context, a front strength of 0.006 represents the 70% quantile of front strength values observed in the current data set. This supports previous findings that kittiwakes prefer areas of moderate rather than maximum stratification (Scott et al. 2010). However, it should also be borne in mind that RSS values for front strength were close to 1.0. Moreover, when average levels of front strength were low or the average distance to the nearest front was high, kittiwake responses to both covariates were relatively flat. Thus, when frontal habitats are less available, birds may switch to targeting other features.

The importance of accounting for spatio-temporal variation in habitat availability is apparent when comparing conditions across years and/or across colonies. At some locations or for certain individuals, areas of higher front strength were not encountered in certain years, constraining the ability of birds to forage in frontal areas (Fig. S5). In such circumstances, the lack of available front habitat could alter kittiwake habitat usage patterns. Likewise, while fronts were generally located close to colonies, suggesting they were readily accessible, in a few cases the typical distance to the nearest front was quite far. For example, for birds from Coquet Island, the median distance to the nearest front was 87 km in 2011 but only 21 km in the following year (Fig. S6). In such a case, birds may either choose to occasionally forage farther from the colony to access profitable environmental conditions related to persistent fronts (Russell et al. 1999, Dean et al. 2015) or to direct their efforts towards other habitats (Cox et al. 2018). In such cases, seabird distributions could change markedly from year to year.

Kittiwake responses to SST showed peaks of usage in both cooler water and warmer waters, with lower usage of areas of more intermediate temperatures. In kittiwakes, higher levels of habitat use in cooler, mixed waters have previously been reported (Robertson et al. 2014, Trevail et al. 2021). Here, selection of areas with cooler SST was demonstrated by the large RSS values calculated for this covariate, which were far larger than for any other covariate considered. Although relative rather than absolute values, they nevertheless highlight the degree of selection of such areas and the importance of SST. Moreover, functional responses demonstrated how, as average SSTs

increased, habitat usage was predicted to increasingly shift towards cooler waters. In cooler waters, cold-adapted plankton species may be larger and more nutritious, with beneficial effects that could cascade up local marine food webs (Beaugrand et al. 2002). Higher temperatures may also be detrimental to the growth, recruitment, and spawning stock biomass of lesser sandeels *Ammodytes marinus*, a key kittiwake prey species (Arnott & Ruxton 2002, Carroll et al. 2017). Further highlighting the importance of cooler, mixed waters, kittiwake productivity has been shown to be positively associated with cooler SST at some breeding colonies (Frederiksen et al. 2005, Carroll et al. 2015).

A preference for foraging in areas with higher SSTs when average SST levels were lower may indicate birds foraging on the warmer, stratified sides of mixing fronts. In general, average SST levels are likely to increase throughout the summer and may also reflect areas of higher stratification at seasonal time scales due to the influence of solar heating (Scott et al. 2006, Sharples et al. 2020). Therefore, while kittiwakes may utilise areas of moderate stratification, they appear to increasingly shift to using areas of cooler water as average SST levels, and hence the degree of stratification, increase. Such behaviour will result in birds shifting their habitat usage patterns both seasonally and across years as environmental conditions related to frontal activity change (Robertson et al. 2014, Cleasby et al. 2015, Bertrand et al. 2021). However, it should be borne in mind that RSS values associated with the use of areas with warmer SSTs were not at the magnitude for cooler SSTs. Thus, while certain conditions may favour the use of such areas, they were still not as strongly selected as cooler regions.

Kittiwakes tended to use areas of higher chlorophyll concentration when the average chlorophyll concentration in the area available to them for foraging was low. Chlorophyll concentration is frequently used as a measure of phytoplankton abundance, which provides the basis for marine food webs on which top predators such as seabirds rely (Suryan et al. 2012). Therefore, kittiwakes may be foraging in patches of high near-surface chlorophyll, indicative of higher primary production at such locations. Positive relationships between kittiwake abundance and chlorophyll concentration have also been observed in other studies, including some based in the North Sea (Scott et al. 2010, Chivers et al. 2013, Robertson et al. 2014). However, it is less clear what drove the higher usage of areas with lower chlorophyll when mean chlorophyll levels were higher. Chlorophyll concentration tends to be higher in coastal areas in the northern North Sea

(Peters et al. 2005). Therefore, greater usage of areas with lower chlorophyll could be driven by birds tending to forage away from the coastline in offshore areas (Grémillet et al. 2008), even though chlorophyll levels themselves are higher in coastal waters. This relationship would be most apparent in birds that typically foraged in inshore areas, as this would result in their available habitat being characterised by a higher mean chlorophyll concentration. In addition, the highest levels of chlorophyll concentration observed in this study largely occurred in the southern North Sea, south of the Flamborough front. In the current data set, we only occasionally observed birds from Filey and Flamborough foraging to the south of the Humber estuary (Fig. 1). Thus, our results could, in part, be driven by birds from the most southerly colonies in our data set tending to avoid foraging in the mixed waters of the southern North Sea. The relatively low use of such areas may also reflect a mechanistic constraint on foraging range when feeding young chicks. For example, tracking data from Flamborough Head in 2017 (Wischnewski et al. 2017) showed kittiwakes foraging more extensively farther south than we observed here. However, Wischnewski et al. (2017) deployed tags on individuals for a longer period (up to 29 d) than in the current study. Thus, our findings may not reflect the strength of habitat associations throughout the entire breeding period, particularly as the magnitude of central-place constraints also varies throughout the breeding cycle. More broadly, associations between chlorophyll abundance and zooplankton biomass can become de-coupled (Díaz-Astudillo et al. 2022). Consequently, areas of lower chlorophyll may not always reflect prey abundance available for predators at higher trophic levels (Grémillet et al. 2008).

4.2. Conservation implications

The predictability of oceanographic features is thought to shape the movement patterns of many marine predators, with habitat usage directed towards areas where favourable conditions persist over time versus more ephemeral food patches (Scales et al. 2014). Tidal mixing fronts represent one such feature, as they are highly productive regions whose location is shaped by the relatively predictable influences of the tides and bathymetry (Belkin 2021). As such, fronts have been cited as dynamic ocean features that could help to identify ecologically important areas suitable for designation as marine protected areas (MPAs) or other conservation measures (Miller & Christodoulou 2014, Scales et al. 2014). Indeed, the location of tidal

fronts underpins the development of recent UK MPAs such as the Irish Sea Front SPA (https://jncc.gov.uk/our-work/irish-sea-front-spa/, accessed on 24 March 2023). The results presented here demonstrate the importance of such areas to kittiwakes and highlight how key marine habitat features such as persistent fronts could be used for MPA identification. However, functional response models also show how, as oceanographic features associated with foraging vary over space and time, the usefulness of specific areas for foraging will likewise shift. For greater resilience of MPA design, the dynamic nature of such features and resulting pattern of space use in seabirds (or other species) should therefore be considered (Game et al. 2009, Chivers et al. 2013, Isaksson et al. 2023).

In this context, climate change is likely to play a key role in shaping kittiwake habitat usage in the future as the number and intensity of physical biophysical processes and, consequently, kittiwake distribution patterns are altered. For example, seasonal stratification could occur earlier in the spring and last for longer, with stratification being stronger and the location of tidal mixing fronts shifting slightly in response to climate change (Holt et al. 2010, Sharples et al. 2020). The growing number of offshore renewable installations may also impact tidal front habitats because the addition of such structures can have important impacts on levels of water column mixing and the distribution of phytoplankton (Carpenter et al. 2016, De Dominicis et al. 2017, Scott 2022). In each case, the kittiwake functional responses reported suggest that habitat usage will shift in response to such changes, which highlights the vulnerability of this species to potential changes in North Sea stratification patterns and climate change in general (Burthe et al. 2014, Carroll et al. 2015). Given the planned increase in offshore renewables, it will become increasingly important to understand impacts on water stratification patterns when planning future offshore developments (Medina-Lopez et al. 2021).

North Sea SSTs are expected to rise under various climate change scenarios (Dieterich et al. 2019). Based on our results, we would expect kittiwake habitat usage to increasingly shift towards areas of cooler SST in the future despite such habitat becoming less available. As a result, kittiwakes may either be forced into smaller pockets of preferred habitat (Bonnet-Lebrun et al. 2022) or increase foraging ranges to find suitable habitat (Osborne et al. 2020). However, there are limits to how much flexibility kittiwakes have to buffer against increasing SSTs before key demographic parameters, such as breeding success, begin to decline (Schlener et al. 2024).

4.3. Extensions to habitat modelling

The use of GFRs allows us to condition habitat usage upon a given definition of habitat availability and therefore account for shifts in habitat use as conditions change (Matthiopoulos et al. 2011). To a degree, the work presented here represents an extension of the modelling approach of Wakefield et al. (2017), who used GFRs to predict kittiwake habitat usage at the UK scale using multiple environmental covariates, including SST and front strength, which were also examined here. However, in that study, the environment available to birds was defined as a covariate's mean in the waters accessible to that colony. Moreover, environmental covariates themselves were averaged over the 5 yr period of the study (summer 2010–2015). Consequently, information on environmental variability experienced between years or between individuals from the same colony foraging over different spatio-temporal extents was not incorporated. Averaging over such a broad spatio-temporal extent will also tend to average across the responses of different individuals in regions of contrasting habitat characteristics, leading to a flattening of model coefficients (Paton & Matthiopoulos 2016). Here, we have been able to incorporate this additional variation, allowing us to assess kittiwake responses over a range of different environmental conditions at much finer spatio-temporal scales. For example, while Wakefield et al. (2017) found a negative association between SST and habitat usage (as we did here), they did not retain a term for the interaction between SST and its availability. However, our findings suggest that not only is kittiwake habitat usage positively associated with lower SSTs but also that this tendency tends to be stronger in habitats where average SST levels are higher. Moreover, we also incorporate new information on the distance to fronts, which was not previously considered but highlights the importance of areas close to fronts when this habitat is more available.

Our results also differ somewhat from those of Trevail et al. (2021), who reported that kittiwakes selected areas of weaker front strength and areas located farther from fronts. In part, we believe this is because the GFR approach allowed us to account for differences in environmental condition experienced by different individuals as outlined above. In addition, the use of RBFs gave additional insight into the non-linearity of observed functional responses, whereas Trevail et al. (2021) were restricted to examining linear relationships. However, our UHCs suggested that capturing non-linearity is important, and UHCs based on assuming simpler, linear relationships may not achieve this as well, even when including random slopes to account for between-individual variation.

The rapid growth in habitat modelling techniques means there is scope to extend the GFR approach further. Unlike Wakefield et al. (2017), the models presented here were not designed to generate predictive spatial distributions but rather to focus on specific covariates linked to tidal fronts. Nevertheless, they could be developed for such purposes via newly proposed machine learning methods (Aldossari et al. 2022). In particular, the use of RBFs, which are commonly used in machine learning processes, should facilitate this. One aspect of using RBFs is choosing the number and location of the centres used. In most cases, a small number of centres or knots (3–5) such as we used here is sufficient to model a non-linear relationship without much risk of over-fitting (Schuster et al. 2022). In addition, we used a relatively simple placement of centres across a uniform set of data quantiles, mirroring the placement of knots typical of many spline fitting procedures (Aarts et al. 2008, Perperoglou et al. 2019). Based on our UHC plots, we judged that our approach was sufficient to capture the non-linear patterns of usage seen in our data. However, using a machine learning approach, it would be possible to tune the exact number and placement of RBF centres.

Similarly, our models only considered 2-way interactions between a given environmental covariate and its own estimated availability. Our reasoning was that the habitat selection response to a given covariate would be most closely linked to the availability of that same covariate rather than another. We chose to do this for simplicity and ease of interpretation. However, a full GFR approach could involve fitting interactions between all of the environmental covariates considered here as well as interactions with the defined availability of each covariate. Likewise, models could be extended further by the addition of more covariates, although UHC plots did not highlight severe discrepancies that suggested the responses we observed were being driven by an important, missing covariate. Nevertheless, given the temporal scale on which remote sensing data are now available, it should be possible to develop seasonal and even daily habitat usage maps using a broader suite of covariates. Advances in tracking technology and data logger miniaturisation allowing for longer tagging deployments on individual birds could also assess how seabird habitat usage alters throughout the breeding season as fronts develop, or across the spring–neap tidal cycle (Scott et al. 2013).

Here, our model included random intercept terms for individual identity and colony given we had multiple measures at both levels, although the variance of these random intercepts was fixed at an arbitrarily large value (Muff et al. 2020). Models in which we attempted to include additional random slopes had a high computation time and failed to converge. In part, this may have arisen because random slopes were applied across the entire set of basis functions for a given covariate, resulting in estimation of multiple random slopes. However, model convergence also remained an issue when modelling covariates using simple, linear terms and fitting individual-level random slopes whenever we included an interaction between a covariate and that covariate's estimated availability (which was calculated at the individual level). Ultimately, we decided that a non-linear GRF performed well in describing non-linear patterns in habitat usage based on UHC plots, hence its application here. As such, our results should be seen as population-level functional responses which may mask individual variation caused individuals whose own response deviates from the population-level response (Newediuk et al. 2022). It has been suggested that individual variation in selection function coefficients could be assessed by sampling an individual over a longer time frame encompassing more environmental conditions (Northrup et al. 2022). Given the short timeframe of GPS tracking in the current study, we did not attempt this, but with longer tracking deployments or a study designed to track the same individual across multiple years, such an approach would be more feasible.

While tidal fronts may represent an important foraging habitat for kittiwakes, exactly how birds use such an environment was not examined here. However, the exact nature of prey availability is likely to differ depending on which side of the tidal front birds forage. For example, prey density was higher and prey were more aggregated at shallower depths in mixed water in the Celtic Sea, but the probability of prey encounters was greater in stratified waters for common guillemot *Uria aalge* and Manx shearwater *Puffinus puffinus* (Waggitt et al. 2018). Similarly, in short-tailed shearwaters *P. tenuirostris*, dense patches of euphausiids near the sea surface on the stratified side of mixing fronts represented an important food source (Vlietstra et al. 2005). Therefore, kittiwakes may utilise different foraging strategies and target different prey species when foraging in mixed versus stratified waters, as seen in other species (Cleasby et al. 2015, Cox et al. 2016). To address such issues, more information is required on spatio-temporal vari-

ation in the prey species consumed across the kittiwake colonies examined here throughout the course of the breeding season. Ideally, data on the distribution of key prey species would also be available at sufficient spatio-temporal resolutions, which is not the case currently (Ruffino et al. 2023). Similarly, because birds were not sexed in the current study, we do not know if there were differences between males and females in habitat use as has been seen in other species that forage in tidal front habitats (Cleasby et al. 2015).

5. CONCLUSIONS

Functional responses of kittiwakes to a suite of environmental covariates highlight the importance of dynamic tidal front habitats for this species. Kittiwake responses to such features varied as their availability changed. However, when the relative availability of frontal habitat was high (i.e. the average distance to fronts was low), we observed peaks in habitat usage close to tidal fronts. Kittiwakes also tended to forage in cooler waters with lower SSTs. Additionally, their preference for areas with lower SST increased as the average SST across the foraging area available to them rose. More broadly, the results highlight the dynamic and non-linear nature of seabird responses to frontal habitats as conditions change. Consequently, the timing and development of fronts both across different years or seasonally within a year (Sharples et al. 2006) as well as the influence of the spring—neap cycle could have a marked influence on the availability of frontal habitats and subsequent seabird habitat use patterns in shelf seas. Therefore, when using fronts or similar features for MPA design, their dynamic nature should be taken into account. For similar reasons, human activities such as marine renewable installation or longer-term processes such as climate change that alter stratification patterns could influence seabird habitat use and at-sea distributions. As a surface-feeding species that may rely upon the actions of tidal fronts to aggregate prey in shallower depths, kittiwakes may be particularly vulnerable to changes in stratification patterns. However, given associations between other marine predators and tidal fronts, our results are likely relevant to a range of different species that utilise tidal fronts.

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