Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird

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SUMMARY

The oceanographic drivers of marine vertebrate habitat use are poorly understood yet fundamental to our knowledge of marine ecosystem functioning. Here we use composite front mapping and high-resolution GPS tracking to determine the significance of mesoscale oceanographic fronts as physical drivers of foraging habitat selection in northern gannets *Morus bassanus*. We tracked 66 breeding gannets from a Celtic Sea colony over two years and used residence time (RT) to identify area-restricted search (ARS) behaviour. Composite front maps identified thermal and chlorophyll-a mesoscale fronts at two different temporal scales – (a) contemporaneous fronts and (b) seasonally persistent frontal zones. Using Generalised Additive Models (GAM), with Generalised Estimating Equations (GEE-GAM) to account for serial autocorrelation in tracking data, we found that gannets do not adjust their behaviour in response to contemporaneous fronts. However, ARS was more likely to occur within spatially predictable, seasonally persistent frontal zones (GAM). Our results provide proof-of-concept that composite front mapping is a useful tool for studying the influence of oceanographic features on animal movements. Moreover, we highlight that frontal persistence is a crucial element of the formation of pelagic foraging hotspots for mobile marine vertebrates.

KEY WORDS

seabird, marine vertebrate, foraging, remote sensing, oceanographic front, habitat use

1.0 INTRODUCTION

Marine predators, such as seabirds, cetaceans, pinnipeds, turtles and sharks, must locate sparsely-distributed prey in vast, heterogeneous and dynamic oceans. Although these diverse taxa differ greatly in foraging ecology, shared scale-dependent foraging strategies have evolved, presumably in response to the patchy, hierarchical distribution of pelagic prey (1-3). These strategies enable predators to locate broad-scale foraging grounds and then adjust the scale of search effort to find prey aggregations nested within (3, 4). Prey distributions are somewhat predictable at large- and meso-scales (10s-100s km; 5), but less so at sub-mesoscales (~1km; 1, 6), which may explain why foraging-site fidelity at large- and meso-scales is common among marine vertebrates (e.g. seabirds, turtles, seals; 5,7-10).

Oceanographic processes operating over a range of spatial and temporal scales regulate pelagic prey availability, and predictability, driving patterns of habitat utilisation for highly mobile marine predators. For instance, a taxonomically diverse range of marine vertebrates is known to associate with meso- (10s-100s kms) and sub-mesoscale (~1km) oceanographic features such as fronts and eddies (5, 11-17). Fronts are transitions between water masses, which manifest at the surface as horizontal gradients in temperature, salinity, density, turbidity or colour (18, 19). Nutrient retention within fronts can significantly enhance primary production (18, 20) and bio-physical coupling leads to aggregation and proliferation of zooplankton (21, 22). These conditions are suitable for pelagic fish, which in turn are prey for higher predators, and hence, fronts may be foraging hotspots (18, 23). Despite the assumed significance of fronts as foraging locations, we still have a poor grasp of their ecological value for higher trophic level predators. Fronts occur throughout the oceans, yet differ considerably in strength, persistence, size and spatial variability (19). This variability, as well as temporal and spatial lags in bio-aggregative effects (18, 21, 24), influences the suitability of fronts for foraging, particularly for piscivores. Persistent fronts are assumed to present more predictable foraging opportunities than small-scale, ephemeral and/or superficial features (25, 26), but direct tests of the significance of frontal predictability for predator foraging are lacking.

Recent methodological developments can address this discrepancy. Bio-logging technology and associated analytical techniques have enabled remote monitoring of individual animal distribution and behaviour, enriching our insight into habitat use by marine predators (27). However, a key constraint is the lack of data describing oceanographic processes and pelagic prey distributions at matching spatio-temporal scales. Although *in-situ* studies have yielded valuable insights into the fine-scale mechanisms underlying animal-oceanography interactions (e.g. 28-31), this eulerian

approach cannot provide information on behaviour throughout a foraging bout, limiting our understanding of broader-scale oceanographic influence. Remotely-sensed data can supplement bio-logging, identifying physical conditions that drive habitat selection in virtual real-time. Sea surface temperature (SST) and chlorophyll-a (chl-a) imagery are most widely used (12, 32), but it is questionable whether these metrics are appropriate for defining foraging habitat, particularly for piscivores (33). Indeed, the use of chl-a imagery in shallow shelf seas could be misleading, as sub-surface chlorophyll maxima in stratified areas can present more attractive foraging opportunities than mixed waters with elevated surface chl-a (28). In contrast, sub-surface processes occurring along thermal fronts are known to increase prey accessibility for diving predators. Convergent flow fields and fine-scale downwelling aggregate plankton in the shallow thermocline (21, 22), attracting higher trophic level consumers, including foraging seabirds (34, 35). Front mapping is able to detect the surface profile of these important sub- and near-surface biophysical processes and is, therefore, a potentially powerful tool for identifying pelagic foraging hotspots.

Composite front mapping (36) is a step forward in automated front detection via remote sensing, addressing the limitations of precursor methods. To date, the majority of studies including a measure of frontal activity have either identified fronts manually or used single-image edge detection (SIED; 37) on single-day (e.g. 38) or temporally averaged (e.g. 16) images. However, limitations of these methods reduce their utility. For example, using single-day imagery can result in sacrifice of tracking data owing to cloud cover. Furthermore, temporally averaged imagery masks spatiotemporal dynamics of fronts, which can be highly variable in shelf seas, giving only an estimated average position of a wandering feature. Using SST/chl-a gradients it is not possible to recognise contiguous curvilinear frontal features and, when using temporally averaged images, can result in erroneous frontal locations. Composite front mapping (36) addresses these limitations, enabling objective, automatic front detection over a sequence of images, removing cloud influence and allowing for the visualisation of frontal dynamics. In addition, high-resolution front metrics, such as the distance to the closest front or density of detected fronts, can be derived. These metrics facilitate objective quantification of the strength of predator-frontal associations and exploration of the effects of spatial scale, persistence, and magnitude of cross-frontal gradient, not always possible previously.

Here we use composite front mapping and high-resolution GPS tracking to investigate oceanographic drivers of habitat use in a piscivorous marine predator, the northern gannet *Morus bassanus* (hereafter, 'gannet'). Gannets are large, medium-ranging marine predators, which feed on

a wide-variety of piscivorous prey (7, 39-41). Foraging plasticity in gannets has been linked to oceanographic variability over a range of scales (40, 42-44). We here assess the influence of mesoscale frontal activity on gannet foraging behaviour, and evaluate the utility of composite front mapping for elucidating oceanographic controls of habitat selection. Moreover, we explicitly address the importance of frontal persistence by investigating gannets' behavioural responses to both contemporaneous and seasonally persistent thermal and chlorophyll fronts.

2.0 METHODS

2.1 Device deployment

Chick-rearing gannets (n=66) were tracked from a large breeding colony (~40,000 breeding pairs) on Grassholm, Wales, UK (51° 43' N, 05° 28' W) over two breeding seasons (n=17, Jul 2010; n=49, Jun-Jul 2011; Fig. 1). All birds were equipped with 30g GPS loggers (i-gotU; MobileAction Technology; http://www.i-gotu.com), TESA-taped to feathers on the centre of the back. Previous studies indicate these devices have no deleterious effects on foraging gannets (7). All birds were caught during changeover at the nest, to minimise time chicks spent alone and to ensure foraging trips began immediately following release. Handling time did not exceed 15 minutes. Devices were programmed to record location fixes at one- or two- minute intervals, and recovered after at least one complete foraging trip.

FIGURE 1 HERE

2.2 Behavioural classification

Area-Restricted Search (ARS) behaviour is characterised by low flight speed and frequent turning (45) and can thus be distinguished from direct and fast transit to and from the colony. Previous work has revealed that ARS is triggered by the detection and pursuit of prey in gannets (44). The pelagic prey field is patchy and hierarchically organised, with dense prey patches nested within broader-scale aggregation zones, and resultantly ARS is often observed at multiple nested scales (4, 6, 46, 47).

We used an approach based on residence time (RT; 48) to identify ARS bouts in all foraging tracks (adehabitatLT R package; 49). To avoid artificial inflation of residence times, we excluded tracking locations recorded during hours of darkness and all locations within a radius of 1km of the colony (because gannets do not forage here but do frequently rest on the water). We then interpolated each daylight movement bout to 60 second intervals and calculated RT at each of these locations, using three radii (1km, 5km, 10km; 2 hours allowed outside circle before re-entering) to detect the

scale at which birds performed ARS. These radii were chosen to cover the range of ARS observed previously in gannets (e.g. 44; average scale of search 9.1 ± 1.9km, with nested finer-scale search at 1.5 ± 0.8km). We used RT at each interpolated location to distinguish ARS from transit using an approach based on Lavielle segmentation (48) , using both the mean and variance of each series with an 'Lmin' value of 3 (minimum number of observations in each segment) and a 'Kmax' value of 10 (maximum number of segments in movement burst; Supp. Fig. 1). We classified segments as periods of ARS or transit using a custom-written R function that identifies each segment as either above or below a threshold of residence time (seconds), with thresholds specified as mean values across all trips at each radius, resulting in a binary response variable (i.e. ARS or transit) for each radius (Supp. Fig. 2). We then used these multi-radii ARS classifications in subsequent analysis, investigating levels of scale-dependence in the influence of fronts on habitat selection at meso- (10s – 100s kms) and submeso- scales (~1km).

2.3 Composite front mapping

Thermal composite front maps were created for the area enclosing accessible habitat (see 50; Fig. 2), using a radius of whole-dataset maximum displacement from colony (432km). Firstly, raw (level 0) Advanced Very High Resolution Radiometer (AVHRR) infrared data were converted to an index of Sea-Surface Temperature (SST; level 2). SST data were then mapped on to the United Kingdom Continental Shelf (UKCS) region in Mercator projection, with a spatial resolution of ~1.1km/pixel. Thermal fronts were detected in each scene using Single-Image Edge Detection (SIED; 37). Thresholds used for SIED front definition are often selected arbitrarily, and yet are central to findings. We therefore actively varied the threshold for thermal front definition, enabling us to objectively assess the effects on model predictions. To investigate the influence of the magnitude of cross-frontal temperature gradient, we created separate thermal composite sets using 0.4°C and 1.0°C thresholds. All fronts detected over 7-day windows were included in composite front maps, rolling by one day and covering the entire tracking duration. We also produced composite chlorophyll-a (hereafter; chl-*a*) front maps from MODIS data using a similar protocol. However we only used a single front detection threshold for chl-*a* owing to the log-space scale of chl-*a* imagery (0.06 log mg chl-a m^{-3}). Resultant composite maps (Fig. 2) quantify frontal activity using arbitrary units (fcomp; 36), which are a combination of thermal gradient, persistence (ratio of front observations to cloud-free views) and proximity of neighbouring fronts.

Composites were used to create a suite of metrics quantifying frontal activity designed for use with tracking data (Fig. 2). We simplified the composite maps to determine contiguous contours through

the strongest front observations, using a novel clustering algorithm (Miller, *unpubl. data*) which first involves smoothing the front map with a Gaussian filter of five pixels width. From these we generated smoothed rasters describing distance to the closest front and frontal density, for use with tracking data. **Frontal distance (fdist)** describes distance from any point to the closest simplified front (Fig. 3). **Frontal density (fdens)** quantifies the relative strength of detected fronts, spatially smoothed to give a continuous distribution of frontal activity (Fig. 3). We selected a smoothing parameter based on the level of detail in resultant products, choosing a value that did not oversmooth small-scale, ephemeral fronts. Thermal and chl-*a* front metrics were extracted for each location along each track using custom software. In addition, we extracted surface chl-*a* (mg m^{-3}; 7-day composite) for each location, as an indicator of levels of primary production in relation to frontal propagation.

Seasonal thermal front climatologies were also generated for each year (Jun-Aug; 2010-11), at 1.2km/pixel resolution. These **frequent front (ffreq)** maps (Fig. 4) identify seasonally persistent frontal zones by highlighting regions in which strong, persistent or frequently-occurring fronts manifest. We used a custom algorithm that estimates the percentage time in which a 'strong' front (here, $F_{comp} \geq 0.015$) is detected within each grid cell over a specified time period (51). This F_{comp} unit combines strength, persistence and proximity to other fronts (36), and this threshold is used to exclude numerous weak and variable fronts that could confuse the seasonal frequency. Seasonal chl-*a* (median) composites were created at the same temporal and spatial resolution, to highlight areas of enhanced productivity in relation to persistent frontal zones.

FIGURE 2 HERE

2.4 Modelling gannet foraging behaviour

2.4.1 Contemporaneous thermal and chlorophyll-a fronts

First, we tested the influence of contemporaneous thermal and chl-*a* fronts on the probability of observing ARS in gannets. Metrics describing frontal density (*fdens*), distance to closest simplified front (*fdist*), and chl-*a* concentration were extracted from rolling 7-day composites centred at the time of animal presence (Fig. 3). To account for the fact that gannet foraging range is influenced by intra-specific interactions and travelling costs (52), we also included distance to the colony of each GPS fix as a proportion of maximum displacement as a covariate in our models (50). All explanatory covariates were standardised before inclusion by subtracting the mean and dividing by the standard deviation (53). We checked for multi-colinearity using Generalised Variance Inflation Factors (GVIF)

and pairwise plots. Owing to observed colinearity, the *fdens* and *fdist* metrics were investigated using separate models for both thermal and chl-*a* fronts.

To account for strong intra-individual temporal autocorrelation, we used Generalised Estimating Equations (GEEs; 54), with each daylight movement bout as the blocking variable (see also 30, 55, 56). We constructed GEE-GAMs with a binomial error structure and logistic ('logit') link function ('geepack' and 'splines' R packages;57). Quasi-likelihood under the model independence criterion (QIC; 58) was used to select between a working independence correlation structure and an autoregressive, AR1, correlation structure.

An approximated version of the QIC (QICu; 58) was used to select the most parsimonious set of explanatory variables from *a priori* candidate models. In order to ascertain the most appropriate form of each explanatory covariate, we compared the QICu of models with each term in its linear form, and as a B-spline with 4 degrees of freedom and a knot positioned at the mean. QICu can be over-conservative (59), so we used repeated Wald's tests to determine significance of retained explanatory covariates.

Goodness-of-fit of final models was evaluated using a confusion matrix comparing binary predictions to observed incidence of ARS in the original dataset. The probability cut-off above which a prediction was classified as an ARS point was selected using a Receiver Operating Characteristic (ROC) curve (60). We computed the area under the ROC curve (AUC) as a further measure of model performance (closer to 1, better performance; 60). To obtain response curves, we predicted from the final model for each of the explanatory terms, holding all other terms constant. Terms retained by QICu model selection but found to be non-significant under more stringent Wald's tests were not removed from the model (55), and only significant relationships were plotted.

2.4.2 Seasonally persistent thermal and chlorophyll-a frontal zones

Second, we tested the influence of seasonally persistent thermal and chl-*a* frontal zones (Fig. 4) on gannet foraging habitat preference. As no intra-individual temporal autocorrelation existed in this time-aggregated dataset, we used a binomial Generalised Additive Model (GAM) with a logistic ('logit') link function to model presence/absence of ARS against front frequency for the 2011 breeding season ('mgcv' R package; 62). To achieve this, we created a grid at a matching spatial resolution to the seasonal frequent front maps (1.2km; 'raster' R package;61), and then determined presence/absence of ARS in each cell across all tracks. We were unable to do the same for 2010

because of low sample size. Environmental covariates were standardised before inclusion as explanatory terms, and multi-colinearity was checked using GVIF and pairwise plots. Co-linearity between the seasonal frequent front and chl-*a* metrics prevented simultaneous inclusion in the same model, so the terms were applied separately. An index of habitat accessibility, derived using the distance of each grid cell to the colony as a proportion of whole-dataset maximum displacement, was also included to control for greater accessibility of fronts close to the colony than in fringes of the foraging range (50).

In order to ascertain the best form for each explanatory covariate, we fitted separate models with both linear and smoothed forms of each term, visualised the shape of smoothers and determined the effect of the inclusion of each form on Akaike Information Criteria (AIC). Smoothers were only included in final models where deemed biologically reasonable. For example, although the smoothed forms of the front frequency metrics (mfreq; cfreq) were associated with lower AIC, linear forms were preferred following visualisation of the smoother, as a conservative approach to prevent over-fitting. Forwards and backwards step-wise model selection using AIC identified the final model, which was then checked for overdispersion. Model residuals were checked for spatial autocorrelation (53).

3.0 RESULTS

3.1 Gannet foraging trips

For the 66 birds tracked over the two breeding seasons, mean number of foraging trips was 3.8 ± 2.8 (range 1-12), with an average duration of 24.8 ± 22.7 hours (range 2 – 168 hours). The majority (76%) involved one or more nights spent away from the colony (mode 1; range 0-7). Maximum foraging range per trip ranged between 22.2 and 432.0 km from the colony, with an average of 178.3 ± 87.2 km. All foraging trips included at least one ARS zone.

3.2 Contemporaneous thermal and chl-a fronts

We found no evidence that gannet ARS was associated with contemporaneous thermal or chlorophyll-*a* fronts, even when varying the threshold used for thermal front definition and the radius used to define ARS through the residence time analysis. Although QICu model selection retained contemporaneous front metrics in some model runs (Supp. Table 1), post-hoc repeated Wald's tests confirmed that only distance to colony explained a significant proportion of deviance in each of these model runs (Supp. Fig. 3).

Model validation confirmed goodness of fit of final models. True positive rates of model predictions, obtained from confusion matrices, are given in Supplementary Table 1. ROC curves confirmed models performed acceptably well. High levels of temporal autocorrelation (within-block correlation, e.g. thermal 0.4°C threshold, 5km RT radius *fdens* = 0.97 ± 0.04) justified the use of GEEs. QIC comparison confirmed an AR1 autoregressive correlation structure as best fit for the data for all models.

FIGURE 3 HERE

TABLE 1 HERE

3.3 Seasonally persistent thermal and chl-a frontal zones

Seasonal thermal front frequency (mfreq; Fig. 4a) was retained by model selection ($\chi^2_1 = 322.5$, $p < 0.001$; Fig. 4c; Table 2), with the probability of ARS twice as likely at high front frequency compared with low (Fig. 4c). A smoothed relationship with habitat accessibility was also retained (HabAccess, df = 8, $p < 0.001$; Supp. Fig. 4; Supp. Table 2). The model explained 33% of deviance and was not over-dispersed (dispersion statistic = 0.83). Colinearity between thermal front frequency (Fig. 4a) and seasonal average surface chl-*a* concentration also confirms that persistent frontal zones are areas of increased primary productivity.

The seasonal front frequency index for chlorophyll-*a* fronts (cfreq; Fig. 4b) was also significant in explaining the spatial distribution of ARS over the breeding season ($\chi^2_1 = 3108$, $p < 0.001$; Fig. 4d; Supp. Table 2), alongside smoothed habitat accessibility ($p < 0.001$; Supp. Fig. 4; Supp. Table 2). The model explained 32% of deviance and was not over-dispersed (dispersion statistic = 0.88).

FIGURE 4 HERE

TABLE 2 HERE

4.0 DISCUSSION

Combining composite front mapping with high-resolution GPS tracking, this work has revealed that gannets are more likely to perform ARS within persistent mesoscale frontal zones than in other regions of accessible habitat. This is of particular significance since it not only shows that mesoscale

fronts influence habitat selection, but also that remote sensing methods are able to identify features relevant to piscivorous marine vertebrates. Moreover, this work also illustrates that temporal scale is crucial - gannets do not tend to forage at ephemeral contemporaneous fronts, instead relying on spatially predictable, seasonally persistent zones of frequent frontal activity.

4.1. Mesoscale fronts and top predator foraging

Predictability of foraging grounds is known to strongly influence seabird habitat selection, and may partially explain our observed differences in front use (5). Many marine predators, including seabirds, are known to repeatedly return to the same foraging areas (5, 7, 40, 63), which is generally attributed to the presence of oceanographic features that are predictable in time and space. In the Celtic Sea, these predictable foraging areas are associated with persistent mesoscale thermal and chl-a frontal zones. The ultimate mechanisms by which these features are located are not known, although a combination of memory effects, local enhancement and colonies acting as information centres strongly influence observed foraging distributions in this species (52). Proximate environmental factors enabling front detection include visual cues associated with the accumulation of foam and detritus (18, 22); flow patterns, including surface convergence (22) and cross-frontal jets (34), or olfactory cues such as dimethyl sulphide (DMS; 65). Persistent fronts probably produce a stronger surface signal than ephemeral features, increasing detectability.

Alongside greater spatial predictability and detectability, persistent mesoscale frontal zones also present more attractive foraging opportunities than ephemeral fronts. The bio-aggregative effects of fronts vary with temporal persistence, spatial scale, temperature gradient, strength of convergent flow and the properties of surrounding water masses, influencing their attractiveness as top predator foraging habitat. Ephemeral, weak or spatially-variable features may not propagate for sufficient time for biological enhancement to attract mid-trophic level consumers such as pelagic fish. In contrast, persistent frontal zones are associated with sustained primary productivity, and therefore more likely to attract the pelagic fish preyed upon by seabirds and other large marine vertebrates.

In contrast to our findings, the closely-related Cape gannet *Morus capensis* is known to initiate ARS-type behaviours at contemporaneous chl-*a* fronts in the Benguela (16). The reasons for these differences are not clear, but are likely to be related to differences in regional oceanography. Small-scale, superficial and ephemeral thermal fronts develop frequently in the Celtic Sea through tidal effects and cycles of stratification and mixing (30), but are not always associated with chl-*a*

enrichment (28, 67). In contrast, the Benguela is a major upwelling zone, in which upwelling filaments, eddies and strong vertically-structured fronts manifest. Although varying in seasonal intensity and position, upwelling fronts in the Benguela are less spatiotemporally variable than tidal fronts in the Celtic Sea over time scales of days to weeks, and so may be more predictable foraging habitats for seabirds using learning and memory effects to locate prey (5). In addition, Cape gannets prey upon the mega-abundant sardines and anchovies in the Benguela (16). These fish are zooplanktivorous, and therefore more closely tied to oceanographic drivers, than the piscivorous fish (e.g mackerel *Scomber scombrus*, garfish *Belone belone*) targeted by northern gannets in the Celtic Sea (39). Differences in the biophysical nature of fronts encountered by prospecting birds within these two contrasting oceanographic regions elicit different responses from these two closely-related species. These differences highlight the need for a comprehensive understanding of regional oceanography when investigating the drivers of habitat selection for mobile marine vertebrates.

Gannets in the Celtic Sea also forage extensively at fishing vessels (39,67, 68), so fisheries activity could also influence the association between fronts and gannets reported here. Nevertheless, we believe that gannets are using persistent frontal zones as natural foraging sites for the following reasons. First, gannets switch between natural foraging and scavenging both within and among trips (39) and must therefore rely upon both natural foraging and scavenging. Second, analysis of a subset of ten gannets in 2011 equipped with bird-borne cameras enabled us to determine frontal activity in the presence and absence of fishing vessels. This revealed little difference between vessel-associated ARS instances, those associated with natural foraging and conditions experienced during transit (see Supp. Fig. 5). Third, the majority of trawlers that gannets follow in the Celtic Sea target demersal fish (39), which would not benefit from fishing in frontal regions.

4.2. Composite front mapping and marine predator foraging habitat

We have used multi-threshold objective front detection to produce composite thermal and chl-*a* front maps at 1km resolution, enabling us to quantify the influence of fronts on foraging habitat selection in gannets. Using this technique has negated sacrifice of tracking data as a result of cloud cover. Furthermore, using both temporally-matched 7-day front composites and seasonal front indices has revealed the importance of considering frontal persistence. However, composite front mapping does have limitations with implications for defining marine predator foraging habitats. In common with all remotely-sensed products, only the surface signature of complex three-dimensional oceanographic processes is visible. Resolution of imagery is also limited by sensor technology, restricting our ability to detect sub-mesoscale (~1km) nearshore tidal fronts, potentially

significant features in shallow shelf-seas (69). Furthermore, using 7-day composites could mask real-time, fine-scale responses to environmental cues. Recent in-situ studies of fine-scale oceanographic influence on seabird foraging have identified tidal state, thermal stratification index, and sub-surface processes such as tidal shear at the thermocline, as significant influences on foraging decisions (55, 70). These fine-scale processes cannot be detected using contemporary remote sensing techniques. However, remote sensing can provide oceanographic context for the movements of known individuals over broader spatial and temporal scales, generating insights of direct relevance to predictive habitat modelling (71) and marine spatial planning (51).

5.0 CONCLUSIONS

We here present proof of concept that objective front detection and composite front mapping (36) can enhance the value of predator tracking data for habitat utilisation studies and improve understanding of mechanistic links between oceanographic processes and marine vertebrate foraging ecology. Novel front metrics used here provide capacity for quantification of the strength of predator-frontal relationships without neglecting the significance of frontal strength, persistence and scale. We have found that persistent frontal zones are preferred foraging habitats of a piscivorous top predator inhabiting a shallow shelf sea, but that responses to contemporaneous thermal and chl-*a* fronts vary. Persistent frontal zones are likely to represent predictably profitable foraging grounds for predators that use learning and memory effects to locate prey. In contrast, ephemeral, superficial fronts may not present attractive foraging opportunities owing to the spatial and temporal lags inherent in bio-aggregation. Furthermore, persistent fronts are more likely to generate environmental cues discernable to overflying gannets, and so more likely to become sites of local enhancement for these network foragers. These findings provide direct evidence that the temporal persistence of mesoscale fronts fundamentally regulates their value as foraging habitats for marine predators.

Although considerable advances have been made in our understanding of the oceanographic drivers of marine vertebrate habitat use in recent years, questions remain regarding the strength and nature of predator-frontal associations. Our methods have considerable scope for further application, providing opportunity for environmental contextualisation of habitat use, across foraging guild, trophic level and oceanographic region. Composite front mapping allows us to objectively detect thermal and chl-*a* fronts anywhere in the global ocean at high resolution, which could help in locating critical at-sea habitats for mobile marine vertebrates, many of which are of immediate conservation concern (72, 73). Furthermore, continuous near-real time global satellite

393 monitoring of environmental conditions, together with animal tracking and biologging, provides
394 capacity for investigation of responses to global change.

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FIGURE AND TABLE CAPTIONS

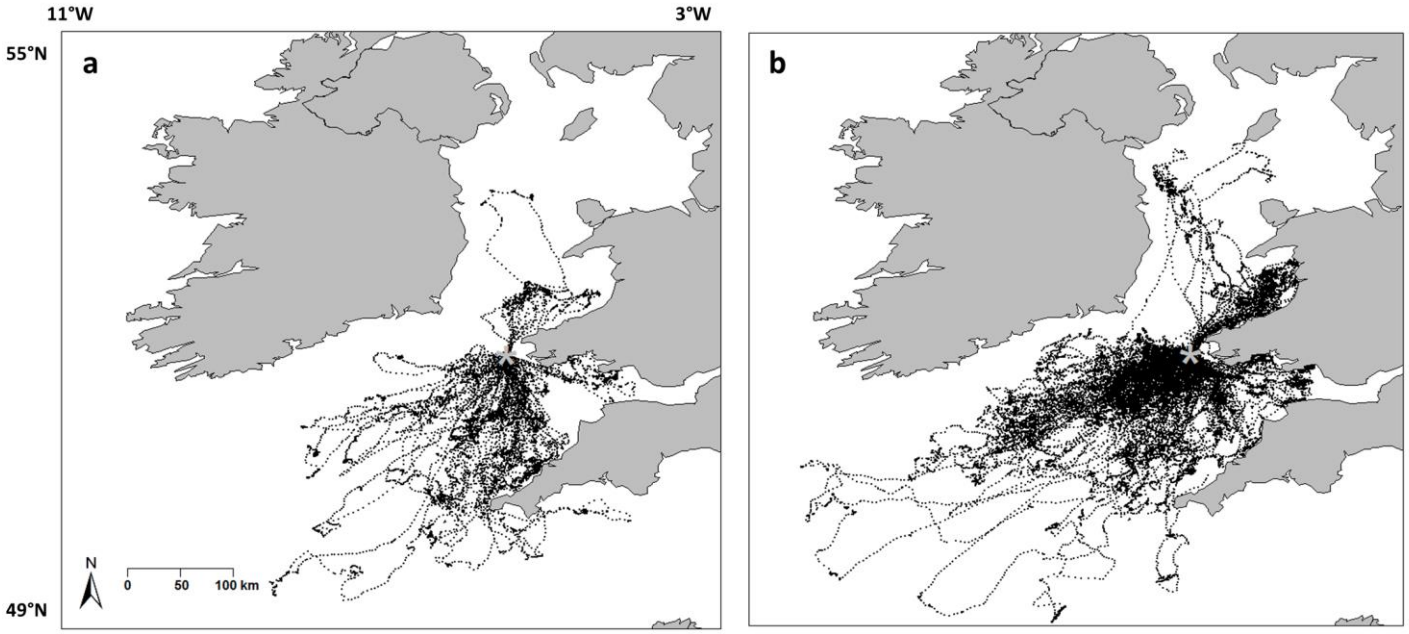
FIGURES

Fig. 1. GPS tracking. All foraging trips of birds GPS-tracked during 2010 (a, n=17) and 2011 breeding seasons (b, n=49). Grassholm colony shown as grey star.

Fig. 2. Composite front mapping. Preparation of thermal composite front maps, and front metrics rasters, from Advanced Very High Resolution Radiometer (AVHRR) sea surface temperature (SST) images. Several satellite passes per day are mapped to the study area (e.g. a,b). Single-Image Edge Detection (SIED) detects fronts in each of these swaths, using a given threshold for front definition, here 0.4°C (c,d). Composite front maps are created from all fronts detected in imagery over a 7-day period (e; Miller, 2009), and spatially smoothed to generate a frontal density (*fdens*) metric (f) or simplified to generate a distance to closest front (*fdist*) metric (g).

Fig. 3. Contemporaneous front metrics time-matched to gannet foraging trip. Distance to closest thermal front (*fdist*; 0.4°C threshold, a), thermal front density (*fdens*; 0.4°C threshold, b), distance to closest chl-*a* front (c) and chl-*a* front density (d) shown for one complete foraging trip (23 July 2011). Points designated as ARS by residence time analysis (5km radius) shown as white track sections, and transit as black track sections. Colony location shown as black star.

Fig. 4. Modelling the effects of persistent frontal zones (thermal, chl-*a*) on the spatial distribution of gannet area-restricted search behaviour. Seasonally persistent (Jun-Aug 2011) thermal frontal zones (a) and chl-*a* frontal zones (b), identified using frequent front (mfreq; cfreq) metrics. Model predictions for effects of seasonal thermal front frequency (c; model 4.1) and seasonal chl-*a* front frequency (d; model 4.2). Gannets are more likely to perform ARS behaviours within regions of frequent frontal activity.



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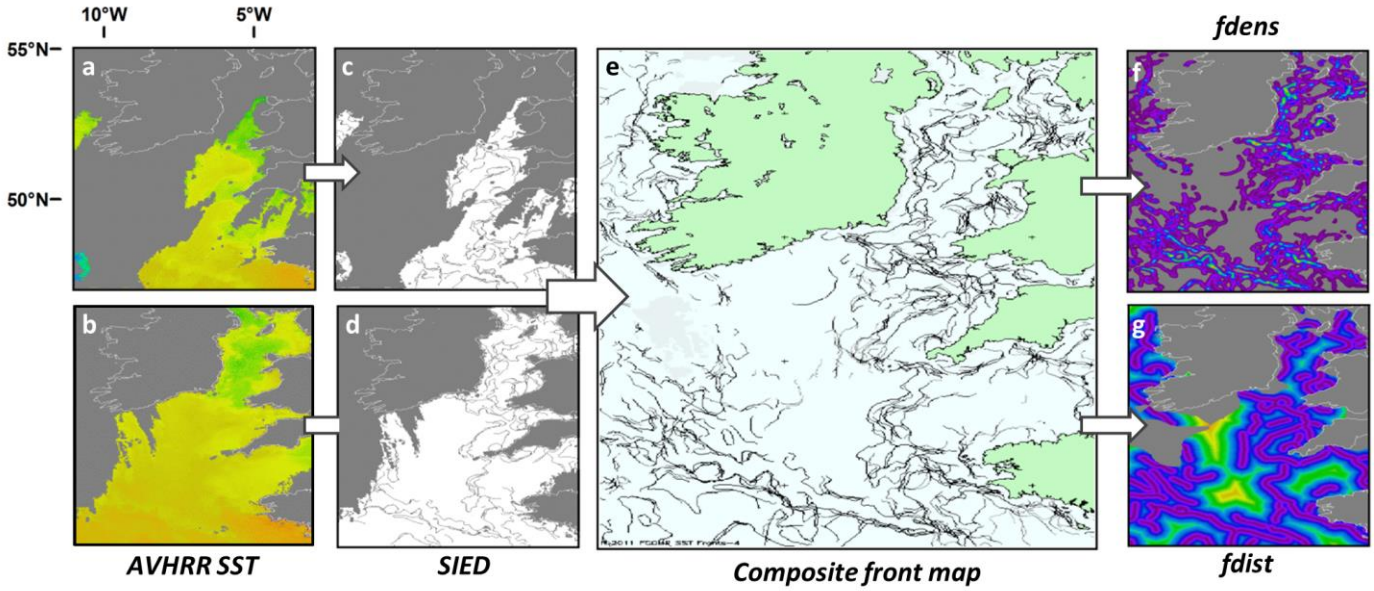

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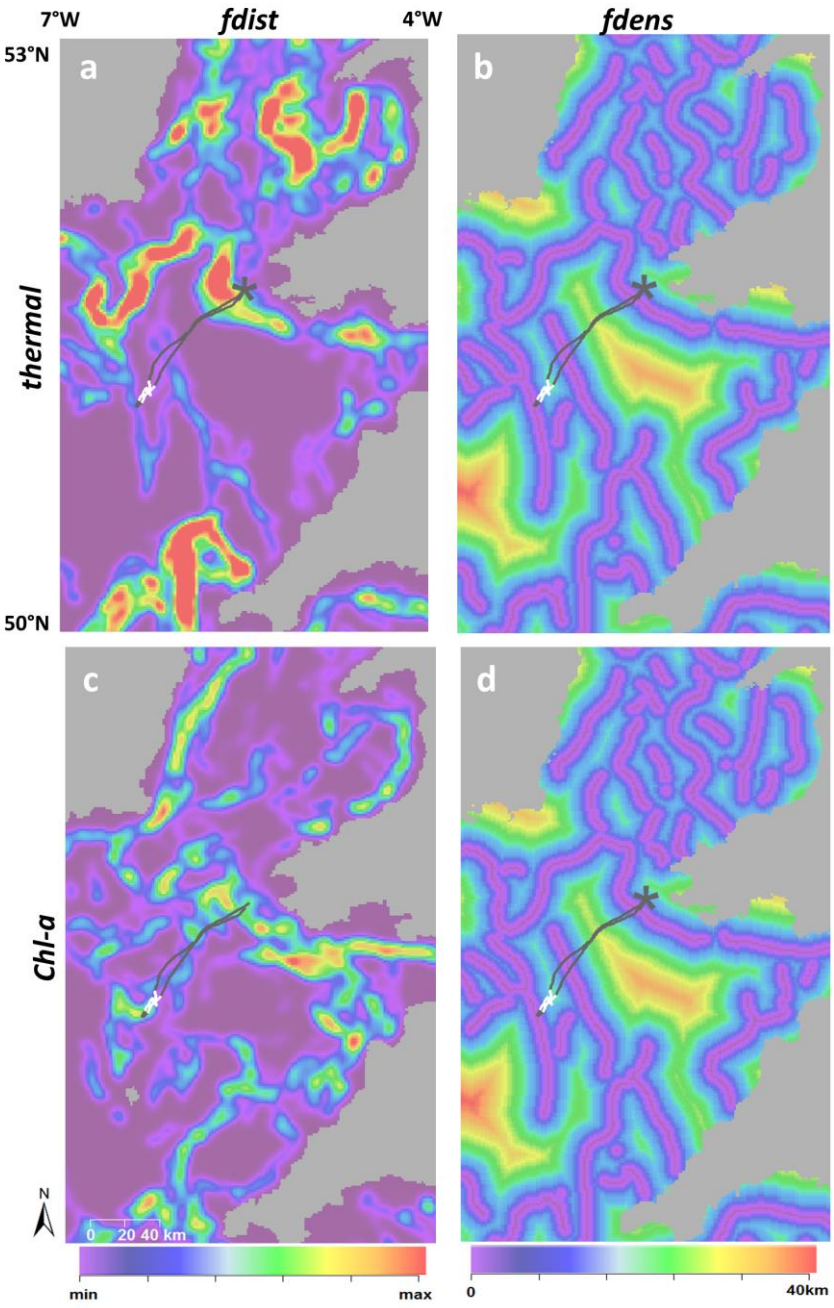

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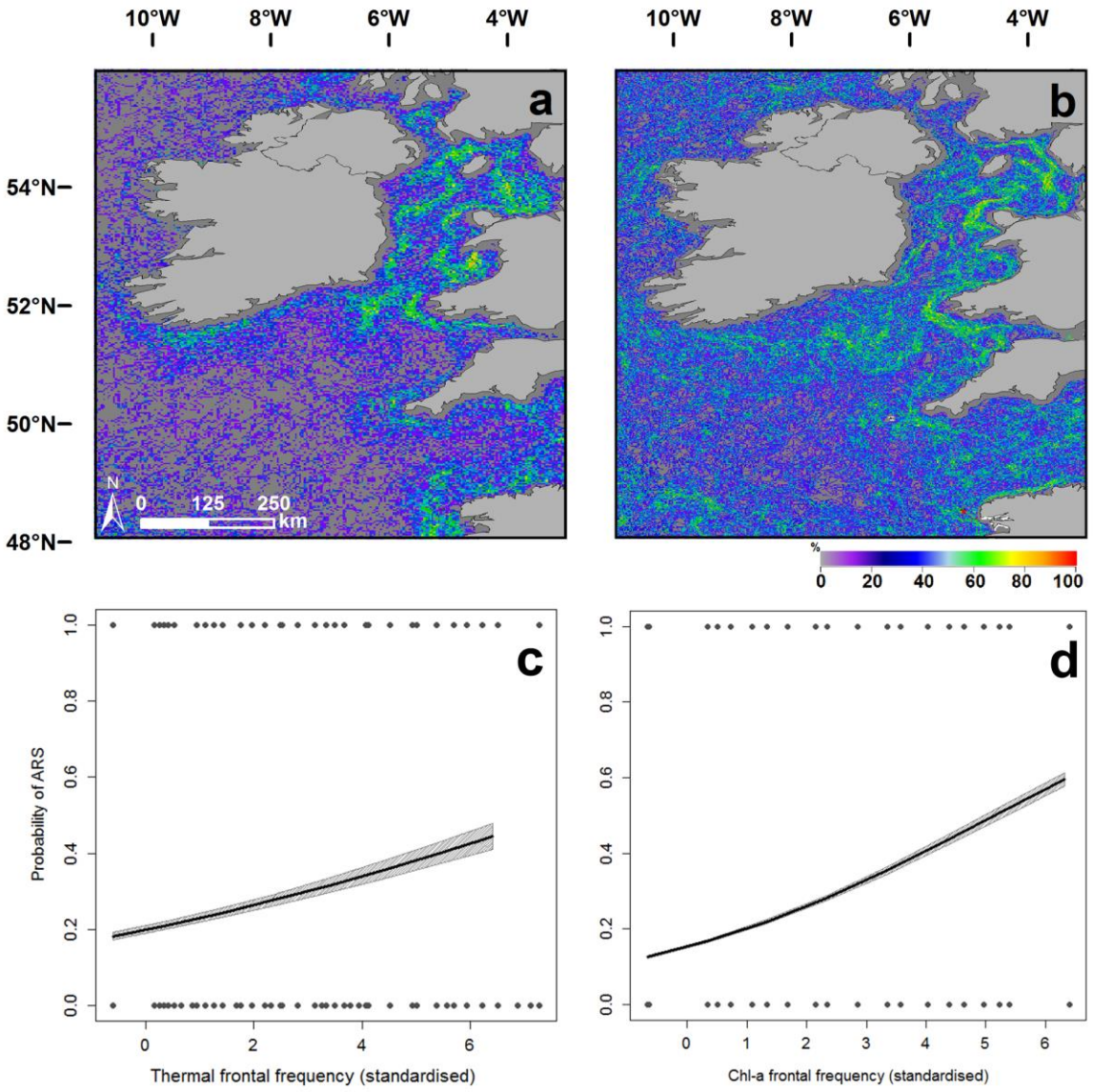

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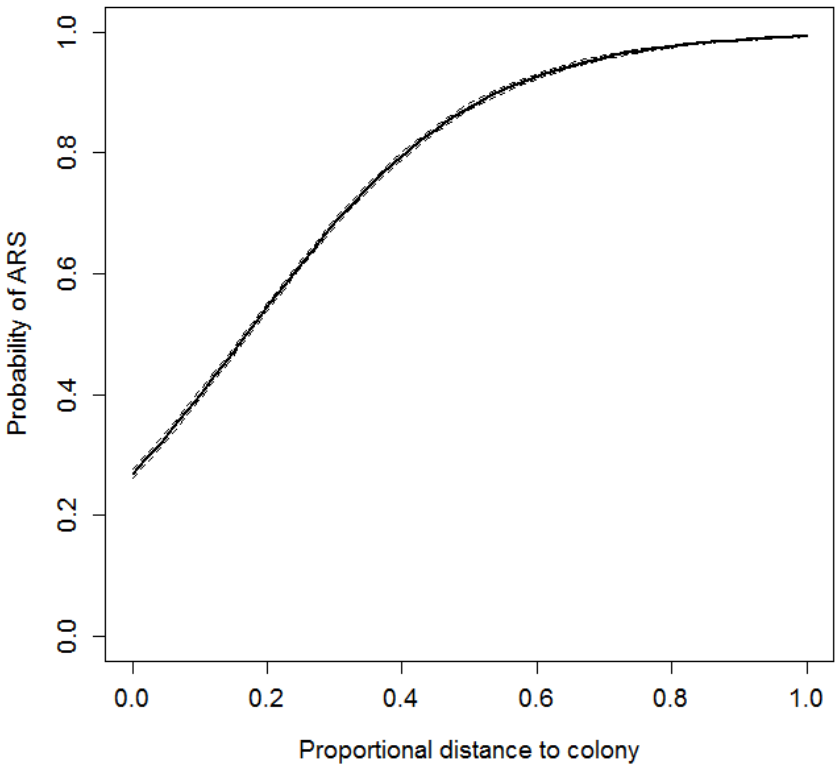
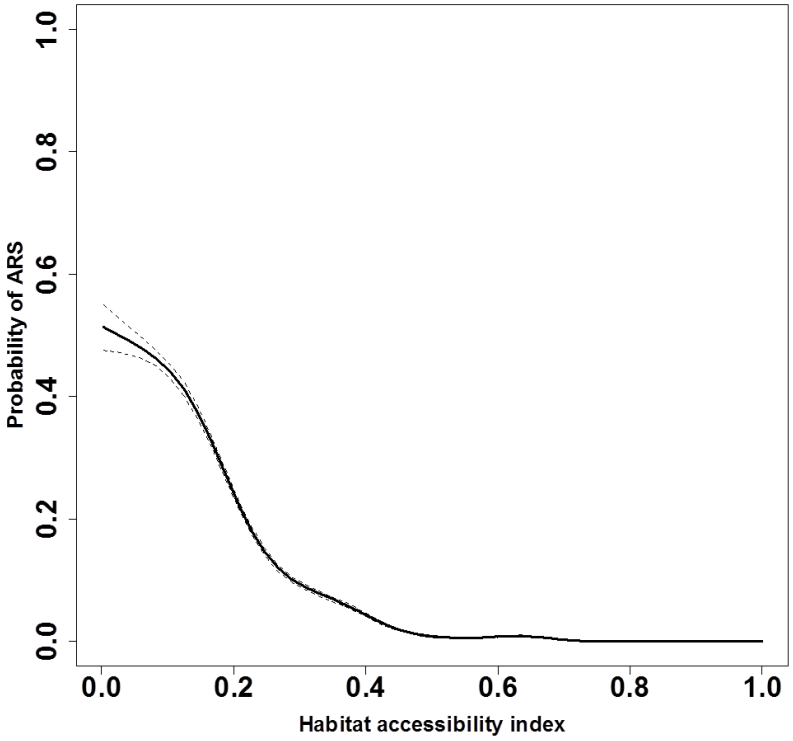


Supplementary Fig. 1. Modelling the effects of contemporaneous thermal fronts on gannet area-restricted search behaviour, using GEE-GAMs. Contemporaneous front GEE-GAM results (model 1.1.2), showing predicted influence of proportional distance to colony. All other explanatory terms, including thermal and chlorophyll front metrics, were not statistically significant, so are not shown here. The higher probability of ARS further from the colony represents the tendency for ARS zones to take place at the distal point of foraging points, as ARS 0/1 along each track was used as the response variable. Confidence Intervals represented by dashed lines, here close to the main effect line, owing to small standard error on this coefficient estimate in model output.



Supplementary Fig. 2. Modelling the effects of persistent frontal zones (thermal, chl-a) on the spatial distribution of gannet area-restricted search behaviour. Habitat Accessibility index fitted to binomial GAM investigating the influence of persistent frontal zones on gannet ARS behaviour (models 4.1, 4.2) as a control for availability of fronts as a function of distance from colony.