

## Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic

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### Summary

1. Understanding the mechanisms that link oceanographic processes and marine vertebrate space use is critical to our knowledge of marine ecosystem functioning, and for effective management of populations of conservation concern.

2. The basking shark *Cetorhinus maximus* has been observed in association with oceanographic fronts – physical interfaces at the transitions between water masses – exploiting foraging opportunities resulting from zooplankton aggregation. However, the scale, significance and variability of these associations have not previously been established.

3. Here, we quantify the influence of thermal and chlorophyll-*a* fronts on basking shark habitat use in the north-east Atlantic. We use animal-mounted archival tracking together with composite front mapping via Earth Observation (EO) remote sensing to provide an oceanographic context to shark movements.

4. We investigate levels of association with fronts occurring over two spatio-temporal scales, (i) broad-scale, seasonally persistent frontal zones and (ii) contemporaneous thermal and chl-*a* fronts. Using random walk simulations and logistic regression within an iterative generalized linear mixed modelling (GLMM) framework, we find that seasonal front frequency is a significant predictor of shark presence.

5. Oceanographic metrics time-matched to shark tracks indicate that sharks show a preference for productive regions and associate with contemporaneous thermal and chl-*a* fronts more frequently than could be expected at random. Moreover, we highlight the importance of front persistence and cross-frontal temperature step, which appear to interact to affect the degree of prey aggregation along thermal fronts in this shelf-sea system.

6. Our findings confirm that surface frontal activity is a predictor of basking shark presence in the north-east Atlantic, both over seasonal timescales and in near real-time. These insights have clear implications for understanding the preferred habitats of basking sharks in the context of anthropogenic threat management and marine spatial planning in the region.

**Key-words:** animal tracking, biologging, front mapping, habitat preference, habitat use, marine megavertebrate, marine vertebrate, remote sensing

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### Introduction

Understanding the ways in which large marine vertebrates optimize foraging efficiency in heterogeneous and dynamic pelagic environments has become a central issue in marine ecology. These animals are often highly mobile, moving over immense spatial scales in order to find suitable

habitats in which to forage and reproduce. Moreover, zooplanktivorous megavertebrates such as the basking shark, *Cetorhinus maximus*; whale shark, *Rhincodon typus*; leatherback turtle, *Dermochelys coriacea*; and manta ray, *Manta birostris* exist on an energetic 'knife-edge', and so must maximize prey encounter rates in patchy pelagic prey seascapes in order to survive (Sims 1999, 2008; Hays *et al.* 2006; Stevens 2007; Fossette *et al.* 2010).

Underlying movement patterns that enhance foraging optimality, such as behaviours approximating theoretically optimal Lévy walks, have been identified in a variety of marine taxa (Viswanathan *et al.* 1999; Sims *et al.* 2008; Humphries *et al.* 2012) and linked to oceanographic context (Hays *et al.* 2006; Humphries *et al.* 2010) and prey fields (Sims *et al.* 2012). Biophysical habitat characteristics, including primary productivity and convergent front propagation, have been shown to influence behavioural switches between Lévy behaviour and Brownian movements in several species, including the basking shark (Humphries *et al.* 2010). Such behavioural switches indicate the concentration of area-restricted search (ARS), a proxy for foraging effort, in productive waters (Humphries *et al.* 2012). Broad-scale movements have also been linked to climatic influence over thermal resources, and finer-scale habitat use closely coupled with prey availability (Cotton *et al.* 2005; Siders *et al.* 2013; Curtis *et al.* 2014), indicating that bottom-up forcing and the propagation of oceanographic features that aggregate prey are likely to mediate foraging behaviour over a continuum of spatial scales.

A diverse range of large marine vertebrates have been shown to associate with mesoscale (10 s–100 s km) and submesoscale (*c.* 1 km) oceanographic features such as fronts, eddies and seamounts as foraging habitats, in contrasting ocean domains (Morato *et al.* 2010; Godø *et al.* 2012; Scales *et al.* 2014b). Here, we focus on mesoscale fronts – physical interfaces at the transitions between water masses that differ in temperature, salinity, density, turbidity or productivity (Belkin, Cornillon & Sherman 2009) – as features of potential significance to the basking shark in seasonally stratified shelf seas in the north-east Atlantic.

Understanding the role of oceanographic processes as drivers of marine vertebrate habitat utilization is fundamental to our knowledge of pelagic ecosystem functioning and pivotal in identifying important habitats for species of conservation concern. Basking shark populations in the north-east Atlantic are still recovering from the effects of historical overexploitation (Southall *et al.* 2006), and the species is currently classified as *vulnerable* globally and *endangered* in the north-east Atlantic by the IUCN Red List of Threatened Species (Fowler 2005). A better understanding of the drivers of habitat utilization is valuable for the management of populations of these enigmatic marine vertebrates, and indeed for marine vertebrates more generally. An ability to predict the locations of important habitats has relevance for the design of marine protected area (MPA) networks and marine spatial planning (Miller & Christodoulou 2014; Paxton, Scott-Hayward & Rexstad

2014; Scales *et al.* 2014b) and could inform projections of habitat shifts occurring in the wake of future climate change.

Seasonal basking shark aggregations occur in coastal regions of Great Britain and Ireland from May to October each year, when they can be observed surface-feeding on dense zooplankton patches (Sims, Fox & Merrett 1997; Sims & Merrett 1997). Although sharks are generally present in shelf and shelf-edge waters year-round in this region (Sims *et al.* 2003), they also spend protracted periods in the open ocean and are rarely sighted at the surface at other times of year. Distinct seasonal sightings 'hotspots' are apparent off the south-west of England, the Isle of Man, western Scotland and in Irish waters (Berrow & Heardman 1994; Southall *et al.* 2005; Leeney *et al.* 2012; Witt *et al.* 2012).

Associations between basking sharks and mesoscale thermal fronts have been observed repeatedly in the region, with sharks using front-associated habitat for both foraging (Sims & Quayle 1998; Priede & Miller 2009) and social interaction (Sims *et al.* 2000). Biophysical coupling along fronts is known to lead to the proliferation and aggregation of zooplankton (Le Fevre 1986; Franks 1992b; Genin *et al.* 2005), creating potentially profitable foraging opportunities for higher trophic-level organisms (Belkin *et al.* 2014; Scales *et al.* 2014b). Tidally mediated thermal fronts in seasonally stratified shelf seas can be highly productive (Pingree *et al.* 1975; Pingree & Griffiths 1978) and are known to be features around which the basking shark exploits foraging opportunities resulting from aggregation of its preferred *Calanus* prey (Sims, Fox & Merrett 1997; Sims & Merrett 1997; Sims & Quayle 1998).

Although broad-scale climatic drivers of basking shark abundance (e.g. North Atlantic Oscillation, NAO; Cotton *et al.* 2005) and the finer-scale influence of prey dynamics on habitat selection (Continuous Plankton Recorder, CPR; Sims *et al.* 2006) have been investigated in some detail, associations between sharks and frontal activity in the region have been described (e.g. Sims *et al.* 2003, 2006; Sims 2008) but not yet adequately quantified. A recent study in the north-western Atlantic linked the movements of sharks tracked using biotelemetry over timescales of days to weeks with remotely sensed oceanographic data, finding significant associations with sharp surface gradients in temperature and productivity in Cape Cod Bay during late summer (Curtis *et al.* 2014). These findings provided valuable insight into preferred oceanographic conditions, and the study represented a methodological forward step in quantitative investigation of habitat selection. However, the spatial resolution (0.05° pixel size) and temporal averaging (monthly composites) of remotely sensed imagery and the use of the gradient method to identify fronts restricted the authors' ability to define mesoscale features accurately. Moreover, the latter study used nonparametric testing to compare oceanographic conditions encountered by tracked sharks to those encountered by 250 random walk simulations. This approach to investigating habitat

preference is limited in its ability to quantify the influence of mesoscale oceanographic conditions.

Here, we use satellite-linked archival tracking to investigate movements of individual sharks through their natural environment over timescales of weeks to months, alongside high-resolution composite front mapping (*c.* 1 km pixel size; 7-day composites; Miller 2009) to characterize oceanographic conditions encountered. We test the hypothesis that surface frontal activity is a predictor of habitat preference for these planktivorous megavertebrates, and use a robust mixed modelling procedure to quantify associations occurring over two spatio-temporal scales: (i) seasonal associations with regions of frequent frontal activity, and (ii) near real-time associations with contemporaneous thermal and chlorophyll-*a* (chl-*a*) fronts. We aim to clarify factors affecting the degree of association between sharks and fronts through explicitly investigating the influence of cross-frontal temperature change and front persistence. In this way, we highlight the key biophysical characteristics of fronts that attract basking sharks, improving understanding of the foraging ecology of the species and building capacity for identification of potentially important habitats.

## Materials and methods

### SATELLITE-LINKED ARCHIVAL TRACKING

Satellite-linked pop-up archival transmitting (PAT) tags (Wildlife Computers, Redmond, WA, USA) were deployed on foraging sharks ( $n = 21$ ) off north-west Scotland and south-west England between May and August in 2001 and 2002. A detailed description of tag deployment and tracking data preparation protocols can be found in Sims *et al.* (2006). Briefly, PAT tags were attached to basking sharks by first approaching them from behind in a small vessel. Using a modified speargun harpoon, tags were placed at the base of the first dorsal fin and held in position by a small stainless steel T-bar dart with a monofilament tether connected to the tag (Sims *et al.* 2003, 2006). Tagging was conducted under licences from the UK Home Office, English Nature and Scottish Natural Heritage. Shark locations during the period of tag attachment were derived using light-based geolocation (GLS), corrected for sea-surface temperature (SST), with a calculated error radius of  $75.5 \pm 54.5$  km (Sims *et al.* 2006). In order to account for this spatial uncertainty, we resampled possible locations ( $n = 10$  per GLS-derived location) from within the mean radius of error (Fig. 1). Resampled presence positions falling on land were

discarded and replaced. We also resampled presence positions ( $n = 10$ ) in the initial (vessel dGPS, error radius  $< 5$  m) and final (Argos pop-up location, error radius  $< 1$  km) locations per track, for equal weighting of all presence positions. All locations derived from this combined data set were treated as near-surface presence positions in further analyses.

### RANDOM WALK SIMULATIONS

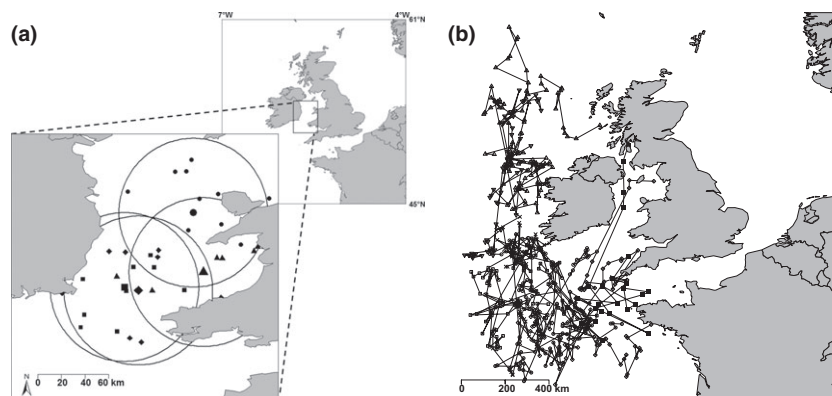
The use of presence-only, serially autocorrelated tracking data to infer habitat preference has inherent complications (Aarts *et al.* 2008; Warton & Aarts 2013). In order to account for regions of habitat accessible to, but not actively utilized by, tracked sharks, we used a randomization procedure (cf. Heithaus *et al.* 2006; Sims *et al.* 2006) to generate correlated random walk simulations ( $n = 1000$  per shark, total = 7000; ADEHABITATLT package for R; Calenge 2006). Simulated tracks were generated per shark such that the total number of locations equalled the original track length, and step lengths and turning angles were derived from distributions in each original track. Simulations were permitted to approach, but not cross, land, were time-matched to original tracks and were constrained within a region defined by the bounding box surrounding all locations obtained across all individuals (Fig. 1;  $45^\circ$  to  $61^\circ$  N,  $-15^\circ$  to  $6^\circ$  W; hereafter 'study area'). This study area includes the UK and Irish continental shelf region, and the shelf-break system (Fig. 2). Locations derived from this simulated data set were treated as pseudo-absences for statistical analysis.

### ENVIRONMENTAL DATA

Composite front maps (7-day, rolling by 1 day; Miller 2009) were prepared for the study area using SST data obtained via the Advanced Very-High Resolution Radiometer (AVHRR) sensor and ocean colour data obtained via the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS; Local Area Coverage, LAC), mapped to the study area at 1.1 km resolution using Mercator projection.

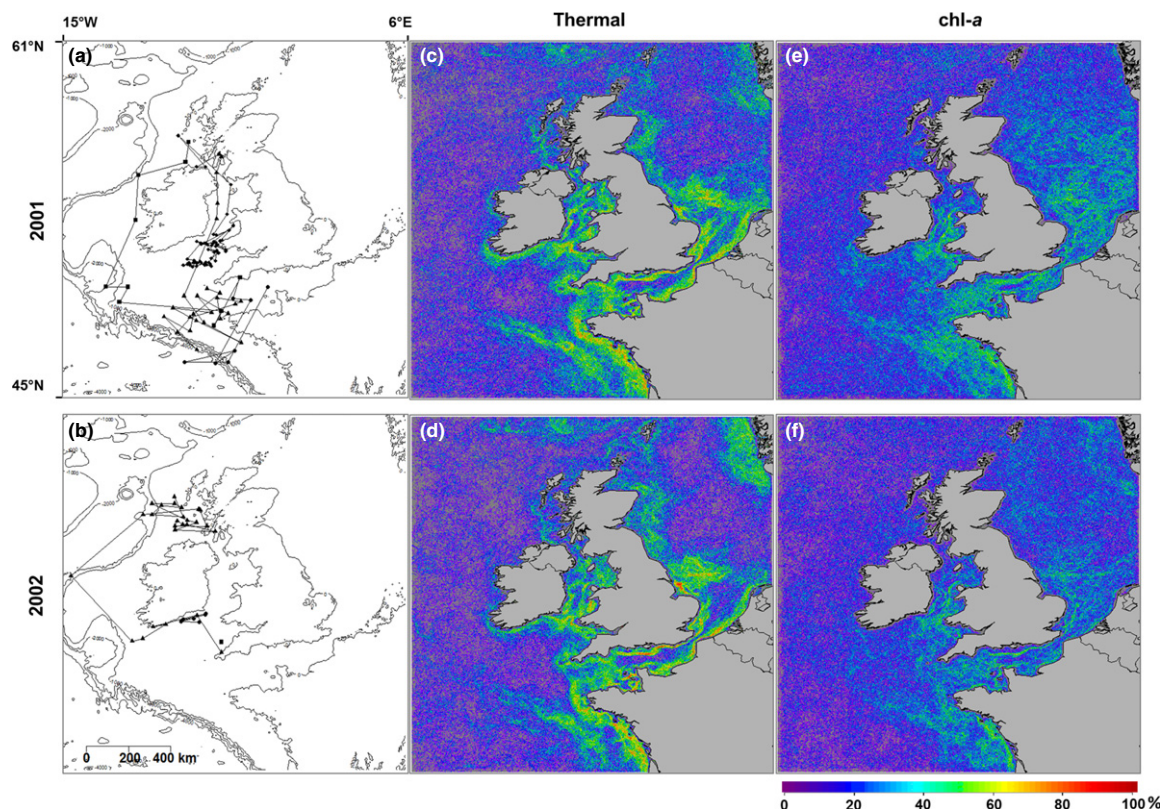
Seasonal front frequency maps quantifying the percentage time in which a front was detected in each pixel of the study area, as a ratio of positive detections to the number of cloud-free observations, were generated for each tracking year (Miller & Christodoulou 2014). As  $> 95\%$  of all tracking locations were obtained during the main UK basking shark sightings season (May–October), we used 7-day composite front maps from this period of each year (2001, 2002) to generate the front frequency data sets (thermal front detection threshold =  $0.4^\circ\text{C}$ ; chl-*a* min. front detection threshold =  $0.06\text{ mg m}^{-3}$ ). We also generated seasonal front frequency maps for the preceding year, to assess the influence of the previous year's conditions on habitat selection (Fig. 2).

Contemporaneous front metrics (front distance *fdist*, front gradient density *gdens*, front persistence *pfront*) were generated from



**Fig. 1.** Derivation of presence/pseudo-absence data set from tracking data. (a) Example of resampling of possible presence locations from within calculated error radius of each geolocation-derived tracking location. (b) Example random walks (10 shown from  $n = 1000$ ), used to derive pseudo-absences for each shark. Geolocation-derived track as bold line.





**Fig. 2.** Associations with broad-scale, seasonally persistent frontal zones. (a), (b) Shark tracking locations obtained from satellite-linked pop-up archival tags, with different icons identifying individual sharks overlaid over bathymetry contours of the study area, derived from the General Bathymetric Chart of the Oceans (GEBCO, 30 arc-second resolution). (c), (d) Seasonal thermal front frequency for the main UK basking shark sightings season (May–October) of each year at 1.1 km resolution (0.4 °C front detection threshold). (e), (f) Seasonal chlorophyll-*a* front frequency for the same period of each year (0.06 mg m<sup>-3</sup> min. front detection threshold).

composite front maps and time-matched to shark tracks (7-day, rolling by 1 day). Front distance (*fdist*) quantifies the distance from any location in the study area to the closest simplified front, using a custom simplification algorithm (P. I. Miller, unpubl. data). Front gradient density (*gdens*) is the result of applying a Gaussian smoothing filter ( $\sigma = 5$  pixels) to a map of the mean gradient magnitude values. It is designed to provide a local neighbourhood average of frontal gradient, avoiding the discrete nature of individual detected front contours. Front persistence (*pf*) is the fraction of cloud-free observations of a pixel for which a front is detected. Again, a Gaussian filter ( $\sigma = 5$  pixels) was applied, to provide a local neighbourhood average of frontal persistence.

Thresholds for front detection (Single-Image Edge Detection, SIED; Cayula & Cornillon 1992) are often chosen arbitrarily, yet the magnitude of cross-frontal temperature change is likely to influence associations between marine vertebrates and fronts (Etnoyer *et al.* 2006). We therefore systematically varied the SIED threshold used in the preparation of thermal composite front maps, from 0.2 °C (minimum detectable owing to SST scaling in original imagery) to 1.0 °C, generating a set of time-matched front metrics at each threshold. Values were obtained for each of these metrics, plus SST and chl-*a* with no front detection, for each location of the full data set (presence, resampled presence, pseudo-absence), and used as predictor variables in subsequent statistical modelling.

#### STATISTICAL ANALYSIS

We carried out a use-availability analysis over two spatiotemporal scales: (i) seasonal associations with zones of frequent frontal activity and (ii) near real-time associations with contemporaneous

mesoscale thermal and chl-*a* fronts. We used logistic regression within a generalized linear mixed modelling framework (GLMM, LME4 package for R; Bates *et al.* 2014) to obtain estimates of the influence of each of the predictor variables on the probability of observing a presence (individual as random effect; binary presence/pseudo-absence response; binomial errors with logistic link function). Owing to serial autocorrelation in both tracking data and simulated tracks, which violates the assumption of independence essential to the use of GLMM, we used a nonparametric bootstrapping regime to iteratively resample both the presence and the pseudo-absence data sets for each model fit (Scales *et al.* 2015). A total of 1000 presence and 1000 pseudo-absence locations, weighted as per the proportion of the complete tracking data set contributed by each individual, were subsampled from each individual data set for each iteration. Resultant presence/pseudo-absence data sets were then used to fit models over 1000 iterations.

We repeated this procedure using (i) seasonal front frequency metrics (thermal, chl-*a*) for both the season in which the sharks were tracked, and the preceding year, and (ii) 7-day contemporaneous front metrics (thermal, chl-*a*; distance to closest front *fdist*, frontal gradient density *gdens*, frontal persistence *pf*), together with time-matched SST and chl-*a* values. All 7-day contemporaneous front metrics and SST were standardized across the entire presence/pseudo-absence data set prior to the modelling procedure, by subtracting the mean and dividing by standard deviation (Zuur, Hilbe & Ieno 2013). This enables comparability of effect sizes between variables that are scaled differently in their original form. The distribution of chl-*a* was highly skewed, with a large predominance of small values. We therefore removed all spurious outlying values ( $>20$  mg m<sup>-3</sup>) and transformed the resulting data

set using a  $\log_{10}$  transformation to generate an explanatory variable with a distribution approaching normal.

Owing to collinearity between predictor variables, which was detected using pairwise plots and generalized variance inflation factors (GVIF; Zuur, Hilbe & Ieno 2013), each variable was fitted via maximum likelihood estimation as a standalone explanatory term in separate model runs (1000 iterations per term). Parameter distributions generated by each set of model iterations were used to obtain the mean and standard deviation of model intercepts, regression coefficients and standard errors of fitted terms, deviance explained and chi-square statistic and *P*-value from a likelihood ratio test against a null model with no fixed effects (with Restricted Maximum Likelihood; Table S1, Supporting information). Confidence intervals (CIs; 95%) were also calculated for each of the parameter distributions. Mean values and CIs of regression coefficients were plotted and used to assess the influence of each term on the probability of shark presence (CIs overlapping zero indicates non-significant term). To assess the influence of thermal gradient magnitude on the strength of associations with fronts, we repeated this modelling procedure for each set of time-matched metrics derived using different front detection thresholds (0.2, 0.4, 0.6, 0.8, 1.0 °C).

## Results

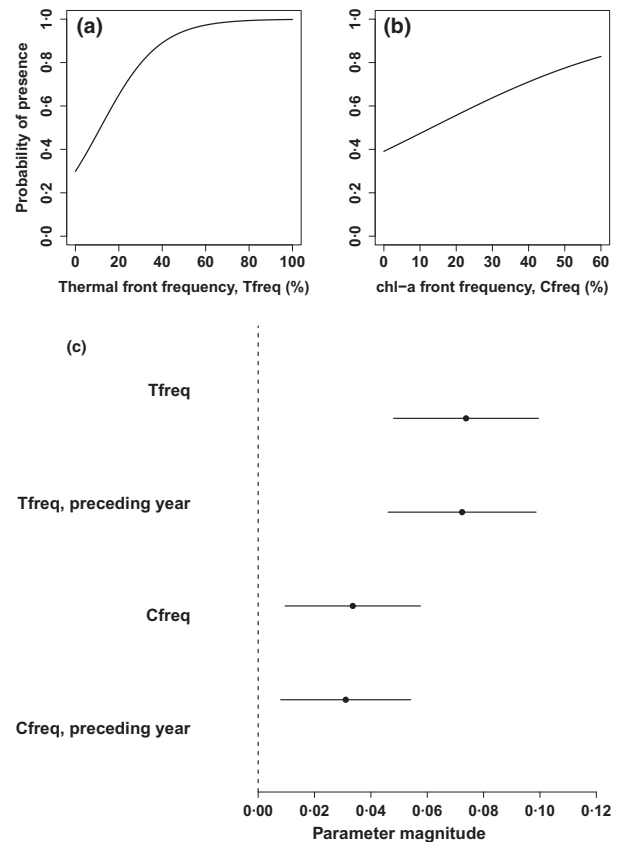
### SATELLITE-LINKED ARCHIVAL TRACKING

Of the 21 basking sharks tagged, sufficient data to reconstruct tracks were received from seven individuals (body length range 2.5–7.0 m), which were tracked for a cumulative total of 964 days, ranging from 72 to 213 days per individual. A total of 186 light-level geolocations were obtained ( $0.2 \pm 0.05$  per day) during this period. Associated dive data indicated that all sharks spent a significant proportion of this time foraging at the sea surface (Sims *et al.* 2006).

### SEASONAL FRONT FREQUENCY

Basking shark tracking locations were clustered within broad-scale regions of high seasonal front frequency, in both SST and chl-*a* fields (Fig. 2). Logistic regression revealed that the probability of shark presence was higher in regions of frequent or persistent frontal activity ('frontal zones') during the basking shark surface sightings season (May–October) over 2 years (Fig. 3; Table S1). Thermal front frequency had a stronger influence over the probability of observing a presence than chl-*a* front frequency, although both contributed significant explanatory power to models (Fig. 3c; Table S1). The proportion of deviance explained was also found to be higher for thermal front frequency than for chl-*a* (thermal =  $8.25 \pm 2.32$ ; chl-*a* =  $1.65 \pm 1.06$ ).

Seasonal front frequency in the preceding year also had an influence on the probability of observing a presence (Fig. 3; Table S1). Model intercepts and regression coefficients were similar when modelling the influence of front frequency from the contemporaneous year and from the preceding year on shark presence (Table S1). Interannual variability in front frequency was low in both thermal and chl-*a* fields between 2000 and 2002 (Fig. 2, Table 1). We also observed a high degree of spatial correlation between the thermal and the chl-*a* seasonal front frequency metrics



**Fig. 3.** Modelling the influence of seasonal front frequency on probability of shark presence. Mean regression coefficients for the influence of (a) thermal front frequency and (b) chl-*a* front frequency on probability of observing a shark presence vs. pseudo-absence derived from random walk simulations. (c) Distribution of each regression coefficient, obtained from 1000 model iterations, as mean with 95% CIs.

**Table 1.** Interannual variability in seasonal front frequency (May–October, 2000–2002). Pearson product-moment correlation coefficient for spatial correlation between years

	2000	2001	2002
Thermal front frequency			
Mean = $0.635 \pm 0.03$			
2000	1.0	0.619	0.617
2001	0.619	1.0	0.670
2002	0.617	0.670	1.0
Chl- <i>a</i> front frequency			
Mean = $0.581 \pm 0.02$			
2000	1.0	0.577	0.566
2001	0.577	1.0	0.599
2002	0.566	0.599	1.0

in each year (mean =  $0.523 \pm 0.04$ ; 2000 = 0.476; 2001 = 0.561; 2002 = 0.533).

### TIME-MATCHED FRONT METRICS

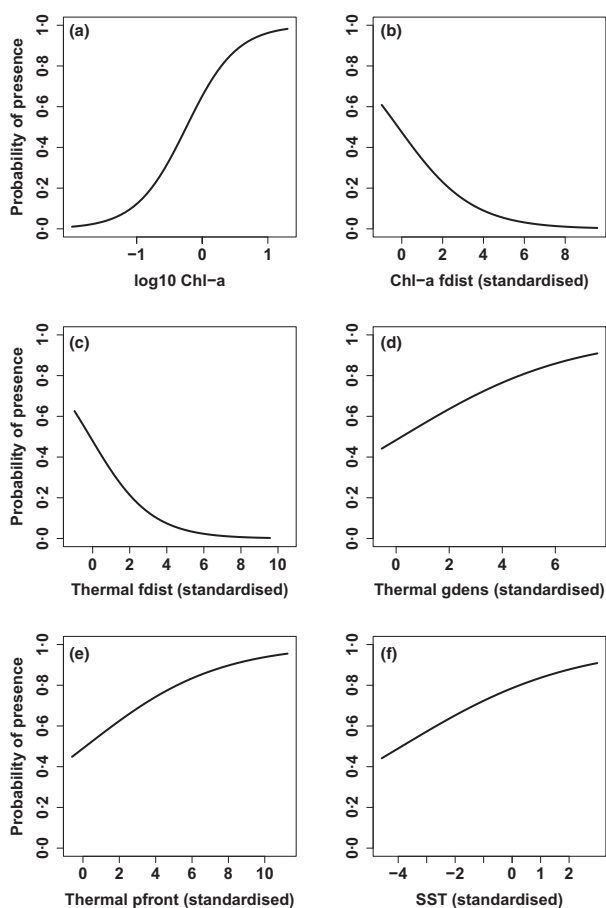
Shark presence locations were significantly more likely to be associated with contemporaneous thermal and chl-*a* fronts than pseudo-absences derived from random walk simula-

tions (Fig. 4; Tables S2 and S3, Supporting information). Distance to closest chl-*a* front (*fdist*) and all 7-day thermal front metrics (distance to closest simplified front, *fdist*; frontal gradient density, *gdens*; front persistence, *pfront*; 0.4 °C front detection threshold) were significant predictors of shark presence. Shark presence was more likely to be observed in closer proximity to thermal and chl-*a* fronts, at higher thermal gradient densities and in association with persistent thermal fronts than pseudo-absences. Indeed, some individuals appeared to spend days to weeks tracking the surface profile of strong thermal fronts, presumably foraging on aggregated prey (see Video S1, Supporting information).

Overall, 7-day chl-*a* front metrics held less explanatory power than thermal metrics, while distance to closest simplified chl-*a* front *fdist* explained a significant proportion of deviance, *gdens* and *pfront* had a less pronounced effect on the probability of shark presence (Fig. 5; Table S3). In addition, confidence intervals of the distribution of regression coefficients from bootstrapping approached zero for chl-*a* *gdens* and overlapped zero for chl-*a* *pfront* (Fig. 5). We can surmise that shark presence positions are more likely to be observed in closer proximity to chl-*a* fronts than

pseudo-absences, but that chl-*a* *gdens* and *pfront* metrics have a lesser influence on probability of shark presence, presumably as a result of the ephemeral nature of chl-*a* blooms at fronts, and the spatial smoothing involved in preparation of these metrics. These results indicate that time-matched thermal front metrics are more useful predictors of shark presence than comparable chl-*a* metrics in this case.

Varying the thermal front detection threshold had a considerable effect on the magnitude of the logistic regression coefficient for the thermal *fdist* metric (Fig. 6; Table S2). Effect size and proportion of deviance explained increased with a higher detection threshold. Shark presences were more likely to be associated with stronger thermal fronts (1.0 °C cross-frontal temperature difference or 'step') than weaker features (0.2 °C difference), although all detection thresholds resulted in significant predictors (Fig. 6; Table S2). In contrast, altering the detection threshold had little influence over the effect sizes of the *gdens* and *pfront* metrics (Table S2), most likely as a result of the inclusion of the cross-frontal gradient in the *gdens* metric, and the tendency of fronts with a stronger cross-frontal gradient to persist through time (Bakun 2006).



**Fig. 4.** Modelling the influence of contemporaneous fronts on probability of shark presence. (a–f) Mean effects of time-matched oceanographic metrics (chl-*a*, distance to closest simplified thermal or chl-*a* front *fdist*, frontal gradient density *gdens*, frontal persistence *pfront*, and sea-surface temperature, SST) over 1000 model iterations.

#### COMPARISON WITH STANDARD SST AND CHL-*A* FIELDS

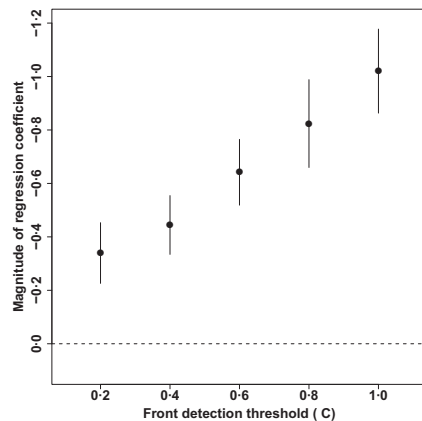
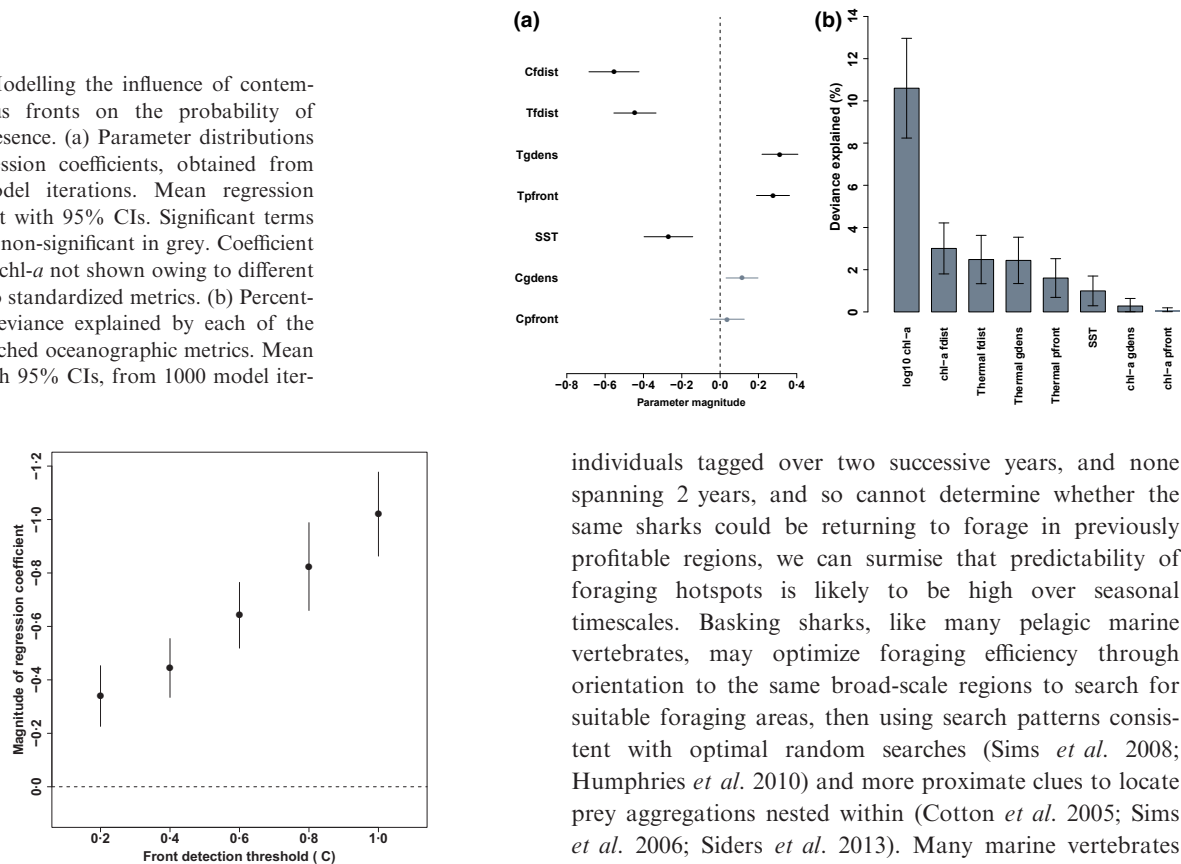
Chlorophyll-*a* concentration was found to have a significant effect on the probability of shark presence, with log<sub>10</sub>-transformed chl-*a* concentration explaining the highest proportion of deviance across model iterations (Fig. 5b; Table S3). Chl-*a* had a strongly positive effect as a predictor of shark presence, indicating that foraging habitat selection is tightly coupled with primary productivity. SST was also found to be a significant predictor, although this variable explained a considerably lower proportion of deviance than chl-*a* and time-matched front metrics, having a weak negative effect on the probability of shark presence (Fig. 5; Table S3).

#### Discussion

Our combined use of animal-attached, satellite-linked archival tracking and composite front mapping (Miller 2009) provides novel insight into the influence of regional oceanography on habitat selection in this wide-ranging marine megavertebrate. This study builds upon prior observations of associations between the planktivorous basking shark and oceanographic fronts in coastal regions of the north-east Atlantic obtained from *in situ* work (Sims & Quayle 1998; Sims *et al.* 2000; Priede & Miller 2009), but is novel in that we provide a robust quantification of the influence of thermal and chl-*a* fronts on habitat selection for sharks tracked over time-scales of weeks to months. Our analysis reveals associations between tracked sharks and seasonally persistent frontal zones, and a more proximate influence of contemporaneous mesoscale thermal and chl-*a* fronts on habitat selection.



**Fig. 5.** Modelling the influence of contemporaneous fronts on the probability of shark presence. (a) Parameter distributions for regression coefficients, obtained from 1000 model iterations. Mean regression coefficient with 95% CIs. Significant terms in black, non-significant in grey. Coefficient for  $\log_{10}$  chl-*a* not shown owing to different scaling to standardized metrics. (b) Percentage of deviance explained by each of the time-matched oceanographic metrics. Mean value with 95% CIs, from 1000 model iterations.



**Fig. 6.** Effect of varying thermal front detection threshold on magnitude of effect size for distance to closest simplified thermal front (*fdist*). Parameter distributions (mean + 95% CIs) for regression coefficient obtained from 1000 model iterations per threshold.

#### ASSOCIATIONS WITH SEASONALLY PERSISTENT FRONTAL ZONES

Seasonal front frequency, that is the number of times a front was detected in any one pixel ( $1.1 \times 1.1$  km) of the study area over the main UK basking shark surface sightings season (May–October), was found to be a significant predictor of shark presence for both thermal and chl-*a* frontal activity. Presence locations of tracked sharks were more likely to be found in association with seasonally persistent frontal zones than in other regions of the study area, although thermal front frequency was found to have a stronger effect than chl-*a*, perhaps owing to the propensity of thermal fronts to manifest in similar locations more frequently than chl-*a* fronts over the season (Kahru *et al.* 2012).

Furthermore, seasonal front frequency metrics from the preceding year were significant predictors of shark presence. Low interannual variability in the spatial extent of these persistent frontal zones over the study period (2000–2002) indicates that sharks may return to spatiotemporally predictable foraging grounds, in which they have previously experienced profitable prey encounter rates. Although we only have tracking data from seven different

individuals tagged over two successive years, and none spanning 2 years, and so cannot determine whether the same sharks could be returning to forage in previously profitable regions, we can surmise that predictability of foraging hotspots is likely to be high over seasonal timescales. Basking sharks, like many pelagic marine vertebrates, may optimize foraging efficiency through orientation to the same broad-scale regions to search for suitable foraging areas, then using search patterns consistent with optimal random searches (Sims *et al.* 2008; Humphries *et al.* 2010) and more proximate clues to locate prey aggregations nested within (Cotton *et al.* 2005; Sims *et al.* 2006; Siders *et al.* 2013). Many marine vertebrates exhibit broad-scale foraging site fidelity over seasonal, annual or interannual timescales (e.g. seals, Bradshaw *et al.* 2004; sharks, Pade *et al.* 2009; Queiroz *et al.* 2012; whales, Irvine *et al.* 2014; seabirds, Patrick *et al.* 2014), indicating that spatio-temporal predictability of prey encounter rates influences habitat selection across taxa (e.g. seabirds, marine mammals; Weimerskirch 2007; Bost *et al.* 2009).

Spatial correlation between the locations of thermal and chl-*a* frontal zones with which sharks associate was also found to be high within the study area, over the 3 years' of remotely sensed data analysed for this study. The locations of thermal and chl-*a* fronts often coincide (Le Fevre 1986; Belkin, Cornillon & Sherman 2009), since chl-*a* fronts frequently manifest where convergent processes occurring around thermal discontinuities aggregate nutrients and plankton in productive regions with high-background chl-*a* concentrations, such as at the peripheries of plankton blooms (Le Fevre 1986; Kahru *et al.* 2012). Although these mechanisms are not yet well understood, objective detection of regions of frequent frontal activity in both thermal and chl-*a* fields, such as that presented here, could aid in the identification of biophysical hotspots. Persistent thermal and chl-*a* frontal zones in the Celtic Sea, identified using the same front frequency indices, have been found to be significant foraging features for breeding northern gannets *Morus bassanus* (Scales *et al.* 2014a). When considered together, these results suggest that persistent mesoscale frontal zones in UK shelf seas may have significant cross-taxa ecological importance, providing spa-

tio-temporally predictable foraging opportunities for both planktivorous and piscivorous marine vertebrates.

#### ASSOCIATIONS WITH CONTEMPORANEOUS THERMAL AND CHL-*a* FRONTS

Basking sharks were found to associate strongly with productive regions of the study area, indicating that the propagation of surface-foraging opportunities is tightly coupled with bottom-up oceanographic forcing. Our analysis also reveals that over timescales of weeks to months, sharks associated with thermal and chl-*a* fronts within these productive areas. Time-matched front metrics were significant predictors of shark presence at the surface. Tracking locations were more likely to be found in close proximity to thermal and chl-*a* fronts, at higher thermal gradient densities and in association with more persistent thermal fronts than pseudo-absences derived from random walk simulations. These findings are in concordance with those of Curtis *et al.* (2014), and with our *a priori* assumption that foraging behaviour of these planktivores is closely tied to low trophic-level enhancement. Comparable associations with thermal fronts in pelagic waters have been documented in other sharks and large teleosts, including the blue shark *Prionace glauca* (Queiroz *et al.* 2012), ocean sunfish *Mola mola* (Sims & Southall 2002), bluefin *Thunnus thynnus* (Schick, Goldstein & Lutcavage 2004), albacore *Thunnus alalunga* and skipjack *Katsuwonus pelamis* tunas (Fiedler & Bernard 1987) and swordfish *Xiphias gladius* (Podestá, Browder & Hoey 1993; Seki *et al.* 2002) in differing oceanographic regions, suggesting that thermal fronts could have multitaxon ecological importance for pelagic predators.

Furthermore, basking shark presence was more likely to be associated with lower SSTs, indicating that fine-scale upwelling and vertical mixing are likely to influence the propagation of profitable foraging opportunities. Upwelling fronts are sites of strong biophysical coupling, along which nutrient retention and vertical mixing increase primary productivity and attract grazers such as the calanoid prey of basking sharks (Smith *et al.* 1986; Franks 1992a; Sims & Quayle 1998; Shanks *et al.* 2000).

Through systematically varying the threshold used for the detection of thermal fronts, our analysis has revealed that cross-frontal temperature difference is likely to be an important influence on foraging decisions. Regression coefficients and proportion of deviance explained across the model iterations per threshold indicate that stronger (1.0 °C cross-frontal step) fronts have more influence over the probability of shark presence than thermal fronts with a weaker cross-frontal temperature step. In addition, the effect of the gradient density *gdens* metric indicates that sharks are more likely to associate with stronger fronts. While part of this effect may be related to the spatial element of this study, in that stronger fronts are less numerous and so less likely to be encountered by random walk simulations, this nevertheless indicates that tracked sharks were

found in closer proximity to these strong fronts than could be expected by chance. These findings highlight the importance of the choice of front detection threshold in studies investigating species–habitat relationships. The influence of relative sizes of fronts detected has not been explicitly considered here owing to methodological considerations, but may be an interesting subject for future research.

The magnitude of cross-frontal temperature difference is likely linked to persistence and the degree of bioaggregation occurring at a front, owing to the spatial and temporal lags inherent in biophysical coupling mechanisms (Le Fevre 1986). Stronger fronts are more likely to persist through time and also potentially more likely to attract foraging sharks. The mechanisms through which basking sharks detect and respond to environmental clues associated with biophysical coupling at fronts are not yet well understood, but frontogenesis and front propagation are likely to induce the development of discernible environmental clues (e.g. surface and subsurface flow patterns, tidal slicks and streams, accumulation of biota; Franks 1992b). These cues are likely to be more pronounced in the vicinity of stronger, more persistent fronts.

Modelling the influence of contemporaneous fronts on habitat selection has revealed that spatio-temporal persistence of thermal fronts is an important aspect of their attractiveness as surface-foraging hotspots. Thermal fronts in shelf seas around Great Britain and Ireland form primarily as a result of interaction between tidal processes, seasonal stratification and bathymetric influence (Pingree & Griffiths 1978; Simpson & Sharples 2012). As a result, fronts range from ephemeral, only manifesting at certain stages of the tidal cycle, to quasi-stationary and seasonally persistent (Belkin, Cornillon & Sherman 2009; Simpson & Sharples 2012).

Persistent fronts are more likely to be sites of bioaggregation (Bakun 2006), and hence more likely to attract foraging marine vertebrates, than ephemeral features. While gannets in the Celtic Sea appear to target foraging effort within seasonally persistent frontal zones, responses to contemporaneous fronts are highly variable (Scales *et al.* 2014a). We here provide evidence that basking sharks may associate with contemporaneous fronts more actively than these piscivorous birds, and while persistence evidently has an influence, sharks may also associate with more ephemeral features. We can surmise that aggregation of the sharks' preferred zooplankton prey does not involve the same spatial and temporal lags that would be required for bioaggregation to propagate through the food chain from plankton to pelagic fish populations and, in turn, to their predators. This work highlights the importance of persistence, and spatio-temporal predictability, of fronts when considering their value as habitats for marine predators.

#### TECHNICAL LIMITATIONS

While this study enhances understanding of associations between basking sharks and fronts in the north-east Atlan-



tic, it is not of course without limitations. Using archival tracking technologies based on light-level geolocation has intrinsic limitations, owing to the low level of spatial accuracy of location estimates. However, we have propagated this uncertainty through modelling by repeatedly resampling potential presence locations from within an experimentally-derived radius of error around each geolocation estimate, and randomly resampling from this presence data set before fitting each model iteration. The future use of more accurate tracking technologies, such as fast-acquisition GPS systems (e.g. Fastloc™-GPS; Wildtrack Telemetry Systems Ltd., Leeds, UK), will enable finer-scale investigations into the drivers of habitat preference in this species and other pelagic marine vertebrates (e.g. Sims *et al.* 2009). The use of GPS-based tracking with composite front mapping or similar techniques would be a logical follow-up to the results presented here.

Moreover, our study has been restricted to the analysis of movements of only a few individuals ( $n = 7$ ) over part of one year of their life cycle, so we are hesitant to extrapolate findings to the population level. Many aspects of the life cycle of the basking shark remain unknown, including the size of the population using shelf seas of the north-east Atlantic, and longer range migratory behaviour (Sims 2008). We cannot ascertain whether fronts are significant habitat features for basking sharks throughout the annual cycle or throughout their range. In the north-west Atlantic, tracked basking sharks move from higher latitudes in summer to equatorial regions in winter (Skomal *et al.* 2009), but in the north-east Atlantic other tracking work has revealed that the shelf-break system, a region of frequent and intense surface frontal activity, may represent an important over-wintering habitat (Sims *et al.* 2003).

Results presented here indicate that sharks also associate with thermal and chl-*a* fronts manifesting in coastal waters of the region in summer, when sharks frequently feed at the surface and occasionally dive to the sea bottom (Sims *et al.* 2005), and so are at their most vulnerable to deleterious anthropogenic interactions [e.g. fisheries bycatch; development of Marine Renewable Energy Installations (MREI); impacts of maritime leisure]. Composite front mapping is useful in identifying key habitats and potential regions of overlap with anthropogenic pressures within the Exclusive Economic Zones (EEZ) of nations, and so could be of value in marine spatial planning and the formulation of management initiatives for species of conservation concern (Miller & Christodoulou 2014; Scales *et al.* 2014b).

Although oceanographic front metrics derived from composite front mapping have proven useful in this context, the technique has some constraints that must be taken into account. Along with all marine remote sensing applications, only the surface profile of complex three-dimensional oceanographic processes can be detected. However, surface frontal activity can be a useful indicator of subsurface biophysical processes that influence prey availability (Le Fevre 1986; Genin *et al.* 2005). Moreover, this study focuses on basking sharks that spend long periods surface-

feeding, which may be more closely associated with surface frontal activity than other deep-diving marine vertebrates (e.g. northern elephant seal *Mirounga angustirostris*; Robinson *et al.* 2012). In addition, the spatial resolution of SST and chl-*a* imagery used to derive the front indices is limited by the satellite-based sensors. Here, we use LAC to obtain 1.1 km resolution products, but we cannot detect finer-scale oceanographic influence on shark movements. The issue of spatial resolution has an impact on the algorithm's ability to detect fine-scale tidal mixing fronts occurring near to the coastline, which have been identified as potentially significant features for marine vertebrates utilizing the nearshore coastal zone (e.g. Jones *et al.* 2014). However, front metrics used here are appropriate for oceanographic contextualization of animal movements occurring across pelagic seascapes over timescales of days–weeks–months, complementing the recent proliferation of data obtained through biologging.

## Conclusions

In summary, we present evidence that basking sharks associate strongly with thermal and chl-*a* frontal activity in shelf seas of the north-east Atlantic. We provide a robust methodological approach to quantification of the influence of fronts on habitat selection by wide-ranging marine vertebrates. This analysis reveals that seasonal front frequency is a useful predictor of shark presence. Moreover, we highlight the tendency of sharks to associate with contemporaneous thermal and chl-*a* fronts, and the significant influence of cross-frontal temperature change and spatio-temporal persistence on the strength of associations. These findings have implications for management and conservation (Miller & Christodoulou 2014; Scales *et al.* 2014b), particularly in regard to the current marine spatial planning agenda in the north-east Atlantic.

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## Data accessibility

GLS tracking data and associated time-matched front metrics are deposited in the Dryad Digital Repository (doi: 10.5061/dryad.d0h7s) (Miller *et al.* 2015).

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## Supporting Information

Additional Supporting information may be found in the online version of this article:

**Table S1.** Modelling the influence of seasonal front frequency on the probability of observing shark presence vs. pseudo-absence derived from random walk simulations ( $n = 1000$  per shark).

**Table S2.** Modelling the influence of contemporaneous mesoscale thermal fronts on habitat selection.

**Table S3.** Modelling the influence of contemporaneous mesoscale chlorophyll-*a* (chl-*a*) fronts, sea surface temperature (SST) and surface chl-*a* concentration on habitat selection.

**Video S1.** Visualising associations between basking sharks and oceanographic fronts in the north-east Atlantic, using a Google-Earth approach to data visualisation for animal tracking data and composite front mapping.