

Oceanic loggerhead turtles *Caretta caretta* associate with thermal fronts: evidence from the Canary Current Large Marine Ecosystem

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ABSTRACT: Oceanographic fronts are physical interfaces between water masses that differ in properties such as temperature, salinity, turbidity and chlorophyll *a* enrichment. Bio-physical coupling along fronts can lead to the development of pelagic biodiversity hotspots. A diverse range of marine vertebrates have been shown to associate with fronts, using them as foraging and migration habitats. Elucidation of the ecological significance of fronts generates a better understanding of marine ecosystem functioning, conferring opportunities to improve management of anthropogenic activities in the oceans. This study presents novel insights into the oceanographic drivers of habitat use in a population of marine turtles characterised by an oceanic–neritic foraging dichotomy. Using satellite tracking data from adult female loggerhead turtles *Caretta caretta* nesting at Cape Verde ($n = 12$), we tested the hypothesis that oceanic-foraging loggerheads associate with mesoscale (10s to 100s of km) thermal fronts. We used high-resolution (1 km) composite front mapping to characterise frontal activity in the Canary Current Large Marine Ecosystem over 2 temporal scales: (1) seasonal front frequency and (2) 7 d front metrics. Our use–availability analysis indicated that oceanic loggerheads show a preference for the highly productive upwelling region between Cape Verde and mainland Africa, an area of intense frontal activity. Within the upwelling region, turtles appear to forage epipelagically around mesoscale thermal fronts, exploiting profitable foraging opportunities resulting from physical aggregation of prey.

KEY WORDS: Oceanographic front · Composite front mapping · Remote sensing · Sea turtle · Pelagic habitat · Foraging · Satellite telemetry

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INTRODUCTION

Anthropogenic impacts on the marine environment are now evident in every major ocean basin and marine ecosystem type (Halpern et al. 2008). These impacts are consequent not only for continued use of marine ecosystem goods and services by humans, but also for management and conservation of marine

biodiversity (Maxwell et al. 2013). Understanding the oceanographic drivers of marine vertebrate habitat use is essential to our knowledge of marine ecosystem functioning, and in locating critical habitats for species of conservation concern.

Oceanographic fronts are potentially significant habitat features, often associated with pelagic biodiversity hotspots (Le Fèvre 1986, Belkin et al. 2009).

Fronts are physical interfaces at the transitions between water masses, manifesting as surface features delineating abrupt changes in physical properties (i.e. temperature, salinity, colour). Fronts occur throughout the oceans, range from metres to thousands of kilometres in length, and can be ephemeral or persistent (Belkin et al. 2009). Along some features, nutrient retention can enhance primary productivity (Traganza et al. 1987, Franks 1992a). Zooplankton and small nekton may also become entrained and aggregated together by convergent flow fields (Franks 1992b, Graham et al. 2001, Genin et al. 2005). Together, this can provide rich foraging opportunities for higher marine vertebrates, from pelagic fish to apex predators.

Evidence suggests that a taxonomically diverse range of marine predators, including seabirds, pinnipeds, predatory fish, cetaceans, elasmobranchs and several species of sea turtle associate with fronts to some degree during their life cycle (see Polovina et al. 2004, Mansfield & Putman 2013, Scales et al. 2014b & references therein). However, the nature, strength and variability of these associations remains unclear in many cases. Alongside taxon-specific aspects of foraging ecology, regional oceanographic character is likely to strongly influence the attractiveness of fronts as foraging features. Spatial scale, gradient magnitude and temporal persistence of fronts vary both within and between oceanographic regions, influencing the linkages between predators, prey, and physical processes. Foraging opportunities associated with bio-aggregation along fronts may be more profitable under certain oceanographic conditions, or exploitation of these opportunities may vary between populations or individuals (Scales et al. 2014a). More research is therefore needed to elucidate the influence of mesoscale oceanographic dynamics on habitat preference in different marine vertebrate populations.

Loggerhead turtles *Caretta caretta* have been shown to migrate along the North Pacific Transition Zone (Polovina et al. 2000, 2004, Kobayashi et al. 2008), forage around coastal upwelling fronts off Baja California (Etnoyer et al. 2006), and raft amongst floating *Sargassum* at fronts as neonates (Witherington 2002, Mansfield et al. 2014). However, loggerheads are circumglobally distributed, migratory predators that exhibit a high degree of foraging plasticity (Hatase et al. 2002, 2013, Hawkes et al. 2006, Frick et al. 2009, Varo-Cruz et al. 2013), so questions remain regarding the generality of these findings across populations. Adult loggerheads in the classic life history model forage benthically in coastal waters of

temperate and subtropical nations (Schroeder et al. 2003), yet oceanic foraging strategies have now been observed in populations in the Atlantic (Cape Verde, Hawkes et al. 2006, Varo-Cruz et al. 2013; western North Atlantic, Mansfield et al. 2009, Reich et al. 2010), Pacific (Hatase et al. 2002), Indian Ocean (Luschi et al. 2003a), the Mediterranean (Casale et al. 2008) and Arabian seas (Rees et al. 2010). Oceanic loggerheads are thought to feed in the epipelagic zone (i.e. near the surface), preying opportunistically on planktonic and neustonic organisms such as jellies, fish, crustaceans and their eggs and larvae (Frick et al. 2009, McClellan et al. 2010, Todd Jones & Seminoff 2013), organisms that are easily entrained along bio-aggregating fronts.

Here, we used high-resolution (1 km) composite front mapping (Miller 2009) to provide a remotely sensed oceanographic context to the movements of post-nesting female loggerheads tracked by satellite from Cape Verde, a population in which the oceanic foraging strategy seems to dominate (Hawkes et al. 2006, Eder et al. 2012, Varo-Cruz et al. 2013). Composite front mapping (Miller 2009) allows us to objectively locate thermal and chlorophyll *a* (chl *a*) fronts over ocean-basin scales, remove any obscuring influence of cloud and visualise spatiotemporal dynamics. High-level metrics describing frontal activity (distance to closest front, front density) can be time-matched to tracking data, and used as part of a suite of remotely sensed products to contextualise animal movements. Using metrics describing oceanographic conditions over 2 temporal scales (seasonal, 7 d) in a multi-scale use-availability analytical framework, we aimed to quantify associations between oceanic loggerheads and thermal fronts in a novel oceanographic region.

MATERIALS AND METHODS

Tracking data

A total of 24 adult females were equipped with Argos-PTT satellite tracking devices over 3 successive nesting seasons (2004, $n = 10$; 2005, $n = 3$; 2006, $n = 11$) at Boa Vista, Cape Verde ($16^{\circ} 06' N$, $22^{\circ} 47' W$; Hawkes et al. 2006, L. A. Hawkes unpubl. data), using previously tested attachment methods (Godley et al. 2002). Transmitters used were Sirtrack Kiwisat model 101 ($n = 16$), Telonics model ST-14 ($n = 2$) and dive-recording Sea Mammal Research Unit (SMRU) 9000x Satellite Relay Data Loggers (SRDLs; $n = 6$). Since tags were attached to adult turtles only (curved

carapace length > 70 cm), we assumed that additional drag effects were minimal, following Todd Jones et al. (2013). Argos data were filtered to include only location classes (LC) A, B, 0, 1, 2 and 3, using the Satellite Tracking and Analysis Tool (Coyne & Godley 2005), excluding LC Z owing to low accuracy (Witt et al. 2010). All inter-nesting locations were removed. Unrealistic locations were also excluded (e.g. swimming speed > 5 km h⁻¹; positions on land). Only those turtles that exhibited an oceanic foraging strategy (n = 12; 98% locations > 500 m depth; Hawkes et al. 2006) were included in further analyses (see Appendix).

Track interpolation using state–space modelling (SSM)

The majority (60%) of filtered Argos locations were of low accuracy (LC A and B) and were irregular, with long data gaps (mean uplink frequency: 1 location per 11.2 h; Fig. 1). We thus excluded large gaps

(>14 d), which reduced mean uplink frequency to 1 location per 8.1 h, but variability remained high (range <1 to 332.5 h between uplinks). Consequently, we interpolated between locations using a first differences correlated random walk SSM (DCRW; Jonsen et al. 2005) in R (R Development Core Team 2012) and Just Another Gibbs Sampler (JAGS) 3.2.0 (www.mcmc-jags.sourceforge.net). Model parameters were estimated for each track using 2 parallel Markov Chain Monte Carlo (MCMC) chains. We used 10 000 iterations after a burn-in phase of 30 000, and a thinning rate of every 10th sample. A time-step of 12 h was used to generate 2 ‘most likely’ locations for each day of the tracking period from the posterior means of resultant distributions (Fig. 1).

Broad-scale use–availability analysis

High-use habitat over seasonal timescales was identified using kernel utilisation distributions (KUD) on interpolated tracks over a 1 km resolution grid.

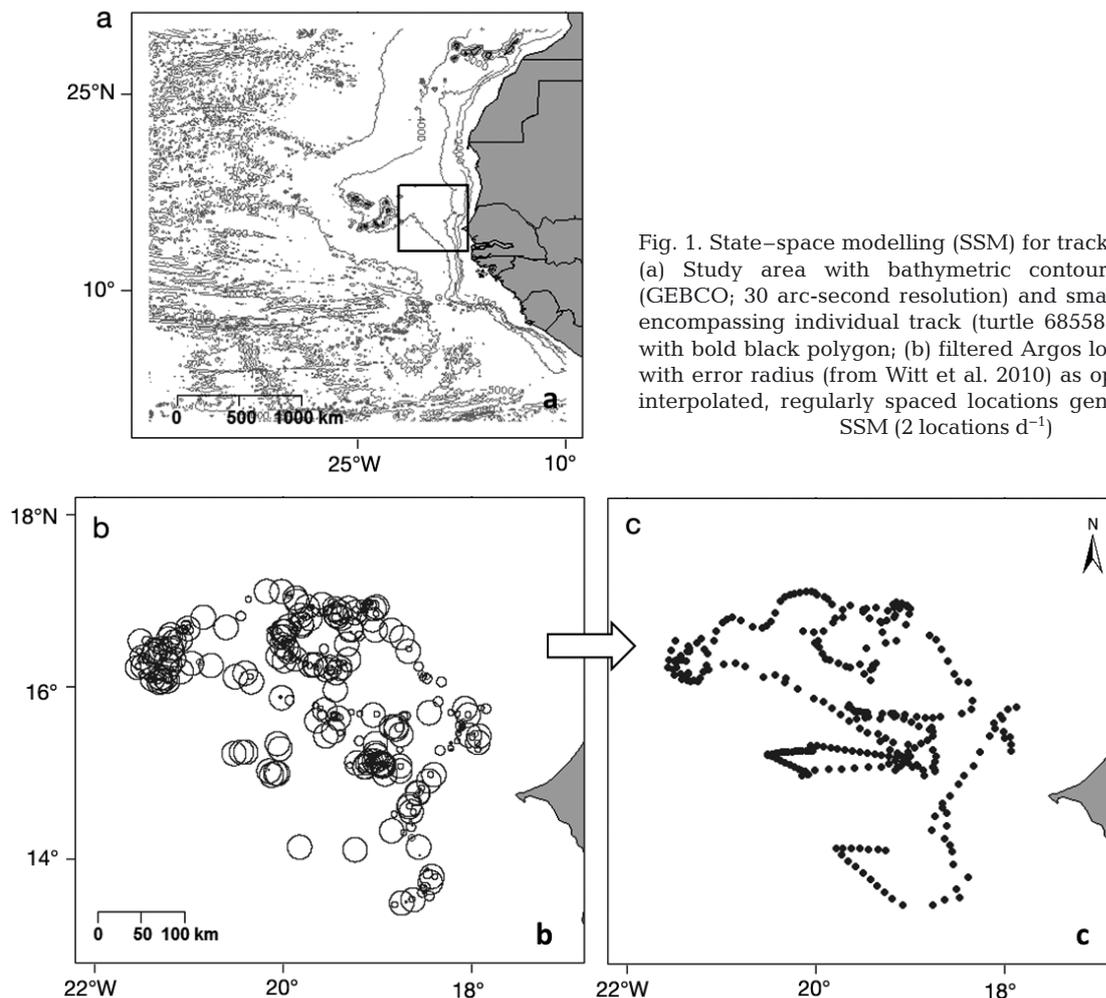


Fig. 1. State–space modelling (SSM) for track interpolation. (a) Study area with bathymetric contours highlighted (GEBCO; 30 arc-second resolution) and smaller inset area encompassing individual track (turtle 68558a) highlighted with bold black polygon; (b) filtered Argos locations shown with error radius (from Witt et al. 2010) as open circles; (c) interpolated, regularly spaced locations generated by the SSM (2 locations d⁻¹)

Data were split into seasons (Winter: Dec through Feb; Spring: Mar through May; Summer: Jun through Aug; Autumn: Sep through Nov) across the entire tracking period and aggregated ('adehabitatHR' library for R; Calenge 2006). Low sample size prohibited further separation into seasons of each year. The KUD smoothing parameter was selected using the reference bandwidth (Kie 2013).

Seasonal environmental data

Thermal composite front maps (Miller 2009) were created at 1 km resolution using NASA Multi-sensor Ultra-high Resolution Sea-Surface Temperature data (MUR SST). Daily SST imagery was mapped to the study area in geographic projection, and thermal fronts were detected in each scene using Single-Image Edge Detection (SIED; Cayula & Cornillon 1992; front detection threshold = 0.4°C). All fronts detected over 7 d windows were incorporated into composite front maps, rolling by 1 d and covering the entire tracking duration (July 2004 to October 2009; see Fig. 2). Using these 7 d composite front maps, seasonal thermal front climatologies were generated for the area enclosed by a radius described by the maximum displacement from origin (0 to 30°N, 10 to 40°W) for each season (Winter, Spring, Summer, Autumn; see Fig. 3) over the entire tracking duration (2004 to 2009). Resultant frequent front maps track each pixel through successive composites, quantifying the percentage of time in which a front is detected and thereby highlighting regions in which fronts persist or manifest frequently (Miller & Christodoulou 2014). Median SST and chl *a* imagery was processed from MODIS data at 4 km resolution and mapped to the same region over matching seasonal timescales. General Bathymetric Chart of the Oceans (GEBCO_08 grid; www.gebco.net/) depth data were also obtained at 30 arc-second resolution, and mapped to the study area ('raster' library for R; Hijmans & van Etten 2012).

Mesoscale use–availability analysis

Random walk simulations

Estimating habitat preference using presence-only, spatio-temporally autocorrelated telemetry data can be complex (Aarts et al. 2008). In order to generate a null model with which to test habitat preference by loggerhead turtles, we used a randomisation proce-

dure (cf. Heithaus et al. 2006) to generate pseudo-absence points for use within a regression-based statistical framework (Warton & Aarts 2013). A total of 1000 correlated random walk (CRW) simulations were generated per individual and were time-matched to original tracks using step lengths, turning angles and total track length from each track ('adehabitatLT' library for R; Calenge 2006). To reflect spatial bias in presence data, random walk simulations had a fixed start at the nesting beach and were constrained within a habitat availability radius defined by the overall maximum displacement distance.

Temporally matched environmental data

Thermal composite front maps (7 d, rolling by 1 d) were processed to generate a suite of time-matched rasters describing frontal activity (Fig. 2). Frontal density (*fdens*) quantified the relative number and strength of all fronts detected over the study area, as a single metric that comprised both strength and persistence. *fdens* was prepared directly from composite front maps (Miller 2009), spatially smoothed to generate a continuous distribution quantifying relative frontal activity over the study area. The frontal distance (*fdist*) metric quantified the distance from any location to the closest simplified front, using a custom simplification algorithm (P. I. Miller unpubl. data). Front metrics, SST and chl *a* were extracted from temporally-matched rasters for each location along each track, both real and simulated.

Statistical analysis

We compared the proportion of time spent in proximity to mesoscale thermal fronts for real and simulated tracks (the null model). We derived the proportion of each track spent within 4 distance bins (2, 5, 7 and 10 km) of the closest front, and compared the distributions. Distance bins were chosen to account for deviation between a front's surface manifestation and its sub-surface profile, advection of aggregated material, sub-mesoscale meanders undetectable at this spatial resolution, and potential measurement error.

A regression-based approach was then used to quantify the influence of oceanographic covariates on the probability of turtle presence. As tracking locations were serially autocorrelated, violating the assumption of independence held central to generalised linear modelling, we used a non-parametric

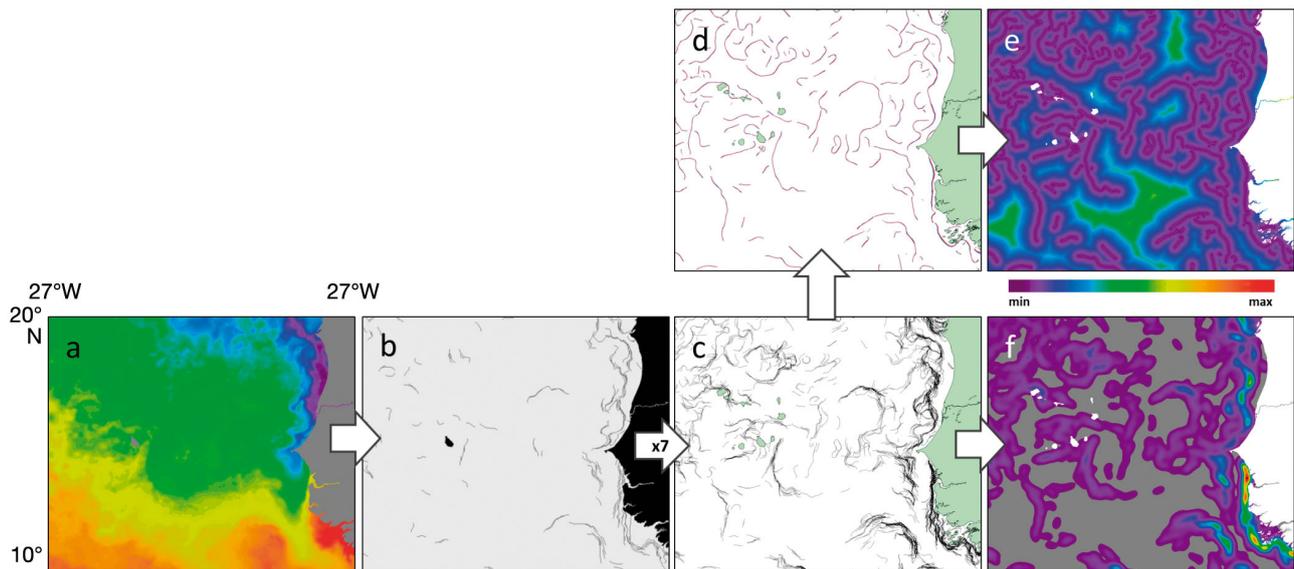


Fig. 2. Composite front mapping protocol. (a) Example daily NASA Multi-sensor Ultra-high Resolution Sea-Surface Temperature (MUR SST) product, (b) single-image edge detection, with edges shown in grey (0.4°C threshold). (c) All fronts detected in 7 daily images combined to create 7 d composite front maps (Miller 2009), rolling by 1 d to cover entire tracking duration. (d) Composites simplified to a single line for each frontal feature (red = warm side, blue = cold side; width = relative strength), and (e) a continuous distance to closest front raster created from this simplified map (*fdist*). (f) Continuous frontal density (*fdens*) raster, created by spatial smoothing of the composite front map in (c)

bootstrap regression to repeatedly sub-sample the real (presence) and simulated (pseudo-absence) tracking datasets. Each sub-sampling iteration selected a total of 1000 presence and 1000 pseudo-absence points from the master dataset, weighted per the proportion of presences for each turtle. Presence/absence was then used as a binary response variable in binomial generalised linear mixed models (GLMM; 'lme4' package for R; Bates et al. 2014), with individual as a random effect, over 1000 bootstrap iterations. All environmental covariates were standardised before inclusion in models, by subtracting the mean and dividing by the standard deviation (Zuur et al. 2013), enabling comparability of coefficient estimates.

Firstly, each environmental covariate was fitted as a stand-alone term in separate models, over 1000 iterations per term, to assess the effect of each on the probability of turtle presence. Parameter distributions drawn from model iterations were used to obtain mean values and standard deviations for model intercepts, regression coefficients and standard errors of fitted terms, percentage deviance explained, chi-square statistic and p-value from a likelihood ratio test of each model iteration against a null model fitted with no fixed effects (see Table 1). Next, multiple regression including all oceanographic covariates

(*fdist*, *fdens*, chl *a*, SST; all standardised) was used to determine relative contributions to the probability of turtle presence. Generalised variance inflation factors (Zuur et al. 2013) confirmed that collinearity between oceanographic covariates was not prohibitively high for inclusion in the same model. We again used a non-parametric bootstrap, using a binomial GLMM with turtle ID as a random effect and removing each term from the maximal model in turn over 1000 iterations per term. We obtained estimates for regression coefficients, change in Akaike's information criterion (AIC) and deviance explained on removal, and chi-square statistic and p-value from a chi-square test against the maximal model, to quantify the relative importance of each term to the model (Table 1).

Dive behaviour

Two individuals were equipped with dive-logging devices, which recorded the location, depth and duration of dives (see Appendix). We mapped dive locations, separated them into day or night using location-specific civil twilight times, and then extracted temporally matched environmental data ('maptools' library for R; Bivand & Lewin-Koh 2013). To test

whether dive behaviour differed in association with mesoscale fronts, a negative binomial generalised additive mixed model (GAMM) was fitted, with maximum dive depth (m) as response and a smoother applied to the *fdist* (distance to closest front) metric, with individual as a random effect. The theta parameter was estimated by performance iteration, and scale parameter and model dispersion statistic were used for model validation (Zuur et al. 2013).

RESULTS

Broad-scale, seasonal habitat associations

At broad scales, high-use habitat of oceanic loggerheads was strongly associated with the upwelling region off the coast of Northwest Africa, characterised by intense frontal activity and elevated chl *a* concentrations (Fig. 3). Thermal front frequency was higher

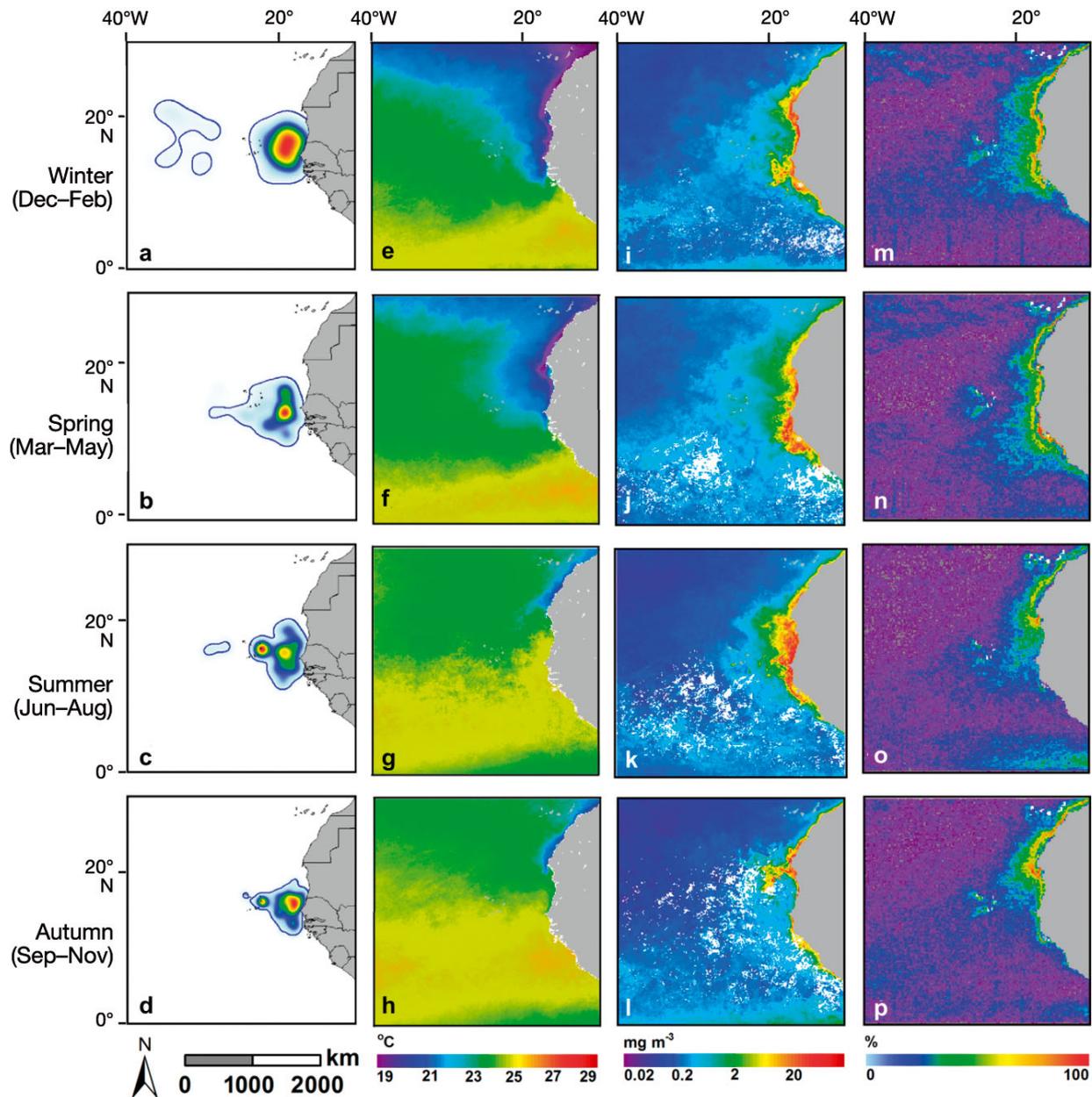


Fig. 3. Broad-scale, seasonal habitat associations. (a–d) Seasonal kernel utilisation distributions (KUD) for oceanic-foraging turtles only ($n = 12$), identifying high-use habitat over the whole tracking duration, binned by season. KUD contours highlighted, with 95% contour as perimeter line. (e–h) Seasonally averaged SST (2006 data) and (i–l) chl *a* concentrations (2006 data). (m–p) Thermal front climatologies highlight areas of frequent, intense frontal activity over the tracking duration (2004 to 2009)

within regions of habitat used by tracked animals than the background level of frontal activity observed within the study area (Fig. 4).

Mesoscale habitat associations

Oceanic-foraging loggerhead turtles associated with mesoscale oceanographic fronts within the upwelling region significantly more than would be

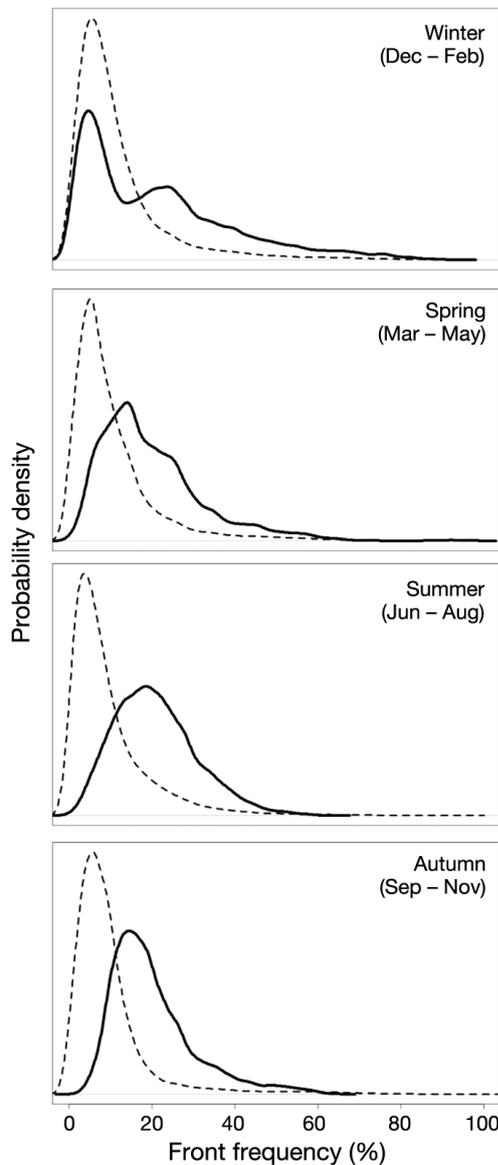


Fig. 4. Broad-scale, seasonal habitat associations of oceanic-foraging loggerheads in the Canary Current Large Marine Ecosystem. Distribution of front frequency from habitat used, as defined by 95 % kernel utilization distribution (KUD) contours (solid line), against background level of front frequency in all accessible habitat, as defined by radius of maximum displacement from nesting location (dashed line)

expected under a scenario of random habitat use. The proportion of each track occurring within a spatial buffer (2, 5, 7 and 10 km) of the closest detected front was, on average, higher for tracked turtles (2 km, 0.10 ± 0.04 ; 5 km, 0.25 ± 0.07 ; 7 km, 0.33 ± 0.07 ; 10 km, 0.47 ± 0.10) than for random walk simulations (2 km, 0.07 ± 0.03 ; 5 km, 0.19 ± 0.05 ; 7 km, 0.26 ± 0.07 ; 10 km, 0.39 ± 0.09), with 4 of 12 turtles associating with fronts significantly more frequently than random walks (Fig. 5; 5 % significance level).

Presence/absence predictions from logistic regression suggest that front metrics (*fdens*, *fdist*) are significant predictors of turtle presence, both as stand-alone terms and in multiple regression. Presence points were more likely to occur closer to fronts and at higher frontal density than pseudo-absences derived from random walks (Fig. 6, Table 1). Confidence intervals (CIs) of distributions of regression coefficient magnitude obtained from 1000 model iterations did not overlap zero for *fdens*, *fdist* or SST, indicating that these terms have significant explanatory power (Fig. 6e).

Further, *fdens* and *fdist* were found to be significant terms using likelihood ratio tests, with p-values indicating significance in all 1000 single-term model

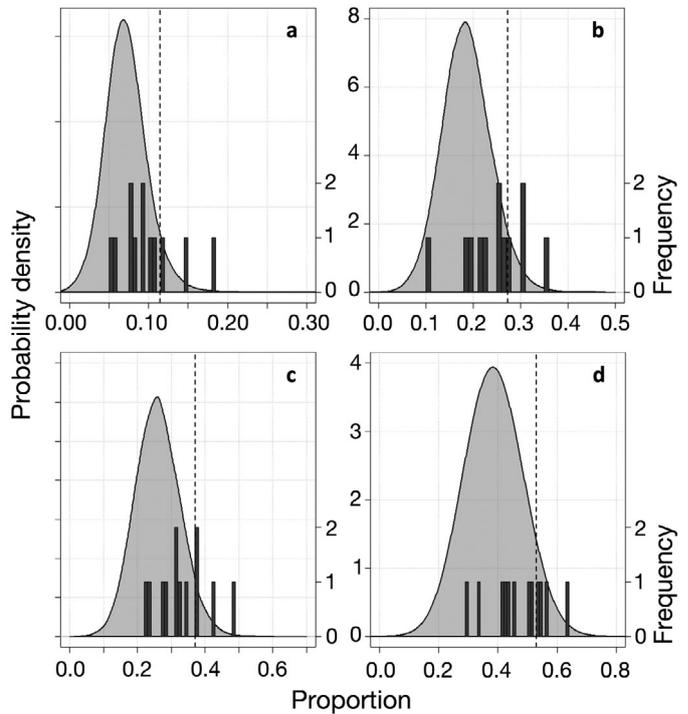


Fig. 5. Use of mesoscale thermal fronts by oceanic-foraging loggerheads. Proportion of each track ($n = 12$) within (a) 2 km, (b) 5 km, (c) 7 km and (d) 10 km of closest front (grey bars). Proportion of simulated tracks ($n = 12000$) within each distance threshold shown as grey curve. Upper 5 % of distribution marked by dashed line

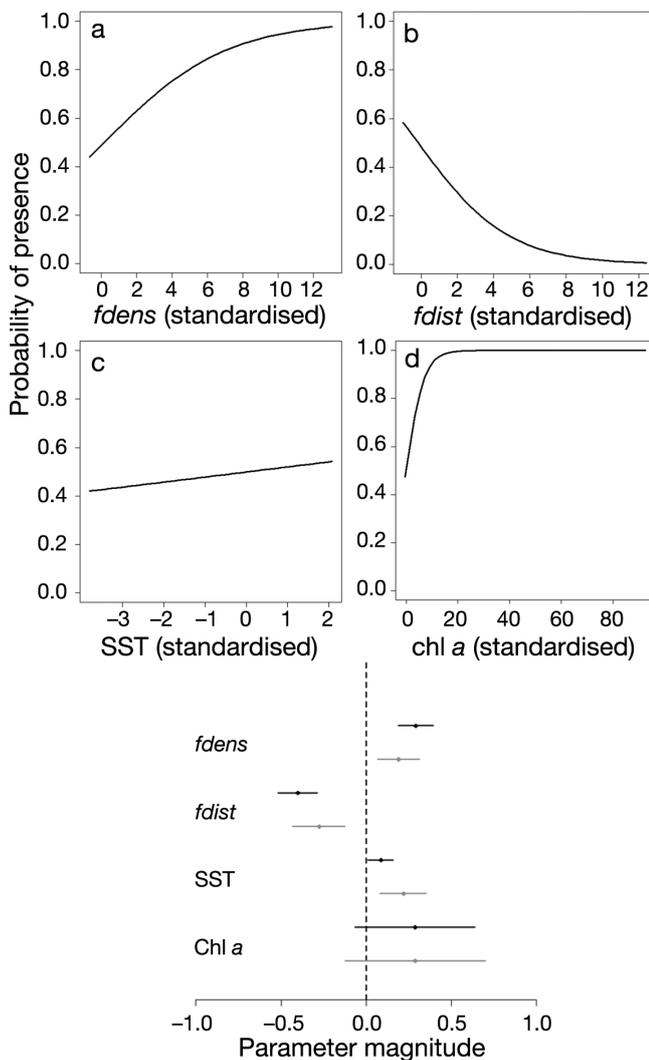


Fig. 6. Modelling the influence of mesoscale fronts on habitat selection. Effect of (a) frontal density (*fdens*), (b) distance to closest front (*fdist*), (c) SST and (d) surface chl *a* concentration on probability of turtle presence (all covariates standardised). (e) Parameter distributions for regression coefficients from binomial generalised linear mixed model (individual as random effect; 1000 iterations) shown for influence of *fdens*, *fdist*, SST and chl *a* concentration. Mean value indicated by filled circle, 95% confidence intervals (CIs) shown as horizontal lines. Outputs from modelling of single terms in black, multiple regression in grey. Mean regression coefficients plotted on response scale (logistic link function; a–d). CIs for *fdens*, *fdist* and SST do not overlap zero, indicating significance explanatory power as predictors of turtle presence

iterations. In contrast, SST and chl *a* were weaker predictors of turtle presence. CIs of regression coefficients for chl *a* overlapped zero, and a lower proportion of significant p-values were generated. In addition, *fdens*, *fdist* and SST made a more significant difference to the AIC of the multiple-regression

model upon removal than chl *a*. These results indicate that the 7 d front metrics *fdens* and *fdist* have better explanatory power in predicting turtle presence than the more commonly used SST and chl *a* metrics.

Dive data

The distribution of dive depth maxima clearly showed a predominance of shallow dives, with a median maximum depth of 14.5 m (Fig. 7a). Dives were marginally deeper during daylight than darkness hours (Fig. 7b). Moreover, dives during daylight hours tended to be shallower when closer to fronts (Fig. 7c).

DISCUSSION

Oceanic-foraging loggerhead turtles inhabiting the Canary Current Large Marine Ecosystem appear to strongly associate with the highly productive upwelling region off Northwest Africa between return migrations to their nesting grounds at Cape Verde. At an ocean-basin scale and over seasonal time-spans, high-use habitat overlapped with a region of intense frontal activity associated with this major eastern boundary upwelling. Within the upwelling region, meso- and sub-mesoscale oceanographic dynamics influence prey availability. Oceanographic features, such as filaments, jets, eddies and internal waves drive spatial structuring and front formation as cool, dense water is forced to the warmer surface (Chavez & Messié 2009). Filaments (tongue-shaped extensions of coastally upwelled water) extend 100s of kms offshore, transporting nutrients and entrained plankton to pelagic waters (Rodríguez et al. 1999). Strong, persistent thermal fronts around filaments and eddies concentrate these nutrients and low trophic-level biota, increasing prey accessibility for higher-level consumers and their predators (Hernández-León et al. 2002).

Our use-availability analysis provides objective evidence that mesoscale oceanographic processes influence habitat selection by loggerhead turtles within this upwelling region. Tracked turtles spent more time in association with mesoscale thermal fronts than expected at random. Loggerheads are thought to be opportunistic foragers, feeding while travelling (Frick et al. 2009, Todd Jones & Seminoff 2013), so presumably use front-associated foraging opportunities as they encounter them.

Table 1. Modelling the influence of mesoscale fronts on habitat selection by loggerhead turtles *Caretta caretta*. Model parameters (mean \pm SD, range; binomial generalised linear mixed model; 1000 iterations) for the influence of frontal density (*fdens*), distance to closest front (*fdist*), sea surface temperature (SST) and chl *a* concentration on probability of observing a presence (locations sampled from filtered Argos dataset) or absence (pseudo-absences sampled from random walk locations). All environmental covariates standardised before inclusion, for comparability of coefficient sizes. Regression coefficients reported on untransformed scale

(a) Single terms: presence (0/1) ~ metric + (1 ID)					
Environmental covariate (standardised)	Intercept	Regression coefficient	Standard error	Deviance explained (%)	p-values < 0.05 (%)
<i>fdens</i>	-0.050 ± 0.01 (-0.08 to -0.03)	0.29 ± 0.05 (0.14 to 0.48)	0.04 ± 0.003 (0.034 to 0.054)	1.9 ± 0.53 (0.62 to 3.8)	100
<i>fdist</i>	-0.07 ± 0.01 (-0.12 to -0.03)	-0.40 ± 0.06 (-0.61 to -0.23)	0.6 ± 0.002 (0.05 to 0.07)	1.9 ± 0.51 (0.65 to 4.30)	100
SST	-0.005 ± 0.003 (-0.02 to 0.003)	0.08 ± 0.04 (-0.02 to 0.22)	0.04 ± 0.0004 (0.041 to 0.044)	0.16 ± 0.13 (0.00 to 0.92)	51
chl <i>a</i>	0.02 ± 0.04 (-0.1 to 0.14)	0.29 ± 0.18 (-0.05 to 1.14)	0.1 ± 0.03 (0.02 to 0.18)	0.64 ± 0.53 (0.00 to 3.48)	75
(b) Multiple regression: presence (0/1) ~ <i>fdens</i> + <i>fdist</i> + chl <i>a</i> + SST + (1 ID)					
Intercept = -0.05 ± 0.05 (-0.19 to 0.08)					
AIC: 1531 ± 33.5 (1430 to 1645)					
Total deviance explained (%) = 4.2 ± 1.0 (1.3 to 7.5)					
Environmental covariate (standardised)	Regression coefficient	Δ AIC on removal	Δ deviance explained on removal (%)	Chi-square statistic (df = 1)	p-values < 0.05 (%)
<i>fdens</i>	0.19 ± 0.06 (0.01 to 0.38)	$+11.0 \pm 7.1$ (-1.9 to 36.6)	0.82 ± 0.45 (0.00 to 2.40)	13.0 ± 7.1 (0.07 to 38.6)	93
<i>fdist</i>	-0.28 ± 0.08 (-0.52 to 0.02)	$+11.4 \pm 6.8$ (-1.9 to 40.3)	0.84 ± 0.43 (0.01 to 2.64)	13.4 ± 6.8 (0.09 to 42.3)	95
SST	0.22 ± 0.68 (-0.01 to 0.47)	$+11.2 \pm 7.6$ (-1.9 to 51.4)	0.83 ± 0.51 (0.00 to 3.37)	13.2 ± 7.6 (0.05 to 53.4)	93
chl <i>a</i>	0.29 ± 0.21 (-0.06 to 1.18)	$+6.6 \pm 8.1$ (-2.0 to 52.5)	0.54 ± 0.51 (0.00 to 3.53)	8.6 ± 8.1 (0.0 to 54.5)	64

While it is difficult to distinguish foraging dives from transit using dive depth alone, our dive data indicate some influence of front proximity on dive behaviour. Overall, dive data suggest that loggerheads forage epipelagically, and most particularly when associated with fronts (see also Polovina et al. 2000, 2003, Mansfield & Putman 2013, Dalleau et al. 2014). As features in which the thermocline breaches the surface, fronts often act to increase prey accessibility in the surface ocean (Le Fèvre 1986). We can therefore surmise that loggerheads likely dive epipelagically around thermal fronts to exploit profitable foraging opportunities resulting from physical aggregation of prey close to the surface.

As ectotherms, turtles must make energetic trade-offs between thermal constraints and availability of food resources when selecting pelagic habitats (Fossette et al. 2012). Habitats associated with the upwelling region favoured by this population are highly thermally dynamic, characterised by the intrusion of

cool water into warmer tropical surface waters. As turtles do not invest in reproduction every year (mean interval 2.3 yr; Marco et al. 2012), energetic trade-offs presumably enable the population to exploit profitable foraging opportunities associated with this upwelling in the intervening period. Seasonal patterns of space use show a range contraction through the year, coincident with variation in upwelling intensity. During the summer (Jun to Aug), when upwelling was at its most intense (Moyano et al. 2014), turtles remained within a core foraging area associated with the highly productive frontal zone.

While our analysis indicated that only 4 of 12 tracked turtles spent a significant proportion of time in the vicinity of strong fronts, use-availability regression models indicated that front metrics are significant predictors of turtle presence at the sampling level even when this inter-individual variability was explicitly accounted for. We postulate that this may

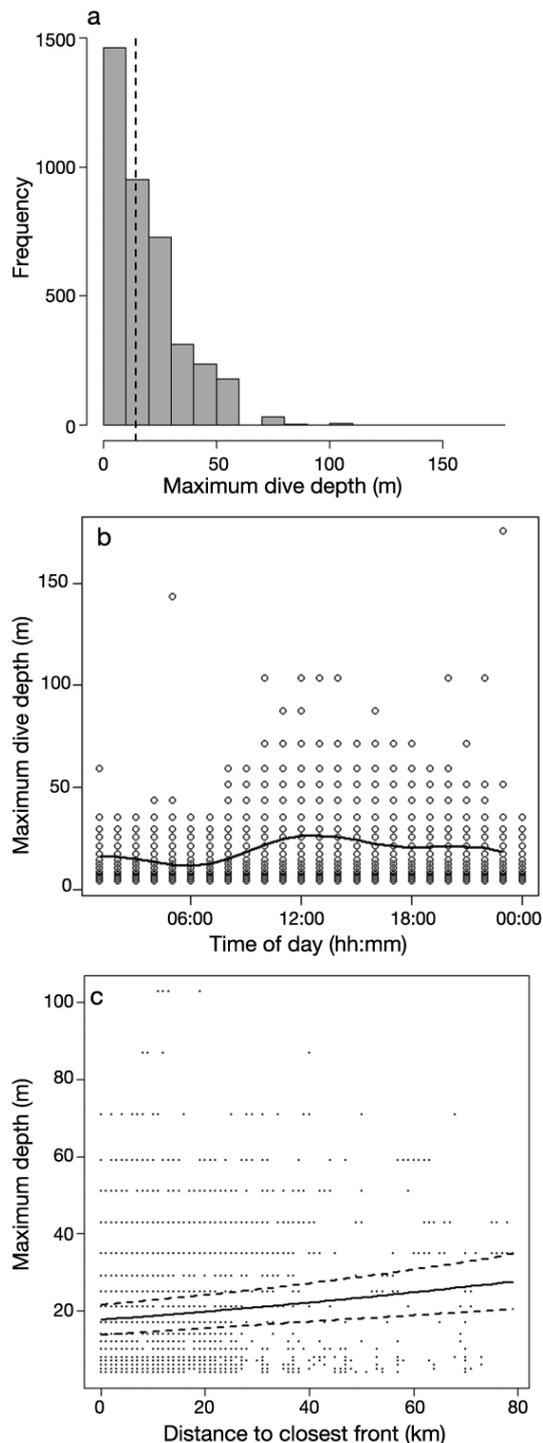


Fig. 7. Dive behaviour of oceanic turtles. (a) Distribution of maximum dive depths, with median shown by dashed line, indicates epipelagic foraging. (b) Diel cycle of dive depths, with deeper dives during daylight hours. Points represent individual dives, aggregated by hour of day. Solid line shows predictions of generalised additive model of diel cycle in dive depths. (c) Modelling the influence of meso-scale fronts on dive behaviour suggests that, during daylight hours, dives are shallower in proximity to fronts. Points represent individual dives. Solid line shows model predictions, with 95% confidence intervals as dashed lines

be a function of limited sample size, or of individual behavioural differences during the tracking period — some turtles may move along fronts, presumably to exploit favourable conditions, while others may associate with front-associated habitat more opportunistically as they navigate the pelagic seascape. In addition, the degree of bio-aggregation at fronts, which varies according to the direction and strength of flow, temporal persistence and the properties of surrounding water masses (Bakun 1996), is likely to make some fronts more attractive than others — it has been shown that persistent fronts are more attractive to some high trophic-level organisms than ephemeral features (Scales et al. 2014a). Moreover, advection of prey items aggregated in convergent fronts could obscure the signal of frontal foraging. Importantly, front metrics (*fdens*, *fdist*) were found to be better predictors of turtle presence than SST or chl *a*, parameters that are widely used to characterise habitat preference (e.g. Kobayashi et al. 2008, McCarthy et al. 2010). Thus, our approach offers advantages for future studies that wish to enumerate, robustly compare or predict the distribution of animals associating with oceanographic features.

Despite using the best available data and a progressive methodological approach, technical limitations meant that we were unable to investigate these mesoscale associations in further detail. We used, for the first time to our knowledge, high-resolution (MUR SST; 1 km) composite front mapping, which addresses many of the caveats of precursor front detection methods, alongside MODIS chl *a* (4 km), to provide a novel context for the movements of tracked animals. Our use-availability analysis considered multiple nested spatial and temporal scales, defined by the oceanographic processes that underlie foraging habitat use and preference. We used a regression-based technique that explicitly accounted for non-independence in tracking data to quantify, rather than just describe, associations with fronts.

However, limitations of data frequency and accuracy precluded further investigation into the role of ocean currents in this system. Consideration of current flow is an important aspect in analysis of marine vertebrate space use (Luschi et al. 2003b, Gaspar et al. 2006). Broad-scale current flows experienced as hatchlings are known to strongly influence foraging site selection in adult turtles (Scott et al. 2014). The influence of currents on the movements and behaviour of adult hard-shelled turtles, which have sufficient motility to actively swim against or across current fields, are less clear — and under

debate (see Hays et al. 2014, Kobayashi et al. 2014). Advances in biologging technologies, including the advent of fast-acquisition GPS-based tags, (e.g. Fastloc™-GPS; Wildtrack Telemetry Systems) enable high resolution investigation of space use (Shillinger et al. 2012). Using directly measured, modelled or remotely sensed oceanographic data (c.f. McCarthy et al. 2010) alongside GPS-tracking technologies to investigate interactions between frontogenesis, mesoscale current fields and turtle habitat selection would be a logical follow-up to this study.

In a wider context, insights into the oceanographic drivers of marine vertebrate habitat use contribute to our understanding of pelagic ecosystem functioning, and thereby confer opportunities to improve biodiversity conservation as anthropogenic impacts on the global ocean intensify (Halpern et al. 2008). Such insights are useful in identifying ecologically significant marine areas, and assessing the extent of overlap between critical habitats and anthropogenic threat (McCarthy et al. 2010, Pikesley et al. 2014). At a regional level, intense fisheries pressure leads to high rates of incidental capture ('bycatch'; Zeeberg et al. 2006), threatening this globally significant loggerhead population which also experiences direct take on the nesting grounds (Marco et al. 2012). Bycatch remains a major threat to many marine vertebrate populations of conservation concern (Lewison et al. 2014). As fisheries also target productive fronts, these threats are likely to be concentrated in ecologically significant frontal zones (see Seki et al. 2002, Alemany et al. 2014, Scales et al. 2014b). As a tool for identification of vulnerability hotspots, front mapping could inform a more spatially dynamic management paradigm (cf. Howell et al. 2008), designed to incorporate the conservation needs of highly mobile marine vertebrates.

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Appendix. Summary of filtered Argos-PTT tracking dataset for oceanic-foraging loggerhead turtles tracked from Boa Vista, Cape Verde from 2004 to 2006 (n = 12; Hawkes et al. 2006). Individuals equipped with dive-loggers (n = 2) are highlighted (*). CCL: curved carapace length

ID	CCL (cm)	Deployment date	Tracking duration (d)	No. of relocations	Max. displacement (km)
4413a	–	18 Aug 2004	24	89	555
4416a	78.50	04 Oct 2004	132	195	663
49819a	71.50	08 Aug 2004	596	1708	746
49827a	74.00	28 Jul 2004	345	1440	683
49829a	76.00	30 Jul 2004	221	747	640
52200a*	84.00	14 Aug 2004	83	158	652
57393a	86.00	07 Jul 2005	144	218	604
34208a*	86.00	19 Aug 2006	250	353	605
64702a	89.00	25 Aug 2006	714	484	635
68125a	–	03 Sep 2006	565	1654	666
68554a	76.00	18 Aug 2006	118	95	1292
68558a	90.00	30 Aug 2006	149	337	540