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Predicting residence time using a continuous-time discrete-space model of leatherback turtle satellite telemetry data

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Abstract. The utilization and capabilities of biotelemetry are expanding enormously as technology and access rapidly improve. These large, correlated datasets pose statistical challenges requiring advanced statistical techniques to appropriately interpret and model animal movement. We used satellite telemetry data of critically endangered Eastern Pacific leatherback turtles (*Dermochelys coriacea*) to develop a habitat-based model of their motility (and conversely residence time) using a hierarchical Bayesian framework, which could be broadly applied across species. To account for the spatiotemporally auto-correlated, unbalanced, and presence-only telemetry observations, in combination with dynamic environmental variables, a novel modeling approach was applied. We expanded a Poisson generalized linear model in a continuous-time discrete-space (CTDS) model framework to predict individual leatherback movement based on environmental drivers, such as sea surface temperature. Population-level movement estimates were then obtained with a Bayesian approach and used to create monthly, near real-time predictions of Eastern Pacific leatherback movement in the South Pacific Ocean. This model framework will inform the development of a dynamic ocean management model, "South Pacific TurtleWatch (SPTW)," and could be applied to telemetry data from other populations and species to predict motility and residence times in dynamic environments, while accounting for statistical uncertainties arising at multiple stages of telemetry analysis.

Key words: animal behavior; Bayesian; biologging; continuous-time discrete-space; *Dermochelys coriacea;* leatherback turtles; movement; telemetry.

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Introduction

With the advancements in telemetry technologies, animal movement data have been collected with increasing duration, resolution, and accuracy (Hooten et al. 2017). These telemetry data provide opportunities for resource selection studies (Johnson et al. 2008*b*), which examine the complex interactions between animal populations and environmental processes. The high dimensionality of

modern animal movement data, however, calls for development of efficient computational methods and the ability to incorporate both static (e.g., bathymetry) and dynamic (e.g., sea surface temperature) environmental drivers that can influence animal movements. For aquatic and exploited species, insights from such studies can in turn enable dynamic ocean management, spatiotemporally varying management based on the incorporation of near real-time data (Howell et al. 2008, Block et al. 2011, Maxwell et al. 2015, Hazen et al. 2016, 2018).

Telemetry data provide valuable animal movement information, but are characterized by many challenging statistical properties, such as non-normal measurement errors (Jonsen et al. 2005), temporal auto-correlation (Fleming et al. 2015), and unbalanced and presence-only sampling design (Aarts et al. 2008). Modern statistical models include state-space model approaches to model measurement errors and dynamics of the movement process (Jonsen et al. 2005), continuous-time models of unbalanced sampling (Johnson et al. 2008*a*), and agent-based or velocity-based models (Hooten et al. 2010, Hanks et al. 2011). These approaches, however, tend to use customized Markov chain Monte Carlo (MCMC) algorithms for statistical inference, which are computationally demanding, and generally focus on statistical inference of individual-level movement (Hooten et al. 2016). With the increasing availability of telemetry observations from multiple individuals, it is natural to generalize this individual-level inference to the population level, although there are the added challenges of individual-level or sampling variability (Aarts et al. 2008).

Telemetry data are increasingly being used in species distribution models (Hazen et al. 2016, 2018). Although terrestrial studies tend to use environmental variables based on static geographic features at a fixed resolution, this may not adequately represent the environmental conditions experienced by marine species within a dynamic seascape (Hidalgo et al. 2016). Thus, it is important to consider movements of highly migratory marine species in relation to the contemporaneous environment they are experiencing, particularly for highly dynamic features (Mannocci et al. 2017).

In order to account for the various sources of uncertainty and complexity inherent within telemetry data, Hooten et al. (2016) and Hanks et al. (2015) proposed a Bayesian hierarchical approach to statistical inference of population-level movement. This hierarchical approach incorporates uncertainties from multiple sources, such as inaccuracy of location observations, process variability from stochastic movement processes, and sampling variability among individuals. In addition, this approach can be formulated in the classical generalized linear mixed model framework. Although previously implemented with static environmental variables, we generalized the modeling approach to incorporate dynamic environmental drivers, essential to understanding and predicting the spatiotemporal distribution of highly migratory species. We utilized and modified this statistically robust approach to study dynamic resource selection using a large telemetry dataset of Eastern Pacific leatherback turtles (*Dermochelys coriacea*). The "ctmcmove" R package (Hanks 2018) was generalized to achieve the input of dynamic environmental drivers (see Data S1). Thus, this dynamic framework can be applied to other populations and species tracked through a dynamic seascape to predict motility and residence time based on changing environmental conditions.

Methods

Leatherback turtle data

Adult females were tagged with Argos satellite transmitters at nesting beaches in Mexico ($n = 1$) and Costa Rica (2003–2008) (Fig. 1; $n = 42$; Shillinger et al. 2008, 2010, Bailey et al. 2012*b*). Two juvenile leatherbacks caught in the Peruvian driftnet fishery were released with Argos tags (2014). Additional data from Mexiquillo, Cahuitán, and Agua Blanca, Mexico ($n = 24$; 1993–2003); Playa Grande, Costa Rica ($n = 8$; 1992–1995); and Peru ($n = 2$; 2014–2015) were not included within the final analyses due to substantial gaps in the availability of associated remotely sensed environmental datasets.

State-space model

We applied a Bayesian switching state-space model (SSSM; Jonsen et al. 2005, 2007) to raw satellite telemetry positions and obtained mean daily location and behavioral mode estimates (classified as transiting or foraging) for each

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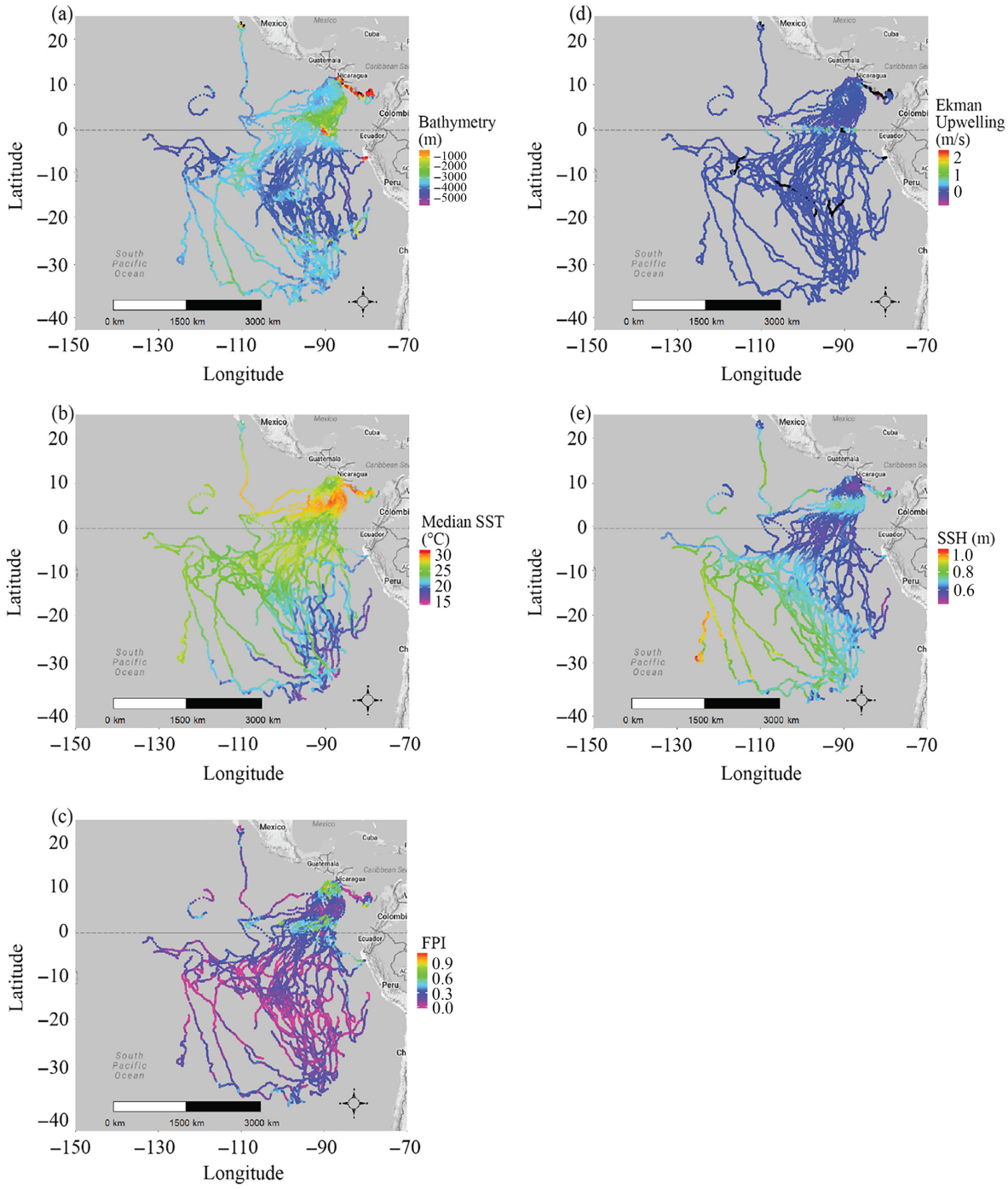


Fig. 1. Monthly values for each of the modeled environmental variables: (a) bathymetry (m), (b) sea surface temperature (°C), (c) frontal probability index, (d) Ekman upwelling (m/s), and (e) sea surface height (m) for leatherback observations based on the estimated mean daily positions from the switching state-space model. Maps were generated using "ggmap" in R (Kahle and Wickham 2013).

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individual track. We distinguished post-nesting behavior from inter-nesting behavior for the leatherbacks tagged on the nesting beaches by removing the initial part of the track that was indicative of inter-nesting behavior as in Bailey et al. (2008, 2012*a*). Only post-nesting portions of the tracks of at least 30-d duration were included in the analysis (Bailey et al. 2012*a*). The SSSM package "bsam" (Jonsen et al. 2005, Jonsen 2016, R Core Team 2017) was chosen over other R packages (e.g., "crawl"; Johnson et al. 2008*a*, Johnson and London 2018) because the SSSM provided the behavioral mode estimation necessary for this track delineation and had been used in previous studies with these tracks (Bailey et al. 2008, 2012*a*, *b*, Shillinger et al. 2008, 2010, Block et al. 2011). By removing inter-nesting females, we assumed sex did not influence movement behavior in this population (James et al. 2005, Benson et al. 2011). Two MCMCs were run with 30,000 samples, a burn-in of 20,000, and thinning of 10. Switching state-space model-derived position estimates on land were corrected to the nearest plausible location at sea. Tracks with gaps too large for the SSSM to accurately interpolate across (≥20 d) were split into track sections (n = 12 tracks split). All analyses were conducted in the R statistical environment (R Core Team 2017).

Environmental covariates

Environmental covariates included in the model were sea surface temperature (SST), bathymetry, sea surface height (SSH), frontal probability index (FPI), and Ekman upwelling (Fig. 1; see Appendix S1: Table S1). Monthly values were obtained from the NOAA/NMFS Southwest Fisheries Science Center, Environmental Research Division's ERDDAP server (https://coastwatch.pfeg.noaa.gov/erddap; Simons 2016), E.U. Copernicus Marine and Environment Monitoring Service (CMEMS; marine.copernicus.eu), and Plymouth Marine Laboratory (following method in Miller et al. 2015) within a latitudinal range of −42° to 30° N and longitude from −140° to −70° E. We chose to build the model over a 0.5° grid cell to provide a cell size that leatherbacks could move across within one day given transiting speed estimates (Shillinger et al. 2008), but as large as possible to reduce computational intensity given the large prediction area (see Appendix S2).

Continuous-time discrete-space model

Continuous-time discrete-space (CTDS; Hanks et al. 2015) is a habitat model that accommodates unbalanced telemetry data from individual Argos tracks and gridded estimates of environmental covariates to provide movement estimates through a given area. Specifically, let $\left\{\widehat{\hat{y}}_i(u), u = 1\ldots, T\right\}$ denote the estimated daily track locations from the SSSM, where i denotes an individual animal. Let β_i denote the CTDS parameter for this individual. We denote the individual CTDS model $\pi(\hat{y}_i|\beta_i)$ as following: discretize the continuous track according to the granularity of the environmental covariates, and let $\boldsymbol{S}_i = \left\{\boldsymbol{g}_i, \boldsymbol{t}_i, \boldsymbol{\tau}_i\right\}$ denote the animal's CTDS path, where $\boldsymbol{g}_i = \{g_{ic}, c = 0, \ldots, C\}$ denotes the sequence of starting cells traversed by the animal, and $t_i = \{\boldsymbol{t}_{ic}, c = 1, \ldots, C\}$ and $\boldsymbol{\tau}_i = \{\tau_{ic}, c = 1, \ldots, C\}$ the time of entry and residence time for each cell $g_{i,c-1}$ before transition into $g_{i,c}$.

Let $k \sim l$ denote two neighboring grid cells, and $\mathbf{x}_{i,kl,t}$ the corresponding vector of environmental drivers. The transition rate between cells can then be modeled with the environmental data via a log link

$$\lambda_{i,kl}(\beta_i, t) = \exp\left\{\mathbf{x}_{i,kl,t}^{\mathrm{T}}\beta_i\right\}. \quad (1)$$

We considered only motility-based covariates and assumed that impacts of gradient-based covariates on turtle movements would be minor at the population level.

$$\lambda_{i,kl}(\beta_i, t) = \exp\left\{\mathbf{x}_{i,k,t}^{\mathrm{T}}\beta_i\right\}. \quad (2)$$

The transition to neighboring cells follows a multinomial process with probability proportional to (1). Let $|N_k|$ denote the number of adjacent cells to cell k, the total transition rate from a cell k equals

$$\lambda_{i,k}(\beta_i, t) = \sum_{l\sim k}\lambda_{i,kl}(\beta_i, t) = |N_k|\exp\left\{\mathbf{x}_{i,k,t}^{\mathrm{T}}\beta_i\right\}, \quad (3)$$

and the corresponding residence time at cell k follows an exponential distribution

$$\tau_{i,g_c} \equiv \tau_{i,c} \sim \text{exponential}\left[\lambda_{i,k}(\beta_i, t)\right], \quad (4)$$

where exponential (λ) denotes the distribution with mean 1/λ.

Assuming conditional independence between transitions and residence time—given the

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environmental drivers—within and across transitions, the likelihood of the CTDS path S_i according to models 1–4 can be written as

$$\prod_{c=1}^{C} \lambda_{i,c-1,c}(\beta_i, t_{i,c}) \exp\{-\tau_{i,c}\lambda_{i,c-1}(\beta_i, t_{i,c})\}, \quad (5)$$

where we write $\lambda_{i,g_{c-1},g_c} \equiv \lambda_{i,c-1,c}$ for brevity of notation. Hanks et al. (2015) introduced the latent variable $z_{c,c'} = 1(g_{c'} = g_{c+1})$ and write the likelihood above as

$$\prod_{c=1}^{C} \prod_{c' \sim c-1} \lambda_{i,c-1,c'}(\beta_i, t_{i,c})^{z_{i,c-1,c'}} \exp\{-\tau_{ic}\lambda_{i,c-1,c'}(\beta_i, t_{ic})\}. \quad (6)$$

The advantage of the parameterization is that model 6 is an independent Poisson likelihood with data $\{z_{i,c,c'}, c = 0, C-1, c \sim c'\}$ and offset $\{\log(\tau_{i,c}), c = 1, \ldots, C\}$, for which the iterative generalized least squares algorithm can be used for estimation in the frequentist framework.

Population-level inference

The CTDS models individual-level association between movement and environmental cues. To account for sampling variabilities among individuals and then generalize the individual response pattern to the population level, we applied a hierarchical model that uses random effects for individual-level parameters (Hooten et al. 2016). Let n denote the number of individuals and $\pi(\hat{y}_i|\beta_i)$ denote the CTDS likelihood function (6) of individual $i = 1, \ldots, n$ as the first stage of the hierarchical model. At the second stage, we specify a conventional normal prior for β_i

$$\beta_i \sim \mathrm{N}(\mu_\beta, \Sigma_\beta), \quad \textit{for} \quad i = 1, \ldots, n, \quad (7)$$

where μ_β, Σ_β denote the population-level parameter and the covariance matrix of individual-level sampling variabilities around μ_β. Letting $\nu = \dim(\mathbf{x})$ denote the dimensionality of the environmental covariates, we assign a vague hyper-prior to complete the hierarchical Bayesian model specification.

$$\mu_\beta \sim N(\mu_0, \Sigma_0), \Sigma^{-1} \sim \mathrm{Wishart}(\nu, Q), \quad (8)$$

where μ_0 is $\nu \times 1$ vector of zero, Σ_0 is $100 \times I$, where I is a $\nu \times \nu$ identity matrix, and $Q = \nu^{-1}I$.

Markov chain Monte Carlo algorithm

The hierarchical model (6–8) follows the generalized linear mixed model family (see Appendix S2). We used the Hamilton MCMC with No-U-Turn algorithm (Hoffman and Gelman 2014) due to its superior convergence performance. The "brms" package (Bürkner 2017) served as an R interface to Stan and model selection. Markov chain Monte Carlo convergence diagnostics were conducted for μ_β, Σ_β, and selected β_i parameters based on the R "coda" package (Brooks and Gelman 1998, Plummer et al. 2006).

Model selection

The full model available for selection was symbolically

$$\begin{aligned} \log(\text{motility}) \sim \text{bathymetry} + f(\text{SST}) \\ + \text{Ekman} + \text{FPI} + \text{SSH} + \text{crw}, \end{aligned} \quad (9)$$

where motility is the total rate of transitions out of a grid cell per day. Each environmental variable is incorporated as a dynamic driver based on the time of entry into the initial cell for each movement c. We incorporated quadratic sea surface temperature and linear bathymetry, Ekman upwelling, frontal probability index, and sea surface height. The crw term is a constructed auto-covariate term (Illian et al. 2012), which measures the directional change between the adjacent moves, and is important in the model to incorporate temporal auto-correlation. The remaining model covariates were selected first using a "top-down" strategy based on posterior leave-one-out (LOO) predictive statistics (Vehtari et al. 2017). We sequentially removed each variable from the hierarchical model (6–8) and compared the LOO statistics between the original model and each simplified model. The variable resulting in the least significant difference in the LOO statistic is removed. This drop-one process stops when no variable can be removed from the model. The automatic model selection was supplemented by manual interpretations.

Model prediction

We used residence time as a metric to map the predictive resource selection (Hanks et al. 2015). Let $\mathbf{x}_j^p, j = 1, \ldots, J$ denote the value of selected covariates at grid cells g_j, which covers the entire

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leatherback habitat in the eastern Pacific. The mean residence time at each cell can be defined as

$$r_j(\mu_b) = \exp\left\{-\mathbf{x}_j^{p\mathrm{T}}\mu_\beta\right\} \quad \text{for} \quad j = 1,\ldots J. \qquad (10)$$

Posterior inference of $r_j(\mu_\beta)$ can be forward simulated based on posterior samples of μ_β, while accounting for the joint distribution of all model parameters. The posterior mean and interquartile-range can be mapped as the estimated residence time and associated uncertainty.

Results

Based on the results of the SSSM, there were 58 tracks from 45 individual turtles used in the modeling process, totaling 10,066 daily positions spanning February 2003 through December 2014 (Table 1). The best model from the posterior LOO model selection was the full model bathymetry, SST, SST^2, FPI, and SSH (ΔLooIC = −4.57, SE(ΔLooIC) = 3.53, $P = 0.20$; see Appendix S1: Table S2). Population-level Eastern Pacific leatherback motility estimates (μ_β) indicate effects for each model covariate given no zero overlap for each 95% confidence interval (Table 2). Leatherbacks are more likely to move (decrease residence time) with high and low values of SST ($\mu_\beta = 0.54$; SST^2: $\mu_\beta = 0.72$) and high FPI ($\mu_\beta = 0.76$), while reducing movement in areas of high SSH ($\mu_\beta = -1.330$). Environmental predictors were checked for collinearity. Residence time in days was predicted for June 2016 (Fig. 2a) and December 2016 (Fig. 2b).

Discussion

This habitat-based movement modeling approach can serve as a foundation for studies utilizing tagging data to overcome statistical challenges for population-level movements (see Appendix S1: Fig. S1). Organismal movement is often highly complex, and this framework accommodates intricate environmental selection by individuals scaled to populations. This process can be applied to tagging studies to account for the spatiotemporally auto-correlated, unbalanced, and presence-only telemetry observations in a dynamic environment. It is broadly applicable, automatable, parallelizable, and interpretable, easing computing demands of vast datasets. This considers and accounts for often-overlooked data source errors, reducing model uncertainty. Overall, this hierarchical modeling approach represents a higher-level estimation of persistent, predictable behavior across any population of study.

Compared to other movement studies, the CTDS model framework does not require the

Table 2. Population-level coefficient estimates (posterior median and 95% credible sets) from continuous-time discrete-space hierarchical model relating motility with environmental covariates.

Coefficient	Estimate	Estimate error	2.5 percentile	97.5 percentile
Intercept	−1.070	0.190	−1.460	−0.680
Bathy	0.080	0.030	0.030	0.130
SST	0.540	0.080	0.380	0.700
SST^2	0.720	0.190	0.370	1.100
FPI	0.760	0.120	0.530	0.970
SSH	−1.330	0.220	−1.760	−0.890
crw	0.670	0.030	0.610	0.730

Notes: crw denotes the direction of the most recent movement at each time point. Tracks ($n = 58$) used were longer than 30 d, include all environmental predictors, and do not exhibit collinearity between predictors. Bathy is bathymetry, SST is sea surface temperature, SST^2 is quadratic sea surface temperature, FPI is the frontal probability index, and SSH is sea surface height.

Table 1. Post-nesting Eastern Pacific leatherback positional information modified from Bailey et al. (2012*a*).

Tagging location	Data type	Years	Total daily positions	No. tags	Track duration (d)		
					Mean	Min	Max
Mexico: nesting	Argos satellite tag	2003	92	1	NA	NA	NA
Costa Rica: nesting	Argos satellite tag	2004–2008	9841	42	179	34	513
Peru: driftnet fisheries bycatch	Argos satellite tag	2014	133	2	67	48	85
Total post-nesting tracks	Argos satellite tag	2003–2014	10,066	45	174	34	513

Notes: All tracks included Argos satellite tag data from starting locations in Mexico, Costa Rica, and Peru with either nesting or fisheries incidentally caught turtles.

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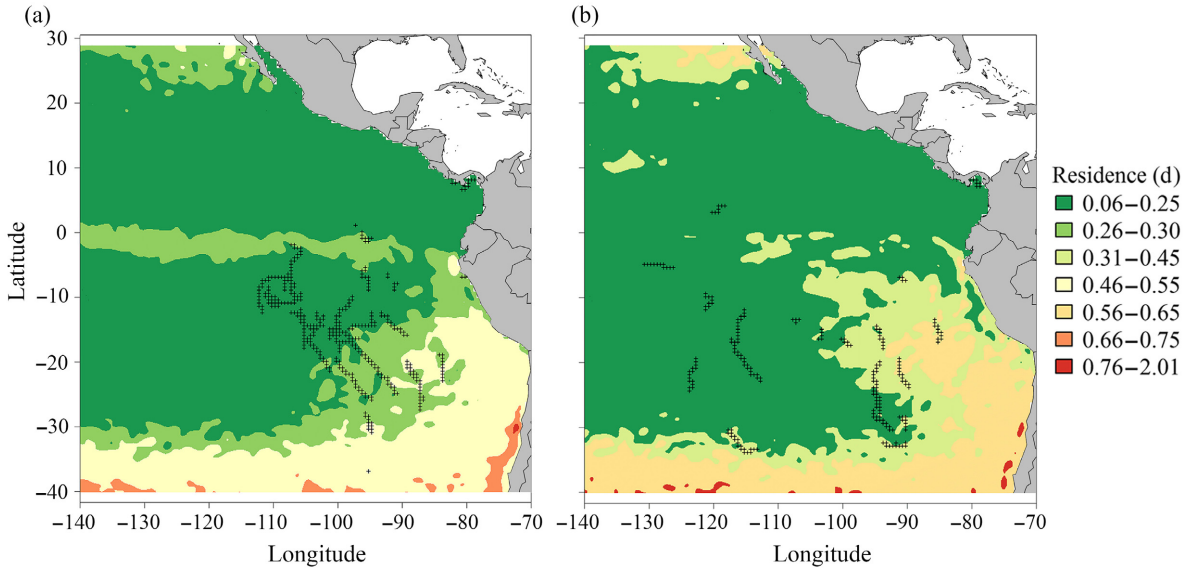


Fig. 2. Leatherback turtle residence time (d) based on continuous-time discrete-space predictions using 45 individuals (n = 58 tracks) and environmental covariates of bathymetry, sea surface temperature, quadratic sea surface temperature, frontal probability index, and sea surface height for (a) June 2016 and (b) December 2016. Plus signs represent daily positions of leatherbacks included in the model during the respective months.

creation of false absences or pseudo-tracks commonly used in generalized additive mixed model analyses of telemetry data (Willis-Norton et al. 2015, Hazen et al. 2016). This framework provides a means strengthening dynamic management models by incorporating multiple data sources, including irregularly spaced data, which strengthens the ability to model available data and maximize sample sizes. The approach reported here is flexible, particularly in that it can be adapted around the same framework indeterminate of the model used. Wilson et al. (2018) utilized a CTDS approach to model species distribution based on static seascape variables. Their approach accounted for unobserved movements into preferred habitats, highlighting these model benefits for marine telemetry data. We incorporated dynamic environmental covariates in CTDS to better reflect changing environmental conditions encountered by migrating marine species through time (e.g., seasonal seascape changes). This enabled short-term forecasting of preferential spatial use at a monthly timescale. The monthly prediction could be more relevant for dynamic ocean management than the long-term utilization density, which was more appropriate for species interacting with static environmental variables. Overall, CTDS provides population-level inference through MCMC compared to many movement studies based on individual-level models.

Using the CTDS modeling framework, we predicted the residence time of leatherback turtles during two months in 2016 (Fig. 2). Residence time estimates should predict leatherbacks transiting quickly from warm, coastal waters in December near the nesting beaches, moving toward productive fronts in the South Pacific Gyre (Fig. 2b). Turtles begin their post-nesting migration southwards through the eastern tropical Pacific in February to May (Shillinger et al. 2008). In the South Pacific Ocean, there is a seasonal pattern with turtles moving south to the South Pacific Subtropical Convergence (Saba et al. 2008) in the austral summer (December to April) when temperatures are higher at these temperate latitudes (~30–40° S) (Shillinger et al. 2011). Leatherbacks generally return north to warmer, tropical waters (~0–20° S) in the winter (May–November; Fig. 2a). As expected, there is a large area in the South Pacific Gyre with low residence time in this warm, less productive water mass during both June and December 2016. In both months, leatherbacks were likely to move

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more slowly through the productive waters west of Peru and Chile. The prediction maps can serve as a valuable tool to assist with dynamic ocean management (Howell et al. 2015) to prevent and ultimately reduce bycatch of leatherback turtles in fisheries through their incorporation into an end-user interface, South Pacific TurtleWatch (SPTW).

Previous studies have conveyed the complex relationship between satellite-derived surface environmental metrics and leatherback distribution (Shillinger et al. 2008, 2011, Bailey et al. 2012*a*). Higher latitudes in the South Pacific are more productive, but temperature is ultimately expected to be a proxy for predicting prey abundance (gelatinous zooplankton), the driver of leatherback movement (Heaslip et al. 2012, Jones et al. 2012). Leatherbacks avoid cooler water farther south where they forage around 19°C and generally avoid warmer water (>31°C) when breeding (Shillinger et al. 2011). This expectation of higher residence time in the north during austral winter and higher probability in the south during summer, creating a north–south seasonal cycle throughout the South Pacific, is generally captured in our model predictions.

Although this modeling approach has many benefits, there are several limitations and complexities to consider. The model must be evaluated for its ability to predict the biologically realistic behavioral responses. If regression coefficients are small at the individual level, patterns across population-level inferences will not be observed. The uncertainty in the estimated movement paths of individuals can be decreased in this framework by applying multiple path imputations (Hooten et al. 2010, Hanks et al. 2015, Wilson et al. 2018), but with larger telemetry datasets, it can become computationally challenging. Within our model, vague priors were used to drive inference. However, priors can be specified to increase predictive power when greater species information is available, a benefit of using this Bayesian approach. A manual backward model selection was conducted, but a Bayesian model averaging approach could make it easier to evaluate overall predictive power of a given set of predictor variables. We used a generalized linear model, having to assume the association between the leatherback movement and environmental variables was parametric. However, a semi-parametric generalized additive mixed model could be incorporated to model more complex associations with the environment.

The amount of telemetry data becoming available is ever-expanding, as are the complex models relating animal behavior to environmental cues, but high computational power is often required. Therefore, it is essential to use a predictive model capable of incorporating robust model estimates of movement over large tracking datasets and vast amounts of environmental information. Here, we utilized a novel approach by incorporating dynamic drivers of animal movement in a broad framework other studies can utilize, and we addressed the data analysis needs of more advanced observational techniques without super-computing computational requirements. The ability to predict motility and residence times of marine species based on environmental conditions can play a valuable role in assisting with their management and conservation in a dynamic ocean.

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