

Ecosphere

Predicting Residence Time

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

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18 Abstract

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

36 **Key Words**

37 animal behavior; Bayesian; biologging; CTDS; leatherback turtles; movement; telemetry.

38 **Introduction**

39 With the advancements in telemetry technologies, animal movement data have been
40 collected with increasing duration, resolution, and accuracy (Hooten et al. 2017). These
41 telemetry data provide opportunities for resource selection studies (Johnson et al. 2008b), which
42 examine the complex interactions between the animal population and environmental processes.
43 The high dimensionality of modern animal movement data, however, calls for development of
44 efficient computational methods and the ability to incorporate both static (e.g. bathymetry) and
45 dynamic (e.g. sea surface temperature) environmental drives that can influence animal
46 movements. For aquatic and exploited species, insights from such studies can in turn enable
47 dynamic ocean management, spatiotemporally varying management based on the incorporation
48 of near real-time data (Howell et al. 2008, Block et al. 2011, Maxwell et al. 2015, Hazen et al.
49 2016, 2018).

50 Telemetry data provide valuable animal movement information, but are characterized by
51 many challenging statistical properties, such as non-normal measurement errors (Jonsen et al.
52 2005), temporal auto-correlation (Fleming et al. 2015), and unbalanced and presence only
53 sampling design (Aarts et al. 2008). Modern statistical models include state-space model
54 approaches to model measurement errors and dynamics of the movement process (Jonsen et al.
55 2005), continuous-time models of unbalanced sampling (Johnson et al. 2008a), and agent-based
56 or velocity-based models (Hooten et al. 2010, Hanks et al. 2011). These approaches, however,
57 tend to use customized Markov chain Monte Carlo (MCMC) algorithms for statistical inference,
58 which are computationally demanding, and generally focus on statistical inference of individual
59 level movement (Hooten et al. 2016). With the increasing availability of telemetry observations
60 from multiple individuals, it is natural to generalize this individual level inference to the

61 population level, although there are the added challenges of individual level or sampling
62 variability (Aarts et al. 2008).

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

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

83 populations and species tracked through a dynamic seascape to predict motility and residence
84 time based on changing environmental conditions.

85 **Methods**

86 **Leatherback turtle data**

87 Adult females were tagged with Argos satellite transmitters at nesting beaches in Mexico
88 ($n = 1$) and Costa Rica (2003 – 2008) (Fig. 1) ($n = 42$; Shillinger et al. 2008, 2010, Bailey et al.
89 2012b). Two juvenile leatherbacks caught in the Peruvian driftnet fishery were released with
90 Argos tags (2014). Additional data from Mexiquillo, Cahuitán, and Agua Blanca, Mexico ($n =$
91 24; 1993 – 2003), Playa Grande, Costa Rica ($n = 8$; 1992 – 1995), and Peru ($n = 2$; 2014 – 2015)
92 were not included within the final analyses due to significant gaps in the availability of
93 associated remotely sensed environmental datasets.

94 **State-space model**

95 We applied a Bayesian switching state-space model (SSSM) (Jonsen et al. 2005, 2007) to
96 raw satellite telemetry positions and obtained mean daily location and behavioral mode estimates
97 (classified as transiting or foraging) for each individual track. We distinguished post-nesting
98 behavior from inter-nesting behavior for the leatherbacks tagged on the nesting beaches by
99 removing the initial part of the track that was indicative of inter-nesting behavior as in Bailey et
100 al. (2008, 2012a). Only post-nesting portions of the tracks of at least 30 days duration were
101 included in the analysis (Bailey et al. 2012a). The SSSM package “bsam” (Jonsen et al. 2005,
102 Jonsen 2016, R Core Team 2017) was chosen over other R packages (e.g. “crawl”; Johnson et al.
103 2008a, Johnson and London 2018) because the SSSM provided the behavioral mode estimation
104 necessary for this track delineation and had been used in previous studies with these tracks
105 (Bailey et al. 2008, 2012a, 2012b, Shillinger et al. 2008, 2010, Block et al. 2011). By removing
106 inter-nesting females, we assumed sex did not influence movement behavior in this population

107 (James et al. 2005, Benson et al. 2011). Two MCMCs were run with 30,000 samples, a burn-in
108 of 20,000, and thinning of 10. SSSM-derived position estimates on land were corrected to the
109 nearest plausible location at sea. Tracks with gaps too large for the SSSM to accurately
110 interpolate across (≥ 20 days) were split into track sections ($n = 12$ tracks split). All analyses
111 were conducted in the R statistical environment (R Core Team 2017).

112 **Environmental covariates**

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

124 **Continuous-time discrete-space model**

125 Continuous-time discrete-space (CTDS) (Hanks et al. 2015) is a habitat model that
126 accommodates unbalanced telemetry data from individual Argos tracks and gridded estimates of
127 environmental covariates to provide movement estimates through a given area. Specifically, let
128 $\{\hat{y}_i(u), u = 1 \dots, T\}$ denote the estimated daily track locations from the SSSM, where i denotes an
129 individual animal. Let β_i denote the CTDS parameter for this individual. We denote the
130 individual CTDS model $\pi(\hat{y}_i|\beta_i)$ as following: discretize the continuous track according to the

131 granularity of the environmental covariates, and let $\mathbf{S}_i = \{\mathbf{g}_i, \mathbf{t}_i, \boldsymbol{\tau}_i\}$ denote the animal's CTDS
 132 path, where $\mathbf{g}_i = \{g_{i,c}, c = 0, \dots, C\}$ denotes the sequence of starting cells traversed by the
 133 animal, $\mathbf{t}_i = \{t_{i,c}, c = 1, \dots, C\}$, and $\boldsymbol{\tau}_i = \{\tau_{i,c}, c = 1, \dots, C\}$ the time of entry and residence time
 134 for each cell $g_{i,c-1}$ before transition into $g_{i,c}$.

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

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

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

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

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

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

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

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

144 where $\text{exponential}(\lambda)$ denotes the distribution with mean $1/\lambda$.

145 Assuming conditional independence between transitions and residence time – given the
 146 environmental drivers – within and across transitions, the likelihood of the CTDS path \mathbf{S}_i
 147 according to models (1 – 4) can be written as

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

148 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
 149 latent variable $z_{c,c'} = 1(g_{c'} = g_{c+1})$ and write the likelihood above as

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

150 The advantage of the parameterization is that (6) is an independent Poisson likelihood with data
 151 $\{z_{i,c,c'}, c = 0, C - 1, c \sim c'\}$ and offset $\{\log(\tau_{i,c}), c = 1, \dots, C\}$, for which the iterative
 152 generalized least squares algorithm can be used for estimation in the frequentist framework.

153 **Population level inference**

154 The CTDS models individual level association between movement and environmental
 155 cues. To account for sampling variabilities among individuals and then generalize the individual
 156 response pattern to the population level, we applied a hierarchical model that uses random effects
 157 for individual level parameters (Hooten et al. 2016). Let n denote the number of individuals and
 158 $\pi(\hat{y}_i | \beta_i)$ denote the CTDS likelihood function (6) of individual $i = 1, \dots, n$ as the first stage of
 159 the hierarchical model. At the second stage, we specify a conventional normal prior for β_i

$$\beta_i \sim \mathbf{N}(\mu_\beta, \Sigma_\beta), \quad \text{for } i = 1, \dots, n, \quad (7)$$

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

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

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

165 Markov chain Monte Carlo algorithm

166 The hierarchical model (6 – 8) follows the generalized linear mixed model family (see
167 Appendix S2). We used the Hamilton MCMC with No-U-Turn algorithm (Hoffman and Gelman
168 2014) due to its superior convergence performance. The “brms” package (Bürkner 2017) served
169 as an R interface to Stan and model selection. MCMC convergence diagnostics were conducted
170 for μ_β, Σ_β , and selected β_i parameters based on the R “coda” package (Brooks and Gelman 1998,
171 Plummer et al. 2006).

172 Model selection

173 The full model available for selection was symbolically

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

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

187 **Model prediction**

188 We used residence time as a metric to map the predictive resource selection (Hanks et al.
 189 2015). Let $\mathbf{x}_j^p, j = 1, \dots, J$ denote the value of selected covariates at grid cells g_j , which covers
 190 the entire leatherback habitat in the eastern Pacific. The mean residence time at each cell can be
 191 defined as

$$r_j(\mu_b) = \exp\{-\mathbf{x}_j^{pT} \mu_\beta\} \text{ for } j = 1, \dots, J. \quad (10)$$

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

195 **Results**

196 Based on the results of the SSSM, there were 58 tracks from 45 individual turtles used
 197 in the modeling process, totaling 10,066 daily positions spanning February 2003 through
 198 December 2014 (Table 1). The best model from the posterior LOO model selection was the full
 199 model bathymetry, SST, SST², FPI, and SSH ($\Delta\text{LooIC} = -4.57$, $\text{SE}(\Delta\text{LooIC}) = 3.53$, $p = 0.20$;
 200 see Appendix S1: Table S2). Population level Eastern Pacific leatherback motility estimates
 201 (μ_β) indicate effects for each model covariate given no zero overlap for each 95% confidence
 202 interval (Table 2). Leatherbacks are more likely to move (decrease residence time) with high
 203 and low values of SST ($\mu_\beta = 0.54$; SST²: $\mu_\beta = 0.72$) and high FPI ($\mu_\beta = 0.76$), while reducing
 204 movement in areas of high SSH ($\mu_\beta = -1.330$). Environmental predictors were checked for
 205 collinearity. Residence time in days were predicted for June 2016 (Fig. 2a) and December 2016
 206 (Fig. 2b).

207 **Discussion**

208 This habitat-based movement modeling approach can serve as a foundation for studies

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

218 Compared to other movement studies, the CTDS model framework does not require the
219 creation of false-absences or pseudo-tracks commonly used in generalized additive mixed model
220 analyses of telemetry data (e.g. Willis-Norton et al. 2015, Hazen et al. 2016). This framework
221 provides a means strengthening dynamic management models by incorporating multiple data
222 sources, including irregularly spaced data, which strengthens the ability to model available data
223 and maximize sample sizes. The approach reported here is flexible, particularly in that it is can
224 be adapted around the same framework indeterminate of the model used. Wilson et al. (2018)
225 utilized a CTDS approach to model species distribution based on static seascape variables. Their
226 approach accounted for unobserved movements into preferred habitats, highlighting these model
227 benefits for marine telemetry data. We incorporated dynamic environmental covariates in CTDS
228 to better reflect changing environmental conditions encountered by migrating marine species
229 through time (e.g. seasonal seascape changes). This enabled short-term forecasting of preferential
230 spatial use at a monthly time-scale. The monthly prediction could be more relevant for dynamic
231 ocean management than the long-term utilization density, which was more appropriate for

232 species interacting with static environmental variables. Overall, CTDS provides population-level
233 inference through MCMC compared to many movement studies based on individual-level
234 models.

235 Using the CTDS modeling framework, we predicted the residence time of leatherback
236 turtles during two months in 2016 (Fig. 2). Residence time estimates should predict
237 leatherbacks transiting quickly from warm, coastal waters in December near the nesting
238 beaches, moving towards productive fronts in the South Pacific Gyre (Fig. 2b). Turtles begin
239 their post-nesting migration southwards through the eastern tropical Pacific in February to May
240 (Shillinger et al. 2008). In the South Pacific Ocean, there is a seasonal pattern with turtles
241 moving south to the South Pacific Subtropical Convergence (Saba et al. 2008) in the austral
242 summer (December to April) when temperatures are higher at these temperate latitudes
243 (approximately 30-40°S) (Shillinger et al. 2011). Leatherbacks generally return north to
244 warmer, tropical waters (approximately 0-20°S) in the winter (May to November) (Fig. 2a). As
245 expected, there is a large area in the South Pacific Gyre with low residence time in this warm,
246 less productive water mass during both June and December 2016. In both months, leatherbacks
247 were likely to move more slowly through the productive waters west of Peru and Chile. The
248 prediction maps can serve as a valuable tool to assist with dynamic ocean management (e.g.
249 Howell et al. 2015) to prevent and ultimately reduce bycatch of leatherback turtles in fisheries
250 through their incorporation into an end-user interface, South Pacific TurtleWatch (SPTW).

251 Previous studies have conveyed the complex relationship between satellite-derived
252 surface environmental metrics and leatherback distribution (e.g. Shillinger et al. 2008, 2011,
253 Bailey et al. 2012a). Higher latitudes in the South Pacific are more productive, but temperature is
254 ultimately expected to be a proxy for predicting prey abundance (gelatinous zooplankton), the

255 driver of leatherback movement (Heaslip et al. 2012, Jones et al. 2012). Leatherbacks avoid
256 cooler water farther south where they forage around 19°C and generally avoid warmer water (>
257 31°C) when breeding (Shillinger et al. 2011). This expectation of higher residence time in the
258 north during austral winter and higher probability in the south during summer, creating a north-
259 south seasonal cycle throughout the South Pacific, is generally captured in our model predictions.

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

274 The amount of telemetry data becoming available is ever-expanding, as are the complex
275 models relating animal behavior to environmental cues, but high computational power is often
276 required. Therefore, it is essential to use a predictive model capable of incorporating robust
277 model estimates of movement over large tracking datasets and vast amounts of environmental

278 information. Here, we utilized a novel approach by incorporating dynamic drivers of animal
279 movement in a broad framework other studies can utilize and addressed the data analysis needs
280 of more advanced observational techniques without super-computing computational
281 requirements. The ability to predict motility and residence times of marine species based on
282 environmental conditions can play a valuable role in assisting with their management and
283 conservation in a dynamic ocean.

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436 **Tables**

437 **Table 1.** Post-nesting Eastern Pacific leatherback positional information modified from Bailey et
 438 al. (2012a). All tracks included Argos satellite tag data from starting locations in Mexico, Costa
 439 Rica, and Peru with either nesting or fisheries incidentally caught turtles.

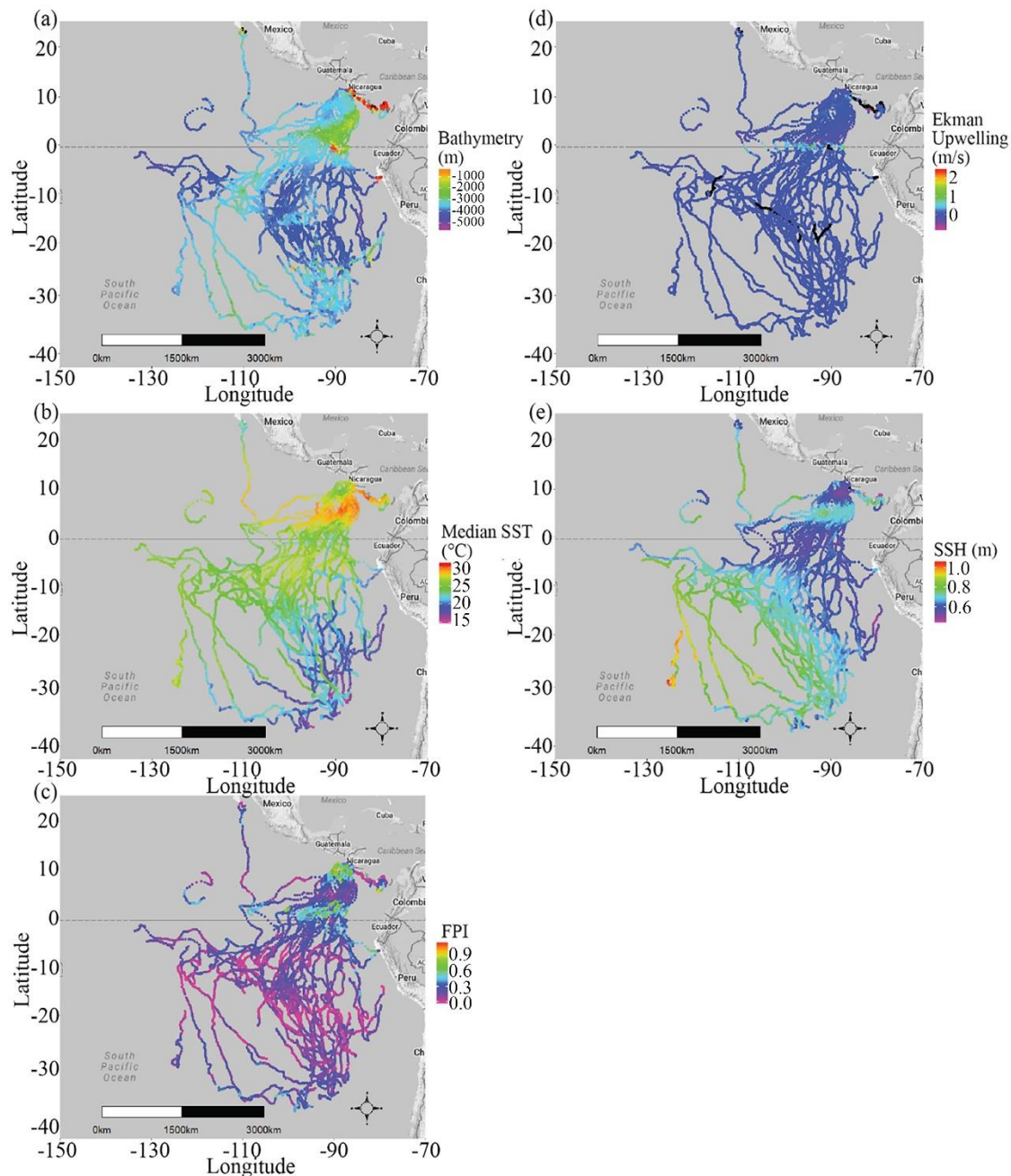
<i>Tagging Location</i>	Data Type	Years	Total Daily Positions	No. Tags	Track Duration (Days)		
					Mean	Min	Max
<i>Mexico: nesting</i>	Argos Satellite Tag	2003	92	1	NA	NA	NA
<i>Costa Rica: nesting</i>	Argos Satellite Tag	2004-2008	9841	42	179	34	513
<i>Peru: driftnet fisheries bycatch</i>	Argos Satellite Tag	2014	133	2	67	48	85
<i>Total Post-Nesting Tracks</i>	Argos Satellite Tag	2003-2014	10,066	45	174	34	513

440

441 **Table 2.** Population level coefficient estimates (posterior median and 95% credible sets) from
 442 CTDS hierarchical model relating motility with environmental covariates. crw denotes the
 443 direction of the most recent movement at each time point. Tracks (n = 58) used were longer than
 444 30 days, include all environmental predictors, and do not exhibit collinearity between predictors.
 445 Bathy is bathymetry, SST is sea surface temperature, SST² is quadratic sea surface temperature,
 446 FPI is the frontal probability index, and SSH is sea surface height.

Coefficient	Estimate	Estimate Error	2.5%ile	97.5%ile
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

447

448 **Figures**

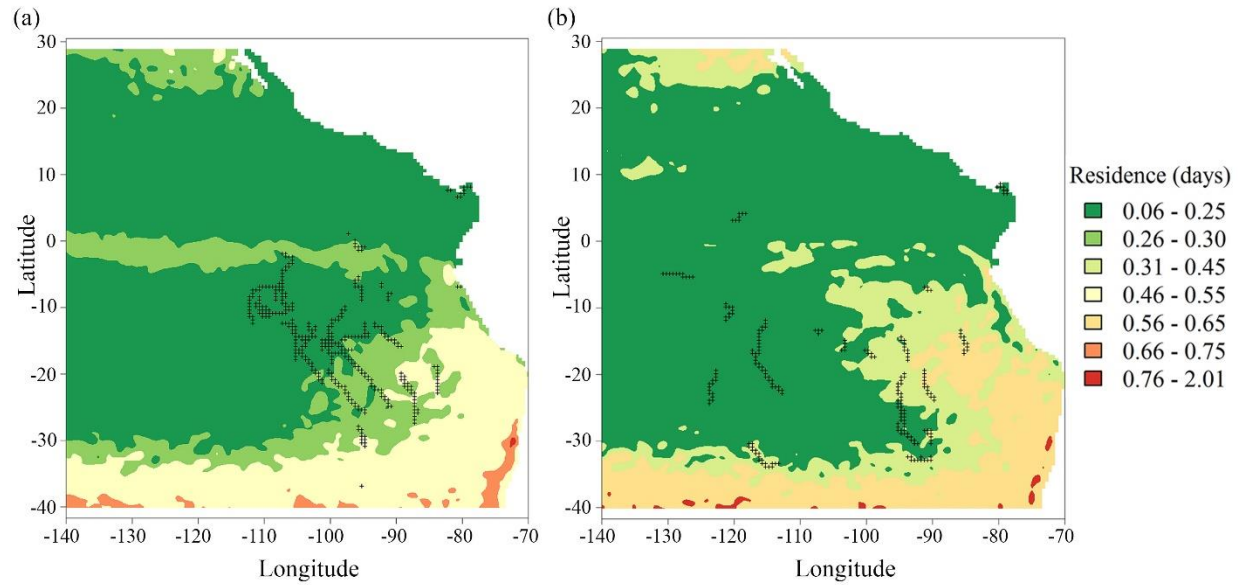
449

450 **Figure 1.** Monthly values for each of the modeled environmental variables: (a) bathymetry (m),451 (b) sea surface temperature ($^{\circ}\text{C}$), (c) frontal probability index, (d) Ekman upwelling (m/s), and

452 (e) sea surface height (m) for leatherback observations based on the estimated mean daily

453 positions from the switching state-space model. Maps were generated using ‘ggmap’ in R (Kahle

454 and Wickham 2013).



455

456 **Figure 2.** Leatherback turtle residence time (days) based on CTDS predictions using 45
457 individuals (n = 58 tracks) and environmental covariates of bathymetry, sea surface temperature,
458 quadratic sea surface temperature, frontal probability index, and sea surface height for (a) June
459 2016 and (b) December 2016. Plus signs represent daily positions of leatherbacks included in the
460 model during the respective months.