Identification of distinct movement patterns in Pacific leatherback turtle populations influenced by ocean conditions

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Abstract. Interactions with fisheries are believed to be a major cause of mortality for adult leatherback turtles (*Dermochelys coriacea*), which is of particular concern in the Pacific Ocean, where they have been rapidly declining. In order to identify where these interactions are occurring and how they may be reduced, it is essential first to understand the movements and behavior of leatherback turtles. There are two regional nesting populations in the East Pacific (EP) and West Pacific (WP), comprising multiple nesting sites. We synthesized tracking data from the two populations and compared their movement patterns. A switching state-space model was applied to 135 Argos satellite tracks to account for observation error, and to distinguish between migratory and area-restricted search behaviors. The tracking data, from the largest leatherback data set ever assembled, indicated that there was a high degree of spatial segregation between EP and WP leatherbacks. Area-restricted search behavior mainly occurred in the southeast Pacific for the EP leatherbacks, whereas the WP leatherbacks had several different search areas in the California Current, central North Pacific, South China Sea, off eastern Indonesia, and off southeastern Australia. We also extracted remotely sensed oceanographic data and applied a generalized linear mixed model to determine if leatherbacks exhibited different behavior in relation to environmental variables. For the WP population, the probability of area-restricted search behavior was positively correlated with chlorophyll-*a* concentration. This response was less strong in the EP population, but these turtles had a higher probability of search behavior where there was greater Ekman upwelling, which may increase the transport of nutrients and consequently prey availability. These divergent responses to oceanographic conditions have implications for leatherback vulnerability to fisheries interactions and to the effects of climate change. The occurrence of leatherback turtles within both coastal and pelagic areas means they have a high risk of exposure to many different fisheries, which may be very distant from their nesting sites. The EP leatherbacks have more limited foraging grounds than the WP leatherbacks, which could make them more susceptible to any temperature or prey changes that occur in response to climate change.

Key words: animal movement; Dermochelys coriacea; *oceanography; Pacific Ocean; satellite telemetry; state-space model.*

INTRODUCTION

Leatherback turtles (*Dermochelys coriacea*) are the widest-ranging marine turtle species, and are known to migrate across entire ocean basins (Hays et al. 2004,

Benson et al. 2007*a*). However, this species is now classified as critically endangered on the 2010 IUCN Red List of Threatened Species, and interactions with fisheries are believed to be a major cause of mortality for adult leatherbacks (Lee Lum 2006, Wallace and Saba 2009). This is of particular concern for leatherback turtle populations in the Pacific Ocean, which have been rapidly declining (Sarti et al. 1996, Spotila et al. 2000). An improved understanding of the spatial and temporal distribution of Pacific leatherback turtles will help us to

identify how and where fisheries interactions may be occurring (Žydelis et al. 2011). This can then be combined with bycatch information to enable suitable mitigation measures to be developed (Howell et al. 2008, McClellan et al. 2009).

There are two regional nesting populations of leatherback turtles in the East Pacific (EP) and West Pacific (WP), composed of multiple nesting sites (Dutton et al. 1999, 2007). Genetic studies have suggested that natal homing occurs (Dutton et al. 1999, 2007), meaning that turtles will periodically return to their natal beaches to breed. Research to date has shown that the WP nesters migrate to multiple foraging destinations in both tropical and temperate latitudes in both hemispheres (Benson et al. 2007a, b, c, 2011). This is in contrast to the EP leatherbacks that generally travel southwards from nesting sites at mid to low northerly latitudes and migrate exclusively into the South Pacific, including areas off the coast of South America (Morreale et al. 1996, Eckert and Sarti 1997, Shillinger et al. 2008, 2011).

These long-distance migrations between coastal and pelagic areas are likely to increase the risk that these animals may be caught in fisheries gear, both on longlines fishing on the high seas and coastal waters, and with gillnets and other gear sets in nearshore waters (Kaplan 2005, Alfaro-Shigueto et al. 2010, Wallace et al. 2010). Furthermore, the apparent lack of diversity in migration routes in EP leatherbacks is believed to make them more vulnerable to adverse anthropogenic impacts and environmental perturbations in the marine environment than WP and Atlantic leatherback populations (Saba et al. 2008b, Wallace and Saba 2009). Additionally, underlying oceanographic features that influence sea turtle foraging and migratory behavior are poorly understood, yet these dynamic features have been linked to changes in the probability of fisheries interaction (Žydelis et al. 2011).

Direct measurements in the field of migrating animals can be a powerful empirical method for quantifying movement and the effects of spatial heterogeneity on individual movements and population redistribution (Turchin 1998). In that regard, satellite telemetry has become a particularly valuable tool for recording the movements of marine species, such as sea turtles, which spend much of their time underwater and offshore (Godley et al. 2008). Satellite tracking data can also be analyzed with newly developed modeling techniques to infer behavioral patterns such as foraging (Jonsen et al. 2007).

When prey resources are patchily distributed, predators are expected to move within localized areas where they have encountered prey, a behavior termed area-restricted search (ARS) (Kareiva and Odell 1987). In the absence of any other information on feeding behavior, identification of ARS behavior, indicated by an increase in turning angle and/or decrease in speed, can be used to determine where foraging behavior may be occurring

(Bailey and Thompson 2006). Combined with satellite-derived environmental data, the effects of ocean conditions on animal movements and behavior can be determined (Polovina et al. 2000, Eckert et al. 2008, Kobayashi et al. 2008, Seminoff et al. 2008).

In this study, we synthesized satellite telemetry data sets for leatherback turtles in the Pacific Ocean, which included tracks from both East and West populations, so that we could identify and compare their movements on a basin scale. A switching state-space model (SSSM) was applied to all tracks to account for observation error, and to distinguish between transiting (migratory) and ARS (foraging) behaviors (Jonsen et al. 2007, Bailey et al. 2008). We tested for seasonal differences in migratory and foraging behavior, and between tagging locations, because this has implications for where and when fisheries interactions could occur, and whether there were differences between nesting sites. We also compared the linearity of foraging patches to gain further insight into leatherback foraging strategies. Finally, we extracted remotely sensed oceanographic data to determine differences in behavior between the populations in relation to environmental variables. This is an important step in understanding the cues individuals may use to select foraging habitats. It can also be a major factor explaining the risk of fisheries bycatch and can be used for developing suitable tools for bycatch reduction (Howell et al. 2008, Žydelis et al. 2011).

METHODS

Tracking data

This study analyzes tracking data from both the EP and WP leatherback turtle populations. Tracks from female EP leatherbacks were obtained by attaching Argos satellite tags to the turtles during nesting. Tagging occurred at Playa Grande, Costa Rica in 1992 to 1995 (Morreale et al. 1996) and in 2004 to 2007 (Shillinger et al. 2008; see Plate 1). The tags deployed in the earlier period were towable hydrodynamic tags ($n = 8$) (Morreale et al. 1996), and the tags deployed in the later period, and at all other sites ($n = 127$), were attached using a harness technique (Eckert and Eckert 1986, Eckert 2002b). There were three tagging sites in Mexico where deployments were made during 1993 to 2003 (seven of these tracks published in Eckert and Sarti 1997) (see also Table 1).

Tracks from WP leatherbacks were obtained using the same harness technique (Benson et al. 2007a) during nesting at two sites in Indonesia, and also at one of the foraging grounds off California, USA, during 2004 to 2007 (Table 1).

State-space model

The Bayesian switching state-space model (SSSM) developed by Jonsen et al. (2007) was applied to all of the raw Argos-acquired surface locations for each of the leatherback turtle tracks, resulting in daily position estimates. This model allows location estimates to be

TABLE 1.   Summary of tracking data for Pacific leatherback turtles.

Tag deployment		Number of tags	Track duration (days)			Mean number of satellite positions per day	Switching state-space model (SSSM) track sections
Location	Years		Mean	Min	Max		
Playa Grande, Costa Rica	1992–1995, 2004–2007	54	260	3	568	2.0	68
Mexiquillo, Mexico	1993–1997	12	199	19	480	1.7	12
Cauhitan, Mexico	1999–2001	12	143	9	373	3.8	15
Agua Blanco, Mexico	2000, 2003	2	104	95	112	5.1	2
East Pacific total		80					97
California, USA	2004–2007	17	271	45	948	4.2	20
Jamursba-Medi, Indonesia	2005–2007	33	328	22	665	3.2	36
Wermon, Indonesia	2007	5	334	303	363	2.9	6
West Pacific total		55					62
Overall mean			234			3.3	
Overall total		135					159

inferred by coupling a statistical model of the observation method (measurement equation) with a model of the movement dynamics (transition equation) (Patterson et al. 2008). The measurement equation accounts for the errors in the observed satellite locations, which were based on published estimates (Vincent et al. 2002). The transition equation was based on a first-difference correlated random walk model, and included a process model for each of two behavioral modes (Jonsen et al. 2005). The transition equation was therefore specified as follows (Jonsen et al. 2007):

$$\mathbf{d}_t \sim \mathcal{N}_2[\gamma_{b_t}\mathbf{T}(\theta_{t})\mathbf{d}_{t-1}, \mathbf{\Sigma}]$$

where $\mathbf{d}_{t-1}$ is the distance between the unobserved coordinate states $\mathbf{x}_{t-1}$ and $\mathbf{x}_{t-2}$ (i.e., locations in latitude and longitude), and $\mathbf{d}_t$ is the distance between $\mathbf{x}_t$ and $\mathbf{x}_{t-1}$. $\mathcal{N}_2$ is a bivariate Gaussian distribution with covariance matrix $\mathbf{\Sigma}$ that represents the randomness in the animal's behavior (Breed et al. 2009). The parameter γ_{b_t} is the autocorrelation in speed and direction ranging from 0 to 1. The transition matrix $\mathbf{T}(\theta_{b_t})$ relates the turning angle to the latitude–longitude coordinates of the data and location estimates, where θ is the mean turning angle. The index b_t denotes the behavioral mode, where mode 1 is considered to represent transiting and mode 2 foraging, or ARS behavior (Bailey et al. 2008). Priors were specified assuming that during transiting, turn angles should be closer to 0 and autocorrelation should be higher than when foraging (Jonsen et al. 2007).

The SSSM was fit using the R software package (R Development Core Team 2008) and WinBUGS software (Lunn et al. 2000). Two chains were run in parallel, each for a total of 20 000 Markov Chain Monte Carlo (MCMC) samples. Trace plots of the parameter values against iteration number were examined for overlap to check for convergence (Spiegelhalter et al. 2003). The first 15 000 samples were discarded to allow the chains to stabilize. The remaining samples were then thinned, retaining every 10th sample to reduce autocorrelation. Thus, posterior distributions for each parameter were based on 500 samples from each chain, yielding a total of 1000 independent samples. When there were 20 or more days of missing satellite positions, the corresponding SSSM positions were removed and the track divided into sections because the error in the SSSM mean positions increases rapidly when there are large data gaps (Bailey et al. 2008).

Analysis of foraging and migration behavior

The behavior of the turtles was inferred from the behavioral mode output by the SSSM. A mean behavioral mode <1.25 was considered transiting or migratory behavior, and a value >1.75 was considered ARS behavior (as in Jonsen et al. [2007]). Values between these were classified as uncertain behavioral mode. The onset of post-nesting (after the end of the nesting period) was identified by a switch in mean behavioral mode from ARS behavior to transiting, where the animal no longer exhibited ARS behavior for at least three or more consecutive daily positions (Bailey et al. 2008). In all subsequent analyses only post-nesting movements were considered, when ARS behavior is most likely to indicate the occurrence of foraging (Jonsen et al. 2007). Based on tag diagnostic information and the similarity of the track to a passive drifter, one turtle tagged at Cauhitan, Mexico was considered dead and the track was removed from all further analyses. The tracks from turtles tagged on the foraging ground off California, USA ($n = 17$), were also excluded from all further statistical analyses because the turtles exhibited a tagging response of rapid movement away from the tagging region, thus confounding our estimates of behavioral mode.

Once the behavioral mode had been determined for all daily track positions, we first tested how the proportion of positions in transiting behavior per month varied seasonally and between tagging locations. We applied generalized linear mixed models (GLMM) with binomial error distribution and logit link function, with the track sections nested within the individual turtle track as a random effect. Season was treated as a cyclical variable by converting it to two vectors that were defined by sine ($\mathbf{M}_s$) and cosine ($\mathbf{M}_c$) terms:

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$$\mathbf{M_s} = \frac{\sin(2\pi \times m)}{12}$$

$$\mathbf{M_c} = \frac{\cos(2\pi \times m)}{12}.$$

Tagging location was included as a categorical variable with the Playa Grande, Costa Rica location as the reference level. We also repeated this with the response variable being designated as the proportion of positions in ARS behavior per month. However, no post-nesting ARS positions were identified for tracks from Agua Blanca, Mexico, and there was only one classified ARS position within the tracks from Cauhitan, Mexico. The analysis of ARS behavior in relation to month therefore did not include these two tagging locations.

We identified ARS patches as consecutive positions in ARS behavior that ended when at least three consecutive positions had a mean behavioral mode <1.75. The linearity of these ARS patches was calculated as the linear distance from the start to the end of the patch divided by the sum of daily distances traveled within the patch. Differences between the two populations in the linearity values of the longest duration ARS patch for each track were tested using a two-sample Wilcoxon test.

Effects of ocean conditions

Oceanographic data were obtained for the time and location of each SSSM-derived daily leatherback turtle position by extracting satellite data products from the OceanWatch Thematic Real-time Environmental Distributed Data System (THREDDS). A mean value for each oceanographic variable was calculated for the area within the SSSM 95% credible limits for each position.

Sea surface temperature (SST) data were obtained from AVHRR (Advanced Very High Resolution Radiometer) Pathfinder version 5.0 at a resolution of 4.4 km with 8-day composites (data *available online*).[15] Chlorophyll-*a* concentration (CHL) data were obtained from SeaWiFS (Sea-viewing Wide Field-of-view Sensor) 8-day composites at a resolution of 8.8 km (data *available online*).[16] We used CHL as a proxy for productivity and hence potential prey availability. Sea-surface height deviation data were derived from AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data; *available online*)[17] calculated within an area of 2 degrees longitude and 1 degree in latitude. The root mean square of these values was calculated (SSHRMS) to indicate the amount of mesoscale variability. Ocean wind velocity data were

obtained from the SeaWinds instrument onboard NASA's QuikSCAT (Quick Scatterometer) satellite at a resolution of 0.25 degrees. These were further processed by NOAA Coastwatch into wind stress and wind stress curl components, which were used to calculate the vertical movement of water in relation to the horizontal displacement from the base of the Ekman layer to the sea surface (Ekman upwelling; data *available online*).[18] The upwelling may impact regional productivity in two ways. First, positive upwelling increases the transport of nutrients, resulting in increased productivity. Second, negative upwelling values (downwelling) are indicative of ocean convergence, which may in turn aggregate organisms and provide increased levels of secondary and higher-level productivity. For high values of either sign, one may expect increased prey availability (Longhurst 2007).

The effect of these key oceanographic variables on the probability of the leatherbacks exhibiting ARS behavior was investigated using a GLMM. The response variable was calculated for each SSSM position as the proportion of MCMC samples in which the behavioral mode had been estimated as ARS behavior (mode 2). Data exploration of the oceanographic variables indicated that a logarithmic transformation was required for CHL and SSHRMS. We then tested for collinearity between the explanatory oceanographic variables by calculating the pairwise correlations and the variance inflation factor. The pairwise correlations were ≤0.10, and the variance inflation factors were ≤1.01, indicating no significant collinearity between the explanatory variables (Zuur et al. 2009). The turtle population, categorized as EP (reference level) and WP, and interaction terms with the oceanographic variables were included in the model to determine if the populations differed in their response to the environment. Only turtle positions with values for each of the four key oceanographic variables were included in the final data set, which resulted in only one track section per individual. The individual tracks were therefore included as a random effect, and a binomial error distribution and logit link function were specified in the model. The model was fit using the R software package (R Development Core Team 2008) and the contributed package lme4 (Bates et al. 2008).

Results

Pacific leatherback turtle tracks

In total, we compiled 135 individual leatherback turtle tracks (Table 1), the largest satellite telemetry data set ever assembled for leatherbacks. The mean satellite tracking duration was 234 days (range = 3–948 days) and the mean number of satellite positions per day was 3.3 (Table 1). Due to long gaps in the satellite data of some of the individual turtle tracks, the resulting SSSM

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[15] http://oceanwatch.pfel.noaa.gov/thredds/Satellite/aggregsatPH/ssta/catalog.html?dataset=satellite/PH/ssta/8day

[16] http://oceanwatch.pfel.noaa.gov/thredds/Satellite/aggregsatSW/chla/catalog.html?dataset=satellite/SW/chla/8day

[17] http://oceanwatch.pfel.noaa.gov/thredds/Satellite/aggregsatTA/sshd/catalog.html?dataset=satellite/TA/sshd/1day

[18] http://oceanwatch.pfel.noaa.gov/thredds/Satellite/aggregsatQS/wekm/catalog.html?dataset=satellite/QS/wekm/8day
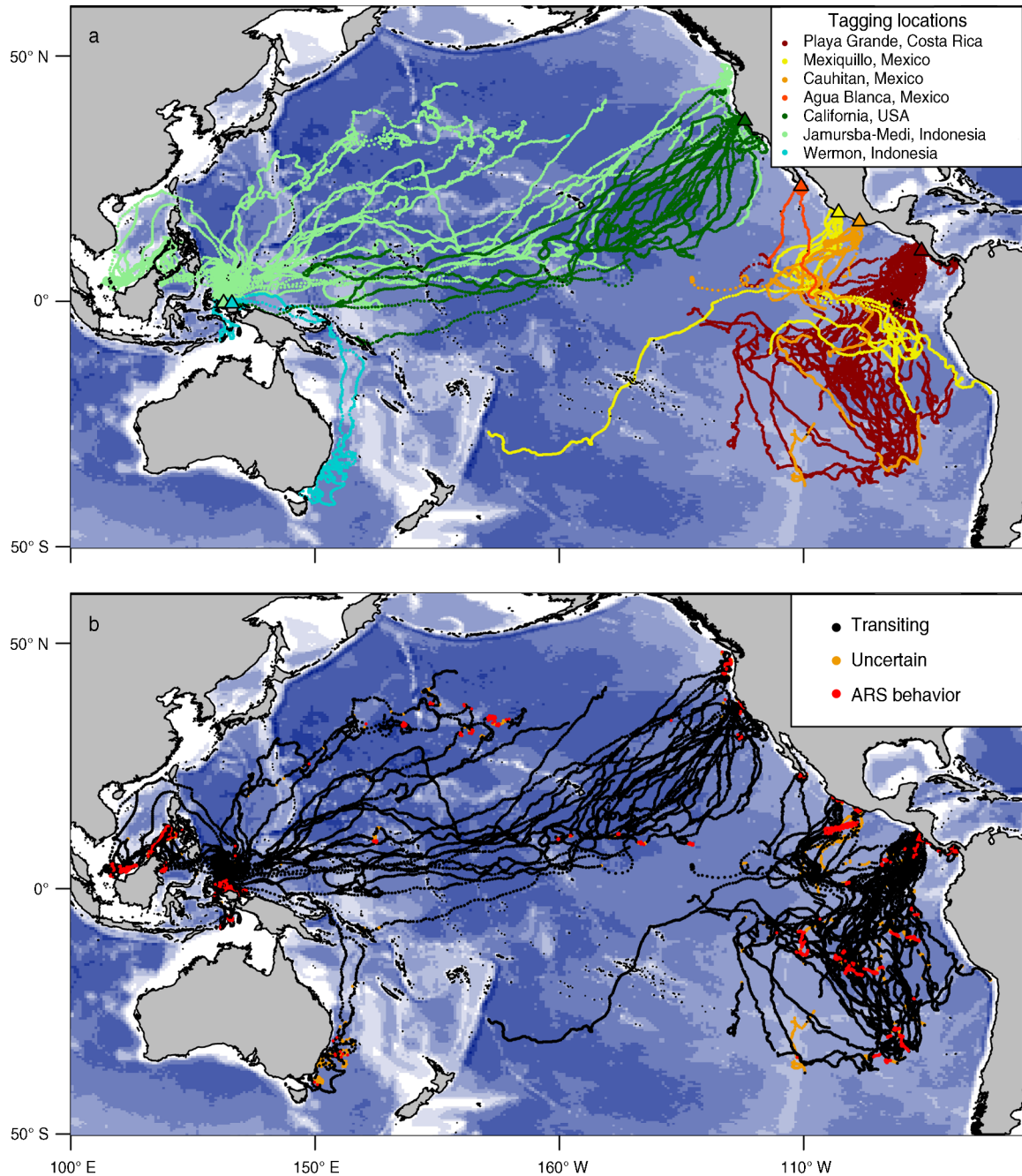
FIG. 1. Switching state-space model (SSSM)-derived daily positions for 135 tracks for Pacific leatherback turtles: (a) color-coded by tagging location and overlaid on bathymetry and (b) color-coded by behavioral mode inferred from the SSSM. Leatherbacks tagged in Costa Rica and Mexico are from the East Pacific (EP) population, and those tagged in California and Indonesia are from the West Pacific (WP) population. The tagging locations are indicated by triangles.

tracks were divided into sections. There was a total of 122 individual tracks and 146 track sections that occurred during post-nesting.

Foraging and migration behavior

Turtles from the EP leatherback population (tagged in Costa Rica and Mexico) generally migrated southwards

into the eastern tropical Pacific and the southeastern Pacific (Fig. 1). In contrast, the WP population migrated to several different areas that were widely separated. Turtles tagged at the two nesting sites in Indonesia migrated to different areas, with those tagged at Wermon Beach, Papua all migrating southwards (Fig. 1a). ARS behavior by the WP population mainly

TABLE 2. Parameter estimates from generalized linear mixed models (GLMMs; binomial error, logit link function) for proportion of tracking days per month with transiting behavior, and ARS behavior, where the tagging location at Playa Grande, Costa Rica was the reference level, and M_s and M_c represent sine and cosine vectors respectively for the month.

Factor	Response: transiting behavior			Response: ARS behavior		
	Estimate	SE	P	Estimate	SE	P
Intercept	2.664	0.409	<0.001*	−8.201	0.797	<0.001*
Month: M_s	0.117	0.031	<0.001*	0.088	0.038	0.021*
Month: M_c	0.459	0.034	<0.001*	−0.588	0.042	<0.001*
Tagging location: Mexiquillo, Mexico	0.210	1.090	0.847	−0.215	2.213	0.955
Cauhitan, Mexico	−2.382	1.162	0.040*	...	...	...
Agua Blanco, Mexico	0.480	2.165	0.824	...	...	...
Jamursba-Medi, Indonesia	0.122	0.696	0.861	3.057	1.185	0.010*
Wermon, Indonesia	−2.194	1.310	0.094	5.850	1.996	0.003*

Note: Variables not included in the final model are indicated by ellipses (...).
* Significant at $P < 0.05$.

occurred when the turtles reached the California Current, central North Pacific, South China Sea, the waters off eastern Indonesia, and southeastern Australia (Fig. 1b). Although both populations had large ranges within the Pacific Ocean, there was no spatial overlap between the EP and WP turtle tracks.

A high proportion of the daily SSSM positions were classified as transiting, with a mean and SD of 80% and 33% of positions per month. This remained high all year, but there was significant seasonal variation (Table 2). The proportion of transiting positions per month was highest from October to March (Fig. 2a). There were also significant differences in the proportion of transiting positions per month for leatherbacks from different nesting sites (Table 2). There were significantly fewer transiting positions per month during the tracks of leatherbacks tagged at the nesting beach in Cauhitan, Mexico than for those tagged at Playa Grande, Costa Rica. However, this is probably the result of a higher proportion of positions from Cauhitan, Mexico being classified as uncertain behavioral mode (30% of positions, compared to <16% for all other tagging locations). Therefore, transiting behavior was likely underestimated.

There was also seasonal variation in the proportion of positions classified as ARS behavior, peaking in June and July (Table 2, Fig. 2b). Significantly more ARS positions per month occurred within tracks of leatherbacks tagged at the nesting beaches in Indonesia (Jamursba-Medi and Wermon) than for individuals tagged at the nesting beach in Playa Grande, Costa Rica (Table 2). The mean latitude at which ARS behavior occurred was generally farther north from April to June and from September to October. There was a greater seasonal change in latitude for turtles tagged at Playa Grande, Costa Rica than at Jamursba-Medi, Indonesia (Fig. 3). For the other EP nesting sites, there was less complete seasonal information, but there seemed to be a similar seasonal pattern between turtles from the Mexiquillo, Mexico nesting site and from Playa Grande, Costa Rica. Turtle tracks from the other WP nesting site at Wermon, Indonesia exhibited relatively

little seasonal change in location of ARS behavior during April to January (Fig. 3). This is because their ARS behavior mainly occurred in the tropical waters off Indonesia.
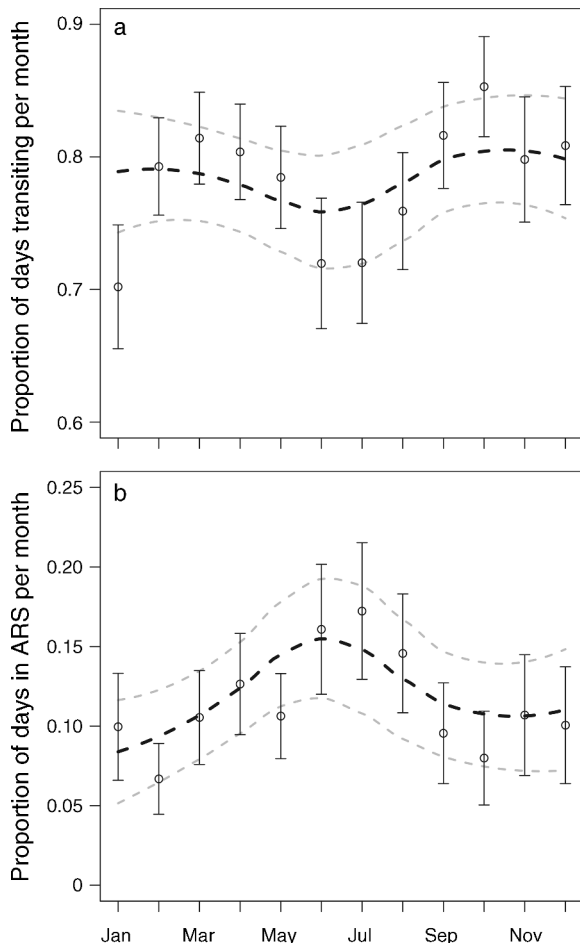

FIG. 2. Mean (±SE) proportion of tracking days in relation to month (circles), with best-fit line from the generalized linear mixed model (GLMM) fitted values (±SE as gray lines), for (a) transiting behavior and (b) area-restricted search (ARS) behavior.

PLATE 1. Leatherback turtle (*Dermochelys coriacea*) at Playa Grande, Costa Rica, nesting beach in Parque Nacional Las Baulas. Photo credit: G. L. Shillinger.

The largest number of consecutive ARS positions within each post-nesting track had a median duration of 24 d (maximum = 257 d). All of the tracks with an ARS patch >100 days were from the WP population and occurred in the South China Sea or just south of the Indonesia nesting sites. There was a significant difference in linearity values of the ARS patches between the two populations (two-sample Wilcoxon Test: $W = 368$, $P = 0.003$). There were higher linearity values for ARS patches by the EP population (median = 0.456), indicating straighter tracks, than for the WP population (median = 0.162).

Effects of ocean conditions

The long distances that the turtles traveled meant that they moved through a range of oceanic regions with different environmental characteristics (Fig. 4). The SST at all tracking locations ranged from 11.3°C to 31.7°C (mean = 24.7°C). The coolest surface temperatures occurred in the northern central North Pacific, off the west coast of the USA, in the southeastern Pacific, and off southeastern Australia (Fig. 4a).

The application of the GLMM indicated that there were significant relationships between the probability of ARS behavior and all of the oceanographic variables investigated (Table 3, Fig. 5). The *P* value for SSHRMS was just above 0.05, but the difference compared with the other coefficients was not itself statistically significant (Gelman and Stern 2006). There were significant interactions between the oceanographic variables and the leatherback populations, indicating that animals from the two populations behaved differently in

response to the environment (Table 3). A higher probability of ARS behavior occurred at lower SSTs for the EP leatherbacks (Fig. 5a). In contrast, the WP leatherbacks had higher probabilities at higher SSTs because of the large number of ARS positions within the warm waters of the South China Sea and around Indonesia (Fig. 1b and 4a).

The probability of ARS behavior showed a slight increase in response to CHL in the EP population, but there was a very strong response in the WP population
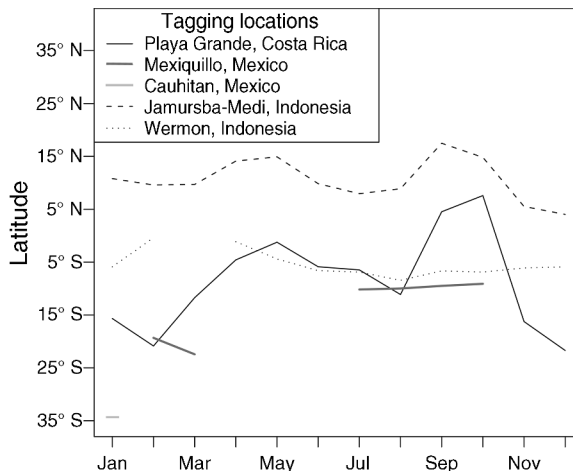

FIG. 3. Mean latitude at which area-restricted search (ARS) behavior occurred in relation to month and tagging location.

(Fig. 5b). The WP turtles exhibited an exponential rise in the probability of ARS behavior with increasing CHL concentration, with the probability reaching 0.5 at a CHL concentration of 2.5 mg/m^3.

There was a significant interaction between the probability of ARS behavior and Ekman upwelling for the two populations (Table 3). There was a negative relationship for the WP population (Fig. 5d), which was driven by the low values around Indonesia and in the South China Sea (Fig. 4d). The probability of ARS behavior increased with increasing Ekman upwelling for the EP leatherbacks (Fig. 5d). These higher Ekman upwelling values mainly occurred in the mid and southern latitudes of the EP population's range (Fig. 4d).

DISCUSSION

This study provides the first pan-Pacific synthesis of telemetry data and gives valuable insights into the distinct movements and behavior of Pacific leatherback turtles. We also confirm differences between the two regional Pacific populations in their behavior and response to oceanographic conditions. These divergent responses have implications for leatherback vulnerability to fisheries interactions and to the effects of climate change.

The satellite tracking data indicated a high degree of segregation in space and time in the distribution of EP and WP leatherbacks, both in their migratory pathways and foraging grounds. The EP leatherbacks mainly foraged in the southeastern Pacific (Morreale et al. 1996, Eckert and Sarti 1997, Shillinger et al. 2008, 2011) whereas the WP leatherbacks had several different foraging areas (Benson et al. 2011). A large number of ARS positions for the WP leatherbacks occurred in areas with high SSTs and negative Ekman upwelling (indicating ocean convergence), which was in contrast to the EP leatherbacks that mainly foraged in areas with low SSTs and higher SSHRMS (indicating high mesoscale variability). Areas with ocean convergences and mesoscale eddies are known to attract leatherback turtles due to their capacity to concentrate prey (Eckert 2006, Doyle et al. 2008).

There may be an energetic advantage to foraging in areas around Indonesia and in the South China Sea because of their relatively close proximity to WP nesting beaches (Benson et al. 2011). There was only one leatherback turtle in the EP tracking data set that similarly foraged in close proximity to a nesting beach. This female nested in Playa Grande, Costa Rica, and then foraged along the coast of Central America (Shillinger et al. 2008, 2011). Another EP leatherback from the nesting beach in Mexiquillo, Mexico, foraged off the coastal waters of Peru and Chile (Eckert and Sarti 1997) (Fig. 1). Saba et al. (2008a) hypothesized that coastal foragers in the EP population may now be a minority because of high mortality rates associated with coastal gillnet fisheries along Central and South

America. Although tagging of WP leatherbacks has been done at the foraging grounds off California, EP leatherbacks have only been tagged during nesting. Similar tracking of EP leatherbacks from foraging grounds and coastal foraging areas is needed to obtain a better understanding of their complete migratory cycles (James et al. 2005b, Benson et al. 2011).

Leatherback turtles specialize on a diet of gelatinous zooplankton (Bjorndal 1997). In this study, we analyzed the effect of chlorophyll-a concentration on the probability of ARS behavior as a proxy for prey availability, with the assumption that areas with high CHL will host greater abundances of zooplankton. This was true for WP leatherbacks, whose foraging grounds all occurred in areas with high CHL, indicating that CHL was a good proxy for leatherback prey abundance. The EP leatherbacks also showed a behavioral response to CHL, but it was less pronounced (Fig. 5b), and they mainly migrated through the high CHL area near the equator. The strong equatorial currents and high temperatures may have made this an unfavorable location for foraging. Instead, the EP leatherbacks appeared to forage in the southern part of their range in the South Pacific Subtropical Convergence, where there is a sharp gradient in primary production (Saba et al. 2008a). Net primary production varies throughout the Pacific where it is mainly on a seasonal cycle, except in the EP dispersal areas where it is dominated by interannual variation (Saba et al. 2008b). It may be that these different oceanic processes in the South Pacific meant CHL was not as good a proxy for leatherback prey in this region and/or that surface CHL may not reflect food availability at deeper depths (Hays et al. 2008, Shillinger et al. 2008, 2011).

Inferences of behavior from the SSSM identified relatively few of the daily positions as ARS behavior (15.4%). The ARS behavior identified is most likely to be indicative of longer foraging bouts, and therefore will not identify individual feeding events or when prey capture did not induce ARS (Weimerskirch et al. 2007). Sims and Quayle (1998) found that another large zooplanktivore, the basking shark (Cetorhinus maximus), foraged while swimming along thermal fronts containing high densities of zooplankton. The lower linearity of the ARS patches by the EP leatherbacks indicated they may be foraging in a similar manner, especially as ARS behavior occurred within the South Pacific Subtropical Convergence where there is a high frequency of thermal fronts (Saba et al. 2008a). When foraging occurs along a relatively straight path, it is much more difficult to distinguish from a migratory movement. The development of models that incorporate other measures indicative of foraging (e.g., dive behavior, jaw movements) will help improve behavioral estimation, particularly when feeding is not occurring by ARS (Fossette et al. 2008, Okuyama et al. 2010). There is the possibility that drag induced by the tagging
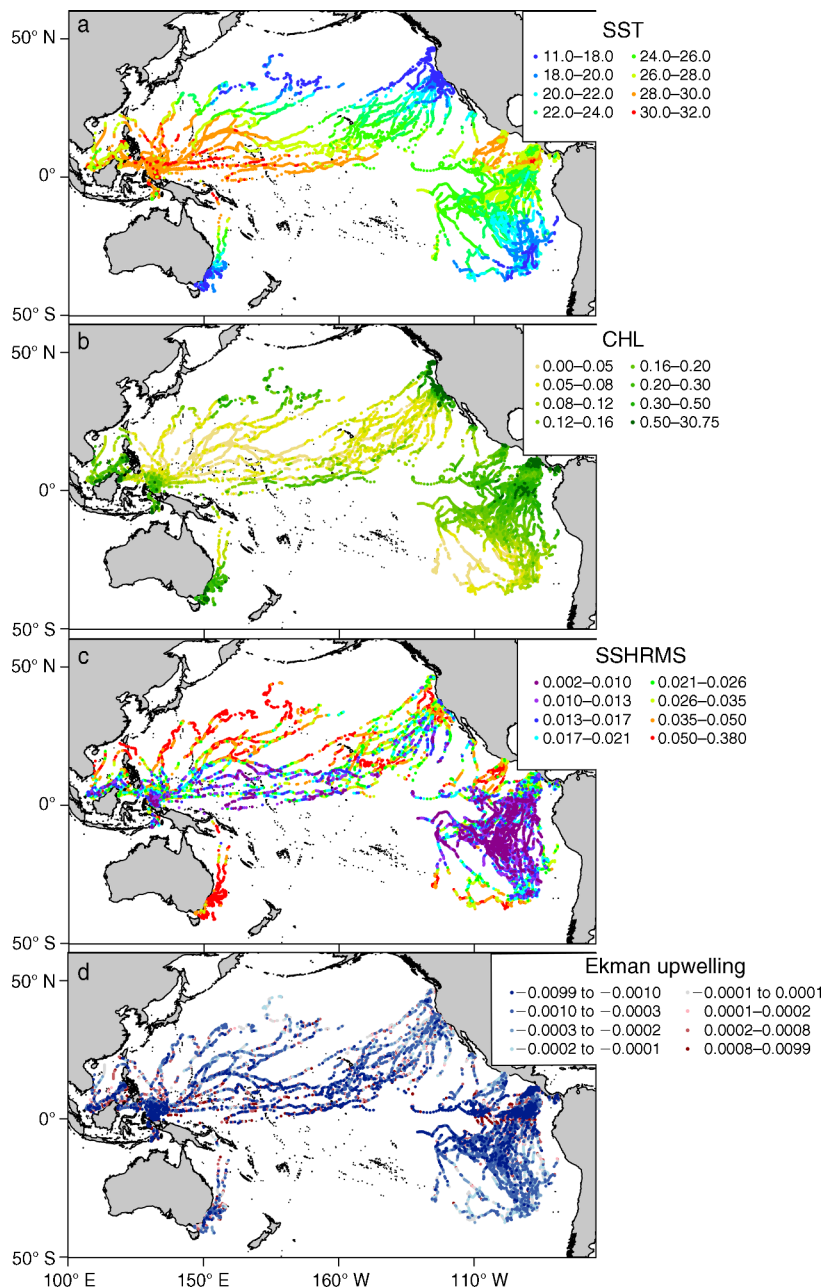
Fig. 4. Maps of (a) Sea surface temperature (SST, °C), (b) chlorophyll-*a* concentration (CHL, mg/m³), (c) sea surface height root mean square (SSHRMS, m), and (d) Ekman upwelling (cm/s) values for all of the switching state-space model (SSSM)-derived daily leatherback turtle positions.

harness may have influenced the turtles' movements. However, turtles with harnesses behaved similarly to those with towed transmitters with very low drag (Morreale et al. 1996). Our study also analyzed only tracks from nesting females as the animals exhibited a tagging response on the foraging ground. Much less is known about the distribution and movements of juvenile or male leatherback turtles (Eckert 2002*a*, James et al. 2005*a*). Given that males were found in the same foraging area off California as the females

(Benson et al. 2011), it is likely that males and females are responding to the environment similarly.

Spatial differences in ARS behavior were found to occur between the two leatherback populations. This is likely driven by differences in seasonal water temperature or prey availability in the two hemispheres. The WP leatherbacks in the Northern Hemisphere foraged farther north in spring and autumn when temperatures were warmer. During this time it is the Austral winter and the EP leatherbacks also foraged farther north.

TABLE 3. Results of the generalized linear mixed model (GLMM; binomial error, logit link function) for the probability of ARS behavior in relation to sea surface temperature (SST), logarithm of chlorophyll-*a* concentration (log CHL), logarithm of root mean square of sea surface height (log SSHRMS), and Ekman upwelling, and the interaction with the leatherback populations.

Factor	Estimate	SE	P
Intercept	1.043	0.719	0.046*
Population: West Pacific	−2.057	0.658	<0.001*
SST	−0.123	0.002	0.002*
log(CHL)	0.341	0.119	0.004*
log(SSHRMS)	−0.268	0.137	0.051
Ekman upwelling	17 360.000	3359.000	<0.001*
Interaction: SST × West Pacific population	0.142	0.025	<0.001*
log(CHL) × West Pacific population	2.148	0.217	<0.001*
log(SSHRMS) × West Pacific population	−0.230	0.259	0.375
Ekman upwelling × West Pacific population	−24 510.000	4945.000	<0.001*

Note: The Eastern Pacific leatherback population was treated as the reference level.

* Significant at $P < 0.05$.
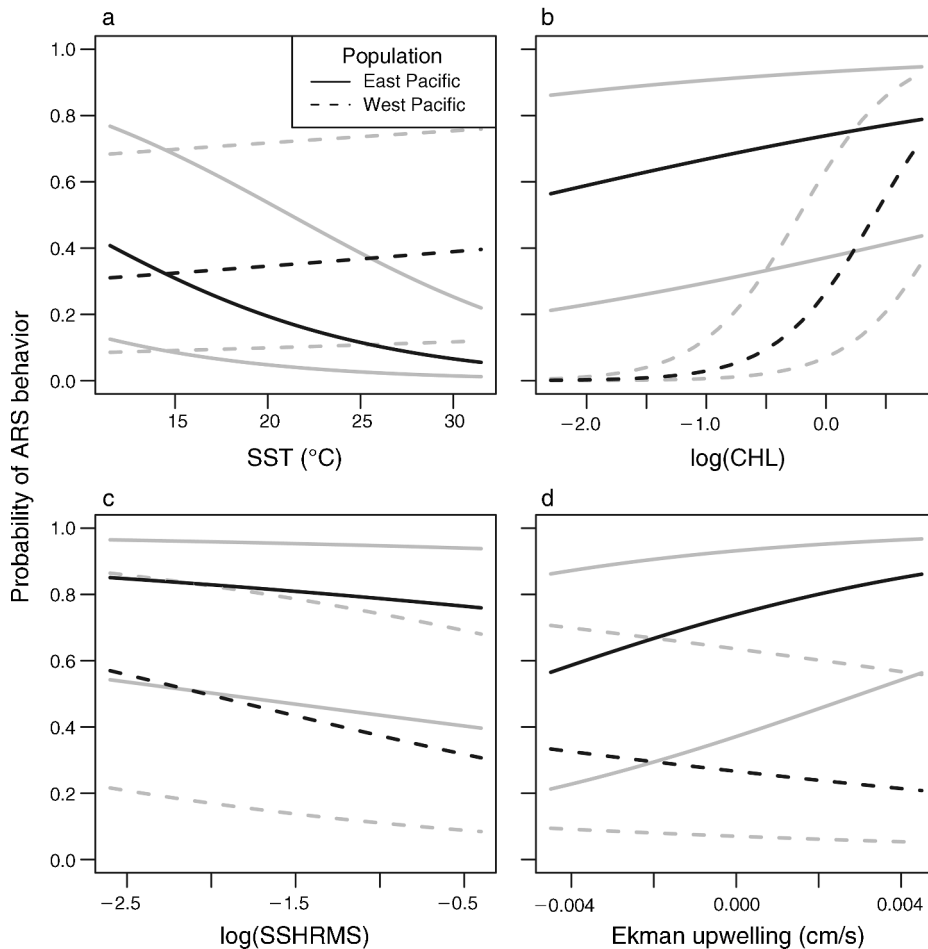
FIG. 5. Generalized linear mixed model (GLMM) predicted probabilities of area-restricted search (ARS) behavior for each leatherback turtle population (solid lines, East Pacific [EP]; dashed lines, West Pacific [WP]). The space between the gray lines shows the variation in the predicted values among individual turtle tracks in relation to (a) sea surface temperature (SST), (b) chlorophyll-*a* concentration (mg/m³) (log[CHL]), (c) sea surface height root mean square (m) (log[SSHRMS]), and (d) Ekman upwelling.

During the Austral summer (November to February), EP leatherbacks foraged at higher southerly latitudes, whereas the WP leatherbacks foraged at much lower latitudes during this corresponding winter period in the Northern Hemisphere (Fig. 3). Although leatherbacks are able to retain metabolic heat (Paladino et al. 1990, Wallace and Jones 2008), these movements suggest that seasonal changes in water temperature at higher latitudes constrain when leatherbacks are able to feed in these regions (McMahon and Hays 2006, Shillinger et al. 2011). Alternatively, it is also possible that these observed movements may reflect seasonal patterns in prey abundance at higher latitudes (Miglietta et al. 2008, Gibbons and Richardson 2009).

The differences in movements and behavior between the two regional populations have implications relative to the impact of climate change. Climate change may result in changes in prey distribution or abundance. The El Niño Southern Oscillation has been shown to influence reproductive frequency of EP leatherbacks, most likely as a result of its impact on prey abundance in the southeast Pacific (Saba et al. 2007). The WP leatherbacks appear to forage in several different areas that are widely separated. This could provide greater flexibility in the event of environmental variation or climate change, which might make the WP population less susceptible to decline as a result of food limitation than the EP population. However, if individuals show site fidelity to particular foraging grounds, these individuals may be affected by changes in their prey due to ocean conditions.

The occurrence of leatherback turtles within both coastal and pelagic areas (Eckert and Sarti 1997, Benson et al. 2007a, b, Shillinger et al. 2008, 2010) means they have a high risk of exposure to many different fisheries, which may be very distant from their nesting sites (Eckert and Sarti 1997, Ferraroli et al. 2004). This makes regulation of fisheries for the purpose of reducing fatal interactions much more challenging (Dutton and Squires 2008, Witt et al. 2008). Bycatch rates suggest that pelagic longlines are not the largest single source of fisheries-related mortality for sea turtles, but they are high enough to warrant management action (Lewison and Crowder 2007). In addition, bycatch data from gillnet and trawl fisheries, particularly in small-scale artisanal fisheries, indicate a high number of sea turtle captures, along with a higher mortality rate, than longlines (Lewison and Crowder 2007, Alfaro-Shigueto et al. 2011). In California, the offshore swordfish and thresher shark drift gillnet fishery has been closed to fishing within a Leatherback Conservation Area from 15 August to 15 November each year since 2001 to protect leatherback turtles (Carretta et al. 2004), and further fine-scale analysis of seasonal movement patterns will improve our understanding of how leatherbacks use this protected area (Benson et al. 2011).

Our study could be used to inform management and improve efforts to reduce bycatch. For example, in the central Pacific, a tool called TurtleWatch has been developed to aid bycatch reduction for loggerhead turtles in the Hawaii-based pelagic longline fishery (Howell et al. 2008). This was developed using information on fishery characteristics and bycatch, and combining these with turtle satellite tracks and environmental data. The development of a similar tool for leatherback turtles using the data and models from our study, and combining it with fisheries information (Žydelis et al. 2011), could provide an effective basis for developing approaches to reduce leatherback and fisheries interactions in the Pacific Ocean.

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