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ARTICLE

Methods, Tools, and Technologies

Integrating telemetry and point observations to inform management and conservation of migratory marine species

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Abstract

Species distribution models have been widely used in both terrestrial and marine systems, and applications have included invasive species management, evaluating potential effects of climate change, and conservation. Generally, only a single type of data can be accommodated within the model structures used, which may lead to higher uncertainty in the predictions when the data are sparse. In this case, it can be beneficial to pool data from multiple sources and data types, such as fishery observations and telemetry data. An integrated

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species distribution model (ISDM) utilizes data integration methods that address the challenges of harnessing multiple data types to estimate species distribution. In this study, an ISDM approach was developed to link turtle locations gathered as part of fishery observations with those derived from satellite telemetry in the East Pacific Ocean to enhance our understanding of a highly migratory and endangered marine species, the leatherback turtle (*Dermochelys coriacea*). These models were developed to support a dynamic management tool, South Pacific TurtleWatch, to identify high-risk areas of management concern and help inform bycatch reduction efforts for this critically endangered species. This data fusion approach could be applied to other populations and species for which telemetry and other point source data are available.

KEYWORDS
data fusion, dynamic Poisson process, habitat-based model, leatherback, Southeast Pacific, specie distribution modeling, telemetry

INTRODUCTION

Species distribution models (SDMs) combine species observations with environmental variables to identify relationships across landscapes and seascapes, and predict distributions in space and time (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). The environmental variables selected for SDMs may directly or indirectly influence the occurrence and abundance of a species, and many environmental variables are publicly available as climatologies, in near real-time, or as a forecast (Elith & Leathwick, 2009; Kerr & Ostrovsky, 2003). This allows SDMs to serve as a management decision support tool for anthropogenic activities that may potentially impact protected and commercial species (Maxwell et al., 2015). In some cases, these SDMs have been further advanced to become operational and provide near-real-time predictions that can inform dynamic management (e.g., Breece et al., 2018; Hazen et al., 2017; Oestreich et al., 2020; Welch et al., 2019).

Applications of SDMs in both terrestrial and marine systems have included invasive species management, evaluating potential effects of climate change, and conservation purposes (Robinson et al., 2011, 2017). In the marine environment, models of target commercial fishery species and nontarget species caught in fishing gear as bycatch have been used to help inform fisheries management and sustainability (Howell et al., 2015; Scales et al., 2017). Such models can provide tools to support dynamic ocean management that uses near-real-time information to more effectively account for variability in environmental conditions and its consequent effects on animal habitat use and human activities (Hazen et al., 2018; Hobday & Hartmann, 2006). For some protected and endangered species, only relatively low bycatch rates may be sustainable, and SDMs can aid in identifying areas of high interaction risk and investigating scenarios to reduce bycatch (Stock et al., 2020; Welch et al., 2019).

Bycatch in fisheries is a major threat to many marine protected species, including sea turtles, marine mammals, and seabirds (Lewison et al., 2009; Wallace, Tiwari, et al., 2013). Information on the number of animals reported (e.g., through log books, human observers, and/or electronic monitoring) incidentally caught in fishing gear can greatly inform the potential risk of interactions (e.g., Alfaro-Shigueto et al., 2012; Degenford et al., 2021; Howell et al., 2015). Fisheries observations of incidental bycatch, which represent a species' presence at a specific point in time and space, are available from multiple jurisdictions and countries. These data have been used in SDMs (e.g., Degenford et al., 2021), but the observations are biased to seasons and areas where there is fishing effort and interpretation of the modeling results may be challenging. Regional-specific bias could be introduced if the opportunistic reporting process from fisheries varies geographically. Patchiness of reporting across countries and jurisdictions could also introduce spatial confounding between dynamic oceanographic conditions and geographic (e.g., fishing effort) locations. To fully describe species' distributions, fisheries observations can be supplemented with additional data streams such as probabilistic surveys to correct for reporting biases (Fithian et al., 2015).

Collecting survey data can be costly and logistically challenging to obtain, resulting in small sample sizes and observations within only small parts of potentially large home ranges of highly migratory species that can reduce

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the accuracy of the SDM (Guillera-Arroita et al., 2015; Stockwell & Peterson, 2002; Wisz et al., 2008). Independent methods of recording animal movements, such as telemetry, can provide a broader picture of the species' distribution or home range (Hussey et al., 2015). Telemetry data also represent repeated observations of individual movements, unlike single point observations from fisheries interactions. For wide-ranging marine species, telemetry data are feasible alternatives to estimate animals' resource selection function in the pelagic habitat, where large-scale surveying is cost-prohibitive and fisheries observations are less abundant or widespread. While resource selection studies are typically applied to individual movement, population-level inference of animal movement is increasingly being used to infer broad-scale species distribution modeling (Hazen et al., 2017, 2018; Hooten et al., 2016).

Where species data are scarce, it can be beneficial to pool data from multiple sources and data types, such as fishery observations and telemetry data. Integrated or hierarchical SDMs (ISDMs) utilize data integration methods that address the challenges of harnessing multiple data types to estimate species distribution (Hefley & Hooten, 2016; Rose et al., 2020). The ISDM framework was built upon the Poisson point process modeling (PPM) (Aarts et al., 2012). ISDM can be applied to fuse data from classical design-based probability surveys with opportunistic presence-only observations, thus utilizing the strengths of both data sources (Miller et al., 2019). For example, Fithian et al. (2015) and Giraud et al. (2016) independently proposed a joint-likelihood approach to correct for the sampling bias in presence-only data by borrowing information from multiple species in probabilistic surveys. Koshkina et al. (2017) incorporated detection probability into the above data fusion framework. Renner et al. (2019) used a penalized joint-likelihood approach to avoid over-fitting of ISDM and enhance its predictive capability. When input data sources have different levels of accuracy or uncertainty, Pacifici et al. (2017) proposed a stepwise approach to data fusion that does not involve the specification of joint-likelihood and is computationally efficient. The approach involves first constructing covariates from high-quality data and then using the covariate to model low-quality data. These developing ISDM approaches can strengthen species distribution modeling, going beyond more traditionally utilized approaches.

In this study, ISDM principles and the stepwise approaches (Pacifici et al., 2017) were applied to link sea turtle locations gathered as part of fishery operations with those derived from satellite telemetry to enhance our understanding of a highly migratory and endangered marine species, the leatherback turtle (*Dermochelys coriacea*). Over the last three to four decades, Pacific leatherback turtles (Benson et al., 2015) have been suffering rapid population declines (Sarti et al., 1996; Spotila et al., 2000; Tapilatu et al., 2013) with bycatch being a major source of mortality at sea, including within gillnet and longline fisheries (Eckert & Sarti, 1997; Tomillo et al., 2008; Wallace, Kot, et al., 2013). Here we build on previous studies on Eastern Pacific leatherback turtles that have separately developed models using telemetry (Hoover et al., 2019; Willis-Norton et al., 2015) and fishery observation data (Degenford et al., 2021). These models were developed to support a dynamic management tool, South Pacific TurtleWatch, following the success of the TurtleWatch project in the North Pacific in reducing bycatch of loggerhead turtles (*Caretta caretta*) (Howell et al., 2008, 2015). In this study, we aim to (1) identify the seascape features that were associated with the population-level movement of Eastern Pacific leatherback turtles; (2) reduce the regional and opportunistic biases in multiple fishery observations; and (3) extrapolate the spatial variation in the species' distribution to identify high interaction risk areas of management concern. This data fusion approach can be applied to other populations and species for which telemetry and other point source data are available, including other species threatened by interaction risks with multiple fisheries.

MATERIALS AND METHODS

Study area, telemetry, and fishery data

Leatherback turtles (*D. coriacea*) are classified as vulnerable to extinction and critically endangered in the East Pacific Ocean (Wallace, Tiwari, & Girondot, 2013), with both East and West Pacific populations in the Pacific Ocean rapidly declining (Sarti et al., 1996; Spotila et al., 2000). This study focuses on the Eastern Pacific Ocean subpopulation, which is genetically distinct and geographically separate from other global populations (Dutton et al., 1999, 2007; Wallace, Tiwari, & Girondot, 2013). Turtles from this population migrate from Mexican and Central American nesting beaches to coastal and oceanic waters off Central and South America (Eckert & Sarti, 1997; Morreale et al., 1996; Schick et al., 2013; Shillinger et al., 2008, 2011). Tracking data were obtained by attaching satellite-linked data loggers and transmitters to female leatherbacks while they were nesting at Playa Grande, Costa Rica in 1992–1995 (Morreale et al., 1996) and 2004–2008 (Shillinger et al., 2008), in Mexico during 1993 (Eckert & Sarti, 1997) and 2019, and to fisheries-bycaught males and females off Peru between 2014 and 2018 (Figure 1). A Bayesian switching state-space model (SSSM)

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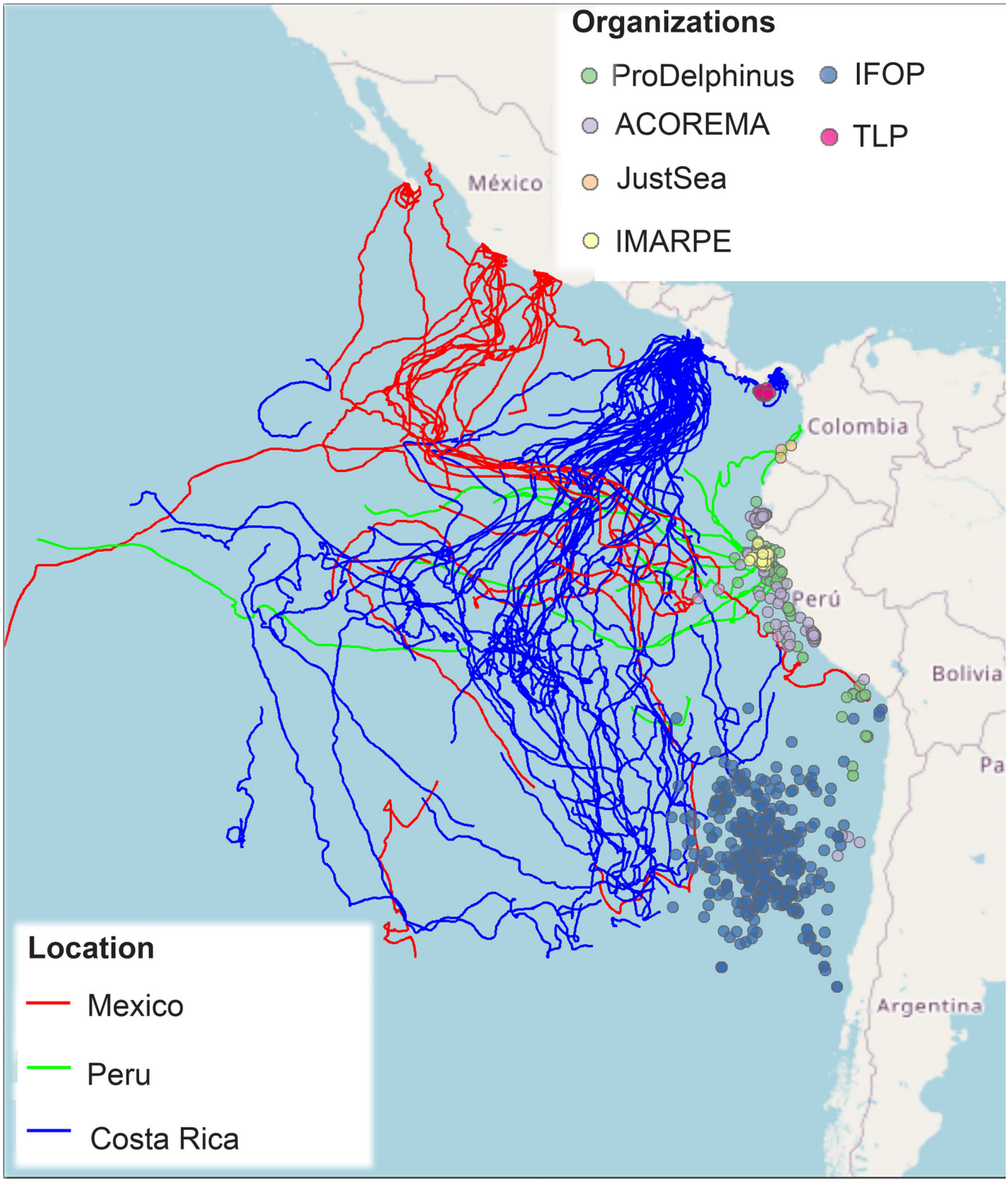


FIGURE 1 Switching state-space model (SSSM)-derived daily positions for 114 tracks between 1993 and 2019 for Pacific leatherback turtles, and distribution of leatherback fisheries observations between 2001 and 2019. Color codes denote tagging locations and organizations providing fishery observation data: ACOREMA (Areas Costeras y Recursos Marinos), Instituto del Mar del Perú (IMARPE), Instituto de Fomento Pesquero (IFOP), The Leatherback Project (TLP).

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was applied to the raw tracking observations to generate daily positional estimates (Bailey, Fossette, et al., 2012). Tracks with more than 20 days of gaps were divided into segments to avoid extrapolation of the SSSM (Bailey, Benson, et al., 2012; Bailey et al., 2008). Data processing was documented in Hoover et al. (2019).

Leatherback observation data from fisheries were provided by organizations in Chile, Columbia, Ecuador, Panama, and Peru for fishery operations in the study area (Figure 1; Degenford et al., 2021). These observations do not solely indicate bycatch, but that turtles were also observed in areas where fishing was taking place. Further, the fisheries data only represent opportunistic leatherback presence in areas where fisheries operate, not the entire leatherback distribution for the region.

Environmental covariates

Oceanographic data were obtained from satellite data for the study area between 1997 and 2019. Bathymetry data were obtained from a calibrated satellite-gravity model (coastwatch.pfeg.noaa.gov/erddap/griddap/usgsCeSrtm30v1.html, Becker et al., 2009). Sea surface temperature (SST) data were obtained from a combination of geostationary and polar-orbiting environmental satellites. The surface reflectance was fused into a global 5-km product with monthly composites (Liu et al., 2014; coastwatch.pfeg.noaa.gov/erddap/griddap/NOAA_DHW_monthly.html). Sea surface height data were derived from high-resolution three-dimensional (3D) temperature and salinity estimates from in situ and satellite observations combined with altimetry (Guinehut et al., 2012; Mulet et al., 2012). Monthly composites were available between 1993 and 2019 at 0.25° resolution (resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012). Monthly chlorophyll *a* composites were obtained from SeaWIFS between 1997 and 2010 and MODIS Aqua (2003–2019) (https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chlamday.html and https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdSW2018chlamday.html). Both data were resampled onto the same grid over the study area. MODIS data after 2003 were fused with available SeaWIFS data into a chlorophyll *a* record between 1997 and 2019. Specifically, SeaWIFS chlorophyll *a* estimates from each grid cell between 2003 and 2010 were used to build a cell-specific regression for the contemporary MODIS data. To calibrate SeaWIFS to MODIS, the predictive capability of the cell-specific regression was estimated using R^2 and leave-one-out cross-validation (LOOCV) criterion. Cells with LOOCV beyond one standard deviation of MODIS Aqua data were removed and interpolated from neighboring cells. The R package gstat was used to perform the interpolation (Pebesma, 2004).

Ocean wind velocity data were obtained from the Sea Winds instrument onboard NASA's QuickSCAT (Quick Scatterometer, https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdQSstressmday_LonPM180.html) satellite between 1999 and 2009, and NASA's Advanced Scatterometer (ASCAT, https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdQAstressmday_LonPM180.html) between 2010 and 2019, both at a resolution of 0.25°. 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. Upwelling values near the equator were removed given the influence of Coriolis force there. Outlier values above 0.02 mm s^{-1} were also removed and interpolated from neighboring cells using inverse distance weighting.

To create a monthly thermal front index, a blended daily 5-km SST product (NOAA Coral Reef Watch, 2018; Skirving et al., 2020) was obtained from NOAA's Environmental Research Division's ERDDAP server (https://coastwatch.pfeg.noaa.gov/erddap/griddap/NOAA_DHW.html). Daily SST front gradients were calculated with the Canny edge detection algorithm, which applies a Gaussian noise filter and then quantifies the magnitude gradient as the hypotenuse of the intensity in the *x*- and *y*-directions of each grid cell ($\sigma = 6$, Canny, 1986; Harris et al., 2020; Oram et al., 2008; Virtanen et al., 2020). A monthly mean front gradient density, representing front strength, was then calculated to examine SST front features (Miller, 2009; Miller et al., 2015; Scales et al., 2015; Suberg et al., 2019).

Environmental data were resampled with a median spatial filter at 56 km resolution over the study area, the resolution was based on the horizontal distance covered by leatherbacks in one day (Bailey, Fossette, et al., 2012; Eckert, 2002). All data were projected to the Lambert Azimutal equal area coordinate system. The temporal resolution was monthly to minimize any missing environmental data (Hazen et al., 2017; Hoover et al., 2019). Geo-processing was conducted using R package raster (Hijmans et al., 2015).

Modeling framework

We start with a model for all individuals in the geographic domain. Next, we derive the movement model based on the initial model for all individuals. The movement model is assumed to be unbiased at population level after considering autocorrelation. We then introduce a presence-only

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process that consists of all individuals observed by the opportunistic sampling process. We end with a discussion of the stepwise estimation process, which fits telemetry and fishery observations to the model framework. In developing the modeling framework, we considered a geographical domain $\mathcal{D}$ where animal locations were characterized by a PPM with intensity (i.e., density of locations per unit area) $\lambda(s_t)$, and s_t denotes location at timestamp t (Hooten et al., 2017; Manly et al., 2007). We assumed each site in $\mathcal{D}$ had associated environmental covariates $x(s_t)$ and that space in $\mathcal{D}$ was discretized into a finite number of cells $\{g \in D\}$. Each cell g was characterized by the same set of covariates. The environmental covariates served as drivers for the PPM in a log-linear form

$$\log \lambda(s_t) = \alpha_0 + x(s_t)^{\mathrm{T}}\beta. \quad (1)$$

The $\beta = \left(\beta_1, ..., \beta_p\right)$ coefficients characterize the environmental space use by the target population and α_0 denotes the unobservable abundance at the average environmental conditions.

To actuate the model, we considered a set of telemetry observations from multiple animals and assumed they contained no gap (e.g., missing daily locations) and had the locational errors integrated out (see references in Jonsen et al., 2007). Telemetry observations were arranged in the form of a continuous time discrete space (CTDS) path (Hanks et al., 2015), and for notational brevity, we removed the dependence of paths on individual animal, *i*. We assigned T to denote the number of cells (i.e., stops) along the path and $g = \{g_c, c = 1, ..., T\}$ to denote the cells each with $\tau = \{\tau_c, c = 1, ..., T\}$ residence time. Without loss of generality, we assumed τ to be in the same temporal unit as the PPM intensity (1). We also assumed, at each time step, that a set of cells were equally available to the animal, and we defined this set indirectly via an adjacency relation "~," thus the availability function $f(g_c) = I(g \tilde{} g_c)$, where I denotes the indicator function (Hooten et al., 2014). To facilitate data fusion between telemetry and fishery observations, we defined the CTDS resource selection function or motility through the PPM model (1)

$$[g|g_c] = \frac{\exp\left\{x(g)^{\mathrm{T}}\tilde{\beta}\right\}}{\sum_{\tilde{g} \tilde{} g_c} \exp\left\{x(\tilde{g})^{\mathrm{T}}\tilde{\beta}\right\}}, \quad g \tilde{} g_c, \quad (2)$$

where $[.|.]$ denotes conditional distribution, $x(g)$ denotes the environmental covariates at neighboring cells, and $\tilde{\beta} = (\delta_1\beta_1, ..., \delta_p\beta_p)$ denotes the scaled resource selection coefficients with scalars $\delta = \left(\delta_1, ..., \delta_p\right)$ linking CTDS motility with PPM intensity. The likelihood function of a CTDS path under model (2) is proportional to the Poisson likelihood with offsets τ, and maximum likelihood or approximate Bayesian estimation can be conducted using the iterated reweighted least-squares algorithm.

The CTDS model (2) can be generalized to allow directional dependence in movements and population-level inference. Directional dependence in movements can be modeled by including direction of the most recent movement as a covariate (Hanks et al., 2015). Random coefficients and intercepts can be used to account for dependence of resource selection within individuals. We, therefore, defined b_i as the $p \times 1$ vector of random coefficients or offsets for individual i and $z(g,i)$ as the constructed covariates of directional dependence, and generalized the individual motility model to

$$[g|g_c^i] = \frac{\exp\{\eta(g,i)\}}{\sum_{\tilde{g} \tilde{} g_c^i} \exp\{\eta(\tilde{g},i)\}},$$

$$\eta(g, i) = x(g)^{\mathrm{T}}\left(\tilde{\beta} + b_i\right) + z(g,i)\gamma, \quad (3)$$

where $g \tilde{} g_c^i$, with g_c^i being the residence cell c of each individual path i.

Fishery observations were modeled through a presence-only model via a thinned Poisson point process (Fithian et al., 2015) to account for the opportunistic observation process. We introduced spatially structured random effects $\xi(s_t)$ to model the potential observational bias in the fishery observations. Additional covariates that were not collinear with the environmental covariates $x(s_t)$ and yet indicative of the bias were incorporated as fixed effects. Data integration between telemetry data and fishery data was implemented through a constructed variable approach (Pacifici et al., 2017). Estimates of resource selection coefficient $\hat{\beta}$ from (3) were used to construct covariates $\hat{\eta}_j(s_t) = x_j(s_t)^{\mathrm{T}}\hat{\beta}$, $j = 1, ..., p$, denoting the expected intensity based on each environmental predictor. We let $\tilde{\lambda}(s_t)$ be the intensity of opportunistic fishery observation per unit area and $\delta = \left(\delta_1, ..., \delta_p\right)$ be the coefficient (2) to scale motility of this constructed variable to the intensity of a Poisson point process

$$\log \tilde{\lambda}(s_t) = \alpha_1 + \sum_j \delta_j\hat{\eta}_j(s_t) + \xi(s_t), \quad (4)$$

where α_1 captures the overall number of reports. We assumed a low-rank Duchon spline for $\xi(s_t)$ to use first-order derivative penalization for 2D space (Wood, 2003). The likelihood function of model (4) can be approximated using a set of quadrature points (Renner et al., 2015).

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The uncertainty in the presence-only observation data was propagated by the following multiple imputation algorithm (Plummer, 2015). We first sampled the resource selection coefficients from a normal approximation to the posterior distribution of $\beta^{(m)} \sim N\left(\widehat{\beta}, \widehat{\Sigma}_\beta\right)$ of model (3) given the CTDS tracking data, where $\widehat{\beta}$ denotes the restricted maximum likelihood estimates and $\widehat{\Sigma}_\beta$ denotes the Bayesian posterior covariance matrix (Wood, 2006), using the approximate normal distribution of regression coefficients. We then used the following $\widehat{\eta}_j^{(m)}(s_t) = x_j(s_t)^{\mathrm{T}}\beta^{(\mathrm{m})}$ to construct the expected species distribution. The random offsets b_i were set to null so that the constructed variable represents the population-level resource selection. Next, we sampled from the posterior distribution of $[\delta, \xi | y_2, \widehat{\eta}]$ of model (4) given y_2—fishery observations and the constructed covariates $\widehat{\eta}$ from model (3). Independent priors were assigned on the scalars $\delta_j \sim N(-1, 0.375)$ such that a priori they are within 25% of −1, reflecting the prior belief that higher motility was associated with lower intensity. The scalar estimates from the fishery observations were assumed to be approximately normal, which leads to a conjugate normal posterior. Normal approximations, spline estimation, and posterior sampling were implemented using the mgcv package in R (Wood, 2017). Statistical significance of the variables was assessed using 95% credible intervals. The R codes along with a simulated example are available online (Liang, 2021).

Intensity was back-predicted for each month from September 1997 to December 2019 using both fisheries and tracking observations. We divided the back-predicted monthly distributions into nonbreeding (April–September) and breeding (October–March) times of the year. Intensities and the associated standard errors for breeding/nonbreeding periods were mapped by aggregating the monthly posterior predictive distributions over each month between 1997 and 2019.

Simulation study

We performed a simulation study to evaluate the predictive performance of the ISDM. We compared predictions from the ISDM with those from a presence-only model. We simulated data from the fitted Bayesian model of a prior telemetry data analysis (Hoover et al., 2019). The spatial extent of the original study was reduced (−100 and −70° longitude and −10 and 20° latitude) to reduce the computational burden of this simulation. The population-level linear coefficients for bathymetry, frontal probability index, sea surface height, and quadratic coefficients for SST were used to generate tracks. Simulation parameters included the number of tracks (20, 80), the average days for each track (20, 40, 60, 80, and 100 days), and the average number of fishery observations (600, 1200). The intensity of the fishery observations was assumed inversely proportional to population-level motility $\lambda = \exp(-\beta)$. Spatially structured observation bias was introduced in the log intensity surface under the fishery observations.

As a basis for simulation, 180 Monte Carlo samples were generated for each of the 40 parameterizations of the simulation. The true intensity was compared with the estimated intensity for two methods: (1) the ISDM combining CTDS and presence-only model (continuous-time discrete-space Markov chain [CTMC] + PPM) and (2) a presence-only PPM. We implemented the presence-only model so that the autocorrelation in the track data was ignored. Instead, telemetry location was assumed independent of each other. The presence-only approach was implemented in R using the methods described in Degenford et al. (2021). The R^2 between the true intensity and the estimates was computed as a measure of the predictive performance.

RESULTS

The predictive R^2 of ISDM started at ~32% with 20 tracks and an average of 20 days (Figure 2). Predictive performance increased as the average length of the tracks increased. The gain in R^2 was more substantial when the average length was 20 days rather than 100 days. A larger number of tracks resulted in around a 3% increase in R^2. The number of fishery observations did not visually alter the ISDM performance. The track length of 60 days resulted in an R^2 close to the maxima. The predictive R^2 of PPM was ~10% and did not change with the increase in track lengths. The number of tracks did not affect the R^2 as well (data not shown). Predictive performance increased slightly when the number of fishery observations doubled from ~600 to ~1200. This indicates that tracking data were not effectively incorporated when the autocorrelation within the tracks was ignored. An ISDM analysis with 20 tracks could significantly outperform the same PPM analysis with doubled fishery observations.

Among the 114 SSSM track segments (denoted tracks hereafter) from 94 female leatherbacks, 19 tracks were before 1997 and removed due to the lack of available environmental data. Three of the remaining tracks were shorter than 8 days and removed to avoid bias toward the tagging location, and a further seven tracks were removed due to highly collinear environmental covariates within

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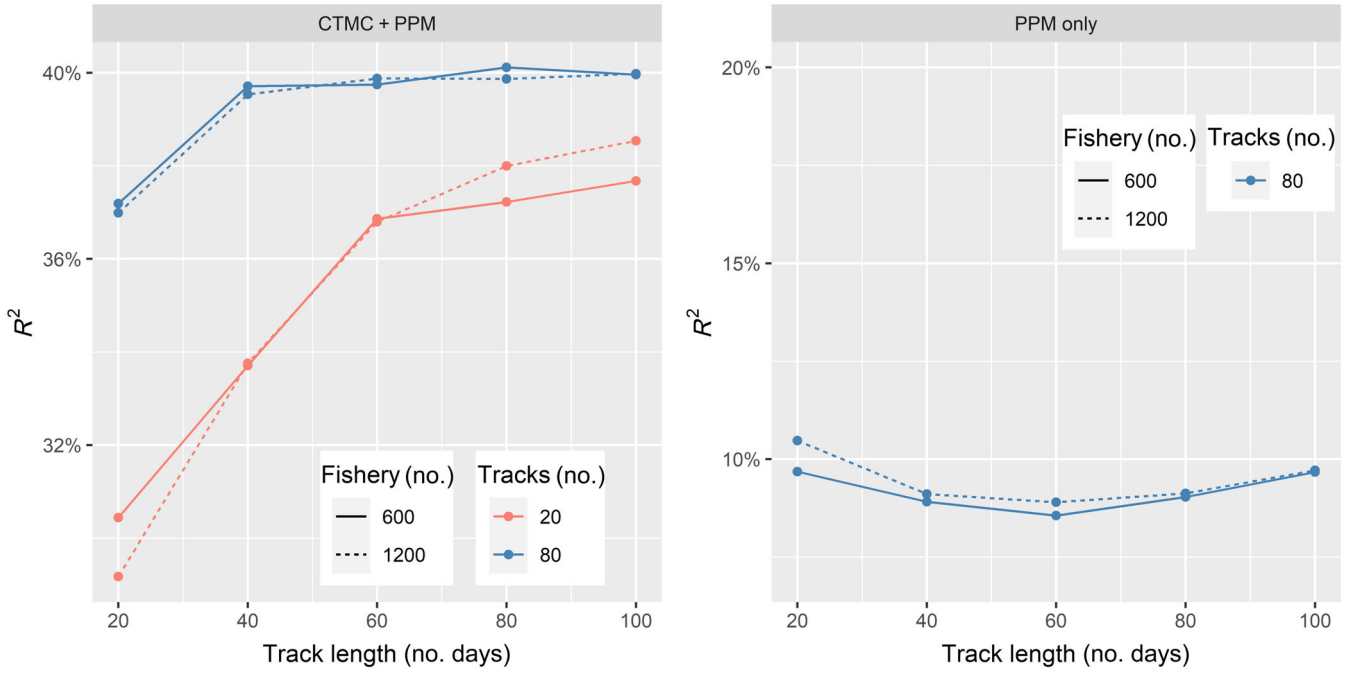


FIGURE 2 Predictive performance of the integrated model. R^2 is the percent variance explained in the simulated intensity. Simulation parameters include the number of tracks, length of tracks, and the number of fishery observations. CTMC, continuous-time discrete-space Markov chain; PPM, Poisson point process model.

the CTDS paths. Thus, a total of 85 tracks were included in the analysis, totaling 33,540 daily positions spanning November 1997 through November 2017. All fishery observations were included in the analysis ($n = 806$). Ekman upwelling was not included in the analyses of the full dataset due to a lack of data coverage before August 1999. Additional analyses with Ekman upwelling only using data after August 1999 are presented in Appendix S1.

We applied backward model selection and none of the variables were removed. Population-level coefficients from the CTDS model were all statistically significant with p-values <0.05 (Table 1). Motility was positively associated with bathymetry and frontal probability index, and negatively associated with sea surface height and chlorophyll *a* concentration. Effects of SST were a priori assumed quadratic (Hoover et al., 2019) with minima around 22°C (Figure 3). The tracks exhibited strong directional dependence as measured by the effects of the direction of the most recent movement denoted by "crw" (Table 1, $p < 0.01$).

Scaling parameters linking estimated motility effects to intensity of the thinned PPM were all statistically significant (95% credible intervals excluding zero, Table 1). Joint analysis indicated that intensity was negatively associated with the bathymetry and frontal probability index due to their positive effects on motility, while intensity was positively associated with sea surface height and chlorophyll *a* concentration. Effects of SST on intensity were concave and quadratic with maxima around 22°C (Figure 3).

The spatial random effects ξ in Equation (4) were estimated within a convex hull containing the fishery observations (Figure 4). The effects were assumed to be null beyond the hull such that predictive mapping was focused on the environmental covariates. Positive spatial random effects (on a log scale) were estimated near two fishing hotspots off Peru and Chile covered by the respective observer programs of the data-providing organizations. Negative effects were estimated in the northwestern part of the convex hull, which indicated a lack of observer coverage and fishery observations.

Intensity was predicted to be high in the coastal areas from Mexico to Chile, the equatorial region, and high seas off northern Chile (Figure 5). Low intensity was predicted at mid-latitudes within areas offshore of Peru and Chile. The long-term average intensity between April and September was similar to that between October and March (Figure 5). Seasonality of intensity was observed in the northern part of the region (low intensity in late summer/early autumn, Appendix S1: Figure S17).

Intensity predictions were drastically different depending on whether adjustments were made according to the spatial random effects ξ, modeling the effects of fishery observational process (Figure 5). The raw prediction from the fishery observations without the

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TABLE 1 Population-level coefficient estimates (along with standard error, test statistic, and *p* value) from continuous time discrete space hierarchical model relating motility with environmental covariates and scalar estimates (along with 95% credible interval [CrI]) from joint species distribution model linking motility with intensity of a Poisson point process model.

Covariate	Estimate	SE	*t*	*p*	Scalar	95% CrI	df	*F*
bathy	0.07	0.03	2.59	0.01	1.53	−0.13, 2.28		
fpi	0.37	0.07	5.51	0.00	1.32	0.59, 1.96		
ssh	−0.51	0.25	−2.06	0.04	−1.61	−2.30, −0.68		
chla	−0.21	0.05	−4.05	0.00	−0.48	−0.93, −0.28		
crw	0.58	0.02	37.62	0.00				
s(sst)	1.95	2.00	10.56	0.00	−1.14	−1.81, −0.53	1.95, 2.00	10.56

Note: Data shown on log scale. s denotes smooth term. *t* tests were used for parametric terms, and *F* test was used for smooth terms. CrI denotes credible interval. df denotes (ecdf, Res. df), where ecdf and Res. df denotes estimated degrees of freedom of the *F* test.

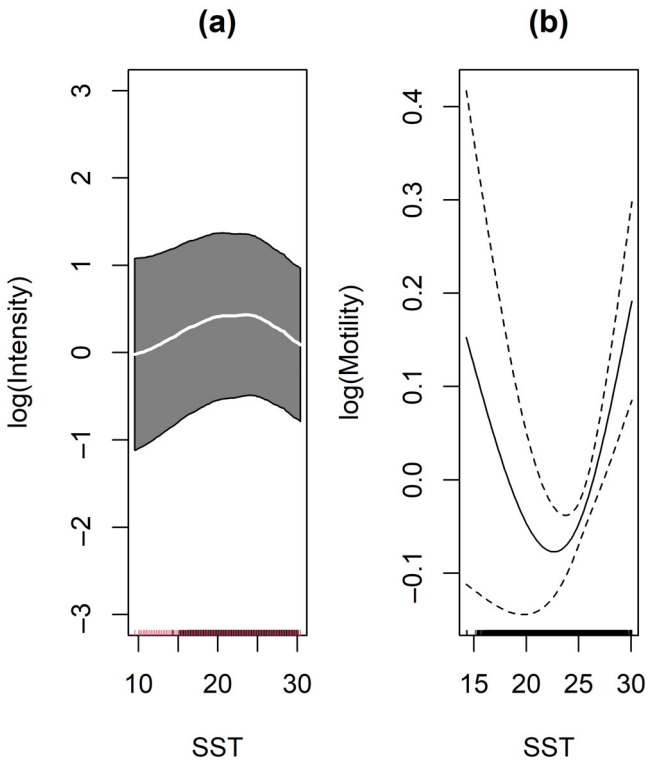


FIGURE 3 Population-level partial effects (estimates and 95% confidence interval), (a) from joint species distribution model relating sea surface temperature (in degrees Celsius) to intensity when other environmental covariates were held at their average values; red rugs denote data from fishery observations, black rugs denote data from tracking observations, and (b) from continuous time discrete space model relating sea surface temperature to motility. SST, sea surface temperature.

adjustment delineated much broader areas of relatively higher intensity in the coastal oceans off Peru and Chile. Based on the raw predictions, coastal Mexico and Costa Rica, as well as the equatorial region, were predicted to be of low seasonal use by the leatherback population.

DISCUSSION

Data from probabilistic surveys or opportunistic sources remain the main inputs for SDMs. Building upon the PPM for telemetry data (Aarts et al., 2008; Miller et al., 2019), we proposed a SDM that synthesized fishery observations with satellite telemetry observations. Our Bayesian approach utilized the telemetry data to estimate the potential reporting bias in fishery observations. We demonstrated the model using long-term (1997–2017) leatherback data in the Eastern Pacific, and we found that fishery records were spatially biased toward Peru and Chile coastal areas, potentially fishing hotspots. Our data synthesis suggests high seasonal leatherback distribution in coastal areas, which concurs with previous studies (Degenford et al., 2021; Shillinger et al., 2008, 2010, 2011).

For other species with long-term tracking data and potentially biased opportunistic observations, this framework can potentially improve our understanding of the drivers of the species' distribution (Rose et al., 2020). The satellite telemetry data represented mostly adult nesting females, but the tracks represent vast pelagic areas of the Southern Pacific Gyre occupied by leatherbacks during the migration. These regions were deficient in fishery observations. The fishery observations, however, represented multiple size and age classes yet are deficient in important postnesting coastal habitats. This framework highlights the importance of considering life stages in accurate species distribution modeling. Telemetry data have been collected for a wide range of marine species (Block et al., 2011; Breece et al., 2018; Yamamoto et al., 2015), which provide valuable information for habitat use of these highly migratory species. Many marine species have declined through anthropogenic threats such as incidental fisheries bycatch. However, fisheries data have rarely been integrated with the telemetry data to map species distributions. We applied a point process framework (Hooten et al., 2014; Manly et al., 2007) to fuse telemetry data with potentially

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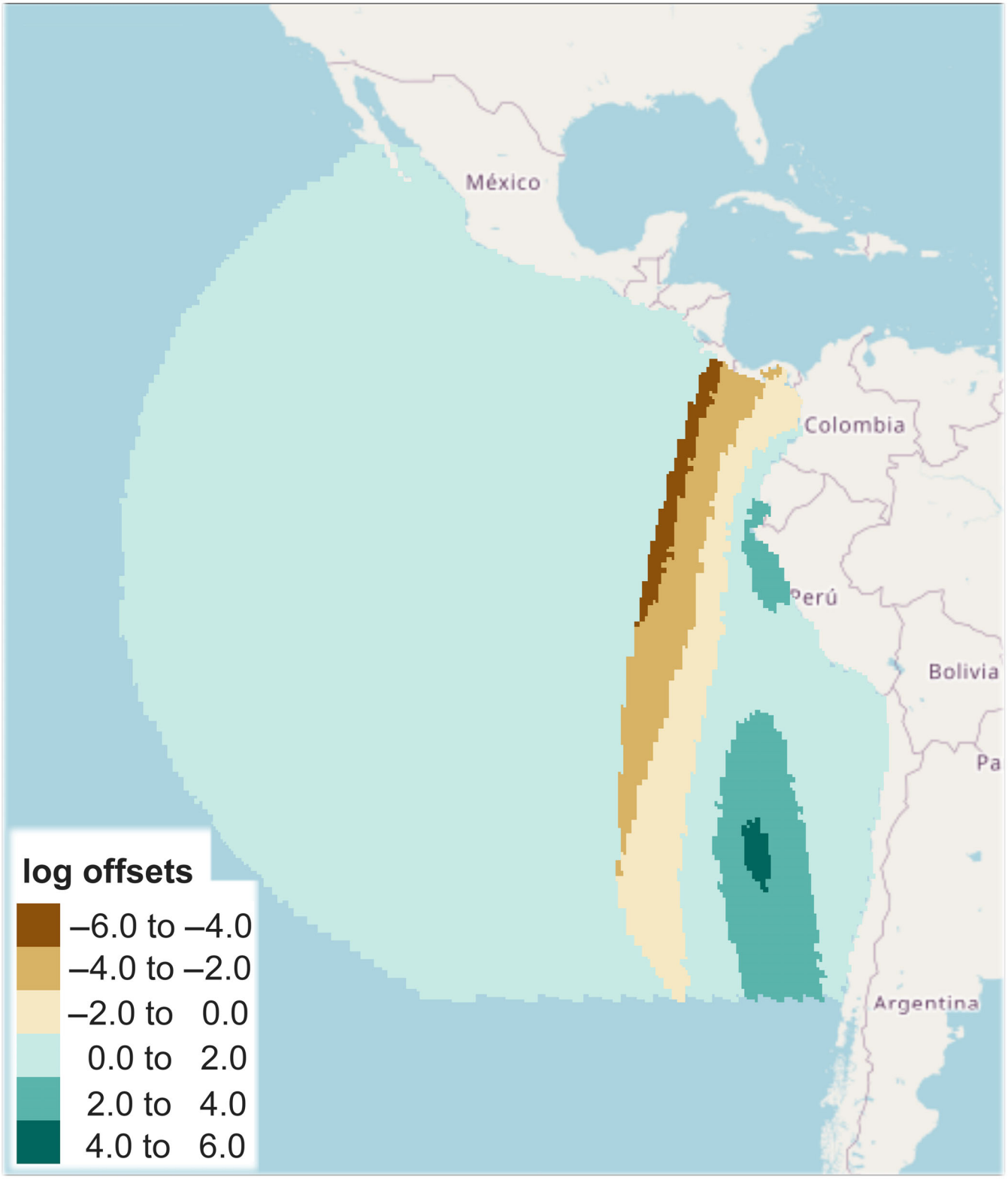


FIGURE 4 Partial effects of spatially structured observational bias in fishery observations, shown as the difference between logarithm of expected distribution from track observations after 1997 and the logarithm of estimated intensity from fishery observations. All environmental data except Ekman upwelling were used.

biased observations, collected from fisheries programs (Pacifici et al., 2017). The PPM has robust predictive performance in some novel periods (Degenford et al., 2021; Rose et al., 2020), collection of more data, such as turtle size and sex, along with systematic reporting of fishing efforts can improve our predictive understanding of a

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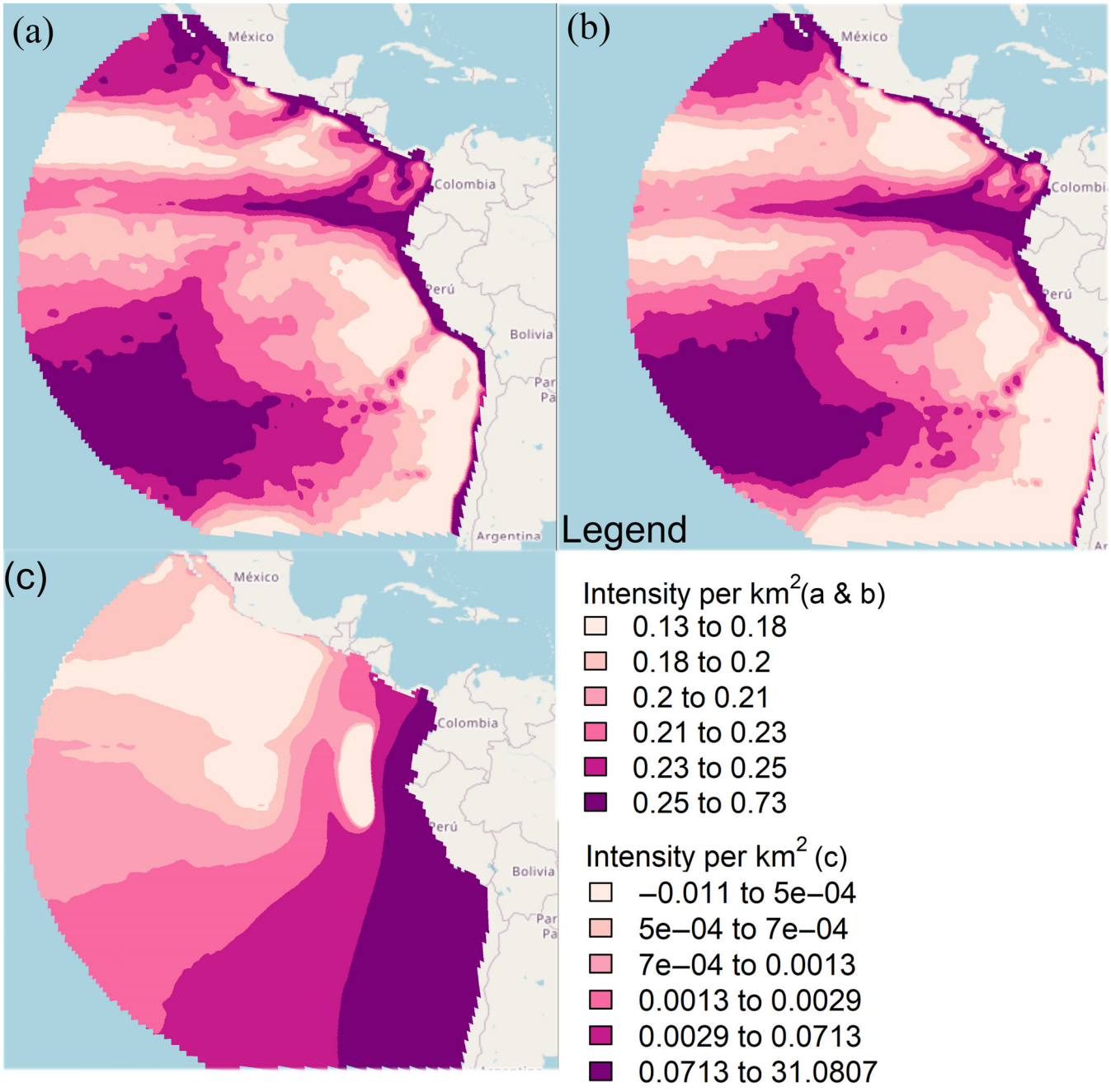


FIGURE 5 Predicted average intensity from 1997 to 2019 between (a) April and September and (b) October and March based on joint distribution model of track and fisheries observations using a limited set of environmental data (without Ekman upwelling). (c) Raw prediction between April and September, without considering observational bias. Intensity is reported in per 1000 grid cells per month. The deep red areas are associated with areas of highest intensity, while paler areas indicate lower leatherback intensity per unit area.

species' distribution (Miller et al., 2019) and its management implications.

The fisheries observation process could generate bias in the development of an SDM (Rose et al., 2020). For example, such bias could result from the confounding between the observational process (e.g., placing observers in a particular fishery or area of fishing effort and interpreting/extrapolating bycatch) and the resource selection of species (Miller et al., 2019). We explicitly modeled the observation process when estimating the relationship between species occurrence and environmental covariates from both the telemetry and fisheries data. A nonparametric spatial smooth demonstrated that observations from several fisheries hotspots, if unaccounted for, could

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weaken the estimates of coefficients of environmental covariates (Komori et al., 2020). Poisson point process framework enables modeling of both the observation process and the ecological process. Further application of the framework is warranted to enhance our ability to utilize fisheries observations in the management of highly migratory marine species.

We developed data fusion by assuming that telemetry data were generated from a point process (Fithian et al., 2015). A preferential sampling approach provides an alternative and general probabilistically coherent framework to synthesize the data (Gelfand & Shirota, 2019). We used the common log-linear form of a PPM, but the framework could be generalized to account for spatial dependence and regularization to improve predictive capability (Renner et al., 2019). A mechanistic model for movement can also be incorporated through a partial differential equation approach (Hooten et al., 2020). Our model uses random effects to achieve population-level inference, but for species with social interactions during migration, dependent movement due to interactions could be relevant for more social animals such as marine mammals and seabirds (Calabrese et al., 2018; Russell et al., 2016). Further, our approach did not explicitly model imperfect detection (Koshkina et al., 2017). Although potential model modifications and assumptions remain, our model is a step toward resolving the challenge of combining two disparate animal distribution data sources.

The intent to effectively synthesize presence-only data within species distribution modeling efforts motivated the development of a joint likelihood approach, which utilizes probabilistic survey data to correct for the potential bias (Fithian et al., 2015; Giraud et al., 2016). The CTDS approach parameterizes the likelihood in a familiar generalized linear model, which allows joint modeling of telemetry data and presence-only records in a fully Bayesian framework (Hanks et al., 2015). The trade-off between data quality and quantity is an important factor in data integration. Here we applied a conceptually simpler stepwise approach by first estimating the CTDS coefficients and then using these coefficients to scale motility to intensity. Such a stepwise approach can be implemented using readily available software and is computationally feasible for analyzing multiple tracks, presence-only observations, and environmental covariates (Hooten et al., 2016; Pacifici et al., 2017). However, a fully joint-model approach remains to be implemented and tested that relaxes such assumptions (Hefley & Hooten, 2016; Pacifici et al., 2017).

In general, resource use is strongly influenced by life stage and gender (Yamamoto et al., 2015). Leatherback populations tend to exhibit distinct movement patterns between internesting (breeding) and postnesting (nonbreeding) periods. Turtle movements in internesting periods are largely driven by predator avoidance, while habitat quality and foraging are important drivers in postnesting periods. Tracked turtles are mostly nesting females, and males are underrepresented. We assumed that telemetry observations give unbiased representations of leatherback resource selection regardless of gender and the internesting and postnesting periods. Our prior analyses using fisheries observations from multiple life stages (both juveniles and adults) and genders seem to support this assumption (Degenford et al., 2021). Habitat-based models for cetaceans have similarly tended to focus on seasonal patterns with monthly outputs and separate models for winter/spring and summer/fall that allow managers to identify key areas of occurrence and high densities (Hazen et al., 2017; Roberts et al., 2016). With the advancement of life-stage specific telemetry studies (Hazen et al., 2012; Mansfield et al., 2021; Shillinger et al., 2011, 2012), a hierarchical model approach that links the life-stage specific movement with relevant fisheries observation data could be developed to account for the nonstationarity of movement due to life stage and sex.

Further joint modeling of telemetry and fishery observations, for example, for leatherbacks during internesting periods, would likely require high-resolution environmental data. Remotely sensed observations are usually processed at multiday composites, and thus insufficient to resolve the high-temporal resolution movement. Joint analysis of internesting data could benefit from expanding beyond satellite-acquired environmental data. Data assimilative ocean models such as the Regional Ocean Modeling System (ROMS) provide subdaily resolution and 3D outputs at high spatial resolution (e.g., Schick et al., 2013). The nowcast from ROMS may be more predictive for species making use of the entire water column (Scales et al., 2017). While a data assimilation system requires extensive effort to set up in large areas such as the Eastern Pacific Ocean, and some important drivers (such as productivity) might still be missing, the data assimilation ocean model is a promising source of environmental data to further improve the predictive capacity of joint modeling of telemetry and fishery data.

Our telemetry observations span between 1993 and 2019, a large period over which there could be global trends across environmental variables. It is challenging to develop environmental covariates with comparable spatial coverage and temporal duration. For example, Ekman upwelling index and chlorophyll a data were not available prior to 1997. This resulted in the truncation of track observations (<5%). Environmental variables were synthesized from multiple satellites and model products. We attempted to use sources with known validation levels and, when possible, developed empirical calibration between multiple products using their overlapping periods, so that the

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environmental covariates could be consistent with the calibration uncertainty quantified (Liang et al., 2016). We conducted supplementary analyses using different sets of environmental variables and study durations, and the results suggested that model outputs were not sensitive to the environmental variables and durations. There is, however, still a possibility of a trend in habitat usage during the last three decades given climatic variability. For example, long-term changes in ocean currents and temperatures could affect habitat availability.

The Eastern Pacific leatherback population exhibits a strong coastal component distribution. This coastal distribution is year-around (Figure 5), which makes this population especially vulnerable to changing climatic conditions and bycatch within neritic foraging and interesting habitats. The integrated analyses suggest that the population distribution is positively associated with chlorophyll *a* and sea surface height, which may suggest population-level feeding and area-restrictive search behaviors in the coastal areas. The ISDM approach uses a PPM framework to separate fisheries observational process from the resource selection in both data types. The results lead to enhanced estimates of the relationship between species distribution and environmental covariates, and enhanced predictive distribution (Figure 5). Our results highlight the benefit of a PPM framework in synthesizing the information from fisheries observations and tracking data. For the leatherback subpopulation in the Southeast Pacific, our results imply areas of high population-level utility. The coastal areas should receive high priority for conservation to protect this population from interactions with fisheries.

Dynamic ocean management is management that can rapidly change in response to the spatiotemporal distribution of selected species (Maxwell et al., 2015). Dynamic management tools provide information on species distributions in space and time, environmental conditions, and activities of interest, to help guide such management (Lewison et al., 2015). The development of these tools for protected species has included whales (WhaleWatch; Hazen et al., 2017), fish (Atlantic Sturgeon Risk of Encounter; Breece et al., 2021), and turtles (TurtleWatch; Howell et al., 2015). In this study, we have improved on our earlier dynamic SDMs for Eastern Leatherback turtles (Degenford et al., 2021; Hoover et al., 2019) by combining different types of data to provide a more holistic estimate of their occurrence based on the environmental conditions to help inform and improve protection for this critically endangered population. The addition of the predictions from this model to the South Pacific TurtleWatch publicly available website (https://www.upwell.org/sptw) will be combined with a communication strategy across different platforms (e.g., mobile, web, printed, radio) aimed at disseminating information to an array of different stakeholders, such as government agencies, the fishing community, and the broader public. Increased protection for this population at sea should be a high priority for this long-lived animal that is rapidly declining as a result of human activity (Santidrián Tomillo et al., 2017).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Anonymized and simulated leatherback data and code (Liang, 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.7120515. The actual leatherback datasets are sensitive. The leatherback telemetry data and the actual fishery observations have not been made publicly available. Telemetry observations from Costa Rica are owned by George L. Shillinger and collaborators. Telemetry observations from Mexico are owned by Scott Eckert and collaborators. Telemetry observations from Peru are owned by Joanna Alfaro-Shigueto, Jeffrey C. Mangel, and collaborators. Fishery observations are owned by ACOREMA

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(Areas Costeras y Recursos Marinos, www.acorema.org.pe), IFOP (Instituto de Fomento Pesquero, www.ifop.cl), IMARPE (Instituto del Mar del Peru, www.imarpe.gob.pe), JUSTSEA Foundation (www.justsea.org), ProDelphinus (www.prodelphinusperu.org), and The Leatherback Project (https://www.leatherbackproject.org/). Interested researchers could contact the owners regarding these data. The environmental covariates can be obtained from the following websites: Bathymetry: coastwatch.pfeg.noaa.gov/erddap/griddap/usgsCeSrtm30v1.html. SST: coastwatch.pfeg.noaa.gov/erddap/griddap/NOAA_DHW_monthly.html. SSH: resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012. Chl-a SeaWIFS: https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chlamday.html. Chl-a MODIS: https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdSW2018chlamday.html. Wind QuickSCAT: https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdQSstressmday_LonPM180.html. Wind ASCAT: https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdQAstressmday_LonPM180.html.

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