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A MACHINE LEARNING SPECIES DISTRIBUTION MODEL FOR THE CRITICALLY ENDANDERED EAST PACIFIC LEATHERBACK TURTLE (*DERMOCHELYS CORIACEA*)

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CONTENTS

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ABSTRACT

The Eastern Pacific leatherback turtle population (*Dermochelys coriacea*) has dramatically declined in recent years, being bycatch from coastal and pelagic fisheries one of the major causes. In this study, we created a machine learning species distribution model trained with fisheries observations and remotely sensed environmental data. Through a highly collaborative international participatory approach, we obtained leatherback observation data from multiple fisheries that operated in the eastern Pacific Ocean between 1995 and 2020. A daily predictive process was applied to predict leatherback habitat suitability (probability of occurrence) for the study period as a function of dynamic and static environmental covariates. This model serves as the basis for dynamic ocean management and Ecological Risk Assessment from which outputs can inform managers and stakeholders as to appropriate management action that can reduce leatherback turtle bycatch while providing a modeling framework for analyzing fisheries observations for other data-limited vulnerable populations and species.

1. INTRODUCTION

Sea turtles represent a unique example of the diversity of life histories of living animals in the world's oceans by straddling the interface between ocean and land throughout their lives. They spend most of their lives at sea, but are tied to terrestrial habitats (i.e., nesting beaches) for reproduction. This life history strategy exposes sea turtles to significant natural (e.g., climate change and habitat loss) and anthropogenic (e.g., fishing, pollution and marine debris, egg consumption, coastal development) threats that currently compromise their population viability, with all species classified by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species as either "vulnerable", "endangered", or "critically endangered"[19]. Consequently, conservation efforts have increased in many regions of the world in an attempt to curb these threats, with varying degrees of success (Wallace et al. 2011).

One species of particular concern is the leatherback turtle (*Dermochelys coriacea*), the largest (~2 m in length) and most geographically widespread of all sea turtle species (Wallace et al. 2010). Distributed circumglobally in tropical to temperate regions, and regularly occurring in coastal as well as high-seas areas, the species comprises seven regional management units (RMUs) or subpopulations (Wallace et al. 2010). Two RMUs—the East Pacific (EP) stock and West Pacific (WP)—exist in the Pacific Ocean, both of which are currently classified as "Critically Endangered" on the IUCN Red List (Tiwari et al. 2013; Wallace et al. 2013). The EP stock in particular has demonstrated a precipitous population decline, with the annual number of nesting females estimated to have declined by over 90% since the 1980s resulting from unsustainable levels of incidental mortality in industrialized and artisanal fisheries, which mainly affect sub-adults and adults, and human consumption of eggs (Laúd OPO Network, 2020).

Given that industrial and artisanal tuna purse seine and longline fisheries cover a high proportion of the species' distribution in the EPO, they unavoidably interact with leatherback turtles, and other sea turtle species, during their normal fishing operations as they target tunas, billfish and other species that share similar epipelagic habitats (IATTC, 2020).

The Inter-American Tropical Tuna Commission (IATTC) is the Regional Fisheries Management Organization (RFMO) that is responsible for the management of these tuna fisheries in the eastern Pacific Ocean (EPO). Since the Antigua Convention entered into force in 2010, which significantly broadened IATTC scope to consider an ecosystem-based approach, several Resolutions pertaining

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[19] The flatback turtle (*Natator depressus*) is the lone exception, as its current IUCN Red List status is Data Deficient.

to the conservation and management of various sensitive bycatch species have been implemented, including sea turtles (Res. C-07-03). However, in light of the declining population of leatherback turtles in the EPO in particular, the IATTC implemented in 2021 more stringent conservation measures to mitigate the fishery impacts on sea turtles through the development of Resolution C-19-04.

Further, the Inter-American Convention for the Protection and Conservation of Sea Turtles (IAC) is an intergovernmental treaty that provides the legal framework for countries in North and South America to take actions to benefit sea turtles, in both nesting beaches and the Parties' territorial waters. Concerned with the critical status of leatherback turtles, the IAC adopted Resolution CIT-COP7-2015-R2 that requests IAC Parties to make efforts to reduce the bycatch of the species in the EPO using recommendations from IAC Resolution COP3/2006/R-2, such as exercising FAO guidelines to reduce sea turtle mortality in fishing operations (FAO, 2009). Other international conservation instruments have been developed for sea turtles as well, such as their inclusion in Appendices I and II of the Convention of Migratory Species (CMS) (CMS, 2015) and under Appendix I of the Convention on International Trade in Endangered Species (CITES) (CITES, 2016). These measures were required to meet regional conservation goals as well as curb international trade of sea turtle products (e.g., eggs, meat, shell material).

Quantitatively demonstrating the sustainability of bycatch species is challenging due to the often lack of reliable biological and catch information available, especially for species of little or no economic value or in data-limited settings. Therefore, assessing bycatch species using traditional stock assessment approaches is often both cost-prohibitive and impractical. As an alternative, the IATTC staff developed a flexible spatially-explicit quantitative ecological risk assessment approach—Ecological Assessment of Sustainable Impacts of Fisheries (EASI-Fish)—to quantify the cumulative impacts of multiple fisheries for data-limited bycatch species, such as sea turtles (Griffiths et al., 2019a). The basic principle of EASI-Fish is to estimate the proportional overlap of fishing effort on the geographic distribution of the species of interest, which is converted into a proxy for species' vulnerability for an assessment period based on well-established biological reference points. Since the extent of overlap between the fishery and species is of critical importance in this approach, a reliable species distribution model (SDM) is required. SDMs are built to describe the relationship between a species and environmental conditions and can predict how environmental variability may affect their distribution and habitat choice (Elith & Leathwick, 2009). Although SDMs have been widely applied in predicting suitable habitats for marine species over past few decades (Melo-Merino et al. 2020), only a few studies have focused on sensitive bycatch species (e.g., Sequeira et al. 2014; Abrahms et al. 2019, Lezama-Ochoa et al 2020, Lopez et al 2020).

Unfortunately for rarely encountered bycatch species, whether their rarity is due to selectivity issues, non-reporting, or declining population size, there is often a small number of observations from which to develop an SDM. This therefore limits the types of models available to develop an SDM that can make use of scant presence records. Unlike other methods, machine learning algorithms, including boosted regression trees (BRT) (Elith et al 2006), are powerful tools in dealing with non-linear relationships, high-dimensional large datasets, imbalanced classes, and limited species occurrences (Elith et al 2008; Mi et al. 2017).

The goal of this study is to generate a reliable high-resolution SDM to inform conservation and management of EP leatherback turtle in the EPO. Previous studies have developed potential methods for producing SDMs for EP leatherbacks using individual-based satellite telemetry data (Hoover et al. 2019) or presence-only observation data (Degenford et al. 2021). Here, we developed a hierarchical machine learning modelling approach that used a region-wide presence-absence dataset for EP leatherback turtles and incorporated different predictive variables and modelling scenarios to: i) understand the potential distribution of the species at different spatio-temporal scales, and ii) identify the environmental preferences of the species, and iii) develop a final prediction map describing to most plausible distribution for the species that will be used in a concurrent study to assess the species' vulnerability. This paper describes the fundamental role of SDMs to quantify and mitigate the impacts of EPO fisheries on EP leatherback turtles, help inform their vulnerability status and guide the development of appropriate conservation and management decisions. The framework presented in this study could also be applied to other data-limited vulnerable species and populations.

2. METHODS

All data processing and analytical work was carried out in the Microsoft R Open environment (MRO 3.4.3; https://mran.microsoft.com/rro). Microsoft R Open is the enhanced distribution of R from Microsoft Corporation and includes additional capabilities for improved performance, parallelization, and reproducibility.

2.1 Fisheries observer data

We used 26 years (1995–2020) of primarily fisheries' observer and logbook data from a variety of industrial and small scale coastal ("artisanal") fisheries (Table 1) operating in 6 countries and the high-seas within the IATTC convention area in the EPO – defined as the region from the coast of the Americas to 150°W between 50°S and 50°N.

The vast majority of the industrial high-seas observations corresponded to the large-scale tuna longline fishing vessels (herein called the "industrial longline fishery") and the tropical tuna large purse-seine fishing fleet (Class 6 with a carrying capacity >363 mt). The data include set-level information on leatherback turtle interactions along with location, date and time of the observation. The distribution of industrial tuna fishing effort mostly concentrated between 20°N and 20°S during the study period. The data for these fleets were collected by IATTC on-board scientific observers, or submitted to the IATTC by its Members under Resolution C-19-08. The observer coverage rate was close to 100% for purse seine vessels of class 6 and around 5% for the industrial longline fishery.

In contrast to the industrial fisheries in the EPO, catch and effort by the numerous artisanal fleets that operate within the EEZs of countries in the EPO generally have very low (if any) observer coverage, and are poorly documented in general. However, leatherback turtles have been shown to be heavily impacted by coastal, artisanal gillnet and longline fisheries, particularly in foraging areas, but also in migratory and reproduction areas (Wallace et al., 2013a). Reasonably detailed effort data for artisanal longline vessels throughout Central America was available from IATTC's long-term research program that examined the effects of different hook types on bycatch rates, in part reported by Andraka et al. (2013). In addition, the IATTC-IAC EP leatherback turtle *ad hoc* working group compiled leatherback turtle interaction and fishing effort information for several artisanal fisheries operating in territorial waters of 6 countries in the EPO (Table 1) (see BYC-11-02 for details).

Duplicate records, data outside the EPO, and observations without reliable date and location information were removed from the dataset (~3.5%). The final dataset included 1,088 leatherback records from nearly 575,000 fishing sets (0.19%) (Table 1) (Fig. 1).

2.1 Predictive variables

A total of 23 variables were included in species distribution models (SDMs), which included 3 spatio-temporal variables, 11 surface variables, 2 subsurface variables, and 2 static variables (Table 2). The three spatio-temporal variables included location and date of set, as seasonality may affect catches. Spatio-temporal variables can be confounded with environmental factors and reflect certain natural processes not captured by the surface and subsurface variables. The majority of environmental data was sourced from daily/weekly fields of global data assimilative models (*i.e.* assimilate available data from satellites and *in situ* platforms) that include the IATTC convention area at 0.25° (~25 km^2) resolution (available at http://marine.copernicus.eu/ and https://www.aviso.altimetry.fr/). The 0.25° spatial resolution, combined with a fine temporal scale, is considered adequate for habitat modeling (Scales *et al*. 2016).

The 11 surface variables chosen included sea surface temperature (SST) and its gradient (SST_grad; calculated as the change in temperature at the same pixel over a period of 7 days), salinity (Sal), sea surface height (SSH), current speed (Vel), current direction (Dir), eddy kinetic energy (EkE), finite size Lyapunov exponents (FSLE), front index (FrontIndex; estimated as a count of the front pixels in the grid cell for the 7-day window), Chlorophyll a (CHL), and Chlorophyll a gradient (CHL_grad; computed as the difference in Chlorophyll a concentration in the same pixel over a 7-day period).

The 2 subsurface variables included temperature at 100 m depth (SST_{100}) and mixed layer depth (MLD). Temperature at 100 m depth and mixed layer depth have proven to be helpful to improve SDMs for large pelagic species (Brodie *et al*. 2018) as help describe the two-dimensional (*i.e.*, vertical and horizontal space) structure of the water column properties.

The 2 static variables included bathymetry (Depth), and the distance to land (LandDistance). These variables were extracted from the Global Marine Environmental Datasets (GMED) (Basher et al., 2018) and MARSPEC Ocean Climate Database (Sbrocco et al., 2013), respectively, and have shown to be important to define leatherback turtle's habitat (e.g. Hazen et al., 2018; Robinson et al., 2016; Willis-Norton et al., 2015).

2.2 Model Specification

In the interest of robustness and to inform comparisons, we took a hierarchical multi-model approach, building 6 presence–absence (catch vs. zero catch per set, binary response) models with each set of variables, from simplest to most complex models. The following models were established for the original model with all presence and absence data: i) spatio-temporal, ii) surface, iii) subsurface, iv) environmental (surface + subsurface), v) static, and vi) full (environmental and static) (Fig. 2).

Because the full model had the best performance metrics (Table 3), subsequent models using different proportions of presence to absence data were only established with this set of variables (full; environmental and static variables) (see section sensitivity analysis for details).

2.2.1 Species Distribution Models: Boosted Regression Trees

a. Model building

Boosted regression trees (BRTs) are a flexible classification algorithm based on machine learning principles (De'ath 2007; Elith *et al*. 2006). Consequently, some of the caveats of more commonly used techniques such as generalized linear models (GLMM) or generalized additive mixed models (GAMM) are not applicable. BRTs have the particular advantage of being tolerant to missing values, outliers, collinearity, non-independence, and allowing for the inclusion of irrelevant predictors (Leathwick et al. 2006). BRTs are also designed to accommodate non-linear relationships, large high-dimensional datasets, imbalanced classes, and limited species occurrences (Elith *et al.* 2008; Mi *et al.* 2017). While GLMMs and GAMMs seek to fit the most parsimonious model to a dataset, BRTs combine predictions of many simple models (i.e., many shallow classification trees) to maximize robustness and predictive performance to reduce associated error (Scales et al. 2017). Accordingly, we fitted BRTs with all available sets of covariates. In the past, authors also fitted GAMM and Random Forest (RF) models to other species presence-absence data to compare and better understand consistency and interpretation between algorithms (e.g., SAC-10-INF-D). In these cases, BRTs performed better than GAMMs and had very similar performance to the RFs. As such, we decided to use BRTs to build all the models in this study, which were implanted in R using the *dismo* package (Hijmans et al. 2017).

In fitting BRTs, we adapted the protocols outlined by Brodie et al. (2018), Elith et al. (2008), Hazen et al. (2018) and Scales et al. (2017). Presence–absence models were built with a binomial (Bernoulli) distribution. We used a tree complexity of 3, a bag fraction of 0.7, and conducted sensitivity analyses on learning rate ("shrinkage") for each model set, aiming for at least 1,000 trees in final model configurations. The sensitivity runs determined 0.01 as the learning rate to be used in all the models, except for the model with the same number of presences and absences (i.e., 50-50 presence-absence ratio; see section on sensitivity analysis), where a value of 0.005 was used. Tree complexity refers to the number of nodes in a tree, which constrains the maximum size of each of the regression trees that together make up a boosted regression tree model. By controlling the number of nodes/branches, tree complexity also sets the maximum number of interactions between predictor variables that are possible (i.e., 3 in this case as a two-way, and perhaps three-way, interactions among variables may be important, but higher-orders unnecessary, in fisheries contexts; Soykan et al. 2014). Bag fraction refers to the percentage of the data that is randomly used for model building at each step, which usually ranges between 0.6-0.75 (Elith et al. 2008). The stochasticity that this step provides to the model building process improves model performance (Soykan et al. 2014).

The potential for model simplification was evaluated with the function *gbm.simplify*. Simplified models were fitted by re-running models without those variables that gave no evidence of improving predictive performance. Deviance explained, variable importance, as well as interactions between variables were also estimated for all the models using the function gbm.interactions. Each of these configuration settings and the performance procedures are described in detail by Elith and Leathwick (2017); Elith et al. (2008); Hazen et al. (2018); Scales et al. (2017) and Soykan et al. (2014).

b. Model validation

A k-fold cross-validation method was used to evaluate the reliability and the predictive performance of final models. This method consists of using independent data sets for model building (i.e., the training data) and model validation (i.e., the test data), where data is partitioned into k equally sized segments or folds through random resampling. Model performance is assessed by successively removing each subset, rebuilding the model on the retained data, and predicting on the omitted data (Elith and Leathwick 2009). In this study, a k = 4 partitioning method was used, meaning that 75% of the observations were used for model building, and the other 25% for model validation. Hold-out validation avoids the overlap between training data and test data, yielding a more accurate estimate of the generalization performance of the algorithm (Villarino et al. 2015).

The predictive power of the model was assessed by computing a set of diagnostic metrics. The mean Area Under the receiver-operating Curve (AUC) (Hanley and McNeil 1982) and the mean True Skill Statistic (TSS) (Allouche et al. 2006) were calculated for each iteration from each confusion matrix. The AUC provides a single measure of overall model accuracy that is threshold independent, with an AUC value of 0.5 indicating the prediction is as good as random, whereas 1 indicates perfect prediction (Fielding and Bell 1997). AUC has been extensively used in SDMs and measures the ability of the model to correctly predict where a species is present or absent (Elith et al. 2006). An AUC value of >0.75 is considered to have a good predictive power and is acceptable for conservation planning (Pearce and Ferrier 2000). TSS is an alternative measure of model accuracy that is threshold dependent and not affected by the size of the validation set (Allouche et al. 2006). It is an appropriate evaluative tool in cases where model predictions are formulated as presence–absence maps (Allouche et al. 2006). TSS is on a scale from -1 to +1, with 0 representing no predictive skill and is calculated from the confusion matrix outputs as sensitivity plus specificity minus 1 (i.e. TSS = sensitivity + specificity - 1). Threshold independent and dependent statistics, such as AUC and TSS, respectively, should be used in combination when evaluating the predictive power of a SDM (Pearson et al. 2006).

c. Sensitivity analyses

The model utilizing all data (hereafter called the "original model") contained 573,883 observations (1088 presences; 0.19%) . To determine the effect of using different proportions of presence on model performance, the relationship between the response variable and the covariates (i.e. environmental and static), as well as the generated predictions, a multi-model approach was conducted using 10 datasets with each having a different presence-absence ratio. The presence-absence ratio in the data used to build the final models was incrementally decreased from 50 to 0.5%. In each case, all 1088 presence observations were included with a variable number of randomly selected absences. For example, the 50:50 model included 1088 absences while the 0.5:99.5 model included 216,512 absences (Table 4). All models (hereafter called "final models") were run using all environmental and static variables, as per the full model) and followed the same model building and validation procedures mentioned above.

2.3 Predictions

a. Daily predictions

Daily predictions of the probability of occurrence of leatherback turtles over the IATTC convention area were conducted for 2002–2020 (i.e. 6935 daily predictions). A series of time-matched environmental data fields (both surface and subsurface as well as static variables) were used to generate daily predictions based on the 11 final models and their best number of trees using function *predict* in the package *raster* (Hijmans *et al*. 2015). Therefore, 11 different predictions were computed for each day of the time series to inform consistency and interpretation, and to visualize the effect of accounting for different proportion of presences on the predictions. The spatial resolution of the predictive surface was set to the lowest common resolution of environmental data fields (0.25°).

b. Prediction averaging and ensemble

Daily predictions (n = 6935) were averaged for 2002–2020 for each of the 11 final models. Visual inspection of predictions, and exploration of performance metrics and the relationships between response the variable and covariates suggested two groups of similar models: i) six models with a presence-absence ratio ranging from 50% to 10%, and ii) five models models with a presence-absence ratio ranging from 5% to 0.19%. All averaged predictions were inspected by experts in leatherback turtle ecology who concurred that the models of the first group best represented the species habitat. Therefore, an ensemble model was created using the average predictions from all models having a presence-absence ratio of 50% to 10%. Similarly, the model with a 25% presence-absence ratio was also identified by both expert opinion and performance metrics as a plausible model (hereafter called the "reference model"). Therefore, a ensemble model was developed using the average predictions from the upper (33:66) and the lower (20:80) models. Generating the two ensemble predictions allowed comparisons between candidates and the exploration of the potential effects of model selection on the final prediction.

c. Probability-of-occupancy (ψ) threshold

The first stage of EASI-Fish in estimating the vulnerability of a species is to determine the number of grid cells where the species is considered to be present and also contains fishing effort. Because SDMs estimate a probability of a species to occur in each grid cell, a probability-of-occupancy threshold value (ψ) must be used to define whether the species is present or absent in each cell. However, the spatial extent of the species' distribution increases and decreases with lower and higher ψ values, respectively, and thus influences the proportion of the species' population that is exposed to fishing. To account for this uncertainty, three ψ values (0.1, 0.2, and 0.3) were applied to each 0.25° cell, based on statistically determined thresholds and verification by experts. This range was determined by overlaying the distribution of predicted probability of presence with that of predicted probability of absences. The ψ value where these two distributions intersected was selected to define the most probable species distribution and upper and lower bounds were selected by visual inspection of the two distributions on either side of the intersection point (Lopez et al. 2020).

Given the critically endangered status of EP leatherbacks, we selected relatively low ψ values to conservatively include areas where experts considered leatherbacks likely to occur, even if in relatively low numbers and for limited periods of time, based on documented patterns of spatio-temporal habitat use (Shillinger et al. 2008; 2011; Donoso and Dutton 2010; Bailey et al. 2012; Quiñones et al. 2021) and previously published SDM maps (Hoover et al. 2019; Degenford et al. 2021). This is key to ensuring that EASI-Fish would be precautionary in its calculations of fishery impacts on leatherbacks throughout their distribution and across fisheries known to interact with the species (see BYC-11-02).

3. RESULTS

3.1 Model performance

Models including all data and environmental and static variables (*i.e.* model vi - full) demonstrated better performance under the diagnostic measures we used (deviance explained, AUC and TSS) (Table 3). In general, complex models (*i.e.* models iv, vii) had better performance than simpler models including sets of variables individually (*i.e.* models i, ii, iii, v). These models explained between 19.71% and 40.57% of the deviance in the data, had AUC values between 0.79 and 0.94, and had TSS values that ranged between 0.51 and 0.76 (Table 3). The number of trees created by the these models ranged between 3600 and 7000. The comparison in model performance led us to recommend the use of this model configuration (model vi - full, environmental and static variables) for further exploration on the sensitivity analysis.

Models including different proportions of presence ratios with environmental and static variables (*i.e.* model vi - full) shown similar but also different performance under the diagnostic measures we used (Table 4). In general, models with balanced or slightly imbalanced dataset (*i.e.* models 50:50, 33:66, 25:75, 20:80, 15:85, 10:90) had better performance than models that used highly imbalanced datasets (*i.e.* models 5:95, 2.5:97.5, 1:99, 0.5:99.5, original - 0.19%). These models explained between 40.57% and 61.54% of the deviance in the data, had AUC values between 0.92 and 0.96, and had TSS values that ranged between 0.76 and 0.81 (Table 4). Based on these diagnostic measures, the model using 25% of presence-absence ratio was identified as the reference model.

3.2 Drivers of leatherback turtle presence

An examination of the relationships between species and the environmental and static variables showed a range of interesting patterns for each of the 11 final models, based on variable importance analysis (Fig. 3) and partial dependence plots (e.g., Fig. 4). These indicators suggested two groups of similar models: i) models with a presence-absence ratio ranging from 50% to 10%, and ii) models with a presence-absence ratio ranging from 5% to 0.19%. The first group showed higher variable importance with SST, SST_{100}, CHL, MLD, FrontIndex, CHL gradient and current direction, whereas the second group showed higher values for Depth, SAL, LandDistance, FSLE and SSH.

A closer look to the reference model showed interesting patterns as well. After simplification, 8 variables were included in the final model, for which relative variable importance was 3.3%-49.9%. EkE, FSLE, LandDistance, SSH, Vel, SST_grad and FrontIndex were dropped from the final model as they did not improve predictive performance. With the exception of CHL_grad (3.3%), all variables contributed more than 5%: SST (49.9%), Depth (12.5%), MLD (9%), SST_{100} (7.5%), Dir (6.7%), CHL (6.2%), and Sal (5%) (Fig. 4).

The model identified higher probabilities of leatheback turtle presence around SST values of 16-20^{o}C. For Depth, higher probabilities of leatherback turtle were found in waters shallower than 1000m. MLD values <100m showed higher probabilities of leatherback turtle presence, whereas SST_{100} showed a positive relationship. Currents with south-west direction showed an evident negative relationship with leatherback turtle presence. A positive relationship was also observed between the leatherback turtle presence probability and CHL, while the opposite relationship was observed for SAL (salinities higher than 30 PSU). Similarly, the model showed higher probabilities of leatherback turtle presence at positive CHL gradient values.

3.3 Predictions

Final models were used to predict species habitat suitability in the convention area for 2002-2020 (Fig. 5).

Predictions revealed spatial differences among models, with, in general, higher probabilities of leatherback turtles predicted by models with presence-absence ratios ranging from 50% to 10%. The predictions of this group of models highlighted several areas expected to support high residence or occurrence by leatherback turtles (Fig. 5). These include coastal areas near nesting beaches in Mexico and Central America, high seas areas through which leatherbacks transit and in which they are presumed to forage, and nearshore foraging areas in southern latitudes. For example, the continental shelf and adjacent high-seas areas within South American EEZs, as well as the higher latitude subtropical convergence zone extending from south-central Chile clearly and consistently supported high probabilities of leatherback turtle presence.

These patterns were also reflected by the ensemble predictions (Fig. 6) and the maps developed after applying the probability of occupancy thresholds mentioned above (Fig. 7).

4. DISCUSSION

Understanding the spatial distributions of marine species is becoming increasingly important as international and regional oceans and fisheries instruments evolve further toward ecosystem-based approaches to conservation and management of marine resources (Aburto et al., 2012; Kirkfeldt, 2019). In a fisheries context, having a reliable prediction of a species' distribution that can be compared with that of fishing effort can allow managers to determine the extent of overlap and implement conservation and management measures (CMM), such as spatial closures, that can reduce fishery interactions, fishing mortality, and thus promote long-term population sustainability.

However, SDMs have traditionally required a large number of species presence locations at fine resolution to be useful for fisheries management in jurisdictions that typically span spatial scales of hundreds, or even thousands, of kilometers. Furthermore, because the largest quantity of data is usually collected for species of high commercial importance (i.e., target species), the application of SDMs has primarily been constrained to these species. However, large scale fisheries such as tuna fisheries that deploy passive gears such as longlines and gillnets to target tunas and other large oceanic predators such as billfish and sharks can be unselective and indiscriminately catch a variety of non-target species such as seabirds, marine mammals and sea turtles, which are mostly discarded at sea and often dead. Some of these bycatch species, such as the leatherback turtle, have life histories of slow growth and low reproductive potential that even low levels of additional mortality applied by fisheries can drive their population to the brink of extinction (Baum et al., 2003; Laúd OPO Network, 2020).

Unfortunately, reliable catch, or even simple occurrence, data is often lacking for bycatch species for a variety of reasons, such as their perceived unimportance to the fishing industry from an economic perspective, the absence of observer programs or policies mandating fishers to record all species interactions in catch logbooks, policies requiring rapid release and no-retention of species, and the typically low frequency of interactions and subsequent issues pertaining to species identification. As was shown in the present study of the critically endangered EP leatherback turtle population, the incidence of interactions in EPO fisheries was extremely low—1088 occurrences from over half a million observations (0.19%). Regardless of whether the low frequency of interactions is attributed to naturally low density in the EPO, rarity of the species following its documented population decline (Laúd OPO Network, 2020), or less than optimal gear selectivity by EPO fisheries, the totality of data available are too few to undertake conventional stock assessments. Therefore, more rudimentary vulnerability assessment approaches that are designed to assess data-limited species (e.g. EASI-Fish) are highly reliant on estimating vulnerability based on the three-dimensional overlap between the species and fisheries, and thus, reliable SDMs.

Nonetheless, the present study showed the improved capability of BRTs to characterize the habitat preferences of a critically endangered species for which very few occurrence records existed in industrial purse-seine and longline fisheries in the EPO (Hall and Roman, 2013; Griffiths and Duffy, 2017; Lezama-Ochoa et al., 2017, SAC-13-10). The SDM that we produced is spatially comprehensive with respect to the full distribution of the EP leatherback population, as well as the distributions of various fisheries that are known to interact with leatherbacks in the EPO region. Performance metrics for the BRTs (i.e., AUC, TSS, Deviance explained) showed that the models were robust to the extreme imbalance between leatherback presences (~1,000) and absences (>570,000). In fact, the performance metrics of our BRTs are in line, or even surpass, the values shown in other BRT models developed for a number of large pelagics, including sharks, tuna, swordfish and leatherback turtles, among others (Brodie et al. 2018, Hazen et al. 2018, Scales et al. 2017). Thus, we suggest that our modeling approach has the potential to be applied to other data-limited vulnerable species and populations. However, we recognize that for many species, researchers might not have access to absence data when generating SDMs and will have to rely on presence-only approaches.

Patterns of leatherback occurrence appeared to be driven largely by SST and bathymetry (Figs. 3 and 4), particularly when models included near parity between numbers of presences and absences. The influence of SST on leatherback occurrence is has been described by telemetry (e.g., Jonsen et al. 2007; Sherrill-Mix et a. 2008; Shillinger et al. 2008; 2011) and modeling studies (e.g., Hoover et al. 2019), which suggest seasonal movements that track preferred SST ranges, particularly in foraging areas. In the EPO, for example, leatherbacks are thought to exploit high latitude foraging areas in the South Pacific Subtropical Convergence during the austral summer (December-April) when SST is higher in this region, later moving northward toward tropical and subtropical latitudes in austral winter (May-November) (Saba et al. 2008; Hoover et al. 2019). Leatherbacks in the Northwest Atlantic Ocean follow a similar general pattern of high latitude occurrence in summer followed by movement to lower latitudes in winter, tracking SSTs above approximately 18-20C (Sherrill-Mix et al. 2008). Leatherbacks might depart high latitude areas when prey abundance declines, rather than specifically because of decreased water temperatures, considering their capacity for effective thermoregulation (Sherrill-Mix et al. 2008; Wallace and Jones 2008).

Further, our model successfully highlighted several areas known, or expected, to support high residence or occurrence by leatherback turtles (Fig. 5), many of which are relatively close to shore; distance to shore was an important covariate (Figs. 3 and 4). These include coastal areas near nesting beaches in Mexico and Central America (e.g., Shillinger et al. 2011), high seas areas through which leatherbacks transit and in which they are presumed to forage (Shillinger et al. 2008; Bailey et al. 2012; Hoover et al. 2019), and nearshore foraging areas in southern latitudes (Alfaro-Shigueto et al. 2007; Donoso and Dutton 2010;

Degenford et al. 2020; Quiñones et al. 2021).

Our SDM predicted similar areas of relatively high probability of occurrence to those highlighted in previous efforts using satellite telemetry data (Hoover et al. 2019) and presence-only observation data in national fisheries, mainly from Peru and Chile (Degenford et al. 2021). For example, the continental shelf and adjacent high-seas areas within South American EEZs, as well as the higher latitude subtropical convergence zone extending from south-central Chile clearly and consistently supported high probabilities of occurrence in our SDM. This result is generally supported by long-term monitoring observations (Donoso and Dutton 2010; Quiñones et al. 2021), telemetry data (Shillinger et al. 2008), and species distribution modeling (Hoover et al. 2019; Degenford et al. 2020). These comparable patterns are encouraging, particularly when considering the distinctly different analytical methods, data, and spatial and temporal scales used in each study, which were each constrained by the amount and types of information available.

In the present case, although our model relied on fisheries-dependent observation data to produce the SDM, it used presences and absences from several different fisheries (industrial and small-scale), each of which use different gear types (e.g., longlines, purse seines, and nets) in different regions (i.e., from Mexico to Chile, and international waters to 150°W), different depths (i.e., surface to ~300 m), and in different habitat types (i.e., temperate to tropical, coastal to high-seas). Therefore, our dataset was derived from a diverse and extensive suite of sampling platforms and should be considered comprehensive for describing patterns of leatherback turtle distribution in the EPO region. In particular, the fact that we were able to include presences as well as absences from the same sampling platforms (i.e., fisheries) improved the strength of our inferences about the magnitude and direction of environmental covariate influence on predicted leatherback occurrence. The resulting SDM prediction maps are thus considered to be robust representations of the probability of leatherback occurrence in the region.

Although BRTs have been applied to many marine species, there have been few, if any, instances of BRTs being used with such a small number of occurrences, which required a deep exploration of specific model diagnostics and sensitivity analyses to determine the utility of BRTs in such data-limited settings. The scarcity of leatherback observation data, and their critically endangered status, motivated our conservative selection of relatively low bounds as threshold values for defining ‘high’ probabilities of occurrence to parameterize the EASI-Fish model to assess vulnerability (see BYC-11-02). As suggested previously, the scarce EP leatherback occurrence data available may be attributable to a combination of several possible reasons. It may be a result of depleted population abundance in the EPO (Laúd OPO Network, 2020) and low observer coverage—and thus leatherback observations—in IATTC tuna longline fisheries and small-scale fisheries throughout the region. Because sea turtle interactions are not generally required to be recorded in catch logbooks in any IATTC tuna fishery or fishery within national jurisdictions of EPO coastal states, their occurrence is generally only recorded by onboard observers when they interact with the gear or are sighted in the vicinity of the fishing operation. Unfortunately, besides the AICDP/IATTC observer program that covers 100% of sets of all large (Class 6; >363 mt) purse-seine vessels in the EPO—where very few sea turtles are caught (Hall and Roman, 2013; Lezama-Ochoa et al., 2017)—observer coverage is very low for most other fleets, especially longline, where sea turtles are frequently hooked or entangled (Swimmer et al., 2017). For example, IATTC Resolution C-19-08 requires only 5% of the fishing effort of vessels greater than 20 m LOA to be observed, but even this low level of coverage is frequently not met by some nations (e.g., IATTC, 2021a). Although the quality of species-specific reporting by this fleet has greatly improved in recent years with C-19-08 mandating reporting of operational level data, the reported information is not considered representative of the fleets in space and time (Griffiths et al., 2021) and therefore, there may be some important habitats for leatherback turtles where data is not currently collected. Given that the IATTC staff has proposed an increase in observer coverage to at least 20% for several years (see IATTC, 2021b), it is hoped that longline observer data will further improve in the near future; a particularly important aspect for data-limited species.

Improving data collection programs, both fisheries-dependent and fisheries-independent, is one of the most important consideration for improving SDMs, not only to better characterize a species' distribution with an increased number of occurrence points, but to disentangle some of the aforementioned issues pertaining to interpretation of increasing or decreasing incidences of the capture of vulnerable species that can guide the subsequent development of appropriate management action. To optimize the utility of data collection programs for SDM development in particular, they need to be carefully designed to cover the widest possible spatial extent of the species of interest that cover the full gradient of environmental variables in which the species is naturally exposed (Araújo and Guisan, 2006; Grenouillet et al., 2011). This maximizes the performance of SDMs since strong and contrasted species-environmental relationships allow the model to better interpolate these relationships into unsampled areas or environmental conditions (Miller, 2010). However, data collection programs can be a costly and logistically difficult proposition for highly migratory wide-ranging pelagic species, such as the leatherback turtle, and fisheries that cover thousands of square kilometres of ocean. Consequently, fishery-dependent data is often the primary source of information from which species occurrence locations can be derived. Although with cooperation and proper coordination with fishers and their national management organizations these programs can be run cost-effectively, occurrence data, and to a lesser extent electronic tagging data, are mainly derived from the fishing grounds, which may not cover the breadth of habitats occupied by the species of interest.

Though we are confident that our EPO-wide SDM provides robust results to evaluate CMM efficacy in the EASI-Fish framework, as well as other conservation applications (see below), we recognize additional potential directions for this SDM work. First, there is clear value in detailed investigation of large-scale environmental cycles (e.g., ENSO regimes, climate change) on inter- and intra-annual leatherback distributions to propose adaptive management options that reflect these dynamics (e.g., Hazen et al 2018, Willis-Norton, 2015, Pons et al 2022). Leatherback movements, habitat use, and life history are known to be strongly influenced by environmental conditions, specifically how those conditions affect resource availability (Saba et al. 2007; 2008; Shillinger et al. 2008; 2010; Wallace and Saba 2009; Bailey et al. 2012; Hoover et al. 2019). Thus, high-resolution predictions of leatherback occurrence in time and space at different scales would be highly informative and useful for fine-tuning conservation strategies in the EPO.

Next, considering that development of EP leatherback SDMs has received significant attention to date (Hoover et al. 2019; Degenford et al. 2020; this study), integration of fisheries-independent data with fisheries-dependent data to validate observation-based models and generate a single SDM for the species would be beneficial. Our model expanded on the fishery-based observation data used by Hoover et al. (2019) to include also the high-seas and higher latitudes, among others, but EP leatherback satellite telemetry data (Shillinger et al. 2008; Degenford et al. 2020) were unavailable for this study. Given the similarities in estimated residence times and occurrence probabilities among the existing studies, it is unclear whether one SDM that included all available fishery-dependent and fishery-independent data would produce significantly different, region-wide results than those we present here. Nonetheless, a single, integrated SDM would avoid confusion among users about which SDM to use in their own work, and thus ensure consistency in research and conservation applications.

On that note, we encourage applications of the high-resolution EP leatherback SDM presented here beyond the current specific application to the EASI-Fish vulnerability assessment and evaluation of CMM efficacy. Improved SDMs can inform dynamic ocean management approaches to identify and manage spatio-temporal overlaps between high-use areas and potential threats, including fisheries activities. For example, a simple environmental envelope model was developed for NOAA's TurtleWatch tool (Howell et al., 2008; Howell et al., 2015) to mitigate loggerhead (Caretta caretta) and leatherback turtle bycatch by longline fisheries in the Central North Pacific Ocean. TurtleWatch identifies potential turtle 'hotspots' based on environmental characteristics, such as favorable sea surface temperatures and the presence of current fronts. However, this model relies heavily upon data collected by observers who have observed 100% of shallow sets in the Hawaiian longline fishery since 2004 (Sippel et al., 2014), providing turtle catch counts as well as information on turtle absences. A conceptually comparable tool is being developed for EP leatherback turtles, but it relies heavily on habitat use data limited to post-nesting females from a single nesting population (Hoover et al., 2019). Further, moving from SDMs for individual species to integrated, multi-species predictions could inform development of ocean planning conservation tools to highlight areas in which effective management of fishing (and other) activities (e.g., shipping) would be most beneficial (Hazen et al. 2018, Abrahams et al. 2019). In addition, simply making SDM outputs publicly available to researchers and conservation practitioners could unlock several potential and yet unforeseen applications of these important resources to various issues at different scales. In this vein, we see value in implementing participatory-inclusive approaches with stakeholders, and fishers in particular, to discuss results and bycatch mitigation ideas, define/propose practical management plans, as well as reinforce capacity building with regards to sensitive species, and the leatherback turtle in particular.

CONCLUSION

The work described in this paper highlighted several ways in which BRTs, and SDMs more generally, may be used to improve our understanding of the spatio-temporal distributional dynamics of marine species, and how this knowledge may translate into improved management of vulnerable species. Further, this effort was the product of an international collaboration under a MoU between two inter-governmental conventions—one established to protect and conserve marine turtles (IAC) and the other to sustainably manage commercially valuable tuna stocks (IATTC). Because this collaborative effort brought together several individual representatives of member countries as well as experts in turtle biology and fisheries operating at multiple scales, the resulting product was able to integrate proprietary datasets whose combined value far exceeds their individual value to understanding comprehensive patterns of leatherback distribution throughout the EPO region. Our results are also encouraging as they reveal that theoretically there is plenty of good habitat for leatherback turtles to thrive, and therefore, if conservation efforts are focused on reducing one of its major threats, the bycatch, the species could find suitable habitat to rebuild its population to levels far lees dire than the current situation.

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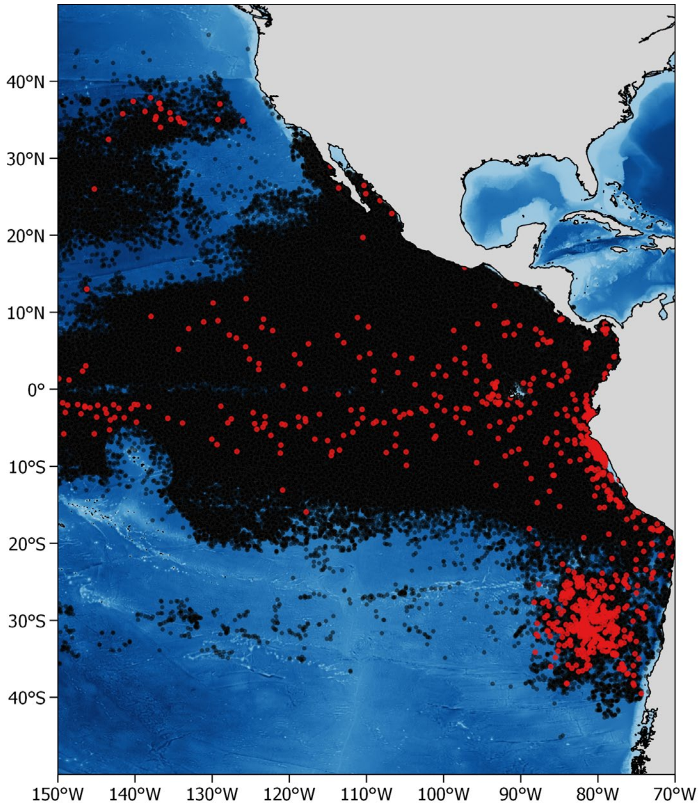

FIGURE 1. Distribution of leatherback presences and absences

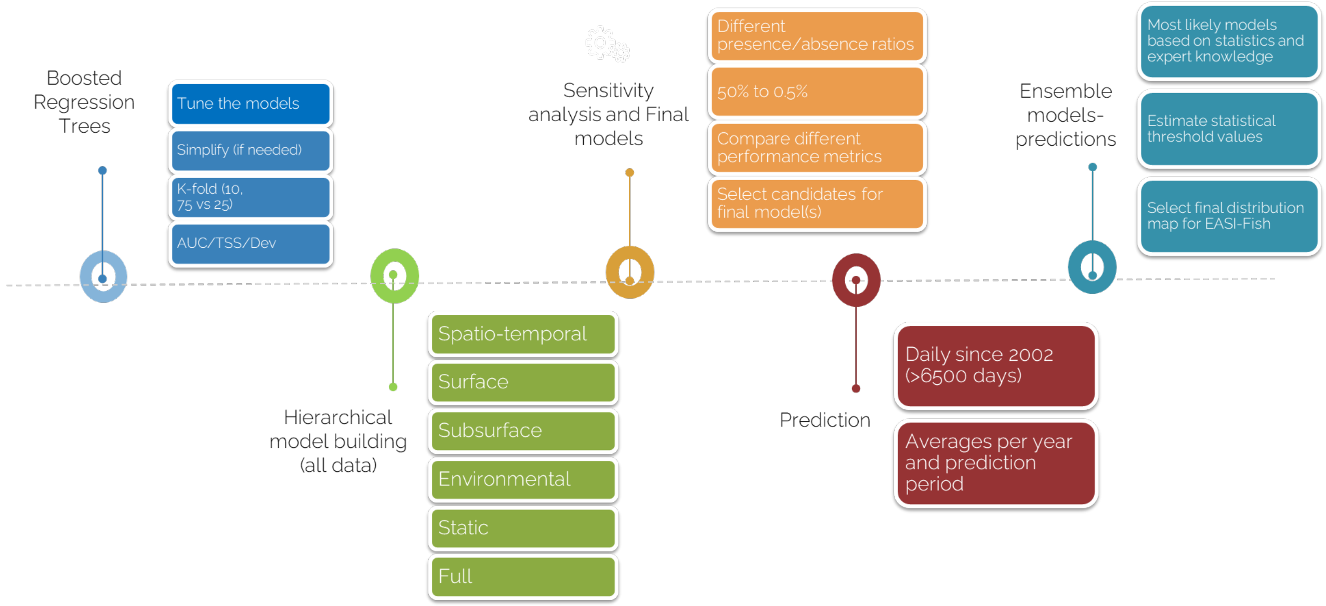

FIGURE 2. Infographic of the methods

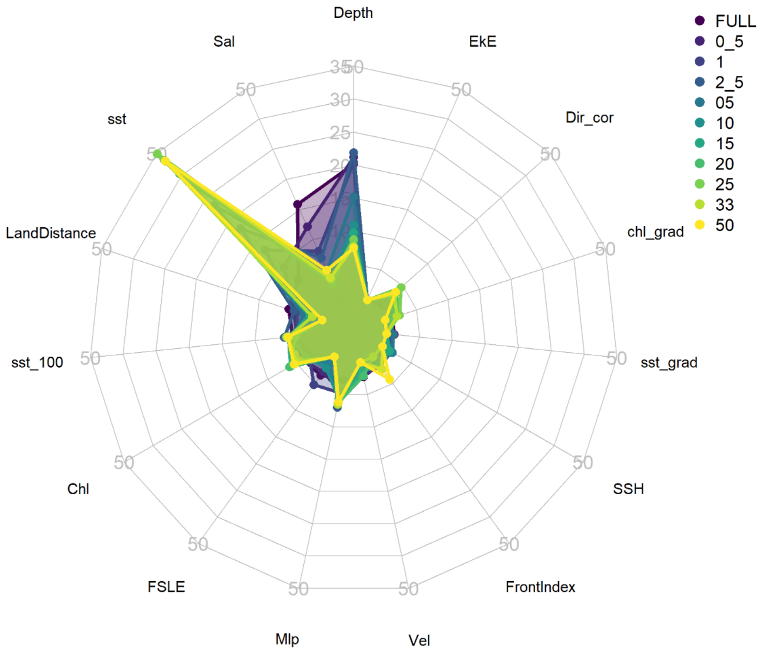

FIGURE 3. Variable importance

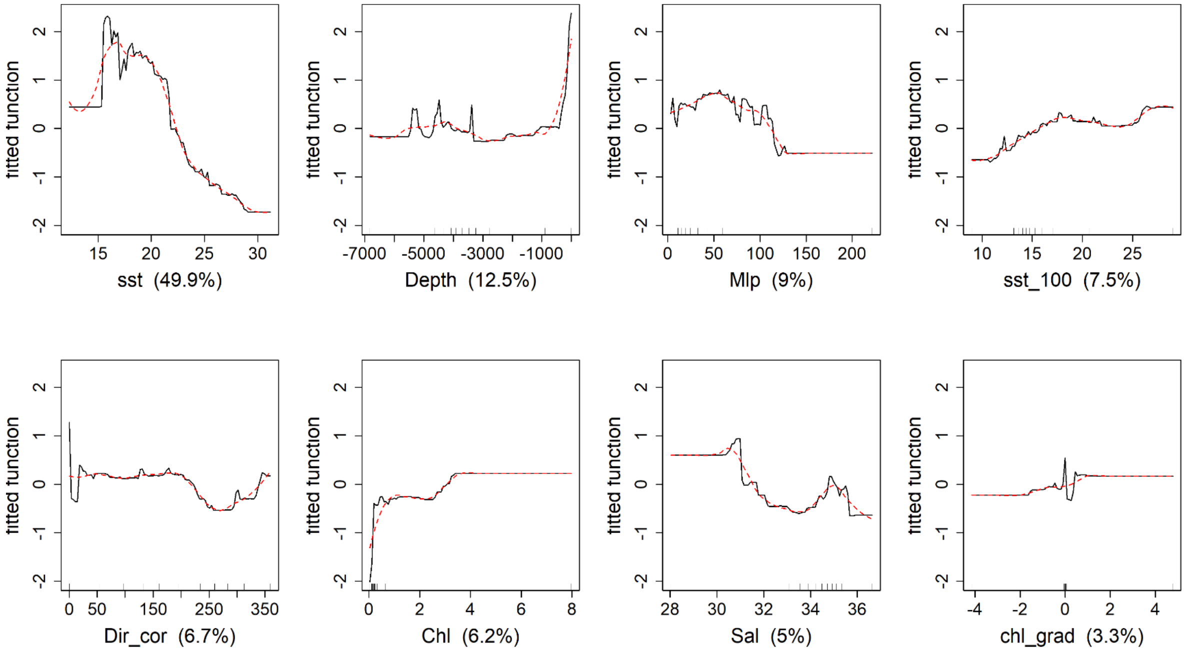

FIGURE 4. Partial dependence plots for leatherback turtle SDMs (example of model with 25% of presences vs 75 absences – reference model)

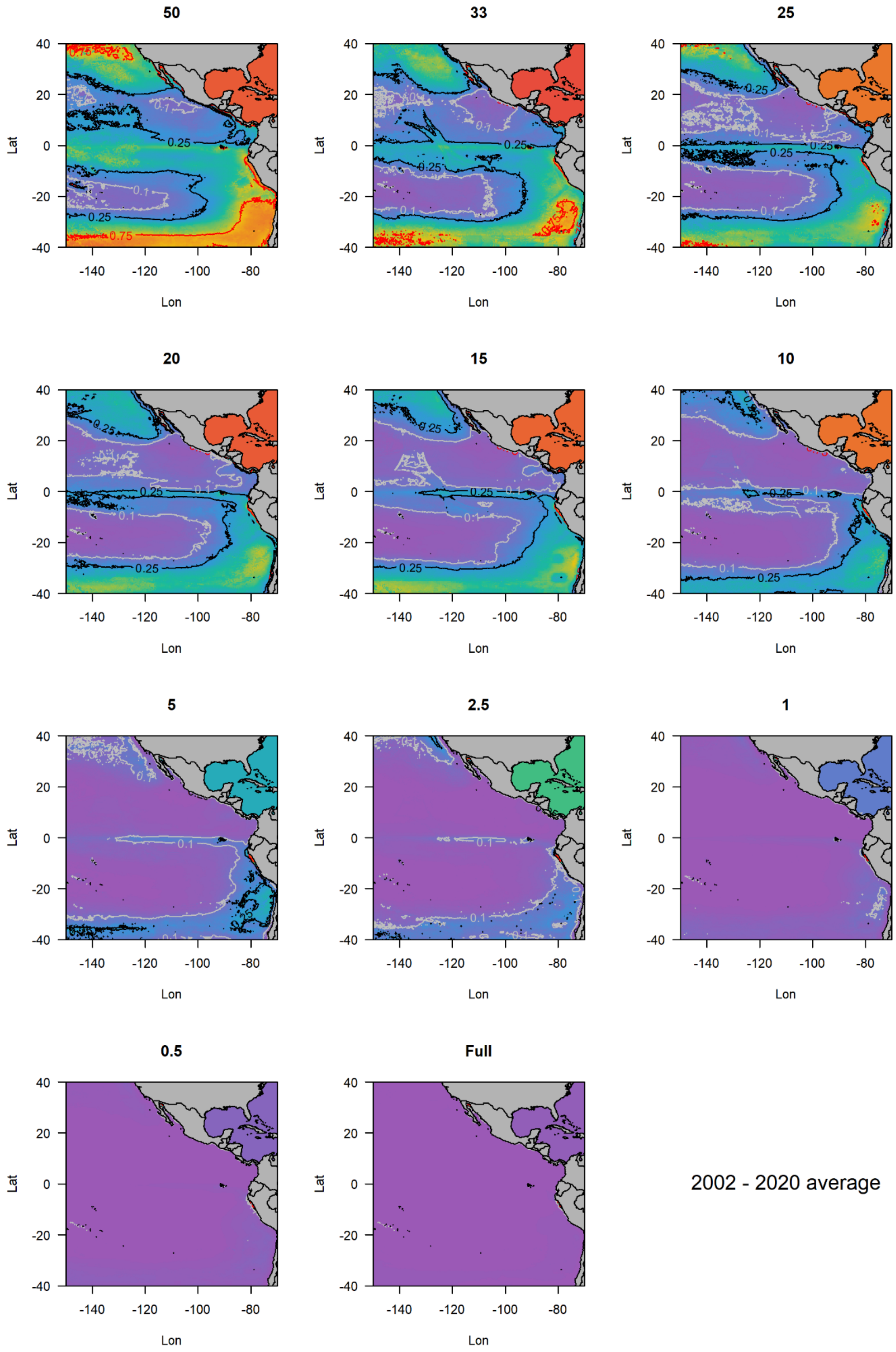

FIGURE 5. Model-specific predictions (averages for daily predictions for the period 2002-2020). The number on top of each panel denotes the ratio of presence to absences used to build the final model (e.g. 50 refers to a 50:50 presence to absence ratio, 33 to a 33:66 presence to absence ratio and so on).

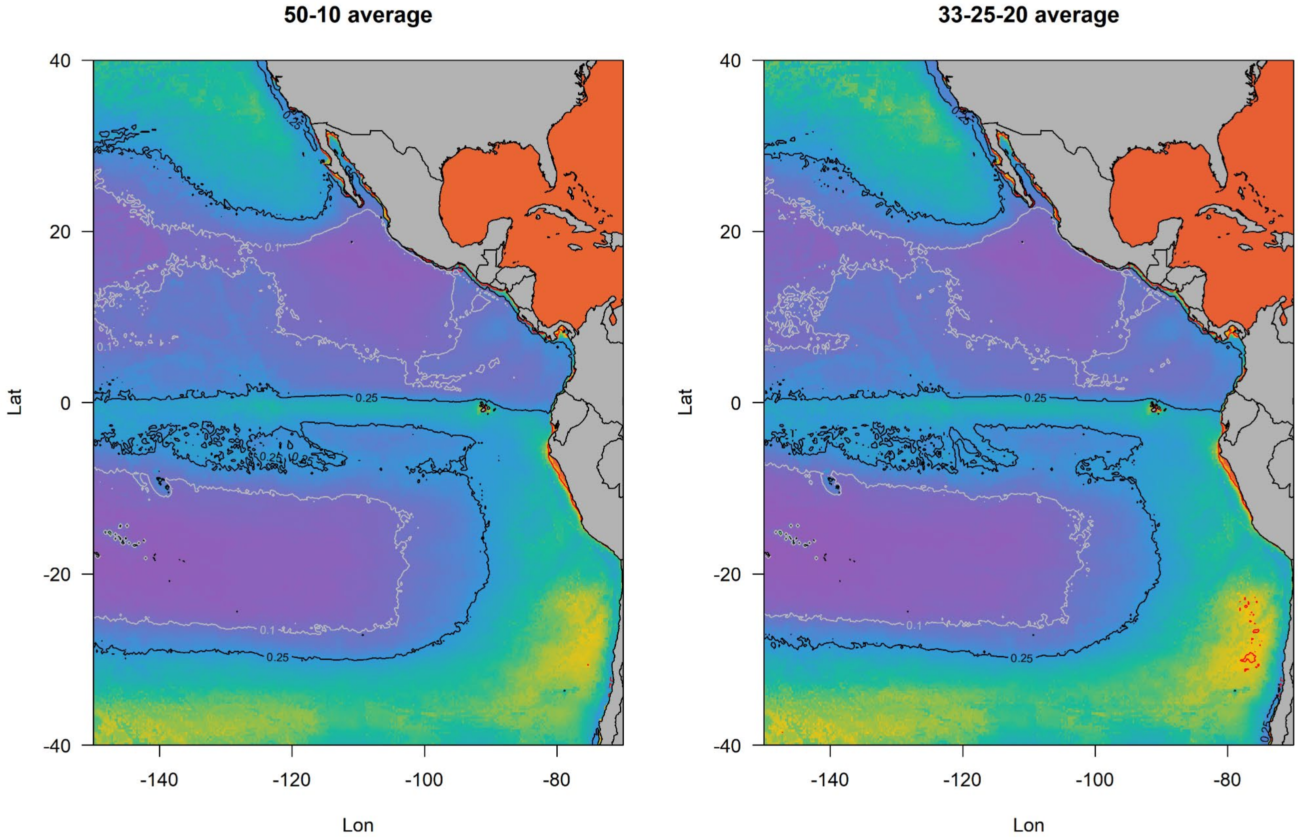

FIGURE 6. Average predictions from an ensemble of SDMs where the ratio of presence to absences were 50-10 (left panel) and 33-25-20 (right panel)

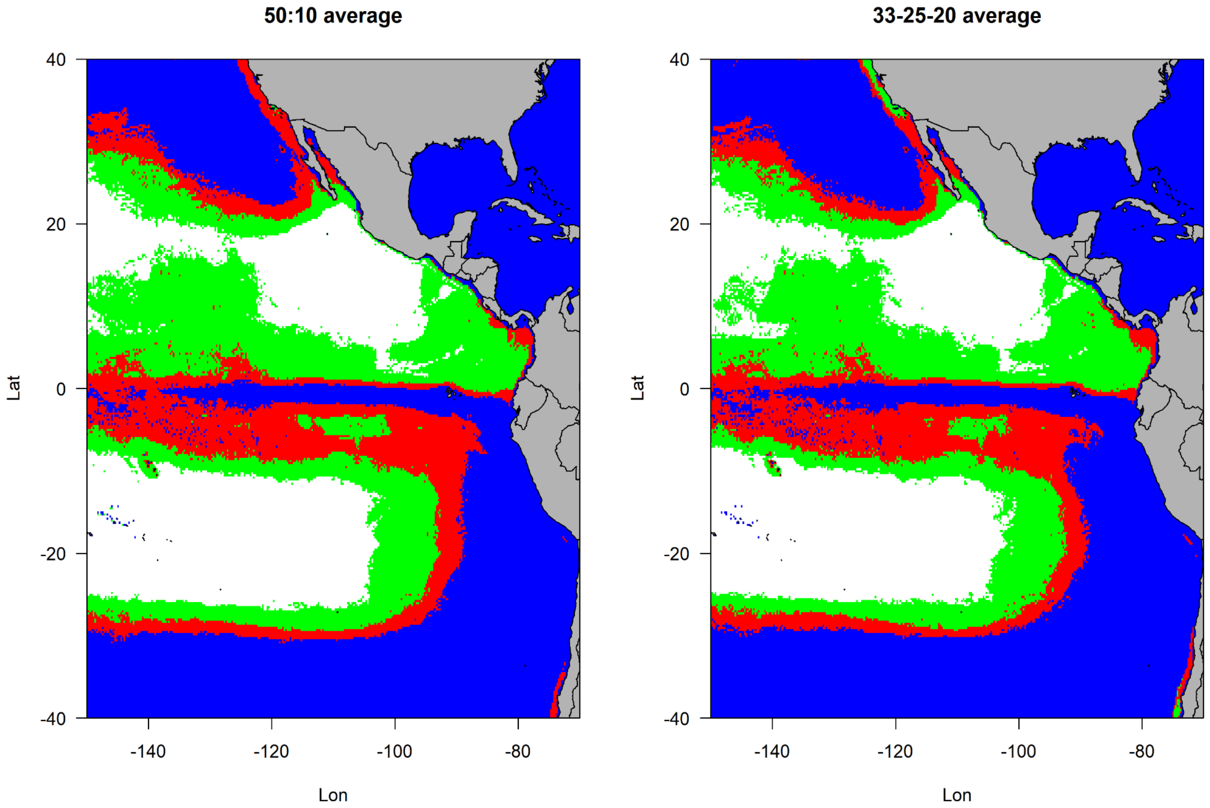

FIGURE 7. The final appearance of the SDM predictions using three threshold values (minimum = 0.3, blue; most probable = 0.2, red; maximum = 0.1, green) upon which the predicted probability of presence is used to create binary values of species presence. For example, at a threshold of 0.2, predicted probabilities of presence above and below 0.2 are predicted to be absence and presence records, respectively.

TABLE 1. Data sources and period of coverage of data used to build the leatherback species distribution model for the EPO.

Country	Gear	First year	Last year	Presence only	Abundance	Effort	No. Presences	No. individuals	No. total sets	% of presences	Source
Chile[1]	Purse-seine	2015	2019	No	No	-	3	3	4396	0.07	Observers
Chile[1]	Industrial longline	2001	2018	No	Yes	Yes (No hooks)	327	365	13828	2.36	Observers
Chile[1]	Artisanal longline	2002	2018	No	Yes	Yes (No hooks)	59	62	1831	3.22	Observers
Chile[1]	Artisanal longline (espinel)	2010	2019	No	No (?)	Yes (No hooks)	2	2	564	0.35	Observers
Chile[1]	Artisanal gillnet	2007	2019	No	Yes	No	22	24	1399	1.57	Observers
Colombia[2]	Gillnet	2017	2018	Yes	No	No	3	3	3	-	Observers
Colombia[2]	Longline	2018	2018	Yes	No	No	2	2	2	-	Observers
IATTC	Purse-seine	1995	2020	No	Yes	No	272	274	532857	0.05	Observers
IATTC	Longline	2013	2020	No	Yes	No	67	67	24005	0.28	Observers
Panama[3]	PS/LL/Gillnet	2018	2020	Yes	No	No	10	10	10	-	Observers
Peru[3] (ProDelphinus)	-	2001	2019	Yes	No	-	186	186	186	-	ProDelphinus
Ecuador[3]	Purse-seine	2019	2020	No	No (?)	-	3	3	2746	0.11	Observers
Ecuador[3]	Longline (bottom)	2017	2020	No	No (?)	No	0	0	766	0.00	Observers
Ecuador[3]	Longline (surface)	2019	2020	No	No (?)	No	2	2	1667	0.12	Observers
Peru[3]	Net	1997	2015	Yes	No	No	141	141	141	-	IMARPE/ACOREMA
Peru[3]	Driftnet/Gillnet	2013	2020	Yes	Yes	No	21	21	21	-	IMARPE (LAMBAYEQUE)
WWF (various) [3]	LL	2004	2009	No	Yes	Yes (Various)	20	20	7539	0.27	WWF-IATTC
Costa Rica[3]	LL	2005	2012	No	Yes	Yes (No hooks)	5	5	2602	0.19	WWF
-	-	**1995**	**2020**	-	-	-	**1145**	**1190**	**594563**	**0.19**	

TABLE 2. Comparing variables' data sources and spatio-temporal resolutions for species distribution models

Variable	**Spatial Resolution**	**Temporal Resolution**	**Source**
Spatio-temporal			
Latitude	GPS	-	-
Longitude	GPS	-	-
Day of the year	-	D	Processed
Environmental surface			
SST	1/4°	D	CMEMS
Δ SST	1/4°	D	Processed
Salinity	1/4°	D	CMEMS
SSH	1/4°	D	CMEMS
Speed	1/4°	D	Processed
Heading	1/4°	D	Processed
EkE	1/4°	D	Processed
FSLE	1/25°	D	AVISO
Front index	1/4°	W	Processed
CHL	1/4°	W	CMEMS
Δ CHL	1/4°	W	Processed
Environmental subsurface			
Temp 100m	1/4°	D	CMEMS
MLD	1/4°	D	CMEMS
Static			
Bathymetry	1/12°	-	GMED
Distance to coast	1/120°	-	MARSPEC (Sbrocco et al 2013)

TABLE 3. Hierarchical models performance metrics with all data (n = 573,889). ST = spatio-temporal variables; SUR = environmental surface variables; SUB = environmental subsurface variables; ENV = environmental Surface and subsurface variables; STA = static variables; FULL = all environmental variables and static variables.

		lr	n.trees	Dev	AUC	TSS	Drop
1	fit	0.01	4500	38.64	0.89	0.66	
ST	simp	-	-	-	-	-	No drop
2	fit	0.01	5150	32.28	-	-	
SUR	simp		5150	32.40	0.92	0.71	EkE
3	fit	0.01	3600	23.62	0.88	0.65	
SUB	simp	-	-	-	-	-	No drop
4	fit	0.01	5600	38.14	0.94	0.74	
ENV	simp	-	-	-	-	-	No drop
5	fit	0.01	4400	19.71	0.79	0.51	
STA	simp	-	-	-	-	-	No drop
6	fit	0.01	7000	40.57	0.94	0.76	
FULL	simp	-	-	-	-	-	No drop

TABLE. 4. Performance metrics of the models conducted during the sensitivity analyses for full models (all environmental and static variables) with different presence-absence ratios (e.g., 50:50 presence-absence ratio)

		lr	n.trees	Dev	AUC	TSS	Drop
50:50	fit	0.005	2900	58.10	-	-	
n = 2176	simp	0.005	3650	59.37	0.92	0.71	7 variables
33:66	fit	0.01	2050	59.16	-	-	
n = 3264	simp	0.01	2650	61.54	0.94	0.76	5 variables
25:75	fit	0.01	2700	59.70	-	-	
n = 4352	simp	0.01	3250	60.42	0.96	0.81	7 variables
20:80	fit	0.01	3200	60.29	-	-	
n = 5440	simp	0.01	3350	59.14	0.94	0.77	6 variables
15:85	fit	0.01	3950	60.21	-	-	
n = 7250	simp	0.01	3650	58.96	0.94	0.76	3 variables
10:90	fit	0.01	5050	60.93	-	-	
n = 10880	simp	0.01	4800	60.16	0.95	0.78	2
5:95	fit	0.01	5300	56.36	0.95	0.78	
n = 21760	simp	-	-	-	-	-	No drop
2.5:97.5	fit	0.01	6400	54.67	-	-	
n = 43520	simp	0.01	5650	52.08	0.95	0.77	7 variables
1:99	fit	0.01	6650	49.24	0.94	0.78	
n = 108800	simp	-	-	-	-	-	No drop
0.5:99.5	fit	0.01	6100	45.23	0.94	0.76	
n = 217600	simp	-	-	-	-	-	No drop
0.19:99.81	fit	0.01	7000	40.57	0.94	0.76	
n = 573889	simp	-	-	-	-	-	No drop